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THE EFFECT OF PROCEDURAL VARIATIONS ON
DISCRIMINATIVE PERFORMANCE: VISUAL ACUITY IN THE
DOMESTIC HEN

A thesis
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ABSTRACT

Changes in discriminative performance as a function of procedural variations were studied, using domestic hens in a visual acuity task. Square-wave gratings and grey stimuli were presented in a successive conditional discrimination. All probe sessions were conducted with increasingly fine gratings. Several methods of analysis were evaluated and various threshold criteria used.

For the first set of experiments, Experiments 1.1 to 1.5, a spatial discrimination procedure was used. A comparison of an ascending and descending series of stimulus presentation showed no consistent difference in discriminative performance. An increase in response requirements to the sample key, from FR1 to FR5 and to FR10 in Experiment 1.2, generally resulted in higher accuracy at most grating values. Increasing response requirements further, resulted in inconsistent improvements in performance. Discriminative performance under a limited range of luminances was assessed in Experiment 1.3. Data showed greater accuracy at the highest compared to the lowest luminance, for most hens and most grating values. In Experiment 1.4 the effects of training hens to stability using a finer grating showed that extended practice on a finer grating value did not consistently improve discriminative performance. A one session probe is thus an accurate description of stable performance. A comparison of performance under a controlled and uncontrolled reinforcement procedure in Experiment 1.5 showed greater overall accuracy of performance with the uncontrolled procedure.

The second set of experiments were a systematic replication of Experiments 1.1, 1.2, 1.3 and 1.5, using a non-spatial conditional discrimination procedure. Results of the comparison of the ascending and descending series of stimulus presentation were replicated.

Increased response requirements from FR1 to FR5 and FR10 generally resulted in increased accuracy at only the coarsest grating. The effects of changing luminance were replicated. The controlled reinforcement procedure gave slightly higher accuracy.

Negative exponential functions fitted to group data described the data well and indicated a lower initial accuracy and greater rate of decay of discriminative performance as a function of grating spatial frequency, for the non-spatial discrimination procedure. Threshold estimates were consistently lower (measured in cycles/degree) for performance with the non-spatial discrimination procedure, than with the spatial discrimination task. Several methods of data analysis were used, and thresholds were estimated using various criteria. Threshold estimates changed, generally reflecting changes in discriminative performance, and as such provided a useful measure of the effects of procedural variations on discriminative performance. However, thresholds estimated from least-squares fitted lines may arguably be more useful than those taken from a unitary value, because they include more of the available data. Problems associated with this and with the use of various criteria are discussed. Furthermore, the use of a constant and variable stimulus as used in these studies, is discussed with regard to the role it may play in encouraging response biases at finer gratings.

The results of these experiments indicate that the measurement of psychophysical phenomena, as exemplified by visual acuity in the domestic hen, may be consistently changed by variables which directly effect the sensory functioning, such as luminance. Discriminative performance was, however, confounded by the effects of non-sensory procedural variations, and the most important of these appears to be task difficulty.

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Discrimination and general concepts of psychophysics

When an organism's behaviour changes as a function of some change in the environment, that behaviour may be termed discriminative (Terrace, 1966). Any aspect of the environment to which an organism responds is termed a stimulus (Blough, 1966).

There are many dimensions along which a physical stimulus may vary. For example, an auditory stimulus may vary along the dimension of loudness or pitch, or a visual stimulus may vary along the dimensions of colour, brightness, and so forth. Functions that relate changes in behaviour to such changes along a stimulus dimension may be termed sensory functions. Psychophysics is the field which is primarily concerned with the behaviour analysis of sensory functions (Stebbins, 1970). The term "psychophysics" was coined by Fechner in 1860 to refer to a methodology for presenting stimuli to an organism to determine the limits and dimensions of its sensory capacities. Fechner was the first to suggest a relation between a stimulus which is measurable in physical units and the resulting sensation. Methodology for studying this has evolved during the last century as a means of answering experimental questions about human sensory acuity (Stebbins, 1970) and has later been extended to the study of the sensory capabilities of animals.

Stebbins (1970) emphasizes an important distinction between sensory and perceptual studies. In sensory studies, prior specification of correct and incorrect responding may be made. The condition of stimulus absence in absolute threshold studies, and of physical equality in differential threshold studies define subthreshold values. That is, a response indicating detection of a

stimulus when this stimulus is in fact absent, or a response indicating a difference in two physically equal stimuli, is defined as incorrect. In perceptual studies, however, (e.g. Vicario, 1972) no such prior specification is possible.

Thresholds. The sensory threshold was considered by Fechner (1860/1966) as the central concept of psychophysics. There are stimuli which an organism can detect and those which it cannot detect. An index of the organism's sensory capacity is determined in terms of either the minimum detectable stimulus magnitude (absolute threshold) or the minimum detectable difference between two stimuli varying only in one dimension (differential threshold) (Blough & Blough, 1977).

The threshold is not a fixed immutable point but has been shown to vary with changes in a variety of different conditions, including momentary unpredicted alterations in both stimulus and organism. Such variations in sensitivity are found in every sense field (Woodworth & Schlosberg, 1954). Repeated measurements of threshold are therefore necessary. The resultant distribution of such thresholds may be described by the normal curve (Woodworth & Schlosberg, 1954), and the value of the threshold is taken as the mean of this distribution. The arbitrary operational definition of the absolute threshold is the correct detection of the stimulus by the organism on 50% of the trials, and is determined directly from the graphed sensory function or obtained through more complex statistical analysis of the data (Dember, 1960). Because the criterion is rarely met exactly, the actual threshold value is usually taken from interpolation on a graph that relates the stimulus and response measures. A function may be fitted to some or all data points prior to interpolation.

Transformation of either the stimulus values or response measure (or both) to result in a function approximately linear may be useful, from which to obtain a straight line fit, especially when data are variable (Blough & Blough, 1977) since inclusion of more data points contributes to the reliability of the threshold estimate.

Although useful sensory information may be provided by the determination of a single threshold value, commonly studies compare several threshold estimates obtained when a second dimension of the stimulus is varied, for example, auditory tones along a range of frequencies (Temple, Foster & O'Donnell, 1984). Sensory thresholds obtained by behavioural means may be compared across species. They may also be compared to those estimates of threshold obtained by other means. For example, an estimate of visual acuity obtained behaviourally for kittens (e.g. Mitchell, Giffin & Timney, 1977) may be compared to another for the same species, determined electrophysiologically by an evoked potential recording (VEP). Here, the threshold is determined as the least intensity of a stimulus which evokes a response from a visual receptor (e.g. Freeman & Marg, 1975). In addition, an estimate of threshold may be compared with that assumed anatomically, by investigation of the actual sensory receptor structure. Here, it is assumed that the arrangement of visual receptors (i.e. the fineness or coarseness of the layers of receptors) within the eye provides some indication of the sharpness or acuity of vision (Riggs, 1965).

Woodworth and Schlosberg (1954) stress, however, that the estimation of thresholds is not purely an empirical matter. Rather, the threshold value may reflect not only the subject's behaviour, but

also the particular measuring procedures employed and the theoretical assumptions through which observed behaviour is translated into a single numerical value. For example, resultant estimates of threshold for the same sensory function and species, may reflect variations across studies in stimulus presentation procedures, response requirements, stimulus type, size and number, difficulty level of the discrimination task, differences in threshold criteria and data analysis employed.

Traditional human psychophysics

In most human psychophysical studies investigating absolute thresholds, the subject is given verbal instructions regarding response requirements. Usually, no specific training is required. There are three stimulus classes which may be employed, including a single stimulus or pairs of stimuli. If a single stimulus is employed, it may be varied along a particular dimension, for example, varying intensities of an auditory tone (Bekesy, 1960), or varying thicknesses of wire against a white background (Hecht & Mintz, 1939). The subject may be required to respond "yes" when the presence of the stimulus is detected. This may be more aptly termed a detection task, considered to be a more simple type of discrimination procedure (Dember, 1960). Alternatively, two variable stimuli may be utilized, differing in one dimension for example, varying grating values which differ only in line orientation. The subject may be required to respond differentially to each grating orientation as the gratings become increasingly finer.

Other procedures may employ a constant or standard stimulus and a variable comparison stimulus, for example, a standard grey stimulus

and a variable grating stimulus, and require the subject to respond differentially to each. Whether stimulus types, for example gratings, consist of two variable stimuli, or one variable and one standard stimulus, as increasingly finer gratings are presented, the discrimination between the two stimuli is assumed to become more difficult.

There are two basic types of responses which may be used by the subject. One involves a simple "yes" or "no" in the stimulus presence or absence respectively, or some other response equivalent. The other involves a forced-choice procedure, in which different responses to each of the stimuli, as specified by the experimenter, are required. When Blackwell (1952) compared the use of the yes/no and forced-choice response types under a variety of conditions, he reported generally greater thresholds (indicating better discrimination) with the forced-choice response. He suggested that the forced-choice procedure was generally more reliable and less easily influenced by irrelevant variables such as the spacing and ordering of stimuli, than the yes/no procedure. The latter procedure was more likely to involve habituation of response.

Each response to a stimulus represents a trial, and many such trials are required to obtain a sensory function. When two stimuli are used, trials may involve either successive or simultaneous stimulus presentation. That is, either only one of the two stimuli is presented on any one trial (successive), or both stimuli may be presented simultaneously.

Woodworth and Schlosberg (1954) refer to two basic methods of

stimulus presentation. The Method of Constant Stimuli involves a relatively small number of stimuli assumed to be around threshold. These are presented to the subject a predetermined number of times, either randomly intermixed or random but grouped in blocks of trials. For the Method of Limits however, the first stimulus value presented is usually one assumed to be well above threshold (i.e. easily discriminable) and the presentation of each successive stimulus is dependent on the subject's previous response. Each stimulus value correctly detected results in presentation of another of a different value, (e.g. presentation of increasingly finer gratings). This is referred to as a descending series of stimulus presentation (Woodworth & Schlosberg, 1954). This series is terminated after a criterion number of failures, and an ascending series begun, commencing with a stimulus value assumed to be below threshold (i.e. not discriminable) and followed by another of a different value (e.g. presentation of increasingly coarser gratings) until a criterion number of successful discriminations are made by the subject.

For the Method of Constant Stimuli, the stimulus values are selected independently of the subject's responses in the experiment. Conversely, in the Method of Limits, although the first stimulus and its successive decrements or increments are pre-selected, the particular point where the descending or ascending series is terminated is partially dependent upon the subject's behaviour (Dember, 1960). Blough and Blough (1977) suggest that a disadvantage of random presentation of stimuli, as in the Method of Constant Stimuli, is that it tends to commit the experimenter to a set of stimulus values that may later prove to be inappropriate. Most other procedures of stimulus presentation are variations of these two basic

methods.

Signal detection theory

The above mentioned methods involve the classical approach which assumes that the threshold is an "all-or none" transition point on the continuum of stimulus intensity, and that stimuli below threshold are not detectable. Because a subject may at times report a particular stimulus as present and at other times as absent, it has been assumed that thresholds change momentarily, and thus a variety of stimulus intensities must be presented to determine the average location of the threshold (Blough, 1966).

Signal detection theory however, (Green & Swets, 1966), the concepts of which were taken from engineering and mathematics, proposes a different approach based on decision theory. D'Amato (1970) points out that signal detection theory dispenses with the concept of thresholds, and requires that each discriminative performance be viewed as the result of two classes of information. Firstly, there is the information about the stimuli, which is mainly a function of the stimulus parameters in the experimental situation, and the subject's sensory capacity. This class of information provides the measure of sensitivity to the stimulus. Then there are several variables such as the subject's motivation, knowledge of the likelihood of stimulus probability and the rewards and costs associated with making correct and incorrect responses respectively. These, although independent of sensitivity, influence discriminative behaviour by affecting the subject's response criterion. That is, these non-sensory variables combine with sensory variables to determine whether the subject will report "yes" or "no" on any given

trial. Variables such as rewards and costs for correct and incorrect responses, and signal presentation probability have been studied under various discriminative conditions, where subjects were required to detect auditory signals, usually imbedded in noisy backgrounds (Stebbins, 1970). Although initially tested with audition, the effect of these non-sensory variables has since been investigated using other sensory modalities, for example, vision (Wright, 1972).

Typically, in the signal detection procedure, the subject must decide whether a sensory event was caused by the signal or by some random process, for example, background noise. Figure 0.0.1 illustrates the stimulus-response matrix of this yes/no signal detection procedure. For any trial there are two stimulus alternatives, that is, the signal (or stimulus) may be present(s) or absent(n), and this results in one of two response alternatives, that is, "yes"(S) or "no"(N). Thus there are four possible outcomes, and the entries in each cell of the matrix represent the probability of any of these. The proportion of correct "yes" and "no" responses are indicated by $P(S/s)$ in the upper left cell, and $P(N/n)$ in the lower right cell, respectively. The proportion of the incorrect "no" and "yes" responses (incorrect rejection and false alarm) respectively, are shown by $P(N/s)$ and $P(S/n)$ in the upper right and lower left cells, respectively.

Green and Swets (1966) suggest that the subject's criterion for saying "yes" (stimulus present) or "no" (stimulus absent) will vary with signal presentation probability. That is, as the probability of the stimulus being present increases, the proportion of "yes" responses by the subject likewise increases. It will also vary with

Figure 0.0.1

		Response	
Stimulus		S(yes)	N(no)
s (on)		$P(S/s)$ Correct detection	$P(N/s)$ Miss
n (off)		$P(S/n)$ False alarm	$P(N/n)$ Correct rejection

Figure 0.0.1:

The stimulus-response matrix of the signal detection procedure. The entries in the cells represent the four possible outcomes of any trial, where $P(S/s)$ and $P(S/n)$ are the probabilities of reporting 'yes' when the signal is 'on' and 'off' respectively. $P(N/s)$ and $P(N/n)$ represent the probabilities of reporting 'no' when the signal is 'on' and 'off', respectively.

the amount of rewards or cost associated with correct or incorrect decisions, respectively. That is, the proportion of "yes" responses may be increased by increased rewards, and decreased by increasing costs for incorrect "yes" responses. Any increase in the proportion of "yes" responses (S/s) may also result in an increase in the proportion of false alarms (S/n). Likewise, an increase in "no" responses may also result in an increase in the proportion of incorrect rejections (N/s).

The ROC curve. In a discrimination task, when the proportion of correct "yes" and "no" responses made by the subject on signal trials, have been entered in the matrix (Figure 0.0.1), the other two can be determined, as the rows must add up to 1.00. The information from the matrix may be represented as a data point on a two-dimensional graph, when the average proportion of correct "yes" responses are plotted against the average proportion of incorrect "yes" responses. When non-sensory variables are manipulated in a discrimination task, and the data plotted, the resultant ROC (receiver operating characteristic) curve represents the different modes of responding (with changes in criterion) that a subject may adopt under particular fixed stimulus conditions. The ROC curve is also termed an "iso-sensitivity" function (Green & Swets, 1966).

If the subject's criterion is very strict (the proportion of "yes" responses and false alarms will be low), this produces points to the lower end of the ROC curve, whilst a more lax criterion (predominantly more "yes" responses and false alarms) will produce more points on the upper end of the ROC curve. The major diagonal line on the graph below the curve indicates totally random responding,

that is, correct and incorrect "yes" responses are close to equal. The area under the ROC curve provides an index of the detectability of the signal (stimulus) that is assumed to be independent of any criterion the subject may use. Criterion in signal detection terms, refers to response bias or preference for responding in a particular way. The sensitivity index, termed d' , increases with increasing distance of the ROC curve from the major diagonal.

In the absence of data necessary to generate complete ROC curves, the signal detection analysis, with the proportion of correct responses in the presence of the stimulus plotted against the proportion of incorrect responses in the absence of the stimulus, may provide a useful description of response bias and stimulus discrimination. For example, when Terman (1970) plotted data obtained from three rats in an audition study, each subject showed relatively constant position biases in different directions. However, despite such biases, data showed similar functions when the sensitivity index, d' , was plotted against stimulus values.

Blough and Blough (1977) suggest that the major impetus for signal detection analysis in human psychophysics was a failure of psychophysical data to correspond to the classical view that on any given trial a detection response is controlled either by sensory input or by some error factor, but not by both. Signal detection theory on the other hand, is presumed to provide the analysis for determining, separately, the contribution of sensory and non-sensory variables in any discriminative performance. However, although signal detection theory predicts that ROC curves plotted on normalized co-ordinates will be straight lines parallel to the major diagonal, Blough and

Blough (1977) report the failure to achieve this, both in human and animal data. When these lines converge, (e.g. Wright, 1972), the sensitivity index, d' , cannot be determined unambiguously, that is, from any point along the major diagonal. Blough and Blough (1977) point out that one explanation for this convergence strikes at the fundamental assumption of the theory, by questioning the actual independence of sensory and non-sensory variables.

If, as the theory predicts, signal detection analysis provides a separate measure of sensitivity and response criteria, then the paradigm may be useful in clarifying the nature of control by the stimulus, over discriminative behaviour. However, in the study of sensory functions, Blough and Blough suggest that it is unlikely to replace the classical paradigm totally. Further, there is no general consensus in the literature regarding the superiority of d' over the more traditional measure of sensitivity, percentages correct. They suggest therefore, that the latter measure, although biased by non-sensory variables, remains an adequate measure for most studies of sensory function.

Animal psychophysics

The fields of human and animal psychophysics are closely related. While in human psychophysics the subject is instructed how to respond, for animals specific training is often required. Blough and Blough (1977) suggest that interest in animal psychophysics is partially a result of the expansion of research on the anatomy and physiology of animal sensory processes. That is, a complete understanding of these sensory functions requires the addition of behavioural data.

Untrained reflexive responses. Some of the early sensory studies required no specific training of the animal, but rather, made use of its reflexive movements to or away from the stimulus. This is termed an atropic response. This method has been used to study the visual acuity of various invertebrates including the fruit fly (Hecht & Wald, 1934), honey bee (Hecht, Wolf & Wald, 1929) and fiddler crab (Clark, 1935). A related reflexive response is termed "optokinetic". These responses consist of movements of the eyes or head, that follow vertical stripes moving horizontally in the visual field. This procedure has been used to study visual acuity in animals, including the development of visual acuity in young prairie deer mice (Vestal & King, 1971).

Classical conditioning. By pairing of stimuli an animal can be trained to respond to stimuli which previously did not elicit the behaviour change. Examples of the use of this procedure include visual acuity studies in which a conditioned increased respiration response to vertical gratings was used in goldfish (Northmore & Dvorak, 1979).

Operant conditioning. Thorndike (1911) formulated the Law of Effect. This law states that a particular behaviour will be strengthened or "reinforced" if it is closely followed by a "satisfying" event, and weakened if closely followed by an "annoying" event. The satisfying consequences of behaviour are termed "reinforcers" and the annoying events "punishers". In 1938 Skinner identified these consequences as measured stimuli and made methodological distinctions between the classical form of conditioning and the behaviour which was strengthened by its consequences. He

coined the term "operant class" for such behaviour. Skinner referred to the operant as "an identifiable part of behavior which it may be said ... that no correlated stimulus can be detected upon occasions when it is observed to occur" (Skinner, 1938, p21). Such responses are said to be "emitted" (D'Amato, 1970), rather than "elicited". While operant behaviour could be modified in various ways by appropriate manipulation of its consequences, the classically conditioned reflex was relatively inflexible (Stebbins, 1970). It may be argued that the Law of Effect, due to its circularity, rather than providing an explanation for events, provides instead a simple description of these events (Brown & Herrnstein, 1975).

Blough and Blough (1977) stress that, regardless of the methods used, acquisition of required behaviour, and establishment of stimulus control over that behaviour, are the two primary behavioural processes of concern, when studying animal sensory functions. In shaping operant behaviour, reinforcement is applied selectively to an animal's behaviour until that particular response chosen by the experimenter is emitted stably at a high frequency (Stebbins, 1970). Correct and incorrect responding are determined by the experimenter.

Stimulus control. Stimulus control refers to

the extent to which the value of an antecedent stimulus determines the probability of occurrence of a conditioned response. It is measured as a change in response probability that results from a change in stimulus value (Terrace, 1966, p171).

That is, if the animal's behaviour changes reliably with the manipulation of a stimulus, then that stimulus is said to exert some control over the animal's behaviour. Blough (1966) states that a controlling stimulus is sometimes said to be "attended to", although it may be argued that such a statement is circular.

Response requirement. Blough and Blough (1977) stress that the selected response should be one that is simple to train in the animal, for example, key pecking in pigeons (Hodos, Leibowitz & Bonbright, 1976), lever pressing in rats (Terman, 1970) and lever pulling in monkeys (Cavonius & Robbins, 1973). They further suggest that equipment which permits many responses with little effort allows the generation of data which provide more reliable thresholds and are more sensitive to differences than equipment in which a discrimination task requires a greater amount of effort. For example, the keypeck response in an experimental chamber requires less effort and allows many more trials per experimental session than responses with jumping stand apparatus (e.g. Fox, Lehmkuhle & Westendorf, 1976) or in a two-choice runway (e.g. Johnson, 1914).

Reinforcement schedules. Reinforcement for correct responding is delivered on a particular schedule, and such schedules involve delivery of reinforcement either after a predetermined number of responses emitted by the animal (ratio schedules) or following the first response emitted after the elapse of a specified interval of time (interval schedules). Schedules may be fixed or variable. For the latter, reinforcement is aperiodic but according to a particular mean value and range. Alternatively, reinforcement may be presented following each correct response. This is referred to as continuous

reinforcement (CRF).

Response bias. In a discrimination task the animal may show a preference or bias for responding to one alternative rather than the other. This response bias has been reported to increase as a function of discrimination difficulty (Terman, 1970). Because behaviour is maintained by reinforcement delivery, reinforcement is clearly an important source of stimulus control. The study of sensory functions, however, places control in other stimuli (e.g. auditory or visual) which precede the response. Therefore, any control by reinforcement delivery is unwanted, and a source of confounding by increasing response bias, and significantly affecting the measure of sensory functions (Blough & Blough, 1977).

Blough (1966) suggests that a requirement of comparable responses to each response alternative and equal reinforcement contingencies for correct responding to each response alternative can minimize response bias. Often, a correction procedure is employed to prevent perseveration on one response alternative from trial to trial (e.g. Hodos *et al.*, 1976). This involves the repeating of an incorrect trial until the animal has responded to the correct response alternative.

Methods of stimulus presentation. The methods of stimulus presentation include the two basic methods (previously mentioned) used in human psychophysics, that is, the Method of Constant Stimuli and the Method of Limits, and variations of these. One variation of the Method of Limits is termed the "tracking" method, also known as the "staircase", "up-down" or "titration" method. Here, the stimulus

values are restricted to those closest to the assumed threshold. Although there is the advantage of employing fewer stimulus values than in the Method of Limits, Blough and Blough (1977) point out that the procedure requires long training, and stimulus control may deteriorate with prolonged discriminations at low levels of stimulus discriminability.

Some comparisons of methods of stimulus presentation have been made. Stebbins (1970) reported that psychophysical functions for conditional discriminations in monkeys obtained using either the Method of Limits or Method of Constant Stimuli were very similar. Blough (1971) also reported similar visual acuity threshold values in pigeons from these two methods. However, she reported better discriminative performance at the coarsest grating values with the descending, compared to the ascending series. Dalland (1970) in an auditory discrimination with bats, used both the descending and ascending series of the Method of Limits and reported a higher rate of errors with the ascending series. Terman (1970) also found that thresholds yielded by the descending series generally indicated better discrimination than the ascending series.

Variations in psychophysical operant training procedures

The investigation of sensory processes of a wide range of species has necessitated the development of a variety of procedures. Most psychophysical procedures require the animal to perform a discrimination between two or more stimuli. When the discrimination requires two different responses, these may be identified with separate manipulanda or differential patterns of responding to the same manipulandum. If the animal is discriminating between two or

more stimuli presented simultaneously, one of these stimuli is pre-specified by the experimenter as the "correct" or "target" stimulus.

Procedures with a single response manipulandum. Procedures using a single response measure include the "go/no go" procedure, and the "conditioned suppression" methods. In the go/no go procedure, the stimulus dimension controls a discriminated operant that is maintained by the appropriate reinforcement contingencies (Blough & Blough, 1977). Trials may be continuous (allowing many responses during a relatively long stimulus presentation time) or discrete (with a short stimulus presentation, requiring only one discriminative response). Traditionally, responses are reinforced in the presence of the target stimulus and not in its absence. The procedure has been used to study various sensory functions, including visual acuity in the sea lion (Schusterman & Balliet, 1970) using conditioned vocalizations in the presence of the grating stimuli, and visual acuity in the pigeon (Bloch & Martinoya, 1982) using key peck responses in the presence of tachistoscopically presented grating stimuli.

Because the procedure is designed to facilitate the response, it may also facilitate response bias. That is, the subject may become biased toward reporting the presence of the target stimulus even in its absence. When Terman and Terman (1972) studied auditory discrimination in rats they modified their procedure in an attempt to alleviate this response bias. They introduced symmetrical contingencies for correct and incorrect responding. Even with such modifications, however, biases toward responding during comparison stimulus presentation persisted. They suggest the bias to be a result

of topographical differences between the two response requirements, that is, the lever press in the presence of the standard, and no lever press in the presence of the comparison stimulus.

In the conditioned suppression method the target stimulus is paired with an aversive stimulus to bring about the suppression of an ongoing operant (Blough & Blough, 1977). As the change in the rate of the responding is used as the psychophysical measure, it is particularly important that a stable baseline of responding is maintained.

Two or more manipulanda. Procedures using different manipulanda for each response alternative are more comparable to most studies in human psychophysics. The use of symmetrical response requirements to both alternatives and symmetrical reinforcement contingencies for correct responses to each alternative, would be expected to minimize response bias, compared to single response procedures.

The "forced-choice" and "yes/no" procedures may generally be differentiated by the class of discrimination used, simultaneous, or successive. In the forced-choice procedure, each of two or more stimuli are associated with a response alternative. The delivery of reinforcement is contingent upon a response to the alternatives corresponding to the correct stimulus. Usually this procedure requires the simultaneous presentation of the stimuli. Frequently, such procedures involve a third response termed an "observing" or "attending" response, which may either initiate the sample stimulus presentation (e.g. Yager & Thorpe, 1970), or act as pre-requisite for

enabling choice response alternatives (e.g. Hodos *et al.*, 1976). As a trial initiating response, it may also serve to ensure that the animal is viewing a visual sample stimulus from a constant distance, (e.g. Blough, 1971). This procedure, using two response alternatives, has been employed extensively to study visual acuity in hens (Johnson, 1914), pigeons (Gundlach, 1933; Blough, 1971) tawny owls (Martin & Gordon, 1974), and cats (Smith, 1936) using two-alley runway apparatus, kittens (Mitchell *et al.*, 1977), falcons (Fox *et al.*, 1976) and gerbils (Baker & Emerson, 1983) using jumping stand-apparatus, and in minks (Dunstone & Sinclair, 1978) and dolphins (Spong & White, 1971), using approach behaviour without such apparatus. The same procedure, using three response alternatives, was used to study both contrast sensitivity and visual acuity in the tree squirrel (Jacobs, Birch & Blakeslee, 1982).

In the "yes/no" procedures, stimuli are generally presented successively. Here, a response to one manipulandum is correct if one stimulus (i.e. the target stimulus) is present ("yes"), and another if the stimulus is absent or another stimulus is present ("no"). This method was used to study auditory discrimination in rats (Irwin & Terman, 1970) and visual acuity in pigeons (Hodos *et al.*, 1976; Hodos, Macko & Bessette, 1984). Although Blough and Blough (1977) suggest that a method using successive presentation of stimuli may produce more bias than simultaneous stimulus presentation, many of these studies using simultaneous presentation of stimuli in the forced-choice procedures (e.g. Johnson, 1914; Fox *et al.*, 1976) report development of position preferences, necessitating modification of stimulus presentation, (correction procedures).

Matching-to-sample procedure. This is a discrimination procedure which may include several variations. In the original procedure the animal is required to choose, from a set of alternative stimuli, one which is physically identical to the sample stimulus. Variations include symbolic matching-to-sample, in which the correct comparison stimulus is determined by an arbitrary relation between the sample and the choice stimulus, which may vary along a different stimulus dimension. For example, the two different sample stimuli may be represented by two different colours, and the comparison stimuli may be represented by two different line tilts. A response to one particular line tilt would be reinforced following the presentation of one particular colour (Carter & Eckerman, 1975). Presentation of the comparison stimuli may be either simultaneous with that of the sample (Cumming & Berryman, 1961) or delayed. The latter has been used to measure the animal's "memory" of the sample over varying temporal durations (e.g. Shimp, 1976).

In some studies the comparison stimuli are spatially determined. That is, for one sample stimulus the correct response may be to the right key, and for the other sample stimulus, the correct response may be to the left key (e.g. Hodos *et al.*, 1976). Alternatively, the spatial factor may be present but irrelevant. For example, the correct response for one sample stimulus may be to the red comparison key, and the correct response for the other sample may be to the green comparison key. However, these red and green comparison stimuli may be programmed to appear on either the left or right keys on any particular trial (e.g. Cumming & Berryman, 1961). Such a procedure might be expected to involve a more complex task for the animal than one in which the comparison stimuli are spatially determined. The

matching-to-sample procedure has been used to study various visual processes in animals, including colour vision in pigeons (Wright & Cumming, 1971; Wright, 1972).

Although there is a wealth of research in sensory processes across various species, there are very few studies which attempt to compare directly, the effects of the procedures themselves on the sensory data generated. These include Blackwell's (1952) comparison of forced-choice and yes/no procedures. He reported the forced-choice procedure to be more reliable (i.e. producing less variable data) for measuring visual thresholds, and suggested that the yes/no procedure may generate data with more bias towards reporting "yes", especially as the discrimination became more difficult. Mentzer's (1966) comparison of the forced-choice and yes/no methods for determining differential thresholds, however, using single responses and discrete trials resulted in functions which were not significantly different. Blough and Blough (1977) caution that such comparisons as these may be difficult to interpret, as many aspects of each situation are arbitrarily chosen, for example, stimulus placement, presentation, response requirement, response force, and so forth, and the effect of these parameters may obscure real methodological differences.

There appears, therefore, to be no general consensus in the literature as to the "best" procedures for any particular species. Stebbins (1970) suggests that this would depend partially upon the extent to which a procedure allows rapid acquisition of stable discriminative responding by the animal, and a stable behavioural baseline over time, allowing replicability. Stebbins further stresses that a major part of evaluative methodology is the analysis of the

procedural variables themselves, to determine the extent to which results may be a function of the procedures used, rather than a function of stimulus discriminability.

Visual acuity

Visual acuity refers to the resolving power of the retina. The "minimum visible" threshold refers to the least visual angle at which a single line or point can be recognised as distinct from its background. The "minimum separable threshold" is given as the smallest interspace, in terms of visual angle or retinal distance, at which two neighbouring objects can be resolved. Usually a distinction is made between these two thresholds, and it has been argued that the former involves a brightness discrimination rather than visual acuity (Wilcox & Purdy, 1932). When visual acuity is measured using grating stimuli, it is defined in terms of the "minimum separable" threshold. Euclid's law of visual angle holds that the visual angle subtended by the space between two points is inversely proportional to the distance between the observer and the points (Kaufman, 1979). Visual angle is thus an inverted measure, that is, the smaller the angle the better the acuity. Acuity is therefore traditionally expressed as the reciprocal of the visual angle (Stevens, 1957).

Acuity may be influenced by a number of factors. These include luminance (Spence, 1934; Hodos *et al.*, 1976), target location (Chard, 1939), target duration (Marshall & Talbot, 1942), the actual type of target stimuli used (Rabideau, 1955; Shlaer, 1938) and stimulus size (Spoehr & Lehmkuhle, 1982).

While various types of target stimuli may be used to determine

visual acuity, commonly a grid or grating is employed (Wilcox & Purdy, 1932). Such stimuli are described both in terms of their contrast and spatial frequency. Contrast refers to the difference between the light and dark bars of the grating. The larger the intensity difference between the bars the greater the contrast (Zusne, 1970). Spatial frequency refers to the measure of a grating and may be expressed in terms of the number of cycles, (i.e. the number of light and dark bars) per degree of visual angle at a particular distance from the subject. Alternatively, spatial frequency may also be expressed in cycles/mm or lines/mm.

Many recent studies use the measure of the grating stimulus, that is, in cycles/degree (c/deg) to express visual acuity, rather than the more traditional measure, the smallest angle subtended at the eye by the stimulus, in minutes of arc. These two measures are interchangeable; for example, 30 c/deg is equivalent to 1 min of arc (1') per light or dark bar, and 15 c/deg is equivalent to 2 min of arc (2') per light or dark bar, and so on.

Visual acuity in birds

Conventionally, human visual acuity, reported at about 30 c/deg or 1 min of arc per light or dark bar (1') (Spence, 1934), acts as a reference point against which to compare that of all other species. The acuity of primates is similar to that of humans, for example 1.4' for the macaque monkey (Yarczower, Wolbarsht, Galloway, Fligsten & Malcolm, 1966), 0.95' for the cebus monkey (Johnson, 1914) or 0.47' for the chimpanzee (Spence, 1934). The acuity of many lower vertebrates however, is much less, including 1.5-2 c/deg (approx. 24'-14') for rodents such as gerbils (Baker & Emerson, 1983), 3.9

c/deg (approx. 7') for tree squirrels (Jacobs *et al.*, 1982) and 5-6 c/deg (6'-5') for cats (Mitchell, Giffin, Wilkinson, Anderson & Smith, 1976) and sea lions (Schusterman & Balliet, 1970).

Acuties of birds vary, according to the particular species under study. For birds of prey such as the eagle (Reymond, 1985), at 137 c/deg, and the falcon (Reymond, 1987; Fox *et al.*, 1976) at 160 c/deg, visual acuity greatly exceeds that of humans. These results were obtained using forced-choice simultaneous discrimination tasks, and modifications of a jumping stand. The acuity of such birds is more dependent on luminance than is that of humans, decreasing sharply with lower light levels (Reymond, 1987). Maximum visual acuity for the falcon was obtained at a luminance of 350 cd/m² (Fox *et al.*, 1976). Studies of such nocturnal species as the tawny owl (Martin & Gordon, 1974) however, yield acuity estimates which are lower than that of humans by a factor of 2.5.

The visual acuity of the pigeon has been determined in several studies and a range of estimates, both greater and less than that of adult humans have been obtained. Most studies have employed simultaneous discriminations and forced-choice procedures. Gundlach (1933) used a two alley runway and required homing pigeons to discriminate at a distance of 15 ft from the stimuli. He estimated the pigeons' acuity to be close to twice as acute as those for humans. His estimates, however, were based on a sequential statistic rather than a more conventional threshold criterion. Two studies used jumping stand apparatus to study acuity as a function of distance from the target stimulus. Of these, Hamilton and Goldstein (1933), reporting estimates from 2.7' to 3.1' at an unspecified brightness,

based their data on relatively few trials (four to eight) and a rather casual criterion of threshold performance. Chard's (1939) study, with 70% correct responses taken as threshold, and illumination of the stimuli at 3.1 foot candles (approx. 32 lx), provided best estimates ranging from 2.7' to 5.2' at 40 cm distance from the stimuli. Discrimination deteriorated at greater distances. Blough (1971) however, using a forced choice procedure and runway apparatus, at a distance of 73 cm obtained estimates from 1.16' to 4.0', compared to 1.19' and 1.22' for humans tested at the same distance. Hodos *et al.* (1976) employed a successive conditional discrimination, using response keys in an experimental chamber, and five different luminances. Visual acuity varied in a sigmoid manner as a function of luminance, and the best acuity obtained was 1.92' (approx. 15 c/deg) with luminance of 2.33 log cd/m² at a near point of accommodation of 62.0 mm. Mean acuity thresholds for 34 pigeons obtained by Hodos, Bessette, Macko and Weiss (1985) measured 12.66 c/deg. Much lower estimates of 1.1 c/deg for lateral and 2.3 c/deg for frontal viewing, at a luminance of 5 cd/m², were reported by Bloch and Martinoya (1982), using a go/no go procedure. They suggest these relatively low estimates to be the result of the short tachistoscopic presentation time of the stimuli (300 ms stimulation). The wide range of acuities obtained for the pigeon indicates that variations in procedure, threshold criteria, data analysis and task difficulty may influence results.

The domestic hen (*Gallus Domesticus*)

Despite its availability, the domestic hen has not been studied as extensively as other animals such as the monkey, rat or pigeon. As in other birds but unlike mammals, there is complete decussation of

the optic nerve in the hen. The right-eye left-hemisphere system contains the pathways necessary for visual discrimination, dominates control of pecking in the binocular field and is involved with switching attention from one stimulus to another (Rogers, 1986).

Typically, the avian eye is both relatively and absolutely large (Walls, 1942; Meyer, 1977) and that of the hen is no exception. King-Smith (1971) estimates the weight ratio of the two eyes to the brain as being almost one to one. Martin (1985) suggests that, optically, the most important parameter of eye size is the anterior focal length or posterior nodal distance, since this determines the size of the retinal area over which the image of an object is spread. The longer the posterior nodal distance, the larger the retinal image of an object (Martin, 1985).

Eye movement in the hen is limited (Salzen & Cornell, 1967), but the position of the eyes in their orbits give a visual field of about 300 deg with a possible binocular field of about 25 deg. Objects are followed by using both head and neck. Both eyes can be focused independently in the lateral field and in part also in the frontal field of vision, indicating that the eyes, as well as their higher processing centres, act as independent units (Schaeffel, Howland & Farkas, 1986).

The depth of the cone packed fovea of the retina is also regarded as a measure of the sharpness of vision. It is especially deep in birds of prey and medium to weak in the remainder of the species. It is shallow in the domestic pigeon and lacking altogether in the domestic hen (Wood, 1914). However, Meyer and May (1973) report that

the retina of the hen has a shallow area of cone concentration which corresponds to the site of the temporal fovea in some birds and may represent the area of most acute vision for the hen.

Hens have a duplex visual system as indicated by the presence of both rods and cones (Myer & May, 1973), and their colour vision, as in other vertebrates, employs a multipigment cone system (Armington & Thiede, 1956). As with other diurnal birds, the retina of the hen contains a relatively high ratio of cones to rods (Bowmaker & Knowles, 1977). This would suggest that the visual acuity of the hen would be affected by varying light levels. Colour vision for the hen and pigeon should be similar. However, because hens lack a distinct fovea, visual acuity may be expected to be less than that of the pigeon. The hen has an accommodation of 17 diopeters (D), which is present in the first day of hatching (Schäefel *et al.*, 1986). They suggest that the chicken's accommodative power should be sufficient to focus on an object as close as about 3 cm, which is comparable to that of the pigeon in behavioural studies (e.g. Macko & Hodos, 1984).

The hen has been described as having a lower ganglion cell density in the retina (Ehrlich, 1981) than that of the pigeon. However, Schäefel *et al.* (1986) state that, due to the large range of accommodation, a good visual acuity can be expected, and suggest that the hen's performance should be comparable to that of the pigeon.

Discrimination studies in the hen have involved visual and auditory stimuli. Bingham (1913) studied size and form perception in the hen. The animals were required to discriminate between geometric forms and different sizes of these forms, (e.g. circles). Ball and

Warren (1960) demonstrated that the rate of simple maze learning in chicks develops more rapidly than their capacity for efficient spatial discrimination and reversal learning. Heat was successfully used as reinforcer for visual (Lee-Teng & Butler, 1971) and spatial (Zolman & Becker, 1968) discriminations.

A yes/no procedure was used by Temple *et al.* (1984) to study the auditory threshold in hens. Estimates of threshold indicate that they detect auditory stimuli within the range of 250 to 7000 Hz. Compared to the pigeon, studies of visual acuity in the domestic hen have been limited. Johnson (1914), using a two-alley runway in a forced-choice procedure, required hens to discriminate between a simultaneous presentation of gratings of two different orientations. Luminance was reported as 3.85 mL (approx. 12.1 cd/m²), and electric shock was used as punishment for incorrect choices. Visual acuity at 4.04' and 4.14' (approx. 7 c/deg) for two hens, was estimated from relatively few trials. Johnson suggested that the results should not be construed too rigidly and are not amenable to statistical treatment. Position preferences were reported to occur as the discrimination task became more difficult, at the finer grating values.

A more recent study by Over and Moore (1981) employed a jumping stand with young chickens, in a forced-choice simultaneous discrimination between gratings and standard grey stimuli. The luminance of the stimuli was 39 cd/m². Visual acuity was reported as 1.2 c/deg. Because, in the several days of testing, discriminative performance did not improve, it was suggested that the hen reaches its limits of acuity very soon after hatching. This seems to be in contradiction to Ball and Warren's (1960) suggestion that capacity for

spatial discrimination in chicks does not does not have such a rapid onset as simple maze learning. The degree of disparity in results from these two visual acuity studies indicates the need for further investigation into the visual acuity of the hen.

The matching approach to signal detection theory

Herrnstein (1961) was the first to describe a matching relation between relative response rate (responses to a key / total responses) and relative reinforcement rate (reinforcement scheduled on one key / total reinforcements scheduled) in concurrent VI VI schedules. Concurrent schedules of reinforcement are continuous choice procedures where two or more alternative schedules of reinforcement are available simultaneously, allowing the subject to chose between responding on one alternative or the other. Herrnstein formulated the following equation to describe the matching function:

$$\frac{P_1}{P_1+P_2} = \frac{R_1}{R_1+R_2} \quad (1)$$

where P_1 and P_2 refer to responses to the two alternatives, and R_1 and R_2 refer to reinforcements obtained from each schedule. Thus the matching law states that the relative response rate on either alternative of a concurrent schedule equals the relative reinforcement rate provided by that schedule. Herrnstein's simple matching relation has been supported by data from a large number of studies, (Catania, 1966; de Villiers, 1977).

Baum (1974) further generalised the matching law to account for data from concurrent schedules which were not directly predicted by

Equation (1). He presents the equation:

$$\log\left(\frac{P_1}{P_2}\right) = a \log\left(\frac{R_1}{R_2}\right) + \log b \quad (2)$$

where a and b are empirical constants, and when data are graphed in log-log co-ordinates refer to the slope and intercept respectively. Bias ($\log b$) accounts for deviations in the intercept from 0.00 and appears as a constant displacement from the matching diagonal. Any changes in a values refer to changes in sensitivity to reinforcement.

Davison and Tustin (1978) suggest that the yes/no signal detection task, traditionally used in human psychophysics could be described as two concurrent Reinforcement Extinction schedules, each operating under a distinctive stimulus. They extended the generalized matching law to describe behaviour in signal detection experiments where the subject makes a particular response (e.g. a left key peck) when one stimulus (S1) is present and another response (e.g. a right key peck) when another stimulus is present (S2) or S1 is absent. With two possible responses (PL and PR) in the presence of two different stimuli (S1 and S2) four possible outcomes are defined. Correct responses are reinforced according to a predetermined schedule. This procedure is illustrated in Figure 0.0.2, where W, X, Y and Z denote the number of events in each cell. Correct responses, that is, PL during S1 (W) or PR during S2 (Z) are reinforced, whereas PR during S1 (X) or PL during S2 (Y) have no consequences or are punished in some way, for example, by blackout, (Irwin & Terman, 1970; McCarthy, 1983).

Figure 0.0.2

		Response	
		yes	no
Stimulus	S1 Present	W (correct)	X (incorrect)
	S2 Absent	Y (incorrect)	Z (correct)

Figure 0.0.2:
The matrix of stimulus and response events, extended from the signal detection procedure (Davison and Tustin, 1976). The letters W, X, Y and Z represents the number of events occurring in each cell.

The generalized matching law suggests that if S1 and S2 are not distinguishable, the distribution of total left and right responses will be determined by the distribution of reinforcement for these responses. Under these conditions, Davison and Tustin suggest that the arrangement becomes simply a concurrent VI VI schedule. However, as the stimulus becomes more discriminable, performance becomes increasingly biased toward making left key responses during S1 and right key responses during S2.

Separate equations were proposed by Davison and Tustin to describe behaviour in the presence of each of the two stimuli, S1 and S2, where only correct responses are reinforced. In the presence of S1:

$$\log\left(\frac{PW}{PX}\right) = a_{r1} \log\left(\frac{RW}{RZ}\right) + \log c + \log d \quad (3)$$

and, in the presence of S2:

$$\log\left(\frac{PY}{PZ}\right) = a_{r2} \log\left(\frac{RW}{RZ}\right) + \log c - \log d \quad (4)$$

where P and R refer to the number of responses made and the number of reinforcements obtained respectively, and W, X, Y and Z refer to the cells of the stimulus-response matrix (Figure 0.0.2). These proposed two equations are based on the assumption that correct responses are controlled by reinforcement for those responses, that there will be a constant bias toward one key ($\log c$) and that the presence of S1 or S2 will bias performance toward left and right key responses respectively ($\log d$). The better the subject can discriminate S1 from S2, the

larger the $\log d$ (sensitivity to the stimulus) and the ratio PW/PX , and the smaller the ratio PY/PZ .

Although each equation refers to responses in the portion of the session in which $S1$ or $S2$ is present, the reinforcement ratio is indicated for the whole session, because it is suggested that the ratio of responses, either PW/PX or PY/PZ is affected by the total reinforcement ratio RW/RZ . It has been argued on the basis of data (McCarthy & Davison, 1980a), that sensitivity to reinforcement is the same in the presence of both $S1$ and $S2$ ($a_{r1} = a_{r2}$). Equation (4) therefore may be subtracted from Equation (3) to remove effects of reinforcement (i.e. reinforcer frequency bias) and inherent bias on performance, as follows:

$$\log\left(\frac{PW}{PX}\right) - \log\left(\frac{PY}{PZ}\right) = 2\log d \quad (5)$$

and a bias-free measure of discriminability ($\log d$) can be determined thus:

$$\log d = .5\left(\log\left(\frac{PW}{PX}\right) - \log\left(\frac{PY}{PZ}\right)\right) \quad (6)$$

McCarthy and Davison (1980a) refer to this as a "stimulus function" because it relates behaviour to the discriminative stimuli, independent of any biaser.

A measure of bias, independent of discriminability may be obtained by adding the equations (3) and (4), as follows:

$$\log\left(\frac{PW}{PX}\right) + \log\left(\frac{PY}{PZ}\right) = 2a_r \log\left(\frac{RW}{RZ}\right) + 2\log c \quad (7)$$

Estimates of response bias (which include both reinforcer frequency bias and inherent bias) can therefore be determined as follows:

$$.5(\log\left(\frac{PW}{PX}\right) + \log\left(\frac{PY}{PZ}\right)) = a_r \log\left(\frac{RW}{RZ}\right) + \log c \quad (8)$$

The measure on the left side of equation (8) is response bias which is analogous to the response criterion measure used in signal detection analysis. The independence of the measure of stimulus discriminability ($\log d$) and response bias ($\log c$) predicted by this model, has been supported in a variety of studies, where reinforcer frequency and signal presentation probability (SPP) have been varied (McCarthy & Davison, 1979; 1980a; 1984) across a range of stimulus values.

$\log d$ is a measure of discriminability independent of response bias when only correct responses are reinforced, and Davison and McCarthy (1980b) have shown that discriminability is affected by reinforcing errors in a detection procedure. That is, the discriminative performance will be degraded by reinforcing errors. Conventional discriminability estimates, therefore, are independent of reinforcer frequency only when no error reinforcement is obtained. Furthermore, discriminability is affected by local variations in reinforcer probability within sessions. For example, both Nevin and MacWilliams (1983) and Stubbs (1968) showed that when detection performance was reinforced on FR schedules, discrimination

systematically increased through the ratio.

As mentioned in a previous section, one major concern in signal detection research has been the finding that the slope of the normalized ROC or iso-sensitivity function departs from unity (e.g. Wright, 1972). This finding questioned the independence of stimulus discriminability d' and response criterion (or bias). In the Davison and Tustin framework, such ROC or iso-sensitivity functions (on normalized co-ordinates) occur only as a result of different sensitivity to reinforcer bias in the presence of the two stimuli (McCarthy & Davison, 1988). For example, it may occur if different responses were required in the presence of S1 and S2 (e.g. Davison & Ferguson, 1978).

Commonly, in signal detection procedures, reinforcement is presented for each correct response (e.g. Hume & Irwin, 1974) or is presented intermittently or probabilistically on VR schedules (e.g. Elsemore, 1972). McCarthy and Davison (1984) refer to these procedures as "uncontrolled reinforcer-ratio procedures", because the relative number of reinforcers obtained for correct detections can vary with the subject's behaviour and with signal presentation probability (SPP). In the uncontrolled reinforcement procedure, discriminability is a function not only of the difference between the two stimuli but also of a reinforcement/stimulus presentation relation. That is, as the difference between S1 and S2 becomes less discriminable, behaviour becomes under control of the reinforcement schedule, as in concurrent reinforcement schedules. The Davison and Tustin model predicts that it is impossible to calculate a constant response bias measure (iso-bias) when an uncontrolled reinforcement

procedure is used, because the bias will not be independent of stimulus discriminability. McCarthy (1980a) proposes that the traditionally reported iso-bias contours are better termed "alloio"-(varying)bias.

Stubbs and Pliskoff (1969) introduced dependent reinforcement schedules in concurrent schedules to ensure that the obtained reinforcer ratio be equal to the scheduled reinforcer ratio. The schedule requires that the two responses are reinforced on two non-independent concurrent schedules. Thus, when a reinforcer is arranged for one of the responses, the schedule associated with the other correct response stops until the arranged reinforcement has been obtained. McCarthy and Davison (1980a) introduced such a controlled reinforcement procedure in a signal detection procedure, to ensure that changes in SPP or in the subject's preference for one response alternative over another would not alter the distribution of reinforcement between the two choice alternatives. That is, that any measure of response bias would not be confounded by variation in reinforcer ratio frequency.

Comparison of performance using both a controlled and uncontrolled reinforcement procedure (McCarthy & Davison, 1984) showed that where the controlled procedure generated iso-bias or equal bias estimates across different stimulus values, the uncontrolled procedure generated alloio-bias, or changing bias estimates across different discriminability levels. These changes in response bias, negligible at large stimulus differences (high discriminability) became more extreme at small stimulus differences. These were due to the changes in reinforcer ratio resulting from the uncontrolled reinforcement

procedure.

The Davison and Tustin model predicts that as discrimination between the two stimuli, S_1 and S_2 , decreases, the value of $\log d$ likewise decreases. A $\log d$ value of zero, therefore, indicates no discrimination between the two stimuli. When values of $\log d$ are plotted as a function of stimulus values, the descending portion of the data function provides a description of decreasing discriminative performance. The stimulus value corresponding to the $\log d$ value of zero may then be taken as a measure of absolute threshold, independent of any response biases the subject may have. Alternatively, the stimulus value corresponding to a $\log d$ value of zero may be obtained by extrapolation from a function fitted to the descending portion of the data. The $\log d$ value of zero has provided a useful description of the absolute threshold of luminance differences in pigeons (McCarthy & Davison, 1984) and audition in hens (Temple *et al.*, 1984).

Threshold criteria

Traditionally, in human studies of visual acuity, each trial involves the presentation of the target stimulus. That is, generally the subject is required to respond to the target stimulus on every trial. The criterion for absolute threshold was conventionally determined for human psychophysics as that stimulus value which the subject could discriminate 50% of the time (Spence, 1934). In some studies, 75% was used, as an adjustment for guessing (e.g. Blackwell, 1952). There can be problems with comparing studies when threshold criteria vary. For example, Dobson and Teller (1978) refer to the variability among acuity values for human infants, when estimates are based on grouped data. Values differed, depending on whether studies

used that stimulus value to which 50%, or 75% of the infants responded.

In animal studies, different procedures may require different criteria for threshold estimation and these criteria may depend on whether or not the target stimulus is presented on each trial. In a forced-choice discrimination task where two stimuli are presented simultaneously, generally threshold estimates are based on the percentages of correct responses to only one of the stimuli (i.e. the "positive" or target stimulus). For example, Martin and Gordon, (1974), using horizontal and vertical gratings, defined responses to the vertical gratings as correct, and Spence (1934) using horizontal gratings and "blank" or grey stimuli defined responses to the gratings as correct. Both studies determined threshold as that grating spatial frequency which was responded to correctly on 75% of the trials. Loop, Smyly, Millican, Leigh and Greifer (1981) however, using the same procedure, determined threshold as that grating value at which 70% of the responses were correct. The threshold criteria for the latter study therefore, was slightly less stringent than that for the other studies mentioned using this procedure.

When a successive discrimination is used, with only one of two stimuli presented on each trial, generally threshold estimates are based on responses in both trial types. For such studies the threshold criterion is generally defined as 75% of total trials (grating and grey stimulus) correct (e.g. Hodos *et al.*, 1976; Hodos *et al.*, 1985).

When a go/no go procedure is used, the discrimination is

successive. That is, there are two trial types, either with gratings of differing orientation, or a grating and grey stimulus. Threshold is generally based on correct responses to the target stimulus and incorrect responses to the "negative" or grey stimulus. For example, Bloch and Martinoya, (1982), using horizontal and vertical gratings required pigeons to respond on the vertical grating presentation ("positive" stimulus) only, and the criterion for threshold was determined as the 50% level of performance. This was based on a performance index of the percentages of correct responses to the "positive" grating, minus the percentage of incorrect responses to the "negative" grating.

Spence (1934) suggested that the selection of any percentage value as threshold criterion is, theoretically at least, an arbitrary matter, as the threshold is a variable that ranges from the last stimulus value which the subject discriminates 100% of the time to the point at which no discrimination is made, or discrimination is 50% by chance. The fact that one may adopt any percentage value within this range, that is, 50% threshold, 60% threshold and so on, adds to the difficulty in comparisons across animal studies.

When the threshold is definitely defined as "that stimulus value which is discriminated as often as it is not", then the 50% correct criterion is often used. However, when the threshold is defined in terms of "the least stimulus value which at which there is clear perception" (the point midway between perfect performance and chance) then the 75% correct criterion is adopted (e.g. Dunstone & Sinclair, 1978). It appears, therefore, that in animal studies, the criterion used is partially dependent on the definition of absolute threshold,

and this may vary across studies.

The criterion may also depend on the number of available response alternatives. Where the 75% value may be taken when two response alternatives are available, the 66% value may be used when three response alternatives are employed (Bartley, 1958). In a study by Jacobs, Birch and Blakeslee (1982), tree squirrels chose between three response alternatives, and a 40% criterion was used. However, this decision may have been based on a 50% criterion for two response alternatives. Martin and Scarborough's (1965) study with hooded rats, using a simultaneous discrimination, employed as threshold the value of stimuli directly preceding the one to which the animal responded correctly 50% of the time. The threshold value chosen here, would necessarily depend on the size of the decrements in stimulus values used. Weiskrantz and Cowey (1963) used the stimulus value corresponding to 75% correct, based only on stimuli immediately above and below the 75% point. Blough (1971) on the other hand, with a simultaneous discrimination, used 75% correct responding to the grating stimuli, extrapolated from a regression line fitted to linearly transformed data from the descending portion of the psychometric function. Some studies use total correct responses to both stimuli (e.g. Herman, Peacock, Yunker & Madsen, 1975) whilst others calculate correct responses to the target stimulus only (e.g. Pepper & Simmons, 1973).

Spence (1934) argued that in animal studies, compared to human studies, a much greater number of random or chance responses occur, as a result of lack of experimental control over all extraneous variables. The effect of such random responses is to lower the

percentages of correct responses made to each stimulus value. However, this effect is not constant for all portions of the psychometric curve, the higher percentages (where discrimination is best) being decreased to a lesser extent than the lower, if the number of random responses is constant for all parts of the curve. This effect would become zero at 50% as this value is itself a chance result. Spence suggested it best to use as a criterion of threshold a percentage value that is the least affected by these random responses. From this point of view the 50% value would be the best criterion, as it alone is not affected by chance factors. However, extended testing at difficult discriminations may also result in loss of stimulus control. As the criterion for threshold becomes higher, the threshold value necessarily decreases.

Across studies, therefore, poorer estimates of threshold may not reflect the animal's visual capacity, but rather, the stringent criterion employed to define threshold. It is possible that, at least in certain procedures, the threshold criterion chosen may depend not only on the arbitrary definition of threshold but also the manner in which the animal's discriminative performance decreases.

Most animal studies require either a simultaneous or successive discrimination between two stimuli. Discrimination may be between a pair of variable grating stimuli, varying only in line orientation such as horizontal and vertical (e.g. Woodburne, 1965). As gratings become finer it becomes more difficult to discriminate between them. However, it is probable that the animal would make as many incorrect responses to one as to the other, regardless of whether the discrimination is simultaneous or successive. Alternatively,

discrimination may be between a variable grating stimulus and an unresolvable grating or grey stimulus (e.g. Hodos et al., 1976). In a simultaneous discrimination as discrimination becomes difficult, the animal is likely to be incorrect equally to both. However, in a successive discrimination, as discrimination becomes more difficult it may be more probable that the animal would respond to the grating as grey than *vice versa*.

In a procedure which employs both a target and a standard stimulus in a successive discrimination there are two extreme response distributions which may occur as discrimination between the two stimuli decreases. All performance which includes discriminative responses to two alternatives would necessarily fall within the range of either of these. Firstly, in a visual acuity task using gratings of increasing spatial frequency and grey stimuli, as discrimination of gratings decreases, discrimination of the grey stimulus may be maintained. That is, the animal may become incorrect on 100% of the grating trials, and still remain 100% correct on grey stimulus trials. The 50% criterion for total performance would be the point at which there was 0% accuracy on grating trials. Therefore, in this case the 75% total correct performance might be used as the criterion as this would be the point at which the animal could discriminate the gratings correctly 50% of the time. If one used the point where $\log d$ becomes zero, to estimate threshold (as suggested previously) for this response distribution, this point would be analogous to the point of 50% correct on total trials. This could result in a threshold value which may overestimate the animal's visual ability, or at least, may not correspond with thresholds based on 50% correct on grating stimulus trials. A $\log d$ value which most closely approximates the

75% total performance may be more appropriate. If one may assume no bias, then a $\log d$ value of 0.48 would be equivalent to 75% total trial accuracy.

A second extreme response distribution could occur when discrimination on both grating and grey stimulus trials decreases equally. That is, as the animal becomes less accurate on grating trials, as a function of increased spatial frequency, it also becomes less accurate on grey stimulus trials. In such a case, the point where the gratings are correctly discriminated on 50% of the trials, is also the point where the grey stimuli are correctly discriminated 50% of the time. If the 75% total performance criterion were used for this response distribution, we would be taking the point where the animal is still discriminating the grating on 75% of trials. The use of this criterion for such a response distribution would result in a threshold value which may underestimate the animal's visual ability. Here, the 50% accuracy of total trial performance coincides with 50% accuracy on gratings trials. For this type of response distribution, a $\log d$ value of zero would possibly be more appropriate.

Because the criterion used to determine threshold is one which is necessarily based on the discriminative performance on one of the two alternatives, (i.e. the grating), it would seem important to analyse performance in such procedures in terms of the response distribution to both response alternatives. If performance falls somewhere between these two hypothetical extreme response distributions, perhaps a threshold value somewhere between the 50% and 75% total correct performance point would be the most appropriate.

The aim of the following series of studies was threefold:

- (a) to investigate visual acuity in the domestic hen,
- (b) to determine the effects of various procedural manipulations on discriminative performance and the resultant estimates of threshold, and
- (c) to compare the effects of task difficulty on discriminative performance under various procedural manipulations.

EXPERIMENT 1.1

Although sensory functions in animals have often been compared across species, and differences between and within species widely documented, the investigation of differences in discrimination which may occur as artefacts of procedural variation has been limited. The method by which stimuli are presented to the subject may affect the discriminative performance, and the estimate of absolute threshold value obtained, as may the techniques of analysis to which data are subjected. Both Dalland (1970) and Terman (1970) reported that the descending series of the Method of Limits stimulus presentation generated higher accuracy than the ascending series.

The present experiment involved a spatial successive discrimination task in a two-alternative procedure with a constant (grey) and variable (grating) stimulus. Such a procedure may be termed a symbolic matching-to-sample procedure, in which the sample designates which of the two comparison stimuli (left or right keys) is correct.

The purpose of this study was:

- (a) to determine the discriminative performance in the domestic hen, using a visual acuity task,
- (b) to determine absolute threshold estimates with a variety of criteria,
- (c) to evaluate the utility of various methods of analysis both traditional and non-traditional, for the present studies, and
- (d) to determine any difference between discriminative performance in a descending and ascending series of stimulus presentation.

Method 1.1

Subjects

Six domestic hens (Ross Tinted) numbered from 71 to 76 served. They were 42 weeks old when the study commenced. All birds had been magazine trained and trained to peck an illuminated key prior to the experiment. They were individually housed and received supplementary food (commercial laying mash) to maintain their weights at 80% +/- 20 g of their free-feeding levels throughout the study. Water and grit were available at all times.

Apparatus

The experimental chamber consisted of a wooden box 414 mm wide, 535 mm high and 570 mm long. Three back-illuminated response keys of clear plate glass, 3 mm thick, 30 mm in diameter, 90 mm apart and 385 mm above the floor, were located centrally on separate aluminium response panels. A piece of clear perspex, 30 mm in diameter and 4 mm thick was placed between the rear of the centre response key and the light source. A small square of thin white cardboard was attached to the exterior of the response wall, between the rear of each of the two side keys and their respective light sources. Access to the solenoid-operated magazine was centrally located 145 mm from the floor. On the bottom of the chamber a grid floor was set in a plastic tray. This was removable for cleaning.

The centre key was made opaque except for a 20 mm diameter circular region in the centre, by applying a coat of black paint around the circumference of the rear of the key. Pecks on the

response keys were effective only if they exceeded a force of 1.5 N for the centre key and 0.75 N for the side keys and if the keys illuminated. An effective peck extinguished the keylight and produced a tone for 35 ms. This tone provided auditory feedback. Experimental events were controlled by a Commodore 64 computer, situated remotely from the experimental chamber.

Target stimuli. These consisted of a series of pairs of black and white stripes (termed gratings) and grey stimuli. Both stimulus types were photographic transparencies. The gratings were photographed reductions of a commercially prepared high contrast square wave grating called Letraset. Both the gratings and grey stimuli measured 24 mm by 35 mm. The gratings ranged in spatial frequency from one to ten line-spaces per mm (cycles/mm). When, for the present series of studies, the widths of bars and spaces were measured using a microscope with stage micrometers, the bar widths and spaces between the bars were found to be slightly different, with spaces less than 0.05 mm wider than bar widths for the coarsest grating (1 cycle/mm). For all grating sizes this slight difference was a constant proportion, as the finer gratings were reductions from the coarsest grating. Therefore, for the purposes of the present studies, the bars and spaces were treated as equal (e.g. one cycle per mm (c/mm) refers to one bar and one space per mm) for clarity and ease of across-study comparison. A photographic enlargement of the original grating is shown as Plate 1.1.1.

Six pairs of gratings and grey stimuli were mounted in alternating order, around the circumference of a 216 mm diameter

Plate 1.1.1

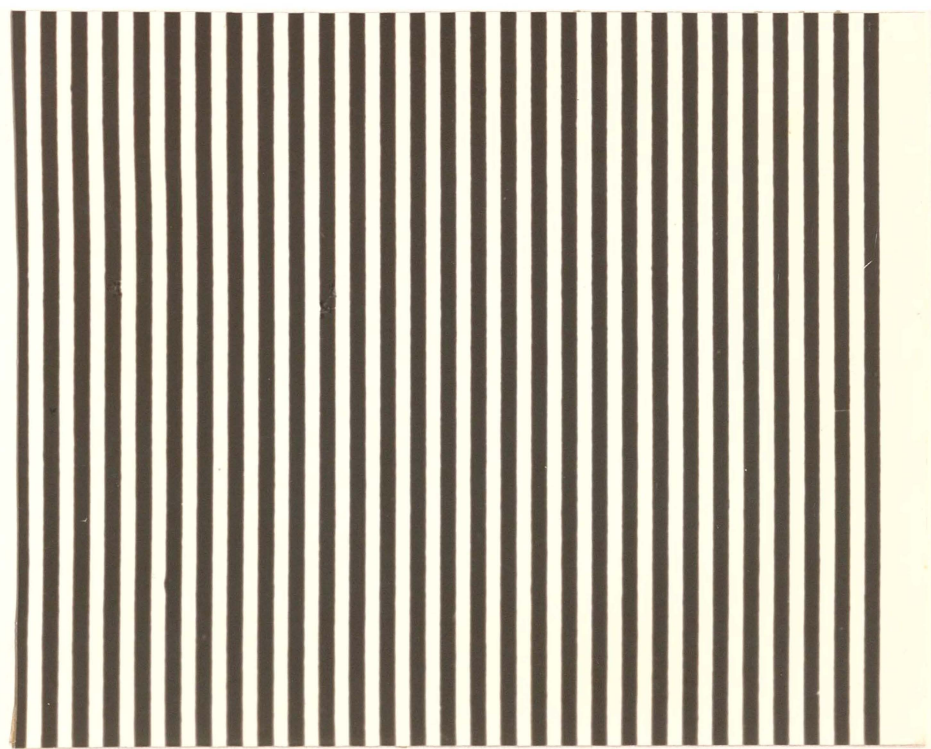


Plate 1.1.1: A Photographic enlargement of the original grating used.

opaque perspex disk, located at the rear of the centre key. The distance from the front surface of the key to the front surface of the stimuli was 26 mm. Fourteen stimulus disks were used throughout the study. On each were mounted six grey stimuli and six gratings of one spatial frequency only. The stimuli on the disks, and the rear of the centre response key were regularly dusted with a fine bristled brush. Figure 1.1.1 shows an illustration of the disk attached to the exterior of the response wall of the chamber.

Contrast of the stimuli. The contrast of seven of the gratings, ranging in spatial frequency from one to 10 c/mm, was measured with a Joyce-Loebl Mark 3CS microdensitometer, with a rectangular measuring slit 50 microns by 500 microns. The following formula was used to calculate contrast:

$$\%C = \frac{L_1 - L_d}{L_1 + L_d} \times 100$$

where %C represents the percentage contrast, L_d is the luminance of the dark bars, and L_1 is the luminance of the spaces. The percentage of contrast was found to vary from 92.5% to 100%. The contrast of each grating is shown in Table 1.1.1.

Luminance values. All key luminances were measured in cd/m^2 with an ASAHI Pentax Spotmeter V. Luminance of the centre sample key measured at 3 cd/m^2 and luminance of the two side keys measured 2.69 cd/m^2 . Luminances of gratings and grey stimuli were equal, with a loss of luminance of 0.16 cd/m^2 at the finest grating (10 c/mm) only.

Figure 1.1.1

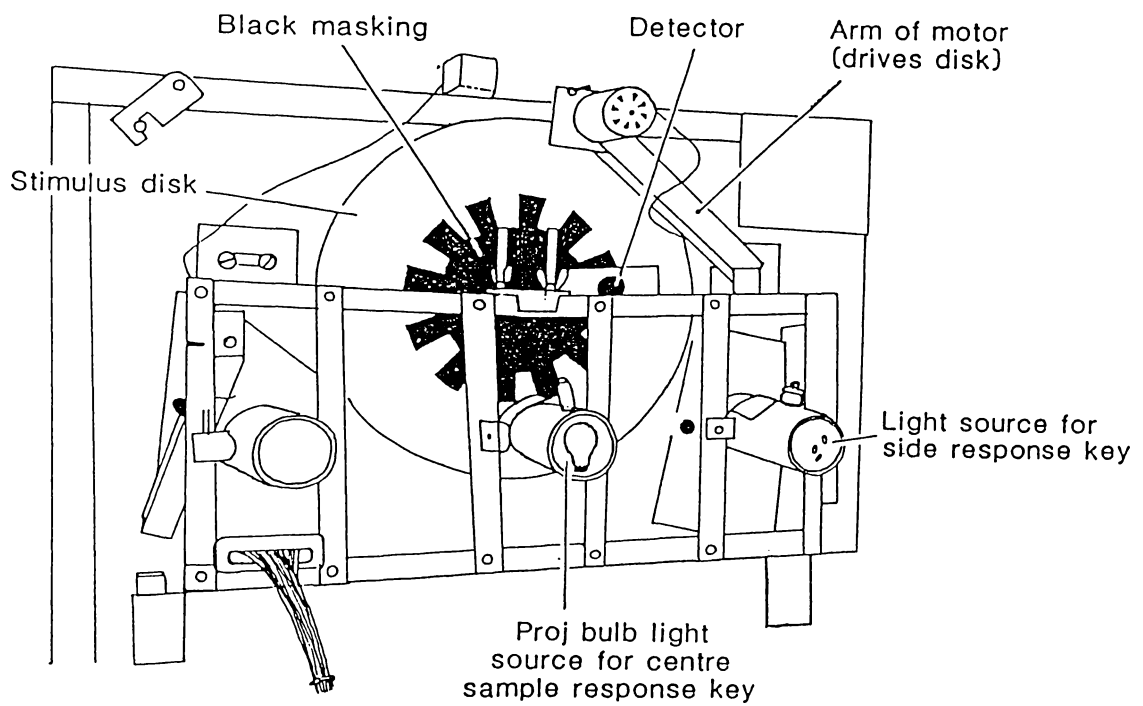


Figure 1.1.1: The exterior of the response wall of the experimental chamber.

Table 1.1.1

Table 1.1.1

Contrast of grating stimuli of each spatial frequency, measured by a Joyce Loebel Mark 3CS microdensitometer

Grating spatial	
frequency (c/mm)	Contrast (%)
1	94.80
2	100
3	94.1 +/- 1.0
4	94.1 +/- 1.0
5	100
6	100
8	92.5 +/- 1.0
10	93.6 +/- 4.8

The three response keys were rear illuminated by 3.75 W projector bulbs. The projector bulb behind the centre key was replaced every eight weeks, and prior to each series of probes, and luminance was checked regularly to ensure that the value remained constant. Illumination of the walls and ceiling remained at approximately 3 Lux, as measured with an L1-170 Quantum Radiometer Photometer. No houselight was used.

Reinforcement. An automatic food delivery hopper contained whole wheat. The hopper could be raised to allow access to the wheat. The food hopper was illuminated by a 1.5 W bulb covered with an opaque plastic cap.

Procedure

General procedure. Six gratings of the same spatial frequency and six grey stimuli were presented during an experimental session. Presentation of the grating or grey stimuli was psuedo-random, a variation of the Gellerman (1933) series. This ensured that the grating and grey stimuli would each be presented on no more than three consecutive trials, and that each would be presented on approximately the same number of trials within each experimental session. A non-correction procedure was used, that is, the occurrence of the grating and grey stimulus behind the centre key was independent of the accuracy of responses on the previous trial.

A variable-interval reinforcement schedule of 30 s (VI 30) was programmed, using a version of the Gellerman series, allotting reinforcement delivery for correct responses on each of the two side keys aperiodically, around an average of 60 s each, or 30 s overall.

The VI schedule consisted of an arithmetic series of 15 intervals, $(a+bx; a=1, b=2 \text{ (i.e. } 1+2x) \text{ } x=0,1,2 \dots 14)$ presented in random order. The schedule of reinforcement was kept constant at VI 30 s throughout the experiment.

A non-independent or controlled reinforcement procedure was used. That is, if a reinforcement came available on one alternative, the animal was denied access to reinforcement for correct responses on the other, until it made a correct response on the alternative where the reinforcement was available. This prevented exclusive responding to one alternative only and controlled the relative obtained reinforcement rate. This schedule was in effect throughout the experiment.

Each trial began with the presentation of either a grating or a grey stimulus (the sample stimulus) behind the illuminated centre key. A single peck on this key resulted in the two side keys being lit. If the grating was present behind the centre key, a peck to the left side key was correct. If the grey stimulus was presented on the centre key, a right side key peck was correct. The centre response key remained lit during this choice. A correct trial resulted in the magazine light coming on for 3 s, and aperiodically this was accompanied by 3 s access to wheat. The three key lights went out and the keys were inoperative during this time. Incorrect responses, that is, a response to the right key when a grating was presented, or a response to the left key when a grey stimulus was presented, resulted in 3 s blackout. During the 3 s of reinforcement or blackout, the stimulus disk turned to position the stimulus for the following trial. Sessions started and ended in black-out. Experimental sessions were

scheduled for seven days a week, for a total of 45 reinforcements or 30 min, whichever was the shortest.

Preliminary Training. Training commenced with a 4 c/mm grating and grey stimuli, and 4 s reinforcement for each correct response (CRF). After seven sessions, training continued on a VI 15 s schedule for correct responding, for a further 18 sessions. During these sessions, when a correct response was not followed by reinforcement, the magazine light went on for 0.5 s. The consequence for an incorrect response was 3 s blackout. For the following 21 sessions the magazine light duration was increased to 2 s when a trial was correct but reinforcement was not available. The magazine light presentation was then increased to 3 s duration, and continued at this duration throughout the experiment. Following a further 35 sessions, the reinforcement schedule was reduced to VI 30 s, and this schedule was continued throughout the experiment. Table 1.1.2 presents the experimental sessions during preliminary training.

Main training sessions. Following the first 40 sessions of main training, the training stimulus was changed from 2 c/mm to 1 c/mm. Thereafter, on training sessions the grating presented was always of the lowest spatial frequency (1 c/mm) and other conditions were as in the general procedure. Training sessions continued for a further 21 sessions, until behaviour met both an accuracy and a stability criterion. Hens were required respond with an 80% accuracy on total (both grating and grey) trials. It was necessary to reduce this testing criterion to 70% accuracy for hen 73, when it became apparent after extensive training that she was not going to reach this degree of accuracy. The stability criterion required that the median

Table 1.1.2

Table 1.1.2

The spatial frequency of the training stimulus, the reinforcement schedule (Rft sched) reinforcement duration (Rft dur) magazine light duration (Mag light) and the number of sessions for each training condition.

Training stimulus

<u>Spatial frequency</u> (c/mm)	<u>Rft</u> <u>sched(s)</u>	<u>Rft</u> <u>dur(s)</u>	<u>Mag. light</u> (s)	<u>No of</u> <u>sessions</u>
2.0	CRF	4	0.5	7
2.0	VI 15	3	0.5	18
2.0	VI 15	3	2.0	21
2.0	VI 15	3	3.0	35

of the proportion of correct responses emitted over five sessions be within 0.05 of the median from the preceding five sessions (Davison, 1976). This criterion had to be met five, not necessarily consecutive, times.

Probe sessions. Once the above criteria were satisfied, testing or probe sessions were commenced. These sessions involved the use of a grating of a higher spatial frequency from that used as the training stimulus. Only one value of spatial frequency was used during a probe session, and, in most cases, only one probe session was undertaken at each grating value. Between probe sessions, training continued with the coarsest grating (1 c/mm) for at least one session, until each hen had reached her individual testing criterion. The testing criterion for each hen was that correct responses be within 0.1 of the highest proportion of total trials correct during the last five days of training, before the probe series began.

Probes included a descending and an ascending series. For the descending series of probes, the gratings presented in each probe session increased in spatial frequency (i.e. progressively finer gratings) from 1 c/mm to 10 c/mm. The ascending series of probes began with the grating of the highest spatial frequency (10 c/mm) and gratings were presented in order of decreasing spatial frequency at each successive probe session. The ascending series of probes commenced immediately following completion of the descending series of probes, when all hens had reached their individual testing criteria. Equipment problems caused rejection of data for the first 53 sessions following commencement of probe sessions.

Data Collection. The data collected included the number of correct and incorrect responses emitted on the left and right keys following presentation of the grating and grey stimulus on the sample key, the latencies of correct and incorrect responding on left and right keys following presentation of the grating and grey stimulus, and the number of reinforcements obtained for responding correctly on the left and right keys.

Determination of visual angle

To calculate near field visual acuity, it was necessary to determine the distance from the surface of the gratings to the retinal surface of the eye. A video film was taken of each hen whilst it was working in the chamber. A ruler with 10 mm markings was set up, extending along the ceiling of the chamber, from a point immediately above the centre key. Filming occurred over several sessions, and the hens seemed undisturbed by the presence of the camera. Lighting conditions in the chamber were unchanged during this time. The video of the hens was subsequently run slowly, stopped and rewound at various points to determine placement of the hen's head just prior to the initiation of a peck on the sample (centre) key. Still photos were taken at these points, just prior to the start of a peck movement. The distance from the centre response key to the anterior surface of the hen's cornea was determined from these photos. Measurements obtained were used to estimate the visual angle subtended by the retinal images of the gratings. A photograph of one of the hens in a typical position prior to pecking the centre key, is shown on Plate 1.1.2.

A histological study was completed by Ms Denyse Harding, a biological sciences technician, to determine the distance from the

Plate 1.1.2

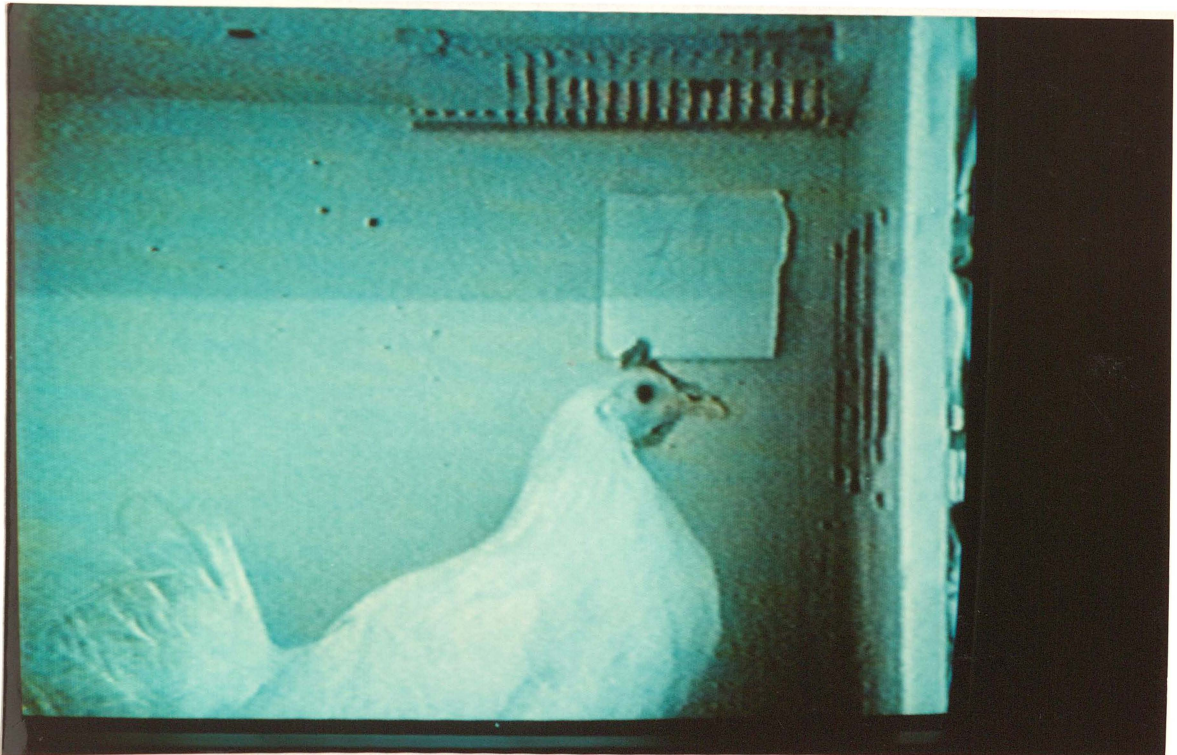


Plate 1.1.2: Hen standing in a typical position in the experimental chamber, prior to pecking the centre sample key.

anterior of the cornea to the retinal surface of the hens' eyes. The extracted left eyes of two recently sacrificed White Shaver adult hens were placed into fixative of 2.5% glutaraldehyde buffered at pH 7.3. As an ocular hemisector was not available, the eyes were hemisected vertically (as carefully as possible) between the cornea and the exit point of the optic nerve, using a disposable microtome blade. Entry of the blade was from the posterior of the globe toward the cornea. An Olympus binocular dissecting microscope with an eyepiece micrometer, was used to determine measurements of the distance from the anterior of the cornea to the anterior surface of the retina. Magnification at 14x was obtained by using 20x eyepieces with magnification at 0.7x.

Results 1.1

Discrimination

Figure 1.1.2 presents the percentages of total trials correct (gratings and grey stimuli) as a function of the spatial frequency of gratings, measured in cycles per mm (c/mm) for all hens and for both the descending and the ascending series of probes. There is close replication in the data for both series and for all hens, with the data showing a monotonically decreasing function at increasingly finer gratings to 3 - 4 c/mm, followed by a levelling off. There are no consistent differences between the data for the descending and ascending series of probes.

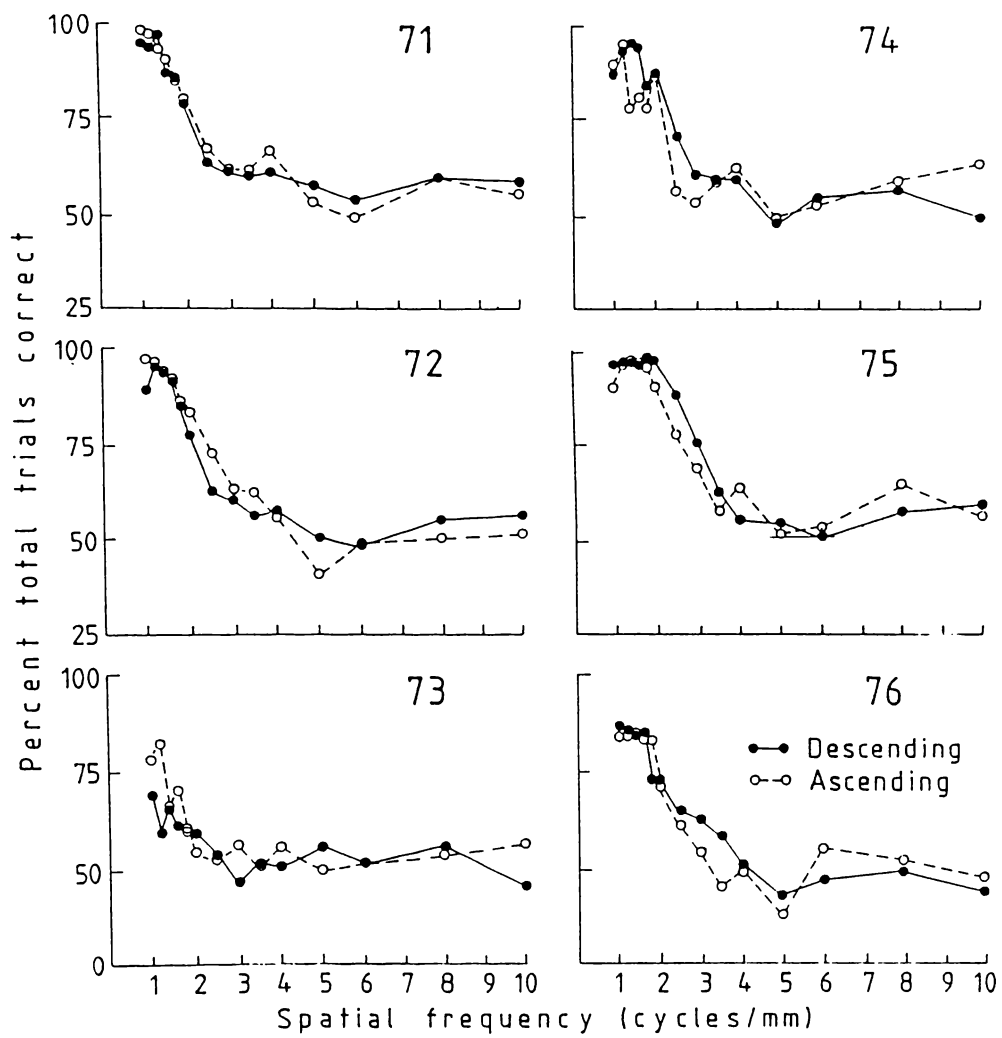
Both at the coarsest gratings, where hens showed highest accuracy, and at the finer gratings, where accuracy is low, there is variability in the data. That is, at grating values where high accuracy indicated that the hens could discriminate, and at grating values where low accuracy indicates little or no discrimination, there are fluctuations in the percentages correct. For example, the percentages of total trials correct for hen 71 were 93% for the probe with a grating of 1.2 c/mm and this increased to 97% at the grating value of 1.4 c/mm. The percentages of total trials correct increased from 54% at the 6 c/mm grating value to 59% correct at the 8 c/mm grating value. Similar fluctuations in accuracy occurred across all hens for both probe series.

The estimates of threshold for each hen for both probe series were determined as that spatial frequency of the gratings at which 75% of total trial performance was correct. This was obtained by

Figure 1.1.2

Figure 1.1.2

The percentages of total trials correct, plotted as a function of grating spatial frequency, measured in c/mm, for all hens, for the descending (filled circles joined by a solid line) and ascending (unfilled circles joined by a broken line) series of probes.



interpolation using the line which joined the data points, to estimate the grating frequency corresponding to 75% of total trials correct. Estimates were also taken from the point at which the plotted function was 50% correct. Where the functions did not decrease to 50%, an estimate was taken by extrapolation from the descending function to the X-axis, by extending a line from the final two data points of the descending portion of the function.

Threshold estimates for all hens for both probe series are shown in Table 1.1.3. Estimates taken from the point at which total performance was 50% correct are greater than those taken from the point of 75% total trial accuracy. The estimates for 75% total trials correct range from 2.1 to 3.0 c/mm for the descending series, and from 1.3 to 2.6 c/mm for the ascending series of probes. Those obtained from the 50% total trials correct criterion range from 2.9 to 5.1 c/mm for the descending series and from 2.3 to 4.3 c/mm for the ascending series of probes.

For three hens, and from both threshold criteria, estimates obtained from the descending series are greater (i.e. indicating more acute vision). For two hens and from both threshold criteria, estimates taken from the ascending series are greater. For one hen, 73, it was not possible to determine a estimate for the descending series as her data did not reach 75% total accuracy. Her performance, however, improved sufficiently to allow estimation of a threshold for the ascending series.

Figure 1.1.3 shows the percentages of correct responses made on grating and grey stimulus trials, plotted separately, as a function of

Table 1.1.3

Table 1.1.3

Threshold estimates measured in c/mm, taken from the data plotted as the percentage of total trials correct, at the stimulus values corresponding to 75% and 50% total trial accuracy for all hens, for the descending and ascending series of probes.

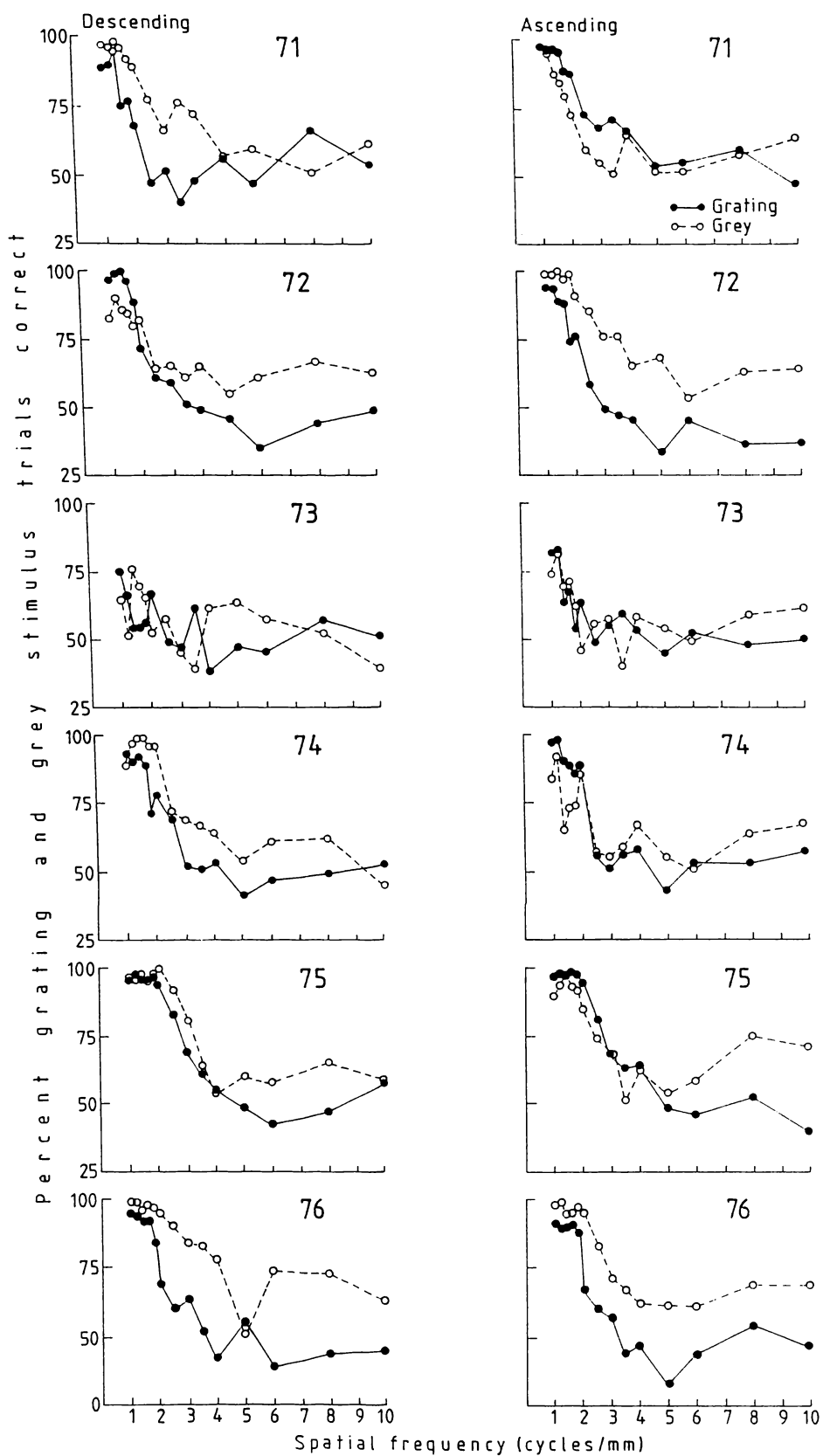
Hen	Descending		Ascending	
	75%	50%	75%	50%
71	2.1	2.9	2.2	3.1
72	2.1	2.9	2.4	3.1
73	*	3.4	1.3	2.3
74	2.4	3.5	2.2	3.1
75	3.0	3.7	2.6	3.9
76	2.5	5.1	2.3	4.3

* Estimate not calculable.

Figure 1.1.3

Figure 1.1.3

The percentages of grating (filled circles joined by a solid line), and grey stimulus trials (unfilled circles joined by a broken line) correct, plotted separately, as a function of grating spatial frequency, measured in c/mm, for all hens, for the descending and ascending series of probes.



grating spatial frequency, measured in c/mm. These are shown for the descending and the ascending series of probes. All functions show decreasing accuracy with increasing values of grating spatial frequency. Generally, the percentages of correct responses on grating trials fell to below 50%. All hens showed decreases in accuracy on grey trials to around 70% or below during probe sessions with finer gratings. However, except for the functions for hens 71 and 73, there is a tendency for the curves to be flatter on grey stimulus trials than for finer grating trials.

Threshold estimates based on the grating trials only, were taken from the stimulus values corresponding to the points at which the plotted functions were 50% correct. Where plotted functions did not decrease to 50%, an estimate of threshold was taken by extrapolation from the descending function to the X-axis, by the extension of a line from the final two data points of the descending portion of the function. Estimates for all hens for both probe series are shown in Table 1.1.4. These range from 2.4 to 4.8 c/mm for the descending series and from 2.5 to 4.9 c/mm for the ascending series. Neither of the two probe series yielded consistently greater threshold values. Estimates were also taken from the points at which the plotted functions were 75% correct. These are also shown in Table 1.1.4 and range from 1.0 to 2.8 c/mm for the descending series and from 1.3 to 2.8 c/mm for the ascending series. Neither probe series consistently provided greater estimates. Although it was not possible to determine an estimate for hen 73 from the point at which the plotted function of percentage of total trials were 75% correct for the descending series, there was sufficient accuracy to calculate this from the grating trials only function. This indicates that the low accuracy of total

Table 1.1.4

Table 1.1.4

Threshold estimates, measured in c/mm, taken from the data plotted as the percentages of grating and grey stimulus trials correct, at the stimulus values corresponding to 50% and 75% grating trial accuracy, for all hens, for the descending and ascending series of probes.

Hen	Descending		Ascending	
	50%	75%	50%	75%
71	2.4	1.9	4.6	2.4
72	3.6	2.0	2.9	1.8
73	2.5	1.0	2.5	1.3
74	3.1	1.8	3.1	2.2
75	4.8	2.8	4.9	2.8
76	3.6	1.9	3.3	1.9

trial performance (Figure 1.1.2) resulted from greater inaccuracy of responding on grey stimulus trials rather than from inaccuracy on grating trials.

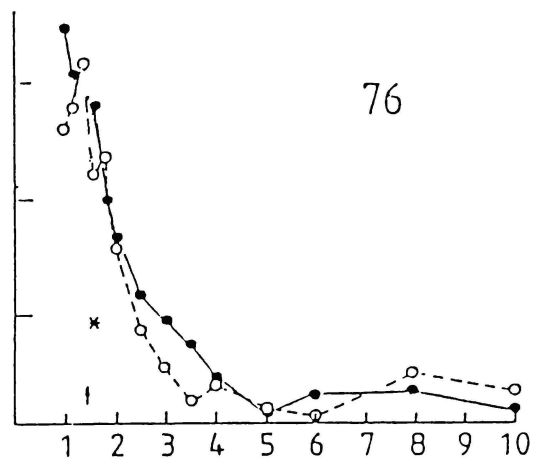
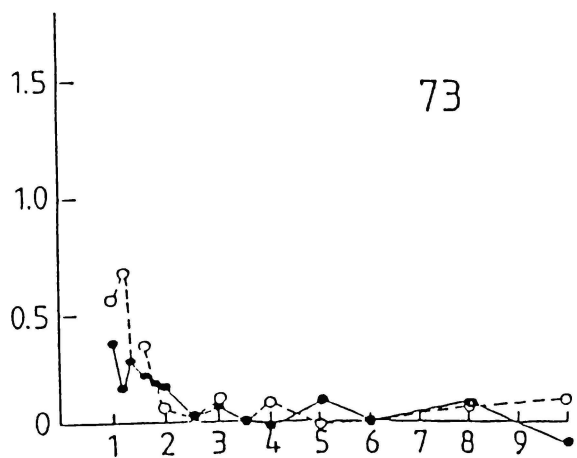
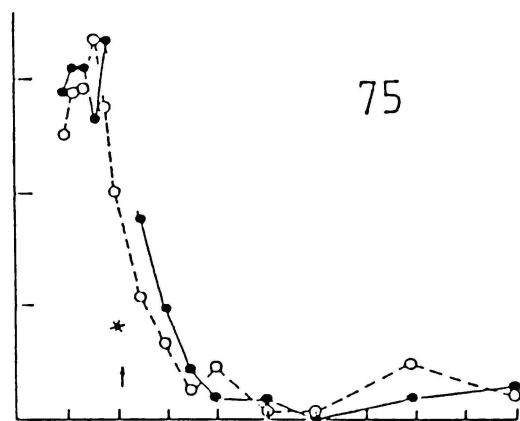
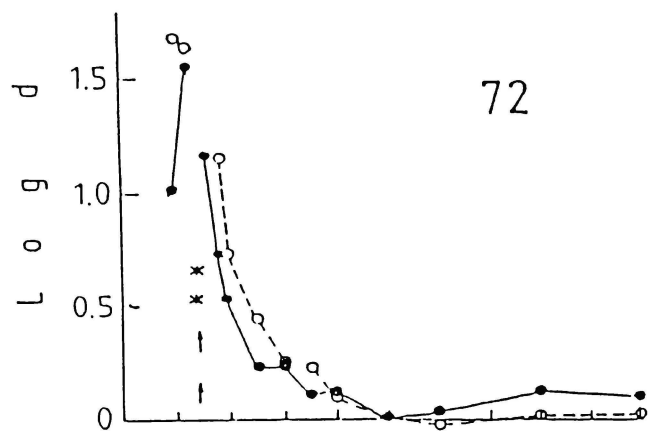
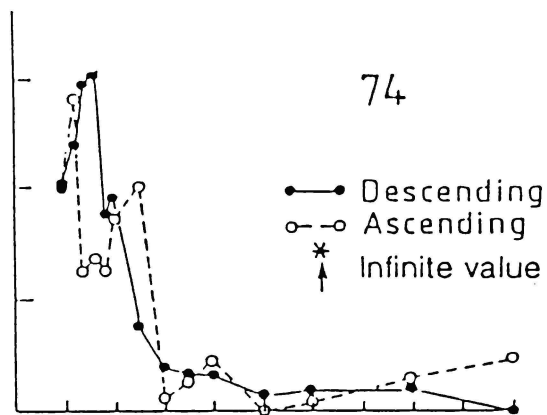
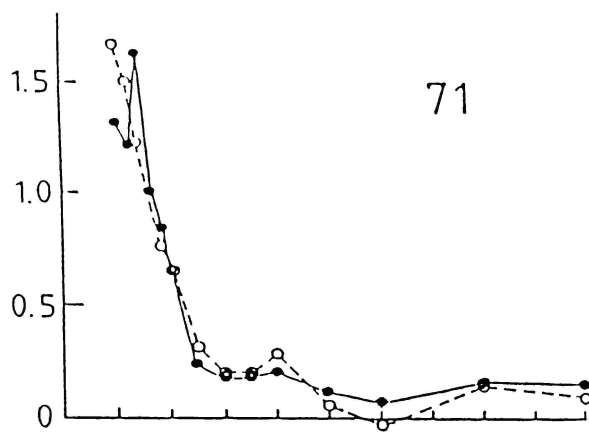
Figure 1.1.4 presents $\log d$ calculated using Equation (6). $\log d$ values are shown for all hens from both probe series, as a function of grating spatial frequency, measured in c/mm. Data replicate well for the two series, showing a steep decrease in $\log d$ with curves flattening out at finer grating probes. In two cases $\log d$ values increased at the highest spatial frequency of gratings.

Threshold estimates were obtained by interpolation to determine the spatial frequency of grating which corresponded to a $\log d$ value of 0.48. The $\log d$ value of 0.48 was chosen as that value which most closely approximates 75% accuracy on total trial performance. Further estimates were taken for both probe series and all hens from the point where the $\log d$ value was 0.00. For most plots, to obtain these estimates, it was necessary to extrapolate by extending a line from the final two data points of descending portion of the function to the X-axis. The estimates of threshold obtained from the $\log d$ values of 0.48 and 0.00 for all hens and both probe series are shown in Table 1.1.5. For the $\log d$ value of 0.48, these range from 2.1 to 3.0 c/mm for the descending series and from 1.3 to 2.8 c/mm for the ascending series. As for estimates obtained from the functions on Figures 1.1.2 for the percentages of total trials correct, neither series of probes consistently yielded greater estimates of threshold. Estimates from the $\log d$ value of 0.00 range from 2.7 to 3.9 c/mm for the descending series and from 2.1 to 3.8 c/mm for the ascending series. For all hens these values are greater than those obtained using the point

Figure 1.1.4

Figure 1.1.4

Values of $\log d$ plotted as a function of grating spatial frequency, measured in c/mm, for all hens, for the descending (filled circles joined by a solid line) and ascending (unfilled circles joined by a broken line) series of probes. Infinite $\log d$ values are indicated by an asterisk and an arrow pointing upwards from the X-axis.



Spatial frequency (cycles/mm)

Table 1.1.5

Table 1.1.5

Estimates of threshold measured in c/mm taken from data, plotted as values of $\log d$, at the stimulus value corresponding to $\log d$ values of 0.48 and 0.00, for all hens, for the descending and ascending probe series.

Hen	Descending		Ascending	
	0.48	0.00	0.48	0.00
71	2.2	2.8	2.3	2.9
72	2.1	2.9	2.4	3.6
73	*	2.7	1.3	2.1
74	2.4	2.9	2.8	3.1
75	3.0	3.9	2.6	3.7
76	3.0	4.2	2.4	3.8

* Estimate not calculable

where the $\log d$ value was 0.48. Neither series of probes consistently yielded greater estimates of threshold.

The data, when plotted as values of $\log d$, generally look like two approximately straight lines, that is, one descending line and one horizontal line. For each hen's data from each probe series, a series of pairs of lines were fitted by the method of least squares. The first lines were fitted by taking the first two data points (the lowest grating spatial frequency) for one line and the remainder for the other. The next pair included the first three points in the first line and the remainder in the other. This process of increasing the number of data points in the first line was continued, to produce a series of line pairs from the data for each hen for each probe series. These line pairs were created for each hen's data for the standard measure of stimulus values used (i.e. c/mm) and a series of transformations of the measures of the stimulus values. Specifically, these transformations were the logarithm of the number of cycles/mm, the width of a cycle (mm) and the logarithm of the width of a cycle. The data are plotted as a function of these in Figures 1.1.5a to 1.1.5d. The lines chosen to describe the descending function of the data are shown in the figures. An attempt was made to choose the first line of the line pair which gave, overall, the least standard error, and included three or more data points in the descending line. In some cases, however, the lines drawn were not those with the lowest standard error, but were those which were judged by three observers to describe the descending portions of the data best. It was possible to fit the line with the least standard error in eight of 12 cases when stimulus values were measured in c/mm (Figure 1.1.5a), in six of 12 cases when stimulus values were transformed to the logarithms of the

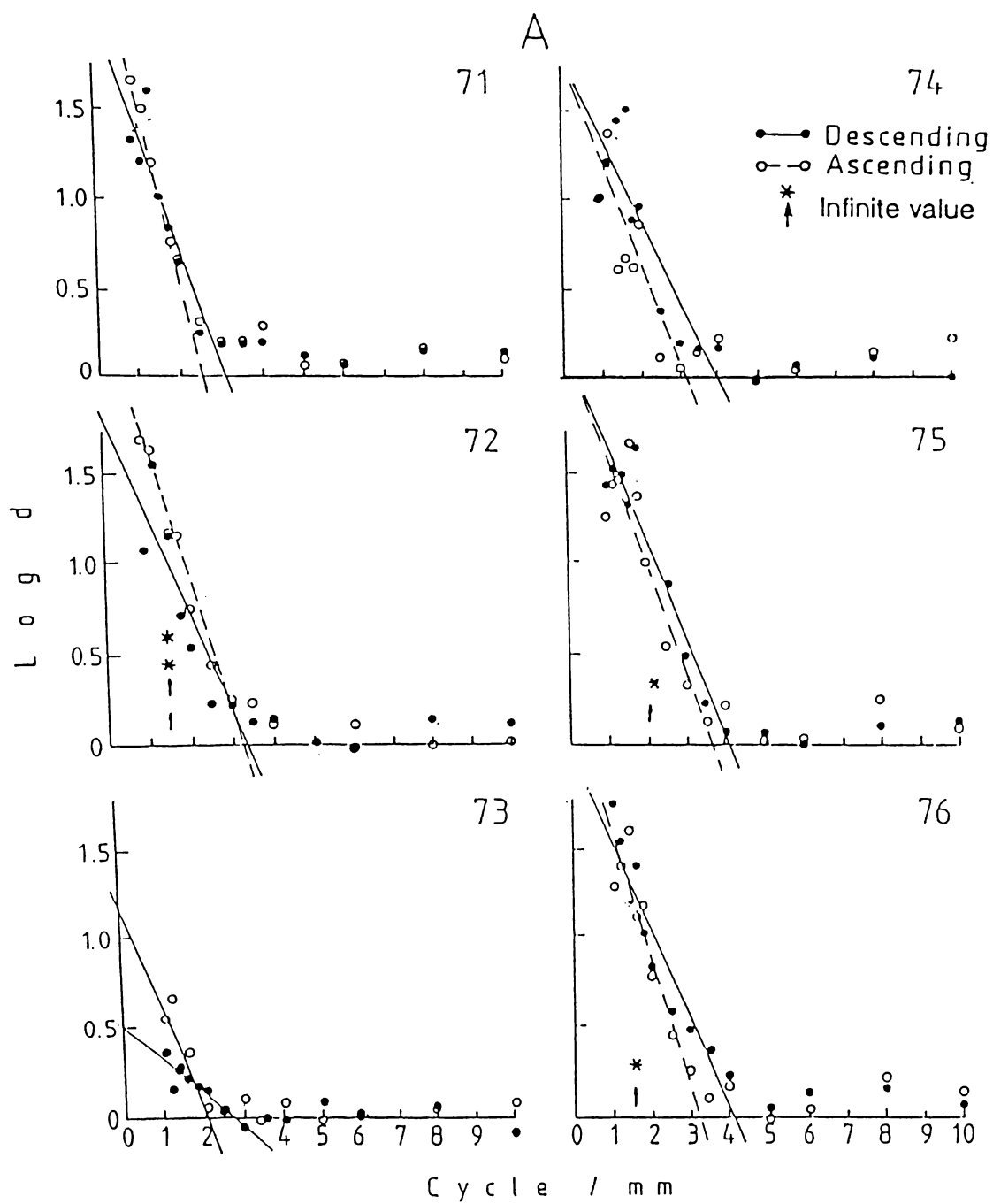
Figure 1.1.5

Figure 1.1.5 (a) to (d)

Values of $\log d$ plotted as a function of grating spatial frequency, for all hens, for the descending and ascending series of probes, plotted as a function of grating spatial frequency, measured in:

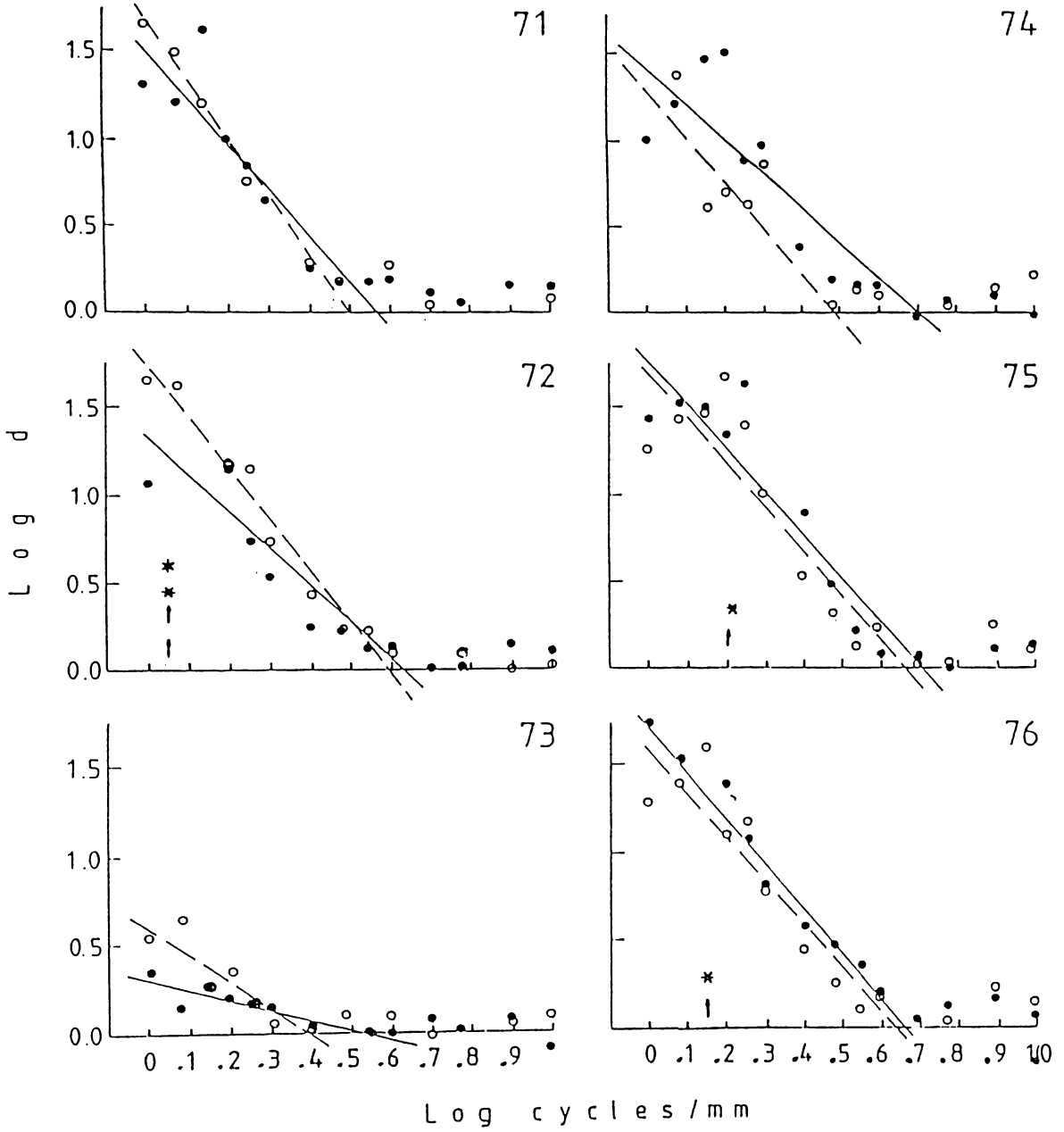
- (a) cycles per mm (c/mm).
- (b) logarithms of the number of cycles per mm.
- (c) width of a cycle (mm).
- (d) logarithms of the width of a cycle.

A line has been fitted to the descending portion of the data from each hen by the method of least squares, and is shown in the figures. The parameters of the fitted lines are given in Table 1.1.6.

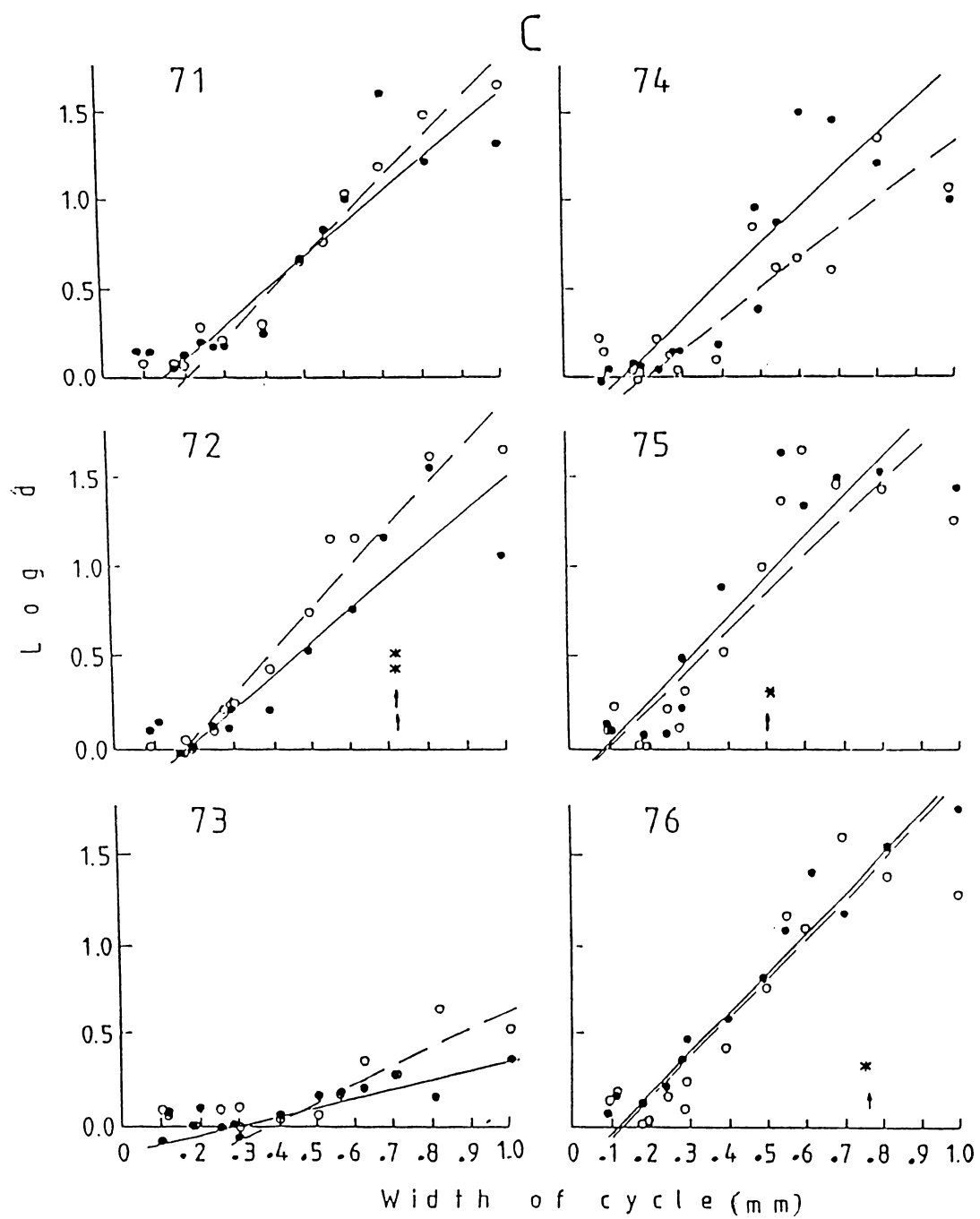


cont.

B

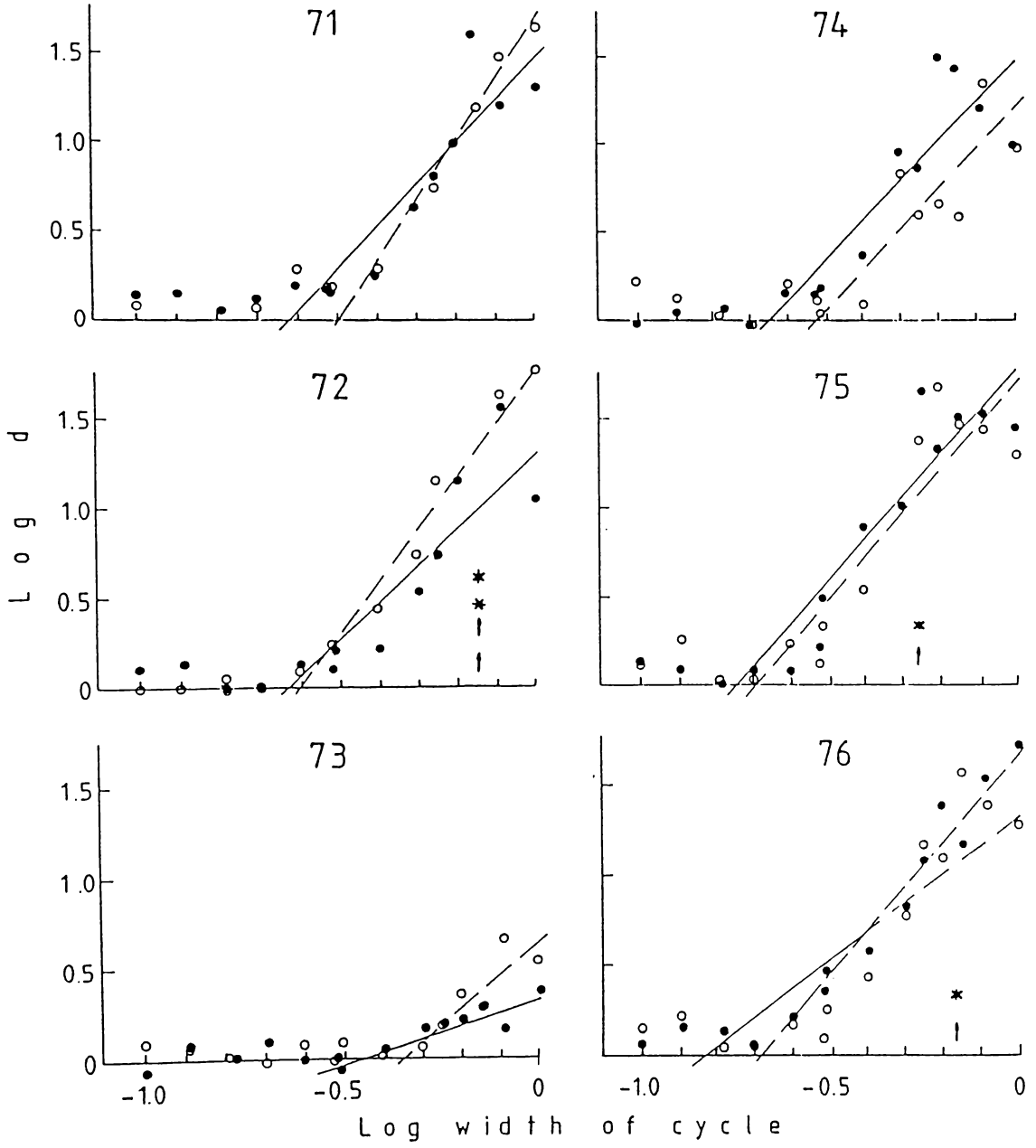


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D



number of cycles/mm (Figure 1.1.5b) and only in five of 12 cases when stimulus values were transformed either to the width of a cycle (mm) or the logarithm of the width of a cycle (Figures 1.1.5c and 1.1.5d). Table 1.1.6 shows the slope, intercept, the number of data points described by the line, the standard error of the estimate and the percentage of variance accounted for (VAC%) by each line chosen to describe the descending portion of the data.

Plotting the data as a function of the logarithms of the number of cycles/mm (Figure 1.1.5b) and as a function of the logarithms of the width of a cycle (Figure 1.1.5d) had the effect of spreading out data points more equally along the X-axis. To estimate threshold, the stimulus values corresponding to a $\log d$ value of 0.48 were determined from the fitted lines. Further estimates were obtained from these functions at the point where the fitted line crossed the X-axis at a $\log d$ value of 0.00. Table 1.1.7 shows these estimates, measured in c/mm, obtained for all hens in both series of probes, for each of the measures of stimulus value and for both of the $\log d$ values, 0.48 and 0.00. The 95% confidence intervals, as derived from the standard error of the line fit, are also shown.

The use of a $\log d$ value of 0.00 consistently yielded threshold estimates greater than those obtained using the $\log d$ value of 0.48, and these were generally greater for the descending series. The range of different estimates obtained for the same data determined from the fitted line at the $\log d$ value of 0.48 was not as great as the range for the same data determined from the fitted line at the $\log d$ value of 0.00. The transformation of stimulus values to the logarithm of the number of cycles/mm generally yielded slightly greater estimates

Table 1.1.6

Table 1.1.6

The slopes and the intercepts of the least squares lines fitted to the values of $\log d$, plotted as a function of grating spatial frequency, measured in cycles/mm(A) logarithm of the number of cycles/mm(B), the width of a cycle (mm)(C) and the logarithm of the width of a cycle (D), for all hens, for the descending (1) and ascending (2) probe series. The number of data points (Data Pts.) described by each line, the amounts of variance accounted for by the lines (VAC%) and the standard errors of the estimates (SE) are also given.

A: Cycles/mm

C: Width of a cycle (mm)

Hen	Probe series	Slope	Intcpt	Data pts.	VAC%	SE	Hen	Probe series	Slope	Intcpt	Data pts.	VAC%	SE
71	1	*-0.70	2.14	8	82.0	0.22	71	1	*1.90	0.29	12	83.2	0.23
	2	*-1.07	2.75	4	98.5	0.03		2	2.28	-0.48	9	97.2	0.09
72	1	*-0.54	1.82	9	77.1	0.25	72	1	*1.83	-0.34	12	81.5	0.24
	2	*-0.76	2.48	5	88.2	0.10		2	2.32	-0.40	12	95.2	0.14
73	1	*-0.18	0.49	8	82.2	0.06	73	1	*0.49	-0.14	10	79.3	0.06
	2	*-0.54	1.16	6	75.4	0.11		2	1.05	-0.39	6	17.1	0.11
74	1	*-0.46	1.81	10	74.0	0.27	74	1	*2.08	-0.31	11	84.2	0.14
	2	*-0.58	1.73	8	71.0	0.24		2	1.67	-0.35	9	72.2	0.24
75	1	-0.54	2.23	10	90.4	0.19	75	1	2.15	-0.20	12	76.8	0.33
	2	-0.61	2.24	9	81.3	0.24		2	2.04	-0.19	11	68.5	0.35
76	1	-0.50	2.03	10	89.8	0.17	76	1	*2.16	-0.25	11	94.4	0.14
	2	-0.66	2.20	8	84.3	0.19		2	2.20	-0.31	11	81.6	0.19

B: Logarithm of number of cycles/cm

D: Logarithm of the width of a cycle

Hen	Probe series	Slope	Intcpt	Data pts.	VAC%	SE	Hen	Probe series	Slope	Intcpt	Data pts.	VAC%	SE
71	1	*-2.68	1.52	9	82.1	0.23	71	1	*2.40	-1.48	10	82.3	0.23
	2	*-3.55	1.72	7	99.0	0.05		2	*3.50	-1.73	7	98.7	0.05
72	1	*-2.14	1.34	11	81.0	0.23	72	1	*1.96	-1.30	12	82.0	0.23
	2	*-2.93	1.75	10	95.8	0.13		2	2.98	-1.78	6	87.3	0.14
73	1	*-0.60	0.32	7	64.4	0.06	73	1	*0.66	-0.33	9	81.8	0.06
	2	*-1.59	0.62	7	78.7	0.11		2	1.80	-0.65	6	73.8	0.12
74	1	-2.02	1.42	12	76.1	0.28	74	1	2.27	-1.48	9	63.5	0.31
	2	-2.44	1.24	8	70.0	0.25		2	2.40	-1.24	7	56.4	0.27
75	1	-2.43	1.76	12	87.3	0.24	75	1	2.37	-1.77	9	74.5	0.27
	2	-2.50	1.70	11	80.8	0.27		2	2.49	-1.71	11	81.7	0.27
76	1	-2.58	1.71	10	95.6	0.11	76	1	*2.46	-1.70	11	96.4	0.11
	2	-2.49	1.59	11	88.5	0.20		2	1.61	-1.35	12	65.5	0.32

* line fitted contains least standard error.

Table 1.1.7

Table 1.1.7

Threshold estimates measured in c/mm, taken from the stimulus value corresponding to a log d value of 0.48 (A) and a log d value of 0.00 (B), as determined by the fitted line, for all hens for the descending and ascending probe series for the following transformations of stimulus values: c/mm, the logarithms of the number of cycles/mm, the width of a cycle in mm and the logarithm of the width of a cycle. The 95% confidence intervals as derived from the standard error of the estimate are shown in brackets. Where estimates were not calculable, an asterisk is shown.

A: Log d value of 0.48

Descending Series					Ascending Series				
Hen	c/mm	log c/mm	width cycle mm	log width cycle	Hen	c/mm	log c/mm	width cycle mm	log width cycle
71	2.4 (0.5)	2.5 (0.4)	2.4 (0.4)	2.6 (0.4)	71	2.1 (0.1)	2.3 (0.2)	2.4 (0.2)	2.3 (0.1)
72	2.5 (0.5)	2.5 (0.2)	2.2 (0.5)	2.5 (0.4)	72	2.6 (0.2)	2.7 (0.2)	2.6 (0.2)	2.8 (0.2)
73	0.1 (0.1)	*	*	*	73	1.2 (0.2)	1.2 (0.2)	1.2 (0.2)	1.2 (0.2)
74	2.9 (0.5)	3.0 (0.5)	2.6 (0.3)	2.8 (0.6)	74	2.3 (0.5)	2.0 (0.5)	2.0 (0.5)	2.1 (0.5)
75	3.2 (0.4)	3.3 (0.5)	3.0 (0.6)	3.4 (0.5)	75	2.9 (0.5)	3.0 (0.5)	3.0 (0.7)	3.1 (0.5)
76	3.1 (0.3)	3.0 (0.2)	2.9 (0.3)	3.1 (0.2)	76	2.6 (0.4)	2.8 (0.4)	2.9 (0.4)	3.3 (0.6)

B: Log d value of 0.00

Descending Series					Ascending Series				
Hen	c/mm	log c/mm	width cycle mm	log width cycle	Hen	c/mm	log c/mm	width cycle mm	log width cycle
71	3.1 (0.5)	3.6 (0.4)	6.7 (0.4)	4.2 (0.4)	71	2.6 (0.1)	3.2 (0.2)	4.5 (0.2)	3.1 (0.1)
72	3.3 (0.5)	4.3 (0.5)	5.6 (0.5)	4.3 (0.4)	72	3.2 (0.2)	3.9 (0.2)	5.6 (0.3)	4.0 (0.3)
73	2.8 (0.1)	3.3 (0.1)	3.3 (0.1)	2.9 (0.1)	73	2.1 (0.2)	2.4 (0.2)	2.6 (0.2)	2.2 (0.2)
74	3.9 (0.5)	5.0 (0.5)	6.7 (0.3)	4.5 (0.6)	74	3.1 (0.5)	3.6 (0.5)	4.5 (0.5)	3.3 (0.5)
75	4.1 (0.4)	5.1 (0.5)	10.0 (0.6)	5.6 (0.5)	75	3.7 (0.5)	4.7 (0.5)	10.0 (0.7)	4.8 (0.5)
76	4.1 (0.3)	4.6 (0.2)	7.7 (0.3)	4.8 (0.2)	76	3.1 (0.4)	4.4 (0.4)	7.1 (0.4)	6.7 (0.6)

* Threshold estimate
incalculable

than for untransformed stimulus values, measured in c/mm, for both probe series, regardless of the $\log d$ value used as the threshold criterion. The transformation of stimulus values to the width of a cycle (mm) generally resulted in the greatest threshold estimates of any method, when determined at the $\log d$ value of 0.00. However for this transformation of stimulus values, estimates were not greater when the $\log d$ value of 0.48 was used.

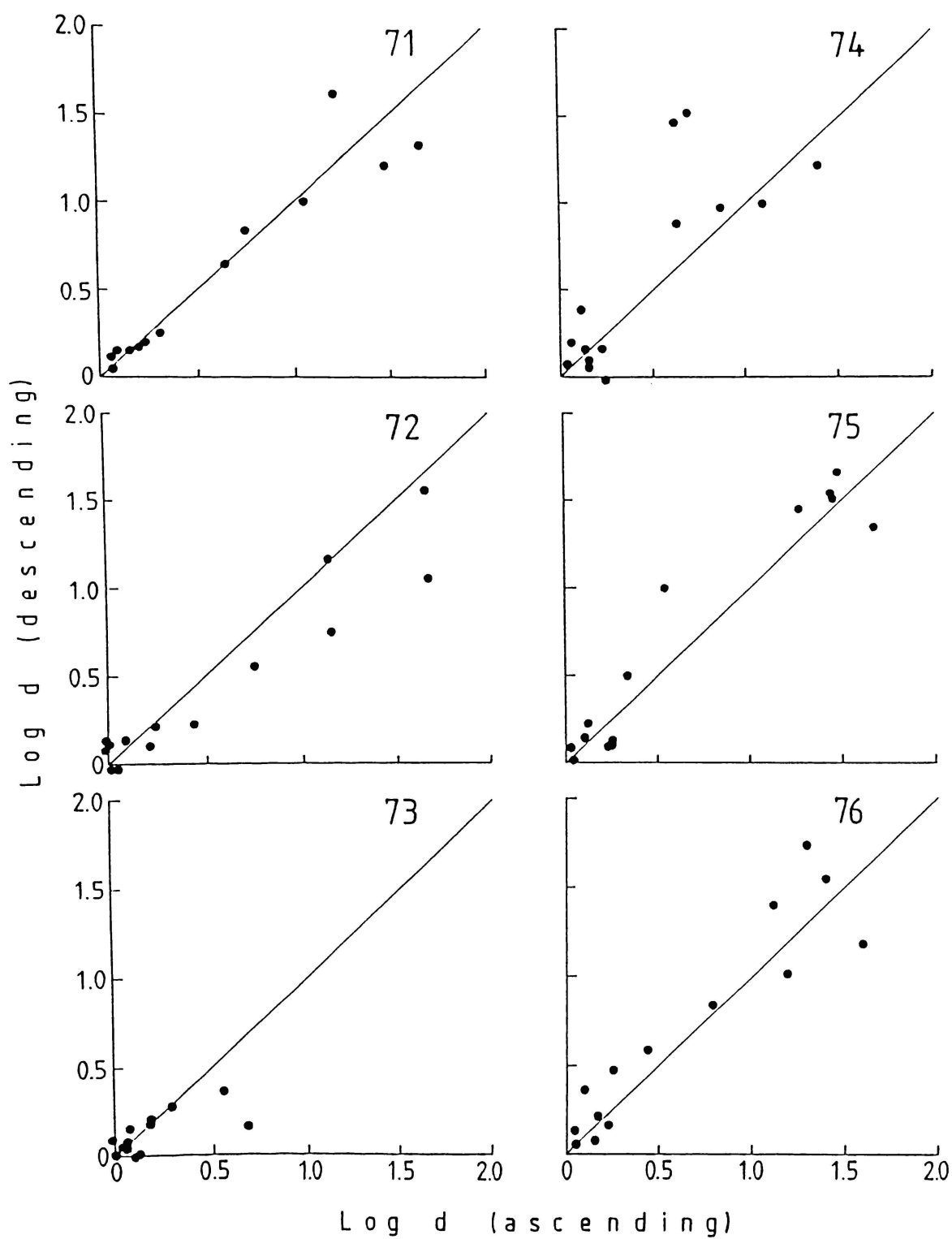
When comparing the estimates of threshold obtained by the use of various criteria it can be seen that there is a tendency for those based on plots using the transformation of stimulus values to the width of a cycle (mm), and using a $\log d$ value of 0.00, to be at a higher grating spatial frequency for all hens and to be more variable than the others. For all hens, threshold estimates determined from the fitted line, based on $\log d$ values of 0.00 were greater and more variable than the estimates based on a $\log d$ value of 0.48. Estimates determined from the fitted line using $\log d$ value of 0.48 generally lie within the range of the 75% of total trials correct and $\log d$ value of 0.48. For four of six hens, the estimates from 50% grating trials correct are greater (indicating more acute vision) than those obtained with a criterion of either 75% total trials correct, 75% grating trials correct or a $\log d$ value of 0.48.

Figure 1.1.6 presents the $\log d$ values for the descending probe series plotted against $\log d$ values for the ascending series, to determine whether performance was more accurate for one probe series than for the other. Common findings show little difference in discrimination at finer gratings, between the two probe series. However, some differences are shown at coarser gratings. For example,

Figure 1.1.6

Figure 1.1.6

The values of $\log d$ for the descending series plotted against the values of $\log d$ for the ascending series of probes, for all hens.



hens 72 and 73 gave a more accurate performance for the ascending series, whilst hens 74, 75 and 76 gave a more accurate performance for the descending series. The data for hen 71 show no difference between the two probe series.

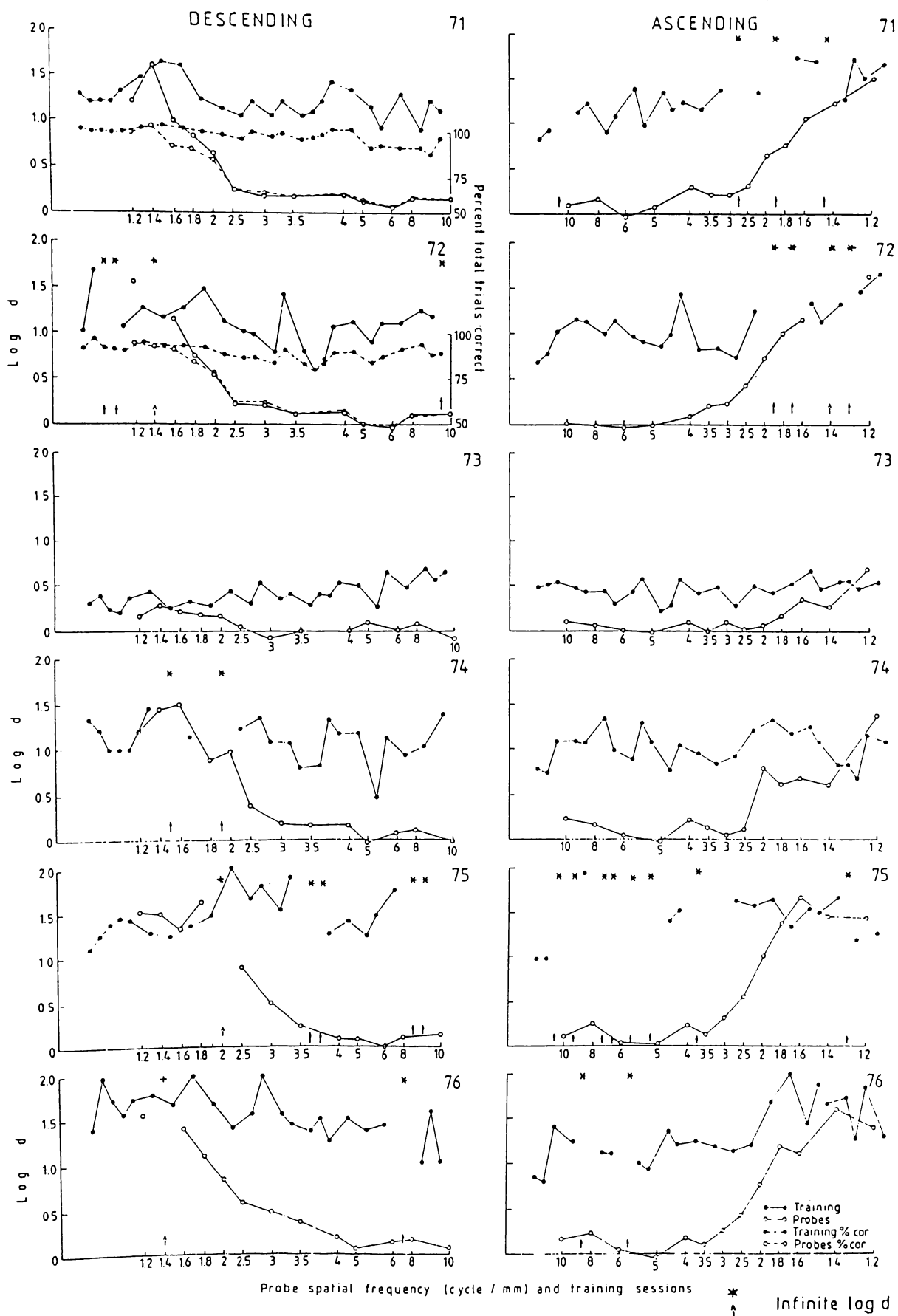
Figure 1.1.7 presents $\log d$ values for each session, as they occurred, including both probes and training sessions, from the last five training sessions prior to the beginning of probes for the descending series. The training and probe sessions are shown as two separate functions. For two hens only, 71 and 72, a second Y-axis is included in Figure 1.1.7, showing the percentages of total trials correct for probe and training sessions, to compare the two functions of percentages of total trials correct with those equivalent $\log d$ values. The plots show that on probe sessions, $\log d$ decreased steeply as a function of grating spatial frequency, and generally levelled off at a $\log d$ value greater than 0.00, between a grating spatial frequency of 2.5 to 3 c/mm. The $\log d$ values for training sessions remained higher. The function of the percentages of total trials correct for the probe sessions at the higher spatial frequencies of gratings, is similar to the function of equivalent $\log d$ values. The functions for the training sessions and those probe sessions at the coarser gratings however, show that the percentages of total trials correct function remains relatively flat whilst the equivalent values of $\log d$ tend to vary when accuracy is high. Because $\log d$ is based on ratios of behaviour, it is sensitive to random variations in responding particularly at high accuracy. When no responses occur in one of the four cells of the stimulus-response matrix (Figure 0.0.2), values of $\log d$ become infinite and cannot be plotted. This occurs when a hen has given a perfect performance on

Figure 1.1.7

Figure 1.1.7

Values of $\log d$ for each session, in order of occurrence, including both probe and training sessions for all hens, for the descending and ascending probe series. Data from the last five training sessions prior to the commencement of probes for the descending series are also shown.

The probe sessions (unfilled circles joined by a solid line) and training sessions (filled circles joined by a solid line) are shown as two separate functions. For two hens only, 71 and 72, a second Y-axis is included in the figure, measuring the percentages of total trials correct for the same probe sessions (unfilled circles joined by a broken line) and training sessions (filled circles joined by a broken line).



grating or grey stimulus trials, or both. Such infinite $\log d$ values are indicated by an asterisk and an arrow pointing upwards from the X-axis. When infinite $\log d$ values were obtained in the present study, they were generally for sessions at the coarsest grating (1 c/mm).

Determination of visual angle

The distances from the centre response key to the anterior surface of the cornea of the eyes of 12 hens, serving in Experiments 1.1 to 1.5 and in Experiments 2.1 to 2.4, (hens 31 to 36, serving later in this study) were determined from the photographs (referred to in the previous section). The distances for individual hens ranged from 70 mm to 85 mm with a mean of 78 mm. The distance from the response key to the target stimulus remained constant at 26 mm. The distances from the anterior surface of the cornea to the retinal surface of the eye, as determined from a histological study of the eyes of two hens, were determined as 13.00 mm and 13.29 mm. The distance of 13 mm was used here. The width of the stimulus subtended by an angle of one degree at the retina was calculated. This was used to determine the number of cycles per degree (c/deg) for the stimulus which was 1 c/mm, for all hens, from each hen's individual distance from the stimulus, and the mean of these distances. These are shown on Table 1.1.8 and range from 1.90 c/deg to 2.16 c/deg for individual hens, with a mean of 2.04 c/deg. This mean is very close to the nominal value of 1 c/mm for the grating stimuli. The distances for individual hens were very similar, and, using the mean distance, the width of the stimulus subtended by an angle of one degree (2.04) is very close to the value of 1 c/mm. Threshold values in c/deg therefore, may be determined by increasing the estimates, measured in

Table 1.1.8

Table 1.1.8

The individual distances and mean distance (mm) for 12 hens, serving in Experiment 1 and Experiment 2, from the cornea of the eye to the surface of the response key, from the surface of the response key to the stimulus, from the cornea to the retina of the eye, and the total of these distances (mm). The width of a 1 c/mm grating subtended by a one degree angle at the retina (c/deg) was calculated from the individual distances and the mean distance and is also shown in the table.

Hen	Distances			Total mm	Width grating	
	Cornea to resp key mm	Key to stim mm	Cornea to retina mm		Total mm	Subtended c/deg
71	85	26	13	124		2.16
72	85	26	13	124		2.16
73	70	26	13	109		1.90
74	75	26	13	114		1.99
75	70	26	13	109		1.90
76	75	26	13	114		1.99
31	85	26	13	124		2.16
32	80	26	13	119		2.08
33	70	26	13	109		1.90
34	85	26	13	124		2.16
35	80	26	13	119		2.08
36	75	26	13	114		1.99
Mean	78	26	13	117		2.04

c/mm, by a factor of two.

The estimates of threshold shown in Table 1.1.3, measured in c/mm taken from the point of 75% total trials correct, were recalculated in c/deg, using both individual and mean distances. These are shown in Table 1.1.9. For the descending series they range from 4.54 to 5.7 c/deg, using individual distances, and from 4.20 to 6.0 c/deg using the mean distance. For the ascending series, these range from 2.47 to 5.18 c/deg using individual distances and from 2.60 to 5.20 c/deg using the mean distance. The use of the mean distance results in a slight increase in the range of threshold estimates for the descending series (by 0.64 c/deg) and a slight reduction in the range of estimates for the ascending series (by 0.11 c/deg). However, if it had been possible to obtain an estimate for hen 73 for descending series, the range of estimates for that probe series would have been reduced also. This is because the use of the mean distance actually results in a value which is 1.0 c/deg greater than that obtained using her individual distance.

Table 1.1.10 shows all threshold estimates obtained from each of the various methods of analysis, for each hen and both probe series, recalculated in c/deg. These estimates are also presented in Figure 1.1.8. This table and the figures show clearly that estimates are higher and more variable for most transformations of stimulus values. Those estimates taken from stimulus values at a log d value of 0.00 are more variable than those taken from either a log d value of 0.48 or 75% total accuracy.

Table 1.1.9

Table 1.1.9

Threshold estimates from Table 1.1.3 taken from the data plotted as the percentage of total trials correct, at the stimulus value corresponding 75% total trial accuracy for the descending and ascending series of probes, recalculated in c/deg, using both the individual distances for each hen and the mean distance.

Hen	Descending		Ascending	
	Distance		Distance	
	Indiv.	Mean	Indiv.	Mean
71	4.54	4.20	4.75	4.40
72	4.54	4.20	5.18	4.80
73	*	*	2.47	2.60
74	4.78	4.80	4.38	4.40
75	5.70	6.00	4.94	5.20
76	4.98	5.00	4.58	4.60

* Estimate not calculable.

Table 1.1.10

Table 1.1.10

All threshold estimates taken from each of the various methods of analysis and criteria, measured in c/deg, for all hens for the descending (desc) and ascending (asc) series of probes. Where the threshold estimate was taken from a fitted line, the 95% confidence interval as determined from the standard error of the line fit, is shown in brackets.

Hen	Probe Series	Total trials		Grating trials		log d	
		75%	50%	50%	75%	0.48	0.00
71	desc	4.2	5.8	4.8	3.8	4.4	5.6
	asc	4.4	6.2	9.2	4.8	4.6	6.0
72	desc	4.2	5.8	7.2	4.0	4.2	5.8
	asc	4.8	7.2	5.8	3.6	4.8	7.2
73	desc	*	6.8	5.0	2.0	*	5.2
	asc	2.6	4.6	5.0	2.6	2.6	4.2
74	desc	4.8	7.0	6.2	3.6	4.8	7.0
	asc	4.4	6.2	6.2	4.4	5.6	6.0
75	desc	6.0	7.4	9.6	5.6	6.0	7.8
	asc	5.2	7.8	9.8	5.6	5.2	7.8
76	desc	5.0	10.2	7.2	3.8	6.0	9.6
	asc	4.6	8.6	6.6	3.8	4.8	7.6

Fitted Line:			Log d of 0.48			Log d of 0.00			
Hen	Probe Series	c/mm	Log c/mm	Width cycle	Log width cyc	c/mm	Log c/mm	Width cycle	Log width cyc
71	desc	4.8	5.0	4.8	5.2	6.2	7.2	13.4	8.4
		(0.5)	(0.1)	(0.4)	(0.4)	(0.5)	(0.4)	(0.4)	(0.5)
	asc	4.2	4.6	4.8	4.6	5.2	6.4	9.0	6.2
		(0.1)	(0.2)	(0.2)	(0.1)	(0.1)	(0.2)	(0.2)	(0.1)
72	desc	5.0	5.0	4.4	5.0	6.6	8.6	11.2	8.6
		(0.5)	(0.2)	(0.5)	(0.4)	(0.5)	(0.5)	(0.5)	(0.5)
	asc	5.2	5.4	5.2	5.6	6.4	7.8	11.2	8.0
		(0.2)	(0.2)	(0.3)	(0.3)	(0.2)	(0.2)	(0.3)	(0.3)
73	desc	0.2	*	*	*	5.4	6.6	6.6	5.8
		(0.1)	*	*	*	(0.1)	(0.1)	(0.1)	(0.1)
	asc	2.4	2.4	2.4	2.4	4.2	4.8	5.2	4.4
		(0.2)	(0.2)	(0.2)	(0.2)	(0.2)	(0.2)	(0.2)	(0.2)
74	desc	5.8	6.0	5.2	5.6	7.8	10.0	13.4	9.0
		(0.5)	(0.5)	(0.3)	(0.6)	(0.5)	(0.5)	(0.3)	(0.6)
	asc	4.6	4.0	4.0	4.2	6.2	6.0	9.0	6.6
		(0.5)	(0.5)	(0.5)	(0.5)	(0.5)	(0.5)	(0.5)	(0.5)
75	desc	6.4	6.6	6.0	6.8	8.2	10.2	20.0	11.2
		(0.4)	(0.5)	(0.6)	(0.5)	(0.4)	(0.5)	(0.6)	(0.5)
	asc	5.8	6.0	6.0	6.2	7.4	9.4	20.0	9.6
		(0.5)	(0.5)	(0.7)	(0.5)	(0.5)	(0.5)	(0.7)	(0.5)
76	desc	6.2	6.0	5.8	6.2	8.2	9.2	15.4	9.6
		(0.3)	(0.2)	(0.3)	(0.2)	(0.3)	(0.2)	(0.3)	(0.2)
	asc	5.2	5.6	5.8	6.6	6.4	8.8	14.2	13.4
		(0.4)	(0.4)	(0.4)	(0.6)	(0.4)	(0.4)	(0.4)	(0.6)

* Estimate not calculable

Figure 1.1.8

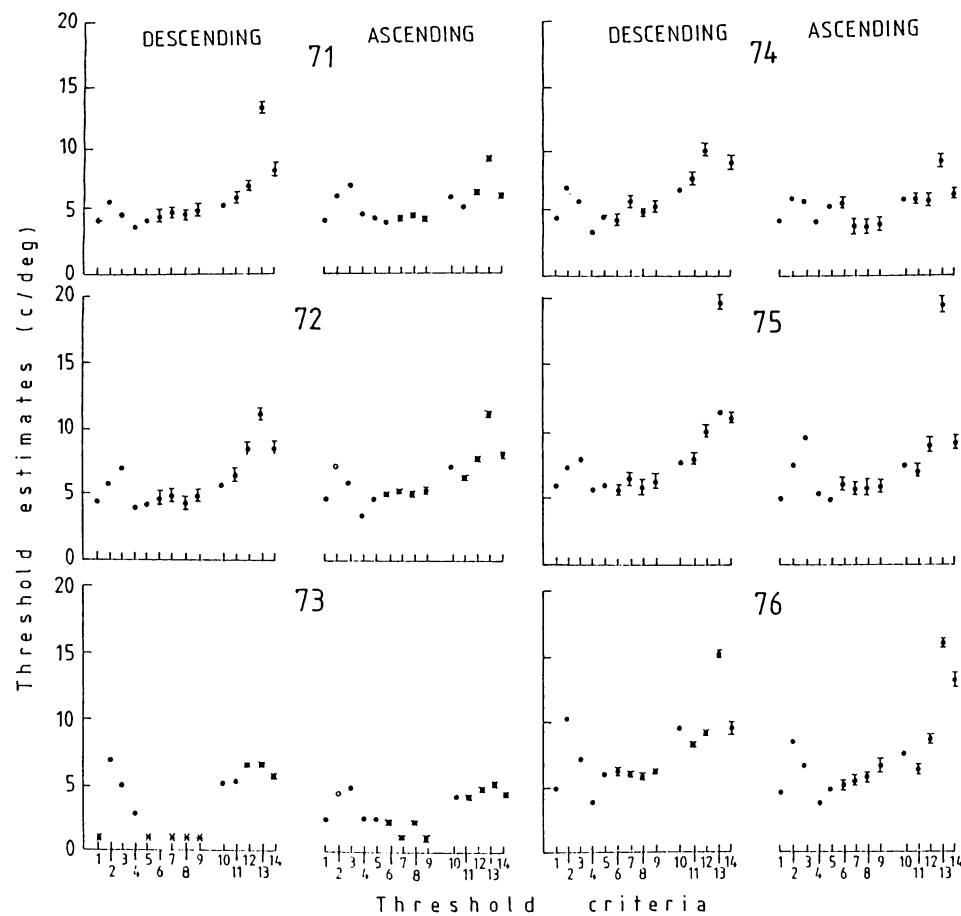
Figure 1.1.8

All threshold estimates from each of the various methods of analysis, and threshold criteria. These estimates were taken from the stimulus values corresponding to 75% (1) and 50% (2) total trial accuracy, 50% (3) and 75% (4) grating trial accuracy, and log d values of 0.48 (5) and 0.00 (10)

Those determined from the fitted line were taken from the stimulus value corresponding to log d values of:

0.48 (6) and 0.00 (11) with spatial frequency measured in cycles/mm,
0.48 (7) and 0.00 (12) with spatial frequency measured in logarithms of cycles/mm,
0.48 (8) and 0.00 (13) with spatial frequency measured in the width of a cycle (mm) and
0.48 (9) and 0.00 (14) with spatial frequency measured in the logarithm of the width of a cycle.

The 95% confidence intervals, determined from the standard error of the line fit, are shown for estimates from the fitted line.



KEY

* Threshold estimate not calculable

- 1 75% total trial accuracy
- 2 50% total trial accuracy
- 3 50% grating trial accuracy
- 4 75% grating trial accuracy
- 5 log d of 0.48

Gratings measured in:

- 6 c/mm
 - 7 log c/mm
 - 8 width cycle (mm)
 - 9 log width cycle
 - 10 log d of 0.00
- } Fitted line at log d of 0.48

Gratings measured in:

- 11 c/mm
 - 12 log c/mm
 - 13 width cycle (mm)
 - 14 log width cycle
- } Fitted line at log d of 0.00

ROC Plots

Figure 1.1.9 shows the proportion of correct responses on grating trials plotted against the proportion of incorrect responses on grey stimulus trials for the descending and ascending series of probes for all hens. Lines join successive probes. The closer the data path to the major diagonal, the lower the discriminative performance. The data path for all hens moves towards the major diagonal, indicating a decrease in accuracy at increasingly finer gratings. Data close to the minor diagonal indicate close to equal left and right key responding. Data to the right of the minor diagonal indicate a greater proportion of left key responding.

In all cases the data paths do not move far from the minor diagonal and the plots show that the descending and ascending conditions replicate well. Points in the upper quadrant come from those hens which tended to respond more to the left key (i.e. as though the stimuli were gratings). This occurred for hen 71 for the ascending series. Points in the lower quadrant came from those hens which tended to respond more to the right key (i.e. as though the stimuli were grey). Hen 71, for the descending series, 72 for the ascending series and 76 for both series show more right key responding.

Response Bias

Figure 1.1.10 shows a measure of response bias, an estimate of $\log c$, for both probe series and all hens. It is assumed that reinforcement delivery to each response alternative is equal (i.e. $RW=RZ$). This was calculated using the following equation, derived from Equation (8):

Figure 1.1.9

Figure 1.1.9

The proportion of correct responses on grating trials, plotted against the proportions of incorrect responses on grey stimulus trials, for all hens, for the descending and ascending series of probes.

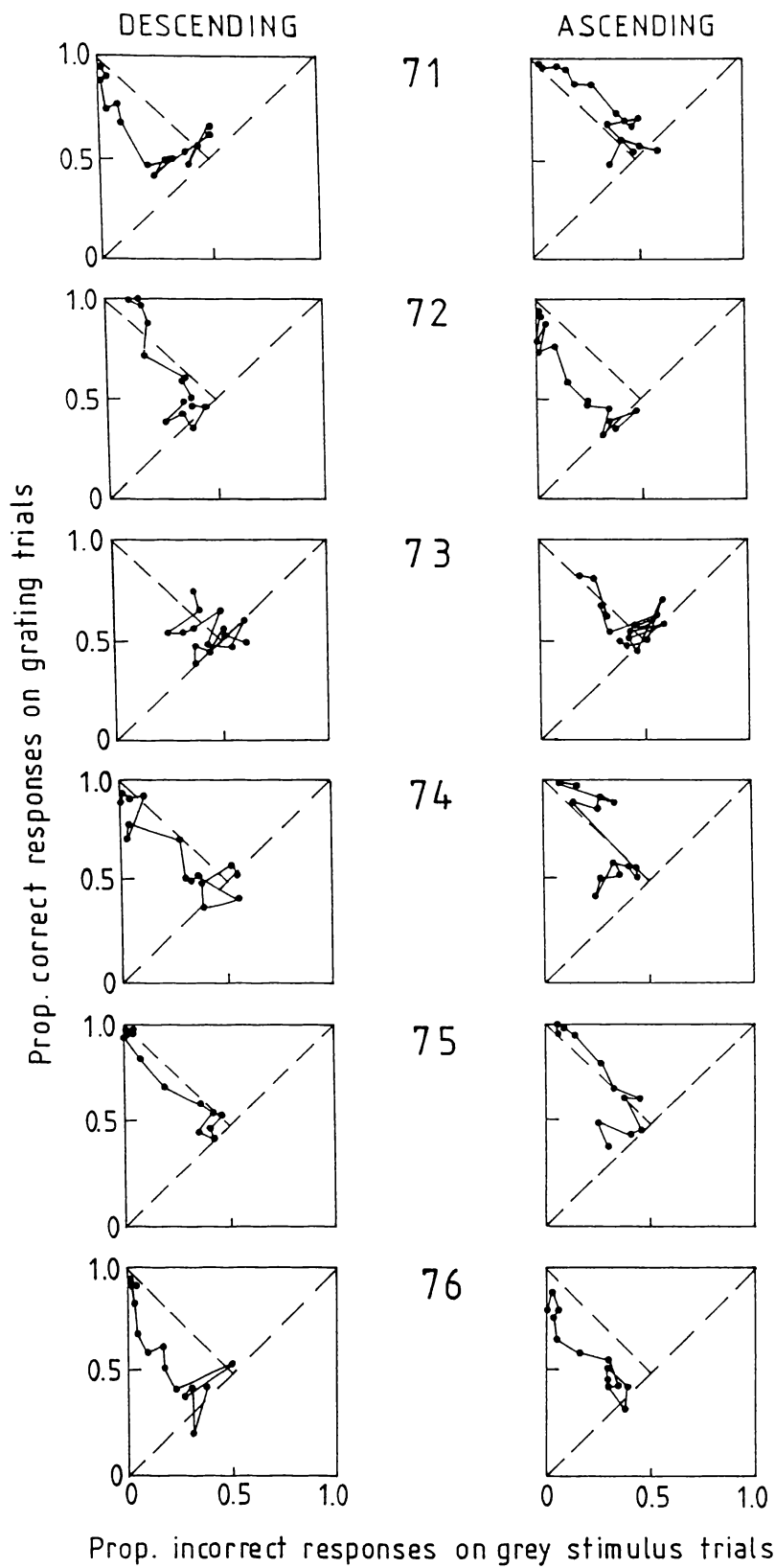
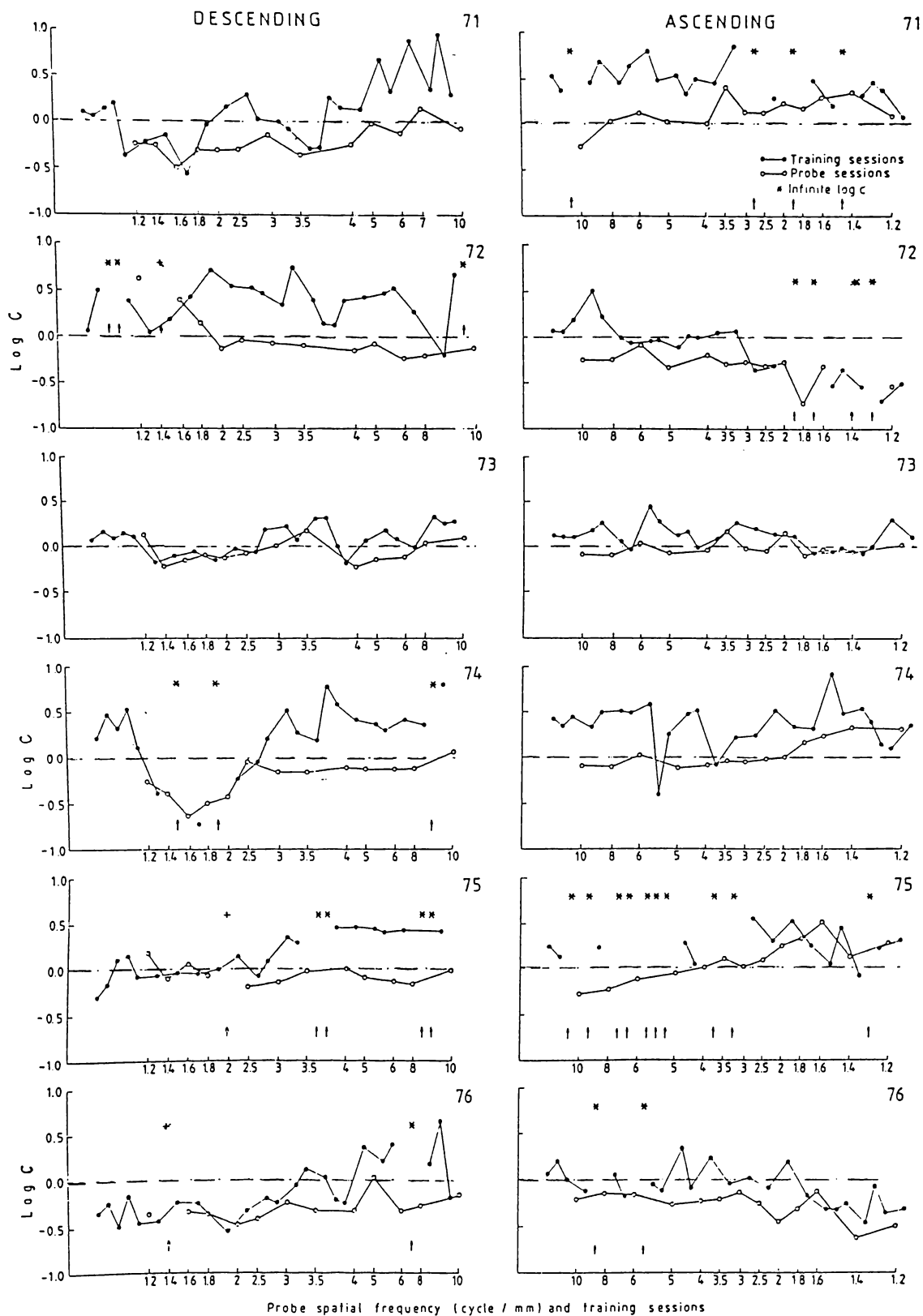


Figure 1.1.10

Figure 1.1.10

Estimates of $\log c$ for each session, in order of occurrence including both probe (filled circles) and training (unfilled circles) sessions for all hens, for the descending and ascending probe series. Data from the last five training sessions prior to the commencement of probes for the descending series are also shown.



$$\log c = \log\left(\frac{P_w}{P_x}\right) \cdot \log\left(\frac{P_y}{P_z}\right) 0.5 \quad (9)$$

where PW represents the number of correct left key responses emitted when the grating is presented, PX is the number of incorrect right key responses emitted during grating presentation, PY is the number of incorrect left key responses when a grey stimulus is presented and PZ is the number of correct right key responses during a grey stimulus presentation.

Estimates of $\log c$ are shown in order, for the descending and ascending probe series, for each training session and probe session as they occurred, for all hens. For the descending series the probe sessions began with gratings of the lowest spatial frequency, and for the ascending series probes began at the highest spatial frequency of gratings. The $\log c$ estimates for probe and training sessions are shown as two separate functions. Positive values of $\log c$ indicate a bias for responding to the left key (as though the stimulus is a grating), and negative values indicate a right-key bias (as though the stimulus is grey).

Generally, differential $\log c$ values for training and probe sessions occurred with probes at finer gratings. On training sessions, $\log c$ estimates were generally higher than for probe sessions. This indicates that the hens tended to respond more to the left key on training sessions (i.e. biased toward reporting "grating"), while probes remained relatively unbiased as spatial frequency of the gratings increased. For both series of probes and all hens, there was generally an immediate increase to the $\log c$

training value following each probe session. Where there were no responses within one of the four response alternatives (Figure 0.0.2), log c values were infinite, and could not be plotted. These are indicated by an asterisk and an arrow pointing upwards from the X-axis. As a measure of bias based on ratios of behaviour, estimates of log c fluctuate with small changes in discrimination, particularly when accuracy is high. For example, the performance of hen 74, on her second training session following the probe at 3.5 c/mm, gave a log c estimate of 0.78, based on 61% of total responses to the left key and a total accuracy of 89%. In contrast, for the probe at 6 c/mm her performance gave a log c estimate of -0.12 based on 57% responses to the right key and a total accuracy of 54%.

Response Latencies

Data for response latencies to side keys following a response to the centre sample key for all hens, in 0.1 s, for both probe series are not plotted, but are presented in Appendix 3. These show no systematic differences between latencies to responding on the side key after viewing the grating or grey stimulus. Latencies were not different for correct and incorrect choices as the discrimination task became more difficult at finer gratings. Hen 76, who achieved the most accurate performance also showed the most regular latencies of responding, whilst hen 73, who showed the least accuracy, provided the most variable latencies.

Discussion 1.1

Visual angle

In the present study the hens were not restrained in any way to ensure that they stood a constant distance from the response key. Some studies have used various means to ensure that the viewing distance from the stimuli remained constant. For example, monkeys were restrained in special chairs during visual acuity studies (Cavonius & Robbins, 1973) and cats viewed the target stimulus through a small tunnel whilst lapping milk from a spoon placed in a constant position (Jacobson *et al.*, 1976).

The visual acuity task in the present study was used primarily as a means to study discriminative performance, and estimates of threshold provided one possible measure of this. Therefore, it was important that consideration be given to the amount of error involved in the calculation of these estimates. This was to ensure that differences between estimates obtained for each hen were the result of differences in discrimination, rather than the result of differences in the distance each hen stood from the response key. In addition, these estimates were useful as a means of comparing discriminative performance across the series of studies.

To calculate near-field visual acuity, it was necessary to determine the distance from the surface of the stimuli to the retinal surface of the eye. A decision was made to use the mean distance from the stimulus to the cornea, across 12 hens serving in the two procedures, Experiment 1 and Experiment 2, to calculate the width of the grating stimulus subtending an angle of one degree at the retinal

surface of the hens' eyes. This decision was based on the threshold estimates for each hen's performance, determined from the point of 75% total trial accuracy, using both the individual and mean distances. The use of the individual distances did not in any way decrease the variance of estimates of threshold across hens. That is, those hens whose data yielded the greatest estimates, as calculated from the individual distances, also yielded the greatest estimates when the mean distance was used. In fact, the variance between estimates, using the mean distance, was slightly less than when individual distances were used. Thus it was not the case that individual distances made estimates more alike.

Using the mean distance estimate, 2.04 cycles of the 1 c/mm grating stimulus subtended an angle of 1 deg. Thus a grating measuring 1 c/mm would be close to 2 c/deg, a grating measuring 2 c/mm would approximate 4 c/deg, and so on. This "rounding off" of the 2.04 c/deg to 2 c/deg resulted in a slight decrease in the estimation of visual angle by a constant fraction.

The use of the mean distance rather than individual distances gave slightly lower estimates of visual angle for the 75% point, by 0.16 c/deg for hens 71 and 72, and slightly increased estimates by 0.10 c/deg for hens 73 and 75, for every 2 c/deg of visual angle. When the 0.04 error for every 2 c/deg is taken into account, these are changed to a reduced estimation of visual ability for hens 71 and 72 by 0.20 c/deg and an increased estimation of visual ability for hens 73 and 75 of 0.06 c/deg, for every 2 c/deg of visual angle.

Thus, a small degree of calculable error results from the use of

the mean distance. However, this error comes from measurements of only a small sample of behaviour. It was neither possible, nor practical to video each hen on each trial in each session for the length of each study, but there was some limit to the range of distance a hen could stand from the centre response key to view the stimulus prior to initiating the trial. Regular observations of the animals during the experimental sessions indicate that the distances obtained were typical of each hen. They pecked the keys from a standing position and each hen stood close to the key prior to and while they were pecking. The distance each hen stood from the keys was very similar.

Because for the present series of studies the order and range of estimates of threshold values resulting from various procedural manipulations were used as possible measures of changes in discrimination, rather than determinants of absolute limits of visual ability, the use of the mean distance was considered justified. The hens' viewing distances from the stimuli were reasonably consistent, thus it was unnecessary to restrain them to ensure a constant distance.

Target stimuli

In discrimination studies it is important to ensure that behaviour is controlled by changes in the stimulus dimension predetermined by the experimenter, rather than by changes in some other dimension of the stimulus not accounted for. Many studies (e.g. Hodos *et al.*, 1976) have used only one sample of the stimuli at each spatial frequency. The present study used six pairs of grey and grating stimuli at each grating value, in an attempt to eliminate

confounding of data by discrimination of extraneous stimuli, for example, smudges or specks of dust on a single target stimulus. In addition, stimuli were regularly dusted with a fine bristled brush. This should mean that discrimination was not based on extraneous cues.

There was a loss of luminance by 0.16 cd/m^2 at the finest grating (10 c/mm) only, compared to the coarser gratings. Hodos *et al.* (1976) also reported some loss of luminance in gratings of higher spatial frequency. If the hens could discriminate on the basis of luminance alone, this could be a problem. However, this does not appear to be the case in the present study. Changes in discrimination occurred with probes at different values of grating stimuli of the same luminance.

Pokorny (1968) stated that the contrast in the grating stimuli should be high, that is, as close to 100% as possible and not less than 50%. The lower the contrast, the more difficult to discriminate even a coarse grating from a grey stimulus. Thus the use of gratings of low contrast in a visual acuity study would introduce a confounding variable. However, the contrast of gratings for the present study, (as previously reported), was well within the suggested limits.

For some hens in the present study, discrimination appeared to improve at the finest gratings. O'Neill (1963) reports that defocussed optical systems take on certain peculiar properties when periodic stimuli such as gratings, are viewed through them. One of these properties is "spurious resolution", in which gratings of certain frequencies, which are not resolved because of the defocussing, appear after further defocussing of the lens. The

contrast of these images is greatly reduced and the images shifted in position by one bar width. This could possibly account for the occasional increased discrimination shown at finer gratings, in the present study.

Millidot (1973) referred to wavy lines at the edges of very fine grating stimuli, which may act as cues. Although an attempt was made, by blacking out all but the centre of the sample key, to prevent edges from coming into view, a periodic displacement of stimuli, sometimes to the left, and sometimes to the right of the centre, due to irregularities of the stimulus positioning detector, occasionally occurred. Independent human observers reported their detection of such wavy images at the edges of stimuli occasionally. It is possible, therefore, that the apparent discrimination of finer gratings was the result of the edges of such gratings. It is suggested that such increases in discrimination be treated as aberrant when they occurred past the point where resolution of the grating is contra-indicated by the prior pattern of discrimination.

Discrimination

The data for all hens showed different levels of discrimination at probes with gratings of different spatial frequency. The data functions analyzed as percentages of total trials correct, could be divided into three levels of discrimination: the high level, which included slight fluctuations, a steep descending portion and a low relatively flat level which also included some fluctuations. Data from probes at several of the finest grating values are included in the low discrimination level, around the 50% total trials correct point. It was initially intended that probes continue to the stimulus

value beyond the point where discrimination for all hens decreased to 50%. Because the performance of all hens did not decrease to this point, probes continued until it was reasonable to assume that the stimuli were not discriminable. Although most studies do not continue testing animals beyond the point where the stimulus is assumed indiscriminable, this range of stimulus values has been retained throughout the following series of studies, to determine whether any changes in discrimination resulting from various procedural manipulations also extended to these gratings of high spatial frequency. Discriminative performance was the most accurate at the coarsest gratings for all hens, and data can be described as a monotonically decreasing function of spatial frequency, which leveled off at the finest gratings, regardless of the measure of discrimination plotted or the series of stimulus presentation (descending or ascending).

Although this function on the descending series was replicated well by the ascending series for most hens, hen 73's performance improved on the ascending series at coarsest grating values. If this was a practice effect, it is interesting that it should occur only for that hen whose initial criterion for probing was lower than that of the others. It is possible that this hen may have improved her discrimination at the coarsest gratings with more sessions of training prior to the commencement of probes. However, given the duration of training she had already experienced (four to five months), it is considered unlikely.

Log d increases with improved discrimination and is regarded as independent of any left-right biases the animal may have (Davison &

Tustin, 1978). McCarthy and Davison (1980a) showed that the $\log d$ measure of discrimination provided a useful description of data from detection tasks when stimuli used were differing durations of a single key light. In the present study the use of $\log d$ as a measure of discriminative performance resulted in a function similar to that of the more traditional measure of total performance (percentages of total trials correct) but showed closer replication between the two probe series. This indicates that some differences in performance between these series of probes, when plotted as percentages of total trials correct, may have been due to response bias, rather than differential discrimination between the two series. Terman (1970) using the bias-free measure of detectability, d' , (Green & Swets, 1966) also reported close agreement between the psychometric functions obtained from three rats, despite a large variation in the degree and direction of response bias.

Although data plotted as $\log d$ values showed the same three levels of discrimination as when plotted as percentages of total trials correct, this would not have been the case if the hens had achieved perfect discrimination at the coarsest grating values. When performance is errorless, either on one or both trial types (i.e. grating and grey stimulus trials) $\log d$ values become infinite, and cannot be plotted. Such perfect discrimination would then result in a loss of the high portion of the data function. Infinite $\log d$ values may not pose a problem when occurring at the coarsest grating values. However, if, as grating values become finer, discrimination on grating trials decrease, but remains perfect on grey stimulus trials, infinite values are also obtained. And, if the first $\log d$ value which is not infinite is less than (for example) 0.3, then this would result in

loss of most of the descending portion of the data function as well, leaving only the low relatively flat level of discrimination. Because of this problem of infinite values, $\log d$ may be more useful as a supplement of, rather than a replacement for the more traditional measure.

Criteria and estimates of threshold

Although in the present study, the use of various criteria and analyses for estimating thresholds resulted in a large variety of values, generally neither series of stimulus presentation (descending nor ascending) yielded consistently greater estimates. This further indicates the similarity of the discrimination functions for both probe series.

The use of any particular criterion to estimate threshold depends not only on the assumptions made about the animal's behaviour, but also on the constraints of the procedure on that behaviour. Chard (1939) suggested that the choice of an absolute threshold criterion is arbitrary. The traditional value is the 50% point, where 50% of the time a grating is present the animal responds correctly to it. That is, discriminative performance on constant (or grey stimulus) trials would not be analysed.

As previously discussed, in such a procedure as that used for the present study, which included analysis of correct responses to both grating and constant (grey) stimuli, there are two extreme response distributions which may possibly result from a gradual loss of discrimination at probes with gratings of increasing spatial frequency. A 50% criterion for total trials correct would be

appropriate if one assumed that when the animals began to fail to discriminate the gratings, they also failed to discriminate on grey stimulus trials to an equal degree. However, when gratings are not discriminable, humans perceive them as grey. It is reasonable to assume therefore, that for animals gratings that cannot be resolved may also appear grey, but not the converse, (i.e. grey stimuli would not appear to be gratings). Therefore, theoretically, it would be more likely that a decrease in discrimination of gratings of higher spatial frequency would result in an overall increase in reporting "grey", and little loss of accuracy on grey stimulus trials. In fact, theoretically, with two stimuli, a grating and a grey stimulus, as discrimination of the grating decreases, it might be responded to incorrectly (i.e. treated as a grey stimulus), while the grey stimulus may continue to be detected correctly. In such a case it could be possible for all grey stimulus trials to be correct, and 50% of grating trials to be correct, at chance level, resulting in a value of 75% of total correct trials to be the appropriate absolute threshold value, that is, the point where discrimination of the grating is reduced to merely chance level.

For the present study, separate analysis of accuracy on grating and grey stimulus trials showed that, generally, as discrimination of gratings decreased, discrimination of grey stimuli also decreased, but not to the same degree, for all hens. That is, the grey stimulus was incorrectly responded to as a grating stimulus on some trials. This mode of responding (i.e. treating grey stimuli as gratings) may be an artefact of the reinforcement procedure, which controlled the relative distribution of reinforcers between the two response alternatives (McCarthy, 1980a). This issue is discussed later in the thesis.

In the present study, comparison of threshold estimates taken from the point of 75% total trial accuracy with those taken from the point of 50% grating trial accuracy, show that the latter were generally greater. This is because, as discrimination of gratings decreased, discrimination of the grey stimulus also decreased. If perfect discrimination had been maintained on all grey stimulus trials, both criteria would have yielded the same values.

The 75% grating trial criterion was also used, to compare the threshold estimates taken at that point with those from the 75% total trial criterion. The difference between the estimate taken from the point of 75% grating trial accuracy and that taken from the point of 75% total trial accuracy must logically be the result of discriminative performance on grey stimulus trials. If the estimate taken from the point of 75% total trial accuracy were a lower value than that taken from the point of 75% grating trial accuracy, this would indicate that discrimination on grey stimulus trials was lower than discrimination on the grating trials at this point. This occurred for hen 73 in the descending series and for hen 75 in the ascending series. But generally, discrimination was better for grey stimulus trials than for grating trials, at the stimulus values that resulted in the descending portion of the data function. This resulted in greater estimates of threshold (indicating more acute vision) from the 75% total trials correct criterion. Therefore, it is possible that when discrimination is analysed as total performance (i.e. the combined performance on both stimulus types) a maintenance of higher accuracy on constant stimulus trials may provide a spuriously high estimate of grating resolution.

Psychophysical studies using two stimulus types, such as a constant and a variable stimulus, usually present data plotted as percentages of total trial correct, and estimates are taken from this total performance, usually the point of 75% accuracy (e.g. Hodos *et al.*, 1976). Very few studies present separate analysis of both trial types, that is, both components which contribute to the total psychometric function. Therefore, it is not known how much of the accuracy at any given stimulus value is actually provided by a maintenance of accuracy on constant stimulus trials. When the purpose of a study is to determine the point of grating resolution, then it would seem to be important to determine exactly how much of the overall accuracy is actually contributed to by discrimination on the grating trials. One study which did analyse separate performance on both the constant and variable stimulus trials (Terman, 1970) investigated discrimination between a constant and variable auditory stimulus in rats. Although the total psychometric function decreased to 58% accuracy at equal stimulus values, accuracy had decreased to 20% for one stimulus type compared to a maintenance of over 90% accuracy for the other.

Where $\log d$ (Davison & Tustin, 1978) was used as the index of discrimination for grating and grey stimulus trials, the $\log d$ value of 0.48 was chosen to estimate threshold values. This value is the equivalent of 75% total trial accuracy, assuming no bias. Resultant estimates of threshold were generally equal to, or slightly greater, as measured in c/deg (indicating more acute vision), than those estimated from the point of 75% accuracy for total trials. Because $\log d$ is a measure of discrimination independent of response bias, the

difference between these two measures would necessarily be the result of such biases. A comparison of estimates taken from the 75% total accuracy and $\log d$ of 0.48 criteria, shows that six were of the same value for both, and five were slightly greater (as measured in c/deg) when analysed as values of $\log d$. McCarthy (1983) reported that response biases at lower levels of discrimination result in lower estimates of threshold (indicating less discrimination) than would be obtained if no response bias were present. Results from the present study may lend some support to the proposition that use of a bias-free measure of discriminative performance may also result in greater estimates of threshold.

The $\log d$ value of 0.00 was also used to estimate thresholds. Performance at chance levels for both response alternatives, that is, equal numbers of correct and incorrect responses, give $\log d$ values of 0.00. Stimulus values which resulted in zero values of $\log d$ were used to estimate absolute thresholds of luminance differences in pigeons (McCarthy, 1983). In addition, Temple *et al.* (1984) predicted the auditory threshold at various frequencies, in hens, using the $\log d$ value of 0.00. All data points for this latter study were above this threshold value and no auditory stimuli were below the intensity of 45 dB(A). A line was fitted by the method of least squares to data obtained at each auditory frequency, to predict the stimulus intensity corresponding to a $\log d$ value of 0.00. In the present study, generally the lowest $\log d$ values plotted, which indicated indiscriminability of the gratings, were greater than a $\log d$ value of 0.00. That is, discriminative performance levelled off at finer grating values, showing a relatively flat function at a value slightly greater than a $\log d$ of 0.00. Generally, discriminative performance

in visual acuity studies decreases to 50% accuracy as stimuli become less discriminable (e.g. Hodos *et al.*, 1976). Therefore, there was no way of knowing in advance that performance in the present study would not do likewise. Thus it is possible that a threshold criterion such as the $\log d$ value of 0.00 may not be appropriate when performance does not decrease to this level. These two previous studies did not analyze performance on the two trial types separately, and it may be that the present results are a consequence of differences in accuracy for the two stimulus types. That is, if performance remains higher than chance on constant stimulus trials, and decreases to chance on variable stimulus trials, then total accuracy will be higher than 50% or a $\log d$ value of 0.00. In the present results, although accuracy decreased on both types of trial, it remained slightly higher on grey than on grating trials.

Transformation of stimulus values. Lines were fitted to the descending portion of $\log d$ values, as a function of a series of transformations of stimulus values. The total function of decreasing accuracy with decreasing stimulus differences possibly provides a more complete description of discriminability than the single value threshold estimates such as the 75% or 50% correct. That is, a line fitted to this portion of the data may take into account all data from the descending portion of the function, rather than only a single point. Also, it was considered that certain transformations of stimulus value may provide a more linear function than others for a straight line fit, by changing the spread of data along the x-axis.

Various studies have estimated threshold from the descending portion of the data function by normalizing the percent correct values

and obtaining a straight-line fit to these descending points (e.g. Terman, 1970; Blough, 1971; 1973). Regardless of the method of analysis, when a line is fitted to the descending portion of the data, judgements need to be made regarding those data which should or should not be included as part of this descending function. For example, it was necessary for McCarthy (1983) and Temple *et al.* (1984) to exclude certain data to obtain the most appropriate line fit to the descending portion of their data. In the latter study a decision had to be made as to whether certain data points were best described by a descending function or by a flat line. When Blough (1971) fitted a straight line to the descending portion of data, only those points corresponding to error rates of 10% or greater were included, since other data points, when plotted in this way were not linear with the rest of the data. Threshold was then estimated by interpolation from the line at a z -score of -0.67 . This value is equivalent to the 25% error point (i.e. 75% correct performance). When straight lines were fitted to $\log d$ values in the plots presented in the present study, no data points were omitted. Instead, an attempt was made to use a logical mathematical criterion, that is, the descending line from the line pair with the least standard error. However, it was necessary to include the qualification that the descending line be the one which best described the descending portion of the data. When data from the present study were re-analysed as normalized percent correct scores, and thresholds estimated by interpolation from the line at a z -score of -0.67 (as for Blough, 1971), the estimates were very similar to those obtained from the fitted line at a $\log d$ value of 0.48 and are presented in Table 1.1.11. This underlines the fact that various transformations of data may result in similar estimates when equivalent threshold criteria are used. The rejection of certain

Table 1.1.11

Table 1.1.11

Threshold estimates determined from the stimulus value corresponding with 75% total trials correct, from the least-squares line at a $\log d$ value of 0.48, and from the least-squares line at a Z score of 0.67 for errors (25% errors).

Threshold Estimate Criteria			
Hen	Total trials cor. 75%	Fitted line c/m $\log d$ 0.48	Distrib. errors. Z score - 0.67
71	4.4	4.2	4.5
72	4.8	5.2	5.2
73	2.6	2.4	2.4
74	4.4	4.6	3.8
75	5.2	5.8	6.0
76	4.6	5.2	5.0

lines to describe the descending portion of data in the present study, seems to be equivalent to the rejection of certain data points from the line fit as used by Blough.

Estimates of threshold from the fitted line at a $\log d$ value of 0.48 generally yielded values close to those from the other criteria ($\log d$ value of 0.48 and the point of 75% accuracy on total trials), regardless of the transformation of threshold values (as shown in Table 1.1.10). However, the use of a $\log d$ value of 0.00 when estimating threshold from the fitted line, consistently resulted in increased variability of estimates, many of which, on visual inspection, would appear to over-estimate visual ability. For example, hen 73's data for the descending series yielded greater estimates than those obtained from the ascending series. Yet, visual inspection indicated that her accuracy was higher on the ascending series, and all other estimates indicated this also. When a line is fitted to functions with a shallow descending slope, such as the function for hen 73's data for the descending series, it tends to include those data points which may be best described by a flat line.

Any line fitted to the descending portion of the data would tend to pivot around the point of a $\log d$ value of 0.48, because, in most cases, the line describes data lying both above and below this value. As a results, thresholds estimated from the point of a $\log d$ value of 0.48 would not be greatly affected by inclusion of data which did not indicate discrimination and are best described by a flat line. On the other hand, any threshold estimated from the $\log d$ value of 0.00 would be greatly affected by inclusion of these "flat" data points which did not indicate discrimination. This is because generally none of the

data lay below this $\log d$ value, and the fitted line at this point was thus more free to change with the change in the spread of "flat" data points across the various transformations of stimulus values, This was especially evident when stimulus values were transformed to the width of a cycle.

Results therefore indicate that a $\log d$ value of 0.48 may be useful in providing an estimate of threshold, equivalent to that of the 75% point of total trial accuracy, but unaffected by left-right biases. However, for the present series of studies, a $\log d$ value of 0.00, being subject to variation and greatly affected by any transformations of stimulus values, does not provide such a consistent measure of performance. The summarizing of the descending portion of the data by a fitted line provides a useful alternative to traditional criteria, when the $\log d$ value of 0.48 is used to estimate a threshold. The straight line fits involved the least standard error when fitted to data plotted as a function of spatial frequency measured in c/mm, compared to other transformations of grating values. Although the estimates of threshold at the points of 50% and 75% accuracy on grating trials vary from those obtained from total performance using the percentages of total trials correct and $\log d$ value of 0.48, they provide a useful indicator of grating discrimination.

Response bias and stimulus control

The problem of response bias is prevalent in animal psychophysics and may be directly related to loss of stimulus control at finer grating values. The present results show that response bias in probe sessions did not vary greatly at finer grating values. The changes in

position preferences between the descending and ascending series of probes, shown in the ROC plots, for three hens, were not reflected their total discriminative performance. That is, there was little difference between discriminative performance in the two probe series despite the change in response bias. This is consistent with the findings of Terman (1970) who also reported that differences in position preferences in three rats, during an auditory discrimination task, were not reflected in their discriminative performance.

Small changes in position preference, that is, response bias, tend to effect $\log c$ estimates in much the same way as $\log d$ is changed by small changes in the response distribution within the four alternatives of the stimulus-response matrix (Figure 0.0.2). The higher the accuracy in performance, the more the estimate of $\log c$ changes. Because accuracy in training sessions was higher than in most probe sessions, small proportions of increased responding to the left key resulted in large changes in $\log c$ estimates. Therefore, although estimates of $\log c$ are assumed to be a measure of response bias independent of discriminability of the stimuli (Davison and Tustin, 1978), there appears to be some relation between changes in this measure and changes in the discriminability of stimuli. Small degrees of right key response bias, which tended to occur during probe sessions at high grating spatial frequency, generally changed to left response biases in the intervening training sessions.

Generally, psychophysical studies which do not control reinforcement ratios to both response alternatives, incorporate within their procedure some attempt to counteract response bias, termed a correction procedure (e.g. Hodos *et al.*, 1976). In such procedures,

when an incorrect response is made, the stimulus remains the same for subsequent trials until the correct choice is made. Responses made during the correction procedure are not counted for psychometric functions, and correct responding with the correction procedure does not usually produce reinforcement. However, the use of this procedure could change the probability of stimulus presentation in a successive discrimination. That is, if an animal responds incorrectly on a trial in which a grating is presented, this trial is repeated until the animal responds correctly to it. This could result in a greater number of grating presentation trials, and a greater number of grating presentation trials that are not reinforced. This could be analogous to unequal reinforcement schedules, which are richer for the constant or grey stimulus trials, and may serve to increase the response bias rather than reduce it.

Generally, response bias was more prevalent at difficult discriminations and appears to bear a close relation to loss of stimulus control. Procedures used to reduce response bias often do so by increasing stimulus control. In the present study, the hens were required to respond to both alternatives in order to obtain the maximum rate of scheduled reinforcers, even when the stimuli may not have been discriminable. This could be considered analogous to reinforcement for errors. That is, it is possible that the hens may perceive the grating as grey at the highest spatial frequency, yet they gain reinforcement for responding as if it were a grating. McCarthy (1980b) reports that when pigeons' errors were reinforced, accuracy decreased as a function of the probability of reinforcers for incorrect responding. Davison and Tustin (1978) suggest that responses to two alternatives, when the stimulus is no longer

discriminable, would be the same as responding under two concurrent schedules of reinforcement. That is, behaviour is no longer under control of the stimulus, but under control of the reinforcement schedule, only. In the present study intervening training sessions were used to re-establish stimulus control. Any loss of stimulus control during the sessions in which the stimuli may have been indiscriminable was immediately regained upon subsequent return to a training session. That is, although $\log d$ values for the probe sessions decreased as a function of probes with gratings of higher spatial frequency, $\log d$ values for the intervening training sessions remained high, indicating a constant level of high accuracy. Although other studies have used various methods, $\log d$ values indicate that intervening training sessions proved an adequate means of re-establishing stimulus control, without affecting the symmetrical contingencies of the procedure.

Latencies

Various studies have reported a relation between response latencies and visual or auditory stimulus intensity; that is latencies were short at easier discriminations and increased progressively with trials at more difficult discriminations. These differential latencies have been reported in various species, including kittens (Mitchell *et al.*, 1977), squirrel monkeys (Woodburne, 1965), pigeons (Blough, 1971), goldfish (Yager & Thorpe, 1970) and rats (Green, Terman & Terman, 1979). Blough reported that latencies in her study were also related to the amount of response bias shown. That is, her pigeons responded more quickly to the preferred response alternative. In the present study, however, no relation was found between response latencies and spatial frequency of

gratings. Where several hens responded slightly more quickly to the right response key, this occurred regardless of whether coarse or fine gratings were present, and whether or not the response was correct. Blough (1978) also failed to find any variation of latencies with stimulus values, when pigeons were tested on a wavelength discrimination task.

Generally, most of those studies reporting differential latencies employed such procedures as jumping stands and two-alley runways. Most of the psychophysical investigations, using a similar procedure to that of the present study, however, do not report findings of differential latencies (e.g. Hodos *et al.*, 1976; Hodos *et al.*, 1985). This may possibly be taken as an indication that no relation between latencies and stimulus values was found. It is possible, therefore, that latencies bear some relation to the difficulty of the discrimination only in certain types of procedures, in which a greater amount of effort is expended on each trial, than in the present study.

Although performance at the coarser gratings was more accurate than at the finer gratings, in no case was there perfect discrimination. If, by some procedural manipulation, it were possible to increase accuracy at the coarsest gratings, then the question is, would accuracy at finer gratings be increased also, resulting in changes of threshold estimates? The following experiment was an attempt to investigate this.

EXPERIMENT 1.2

In the previous study, although discriminative performance was high at the coarsest gratings compared to performance at the finer gratings, none of the hens demonstrated perfect accuracy. One procedural manipulation reported to improve performance on difficult discrimination tasks is the requirement of multiple responses to the sample key. Such a requirement is common in the matching-to-sample procedure (e.g. Cumming & Berryman, 1961). Farthing and Opuda (1974) reported that pigeons discriminating compound stimuli in a matching-to-sample task performed very poorly if only required to peck once at the sample, but discriminative performance improved when they were required to peck 10 times.

These response requirements to the sample stimulus may be termed "fixed ratio" (FR) response requirements. Some studies have found that an increase from an FR1 to an FR5 response requirement improves discrimination of colour and form (e.g. Roberts & Kraemer, 1982), while others report that such an increase was insufficient to improve accuracy (Berryman, Cumming & Nevin, 1963). The response requirement which results in the best discriminative performance for any group of subjects, varies across studies, to FR40 (e.g. Sacks, Kamil & Mack, 1972).

For the following study the FR response requirement to the sample key was increased, to determine:

- a) whether this resulted in improved baseline discriminative performance, and if so,
- b) the FR response requirement at which the most accurate performance

would be achieved for most hens,

c) whether any improvement in accuracy was maintained during probes at increasingly finer grating stimuli, and

d) whether any improvement in performance was maintained upon returning to a single observing response requirement (FR1).

Method 1.2

Subjects and apparatus

The six hens in Experiment 1.1 served. The apparatus was the same as that used for the previous study.

Procedure

The procedure was similar to that used in the previous study, and the controlled reinforcement schedule remained the same, at VI 30 s. There were, however, several variations in the procedure from that for Experiment 1.1. The study included six conditions which involved manipulation of the sample key response requirement. For the first five consecutive conditions increased response requirements were programmed. These were FR5, FR10, FR15, FR25 and FR40, in that order. For the sixth condition, the response requirement was decreased to FR1.

At the beginning of each condition, hens were trained to an accuracy and a stability criterion prior to a descending series of probes, as conducted in Experiment 1.1. Table 1.2.1 presents the six conditions and the number of sessions to stability for each. Stimulus presentation included a descending series of probes only. The number of probe values was decreased from 14 to seven. However, the range of values remained the same, from 1 to 10 c/mm. Grating values used for probes were 1, 2, 3, 4, 6, 8 and 10 c/mm. Upon completion of the series of probes with each FR response requirement, hens were trained for approximately five days with an FR1 response requirement, before the next training condition. Data were collected as for Experiment 1.1.

Table 1.2.1

Table 1.2.1

The order of each probe series, the sample key response requirement in effect, and the number of training sessions to stability prior to commencement of probes, for each probe series.

Order of Probe Series	Response Requirement	Sessions to Stability
1	5	14
2	10	13
3	15	17
4	25	32
5	40	19
6	1	13

Results 1.2

Discrimination

Figure 1.2.1a presents the percentages of total trials correct as a function of grating spatial frequency, measured in c/mm, for all hens, for each probe series with a different FR response requirement to the sample key. Data from the descending series of probes in Experiment 1.1 with an FR1 response requirement, are presented in all figures as unfilled circles joined by a broken line, for comparison.

Figure 1.2.1b presents the percentages of total trials correct at three grating values only (1, 2 and 3 c/mm), plotted as a function of the response requirements to the sample key, for each hen. Equivalent data from the FR1 response requirement in Experiment 1.1 are included. Data for the FR1 response requirement in the present study, following all probe series with the increased response requirements, are plotted as a separate data point, not joined by a solid line. While Figure 1.2.1a shows the effect of each response requirement on the percentages of total trials correct, compared to performance with the single response requirement (Experiment 1.1), Figure 1.2.1b allows a comparison of the effect of each of the different response requirements on discriminative performance at three gratings (1, 2 and 3 c/mm).

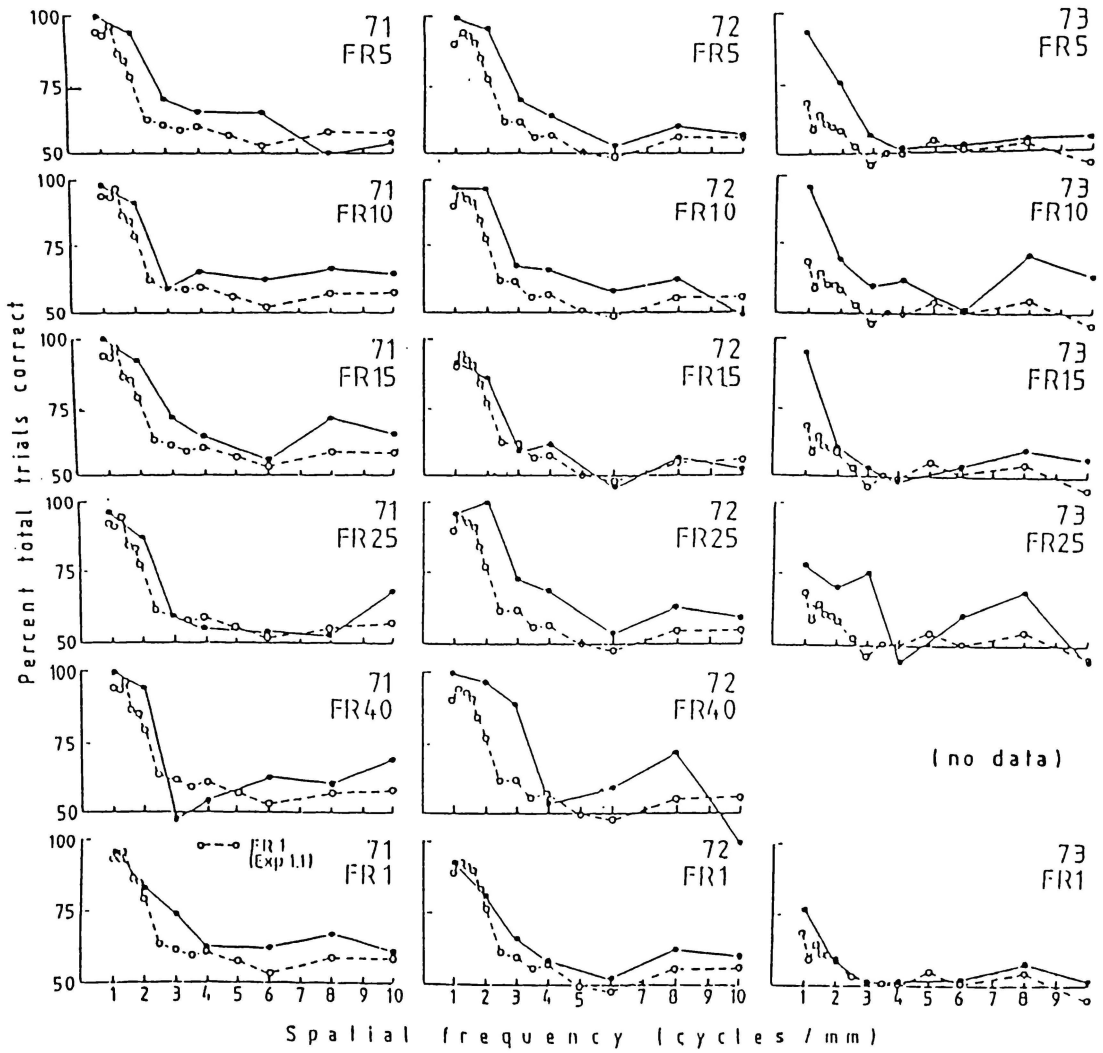
Generally, all data in Figure 1.2.1a show a monotonically decreasing function at probes with increasingly finer gratings, followed by a levelling off. Probes with the FR5 response requirement resulted, for most hens, in an increase in total trial accuracy at the coarsest gratings, compared to probes with FR1. Figure 1.2.1b shows

Figure 1.2.1

Figure 1.2.1a

The percentages of total trials correct, plotted as a function of grating spatial frequency, measured in c/mm, for all hens, for each probe series with a different response requirement. Data from the descending probe series with an FR1 response requirement (Experiment 1.1) are also presented, and are shown in the figure as unfilled circles joined by a broken line.

A



cont.

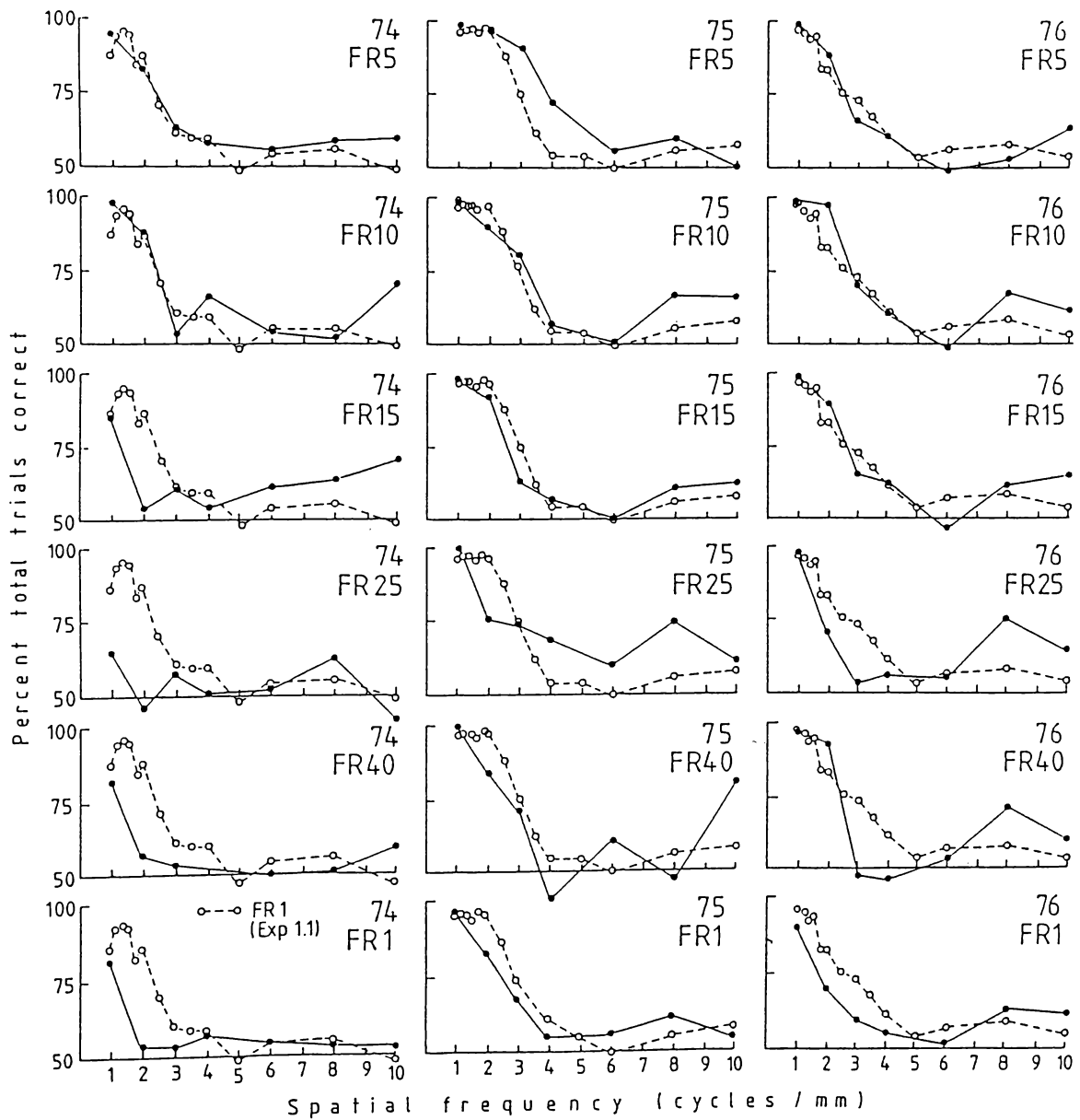
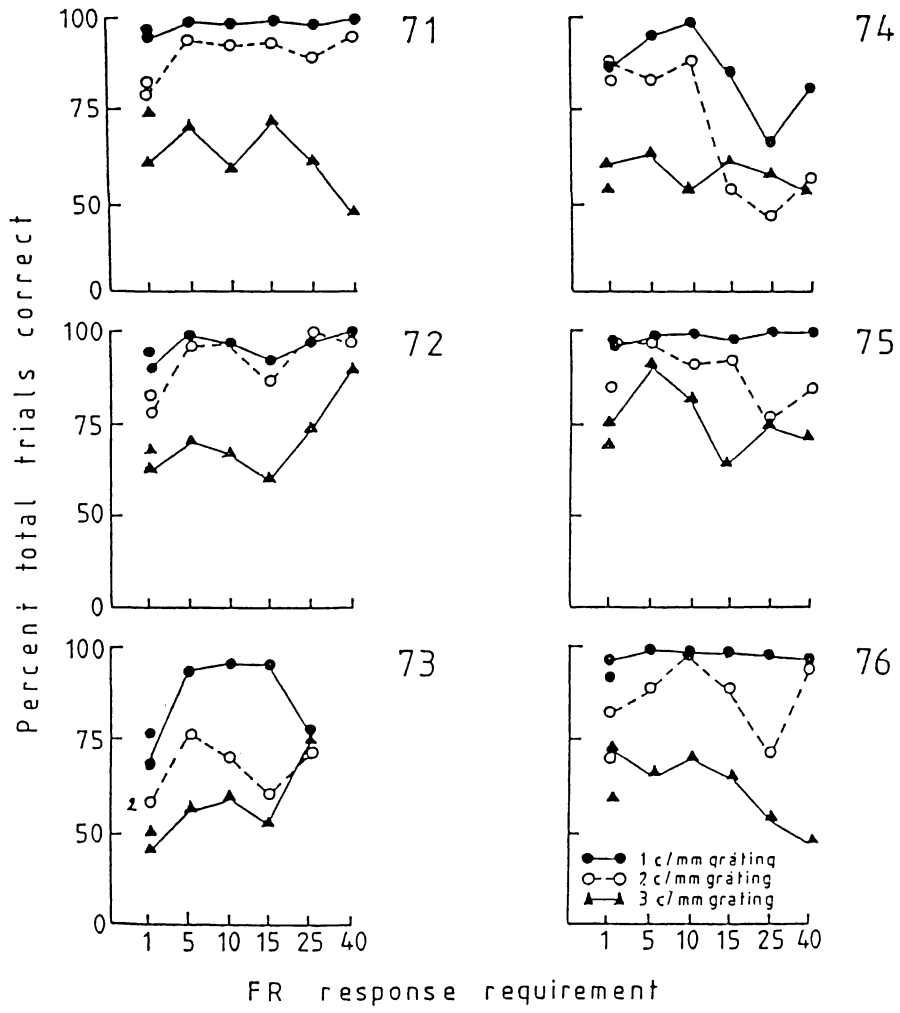


Figure 1.2.1b

The percentages of total trials correct at three grating values (1,2 and 3 c/mm), plotted as a function of the FR response requirements, for each hen. Data from the descending probe series with the FR1 response requirement (Experiment 1.1) are included in the figures.

Data for the probe series with the FR1 response requirement in the present study, following all probe series with the increased response requirements are plotted as separate data points, not joined by a solid line.

B



this more clearly. Generally, this increase in accuracy was maintained over most grating values. This increased accuracy was most evident in the data for hen 73. Her accuracy at the coarsest grating increased from below 70% with FR1 to 94% with FR5, and from below 60% at the 2 c/mm grating with FR1, to 77% with FR5.

Probes with the FR10 response requirement also generally resulted in an increase in total trials correct over probes at most grating values, compared to probes with FR1. For some hens, 73, 74 and 76, the percentages of total trials correct were higher at some gratings than for probes with FR5 responses. For hens 71 and 72, there was little difference and for hen 75, total trial accuracy was slightly less with FR10 than with FR5.

Probes with the FR15 response requirement also resulted in an increase in total trial accuracy, for most hens, over most grating values, compared to probes with FR1. For hen 71, the percentages of total trials correct were higher than for probes with FR5, for hen 76 there is little difference, and for others, 72, 74 and 75, they were slightly less.

Probes with the FR25 response requirement resulted in an increase in the percentages of total trials correct over most grating values for hens 72 and 73, compared to probes with FR1. For hen 71 the percentages of total trials correct were very similar to that with FR1 and for two hens, 74 and 76, they were lower.

Probes with FR40 resulted in an increase in the percentages of total trials correct compared to probes with FR1 over most grating

values for two hens only, 71 and 72. For the remaining hens generally total trial accuracy was lower than with FR1 at most grating values.

The percentages of total trials correct for hens at probes with FR1, following the series of probes with the higher response requirements, were very similar to those obtained with FR1 in Experiment 1.1, for most hens. For two hens only, 71 and 73, performance was slightly better.

Thus, in summary, for most hens, a response requirement greater than FR1 resulted in an increase in total trial accuracy. However, the effect of each response requirement on performance was not the same across hens. In some cases improved performance was maintained to the highest response requirement, (e.g. hen 72), in others an initially improved performance at FR5 was not maintained at higher FR requirements. In addition, as Figure 1.2.b clearly shows, the effect of each response requirement was not the same at each of the three gratings (1, 2 and 3 c/mm), for all hens. The most dramatic improvement was that by hen 73, which was maintained at most increased response requirements to FR25. During training sessions with the FR40 response requirement this hen's accuracy decreased, and responding stopped prior to probes. As a result no probe data were obtained for her at the FR40 response requirement. She resumed responding during retraining with the FR1 response requirement. For some hens there appears to have been an increase in accuracy at some finer gratings, but this did not occur at any one particular grating value or response requirement, for all hens. Accuracy, during probes with FR1 following the series of probes with higher response requirements, decreased for all hens, compared with performance at some of the higher response

requirements.

Threshold estimates for all hens and each probe series were determined as that spatial frequency of grating at which 75% of the total trials were correct. These were obtained by interpolation, as in Experiment 1.1. The estimates, calculated in c/deg, are shown in Table 1.2.2 as Criterion 1. These estimates range from 2.2 c/deg for hen 73 for probes with FR1 following all probe series with the higher response requirements, to 7.2 c/deg for hen 75 for probes with FR5. For most hens, estimates from probes with FR5, FR10 and FR15 were greater than those obtained from probes with FR1. Three estimates from probes with FR25, and only two estimates obtained from probes with FR40 were greater than those obtained with FR1 (Experiment 1.1). Estimates of threshold from probes with FR1, following probes with the higher response requirements, were greater for three hens, and lower for the others, compared to those obtained from probes with FR1 from Experiment 1.1. These results indicate that probes with a response requirement greater than FR1 improved total trials accuracy, not only at the coarsest grating values, but also at some of the finer gratings, resulting in greater estimates of threshold.

Figure 1.2.2 shows the mean of the percentages of total trials correct for the last five days training with each increased response requirement prior to the commencement of probe sessions, and the mean of the percentages of total trials correct for the last five days training with FR1, both from Experiment 1.1 and following each probe series with higher response requirements. Data from FR1 are shown as unfilled circles joined by a broken line, and data from the increased response requirements are plotted as filled circles joined by a solid

Table 1.2.2

Table 1.2.2

Estimates of threshold measured in c/deg obtained from the various methods of analyses and threshold criteria, for all hens, for all probe series with each response requirement. Estimates from the descending series with the FR1 response requirement (Experiment 1.1) are included for comparison. Where estimates were determined from the fitted line (Criterion 5), the 95% confidence intervals are given in brackets.

Hen	Threshold Criterion	Response requirement						
		1 (Expl.1)	5	10	15	25	40	1
71	1	4.2	5.6	5.0	5.8	5.2	5.0	5.8
	2	4.8	8.0	5.4	7.2	5.4	4.8	*
	3	3.6	5.0	4.4	4.8	4.2	4.2	4.0
	4	4.4	6.0	5.4	6.2	5.4	*	6.2
	5	*	6.6 (1.9)	6.0 (1.8)	6.8 (0.6)	6.4 (1.2)	*	6.2 (0.8)
72	1	4.4	5.6	5.0	4.8	5.8	6.8	4.8
	2	7.4	7.0	5.8	5.4	10.4	18.0	6.6
	3	3.6	4.8	4.6	4.2	5.2	6.6	4.2
	4	4.2	*	5.8	5.2	6.6	*	5.2
	5	*	5.2	6.8 (1.4)	5.0 (0.4)	6.4	*	5.4 (0.8)
73	1	*	4.2	3.6	3.2	2.8	*	2.2
	2	4.8	5.6	7.6	4.6	4.6	*	3.8
	3	2.0	3.4	3.4	2.8	4.0	*	*
	4	*	4.4	3.8	3.2	3.2	*	2.4
	5	*	4.4 (0.2)	4.6 (1.4)	3.6 (1.2)	2.8	*	2.4 (0.4)
74	1	4.8	4.8	4.8	2.8	*	2.6	2.6
	2	8.6	5.6	5.4	2.8	2.2	3.4	4.0
	3	3.4	3.4	4.2	*	*	2.6	2.8
	4	4.8	5.4	5.0	*	*	*	2.8
	5	5.8 (1.0)	5.8 (1.0)	6.0 (2.0)	*	*	*	3.0 (1.0)
75	1	6.0	7.2	6.4	5.6	4.0	5.4	5.0
	2	9.8	13.8	6.8	5.6	5.2	5.2	3.4
	3	5.6	7.4	5.0	4.4	3.4	4.0	4.4
	4	6.0	7.8	7.2	6.4	7.0	*	5.4
	5	6.4 (0.8)	7.8 (0.2)	8.2 (1.0)	6.2 (0.4)	6.4 (0.4)	*	5.4 (1.0)
76	1	4.8	5.2	5.6	5.2	3.6	4.8	3.4
	2	7.2	5.4	7.2	5.8	3.6	5.0	4.4
	3	3.8	4.0	5.0	4.4	2.6	4.4	2.6
	4	6.0	5.0	*	5.6	4.6	5.2	4.0
	5	6.2 (0.6)	6.6 (1.0)	5.0 (0.2)	7.0 (1.2)	4.6 (1.0)	5.6 (1.8)	4.8 (1.2)

* Estimate not calculable

Criteria:

1 = 75% total trials correct
2 = 50% grating trials correct

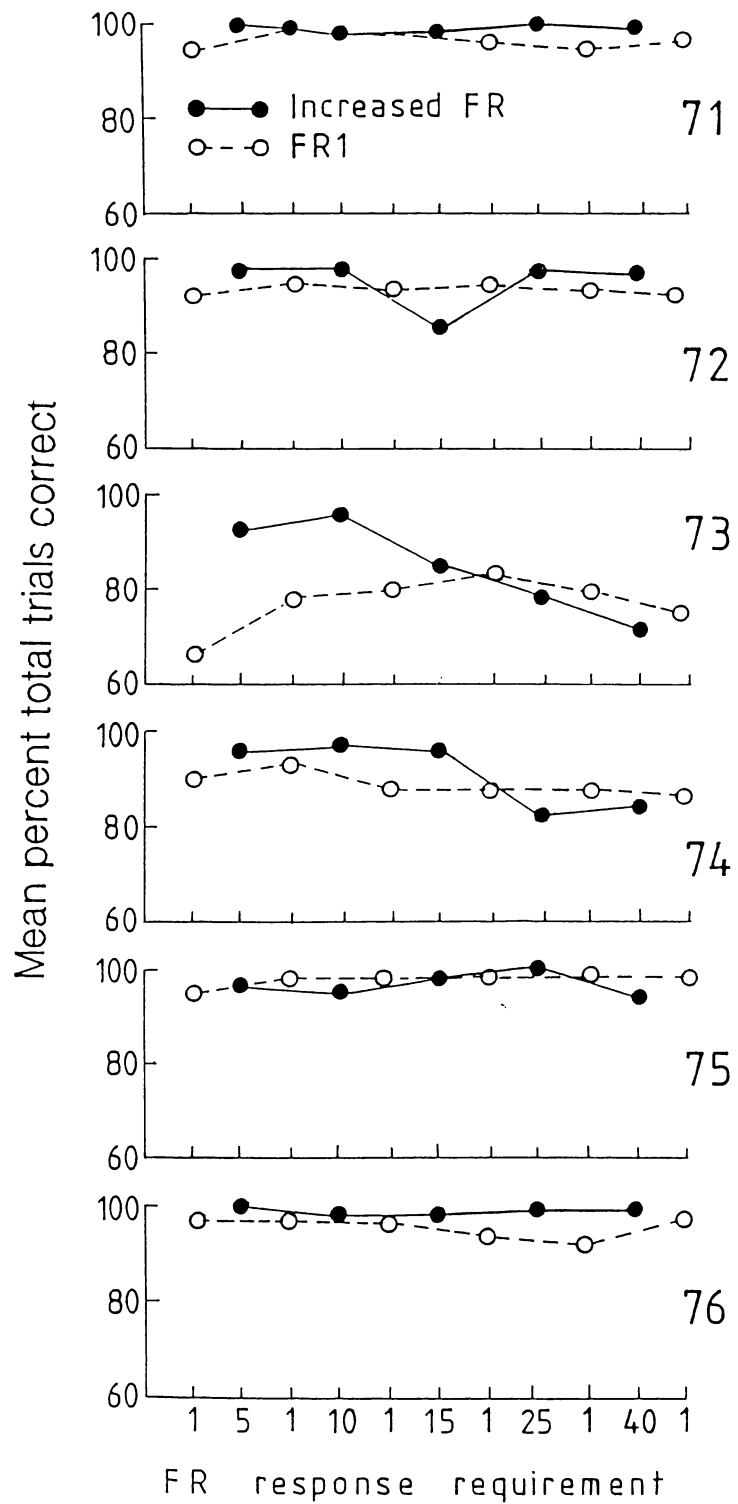
3 = 75% grating trials correct
4 = log d value of 0.48

5 = determined from least-squares
line at log d value of 0.48

Figure 1.2.2

Figure 1.2.2

The mean of the percentages of total trials correct for the last five days of training with each response requirement greater than FR1, prior to the commencement of probe sessions, and the mean of the percentages of total trials correct for the last five days of training with the FR1 response requirement, both from Experiment 1.1, and following each probe series with increased response requirements. Data from sessions with the FR1 response requirement are shown as unfilled circles joined by a broken line, and data from sessions with the increased response requirements are plotted as filled circles joined by a solid line. Data are plotted in order of occurrence, and the response requirement in effect is shown along the X-axis.



line. The data are plotted in the order of occurrence, and the response requirement in effect for data represented by each circle, is shown along the X-axis. For example, the first unfilled circle plotted in each figure represents the data from training with FR1, prior to the training data with the FR5 response requirement (the first filled circle plotted), the second unfilled circle represents data from training with FR1 following the FR5 probe series, and prior to those training data obtained with the FR10 response requirement.

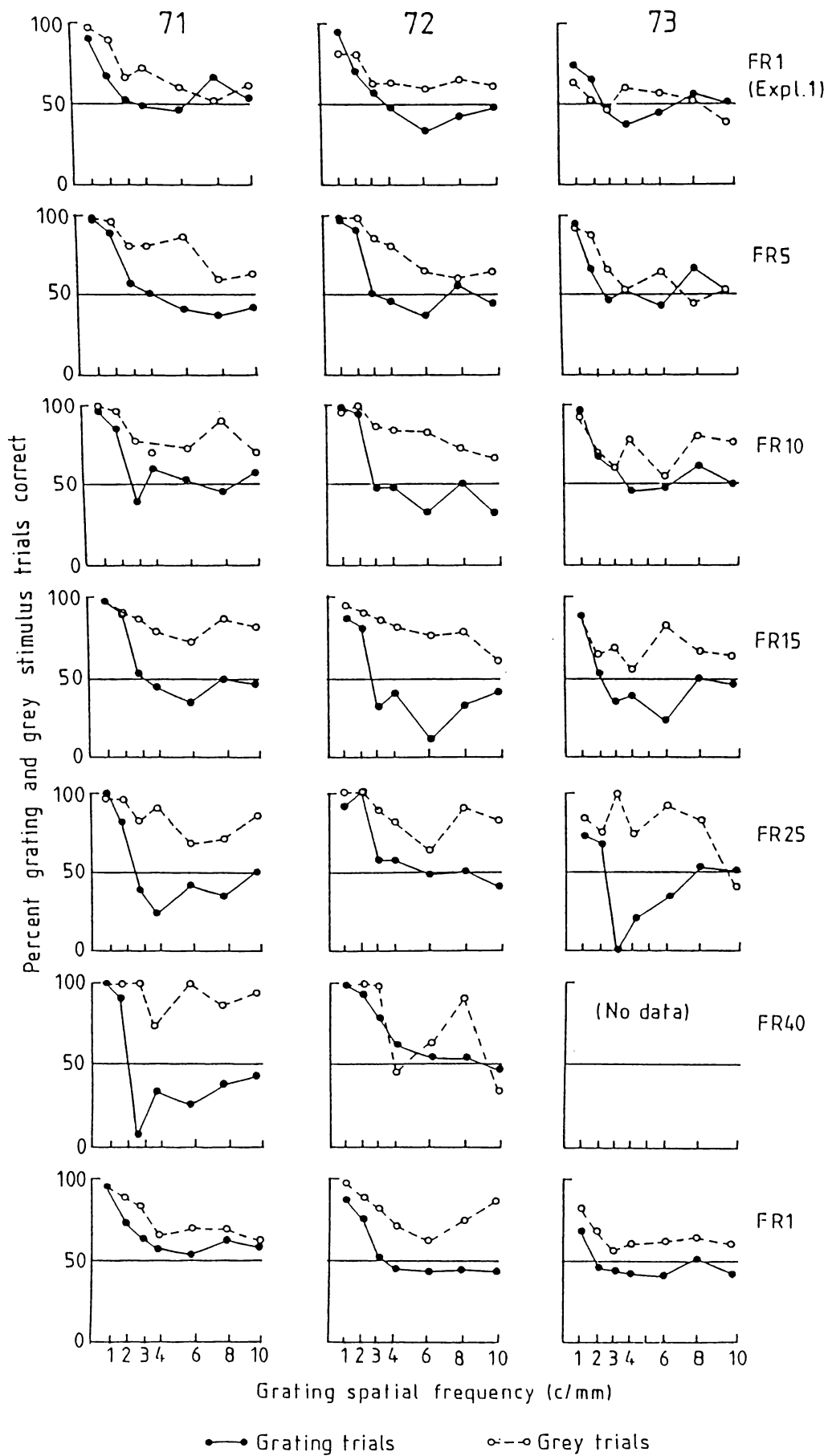
For all hens, the mean percentages of total trials correct during training were higher when the response requirement was increased from FR1 to FR5. Generally, training with response requirements greater than FR1 resulted in a higher mean percentage of correct trials than training with the FR1 response requirement. The response requirement which produced the highest mean percentages of total trials correct varied across hens, but for three hens (72, 73 and 74) it was FR10. The response requirement which produced the highest accuracy for other hens varied from FR5 for hen 76 to FR25 for hens 71 and 75. The mean percentages of total trials correct for training with FR1, prior to the final probe series with FR1, were slightly higher for three hens, and slightly lower for the remaining three hens, than for training with FR1 in Experiment 1.1. For two hens, 73 and 74, the mean of the last five days training with FR25 and FR40 was lower than for training with the FR1 response requirement. Thus, the data indicate that there may have been a certain critical value of response requirement resulting in the best performance for each hen, which, if exceeded, resulted in decreased accuracy.

Figure 1.2.3 presents the percentages of correct responses made on grating and grey stimulus trials separately, plotted as a function of grating spatial frequency, measured in c/mm, for all probe series. Data from Experiment 1.1 with FR1 are also shown, for comparison. For all hens the percentages of grating trials correct decreased to less than 50%, as a function of probes at increasingly finer gratings, and then levelled off. For some probe series with response requirements greater than FR1, the percentages of correct grating trials decreased to a much lower level than for probes with FR1. The percentages of grey stimulus trials, however, for most probe series with the increased response requirements, remained much higher than for probes with FR1. That is, generally, while accuracy decreased on grating trials during probes with the increased response requirements, accuracy was maintained on grey stimulus trials, at finer grating values. For probes with FR1, from Experiment 1.1, the percentages of correct grating trials decreased to approximately 40 - 50% while accuracy on grey stimulus trials remained at about 60%. However, at probes with the higher response requirements, grating trial accuracy decreased to below this value while grey trial accuracy remained much higher than 60% correct. For example, grating trial accuracy for hen 71 at the 3 c/mm probe value with FR40, decreased to 10%, while grey stimulus trials were 100% correct. For hen 73, grating trials accuracy at the 6 c/mm probes with FR25 decreased to 0%, while grey trials were 100% correct. However, at probes with FR1, following the series of probes with increased FRs, this separation of grating and grey stimulus trials lessened, and the data functions are similar to those of the initial series of probes with FR1, from Experiment 1.1. The data function however, for one hen, 76, shows more separation of grating and grey trial accuracy than the other hens for probes with

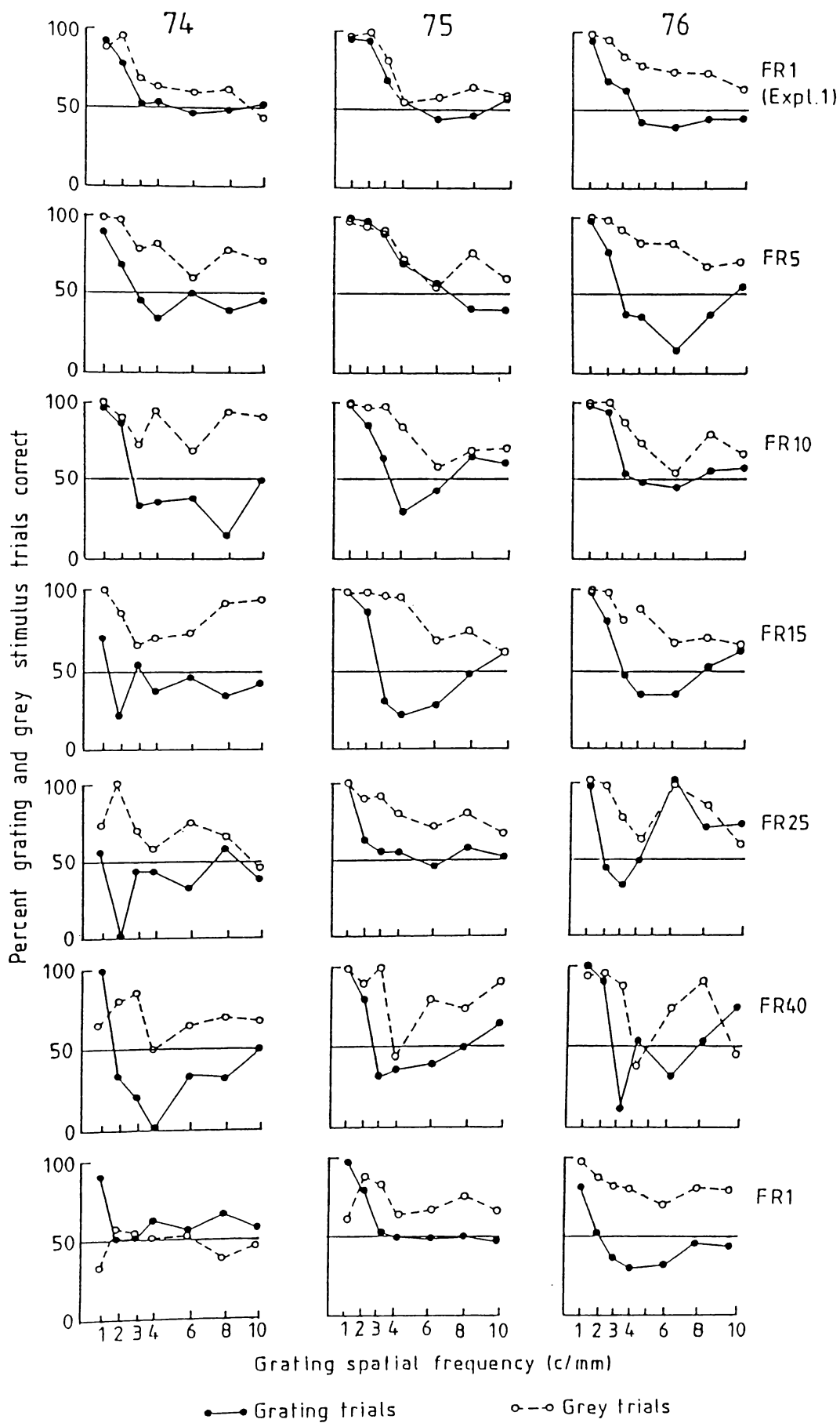
Figure 1.2.3

Figure 1.2.3

The percentages of grating and grey stimulus trials correct, plotted separately as a function of grating spatial frequency, measured in c/mm, for each probe series with an increased response requirement. Data from the descending probe series with the FR1 response requirement (Experiment 1.1) are also shown.



cont.



FR1, and this function does not change very much during probes with increased response requirements. To summarize, generally the two data functions (for grating and for grey stimulus trials) are much more separate at probes with increased response requirements than for probes with the single response requirement.

Threshold estimates based on the grating trials only, were taken from the points at which the plotted functions were 50% correct, as for Experiment 1.1. These estimates are shown in Table 1.2.2 as Criterion 2. They range from 2.8 c/deg for hen 74 for probes with FR15, to 18.0 c/deg for hen 72 for probes with FR40. No probe series with any one particular FR response requirement provided the greatest threshold estimate. All estimates from probes with FR1, following the probes with the increased response requirements, were lower than those taken from probes with FR1 from Experiment 1.1.

Threshold estimates, for grating trials only, were also taken from the points at which the plotted functions were 75% correct. These are also shown in Table 1.2.2 and are presented as Criterion 3. The greatest estimates did not come from the same probe series as the greatest for either of the two previous criteria. They range from 2.0 c/deg for hen 73 for probes with FR1, from Experiment 1.1, to 7.4 c/deg for hen 75, for probes with FR5. Generally, these estimates were not as great as those obtained from the 75% total trials correct. That is, they show lower discriminative performance. This indicates that the threshold estimates taken from total trial accuracy were improved or "inflated" by the higher accuracy on grey stimulus trials, for probes at intermediate grating values.

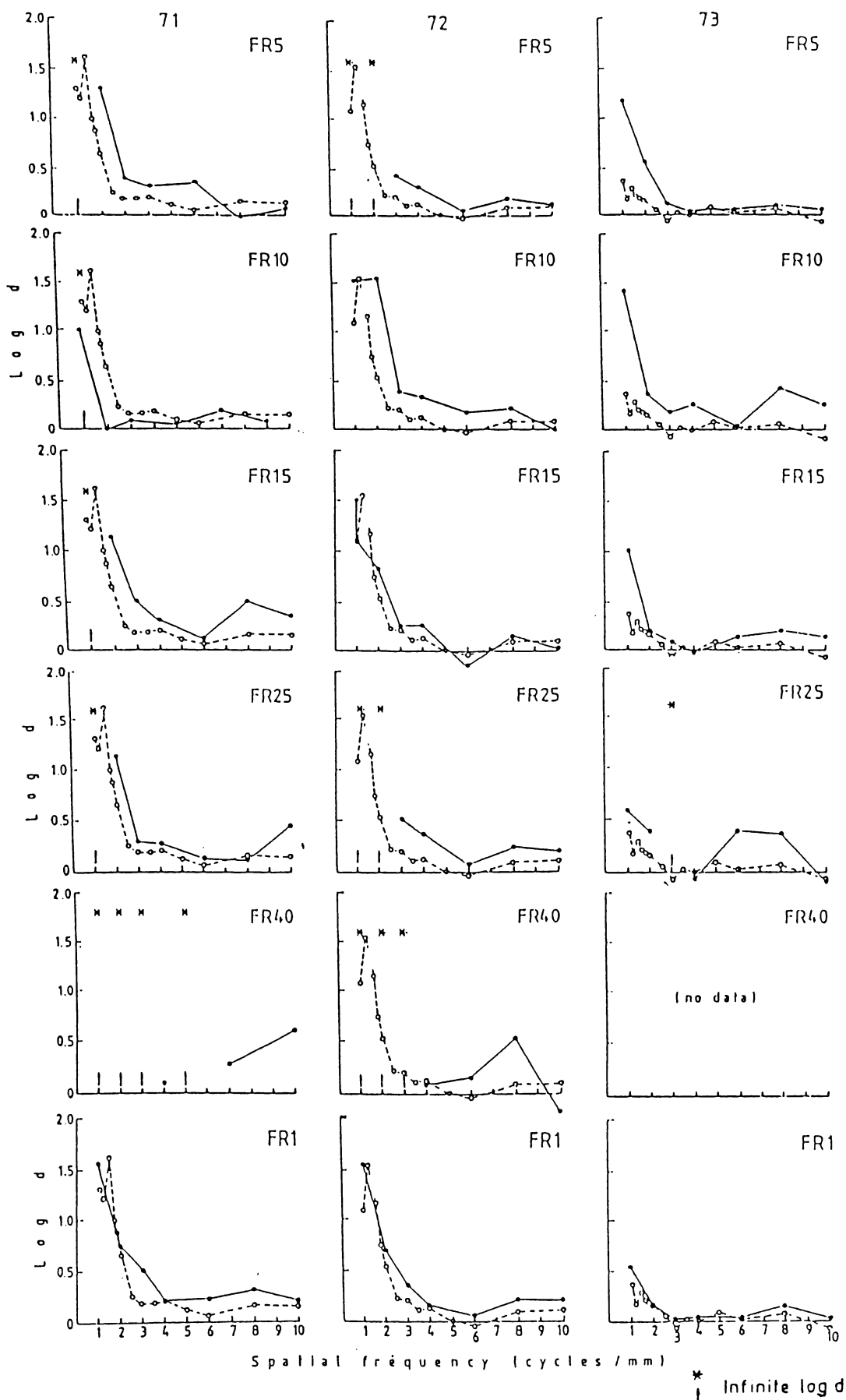
Figure 1.2.4 shows $\log d$ values (Equation 6) plotted as a function of grating spatial frequency for all hens, for all probe series. A high number of infinite values of $\log d$ were obtained during probes with response requirements greater than FR1, especially at the coarser gratings. This indicates that, for those particular stimulus values, 100% accuracy was obtained either on grating or grey stimulus trials or on both grating and grey stimulus trials). That is, no responses were emitted in at least one of the two error cells of the stimulus-response matrix (Figure 0.0.2). Infinite $\log d$ values are indicated in the figures by an asterisk and an arrow pointing upwards from the X-axis. Infinite $\log d$ values were also obtained for probes at some finer gratings. For example, hen 71 for probes at 4 c/mm with FR40, hen 75 for probes at 3 c/mm with FR40 and hen 76 for probes at 6 c/mm with FR25. For hen 71, four of the $\log d$ values obtained for seven probe sessions, were infinite. However, few infinite $\log d$ values were obtained from either series of probes with FR1.

Thresholds estimates were obtained by interpolation (as for Experiment 1.1) to determine the spatial frequency of grating which corresponded to a $\log d$ value of 0.48. These are shown in Table 1.2.2 as Criterion 4. It was not possible to determine thresholds from the data of some hens because of infinite $\log d$ values. Because infinite $\log d$ values cannot be plotted, the lack of data points at the lower stimulus values may result in loss of a descending function from which to determine a threshold. This occurred mainly at probes with the FR40 response requirement. Threshold estimates range from 2.4 c/deg for hen 73 for probes with FR1 following the probe series with increased response requirements, to 7.8 c/deg for hen 75 for probes

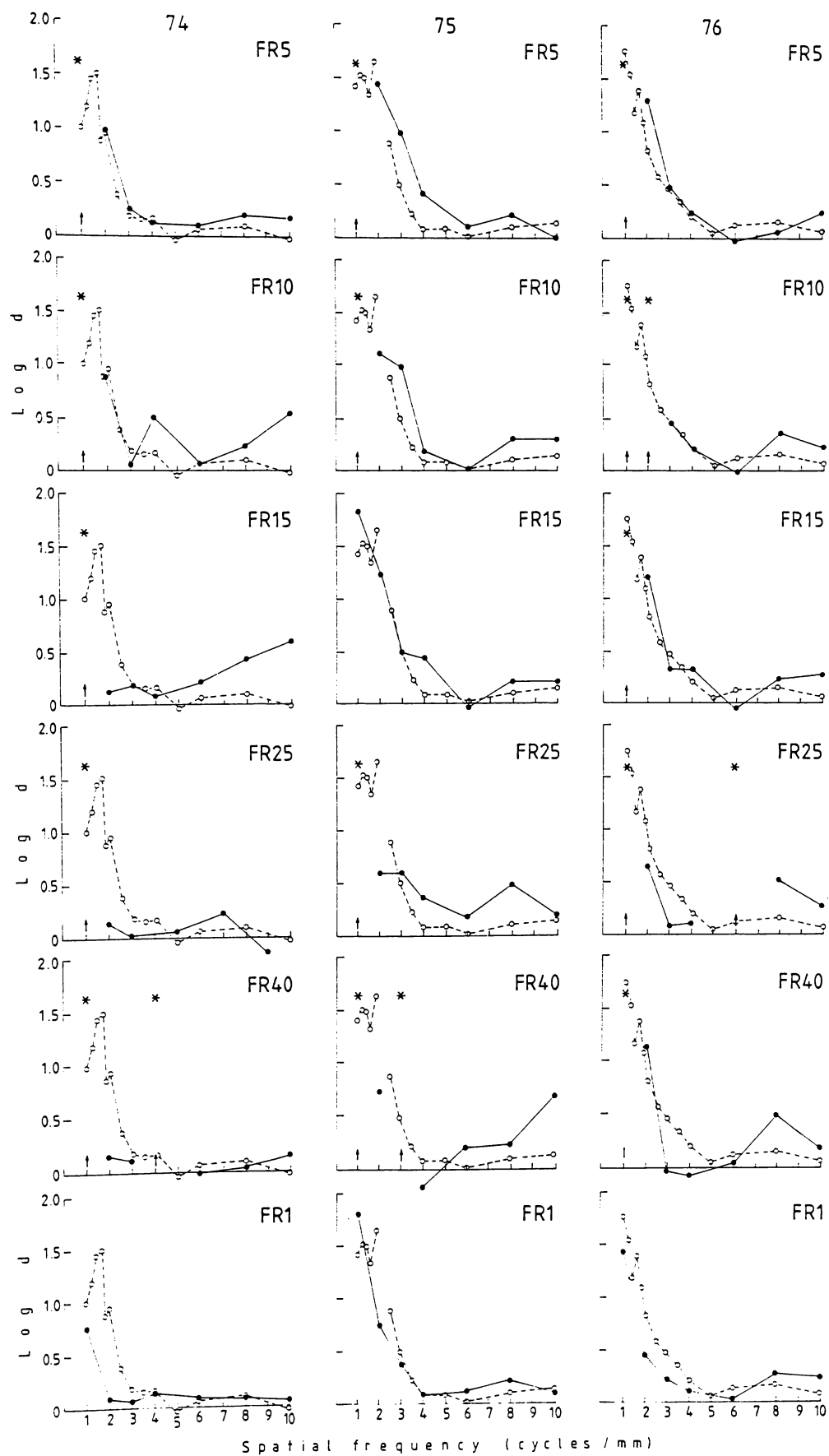
Figure 1.2.4

Figure 1.2.4

Values of $\log d$, plotted as a function of grating spatial frequency, measured in c/mm, for all hens, for each probe series with an increased response requirement. Data from the descending probe series with the FR1 response requirement (Experiment 1.1) are shown in the figures as unfilled circles joined by a broken line.



cont.



with FR5. Most estimates taken from the plotted $\log d$ values were greater than those obtained from the point of 75% total trial accuracy.

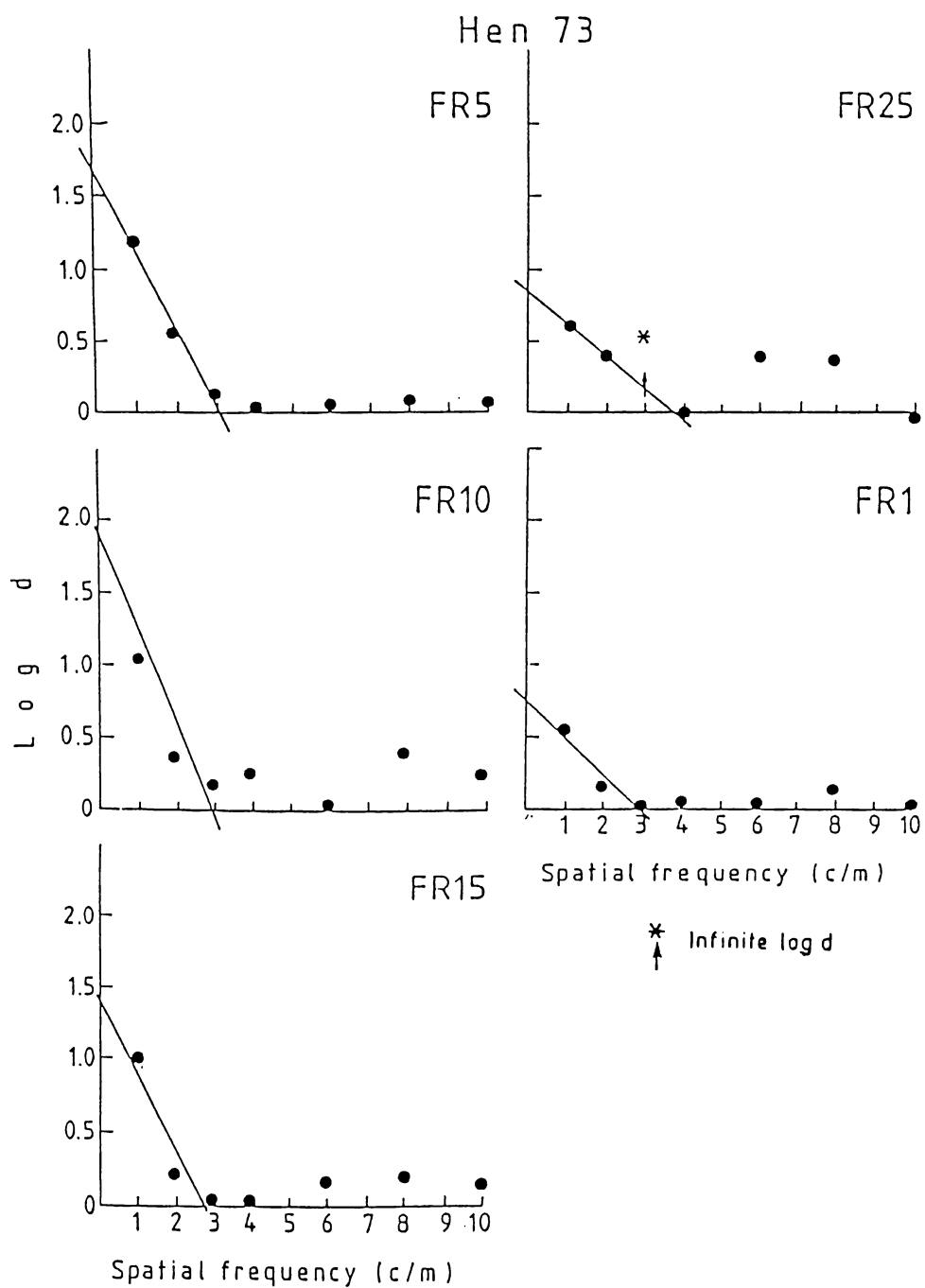
The same $\log d$ values presented in Figure 1.2.4 are plotted in Figure 1.2.5 for two hens only, 73 and 76, as examples of the least and most accurate performance, respectively. Lines have been fitted to most of the hens' data by the method of least squares, (as in Experiment 1.1). The lines chosen to fit the descending portion of the data from hens 73 and 76 are shown in the figures. The slopes, intercepts, standard error and amounts of variance accounted for (VAC%) by each line chosen to describe the descending portion of the data for all hens, are presented in Table 1.2.3. The number of data points from the descending portion of the data, described by each line, is also given. It was not possible to fit lines to some data, because of infinite $\log d$ values. Where $\log d$ values were infinite for probes at the coarser gratings, and the first data point was plotted close to a $\log d$ value of 0.00, there was no descending portion of data to which a line could be fitted. This occurred for hen 74 at probe with FR15 and for several hens at probes with FR40.

In all cases the line chosen was the one that visually best fitted the descending portion of the data, included at least three data points, and in most cases was the line with the least standard error. Lines chosen which did not contain the least standard error include those for the FR10 probe series for hens 71 and 74, for the FR15 probe series for hen 73, the FR25 probe series for hen 71. Table 1.2.3 shows that the standard error of the lines ranged from 0.00 to 0.51. Lines fitted to data from the probe series with FR10

Figure 1.2.5

Figure 1.2.5

Values of $\log d$ for two hens, 73 and 76, plotted as a function of grating spatial frequency, measured in c/mm, for each probe series with an increased response requirement. Lines have been fitted to the descending portions of the data by the method of least squares and are shown in the figures. Parameters of all fitted lines are given in Table 1.2.3.



cont

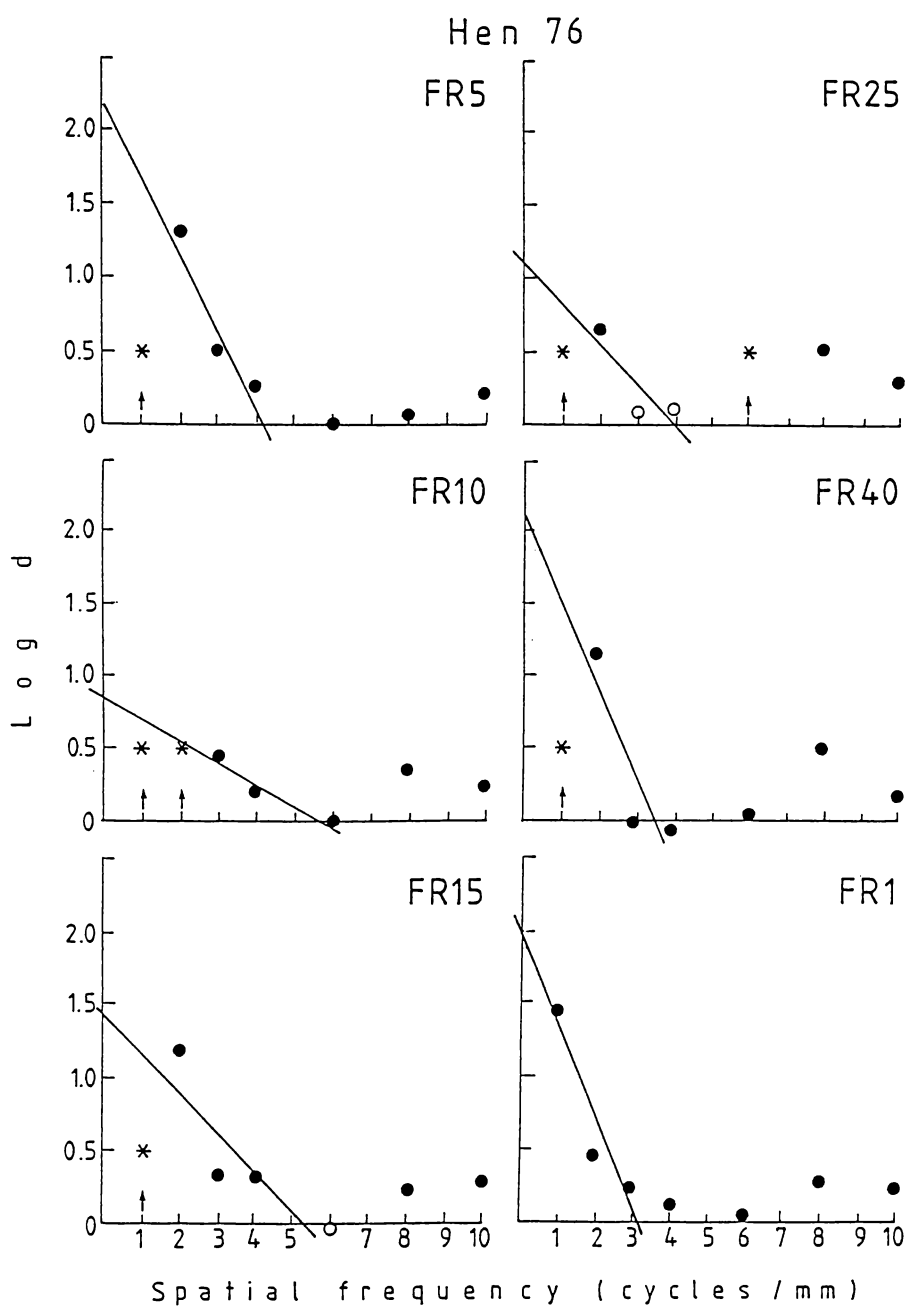


Table 1.2.3

Table 1.2.3

The slopes and the intercepts of the least-squares lines fitted to the values of $\log d$ for all hens, for the probe series with each response requirement. The number of data points described by each line, the amount of variance accounted for by the lines (VAC%) and the standard errors of the estimates (SE) are also given.

FR5						FR10					FR15				
Hen	Slope	Intcpt	Data pts.	VAC%	SE	Slope	Intcpt	Data pts.	VAC%	SE	Slope	Intcpt	Data pts.	VAC%	SE
71	-0.49	2.17	4	61.6	0.34	x-0.46	1.94	4	35.9	0.44	-0.41	1.87	4	84.9	0.17
72	-0.13	0.83	5	100.0	0.00	-0.47	2.13	4	71.7	0.36	-0.42	1.58	3	92.3	0.12
73	-0.53	1.69	3	98.6	0.06	-0.62	1.90	3	71.9	0.36	x-0.48	1.38	3	65.4	0.29
74	-0.39	1.66	4	60.4	0.28	x-0.19	1.06	4	0.0	0.51	*	*		*	*
75	-0.52	2.49	4	99.4	0.04	-0.30	1.69	5	75.8	0.27	-0.62	2.39	3	97.7	0.09
76	-0.53	2.26	4	82.3	0.23	-0.15	0.86	5	91.1	0.07	-0.27	1.46	5	65.2	0.31

FR25						FR40					FR1				
Hen	Slope	Intcpt	Data pts.	VAC%	SE	Slope	Intcpt	Data pts.	VAC%	SE	Slope	Intcpt	Data pts.	VAC%	SE
71	x-0.40	1.73	4	54.0	0.31	*	*		*	*	-0.43	1.83	4	86.3	0.22
72	-0.15	0.97	5	99.9	0.01	*	*		*	*	-0.59	2.05	3	87.7	0.21
73	-0.22	0.80	4	99.6	0.02	*	*		*	*	-0.26	0.77	3	87.3	0.10
74	-0.09	0.37	4	97.5	0.21	*	*		*	*	-0.35	0.99	3	53.2	0.27
75	-0.11	0.86	5	88.6	0.07	*	*		*	*	-0.71	2.40	3	85.8	0.28
76	-0.27	1.10	4	43.3	0.24	-0.61	2.18	4	55.4	0.46	-0.61	1.93	3	77.0	0.31

* line not fitted

x not least standard error

generally contained greater standard error than lines fitted to data from the other probe series. Across all probe series, three to five of a possible seven data points were described by the fitted lines.

To estimate thresholds, the stimulus value corresponding to a log d value of 0.48 was determined from the fitted lines (as for Experiment 1.1). It was not possible to take estimates from data for hen 74 at FR25 because the line crossed the Y-axis at a log d value lower than 0.48. The threshold estimates are shown in Table 1.2.2 as Criterion 5, and include the 95% confidence intervals, as determined by the standard error of the line fit. The estimates range from 2.4 c/deg for hen 73 for probes with FR1, following probes at the higher response requirements, to 8.2 c/deg for hen 75 for probes with FR10. Most of these estimates are slightly greater than those obtained by interpolation at the log d value of 0.48.

A comparison of all threshold estimates taken from the various methods of analysis and criteria generally show that those obtained from probes with an increased response requirement are greater than those obtained from either probe series with FR1. For one hen only, 75, the estimates from the probe series with FR5 consistently were greater than those from any of the other probe series. For the other hens, the FR response requirement providing the greatest estimates differed according to the various criteria used. However, the FR10 probe series generally provided the greatest estimates.

ROC plots

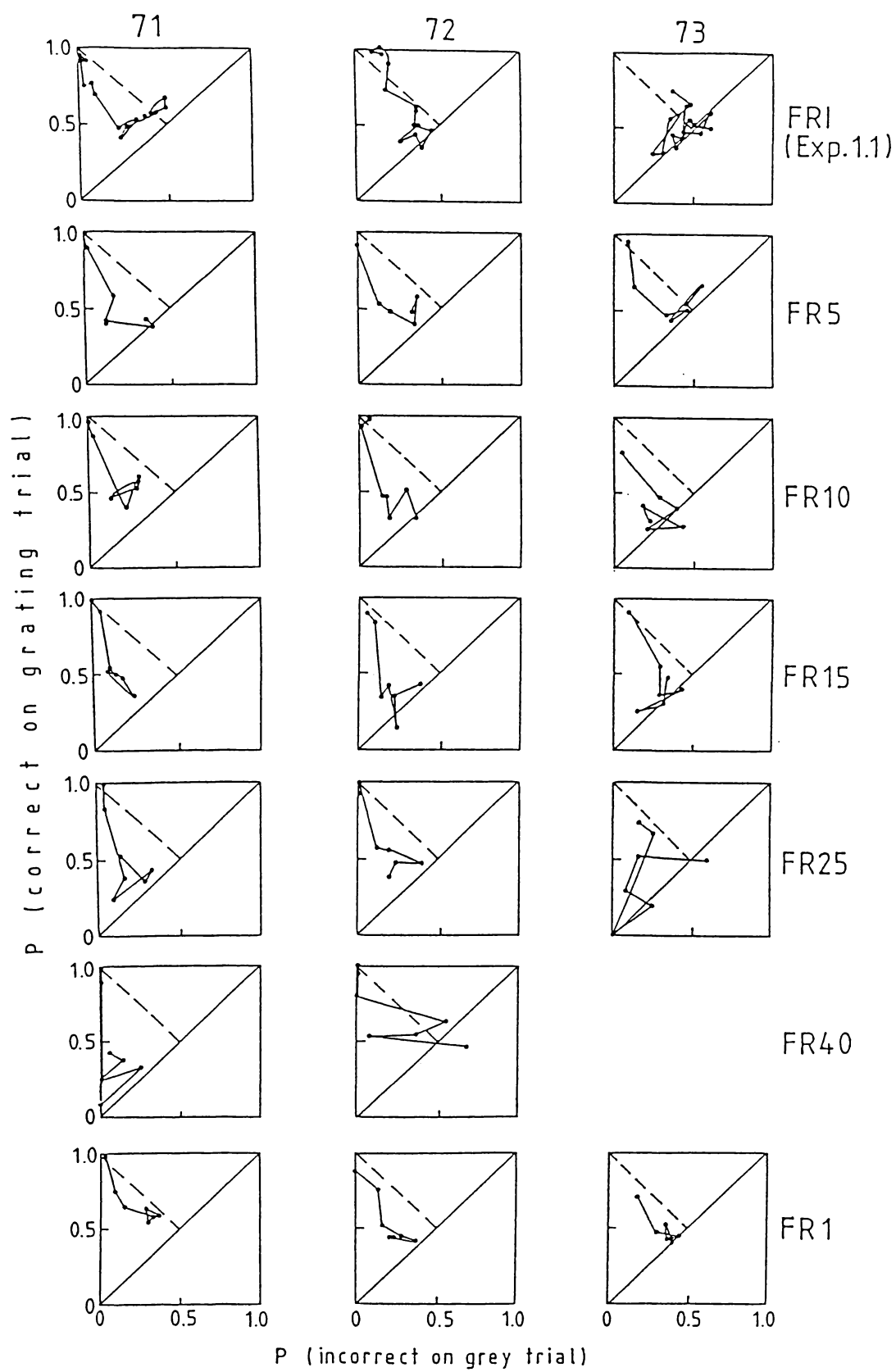
Figure 1.2.6 shows the proportion of correct responses to the left key on grating trials, plotted against the proportion of

incorrect responses to the left key on grey stimulus trials. These are plotted as a function of spatial frequency of gratings, measured in c/mm, for all hens, for all probe series. Lines join successive probes. Generally, the data paths for probes with FR1 (from Experiment 1.1) are close to the minor diagonal. For all series of probes with the higher response requirements, for most hens, the data paths move left of the minor diagonal, especially at probes with finer gratings, and for some probe series, move to the extreme left. However, for probes with FR1, following all probe series with the increased response requirements, the data paths returned closer to the minor diagonal. These data indicate that right key response biases, which were negligible at probes with FR1, developed and increased at probes with increased response requirements, and at some points led to exclusive responding to the right key only (as though all stimuli were grey). This occurred mainly for probes with FR25 and FR40, at the finer gratings.

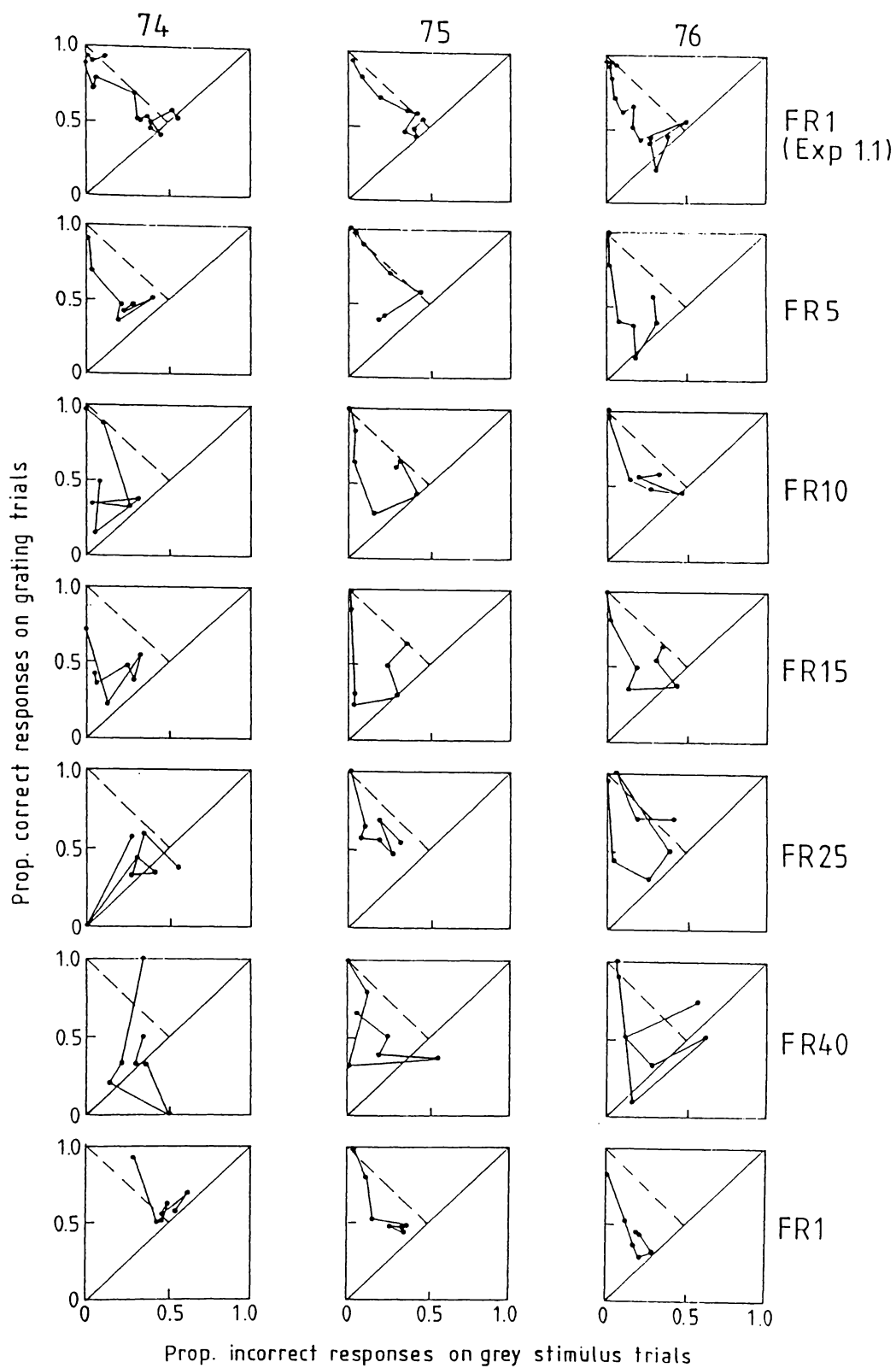
Figure 1.2.6

Figure 1.2.6

The proportion of correct responses to the left key on grating trials plotted against the proportion of incorrect responses to the left key on grey stimulus trials, for all hens, for each probe series with an increased response requirement. Data for the descending probe series with the FR1 response requirement (Experiment 1.1) are also shown.



cont.



Discussion 1.2

Data analysis

Various data analyses included in the previous study were omitted from the present results. For example, thresholds were not estimated from the stimulus value corresponding to a $\log d$ value of 0.00. It was considered, in the previous discussion, that the use of such estimates may not be appropriate in the present discrimination task. The three alternative transformations of stimulus values (logarithm of cycles/mm, width of a cycle in mm and logarithm of the width of a cycle), were omitted, because no additional information was obtained by their use in the previous study.

For Experiment 1.1 the lines chosen to fit the descending portion of the data, plotted as $\log d$ values, were those either from the line pair with the least overall standard error, or the line which visually best described the descending portion of the data. For the present study, however, because of the reduction of probe values from 14 to seven, and the further loss of data points due to infinite $\log d$ values, it was generally not possible to compare the standard error of several line pairs as in the previous study. Therefore, the standard error of the lines generated to fit the descending portion of the data only, were compared. This practice was continued for subsequent studies where probe values were reduced from 14 to seven. In most cases, in Experiment 1.1, the descending line with the least standard error, was also from the line pair which contained the least standard error. Thus, there is likely to be little difference between the two criteria.

Latencies were analysed for the present study, and, as for Experiment 1.1, no systematic relation was found between these and spatial frequency of gratings for any probe series. These were therefore not presented, and further analyses of these does not appear justified.

Discrimination

The common finding in the present study was that discrimination changed with changes of the response requirement to the sample key. Generally, discrimination improved when the FR5 and FR10 response requirements were in effect, compared to performance with an FR1. This is in agreement with a wide range of studies in which an increase from a single response to multiple responses to the sample have resulted in increased accuracy in various discrimination tasks, using the matching-to-sample procedure (e.g. Roberts, 1972; Sacks *et al.*, 1972).

Berryman, Cumming and Nevin (1963) however, failed to find improved discrimination in pigeons on a matching task, with an FR5 compared to an FR1 response requirement. They used a procedure in which the sample was present during the response to the choice alternative, as in the present study. This is termed a simultaneous matching procedure. Sacks *et al.* (1972) suggested that increased response requirements to the sample may not affect performance in simultaneous matching procedures. However, results from the present study are inconsistent with this proposition. On the contrary, an increase from FR1 to FR5 provided more change in accuracy generally across hens compared to performance with an FR1, than any of the other increased response requirements.

Cumming, Berryman and Cohen (1965), using a 0-s delay matching-to-sample procedure failed to find improved accuracy when they increased the sample response requirement to FR5 following 13 sessions with an FR1. Sacks *et al.* propose that the pigeons' previous training with an FR1 response requirement may have obscured any facilitative effects of the increased FR requirement, by "disrupting the well established chain of responses" that is, peck sample once then peck the side. This suggestion is also inconsistent with the present results, which indicate that extensive prior training with a single sample response requirement (i.e. around 300+ sessions) does not prevent an improvement in discriminative performance when an increased response requirement is in effect.

Discrimination at response requirements greater than FR10 was not the same for all hens. For some, accuracy further increased, for others the accuracy attained at FR10 was maintained, and for the rest, accuracy decreased. This indicates that the multiple response requirement necessary for the best discriminative performance varied across hens. Other studies (e.g. Lyderson, Perkins & Chairez, 1977) have also found variations in discriminative performance between pigeons, at different response requirements. There is no consensus in the literature as to the "best" response requirement for discriminative performance. For example, response requirements resulting in greatest accuracy range from FR5 for some studies (e.g. Roberts & Kraemer, 1982) to FR40 for others (e.g. Sacks *et al.*, 1972). In the present study, when the sample key response requirement was decreased to FR1, subsequent to a series of conditions with increased FRs, accuracy decreased, showing that the improved performance was not

a practice effect. This finding was common across all hens, and is consistent with results reported in the literature (e.g. Eckerman, Lanson & Cumming, 1968). Therefore, although there is consensus across studies that a sample response requirement greater than FR1 results in improved discriminative performance, there are variations within and between studies regarding the degree of improvement and the actual value of the response requirement that results in the best performance.

Discrimination at coarser gratings. Separate analysis of the data from grating and grey stimulus trials indicated that both grating and grey trial accuracy increased at the coarser gratings (assumed to be discriminable) for most hens, when the response requirement was increased to FR5 and FR10. That is, the improvement in total performance was not merely a result of increased accuracy on grating or grey trials alone. Various theories have been offered to account for changes in discrimination with increased response requirements to the sample. Generally, studies which have investigated the effects of increased response requirements to the sample have employed a delayed matching-to-sample (DMTS) procedure, where the delay between offset of the sample and onset of comparison keys is varied. Commonly, accuracy decreases as a function of the length of the delay. However, with increased response requirements, they report greater matching accuracy at all delay intervals, compared to performance with a single response requirement (Roberts, 1972). Such findings led to the proposal of the coding hypothesis (Cumming *et al.*, 1965). According to this, the response to the comparison stimulus, following responses to the sample key is under control of specific mediating stimuli associated with each sample. This explanation accounts for the greater proportion of

correct choice responses in the absence of the sample stimulus. The increased response requirement is assumed to increase the strength of the mediating events which control the response made to the comparison stimulus; the larger the response requirement, the greater the strength of these mediating events. Similarly the trace-decay theory (e.g. Roberts & Grant, 1976) proposes that a memory trace of the sample develops and increases in strength as a function of exposure to the sample, and decays in its absence. In such a simultaneous discrimination task as the present procedure, it is possible that the multiple responses to the sample may serve to separate one trial from another and thereby prevent pro-active interference (Grant, 1973). That is, the sample stimulus and choice response from the previous trial is less likely to interfere with performance on the present trial if there is some delay between trials. Increases in inter-trial-intervals (ITIs) have been reported to result in increased accuracy in a manner similar to increased response requirements to the sample (Roberts & Kraemer, 1984).

The responses to the sample are sometimes termed observing responses and it has been suggested that these increase attention to the sample. However, the term "attention" is itself somewhat circular, as it is determined by the degree of accuracy obtained. That is, if the animal discriminates well it must be attending to the sample, and if it is not discriminating well it cannot be attending to the sample. Therefore, such an explanation for the present results may not be adequate.

It is of interest also, that, in the present study, when an increased response requirement was in effect, generally discrimination

increased not only at the coarsest grating values, but also at some finer gratings as well. This resulted in a shift of the descending portion of the psychometric function to the right. Estimates of threshold were greater, indicating more acute vision. It may be reasonable to assume that any variable shown to affect performance in a discrimination task would also affect performance on a visual acuity task, when gratings are discriminable. However, it would not be expected that such a variable would increase discrimination of gratings which, on the basis of the animals' prior performance were not discriminable. That is, it is surprising that the increased response requirements would result in greater estimates of threshold, thereby indicating more acute vision, unless somehow the increased response requirements provided the necessary conditions for the hens to demonstrate already existing capabilities.

Eisler (1984) suggests that discrimination of one's behaviour having met a contingency is a necessary but not a sufficient condition for one's behaviour being controlled by the contingency. Eisler's rats, following an interruption in a tone, obtained reinforcement for lever presses provided they had refrained from lever pressing before the interruption. Long before the rats refrained reliably from lever pressing prior to the interruption, they demonstrated differential latencies of lever pressing following interruption of the tone. That is, short latencies occurred for lever presses which would be reinforced (because the rats had refrained from lever pressing during the tone) and long latencies occurred for lever presses which would not be reinforced (because the animals had not refrained from lever pressing during the tone). Eisler concluded from these results, that the rats had learned which behaviour would be reinforced, before

consistently demonstrating that behaviour. The results of the present study could possibly be explained by extending Eisler's proposal; that learning a task does not necessarily provide sufficient condition for the animal to demonstrate that learning. An increase in response requirements to the sample may in some way provide these necessary conditions. In the present study, accuracy decreased upon return to a single response requirement, which further supports this notion. Although accuracy decreased, the animals would not have become insensitive to the reinforcement-producing aspects of their behaviour, (i.e. which behaviours were correct and incorrect), but the necessary conditions to demonstrate that sensitivity consistently, were removed. Findings of Nevin and MacWilliams (1983) and Stubbs (1968) lend further support to this notion that animals do not always demonstrate what they have learned. They reported that when detection performance was reinforced on FR schedules, discrimination systematically increased through the ratio. This indicates that animals could be accurate, but did not demonstrate it until the reinforcer was temporally closer.

If Eisler's proposal is correct, then this could have important implications for studies of animals' sensory capacities. This may indicate that many procedures used to determine sensory functions may not provide the necessary conditions for animals to demonstrate the limits of their capabilities. Such a possibility has already been demonstrated by the discrepancies between visual acuities predicted from anatomical studies, for example, retinal ganglion cell density (Hughes, 1977) and behavioural studies with the same species (Blake, Cool & Crawford, 1974).

Effort and reinforcement probability. If the increased response requirement to the sample does provide the necessary conditions for improved discrimination, this raises a query as to the processes involved. Any increase in the response requirement to the sample increases both the duration of the single trial and the effort the animal expends on that trial. In the present study, when a single response was required, often many trials were completed before reinforcement for a correct response was available, and occasional errors would not have greatly affected the number of reinforcements obtained within a particular duration of time. That is, errors were not very costly in terms of time and effort. However, with increased responses to the sample, the duration of each trial was lengthened, and more effort was required. Errors then became more costly in terms of time and effort. Blough (1966) suggested that hard work and punishment may work in similar ways to improve stimulus control. He argues that rats look before they run when shock accompanies incorrect responses. In the present study, animals may look more carefully before they respond when each trial involves multiple responses. That is, they may behave more cautiously.

In this study, increasing the FR may have confounded with another variable: the reinforcement schedule. As the response requirement to the sample increased, the animals took longer to finish each trial. Because a VI reinforcement schedule was in effect, the number of correct trials per reinforcement decreased. That is, the probability of reinforcement for any correct trial was increased.

Spetch and Treit (1986), report that their results do not support the role of effort as an explanation of improved performance at

increased sample response requirements. They used a simultaneous matching-to-sample procedure and varied the response requirements to both the sample and a trial-initiating stimulus. Although accuracy increased as a function of an increase in the FR to the sample, it was not significantly affected by a similar increase in the FR to the trial-initiating stimulus. Trial-initiating responses made to the white centre key changed this key to either red or green (the sample stimulus). The results were based on mean data from five sessions, over four pigeons and differences were very small. If the first two conditions are compared (an initiating response requirement of FR1, and an FR1 to the sample), with an initiating response requirement of FR10 and an FR1 to the sample the latter shows a mean improvement of 3% across subjects. However, when comparing an initiating response requirement of FR1 and an FR10 to the sample (total of FR11) with an initiating response requirement of FR10 and FR10 to the sample (total of FR20), the mean accuracy for the latter was 2% lower. There seems to be an implicit assumption here that all behaviour emitted during a trial may contribute to effort required on a trial. However, this may not be so. It is possible that the effort required on the trial-initiating stimulus and the sample stimulus is not cumulative. That is, the effort required to initiate the trial may have been irrelevant.

Decreased accuracy with some high FRs. Results of the present study indicate that increased response requirements greater than a certain value did not further improve discriminative performance in some hens, but resulted in decreased accuracy. For example, hen 73 decreased responding at FR25 and stopped responding when FR40 was in effect. Very large response requirements may be punishing to some

animals, in a similar way to very long FR reinforcement schedules. The aversive effects of long FR reinforcement schedules has been documented. For example, Azrin (1961) states that an organism will sometimes acquire and maintain a response which changes or even removes certain conditions associated with positive reinforcement. He reported that the duration of the self-imposed time-out was a function of the number of responses required for reinforcement. Gentry (1968) and Cherek and Pickens (1970) found that pigeons demonstrated aggressive behaviour to target animals on long FR reinforcement schedules but not under no-reinforcement conditions. Furthermore, Zimmerman and Ferster (1963) report that pigeons increased matching accuracy as punishment for incorrect responding (TO) increased to intermediate values of 10 s. That is, when the cost of being incorrect was increased, accuracy increased. However, when the cost became very great (10 min TO) accuracy then decreased. The results of the present study, where very high FRs resulted in decreased accuracy, therefore, lend some support to the notion of the aversive effects of greatly increased "response cost".

Discrimination at finer gratings. At finer grating values (assumed to be indiscriminable), a maintenance of accuracy on grey stimulus trials was accompanied by a decrease in accuracy on grating trials, to below the level shown when FR1 was in effect in Experiment 1.1. That is, the discrepancy between grating and grey stimulus accuracy increased at trials with increasingly finer gratings. While effort and increased probability of reinforcement may account for improved discrimination at coarser gratings, it is more difficult to account for the separation in grating and grey trials, that is, response bias at finer gratings. It may be that, as discrimination

became more difficult and gratings could not be discriminated from grey stimuli, that the hens treated most trials as though they were grey trials (thus generally maintaining higher accuracy on grey stimulus trials) and responded as though the stimuli were gratings only when reinforcement for responding to the right alternative had not occurred for a while. This way, reinforcement would be maintained for responding to the right key. The hens would possibly be less likely to respond in this way with an FR1, because trials with FR1 are completed faster, and more reinforcements are obtained for correct responding. Thus overall, they would lose a large number of reinforcements by doing this. If, however, as in the present study, the overall number of reinforcements per session is decreased (due to time taken with the increased response requirements), the overall loss in reinforcements would be much less.

It therefore appears that the total discriminative performance, as measured in percentages of total trials correct, and the resultant threshold estimates which reflect the performance, increased as a result of a combination of two factors; firstly by increasing discrimination of both gratings and grey stimuli at the coarser gratings, and secondly, by increasing right key responding, that is right key response bias, and maintaining accuracy on grey trials, thus producing a higher total discriminative performance.

Response bias

In the discussion of the previous study, it was suggested that performance was constrained by the controlled reinforcement procedure. It is interesting that, to some degree, these constraints seem to have been reduced as the FR requirements were increased. Because the

discrepancy in accuracy between gratings and grey stimuli decreased upon return to a single response requirement, it appears that this effect was a function of the increased FR, rather than a gradual change in the overall pattern of responding.

This pattern of increased right key responding (treating most trials as though the stimulus were grey) is again illustrated by the ROC plots (Figure 1.2.6), where right key bias generally increased at finer grating values, as a function of the increased FR requirement. Some ROC plots show a varying bias, more indicative of responding in an uncontrolled reinforcement procedure (McCarthy & Davison, 1980a). However, although the majority of correct responses were to the right, the hens did maintain some responding to the left key. That is, in no case has the increased response bias at finer gratings led to exclusivity. It is likely, then, that the controlled procedure had constrained performance to some degree. At high FR requirements, even an occasional correct response to the left key would be likely to be reinforced, and this would ensure that correct responding to the right key would continue to result in reinforcement from that alternative.

In this study, the increased response requirements resulted in improved discriminative performance not only at the coarser, but also at the finer gratings. Although the discriminability of the stimuli remained constant, the improvement in discrimination was reflected in greater estimates of threshold, indicating apparently more acute vision.

EXPERIMENT 1.3

In Experiment 1.2, the hens' discriminative performance improved when a response requirement greater than FR1 was programmed to the sample key. This improved performance extended to finer gratings, and resulted in greater estimates of threshold. Such a finding indicates that the hens may have been capable of producing this higher level of discriminative performance with the FR1 response requirement, but did not demonstrate this until multiple responses to the sample were required. That is, the increased response requirement would not be expected to change the animals' visual capacity. Rather, their ability to discriminate at a higher level of accuracy may be a necessary, but not a sufficient condition for their demonstration of such ability.

One variable, however, which has been widely reported to affect discrimination by changing the animals' visual ability, is luminance. The manipulation of luminance is a common procedure in studies of visual acuity. Where species are known to have a functional duplex visual system, visual acuity is reported to vary as a function of the luminance of the target stimulus, and the relation between the two is reported to be ogival in form (Wilcox, 1932). Visual acuity varies as a function of luminance for humans and primates (Spence, 1934), sea lions (Schusterman & Balliet, 1971), cats (Loop, Smyly, Millican, Leigh & Greifer, 1981) and for such avian species as the pigeon (Hodos, Leibowitz & Bonbright, 1976), falcon (Fox, Lehmkuhle & Westendorf, 1976), and eagle (Reymond, 1985). The visual acuity of these animals has previously been discussed in the general introduction.

For those animals with rod dominated vision however, for example, nocturnal species such as the opossum (Silviera, Picanco-Diniz & Oswaldo-Cruz, 1982) and the rat (Birch & Jacobs, 1979), acuity is reportedly not affected by luminance variation. However, nocturnal habits alone do not necessarily indicate the lack of duplex vision. Neither does the presence of cones in the retina of an animal indicate a well developed visual duplex system. The acuity-luminance function depends not only on the degree of the animals' nocturnality, but also in the extent to which their behaviour is mediated by the visual sense (Martin & Gordon, 1974).

When Johnson (1914) studied acuity in the domestic hen, he used a constant luminance of 3.85 mL (approx. 12.25 cd/m²) and Over and Moore (1981) reported a constant luminance of 39 cd/m² for their study of visual acuity in young chickens. There are, therefore, no data on the effect of varying luminance on visual acuity in the hen. However, because it is a diurnal animal with a functional cone system (Govardovskii & Zueva, 1977) acuity would be expected to vary as a function of luminance.

The aim of the following study was to vary the luminance of the stimuli within a limited range, to determine the effect of luminance change on discriminative performance.

Method 1.3

Subjects and Apparatus

The six hens from the two previous studies served. The apparatus was the same as that used for the two previous studies.

Luminance. The luminance of the centre sample key was varied in order of intensity, from 0.28 cd/m², to 3.48 cd/m² and 5.48 cd/m². Luminance was changed by varying the amount of light from the centre projector bulb immediately behind the stimulus disk. The lowest luminance, 0.28 cd/m², was obtained by placing a Kodak Wratten neutral density filter, No. 3.0, between the light beam from the centre projector bulb and the stimulus disk. A higher luminance, 3.48 cd/m², was obtained by removing the neutral density filter, and the small perspex disk between the light beam and stimulus disk. The highest luminance, 5.48 cd/m², was obtained by securing silver foil over the open end of the plastic tubing which held the projector bulb, so that more light was reflected toward the stimulus disk.

Procedure

The procedure was similar to that of Experiment 1.2, except that 10 responses were required to the sample key (FR10). The controlled reinforcement schedule remained the same as that used for the two previous studies, at VI 30 s. Hens were trained to both a stability and an accuracy criterion before being tested in a descending series of probes at each luminance. As for Experiment 1.2, seven grating values, ranging from 1 to 10 c/mm, were used. The hens were trained for 17 sessions at the first luminance (3.48 cd/m²), 16 sessions at the second luminance (5.48 cd/m²) and 18 sessions at the third luminance (0.28 cd/m²). Data were collected as for Experiment 1.2.

Results 1.3

Discrimination

Figure 1.3.1 presents the percentages of total trials correct, plotted as a function of grating spatial frequency, measured in c/mm, for all hens for the probe series at the high (5.48 cd/m²) and the low (0.28 cd/m²) luminance. For four of six hens accuracy was slightly higher at the high luminance, but for hen 71 accuracy was slightly higher at the low luminance. For hen 73, accuracy was higher for probes at the high luminance for all but the coarsest grating value. The data indicate that when the hens could discriminate, they were generally more accurate at the high luminance.

Data for the medium luminance (3.48 cd/m²) are not plotted here, because they were highly variable. These data were, for some hens, more accurate than at the high luminance, and for other hens, less accurate than at the low luminance, at the coarser gratings. These data for the medium luminance, shown as the percentages of total trials correct, and the percentages of grating trials correct, are presented in Table 1.3.1.

Estimates of thresholds for each hen and for both luminances were taken from that spatial frequency of the grating at which 75% of total trial performance was correct. Estimates for the probe series at the high luminance range from 3.2 to 6.4 c/deg and those for the probe series at the low luminance range from 2.8 to 5.6 c/deg. These estimates of threshold are presented in Table 1.3.2 as Criterion 1, and indicate that greater estimates, for five of six hens, were from the probe series at the high luminance.

Figure 1.3.1

Figure 1.3.1

The percentages of total trials correct, plotted as a function of grating spatial frequency, measured in c/mm, for all hens, for the probe series at the high (5.48 cd/m^2) (filled circles joined by a solid line) and at the low (0.28 cd/m^2) (unfilled circles joined by a broken line) luminance.

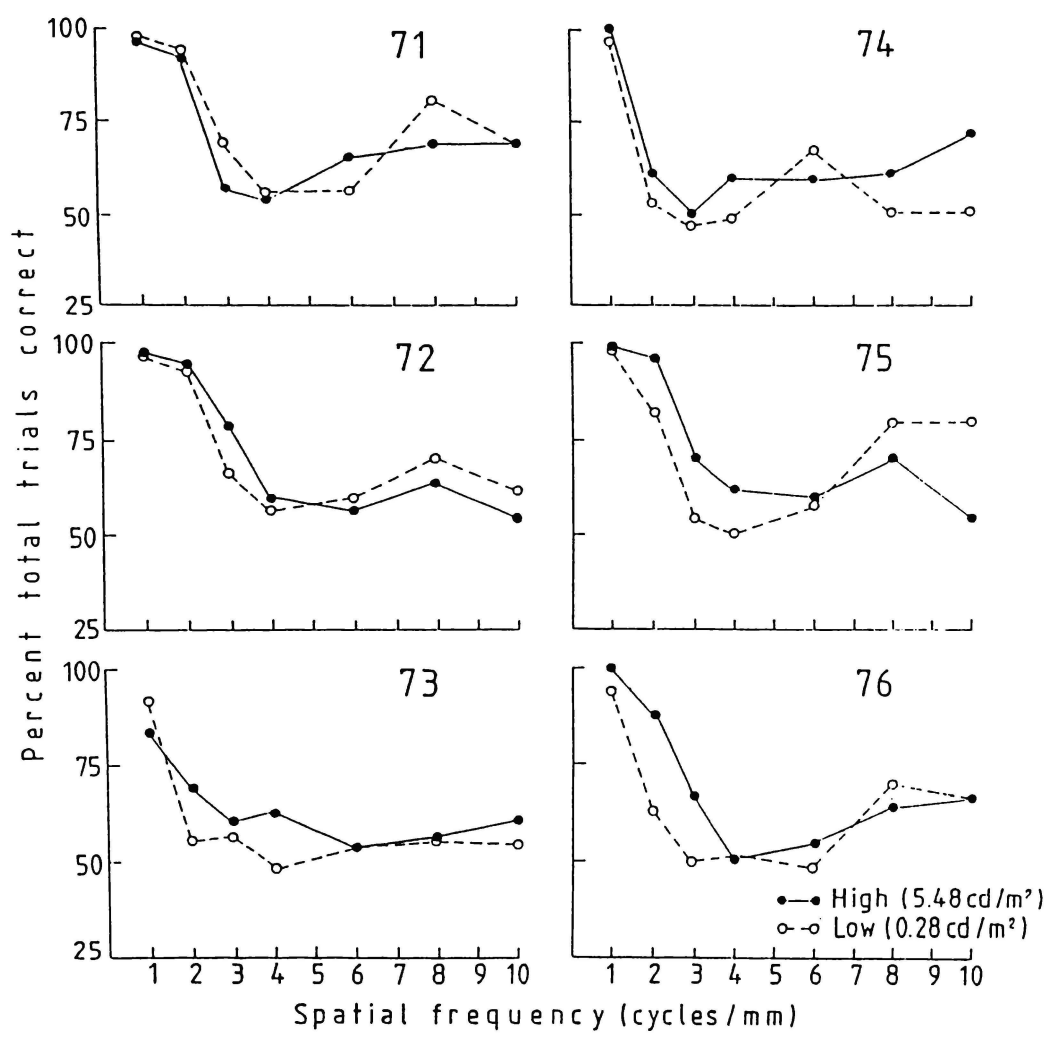


Table 1.3.1

Table 1.3.1

Data from the probe series at the medium luminance (3.48 cd/m^2). These include the percentages of total trials correct and the percentages of grating trials correct, for all hens.

Grating c/mm	% total trials correct					
	71	72	73	74	75	76
1	98	99	83	97	99	98
2	97	92	57	65	97	89
3	57	84	54	52	76	52
4	56	60	58	59	58	55
6	66	55	51	45	60	60
8	78	59	48	66	66	67
10	75	46	63	62	71	69
	% grating trials correct					
	71	72	73	74	75	76
1	95	99	84	98	100	99
2	97	90	50	52	95	82
3	57	71	46	61	67	99
4	53	24	52	50	26	33
6	71	24	51	41	37	48
8	84	31	44	46	46	60
10	78	47	63	53	65	74

Table 1.3.2

Table 1.3.2

Threshold estimates, measured in c/deg, from the various methods of analysis and criteria, for all hens, for the probe series at the high (5.48 cd/m²) and low (0.28 cd/m²) luminance. Where estimates were determined from the fitted line (Criterion 5), 95% confidence intervals are given in brackets.

Hen	Threshold Criterion	Luminance (cd/m ²)	
		High (5.48)	Low (0.28)
71	1	5.0	5.6
	2	6.6	7.2
	3	5.2	5.2
	4	*	6.0
	5	*	6.4 (0.7)
72	1	6.4	5.4
	2	7.6	5.4
	3	6.2	4.4
	4	6.4	6.2
	5	6.8 (0.6)	6.4 (0.2)
73	1	3.2	2.8
	2	6.6	3.8
	3	3.6	2.6
	4	3.4	3.2
	5	4.0 (0.3)	3.8 (0.7)
74	1	3.4	3.0
	2	3.6	3.8
	3	2.8	2.8
	4	*	3.6
	5	*	4.0 (1.1)
75	1	5.8	4.4
	2	6.8	5.6
	3	5.0	3.6
	4	6.0	4.8
	5	6.8 (0.8)	5.0 (0.6)
76	1	5.2	3.2
	2	6.6	4.4
	3	4.6	2.8
	4	5.6	3.4
	5	5.8 (0.2)	4.0 (0.7)

*Estimate not calculable

CRITERIA:

1 = 75% total trials correct

2 = 50% grating trials correct

3 = 75% grating trials correct

4 = log *d* value of 0.48

5 = determined from fitted line at log *d* value of 0.48

Figure 1.3.2 shows the percentages of correct responses made on grating and grey stimulus trials, plotted separately, as a function of grating spatial frequency, measured in c/mm, for the two probe series. Although the function for grey trials is flatter than the function for grating trials for most hens, this is most apparent in the data of two hens, 72 and 75. Their percentages correct for the grey trials at both luminances averaged approximately 75 - 80% correct. For both of these hens, the percentages of grating trials correct decreased to 30 - 35%, which was lower than that for the data from the other hens.

Threshold estimates based on the grating trials, were taken from the points at which the plotted functions were 50% correct. Estimates for all hens and for both probe series at the high and the low luminances are shown in Table 1.3.2 as Criterion 2. These range from 3.6 to 7.6 c/deg for the probe series at the high luminance and from 3.8 to 7.2 c/deg for the probe series at the low luminance. For four of six hens, greater estimates were taken from the probe series at the high luminance. Estimates of threshold were also obtained from the points at which the plotted functions were 75% correct. These are shown in Table 1.3.2 as Criterion 3, and range from 2.8 to 6.2 c/deg for the probe series at the high luminance and from 2.6 to 5.2 c/deg for the probe series at the low luminance. For four of six hens, greater estimates were taken from the probe series at the high luminance, and for two hens the estimates from both probe series were the same.

Figure 1.3.3 presents values of $\log d$ (Equation 6) plotted as a function of grating spatial frequency, measured in c/mm, for all hens

Figure 1.3.2

Figure 1.3.2

The percentages of grating (filled circles joined by a solid line) and grey stimulus trials (unfilled circles joined by a broken line) correct, plotted as a function of grating spatial frequency, measured in c/mm, for all hens for the probe series at the high (5.48 cd/m²) and the low (0.28 cd/m²) luminance.

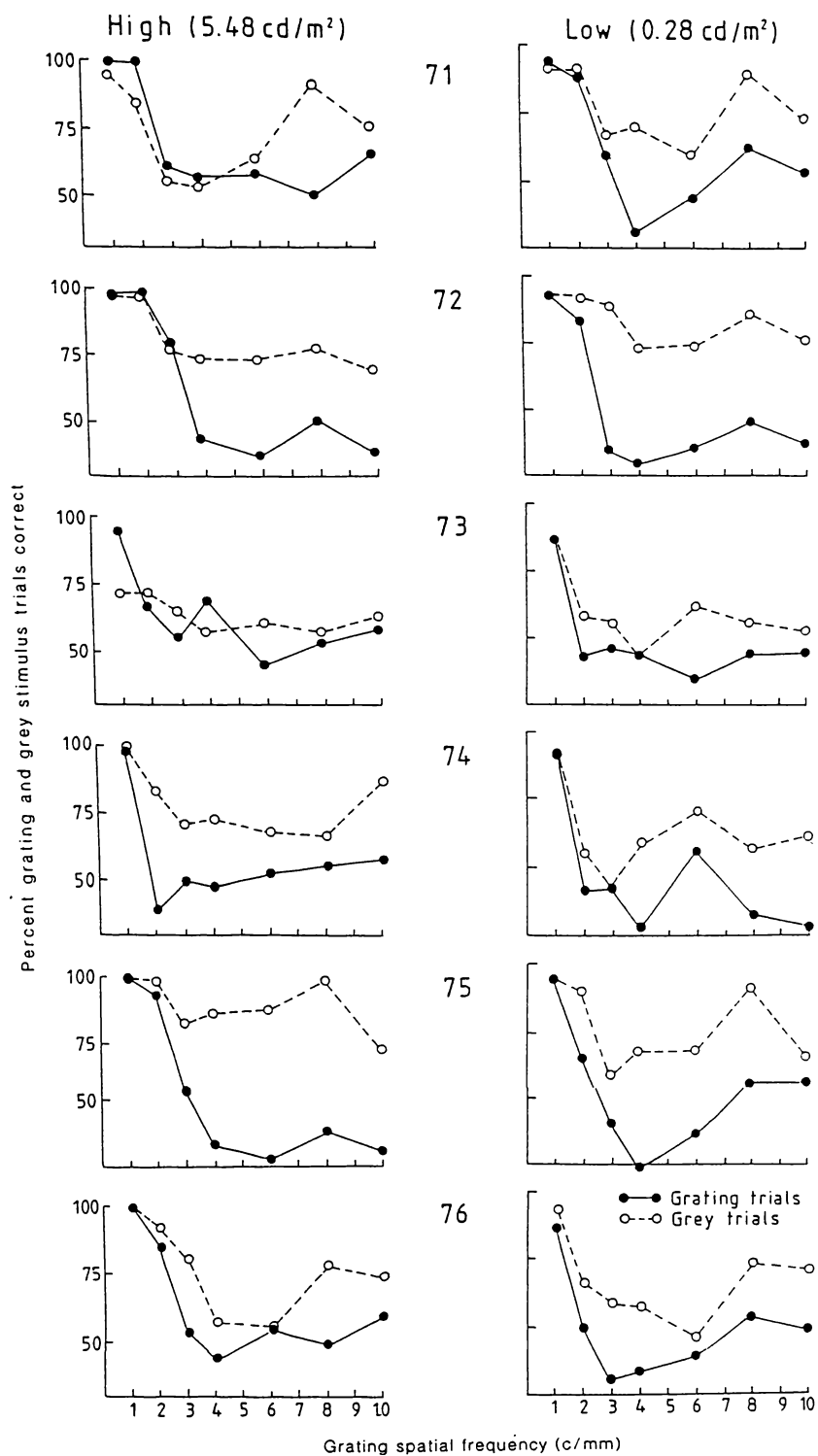
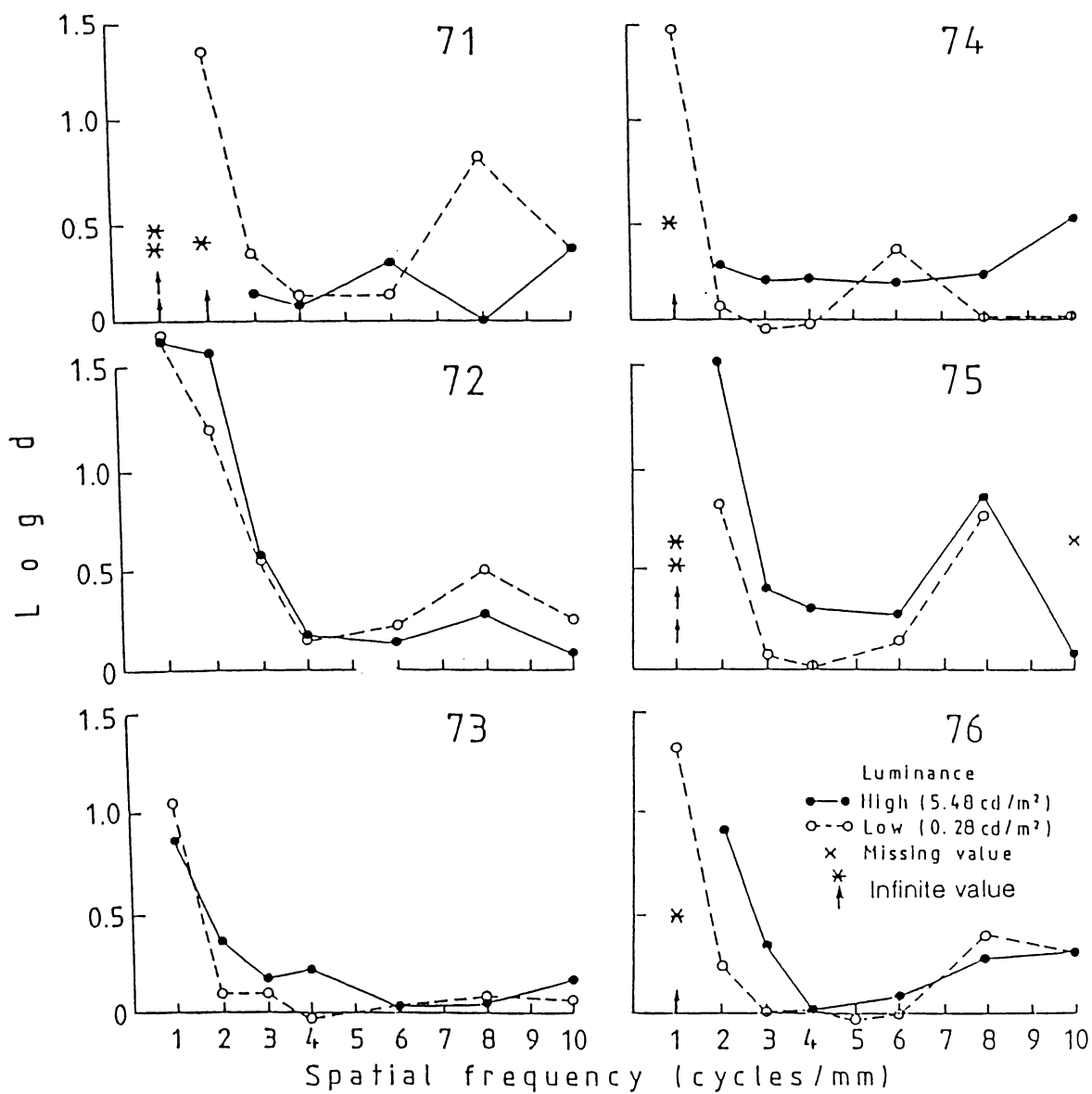


Figure 1.3.3

Figure 1.3.3

Values of $\log d$ plotted as a function of grating spatial frequency, measured in c/mm, for all hens, for the probe series at the high (5.48 cd/m^2) (filled circles joined by a solid line) and the low (0.28 cd/m^2) (unfilled circles joined by a broken line) luminance.



for both probe series. Infinite $\log d$ values were obtained from probes with the coarsest grating, at both luminances, for two hens. Other infinite $\log d$ values were obtained for the probe series at the high luminance only. Generally, greater accuracy was maintained across most grating values when the probe series was conducted using the high luminance, compared to the probe series with the low luminance.

Threshold estimates were obtained by interpolation to determine the spatial frequency of grating which corresponded to a $\log d$ value of 0.48, as for Experiment 1.1. It was not possible to estimate a threshold from two hens' data, 71 and 74, for the probe series at the high luminance, due to infinite $\log d$ values. Threshold estimates are presented in Table 1.3.2 as Criterion 4. These range from 3.4 to 6.4 c/deg for the probe series at the high luminance and from 3.2 to 6.0 c/deg for the probe series at the low luminance. All four estimates from the probe series at the high luminance, were greater than those from the probe series at the low luminance.

The same $\log d$ values in Figure 1.3.3 are plotted in Figure 1.3.4 for two hens only, 73 and 76, for both probe series, and a line has been fitted to the descending portion of the data by the method of least squares. The line is shown in the figures. The slope, intercept, standard error of the estimate and variance accounted for by each line fitted to the descending portion of the data for most hens, for each probe series, is described in Table 1.3.3. All lines fitted were those with the least standard error. The number of data points from the descending portion of the data, described by each line, is also given. It was not possible to fit a line to the data

Figure 1.3.4

Figure 1.3.4

Values of $\log d$ plotted as a function of grating spatial frequency, measured in c/mm, for hens 73 and 76, for the probe series at the high (5.48 cd/m^2) and the low (0.28 cd/m^2) luminance.

A line has been fitted to the descending portion of the data by the method of least squares and is shown in the figures. The parameters of the lines chosen to describe the descending portion of the data from all hens, at the high and low luminance, are given in Table 1.3.3.

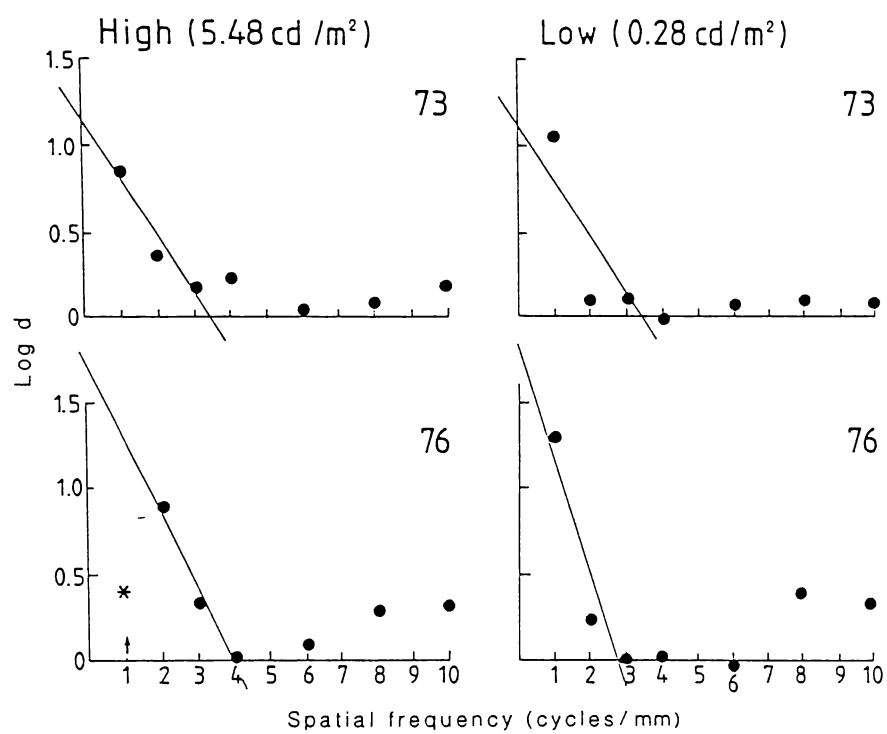


Table 1.3.3

Table 1.3.3

The slopes and the intercepts of the least-squares lines fitted to the values of $\log d$, for all hens, for the probe series at the high (5.48 cd/m^2) and the low (0.28 cd/m^2) luminance. The number of data points (Data Pts.) described by each line, the amounts of variance accounted for by the lines (VAC%) and the standard errors of the estimates (SE) are also given.

Hen	5.48 cd/m^2					0.28 cd/m^2				
	Slope	Intcpt	Data Pts.	VAC%	SE	Slope	Intcpt	Data Pts.	VAC%	SE
71	*	*		*	*	-0.61	2.43	4	74.9	0.33
72	-0.54	2.33	4	85.6	0.28	-0.52	2.18	4	98.4	0.09
73	-0.34	1.15	3	86.4	-.13	-0.32	1.11	4	54.3	0.34
74	*	*		*	*	-0.81	2.15	3	59.6	0.58
75	-0.61	2.57	4	62.3	0.42	-0.40	1.49	4	60.4	0.28
76	-0.44	1.74	4	95.7	0.09	-0.66	1.83	3	75.3	0.35

* line not fitted

for hens 71 and 74 for the probe series at the high luminance because of infinite $\log d$ values.

Threshold estimates were taken from the spatial frequency of grating corresponding to a $\log d$ value of 0.48 as determined from the fitted line (as for Experiment 1.1). These are presented in Table 1.3.2 as Criterion 5. The 95% confidence intervals, as derived from the standard error of the line fit are shown in brackets. The threshold estimates range from 4.0 to 6.8 c/deg for the probe series at the high luminance, and from 3.8 to 6.4 c/deg for the probe series at the low luminance. All estimates from the probe series at the high luminance were greater than those obtained from the probe series at the low luminance.

Figure 1.3.5 presents threshold estimates (c/deg) taken from both the criteria of 75% total trials correct, and 50% grating trials correct, plotted as a function of the low and high luminance. For most hens these show that threshold estimates are greater (indicating more acute vision), for the probe series at the high luminance, compared to those for the probe series at the low luminance.

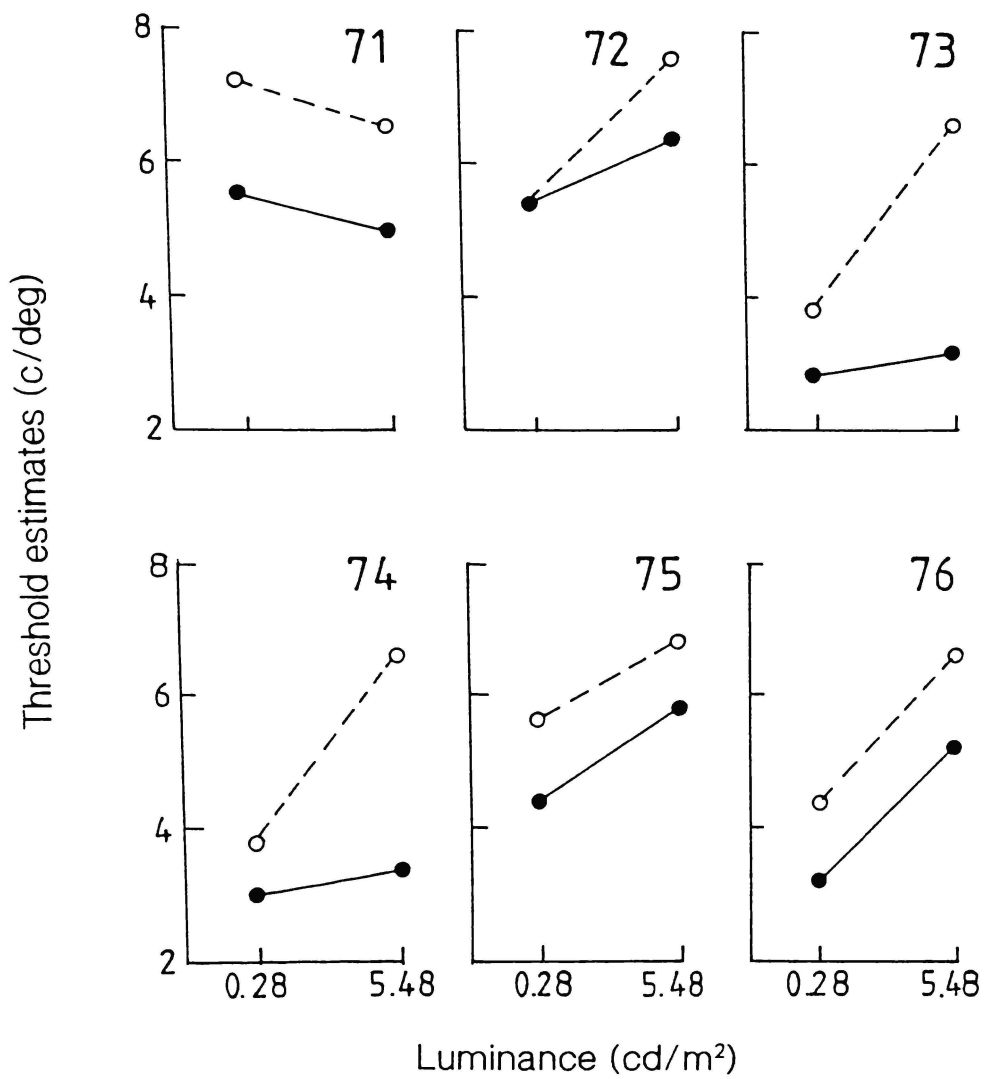
ROC Plots

Figure 1.3.6 shows the proportion of correct responses on grating trials plotted against the proportion of incorrect responses on grey stimulus trials for the two probe series at the high and low luminance. Lines join successive probes. For three hens, 71, 72 and 73, the data path changes from left of the minor diagonal for the probe series at the low luminance value to right of the minor diagonal for the probe series at the high luminance. This indicates a change

Figure 1.3.5

Figure 1.3.5

Estimates of threshold taken from the stimulus values corresponding to 75% total trials correct and 50% grating trials correct, plotted as a function of the low (0.28 cd/m^2) and high (5.48 cd/m^2) luminance, for all hens.

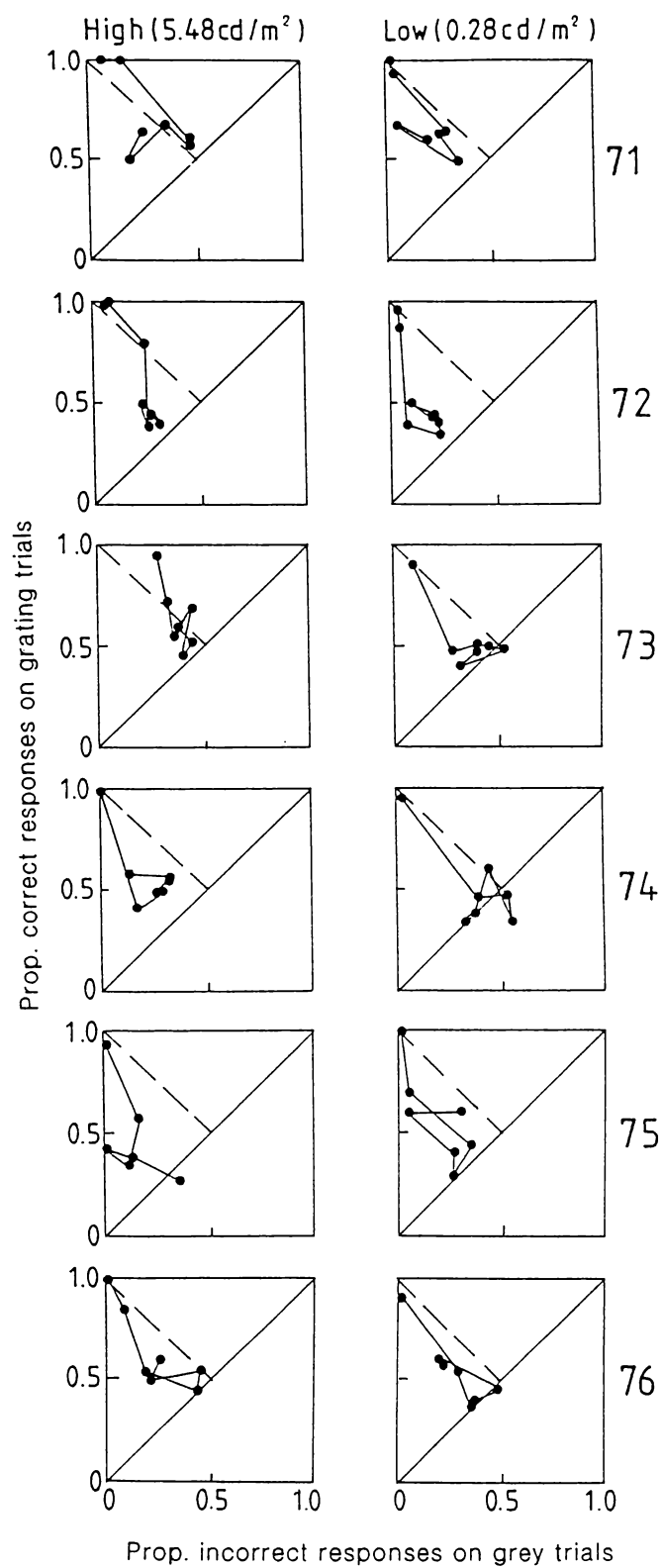


●—● 75% total trials correct
○--○ 50% grating trials correct

Figure 1.3.6

Figure 1.3.6

The proportion of correct responses on grating trials plotted against the proportion of incorrect responses on grey stimulus trials, for all hen for the probe series at the high (5.48 cd/m^2) and the low (0.28 cd/m^2) luminance.



in response bias. These hens responded more to the right key (as though the stimuli were grey) at the low luminance, and responded more to the left key (as though the stimuli were gratings), for some probes at the high luminance. There was little change in bias for the data of the other three hens. That is, for hens 74, 75 and 76 the data path remains to the left of the minor diagonal, indicating a tendency toward right key responding for both probe series. Data for hen 75 showed very strong right biases for both probe series.

Discussion 1.3

Discrimination

Total discriminative performance. Although data obtained at only two luminances were plotted, generally these indicated that discrimination increased as a function of increased luminance. The difference in threshold estimates for both luminances was small. However, with the changes in luminance restricted to a range of less than one log unit, it is perhaps surprising to find such a consistent difference in performance. The low luminance at 0.28 cd/m^2 , is approximately two log units above the "rod-cone" break of the pigeon's adaptation function, as reported by Blough (1956), and is therefore assumed to also be above that level which would require scotopic vision in the hen. That is, it is not likely that the lower visual acuity obtained at this luminance represents a shift from cone to rod vision.

These results are consistent with those of studies in which visual acuity increased as a function of increased luminance, using various species known to have a well developed, functional duplex visual system as does the hen, for example pigeons (Hodos *et al.*, 1976), primates (Spence, 1934), cats (Loop *et al.*, 1981) falcons (Fox *et al.*, 1976) and eagles (Reymond, 1985).

The variability in the unplotted data (Table 1.3.1) obtained at the medium luminance, (3.48 cd/m^2) indicates that the difference between this value and the others (0.28 cd/m^2 and 5.48 cd/m^2) was insufficient to show a consistent change in discriminative performance. The use of a wider range of luminances may have resulted

a greater change in discriminative performance, indicating better visual acuity at higher luminances than those used in the present study. Hodos *et al.* (1976) tested two pigeons at five different luminances ranging over 3 log units, (from $-0.07 \log \text{ cd/m}^2$ to $3.29 \log \text{ cd/m}^2$), in a similar procedure to the present study, and also estimated thresholds from the 75% total correct trial criterion. They reported that pigeons reach their peak acuity of 1.92 min of arc (approx. 15 c/deg) at a luminance of $2.33 \log \text{ cd/m}^2$. At the high luminance in present study, the greatest threshold estimate taken from 75% total trials correct criterion was 6.4 c/deg at 5.48 cd/m^2 (or $0.74 \log \text{ cd/m}^2$). This estimate is close to the estimates obtained for pigeons at a luminance value of $0.42 \log \text{ cd/m}^2$, which was $0.32 \log \text{ cd/m}^2$ dimmer. That is, the hens in the present study required greater luminance than the pigeons in Hodos *et al.*'s study, to provide a similar estimate of visual acuity. Hodos *et al.*'s data are consistent with other studies of pigeons (e.g. Hamilton & Goldstein, 1933; Blough, 1971; Hodos *et al.*, 1985) reporting acuities which exceed those obtained for the hen in the present and previous studies (e.g. Johnson, 1914; Over & Moore, 1981). However, the estimates obtained in the present study are within the range of those obtained by Johnson (1914) at a higher luminance.

Hodos *et al.* (1976) report that pigeons ceased responding at luminances below $-0.07 \log \text{ cd/m}^2$ (0.85 cd/m^2), a higher value than the low luminance (0.28 cd/m^2) used in this study. Although in the present study, responding at the low luminance was generally less accurate than at the high luminance, the rate of responding remained constant. The dimly lit stimulus key may have appeared brighter to the hens in the present study than for the pigeons in the Hodos *et al.*

study however, because in that study the experimental chamber was highly illuminated, whereas in the present study no additional illumination was provided in the chamber.

Discrimination on grating and grey trials. At the high luminance, accuracy on grating trials was generally higher than at the low luminance. Accuracy on grey stimulus trials, was also higher than at the low luminance for three hens. The total performance of only one hen, 71, provided a greater threshold estimate at the low luminance. This resulted from the contribution of greater accuracy on grey trials for the probe series with the low luminance, compared to the probe series with the high luminance. For this hen, it appears that increased right key response bias has resulted in a greater estimate of threshold. A measure of discrimination such as $\log d$ would have provided an unbiased estimate of threshold which may have been greater at the high luminance. However, due to infinite $\log d$ values at the high luminance, no threshold estimates could be determined with this measure, for this hen.

Generally, the discrepancy between accuracy on grating and grey stimulus trials, found at higher sample-key response requirements in the previous study (Experiment 1.2) were replicated in the present results. That is, as gratings became finer, accuracy for grey stimuli was much higher than for gratings. This type of response distribution therefore, appears to be a function of the higher response requirement (FR10).

In the previous study, although discriminative performance improved with some increased response requirements, resulting in

greater threshold estimates than those obtained with FR1, it could not have been the result of increased discriminability of the stimuli, and the increased accuracy was not maintained upon subsequent return to FR1. It was suggested that when response requirements were increased, higher accuracy at coarser gratings, with increased response requirements, resulted from an increase both in effort and in the probability of reinforcement, and that the improved total performance at finer grating values resulted from the higher maintenance of accuracy on grey trials. In the present study, which employed a response requirement of FR10, the improvement in discriminative performance at the high, compared to the low luminance was a result of increased discriminability of the stimuli. If, as previously suggested, the discriminative performance would further improve at an even higher luminance than that used in this study, then it may be possible to obtain similar results using a single-response requirement to the sample key (FR1) and a higher luminance. That is, it may be possible to obtain various degrees of discriminative performance by manipulation of these two parameters, the sample key response requirement and the luminance.

Response bias

For three hens, response bias changed from left, at the high luminance to right at the low luminance. This indicates that they responded more as though the stimuli were grey at the low luminance, and more as though the stimuli were gratings at the high luminance. The change in response bias occurred only at coarser gratings. This change in bias in the condition with the low luminance (subsequent to the condition with the high luminance), may have been a result of loss of discriminability of the gratings (i.e. they were perceived as

grey), compared to the increased discriminability at the high luminance.

Generally, response bias was constant at all stimulus values, but was greater at the low luminance. Hodos *et al.* (1976) reported that, in their results, there was no consistent relation between response bias and luminance, and that response biases were greater at the coarsest gratings. They plotted percentage bias as a function of the spatial frequency of gratings with luminance as a parameter, and reported zero biases at the finest gratings. This seemed surprising, as they used an uncontrolled reinforcement procedure which allows the ratio of reinforcers for the two alternatives to vary with the animals' behaviour. That is, such a procedure which does not control the ratio of reinforcers between the two alternatives (such as the controlled reinforcement procedure used in the present study), may allow the generation of extreme response biases, especially when stimuli are indiscriminable, as at high spatial frequency of gratings, and low luminance. However, when McCarthy (1983) reanalysed their data, using the estimate of response bias, $\log c$, she reported a large degree of bias at finer gratings, and when data were plotted as a function of luminance, extreme biases were shown to have developed at the lowest luminance for both birds at all grating values. Hodos' (1970) percentage bias measure and the Davison and Tustin (1978) log response bias measure therefore, were shown to provide quite different estimates of bias. Log estimates of response bias (e.g. estimates of $\log c$) however, cannot be plotted when the values become infinite. For the purposes of the present studies, therefore, the ROC plots provide a useful description of changes in response bias at successive probe values.

In the present study the discriminability of the stimuli was varied by changing the luminance. Results show an improved total performance at the high luminance compared to the low luminance, in a similar way that the higher FR response requirements improved performance in Experiment 1.2. Similarly, the threshold estimates in the present study increased, reflecting the improved discriminative performance at the high luminance. Although the overall analyses show similar results for the two studies, finer grain analysis (i.e. separate grating and grey trial accuracy) provides evidence that different processes were involved. That is, where improvement in total performance in Experiment 1.2 at finer gratings resulted from increased response bias, and maintenance of grey stimulus trial accuracy, in the present study improved performance at finer gratings occurred on both trial types, and appears to have resulted instead from greater discriminability of these previously assumed indiscriminable stimulus values. Because of the limited range of luminances studied, a need for further research with a much greater range of luminances is indicated.

EXPERIMENT 1.4

Although data from Experiment 1.2 indicated that the hens generally improved their discriminative performance during most conditions where multiple responses to the sample stimulus were required, they did not maintain this level of accuracy upon return to a single response requirement. In Experiment 1.3 generally, discriminative performance was more accurate at the high, compared to the low luminance. In both experiments the improved discriminative performance resulted in greater threshold estimates, indicating more acute vision.

During preliminary training for Experiment 1.1, the hens were initially trained with a grating stimulus of 2 c/mm. This was later changed to a grating stimulus of 1 c/mm in an attempt to improve accuracy prior to commencement of probes at finer gratings. Practice with a grating of 1 c/mm improved discriminative performance at that grating value, following acquisition of the discrimination task. Therefore, it is possible that extensive practice on an even finer grating may improve discrimination at that stimulus value.

There is some reference, in the literature, to the further improvement in measurements of animal visual acuity as a result of practice, following acquisition. For example, when Jacobson, Franklin and McDonald (1976) studied visual acuity in cats, using a punishment procedure, they reported shallow slopes of psychometric functions unlike steep sloped curves typical of human subjects. They suggest that a possible explanation for the shape of the curves is that performance improved as testing proceeded even though it was

apparently stable when testing began. This notion was supported when discriminative performance with gratings of 6 c/deg and finer had increased to nearly 100% accuracy upon their re-presentation as performance checks, in the later months of testing. Furthermore, the animals demonstrated detection of gratings which had previously been below the 50% accuracy threshold criterion (i.e. previously indiscriminable stimuli). Mitchell, Giffin, Wilkinson, Anderson and Smith (1976), employing jumping stand apparatus in a simultaneous forced-choice discrimination task, report that consecutive estimates of acuity for young cats improved with repetition, even though stability had apparently been reached. Unlike the study by Jacobson *et al.* (1976) however, these estimates improved within the same testing session.

In the present series of studies, the hens were exposed to the training stimulus value for approximately 150 trials each session for about 14 to 18 sessions. In comparison, they were presented with gratings of various spatial frequencies on probe sessions for the one session only. Therefore, if discrimination is an increased function of the number of trials on which the subject is exposed to a particular stimulus value, then training to stability with a finer grating may be expected to increase discrimination at that stimulus value. And if this should occur, then this may cast doubts on the utility of a single probe session as a valid indicator of optimal performance at that stimulus value.

The purpose of the present study was to determine
(a) whether hens could learn to discriminate better with prolonged practice with a grating of higher spatial frequency than had been used

for training in the previous studies,

(b) whether any improvement was extended to gratings of even higher spatial frequency, resulting in greater estimates of thresholds, and
(c) whether probing with a grating at a particular stimulus value for one session only, is a valid indicator of hens' stable performance on a grating of that spatial frequency.

Method 1.4

Subjects and Apparatus

The six hens from the three previous studies served. The apparatus was the same as that used for the previous studies. The luminance of the sample key was maintained at 5.48 cd/m².

Procedure

The procedure used was similar to that of Experiment 1.3. The response requirement to the sample key was maintained at FR10. A controlled reinforcement procedure was used and the reinforcement schedule was VI 30 s, as for the previous studies. The hens were trained to both an accuracy and a stability criterion, as for the previous studies. The training grating stimuli was changed, however, and measured 2 c/mm in spatial frequency. Probe sessions began when the hens had reached both the accuracy and stability criteria, as for the previous studies. The first probe session involved presentation of the coarser grating stimuli, measuring 1 c/mm in spatial frequency. The remaining probes were with grating stimuli of increasing spatial frequency, that is a descending series of probes as conducted for the previous studies. Data were collected as for the previous studies.

Results 1.4

Figure 1.4.1 shows the percentages of total trials correct as a function of grating spatial frequency, measured in c/mm, following training with a 2 c/mm grating stimulus. Data from Exp 1.3, at the same luminance, following training on a 1 c/mm grating, are included and shown as open circles joined by a broken line, in each of the figures, for comparison. Probes at a grating value of 2 c/mm resulted in a slightly more accurate performance for four hens following training with a 2 c/mm grating, compared to probes following training with a 1 c/mm grating. For hen 74, total trial accuracy increased from 62% following training on 1 c/mm gratings, to 90% following training on 2 c/mm gratings.

Table 1.4.1 presents threshold estimates for all hens, taken from the stimulus value corresponding to 75% of total trials correct, for the present study. Threshold estimates from the data from Experiment 1.3 are also shown for comparison. For four hens, estimates are greater for the probe series following training with the grating value of 2 c/mm than for the probe series following training with the 1 c/mm grating value. For hen 72 estimates were greater for the probe series following training with the grating value of 1 c/mm, and for one hen, 76, the estimates taken from both probe series were the same. In summary, no consistent differences were found across the two probe series.

Figure 1.4.2 shows the mean and range of the percentages of total trials correct for the last five days' training with the 2 c/mm grating, compared to probes with gratings of 2 c/mm from the present

Figure 1.4.1

Figure 1.4.1

The percentages of total trials correct, plotted as a function of grating spatial frequency, measured in c/mm, for all hens, following training with a 2 c/mm grating stimulus (filled circles and a solid line). Data from Experiment 1.3, following training with a 1 c/mm grating are presented in the figures as unfilled circles joined by a broken line.

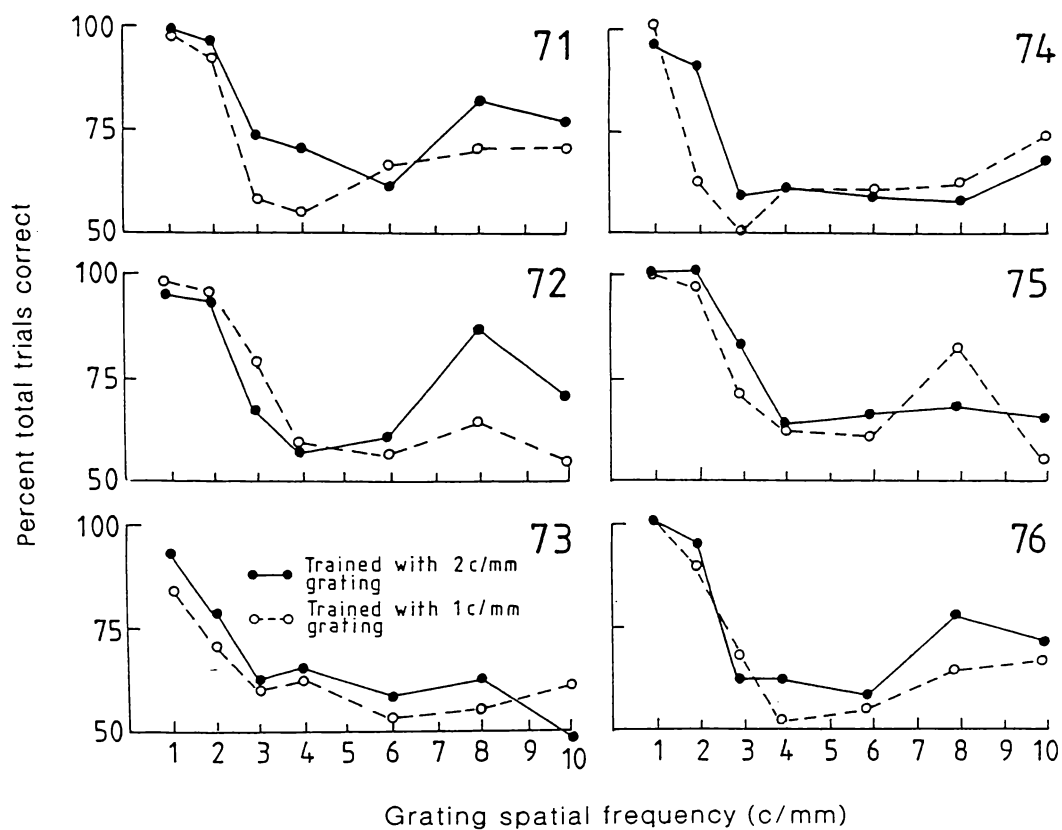


Table 1.4.1

Table 1.4.1

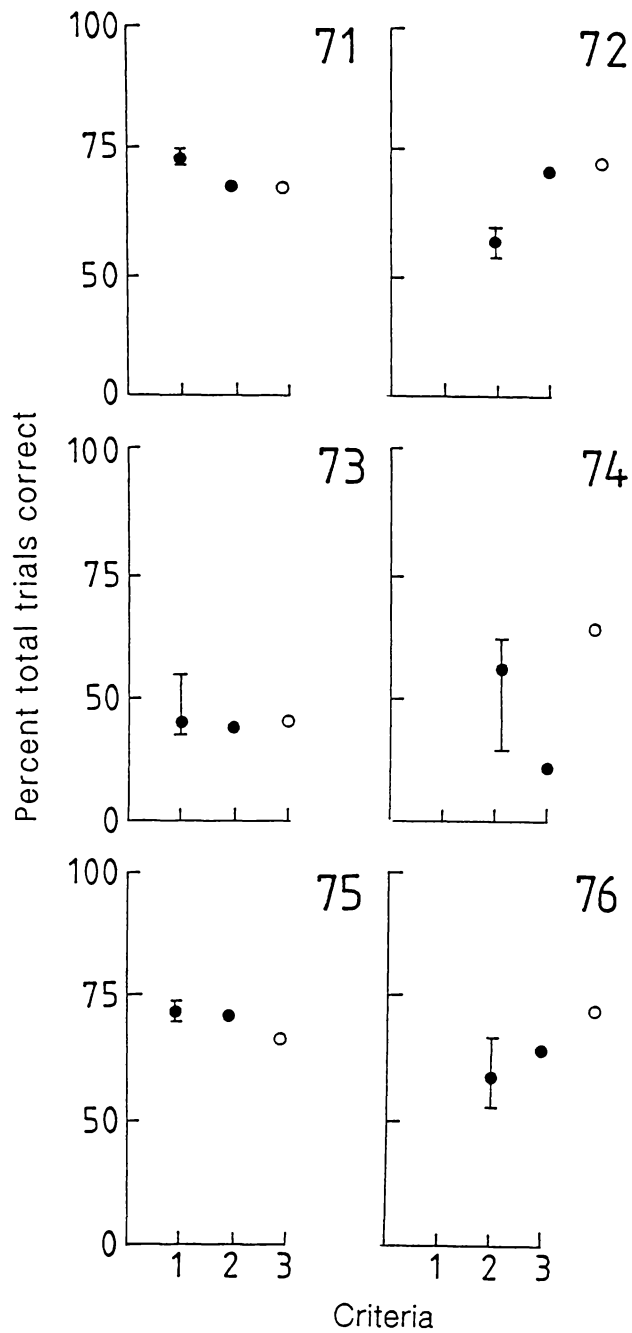
Threshold estimates (c/deg) taken from data plotted as the percentage of total trials correct, at the stimulus value corresponding to 75% total trial accuracy for all hens. Estimates from the data from Experiment 1.3 are also shown for comparison.

Hen	Training grating (c/mm)	Threshold estimate
71	1 (Exp. 1.3)	5.0
	2	5.8
72	1 (Exp. 1.3)	6.4
	2	5.4
73	1 (Exp. 1.3)	3.2
	2	4.4
74	1 (Exp. 1.3)	3.4
	2	5.0
75	1 (Exp. 1.3)	5.8
	2	6.4
76	1 (Exp. 1.3)	5.2
	2	5.2

Figure 1.4.2

Figure 1.4.2

The mean and range of the percentages of total trials correct for the last five days of training with the 2 c/mm grating (1), compared to the percentages of total trials correct for probes with gratings of 2 c/mm from the present study (2), and for the descending probe series from Experiment 1.3 (3), following training with 1 c/mm gratings, for all hens.



- 1: $\bar{x}$ and range of last five training days with 2 c/mm grating
- 2: Probe at 2 c/mm following training with 2 c/mm grating
- 3: Probe at 2 c/mm following training with 1 c/mm grating

study, and for the descending probe series from Experiment 1.3, following training with 1 c/mm gratings, for each hen. Generally, results indicate that data from training to stability on 2 c/mm gratings were not very different from probes at that same stimulus value. For one hen only, 71, the data for the last five days training with the 2 c/mm gratings clearly indicate a superior performance.

- Discussion 1.4

If there had been a consistent improvement in performance at the finer training grating of 2 c/mm, compared to probes at that grating value, whether or not it extended to even finer gratings, the practice effect would have been supported. Generally though, the present results indicate that extensive training on finer gratings did not consistently change discriminative performance or estimates of threshold. That is, once the animal was performing the task accurately, the repeated sessions did not improve performance. Speed of task acquisition however, may be affected by the spatial frequency of the training grating. That is, training to a stability criterion with coarser gratings could be faster because the animal would be likely to reach a higher degree of accuracy than on a finer grating. However, once the task is learned it appears that one session probes at finer gratings produce the same results as training to stability at these grating values. Such findings imply that, as long as stimulus control is maintained, that is some demonstration of criterion accuracy on coarsest gratings, changes in experimental conditions would not require a number of sessions to stability.

The present results are consistent with those of Temple, Foster and Blackman (1983) where the performance accuracy of hens on a number discrimination task did not change, whether conditions were tested as occasional probes within sessions, or throughout a complete session. The results also support the findings of Breen (1987). She studied the discriminative performance of hens in a delayed matching-to-sample procedure at various delays, and found that generally, there was no significant difference between estimates from stable data according to

Davison's (1976) criterion, and the initial estimates. She concluded that repeated performance on delayed-matching-to-sample tasks does not increase performance accuracy, and that therefore the assumption that training past task acquisition improves performance accuracy is not supported.

If probe sessions replicate stable data, as results of the present study and some past research indicate, then this has important implications in animal research, where often acquisition of the psychophysical task alone may be lengthy. For example, Martin and Gordon (1974) report that the tawny owl required nine months of initial training in a forced-choice simultaneous discrimination task. In the present thesis, two criteria were used for probing; a strict mathematically derived stability criterion (Davison, 1976) which required a minimum of 14 sessions, and an accuracy criterion which required that discriminative performance prior to probe sessions be 80% correct on the training stimulus value. Any changes in experimental conditions, such as sample key response requirements (e.g. Experiment 1.2) or luminance (e.g. Experiment 1.3) required that the animals met both of these criteria prior to commencement of probes. McCarthy (1983), employed the same stability criterion when studying the detection of luminance changes in pigeons. In that experiment, discriminative performance was determined under 12 different luminance changes and in two different procedures (a total of 24 experimental conditions) with 150 trials within each session. Training to stability involved a total of 407 sessions (more than 13 months), in addition to the initial stability training prior to the commencement of the first condition in each procedure. It is possible that the same performance obtained following stability in each

condition may have been obtained in single session probes at each of the 12 luminance changes.

Hodos *et al.* (1976), on the other hand, when testing pigeon visual acuity at five different luminances did not train to stability at each luminance, following acquisition. Rather, three sessions only were used at each luminance, starting with training block of 20 trials at the coarsest grating. If accuracy was less than 90%, then it remained as a training session. Otherwise, probes were given on blocks of trials with different values of stimuli presented by the Method of Constant Stimuli. They reported orderly psychometric curves which became more shallow as a function of probes at finer grating values, and higher luminances. That is, no practice effects were evident in the data. This method of post-acquisition training, or variations of this, is typical of many psychophysical studies (e.g. Blough, 1971; 1973; Bloch & Martinoya, 1982). Accuracy criteria across such studies range from 75% (Bloch & Martinoya, 1982) to 90% (Bloom & Berkley, 1977; Hodos *et al.*, 1976). Bloch and Martinoya (1982) also report no general improvement of pigeons' acuity thresholds, subsequent to their attainment of the baseline criterion, and no statistical correlation was obtained between the order of testing and values obtained. Thus their findings support the present results.

It is possible that some variable other than practice may account for improved performance as reported by Jacobson *et al.* (1976) when testing visual acuity in cats. Testing took place over 6 months, and the ages of the cats were not given. If the animals were young, it is possible that some further development of visual acuity may have

occurred during that time. Mitchell *et al.* (1976) report that visual acuity continues to improve in cats to the age of 4-6 months. Alternatively, the use of a punishment procedure may have resulted in a bias towards response suppression, as contingencies for both behaviours (i.e. responding and not responding) were asymmetrical. That is, the animal was punished with shock for not suppressing responses during grating presentation only.

Mitchell *et al.* (1976) reported improved estimates of visual acuity threshold for young kittens, as a function of the session duration. That is, when several thresholds were estimated during a single session, those obtained later in the session were consistently greater (indicating more acute vision) than those obtained early in the session. This may have resulted from the actual discrimination task with the jumping stand. The improved performance and corresponding shorter response latencies may have resulted from the young animals' habituation to the procedure (i.e. jumping a given distance onto one of two stimuli) as a function of session duration, rather than from increased discriminability of the stimuli following repeated presentations.

The results of this present study suggest that, once the hens have learned their task, discriminative performance does not improve with prolonged practice, and that data from a single probe session, as used in the previous experiments, appear to be a valid representation of stable performance.

EXPERIMENT 1.5

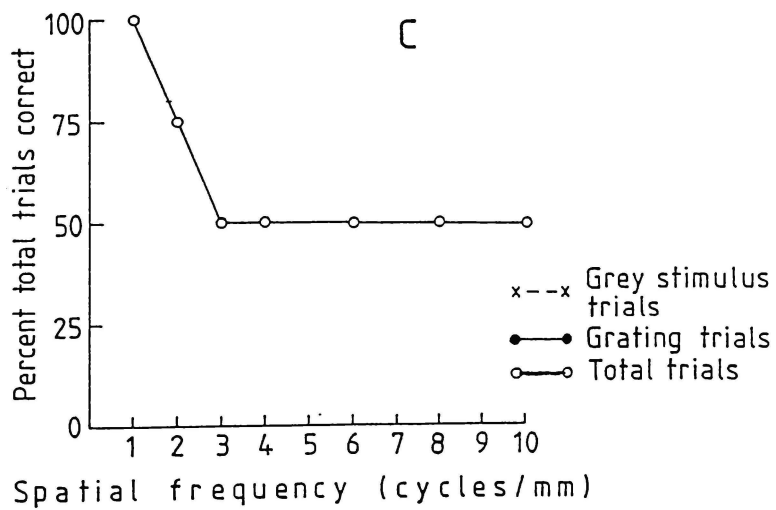
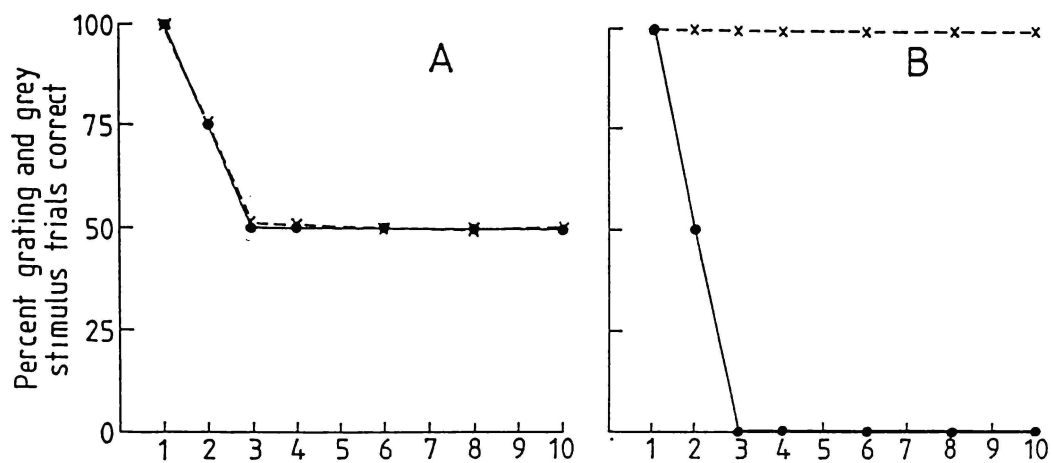
Animals perform on a discrimination task in order to obtain reinforcement. It follows, therefore, that the way in which a reinforcement procedure dispenses the scheduled reinforcers, may well affect the discriminative performance. Typically, psychophysical experiments have scheduled reinforcement for correct responses probabilistically, with all correct responses contributing to the same schedule, or as continuous reinforcement for each correct response (Hodos *et al.*, 1976). This is an uncontrolled reinforcement procedure (McCarthy & Davison, 1980a), which allows reinforcement obtained for left and right key responses to vary with the subject's behaviour. Such a procedure may make it difficult to determine whether the stimulus presentation probability (SPP) or the relative reinforcement rate is effectively controlling behaviour. For example, if, in the present study, the grating stimuli were presented on the majority of trials, and more reinforcers were obtained from correct left key responses, then this could lead to exclusive responding to that key, with little loss of reinforcement. If no responses were emitted on the right key, the animal would experience no consequences, that is, no reinforcement for a correct right key response, to increase the probability of repeating that response in the presence of the grey stimulus. On the other hand, a controlled reinforcement procedure ensures that obtained reinforcer ratios are equal, regardless of changes in the distribution of responses.

Figure 1.5.1 presents diagrams of extreme, but possible patterns of behaviour. Diagrams A and B show the percentage of grating and grey stimulus trials correct, separately plotted as a function of

Figure 1.5.1

Figure 1.5.1

Two hypothetical response distributions of the percentages of grating and grey stimulus trials correct, plotted as a function of grating spatial frequency, measured in c/mm, (Diagrams A and B), and a hypothetical response distribution of the percentages of total trials correct, plotted as a function of grating spatial frequency, measured in c/mm, (Diagram C).



spatial frequency of gratings. The pattern of responding on grating and grey stimulus trials in Diagram A is distinctly different from that in Diagram B. In Diagram A, the discriminative performance (percentages correct) falls equally on both grey and grating trials, whereas in Diagram B the animal's performance remains correct on grey trials, but falls very steeply to 0% correct on grating trials. All performance which includes discriminative responses to two alternatives would necessarily fall within the range of either of these (as previously discussed). Diagram C shows the percentages of total trials correct, plotted as a function of grating spatial frequency. This function is one which could possibly be generated from either performance shown in Diagrams A or B. That is, the different patterns of behaviour shown in Diagrams A and B would generate the same estimates of threshold, when taken from either the 75% or 50% total trials correct criterion.

The distribution of responses in Diagram A may be more likely to occur with a controlled reinforcement procedure. Because the animal is constrained to respond to both alternatives to obtain reinforcement, it is more probable that, as discriminative performance falls, the animal would continue respond to both alternatives. Reinforcers obtained for correct responding on both alternatives would maintain that pattern of responding. That is, as accuracy on grating trials decreases, accuracy on grey trials may also decrease.

Diagram B shows a pattern of behaviour which may be more likely to occur with an uncontrolled reinforcement procedure. This shows that by the 2 c/mm grating value, bias towards right key responding has developed, which increases to exclusivity. Therefore, in such a

hypothetical situation, even though programmed reinforcers to both alternatives may be equal, all reinforcers would be obtained from one alternative, further biasing responding to that alternative. Thus the scheduled equal reinforcer ratios would become irrelevant in a situation where the animal samples only one alternative.

Estimates of threshold taken from the diagrams in Figure 1.5.1 at the stimulus value corresponding to 50% of grating trials correct, would be 3 c/mm and 2 c/mm for the performance in Diagrams A and B respectively. The point taken from the function at 75% grating trials correct corresponds to a stimulus value of 2 c/mm and 1.5 c/mm for performance in Diagrams A and B respectively. Diagram A (showing a pattern of behaviour which may be more likely to occur with the controlled reinforcement procedure) thus produces the greater estimate of threshold (indicating better discrimination). However, if these estimates are taken from the total trial performance (Diagram C), they would be the same for both response distributions shown in Diagrams A and B. This is because the discriminative performance shown in Diagram B would be "inflated" by inclusion of the high level of correct responding on grey trials. That is, analysis of total performance under uncontrolled procedures may indicate a level of grating discrimination that does not actually exist. This is of particular concern when one of the two stimuli is a constant, which, in a visual acuity task for example, is either "neutral" or grey (e.g. Bloom & Berkley, 1977; Hodos *et al.*, 1976) or deemed to be non-resolvable (e.g. Dunstone & Sinclair, 1978; Schusterman & Balliet, 1970).

McCarthy and Davison (1980a) refer to response bias functions as

iso-bias and alloio-bias in controlled and uncontrolled procedures respectively. They state that once relative reinforcement and not relative stimulus frequency is identified as the cause of the response bias in detection experiments, a constant measure of response bias (iso-bias) can be obtained only from a controlled procedure. McCarthy (1983), on investigating the effect of uncontrolled and controlled reinforcement procedures on pigeon's performance in detecting luminance changes, found that the extreme response bias at low luminance levels which developed in the uncontrolled procedure, was absent in the controlled reinforcement procedure. She reported that, although $\log d$ was greater for performance with the uncontrolled, compared to the controlled reinforcement procedure during high discriminability levels, at low discriminability values, the controlled reinforcement procedure provided the higher estimates of $\log d$ and thus produced greater threshold estimates. Her re-analysis of data from the study by Hodos, Leibowitz and Bonbright (1976), which employed an uncontrolled reinforcement procedure for threshold studies, also indicated the presence of increasing response biases at and around threshold.

In the first study of this series (Experiment 1.1) the response distribution of grating and grey stimulus trials was more similar to that of Diagram A, with a similar decrease in discriminative performance for both trial types, as a function of probes with increasingly finer gratings. In Experiment 1.2, when response requirements greater than FR1 were programmed, the data functions for grating and grey trials became more separate than with the single response requirement. It was suggested then, that the increased response requirements seemed to result in an increase of response bias

at lower stimulus discriminability levels. The corresponding grating and grey trial response distributions appeared more indicative of performance under a procedure in which the obtained reinforcer ratio was uncontrolled. It was also suggested however, that some constraints of the controlled reinforcement procedure in effect were evident, because the increased right-key response biases with higher response requirements did not, in any case, lead to exclusivity. This more separate response distribution for grating and grey stimulus trials appears to have been a function of the increased response requirement because it has been maintained in subsequent studies (i.e. Experiments 1.3 and 1.4). However, the degree of constraint exercised by the controlled reinforcement procedure can only be determined by a comparison of grating and grey trial response distributions under both procedures.

The purpose of the present study was to provide uncontrolled reinforcement data for comparison with previous controlled reinforcement data, from Experiment 1.3. If the controlled procedure does indeed provide a constraint to exclusivity at finer grating values, then performance with the uncontrolled procedure should show even greater separation of discriminative performance on grating and grey stimulus trials, and a corresponding increase in right-key response bias, leading to exclusivity. According to the results of McCarthy (1983), discriminative performance at the coarsest gratings could be better for the uncontrolled procedure, (because if a sequence of the same stimulus type is presented, there is no diminishing probability of reinforcers for correct responses to only one alternative). However, because only performance with a controlled procedure remains under joint control of stimulus and the reinforcer,

as stimuli become less discriminable, performance at finer gratings should be more accurate, and resultant threshold estimates should thus be greater with the controlled, than the uncontrolled reinforcement procedure.

Method 1.5

Subjects and Apparatus

The six hens from the previous studies served. The apparatus was the same as that used for the previous studies. The luminance value of the sample key was maintained at 5.48 cd/m².

Procedure

A sample key response requirement of FR10, as used in the two previous studies (Experiment 1.3 and 1.4), was programmed. A single VI 30 s reinforcement schedule was used, as for the previous studies. An uncontrolled reinforcement procedure was programmed. That is, correct detections were reinforced on a single VI schedule and the reinforcements were not scheduled to be equally allotted for correct left and right key responses. Therefore, the hens were not required to respond equally to both alternatives to obtain all scheduled reinforcements.

Training and probe sessions. The hens were trained to an accuracy and stability criterion, as for the previous studies. The grating stimulus value used for training measured 1 c/mm. When both the accuracy and stability criteria had been reached by all hens, after 16 training sessions, they were tested with a descending series of probes, at gratings of increasing spatial frequency, immediately followed by an ascending series of probes. These two probe series were conducted as for Experiment 1.1. The data were collected as for the previous studies.

Results 1.5

Discrimination

Figure 1.5.2 presents the percentages of total trials correct as a function of grating spatial frequency, measured in c/mm, for all hens for the descending and ascending series of probes with the uncontrolled reinforcement procedure. Data from the descending series of probes from Experiment 1.3 at the same luminance value, with a controlled reinforcement procedure, are also presented. These are shown as open circles joined by a broken line, in the figures with the descending probe series, to allow a comparison of both descending series. A comparison of these descending series shows that, for most hens, the percentages of total trials correct was slightly higher for the probes with the uncontrolled procedure, and this higher accuracy was generally maintained at most grating values. There was little consistent difference between performance for the descending and ascending series of probes using the uncontrolled procedure.

The estimates of threshold for each hen, for each probe series with the uncontrolled reinforcement procedure, were determined from that spatial frequency of the grating at which 75% of total trial performance was correct (as in Experiment 1.1). Estimates from the descending probe series with the controlled reinforcement procedure (Experiment 1.3) are included for comparison. Threshold estimates are presented in Table 1.5.1 as Criterion 1, and range from 3.2 to 8.6 c/deg. Four estimates from the descending probe series with the uncontrolled procedure were greater than those obtained with the controlled procedure. Three estimates taken from the ascending series of probes were greater than those obtained from either of the

Figure 1.5.2

Figure 1.5.2

The percentages of total trials correct, plotted as a function of grating spatial frequency, measured in c/mm, for all hens, for the descending and ascending probe series with the uncontrolled reinforcement procedure. Data from Experiment 1.3, from the descending probe series with the controlled reinforcement procedure (Experiment 1.3) are also presented for comparison, and are shown in the figures as unfilled circles joined by a broken line.

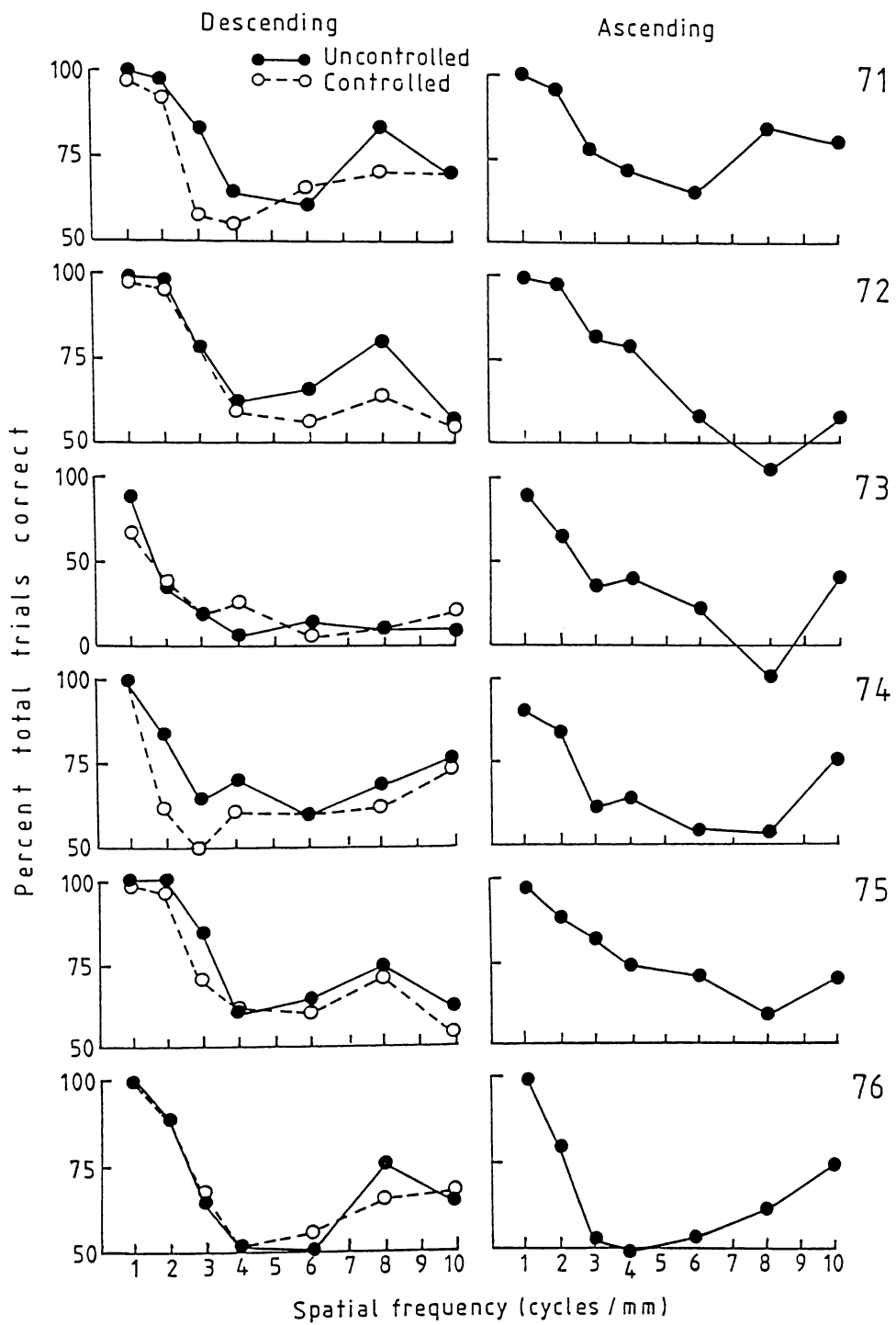


Table 1.5.1

Table 1.5.1

Threshold estimates measured in c/deg, from the various methods of analysis and criteria, for all hens for the descending and ascending series of probes with the uncontrolled reinforcement procedure. Estimates from the descending probe series with the controlled procedure (Experiment 1.3) are also shown, for comparison. Where estimates were determined from the fitted line (Criterion 5), 95% confidence intervals are given in brackets.

Hen	Reinforcement Procedures			
	Threshold Criteria	Contr (Exp 1.3)	Uncontr (Desc)	Uncontr (Asc)
71	1	5.0	6.8	6.8
	2	6.6	5.8	7.8
	3	5.4	5.0	6.2
	4	*	*	9.2
	5	*	*	7.6 (0.8)
72	1	6.4	6.6	8.6
	2	7.6	7.2	10.8
	3	6.2	5.8	8.0
	4	6.4	7.0	9.2
	5	6.8 (0.6)	*	9.0 (0.5)
73	1	3.8	3.4	5.0
	2	6.4	4.2	6.4
	3	3.8	3.0	4.4
	4	3.6	3.6	5.0
	5	4.0 (0.3)	5.0 (0.6)	6.0 (0.2)
74	1	3.2	5.0	4.8
	2	3.6	6.2	5.6
	3	2.8	3.4	4.4
	4	*	*	5.0
	5	*	*	5.0 (0.1)
75	1	5.6	6.8	7.6
	2	6.8	7.2	9.8
	3	5.0	6.2	5.6
	4	5.6	7.2	10.2
	5	6.8 (0.8)	*	6.6 (0.5)
76	1	5.2	5.0	4.2
	2	6.6	5.2	4.4
	3	4.6	4.2	4.0
	4	5.6	5.6	4.6
	5	5.8 (0.2)	6.2 (0.4)	4.4 (0.2)

* Estimate not calculable

CRITERIA: 1 = 75% total trials correct
2 = 50% grating trials correct

3 = 75% grating trials correct

4 = log d value of 0.48

5 = determined from fitted line at a log d value of 0.48

descending series.

Figure 1.5.3a shows the percentages of correct responses made on grating and grey trials separately, plotted as a function of grating spatial frequency, measured in c/mm. These are shown for each probe series. All plots indicate that while accuracy on grating trials decreased, accuracy on grey trials remained high. A comparison of the functions for the two descending series of probes shows that, for most hens, the grating and grey trial functions were more separate for probes with the uncontrolled reinforcement procedure. For hen 75, whose grating and grey trial response distributions were very separate under the controlled procedure (from 30% gratings correct to 90% grey trials correct), there was little room for change. The performance of hen 76 however, showed the greatest change across procedures, from approx 40-50% grating and 55% grey trials correct with the controlled procedure, to 0% grating and 100% grey trials correct for probes at the 6 c/mm grating value, with the uncontrolled reinforcement procedure.

Figure 1.5.3b presents the percentages of correct responses made on grating trials only, plotted as a function of the four coarsest gratings (1, 2, 3 and 4 c/mm) for the two series of probes with the uncontrolled procedure. The figures show that for most hens, the descending function of correct grating trials is steeper for the descending than the ascending probe series. This indicates a somewhat superior discriminative performance for the ascending probes at the four coarsest grating values.

Estimates of threshold based on the grating trials only, were

Figure 1.5.3

Figure 1.5.3a

The percentages of grating and grey stimulus trials correct, plotted separately, as a function of grating spatial frequency, measured in c/mm, for the descending and the ascending probe series with the uncontrolled reinforcement procedure. Data from the descending series of probes with a controlled reinforcement procedure (Experiment 1.3) are also presented for comparison.

A

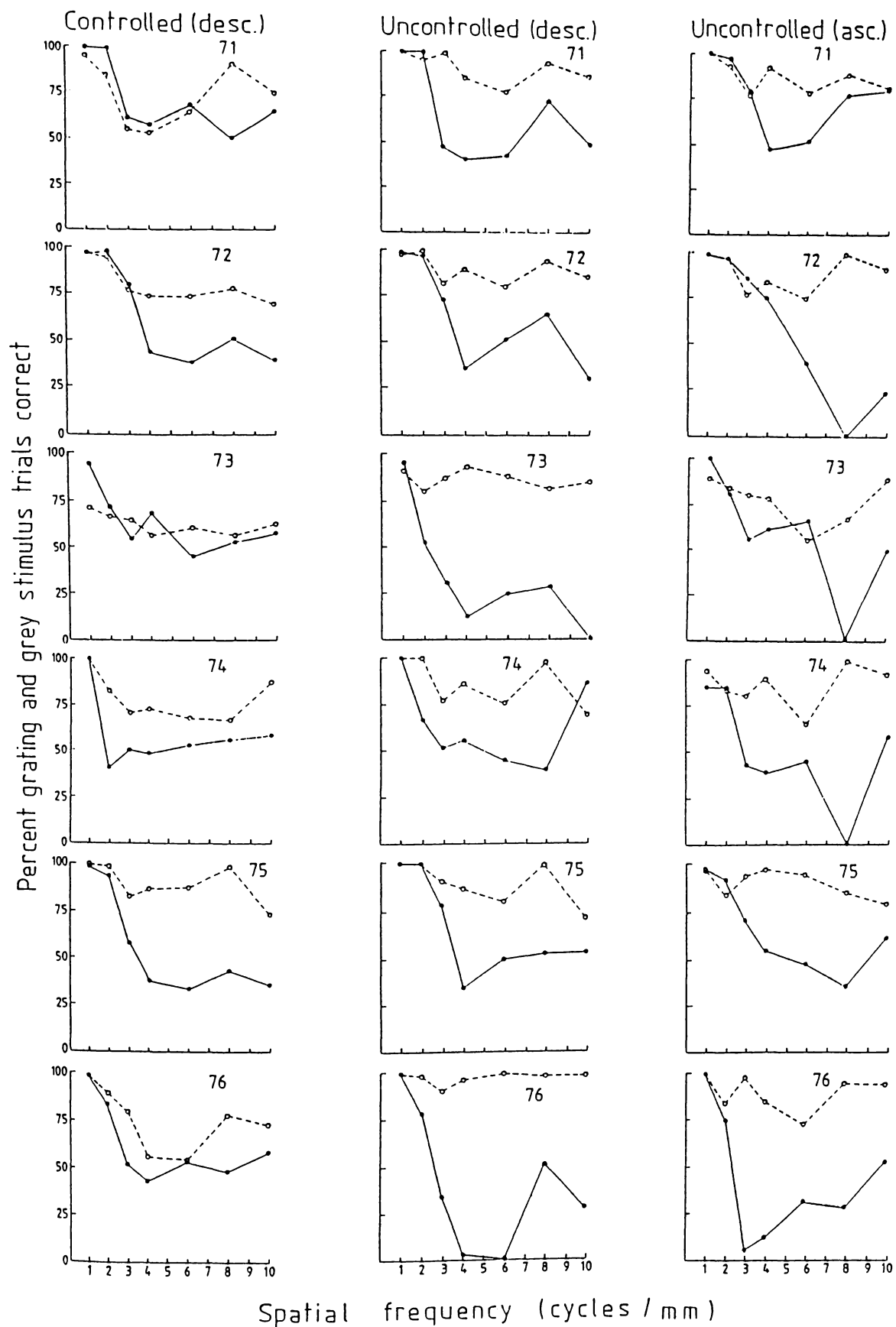
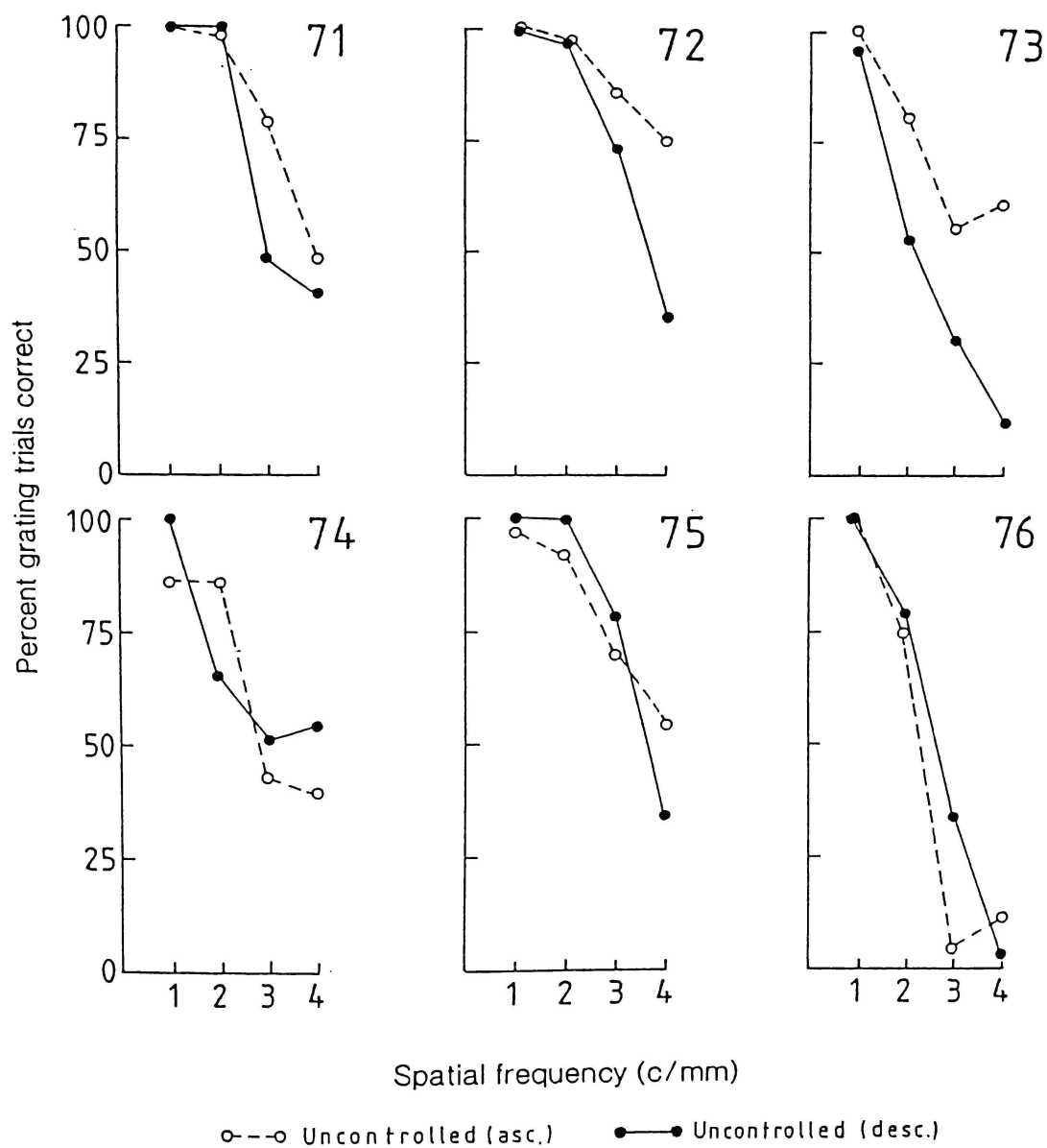


Figure 1.5.3b

The percentages of correct responses made on grating trials only, as a function of the spatial frequency of the four gratings measuring 1, 2, 3 and 4 c/mm, for the descending (filled circles) and ascending (unfilled circles) series of probes with the uncontrolled reinforcement procedure.

B



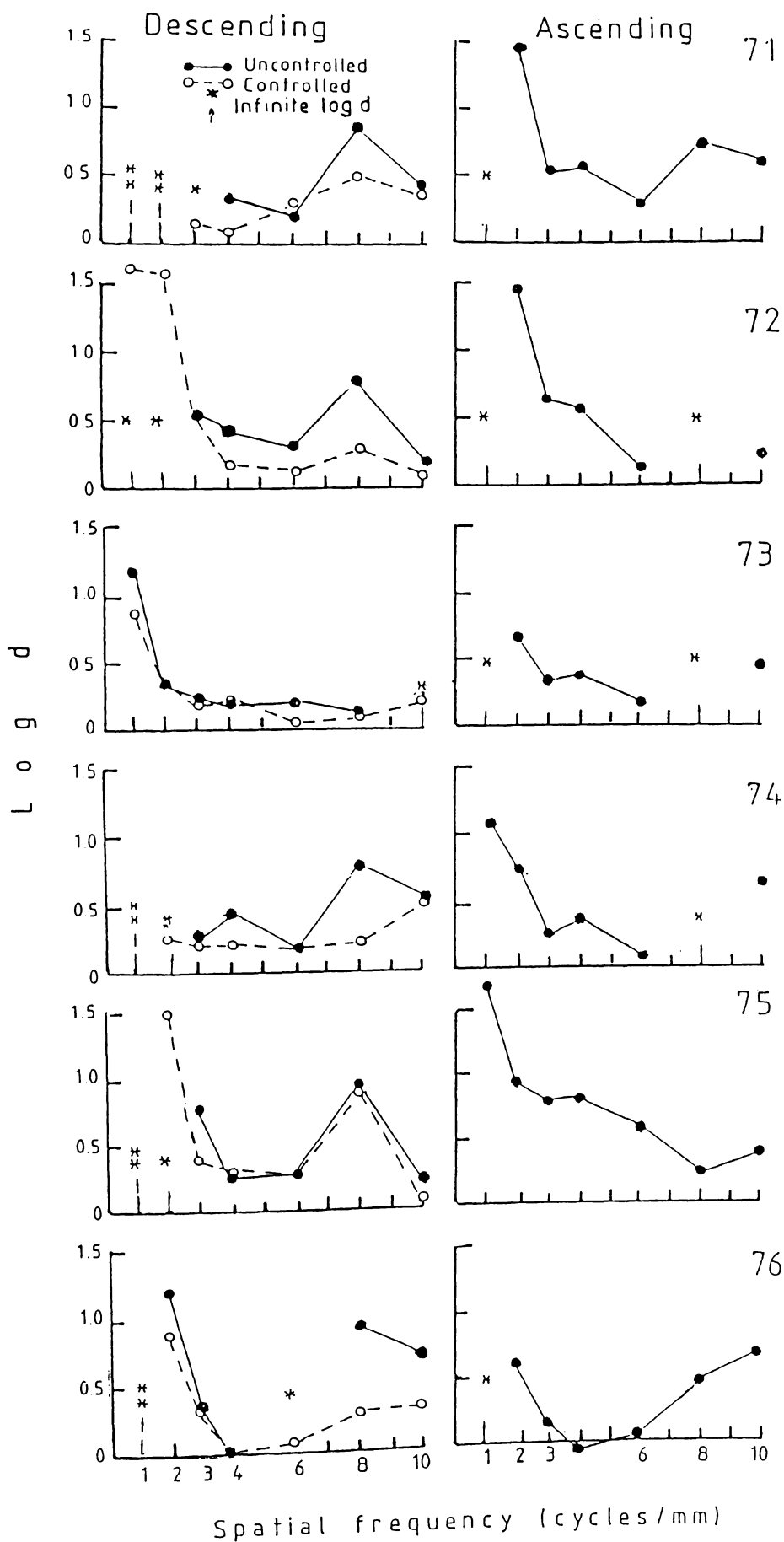
taken from the points at which the plotted functions were 50% correct. These are presented for all hens for each probe series in Table 1.5.1 as Criterion 2. Generally, greater estimates of threshold were taken from the descending series with the controlled, compared to the descending series with the uncontrolled reinforcement procedure. The ascending series of probes with the uncontrolled reinforcement procedure yielded greater estimates for three hens however, than either of the two descending series. Threshold estimates were also obtained from the points at which the plotted functions were 75% correct. These are shown in Table 1.5.1 as Criterion 3. All estimates were slightly lower than those obtained from the 50% grating trial criterion, and similarly show that generally greater estimates were taken from the probes with the controlled reinforcement procedure. The ascending series of probes with the uncontrolled procedure provided greater estimates for four hens than either of the descending series.

Figure 1.5.4 shows $\log d$ values plotted as a function of grating spatial frequency, measured in c/mm, for all hens, for each probe series. These plots show that a larger number of infinite $\log d$ values were obtained for probes with the uncontrolled reinforcement procedure, not only at the coarsest gratings, but also at finer gratings. Those at the finer grating values, which presumably were not discriminable, indicate exclusive responding to one choice alternative. Threshold estimates were obtained by interpolation to determine the spatial frequency of grating which corresponded to a $\log d$ value of 0.48, (as in Experiment 1.1) except where prevented by infinite $\log d$ values. Estimates of threshold are shown on Table 1.5.1 as Criterion 4. Generally these are similar to, or slightly

Figure 1.5.4

Figure 1.5.4

Values of $\log d$ plotted as a function of grating spatial frequency, measured in c/mm, for all hens, for the descending and ascending series of probes with the uncontrolled reinforcement procedure. Data from the descending probe series with the controlled reinforcement procedure (Experiment 1.3) are also presented for comparison, and shown as unfilled circles joined by a broken line.



greater than those obtained from the 75% total trial criterion, ranging from 3.6 to 10.2 c/deg. Three out of a possible four estimates taken from the ascending series of probes with the uncontrolled reinforcement procedure, were greater than those taken from either of the two descending series.

The same $\log d$ values shown in Figure 1.5.4 are plotted in Figure 1.5.5 for the data of two hens only, 73 and 76, for the two probe series with the uncontrolled reinforcement procedure, and a line has been fitted to the descending portion of the data by the method of least squares. The lines are shown in the figures. Table 1.5.2 describes the slope, intercept, standard error and variance accounted for by each line chosen to fit the data from most hens. The number of data points from the descending portion of the data described by the fitted lines, is also given. It was not possible to fit a line to the data from some hens, because of infinite values of $\log d$. All lines chosen to fit the descending portion of the data, except for the line fitted to the ascending probe series for hen 71, were those which contained the least standard error.

To estimate thresholds, the stimulus value corresponding to a $\log d$ value of 0.48 was determined from the fitted lines (as for Experiment 1.1). These estimates are shown on Table 1.5.1 as Criterion 5, and range from 4.0 to 9.0 c/deg. It was possible to compare estimates obtained from the data of two hens only, across the two descending series of probes, and both of these were greater from probes with the uncontrolled reinforcement procedure.

Figure 1.5.6 presents all threshold estimates obtained by the

Figure 1.5.5

Figure 1.5.5

Values of $\log d$ plotted as a function of grating spatial frequency, measured in c/mm, for hens 73 and 76, for the descending and ascending probe series, with the uncontrolled reinforcement procedure.

A line has been fitted to the descending portion of the data by the method of least squares and is shown in the figures. The parameters of the lines chosen to describe the descending portion of the data from all hens, for both probe series with the uncontrolled reinforcement procedure, are given in Table 1.5.2.

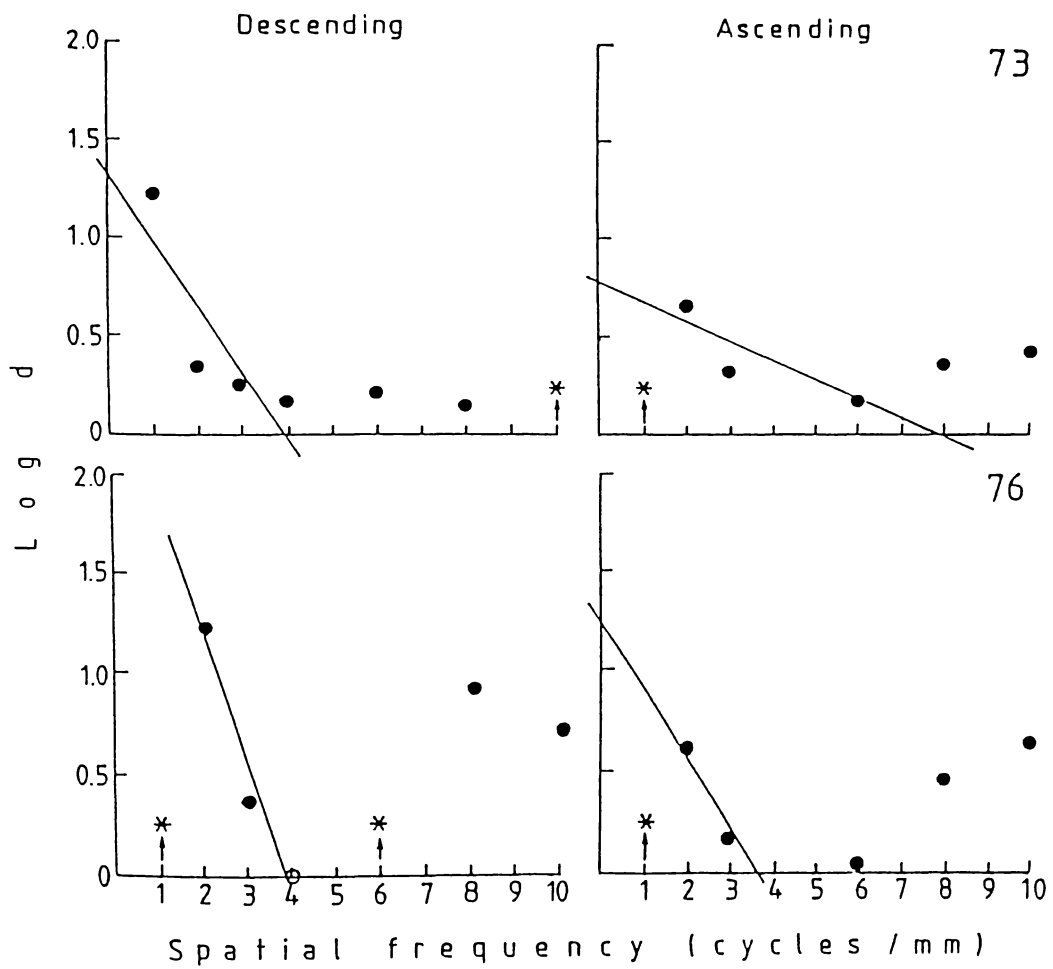


Table 1.5.2

Table 1.5.2

The slopes and the intercepts of the least squares lines fitted to the values of $\log d$ for all hens, for the descending and ascending series of probes with the uncontrolled reinforcement procedure. The number of data points described by each line (Data Pts.), the amounts of variance accounted for by the lines (VAC%) and the standard error of the estimates (SE) are also given.

Descending						Ascending				
Hen	Slope	Intcpt	Data Pts.	VAC%	SE	Slope	Intcpt	Data Pts.	VAC%	SE
71	*	*	*	*	*	x-0.45	2.20	4	46.4	0.38
72	*	*	*	*	*	-0.30	1.83	5	76.6	0.27
73	-0.32	1.29	4	61.0	0.30	-0.10	0.77	5	67.0	0.11
74	*	*	*	*	*	-0.41	1.51	3	97.5	0.06
75	*	*	*	*	*	-0.44	1.99	3	70.3	0.26
76	-0.61	2.36	5	89.4	0.20	-0.33	1.22	4	92.0	0.09

* line not fitted

x not least standard error.

Figure 1.5.6

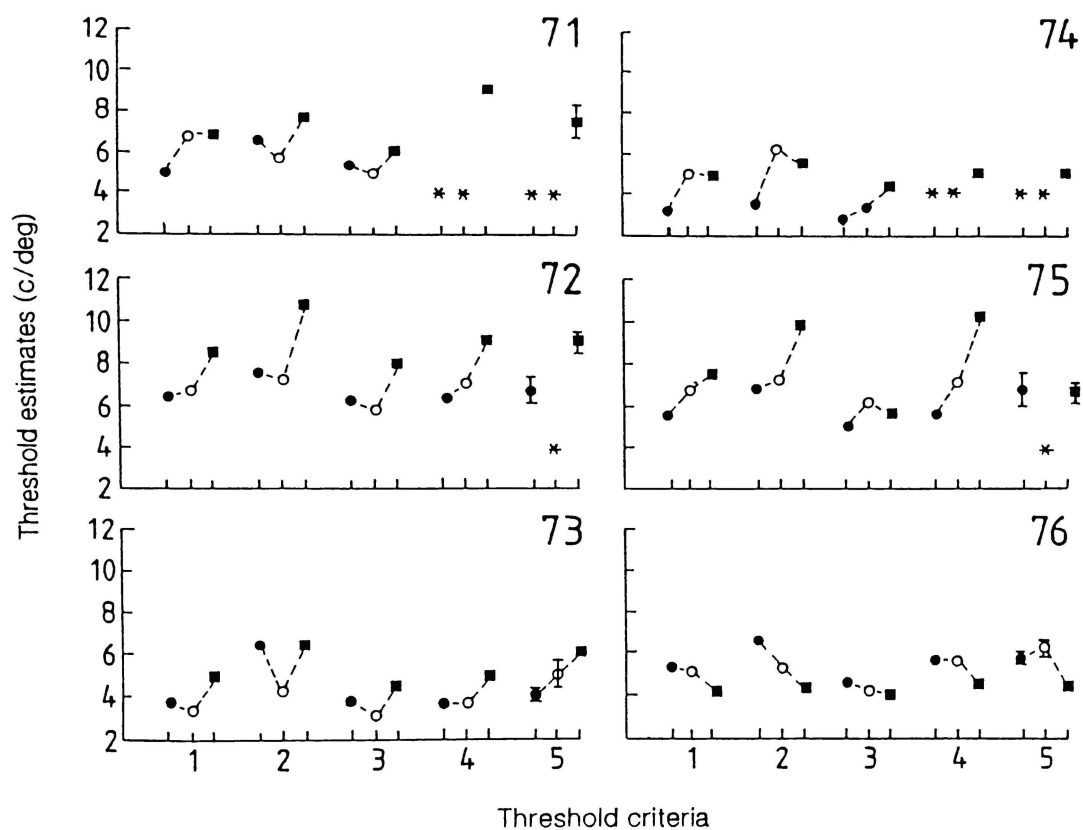
Figure 1.5.6

Threshold estimates taken from each method of analysis using the various threshold criteria.

These estimates were taken from the stimulus value corresponding to:

1. 75% total trial accuracy
2. 50% grating trial accuracy
3. 75% grating trial accuracy
4. $\log d$ value of 0.48
5. $\log d$ value of 0.48, determined from the fitted line

The 95% confidence intervals, determined from the standard error of the line fit, are shown for estimates from the fitted line.



- Controlled (desc.)
- Uncontrolled (desc.)
- Uncontrolled (asc.)
- * Estimate not calculable

- 1 : 75% total trials correct
- 2 : 50% grating trials correct
- 3 : 75% grating trials correct
- 4 : Log d of 0.48
- 5 : From fitted line at log d of 0.48

various methods of analysis, measured in c/deg, plotted as a function of the various threshold criteria. Generally, the greater estimates determined from the analysis of total trial performance, were obtained from the descending series with the uncontrolled, rather than the controlled reinforcement procedure. When estimates were taken from grating trials only however, the controlled procedure generally produced the greater values. This indicates that the higher total trial accuracy for probes with the uncontrolled procedure, compared to the controlled, resulted from the higher accuracy maintained for grey trials, for probes at most grating values. However, estimates from the ascending series of probes were generally greater than either of the two descending series, regardless of the method of analysis, or criteria. This results from the more shallow curve (compared to the curves of the two descending series), indicating a slower decrease in accuracy at probes with the increasingly finer gratings.

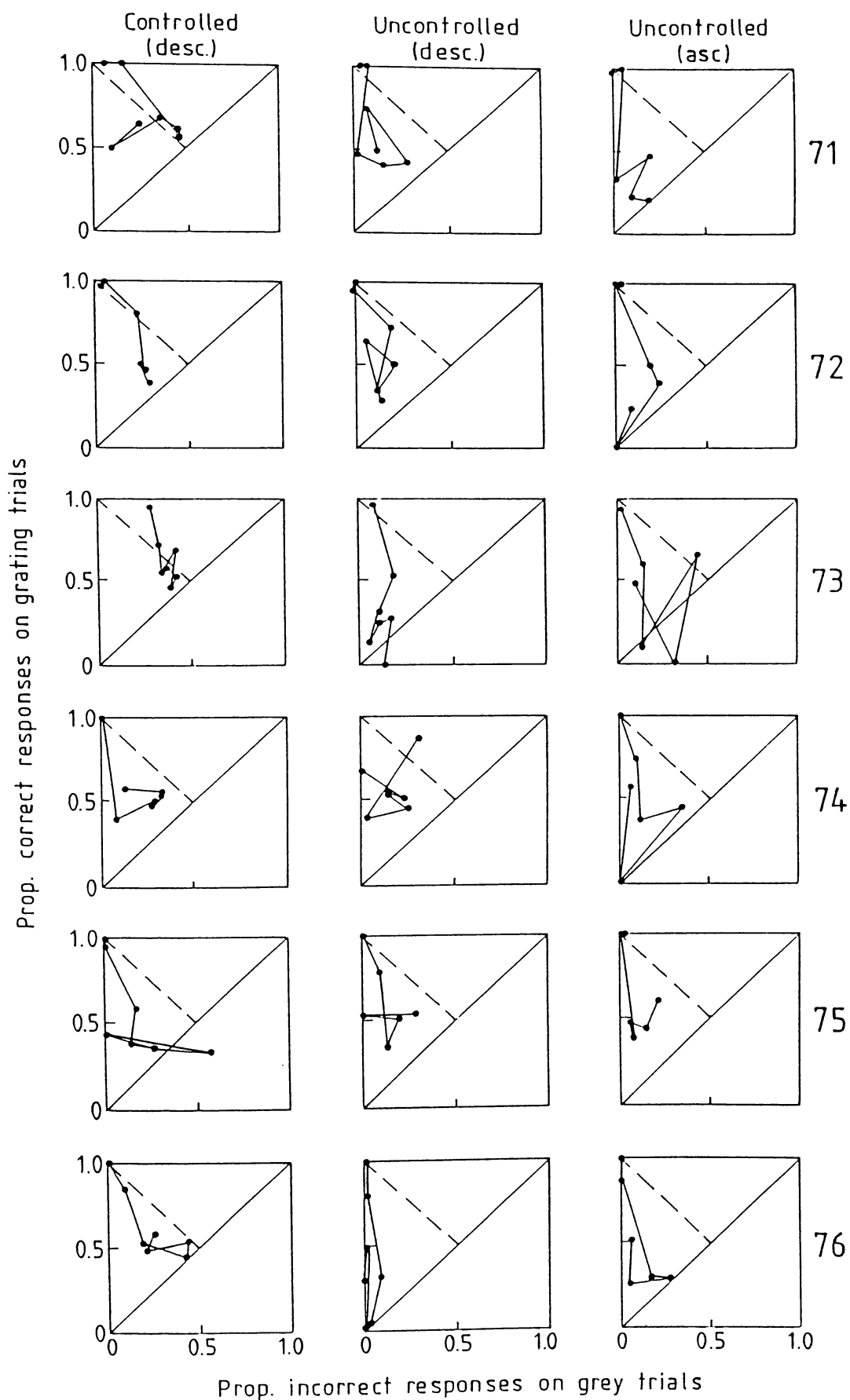
ROC Plots

Figure 1.5.7 shows the proportion of correct responses on grating trials plotted against the proportion of incorrect responses on grey stimulus trials for each probe series. Generally, more extreme bias changes occurred in the probe series with the uncontrolled procedure. All data paths are to the left of the minor diagonal, indicating a tendency to respond more as though most stimuli were grey, and typically these become more extreme at the finer grating values. Hen 75 showed extreme right bias in the controlled reinforcement procedure, and this did not change in the probe series with the uncontrolled reinforcement procedure. There was little difference in response biases between the two probe series with the uncontrolled reinforcement procedure.

Figure 1.5.7

Figure 1.5.7

The proportion of correct responses on grating trials plotted against the proportion of incorrect responses on grey stimulus trials, for all hens, for the descending and ascending series probes with the uncontrolled reinforcement procedure. Data from the descending series of probes with the uncontrolled reinforcement procedure (Experiment 1.3) are also presented, for comparison.



Reinforcement

Figure 1.5.8 shows the proportion of reinforcements delivered for correct responses to the left key, plotted as a function of grating spatial frequency, for all hens, for each probe series. These data indicate that the proportion of reinforcements for correct left and right key responding at probes with the controlled reinforcement procedure were close to equal, while reinforcement obtained for the two probe series with the uncontrolled reinforcement procedure varied widely. For three hens, 72, 73, and 74, at the 8 c/mm grating value, all reinforcements were delivered for correct right key responses. Generally, probes with the uncontrolled reinforcement procedure showed a higher proportion of reinforcements for right key responding, especially as gratings became finer. This reflected the degree of response bias shown in the ROC plots.

Figure 1.5.9 presents the proportion of reinforcements obtained for left key responding, for both probe sessions and training sessions as they occurred, plotted as a function of grating spatial frequency (c/mm), for the descending series with the controlled and uncontrolled reinforcement procedure. Data from probe and training sessions are plotted as separate functions. Data from only two hens, 71 and 76, are plotted. These data are typical of those from the other hens. The figures show that the proportion of reinforcements for left key responding was close to 0.05 for both the training sessions and the probe sessions at all grating values when the controlled reinforcement procedure was used. However, for the probe series with the uncontrolled reinforcement procedure, the proportion of reinforcements for left key responding fell below 0.5 on probe sessions, while

Figure 1.5.8

Figure 1.5.8

Reinforcements for correct responses to the left key on probe sessions. and plotted as a function of grating spatial frequency measured in c/mm, for all hens, for the descending series of probes with the controlled (Experiment 1.3) and uncontrolled reinforcement procedures.

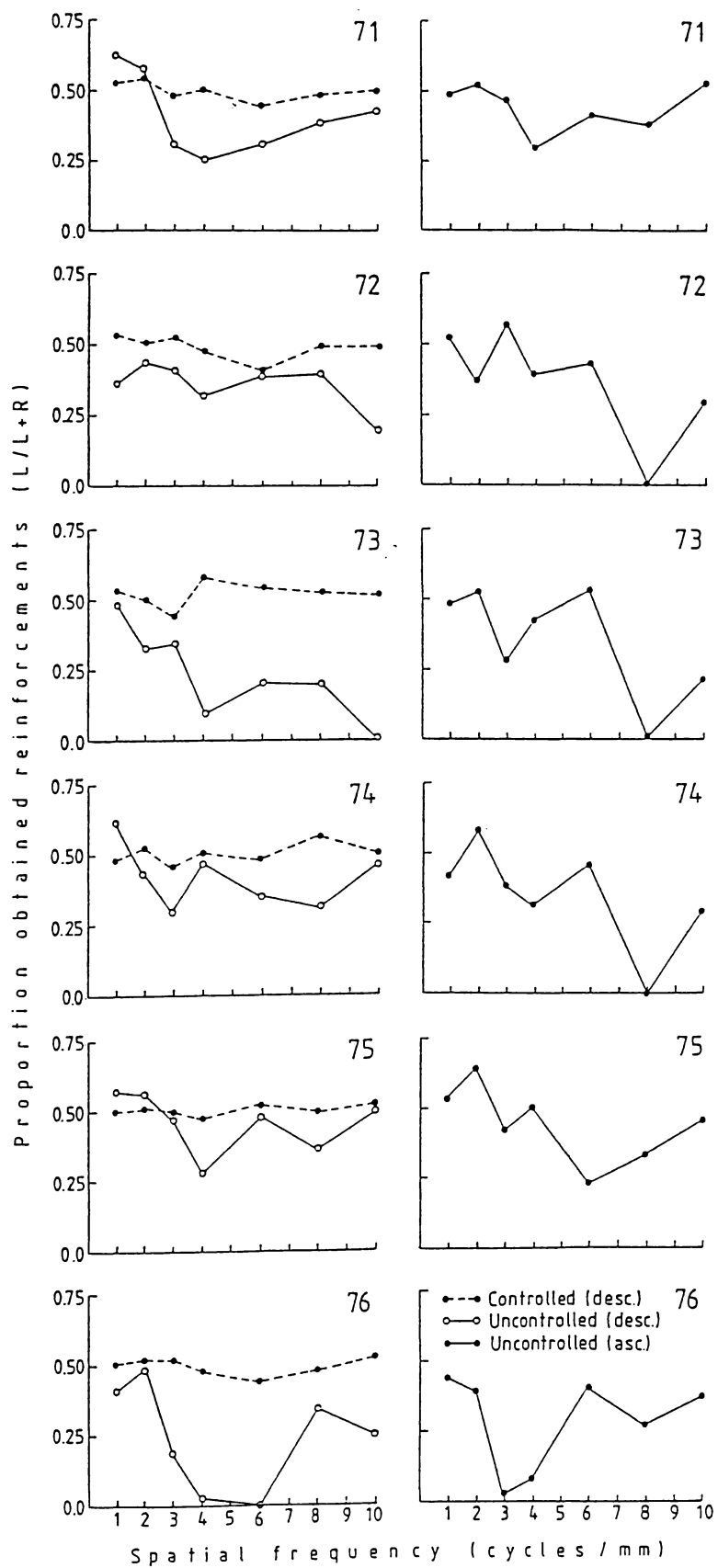
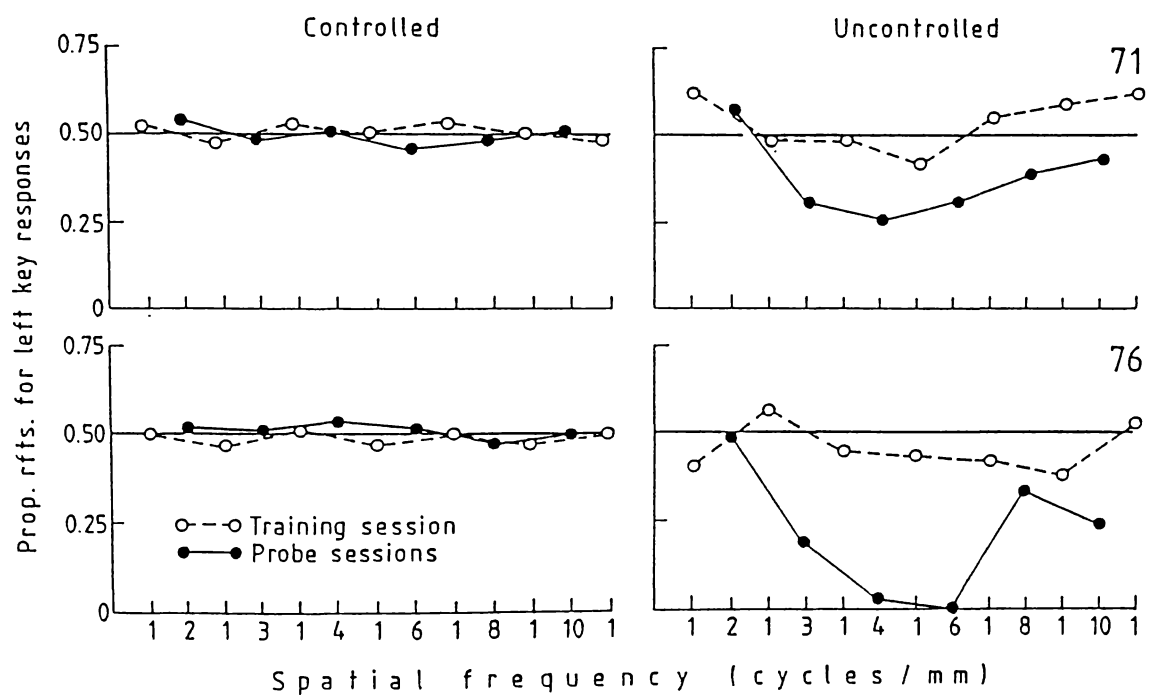


Figure 1.5.9

Figure 1.5.9

The proportion of reinforcements obtained for left key responses, plotted for two hens, 71 and 76, for both probe and training sessions as they occurred, plotted as a function of grating spatial frequency (c/mm), for the descending probe series with the controlled and uncontrolled reinforcement procedure.



remaining close to 0.5 on training sessions. This indicates that, while the hens obtained a close to equal number of reinforcements from both response alternatives on training sessions, a greater proportion of reinforcements were obtained for right key responding on probe sessions, especially as gratings became finer. Thus, the proportion of reinforcements obtained for left key responding was effected both by the value of grating and the type of reinforcement procedure in effect.

Discussion 1.5

Total discriminative performance

Generally, discriminative performance for the descending series, analysed either as percentages of total trials correct or as values of $\log d$, was slightly better with the uncontrolled reinforcement procedure. The slower decrease in discriminative performance with the uncontrolled reinforcement procedure was reflected in generally greater threshold estimates (as measured in c/deg).

Although the higher discriminative performance at the coarsest gratings with the uncontrolled reinforcement procedure is consistent with the findings of McCarthy (1983), the greater estimates of threshold for both series with the uncontrolled procedure are not. In McCarthy's (1983) study, thresholds were estimated by interpolation from a best fit line at a $\log d$ value of 0.00, whereas those for the present experiment were taken from the stimulus values corresponding to a $\log d$ value of 0.48. However, a re-estimate of thresholds from the present data, corresponding to a $\log d$ value of 0.00, still provide greater estimates generally, for performance with the uncontrolled procedure. A comparison of $\log d$ values obtained at stimulus values of 3 c/mm and 4 c/mm, where stimulus discriminability levels have decreased, shows that these were consistently higher for both series with the uncontrolled procedure. This is with the exception of data for only one hen, 76, whose discriminative functions and resultant estimates of threshold were very similar for both descending series. This indicates then that the criterion for estimating threshold does not account for the differences between the present findings and those of McCarthy (1983).

McCarthy's suggestion that increased bias functions at the lower levels of stimulus discriminability result in poorer estimates of threshold, are probably based on previous findings by McCarthy and Davison (1979). In that study also, pigeons were trained to detect luminance differences under a controlled and an uncontrolled reinforcement procedure. They report no difference in discriminative performance with the controlled and uncontrolled performance, and also no difference in the response bias functions under both procedures. However, in spite of the development of greater response biases with the uncontrolled than the controlled procedure in the present study, estimates of threshold for performance under the uncontrolled procedure were generally greater.

In addition, the present results are not consistent with those of McCarthy and Davison (1980a). They also found greater estimates of discriminability with a controlled than an uncontrolled reinforcement procedure, when using a duration discrimination task. A further suggestion by McCarthy and Davison was that the differences in performance under the two procedures might have been the result of differences in the number of responses emitted per reinforcers obtained. That is, the responses per reinforcer were fewer for the controlled procedure. However, when McCarthy (1982) varied responses per reinforcer in a further study in which pigeons detected differences in stimulus duration, she demonstrated empirically that changing the number of responses per reinforcer did not affect discriminability measures. On the other hand, Nevin, Jenkins, Whittaker and Yarensky (1982), training pigeons in a similar temporal discrimination task, reported that the level of discrimination was

positively related to the overall rate of reinforcement.

In Experiment 1.2 (of the present series of studies) the overall rate of responses per reinforcer changed as a function of the increased response requirement to the sample key. Thus, as the response requirement to the sample key increased, the probability of reinforcement for any correct response to the comparison stimuli likewise increased, and, to a certain FR value, accuracy also increased. In the present study, the response requirement (FR10) and the reinforcement schedule were symmetrical across both the controlled and uncontrolled procedures. However, perusal of the data indicates that fewer correct trials per reinforcer were required in the performance with the uncontrolled procedure. That is, the probability of reinforcement for correct trials was actually higher in the performance with the uncontrolled reinforcement procedure, for all hens and all stimulus values. The increase in discriminative performance as a function of increased probability of reinforcements has been well documented in the literature (e.g. Stubbs, 1968; Nevin *et al.*, 1982; Nevin & MacWilliams, 1983) and previously referred to in the discussion of Experiment 1.2. Past research and results of previous studies in the present series thus support the present finding.

McCarthy (1983) states that the higher accuracy obtained by pigeons under the controlled, compared to the uncontrolled reinforcement procedure, was not a result of differences in responses per reinforcers for the two procedures. In her study however, different reinforcement schedules for each procedure may have confounded results. For the uncontrolled procedure a single VI 30

schedule was programmed while for the controlled procedure, VI 45 VI 45 reinforcement schedules were used. The latter would be equivalent to a single VI 22.5 s reinforcement schedule, somewhat richer than that programmed for the uncontrolled reinforcement schedule. No explanation was given as to why a richer reinforcement schedule was used for one procedure. In the present study, equivalent schedules (VI 60 VI 60 and single VI 30) were used for the controlled and uncontrolled procedure, respectively. It would seem that a comparison of performance under two different procedures of reinforcement delivery would necessitate symmetry of the actual reinforcement schedules. Therefore, it is possible that McCarthy's (1983) finding of higher accuracy of performance with the controlled compared to the uncontrolled reinforcement procedure may have been a result of the richer reinforcement schedule programmed for the controlled reinforcement procedure.

Response distributions and response bias. The difference in the grating and grey trial response distributions for most hens under both procedures does to some extent reflect the differences in the hypothetical response distributions shown in Diagrams A and B (Figure 1.5.1), respectively. A comparison of these response distributions for grating and grey stimulus trials for both descending series show that generally there was greater separation of these two functions with the uncontrolled procedure. That is, accuracy was maintained on grey trials while decreasing on grating trials as a function of grating spatial frequency. The psychometric function obtained for hen 76, looked most similar to that of Diagram B (Figure 1.5.1) for the uncontrolled procedure, with development of right key response biases at finer gratings leading to exclusivity. This increase in response

biases in the uncontrolled procedure is consistent with the findings of McCarthy (1983).

In Experiment 1.1 (of the present series of studies) performance for the ascending and descending series of stimulus presentation was compared. Data replicated well for the ascending series, and neither series provided consistently greater estimates of threshold. In the present study however, the ascending series with the uncontrolled procedure generated a better discriminative performance than either of the two descending series. It is puzzling that the grating trial function for the ascending series for some hens, was generally more shallow than that for either of the two descending series. Instead of maintaining higher accuracy on grey trials than on grating trials, some of the hens were more accurate on grating trials. Perhaps this was a series effect. Due to the ascending order of stimulus presentation, for several probe sessions (alternating with training sessions) animals obtained reinforcement for correct responding when stimuli were presumably indiscriminable. Because the animals did not develop exclusive response biases at all stimulus values, (accuracy on grating and grey stimulus trials was not 0% and 100% correct respectively), there must have been trials in which the animal received reinforcers for correct responding on grating trials when the stimuli were indiscriminable. Such feedback could be interpreted as reinforcement for errors. That is, the feedback that the animals received at indiscriminable levels of stimulus values (where it is assumed all gratings were perceived as grey) was that reinforcement was delivered when responding correctly (as though stimuli were grey), and sometimes it was delivered for errors (as though indiscriminable stimuli were gratings). Errors made on grey trials therefore, at more

discriminable stimulus values, may have been result of the earlier ambiguous feedback at the least discriminable stimulus values. Why discriminative performance should be better for the ascending series when an uncontrolled procedure is used, but not when a controlled procedure is in use, is uncertain. A possible explanation is that it results from interaction between a series effect and lack of constraint by the uncontrolled, compared to the controlled reinforcement procedure.

This difference in the response distribution for grating and grey stimulus trials with the uncontrolled procedure may provide an alternative explanation for the better total discriminative performance found in this study, with the uncontrolled procedure. Such a performance may possibly be a result of the types of stimuli employed in the present study, a constant and a variable stimulus. When a variable and a constant stimulus is used, estimates of threshold from total performance may be increased or "inflated" by high accuracy on grey trials. Such a distribution of responses is shown in the present study to be more likely to occur with an uncontrolled reinforcement procedure.

More biases developed in both probe series with the uncontrolled procedure compared to the controlled procedure, at lower levels of stimulus discriminability. This alloio-bias is consistent with that often reported in uncontrolled procedures (e.g. Irwin & Terman, 1970; Hodos *et al.*, 1976; McCarthy, 1983). Although constant bias functions in uncontrolled procedures are not unknown in the literature (e.g. McCarthy & Davison, 1979) they are certainly less common.

Response bias in the controlled procedure was more constant at most grating values. At the finest grating values however, bias also tended to vary, possibly more than would be expected in a controlled procedure. However, unlike the experiments in this present thesis, most studies do not usually continue to probe at stimulus values which are considered indiscriminable. Therefore, there is no typical performance at several indiscriminable stimulus values in the literature against which to compare the present data. The Davison and Tustin (1978) matching model of detection performance predicts that when two stimuli are no longer discriminable (i.e. $S_1 = S_2$) the performance is analogous to performance under concurrent schedules of reinforcement. There was a similar tendency in the data of the previous studies of the series to show more change in response bias at the finest gratings, especially when a response requirement greater than FR1 was programmed to the sample key. It is therefore possible that the changing bias at lowest stimulus values in the controlled procedure may be typical of performance at indiscriminable stimulus values when multiple responses to the sample are required.

In the uncontrolled procedure, where animals are not penalized for responding exclusively to one alternative, it is perhaps surprising that, in the present study, more hens did not develop biases leading to exclusivity at most of the finer grating values. For example, when hen 75 developed response biases during training with the coarsest grating stimulus, she was penalized by receiving about 10 reinforcements fewer than for a comparable performance with the uncontrolled procedure. Perhaps this could be accounted for by their long past history of responding to both alternatives even at indiscriminable stimulus values. Although McCarthy's (1983)

reanalysis of the data from the study by Hodos *et al.* (1976), in which they used an uncontrolled procedure, also revealed increased biases at lower stimulus values, responding there, too, was never exclusive to one alternative.

Conclusion

Comparison of performance under controlled and uncontrolled reinforcement procedures shows that discriminative performance is indeed a function of the manner in which reinforcers are delivered. If a reinforcement procedure which generates a total performance providing greater estimates of threshold is the criterion of a better procedure, then results of this study indicate that the uncontrolled is superior to the controlled reinforcement procedure. However, if the criterion is a procedure which minimizes response biases and thereby maximizes control by the stimulus, then the best procedure is necessarily one which controls the relative reinforcer ratio for responding to both alternatives. The problem of stimulus control and response biases at lower stimulus discriminability is one which has persisted throughout the past decades of studies of animal sensory functions (Blough & Blough, 1977). Any procedure which can thus minimize these has to be superior to one which does not.

Not only the method of reinforcer delivery, but the stimulus types employed should be considered. Many psychophysical studies employ a constant and variable stimulus (e.g. Hodos *et al.*, 1976; Bloom & Berkley, 1977) as used for the present series of studies. The use of these stimulus types may actually encourage the development of biases as stimuli become less discriminable. That is, at lower levels of stimulus discriminability there is a greater tendency to confuse

the grating with the constant stimulus, and respond accordingly, than *vice versa*. However, if two variable gratings are used, differing only in orientation (e.g. Van Hof, 1967; Hodos & Yolen, 1976; Vaney, 1980), performance may be expected to be as incorrect on one alternative as on the other. Although the use of pairs of variable gratings may not prevent biases (e. g. Johnson, 1914) such stimuli may be less likely to encourage them. Studies using a constant and variable stimulus mainly analyse total performance only (e.g. Hodos *et al.*, 1976). Terman's (1970) study of auditory discrimination in rats is one of the few using a variable and a constant stimulus, which included analysis of the two component response distributions. When a constant and a variable stimulus are employed it is important to determine the contribution of each trial type to the total discriminative performance.

Perhaps estimates of threshold obtained from discriminative performance with a constant and a variable stimulus, often referred to as "grating thresholds" may be more appropriately termed "total performance thresholds" as compared to those estimates taken from discriminative performance on grating trials alone. Because discriminative performance on grating trials is not independent of discriminative performance on grey trials when constant and variable stimuli are used, it is questionable as to whether these would be comparable to estimates using only one response alternative (e.g. Bloch & Martinoya, 1982). Perhaps then, it may be that only those estimates taken from total performance on two variable gratings can validly be termed "grating thresholds".

In Experiments 1.2 and 1.3 discriminative performance was changed

by varying firstly the response requirement and secondly the luminance. In the present experiment total performance improved with an uncontrolled reinforcement procedure which did not penalize increased response bias. Fine-grain analysis however, indicated that grating accuracy was actually better maintained with a procedure which controls the reinforcer-ratio, thereby discouraging increases of response bias.

EXPERIMENT 2.1

The procedure employed for Experiments 1.1 to 1.5 was a conditional discrimination in which the correct spatial response alternative (i.e. left or right key), was conditional upon the presentation of a particular sample (i.e. grating or grey stimulus). The literature indicates that other "symbolic" matching-to-sample procedures in which a spatial factor is present, but irrelevant, may involve a more difficult task for the animal. For example, when Smith (1967) trained three pigeons in a delayed-matching-to-sample (DMTS) task with both a spatial and a non-spatial procedure, not only did the pigeons take much longer to acquire the non-spatial task, but increasing the delays from the offset of the sample to the onset of the comparison stimuli from 1 s to 7 s, resulted in a much greater decrease in accuracy in the non-spatial, than in the spatial discrimination task. In a study by Lyderson, Perkins and Chairez (1973) (cited in Lyderson & Perkins, 1974), when pigeons discriminated between different FR response requirements which served as samples corresponding to different comparison stimuli, the non-spatial FR discrimination task controlled lower accuracy when compared with a spatial FR discrimination procedure.

For this study, the animal was required to respond to a red or green lit side key, each of which could be presented to the left or to the right on any given trial. However, apart from the presumed greater difficulty of the animals' task, each of the following studies was directly comparable to a study from Experiment 1. Both experiments were run concurrently. The rationale for the present study was the same as for Experiment 1.1. Discriminative performance

of the domestic hen, was investigated using a descending and an ascending series of probes. The utility of various methods of analysis were evaluated, and estimates of threshold determined using a variety of criteria. Results were compared with those obtained from Experiment 1.1, to ascertain whether, and in what manner, the non-spatial procedure changed discriminative performance. On the basis of the literature, the non-spatial procedure would be expected to control lower accuracy.

Method 2.1

Subjects

Six domestic hens (White Shaver) numbered from 31 to 36 served. They were 85 weeks old when the study commenced. All birds had been magazine trained and trained to peck both red and green illuminated keys prior to the experiment. They were individually housed and received supplementary food (commercial laying mash), to maintain their weights at 80% +/- 20 g of their free-feeding levels throughout the study. Water and grit were available at all times in the home cages.

Apparatus

The apparatus was similar to that used for Experiment 1.1 except for a modification in the mounting of the stimulus disk behind the response wall to make the changing of stimulus disks for probe sessions easier. As for Experiment 1.1, the centre key was made opaque except for a 20 mm diameter circular region in the centre, by applying a coat of black paint around the circumference of the rear of the key. Pecks on illuminated response keys were effective only if they exceeded a force of 1.5 N for the centre key and 0.75 N for the side keys (and closed a microswitch). An effective peck both extinguished the keylight and produced a tone for 35 ms. This tone provided auditory feedback. Experimental events were controlled by a Vic 20 (Commodore) computer, situated remotely from the experimental chamber. An automatic food delivery hopper contained whole wheat. The hopper could be raised to allow access to the wheat. The food hopper was illuminated by a 1.5 W bulb covered with an opaque plastic cap.

Target stimuli. These were the same as those used for Experiment 1.1. Fourteen stimulus disks were used throughout the study. On each were mounted six grey stimuli and six gratings of one spatial frequency only, as for Experiment 1.1.

Luminance. All key luminances and illumination of the experimental chamber were the same as for Experiment 1.1. Behind each of the two side keys were two 1.75 W red and green bulbs. This allowed each of these side keys to be illuminated red or green.

Procedure

General procedure. As for Experiment 1, six gratings of the same spatial frequency and six grey stimuli were presented during an experimental session. Presentation of the grating or grey stimulus was psuedo-random, as in Experiment 1.1. Similarly, a non-correction procedure was used, that is the occurence of the grating and grey stimulus behind the centre key was independent of the accuracy of responses on the previous trial.

Presentation of the comparison stimuli. The presentation of red and green on the left and right side keys was controlled by a variation of the Gellerman series, ensuring that neither colour would be presented on the same key on more than three consecutive trials, and that each key would be red illuminated and green illuminated for the same number of trials, within a session.

A non-independent or controlled reinforcement procedure was used to ensure that scheduled reinforcements were allotted equally to red and green keys. That is, if a reinforcement was available on one

alternative, the red key, the animal was denied access to reinforcement for correct responses on the other, the green key, until it made a correct response on the red key. This prevented exclusive responding to a key of one colour and controlled the relative obtained reinforcement rate. The animals could, however, respond exclusively to a left or right positioned key, without overall loss of scheduled reinforcements. That is, the reinforcement procedure was controlled for key colour, but not for key position. This procedure was in effect throughout the experiment.

Each trial began with the presentation of either a grating or a grey stimulus (the sample stimulus) behind the illuminated centre key. A single peck on this key resulted in the two side keys being lit, one red and one green. If the grating was present behind the centre key, a peck to the red side key was correct. If the grey stimulus was presented on the centre key, a peck to the green side key was correct. The centre response key remained lit during this choice. A correct trial resulted in the magazine light coming on for 3 s, and aperiodically this was accompanied by 3 s access to wheat. The three key lights went out and the keys were inoperative during this time. Incorrect responses, that is, a response to the green key when a grating was presented, or a response to the red key when a grey stimulus was presented, resulted in 3 s blackout. During the 3 s of reinforcement or blackout, the stimulus disk turned to position the stimulus for the following trial. Sessions started and ended in black-out. Experimental sessions were scheduled for seven days a week, for a total of 45 reinforcements or 30 min, whichever was the shorter.

Reinforcement schedule. A variable interval reinforcement schedule of 30 s (VI 30) was programmed. A version of the Gellerman series was used, allotting reinforcement delivery for correct responses on each of the two side keys aperiodically, around an average of 60 s each, or 30 s overall, as for Experiment 1.1. The schedule of reinforcement was kept constant at VI 30 s following preliminary training.

Preliminary Training. Training commenced with a set of six 1 c/mm grating and six grey stimuli. Reinforcement of 3 s duration was delivered for each correct response (CRF). After 56 sessions, training continued on a VI 15 s schedule for correct responding, for a further 39 sessions. During these sessions, when a correct response was not followed by reinforcement, the magazine light went on for 3 s. The consequence for an incorrect response was 3 s blackout. These sessions are described in Table 2.1.1.

Main training sessions. On training sessions the grating presented was always of the lowest spatial frequency (1 c/mm) and other conditions were as in the general procedure. Training sessions continued for a further 47 sessions, until behaviour met both an accuracy and a stability criterion. The initial criterion required that hens respond with an 80% accuracy on total (both grating and grey) trials. However it was necessary to relax the accuracy criterion for this study. Following 142 sessions of training and after all hens had reached a stability criterion (as in Experiment 1.1), although only one hen had reached the 80% accuracy criterion, probe sessions commenced. Table 2.1.2 shows the highest percentage of total trials correct, for each hen for the last five days of training

Table 2.1.1

Table 2.1.1

The grating value, reinforcement schedule and duration, magazine light duration and the number of sessions each condition was in effect during preliminary training.

Stimulus value (c/mm)	Rft sched.	Rft (s)	Mag light(s)	No sessions
1	CRF	3	3	56
1	VI 15	3	3	39

Table 2.1.2

Table 2.1.2

The highest percentages of total trials correct for the last five days prior to commencement of the descending series of probes, for each hen. The same data from Experiment 1.1 are also shown, for comparison.

Experiment 2.1		Experiment 1.1	
Hen	% cor.	Hen	% cor.
31	77	71	95
32	91	72	97
33	77	73	70
34	79	74	95
35	64	75	97
36	75	76	99
Total Sessions	142		129

prior to commencement of probe sessions. Those from Experiment 1.1 are included for comparison. The stability criterion was the same as for Experiment 1.1.

Probe sessions. Once the above criterion was satisfied, probe sessions began. These sessions involved the use of a grating of a higher spatial frequency from that used as the training stimulus. Only one value of grating was used during a probe session, and only one probe session was undertaken at each grating value for each probe series. Between probe sessions, training continued with the coarsest grating (1 c/mm) for at least one session, until each hen had reached her individual testing criterion. The testing criterion for each hen was that the proportion of total correct responses be within 0.1 of the highest proportion of total trials correct during the last five days of training, before the probe series began. However if, after five sessions of training between probe sessions a hen had still not reached its testing criterion, the probe session was commenced. Probes included a descending and an ascending series, as for Experiment 1.1.

Data collection. The data collected included the following: the number of correct responses emitted to the left and right red keys following presentation of the grating on the sample key, the number of incorrect responses to the left and right green keys following presentation of the grating, the number of correct responses to the left and right green keys following presentation of the grey stimulus and the number of incorrect responses to the left and right red keys following presentation of the grey stimulus; the latencies of correct and incorrect responding on the left and right red keys and left and

right green keys respectively, following presentation of the grating and the latencies of correct and incorrect responding on the left and right green keys and the left and right red keys respectively, following presentation of the grey stimulus; the number of reinforcements obtained for responding correctly on the left and right red keys following presentation of the grating and the number of reinforcements obtained for correctly responding on the left and right green keys following presentation of the grey stimulus. Threshold estimates were determined as for Experiment 1.1.

Results 2.1

Discrimination

Figure 2.1.1 presents the percentages of total trials correct as a function of spatial frequency of gratings, measured in c/mm, for all hens, for both the descending and ascending series of probes. There is close replication in the data from both probe series for all hens. The percentages correct monotonically decreased and levelled off at gratings of 2 - 4 c/mm. For some hens there was a slight increase in accuracy for probes at the finest gratings, measuring 8 and 10 c/mm. Hen 32 gave the highest discriminative performance of all hens at the coarsest gratings for both series of probes.

The threshold estimates for all hens and for each probe series were determined from that spatial frequency of the grating at which 75% and 50% of the total trials were correct, as for Experiment 1.1. For three of the hens, 31, 33 and 35, it was not possible to estimate a threshold for either probe series as their data did not reach 75% total trial accuracy. For this reason, it was also not possible to estimate thresholds from the ascending series for hen 34, nor the descending series for hen 36. The estimates (c/deg), were 3.0 and 3.4 c/deg from the descending series for hens 32 and 34 respectively, and 3.0 and 2.0 c/deg from the ascending series for hens 32 and 36, respectively. These are shown in Table 2.1.3. Estimates taken from the stimulus value corresponding to 50% total trial accuracy are also shown on Table 2.1.3 and range from 3.4 to 7.0 c/deg for the descending series and from 4.0 to 5.8 c/deg for the ascending series.

Figure 2.1.2 shows the mean percentages of total trials correct

Figure 2.1.1

Figure 2.1.1

The percentages of total trials correct, plotted as a function of grating spatial frequency, measured in c/mm, for all hens, for the descending (filled circles joined by a solid line) and ascending (unfilled circles joined by a broken line) series of probes.

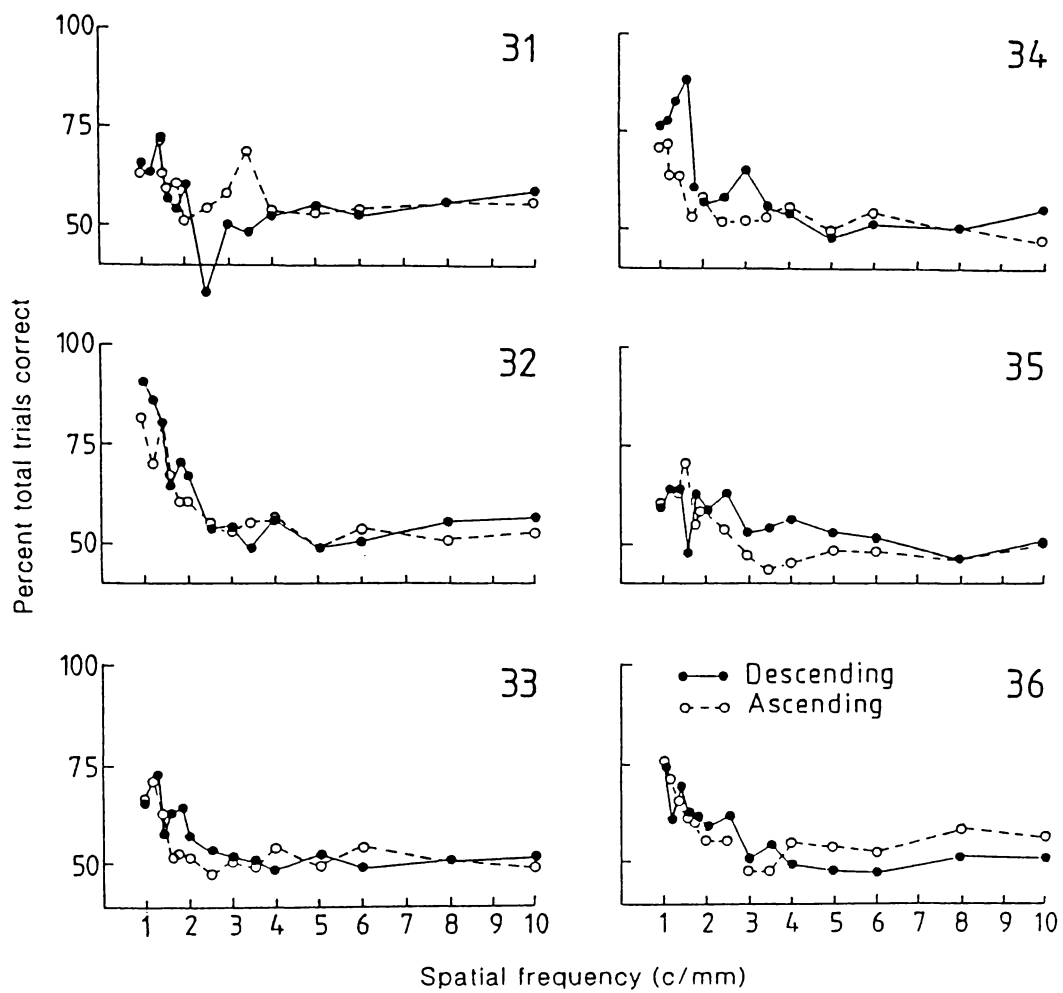


Table 2.1.3

Table 2.1.3

All threshold estimates taken from each of the various methods of analysis and criteria, measured in c/deg, for all hens, for the descending (desc) and ascending (asc) series of probes. Where the estimate was taken from a fitted line, the 95% confidence interval, as determined from the standard error of the line fit, is shown in brackets.

Hen	Probe Series	Total trials		Grating trials		Log d	
		75%	50%	50%	75%	0.48	0.00
31	desc	*	4.4	3.0	*	*	6.0
	asc	*	4.0	3.6	*	*	4.0
32	desc	3.0	7.0	3.2	2.8	3.0	6.0
	asc	3.0	5.8	4.6	2.8	3.0	5.8
33	desc	*	7.0	4.8	2.2	*	7.0
	asc	*	4.4	3.2	2.2	*	4.4
34	desc	3.4	5.0	3.0	2.8	3.0	5.2
	asc	*	5.0	3.6	*	*	3.6
35	desc	*	3.4	3.2	*	*	3.2
	asc	*	5.6	5.2	*	*	5.6
36	desc	*	6.0	5.8	2.2	2.2	6.0
	asc	2.0	5.8	3.2	2.2	2.2	5.6

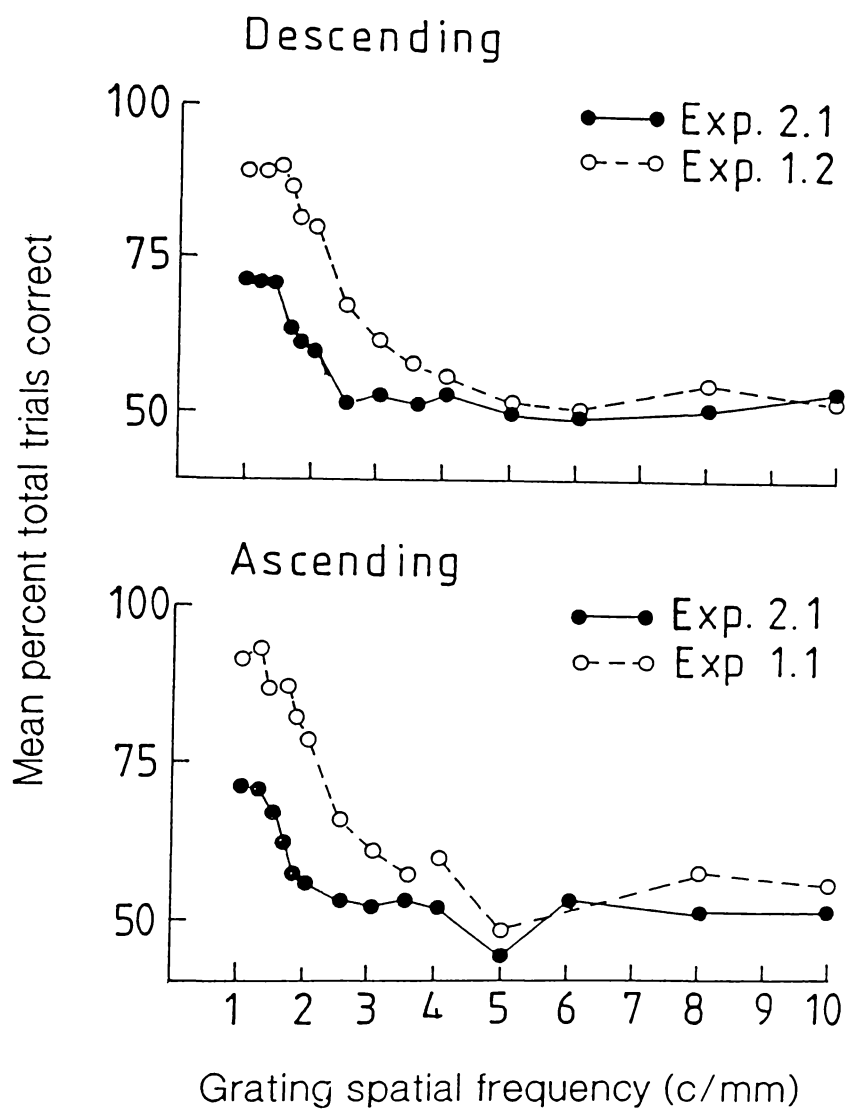
Fitted Line:		Log d of 0.48				Log d of 0.00			
Hen	Probe Series	c/mm	Log c/mm	Width cycle	Log width cyc	c/mm	Log c/mm	Width cycle	Log width cyc
31	desc	*	*	*	*	5.8 (0.2)	6.2 (0.2)	8.4 (0.2)	5.2 (0.3)
	asc	*	*	*	*	7.2 (0.1)	10.8 (0.1)	9.0 (0.1)	5.6 (0.1)
32	desc	3.0 (0.3)	4.0 (0.2)	1.5 (0.2)	1.7 (0.2)	5.0 (0.3)	4.6 (0.0)	5.2 (0.2)	5.0 (0.2)
	asc	3.0 (0.2)	3.2 (0.2)	1.4 (0.2)	1.4 (0.2)	5.0 (0.2)	5.4 (0.2)	6.0 (0.2)	5.2 (0.2)
33	desc	*	*	*	*	9.6 (0.2)	7.0 (0.2)	9.0 (0.2)	6.0 (0.2)
	asc	1.0 (0.2)	*	*	*	4.2 (0.2)	4.0 (0.2)	4.4 (0.2)	3.8 (0.2)
34	desc	2.6 (0.3)	2.4 (0.3)	1.3 (0.3)	1.3 (0.3)	5.2 (0.3)	4.8 (0.3)	6.0 (0.3)	5.2 (0.1)
	asc	2.4 (0.1)	*	1.1 (0.1)	*	4.8 (0.1)	6.6 (0.1)	3.4 (0.2)	4.2 (0.1)
35	desc	*	*	*	*	7.6 (0.2)	4.0 (0.3)	20.0 (0.1)	4.4 (0.3)
	asc	*	*	*	*	5.4 (0.1)	7.6 (0.1)	5.4 (0.1)	7.6 (0.1)
36	desc	0.6 (0.2)	*	0.6 (0.1)	*	6.6 (0.2)	7.8 (0.1)	11.2 (0.1)	6.2 (0.2)
	asc	2.4 (0.1)	0.2 (0.0)	1.1 (0.0)	1.1 (0.0)	5.4 (0.1)	4.2 (0.0)	6.0 (0.0)	4.8 (0.0)

* Estimate not calculable

Figure 2.1.2

Figure 2.1.2

The mean percentages of total trials correct, plotted as a function of grating spatial frequency, measured in c/mm, for group data from the present study (filled circles) and Experiment 1.1 (unfilled circles), for the descending and ascending series of probes. The two functions for the descending probe series are shown in one figure, and the two functions for the ascending probe series are shown in the other figure, for comparison.



from group data for the present study, and for Experiment 1.1, for both series of probes. The functions for the descending series from the present study and Experiment 1.1 are plotted in one figure, and the two functions for the ascending series are plotted in the other, for comparison. Although the shapes of the two functions are similar, the percentages correct were much lower for both series of probes in the present study, compared to the data from Experiment 1.1, at most grating values.

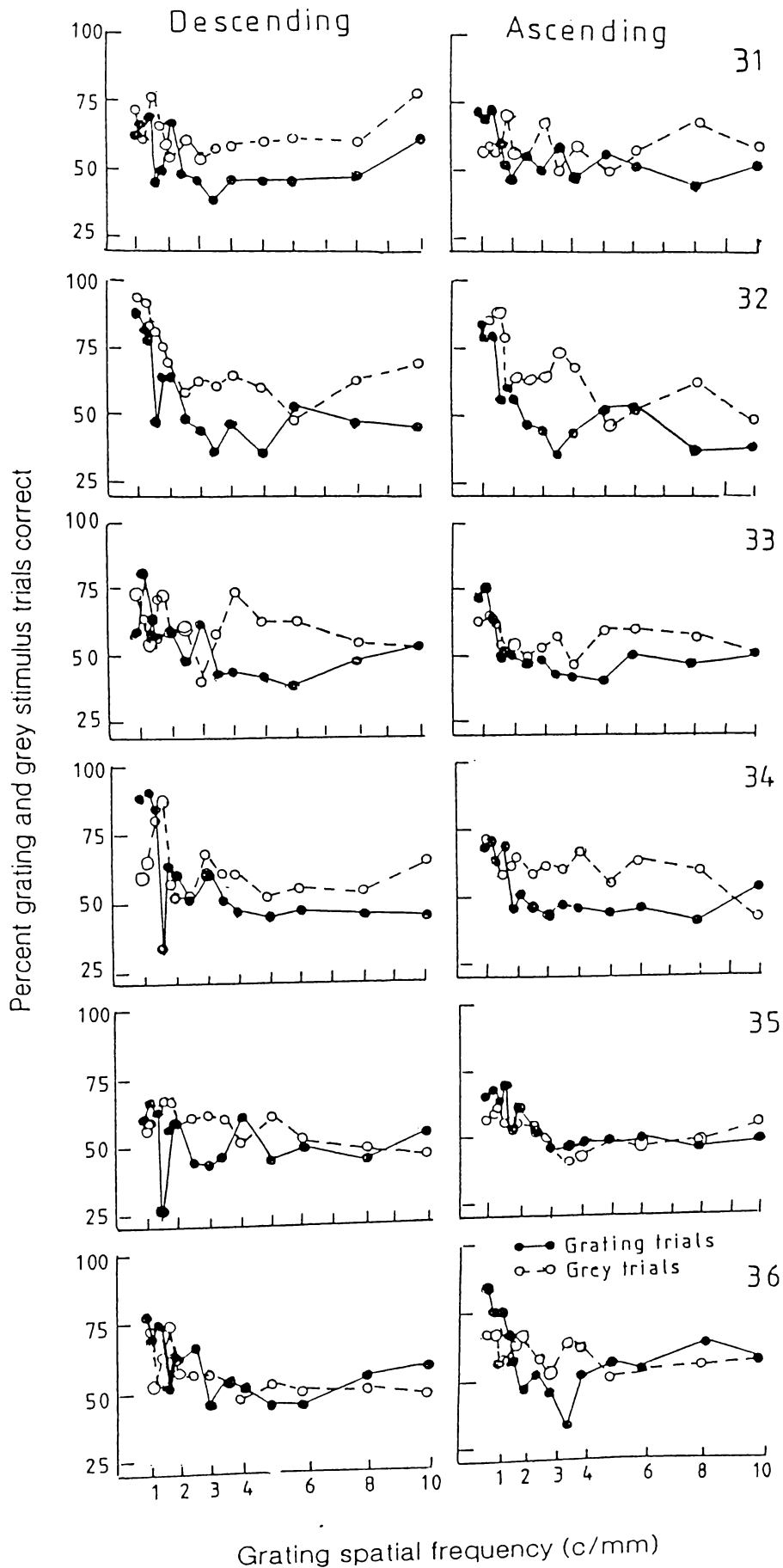
Figure 2.1.3 shows the percentages of correct responses made on grating and grey stimulus trials separately, plotted as a function of grating spatial frequency, measured in c/mm. These are shown for both the descending and the ascending series of probes. All functions show that the percentages correct on grating trials decrease to below 50% with probes at increasingly finer gratings. The percentages correct on grey stimulus trials generally remained above this value. Generally, at the coarser gratings, performance was lower for grating than grey trials. Accuracy on both grating and grey trials tended to be similar at finer grating values, for both probe series. The psychometric functions for the grating and grey stimulus trials are very similar in shape to those obtained for Experiment 1.1, except for the lower accuracy in both grating and grey trials in the present study.

Estimates of threshold from grating trials only, were taken from the points at which the plotted functions were 50% correct. These are shown on Table 2.1.3 and range from 3.0 to 5.8 c/deg for the descending series, and from 3.2 to 5.2 c/deg for the ascending series of probes. Neither probe series consistently provided greater

Figure 2.1.3

Figure 2.1.3

The percentages of grating (filled circles joined by a solid line) and grey stimulus trials (unfilled circles joined by a broken line) correct, plotted separately, as a function of grating spatial frequency, measured in c/mm, for all hens, for the descending and ascending series of probes.



estimates than the other. These estimates are lower than the equivalent estimates for Experiment 1.1.

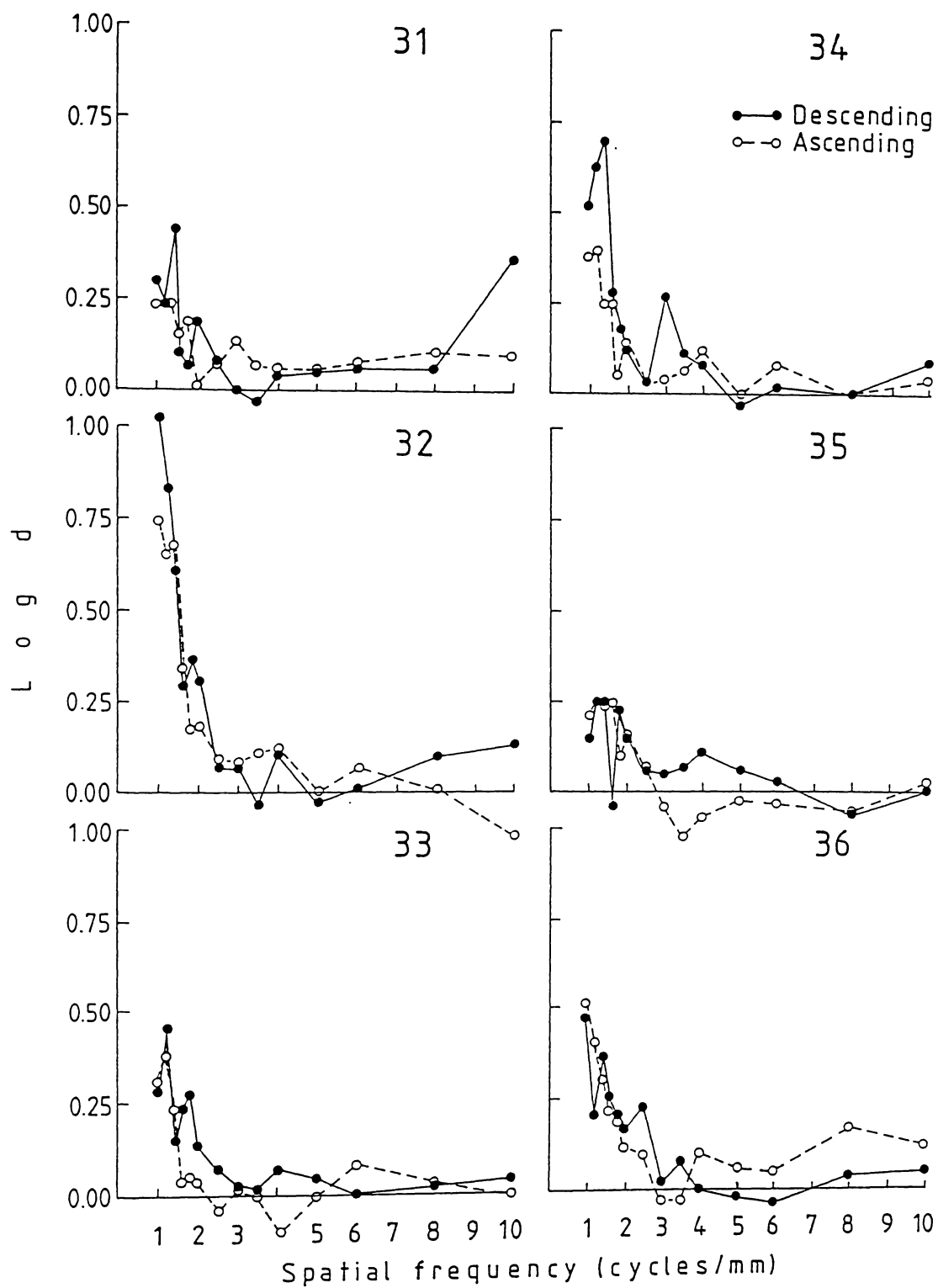
Threshold estimates from the data for four hens were also taken from the points at which the plotted grating trials were 75% correct, and are included in Table 2.1.3. They range from 2.2 to 2.8 c/deg for each probe series. It was not possible to estimate thresholds for two hens, 31 and 35 for either probe series, nor for hen 34 for the ascending series, as accuracy on grating trials did not reach 75%. However, two of the hens whose total trial performance did not reach 75% accuracy did reach 75% accuracy on grating trials. These were hen 33 for the ascending series and hen 36 for the descending series. Their low total trial performance resulted from lower accuracy on grey stimulus trials at the coarsest grating values.

Figure 2.1.4 presents $\log d$ values (Equation 6) plotted as a function of increasing spatial frequency of gratings, measured in c/mm, for all hens and for both probe series. Data replicated well. Generally, $\log d$ decreased as a function of probes with finer gratings to a value close to zero, before levelling off at a stimulus value between 2 - 3 c/mm. Estimates of threshold were obtained by interpolation, as in Experiment 1.1, to determine the spatial frequency of grating which corresponded to a $\log d$ value of 0.48. Further estimates of threshold were obtained for both probe series for all hens from the point at which the $\log d$ value was 0.00. Where necessary, these estimates were taken by extending a line from the final two data points of the descending portion of the function to the x-axis, as in Experiment 1.1. The estimates taken from the $\log d$ values of 0.48 and 0.00 for all hens and both probe series are shown on Table 2.1.3. For the $\log d$ value of 0.48, these range from 2.2 to

Figure 2.1.4

Figure 2.1.4

Values of $\log d$ plotted as a function of grating spatial frequency, measured in c/mm for the descending (filled circles joined by a solid line) and ascending (unfilled circles joined by a broken line) series of probes.



3.0 c/deg for both probe series. For three hens, 31, 33 and 35, no estimates were taken for either probe series, and no estimate was obtained for hen 34 for the ascending series, as all values of $\log d$ were below 0.48. Estimates of threshold from the $\log d$ value of 0.00 range from 3.2 to 7.0 c/deg for the descending series and from 3.6 to 5.8 c/deg for the ascending series of probes. For five of six hens, these were greater (indicating more acute vision) for the descending series of probes.

Figures 2.1.5a to 2.1.5d present the same $\log d$ values as Figure 2.1.4 for all hens for both probe series. For each hen's data and for both probe series a series of pairs of lines were fitted by the method of least squares, as for Experiment 1.1. These line pairs were created for all hens' data for the standard measure of stimulus values used (i.e. c/mm) and a series of transformations of the measures of the stimulus values. Specifically, those transformations were the logarithm of the number of cycles/mm, the width of a cycle (mm) and the logarithm of the width of a cycle. The data were plotted as a function of these in Figures 2.1.5a to 2.1.5d. The lines chosen to describe the descending function of the data are shown in the figures. An attempt was made to choose the first line of the pairs of lines which had, overall, the least standard error, and included three or more data points. However, in some cases the lines drawn were not those with the lowest standard error but were those which were judged by three observers to describe the descending portions of the data best.

When the data were plotted as a function of the logarithms of the number of cycles per mm (Figure 2.1.5b) and as a function of the

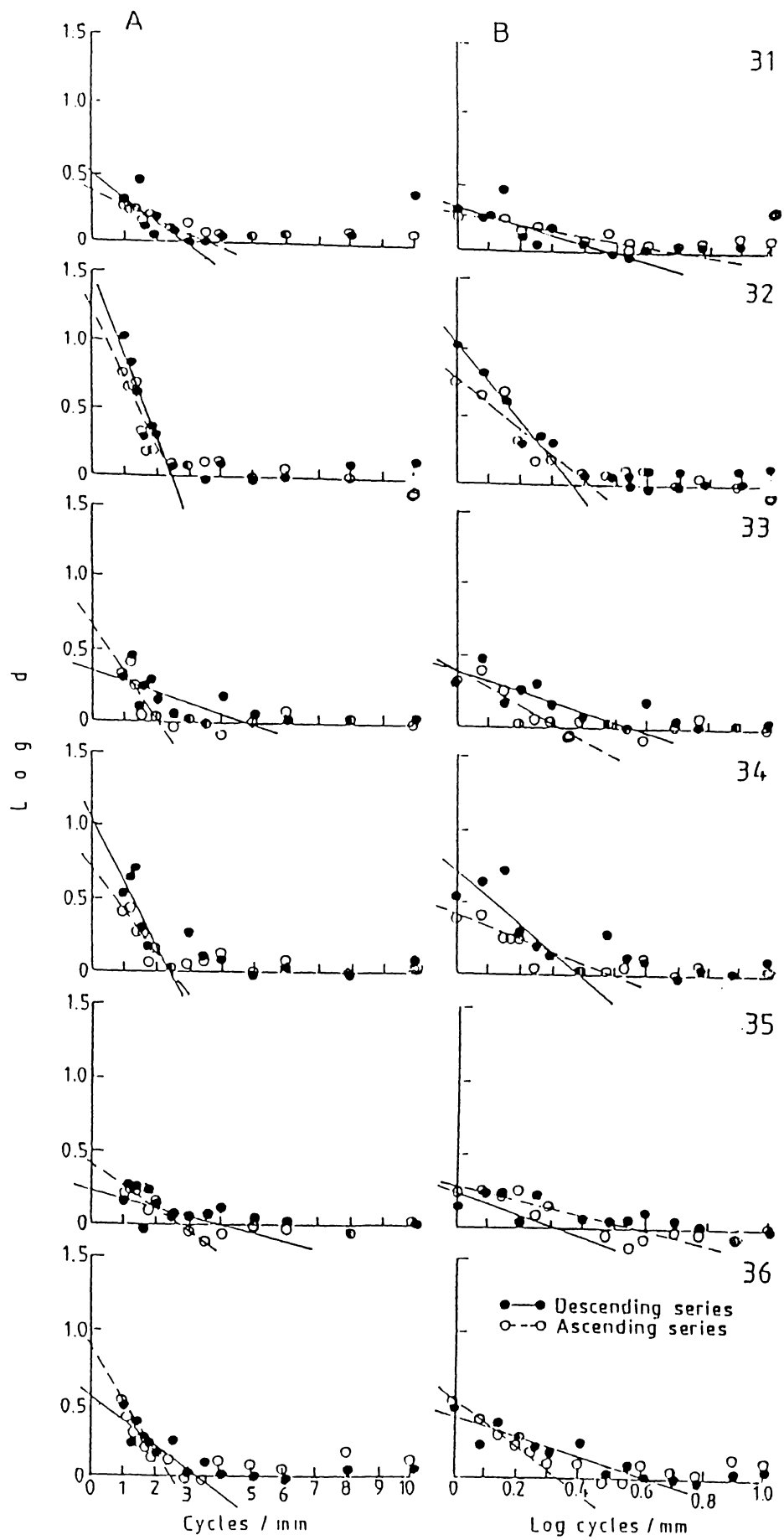
Figure 2.1.5

Figures 2.1.5 (a) to (d)

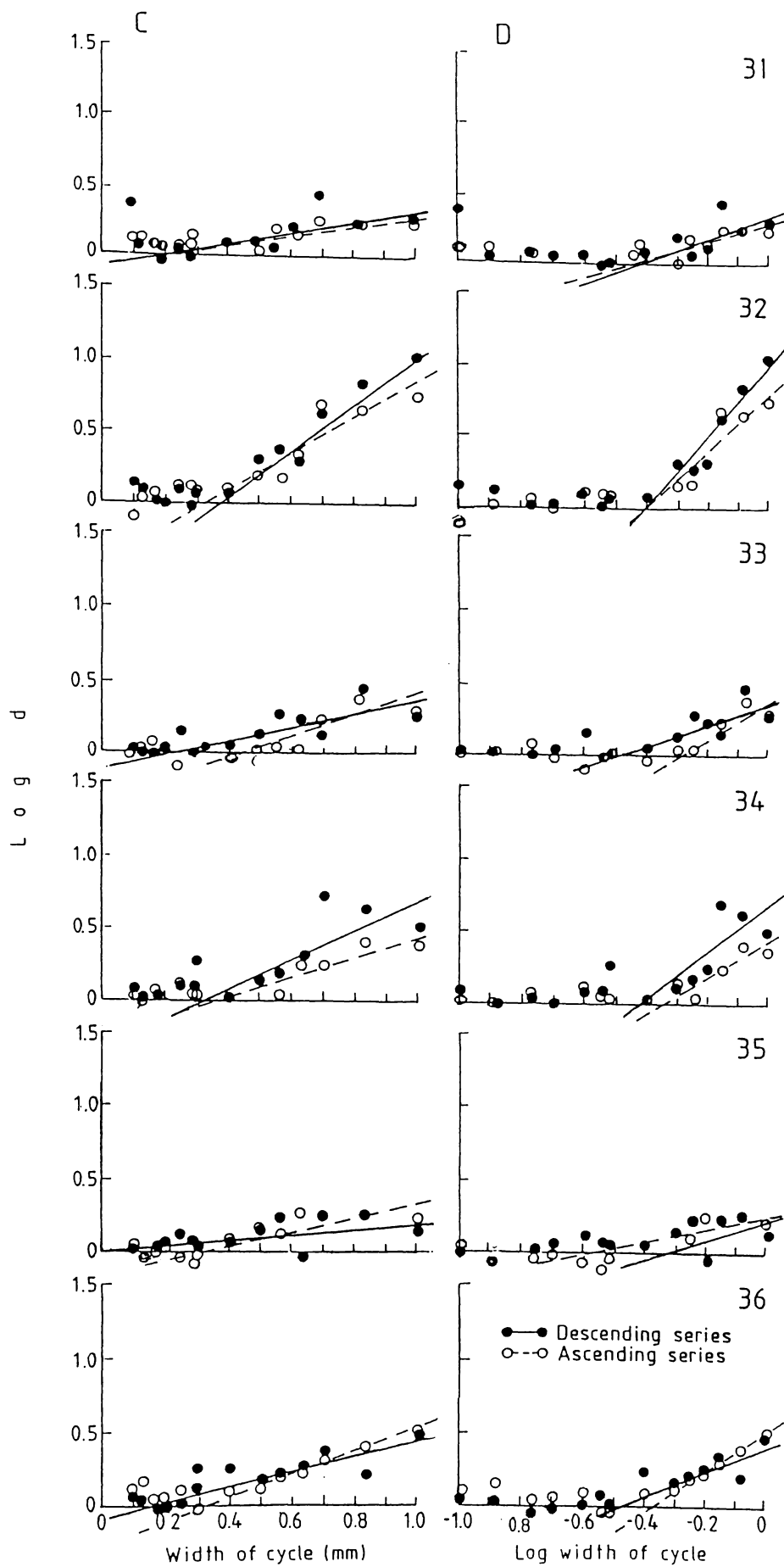
Values of $\log d$ for all hens for the descending and ascending series of probes, plotted as a function of grating spatial frequency, measured in:

- (a) cycles per mm (c/mm).
- (b) logarithms of the number of cycles/mm.
- (c) width of a cycle (mm).
- (d) logarithms of the width of a cycle.

A line has been fitted to the descending portion of the data from each hen by the method of least squares, and is shown in the figures. The parameters of the fitted lines are given in Table 2.1.4.



cont.



logarithms of the width of a cycle (mm) (Figure 2.1.5d), the figures show that the data points were spread out more equally than for the width of a cycle in mm. Where the line was fitted to the data with grating spatial frequency measured in c/mm (Figure 2.1.5a), lines chosen for the data from hens 34 and 35 for the ascending series and hens 31 and 33 for the descending series were those with the least standard error. When grating spatial frequency was measured in the logarithm of the number of cycles/mm (Figure 2.1.5b), only the lines chosen to fit the data from hen 32 from the descending series and hen 35 from the ascending series were those with the least standard error. When spatial frequency was measured in the width of a cycle (mm) (Figure 2.1.5c), lines chosen to fit the data from hens 31, 32 and 35 for the descending series, and hen 36 for both probe series, contained the least standard error. When grating spatial frequency was measured in the logarithm of the width of a cycle (Figure 2.1.5d), those lines fitted to the data from hen 32 for the descending series, and hen 36 for the ascending series, were those with the least standard error.

In summary, only 13 of the 48 fitted lines were those with the least overall standard error. This is because many of those lines with the least standard error did not provide the best description of the descending portion of the data function. Due to the low discriminative performance of most hens, the lines with the least standard error were those which included many low $\log d$ values, which indicated indiscriminability of the stimuli.

Table 2.1.4 gives the slope, intercept, the number of data points described by the fitted line, the standard error of the estimate and the proportion of variance accounted for (VAC%) by each regression

Table 2.1.4

Table 2.1.4

The slopes and the intercepts of the least squares lines fitted to the values of log d for each hen, for the descending (1) and ascending (2) series of probes, the number of data points described by each line (Data pts.), the amounts of variance accounted for by the fitted lines (VAC%) and the standard errors of the estimates (SE) are also given.

Hen	Cond	Cycle/mm					Log cycle/mm					Width of cycle (mm)					Log width of cycle				
		Slope	Intcpt	Data Pts.	VAC%	SE	Slope	Intcpt	Data Pts.	VAC%	SE	Slope	Intcpt	Data Pts.	VAC%	SE	Slope	Intcpt	Data pts.	VAC%	SE
31	1	*-0.16	0.47	8	47.5	0.11	-0.58	0.31	10	56.8	0.97	*0.46	-0.11	8	42.4	0.11	0.85	-0.35	5	0.4	0.15
	2	-0.09	0.35	5	38.3	0.03	-0.29	0.25	5	36.9	0.03	0.35	-0.07	6	41.0	0.07	0.62	-0.28	6	50.4	0.06
32	1	-0.62	1.51	7	83.9	0.14	*-2.84	1.04	3	98.8	0.02	*1.37	-0.38	10	92.0	0.10	*2.40	-0.98	7	90.5	0.10
	2	-0.50	1.23	7	80.3	0.12	-1.93	0.79	7	84.6	0.11	1.25	-0.42	7	80.9	0.12	1.92	-0.79	7	82.3	0.12
33	1	*-0.07	0.35	11	40.1	0.11	-0.66	0.36	9	64.7	0.09	0.49	-0.10	9	60.8	0.09	0.67	-0.37	7	39.7	0.10
	2	-0.28	0.61	7	72.7	0.09	-1.08	0.36	7	76.9	0.08	0.72	-0.33	5	52.8	0.11	1.29	-0.39	4	35.3	0.12
34	1	-0.45	1.08	7	69.7	0.15	-1.65	0.68	7	67.2	0.15	1.02	-0.33	7	56.6	0.17	1.64	-0.68	7	64.3	0.16
	2	*-0.28	0.68	4	59.5	0.05	-0.81	0.41	4	57.1	0.06	0.69	-0.25	5	63.7	0.09	1.26	-0.44	5	71.9	0.08
35	1	-0.03	0.21	11	12.6	0.09	-0.79	0.24	4	0.0	0.15	*0.31	-0.48	3	57.8	0.03	0.72	-0.23	4	0.0	0.14
	2	*-0.15	0.42	9	89.9	0.04	*-0.42	0.26	7	53.7	0.05	0.48	-0.16	10	72.1	0.07	0.42	-0.26	7	52.7	0.50
36	1	-0.16	0.54	8	58.0	0.09	-0.64	0.40	10	73.8	0.08	*0.54	-0.10	11	78.7	0.07	0.81	-0.42	6	45.0	0.09
	2	-0.40	0.88	6	95.4	0.03	-1.50	0.52	4	99.7	0.01	*0.78	-0.25	9	98.8	0.02	*1.35	-0.52	6	98.9	0.02

* Lowest standard error.

line chosen to describe the descending portion of the data. Although many of the lines chosen were not those with the least standard error, the amount of standard error of the fitted lines was in most cases less than 0.16.

Estimates of threshold were taken from the stimulus value corresponding to a $\log d$ value of 0.48, determined from the fitted lines. Further estimates of threshold were obtained from these functions at the point where the fitted line crossed the x-axis at a $\log d$ value of 0.00. Table 2.1.3 shows all threshold estimates obtained for hens in both probe series, for each of the measures of stimulus values corresponding to a $\log d$ value of 0.48 and 0.00. The 95% confidence intervals, derived from the standard error of the line fit, are shown in brackets. It was not possible to determine estimates at the $\log d$ value of 0.48 for hens 31 and 35 for either probe series, nor for hen 33 for the descending series, as extrapolation from the line to this point would have given negative threshold estimates.

Estimates taken from the fitted line with grating spatial frequency measured in c/mm (Figure 2.1.5a) at the $\log d$ value of 0.48, range from 0.6 to 3.0 c/deg for the descending series and from 1.0 to 3.0 c/deg for the ascending series. Neither probe series yielded consistently greater thresholds. When a $\log d$ value of 0.00 was used, these values were greater and range from 5.0 to 9.6 c/deg for the descending series and from 4.2 to 7.2 c/deg for the ascending series. For four of six hens, greater estimates were obtained from the descending series. When grating spatial frequency was measured as the logarithm of the number of cycles/mm (Figure 2.1.5b), the fitted line

at the $\log d$ value of 0.48 gave estimates of 2.4 and 4.0 c/deg for the descending series and 0.2 and 3.2 c/deg for the ascending series of probes. Estimates could not be obtained for hen 34 for the ascending series or for hen 36 for the descending series. Estimates taken at the $\log d$ value of 0.00 with grating spatial frequency measured as the number of logarithms of cycles/mm, for all hens, range from 4.0 to 7.8 c/deg for the descending series and from 4.0 to 10.8 for the ascending series of probes. For four hens, greater threshold values were obtained from the ascending series of probes. With grating spatial frequency measured as the width of a cycle in mm, (Figure 2.1.5c) the fitted line at the $\log d$ value of 0.48 gave thresholds ranging from 0.6 to 1.5 c/deg for the descending, and from 1.1 to 1.4 c/deg for the ascending series of probes, for the three hens' data for which this was possible (hens 32, 34 and 36). Two of the three estimates were greater from the descending series. When a $\log d$ value of 0.00 was used, threshold estimates were taken for all hens' data and range from 5.2 to 20 c/deg for the descending series and from 4.4 to 9.0 c/deg for the ascending series of probes. For four of six hens, the descending series yielded greater estimates. With grating spatial frequency measured as the logarithm of the width of a cycle (Figure 2.1.5d) the estimates taken at the $\log d$ value of 0.48 were 1.3 and 1.7 c/deg for the descending series for two hens only, (32 and 34) and 1.1 and 1.4 c/deg for the ascending series of probes for two hens, (32 and 36). Those estimates taken at the $\log d$ value of 0.00 range from 4.4 to 6.2 c/deg for the descending series and from 3.8 to 7.6 c/deg for the ascending series of probes. Neither probe series gave consistently greater estimates of threshold.

A perusal of all threshold estimates obtained by each of the

various methods of analysis for both probe series (Table 2.1.3), shows that when the 50% grating trials correct criterion was used, the ascending series yielded greater estimates of threshold for most hens. For hen 36, the 50% gratings trials correct criterion gave greater estimates for the descending series, and the $\log d$ value of 0.48 gave identical estimates for both. Where estimates from the logarithm of the width of a cycle in mm were calculated, they tended to give lower values as measured in c/deg (indicating a worse performance) than the other criteria. Estimates taken from the stimulus value corresponding to the $\log d$ value of 0.00 gave greater values than the other criteria, and these estimates varied according to the transformation of stimulus value used. In summary, all estimates were lower than those obtained by the equivalent analyses and criteria for Experiment 1.1. They indicate no consistent difference between the discriminative performance for the descending and ascending probe series.

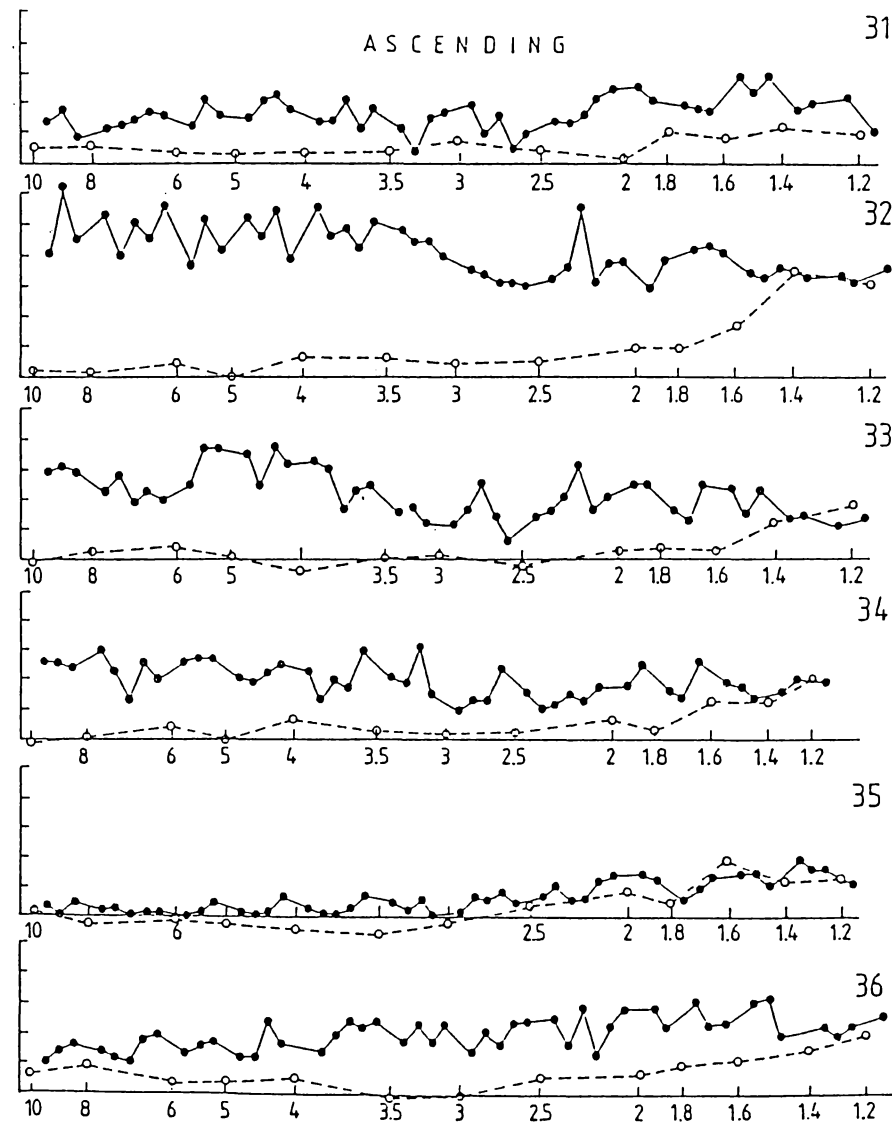
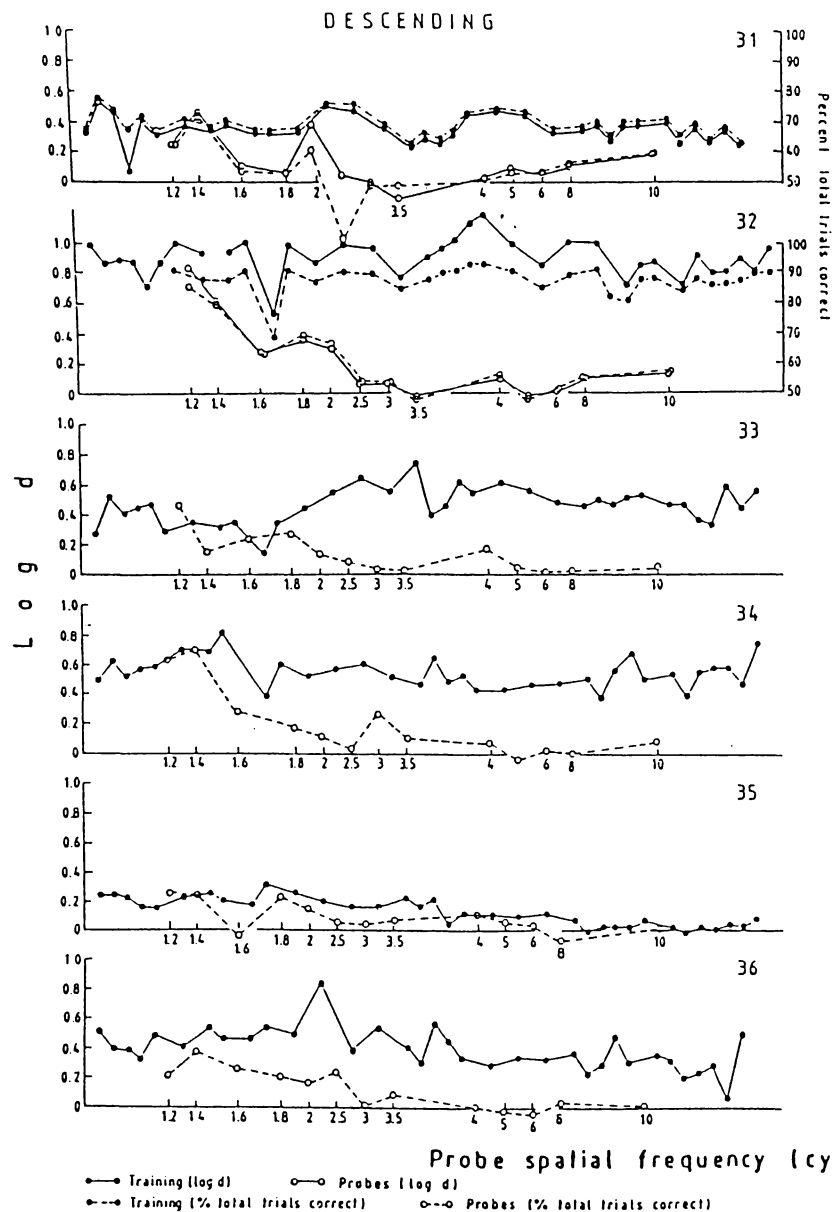
Figure 2.1.6 shows $\log d$ values for each session, as they occurred over the period of the probes, including both probe and intervening training sessions. The data from the last six training sessions prior to the commencement of probes for the descending series are also shown. Data from the training and probe sessions are shown as two separate functions, with filled circles for the training sessions and unfilled circles for the probing sessions. For each of these functions the data are joined by a solid line. The plots show that $\log d$ values from the probe sessions decreased with probes at increasingly finer gratings, to a stimulus value around 3.5 c/mm. With probes at increasingly finer gratings, $\log d$ stayed close to 0.00. The $\log d$ values for the training sessions, however, remained

Figure 2.1.6

Figure 2.1.6

Values of $\log d$ for each session, in order of occurrence, including both probe and training sessions for all hens, for the descending and ascending series of probes. Data from the last six training sessions prior to the commencement of probes for the descending series are also shown.

The training sessions (filled circles joined by a solid line) and probe sessions (unfilled circles joined by a solid line) are shown as two separate functions. For two hens only, 31 and 32, a second Y-axis is included in the figure, measuring the percentages of total trials correct for the same training (filled circles joined by a broken line) and probe sessions (unfilled circles joined by a broken line).



at a higher value for most hens and did not trend. The same data for the ascending series of probes show that $\log d$ values for the probe sessions were relatively low at all gratings finer than around 2.5 c/mm, and increased as a function of probe sessions with increasingly coarser gratings, to 1 c/mm. $\log d$ values for the intervening training sessions for all hens except 35, were higher than those for probe sessions, except at the coarsest values. The greater number of intervening training sessions for the ascending series compared to the descending series, is clearly shown. For the data from hen 35, $\log d$ values for training sessions were not very different from $\log d$ values for probe sessions, especially for the ascending series of probes. This hen also had the lowest $\log d$ of all hens prior to the commencement of probes.

For two hens only, 31 and 32, a second Y-axis was included, and the percentages of total trials correct are shown in the figure, to compare the function for the percentages of total trials correct with that of equivalent $\log d$ values. Although the functions for the percentage of total trials correct generally parallel the $\log d$ values for the same sessions, for hen 32, $\log d$ values tended to fluctuate more. This is because $\log d$ is a measure of discriminability based on two ratios of behaviour measures and thus, when high, is sensitive to small changes in the number of errors.

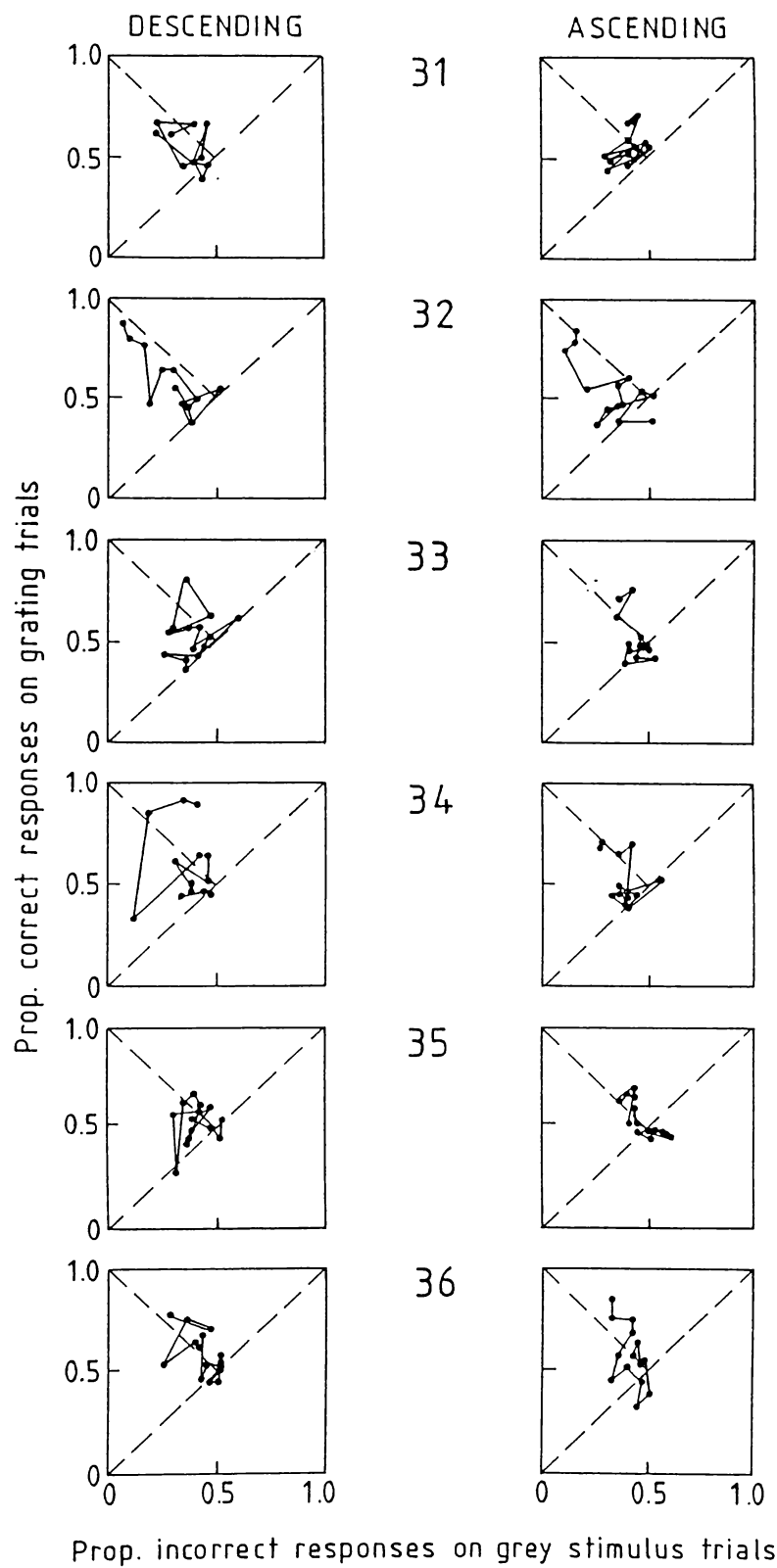
ROC plots

Figure 2.1.7 shows the proportion of correct responses to the red key on grating trials, plotted against the proportion of incorrect responses to the red key on grey stimulus trials, over all probe values, for each hen, for both probe series. For all plots, lines

Figure 2.1.7

Figure 2.1.7

The proportion of correct responses to the red key on grating trials plotted against the proportion of incorrect responses to the red key on grey stimulus trials, for the descending and the ascending series of probes. Lines join successive probes.



join the successive probes. The plots show that the data paths are very close to the minor diagonal for both probe series, indicating that the hens were responding almost equally to red and green response keys. Data points to the left of the minor diagonal for hen 32, for both conditions, indicate some preference for green key responding (i.e. responding as though a grey stimulus was present). At the finest gratings, data for hens 35 and 36 fell below the major diagonal, indicating a reverse discrimination.

Response bias

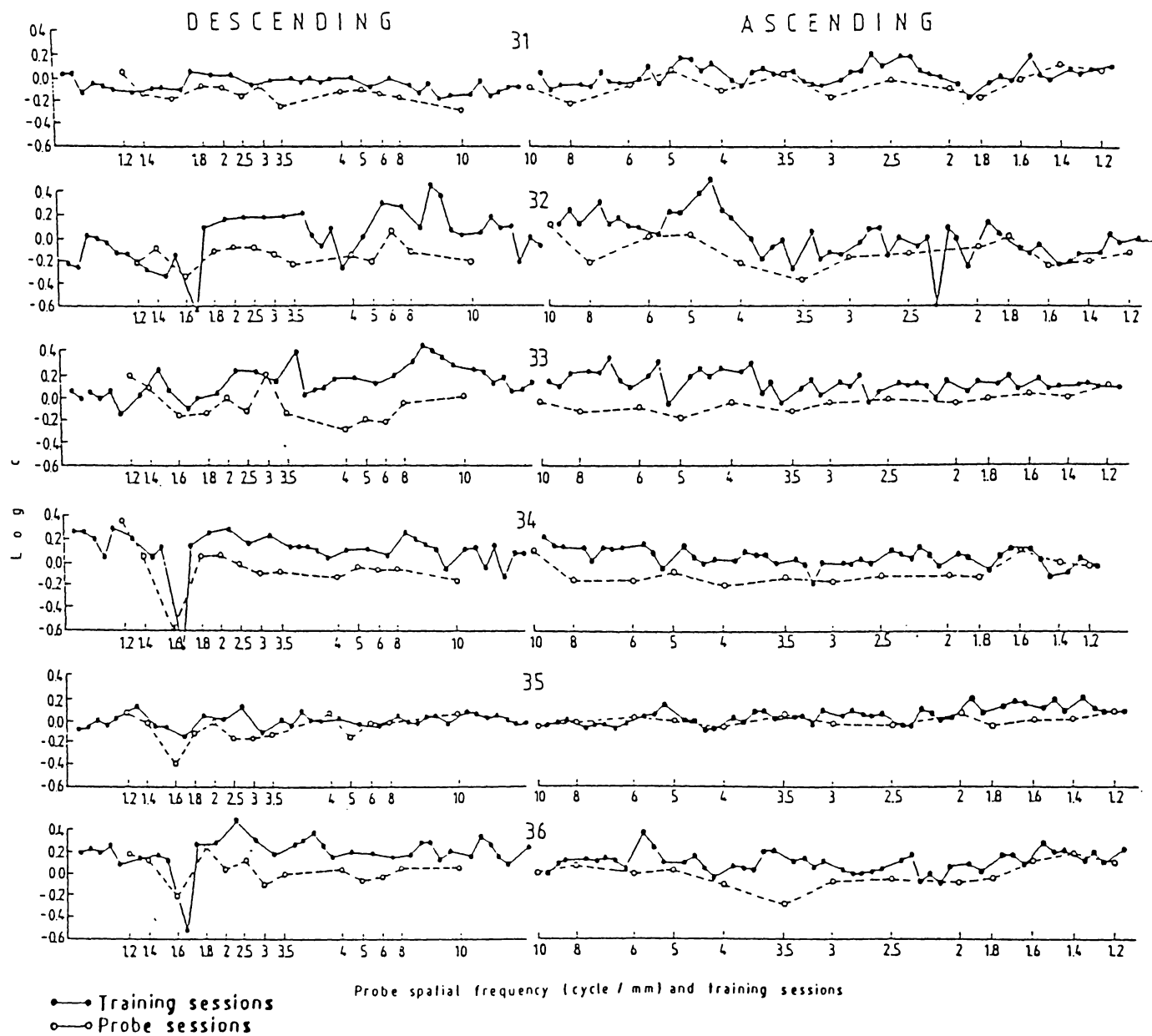
Figure 2.1.8 shows estimates of response bias, $\log c$ (Equation 8) for colour bias, for the data from each hen, from the descending and ascending series of probes, plotted as a function of grating spatial frequency. The estimates of $\log c$ are shown in order for the descending and ascending probe series, for each intervening training session and probe session as they occurred. The $\log c$ estimates for probes are shown as filled circles joined by a solid line, and those data from training sessions are shown as unfilled circles joined by a broken line. Positive values of $\log c$ indicate a bias for responding to the red key (as though the stimulus were a grating), and negative values indicate a green key preference.

$\log c$ values for the probe sessions did not vary very much from zero. Generally, any biases were towards green key responding, as indicated by negative $\log c$ values. In most cases, $\log c$ for training sessions was at a higher value than $\log c$ for probe sessions and showed a bias towards the red key. Thus the bias towards green key responding, evident in probe sessions, was not generally evident in the data from the intervening training sessions. For hen 35, $\log c$

Figure 2.1.8

Figure 2.1.8

Estimates of $\log c$ for the descending and ascending series of probes, plotted as a function of grating spatial frequency, measured in c/mm. Estimates of $\log c$ are shown in order for the descending series and the ascending series, for each probe session and intervening training series, as they occurred. Estimates of $\log c$ plotted for each session, in order of occurrence, including both probe (unfilled circles) and training (filled circles) sessions for all hens, for the descending and ascending probe series. Data from the last five training sessions prior to the commencement of probes for the descending series are also shown.



values tended to be similar for both probe and training sessions. There was little difference between log c values for the descending and ascending probe series.

Figure 2.1.9 presents the proportion of correct and incorrect left key responses, plotted as a function of grating spatial frequency, measured in c/mm , for all hens, for both probe series. The functions for the grating and grey stimulus trials are plotted separately. Data plotted above 0.5 indicate more left key responding and data plotted below 0.5 indicate more right key responding. For most hens there was generally a tendency toward more left key responding across both probe series. Hen 33 however, showed a bias towards right key responding which was even more pronounced for the ascending series of probes. The proportion of left key responses for both grating and grey stimulus trials replicates very closely for all hens. These clearly indicate that position biases were not a function of the grating and grey stimulus trials, and tended to vary unsystematically.

Reinforcement

Figure 2.1.10 shows the proportion of total reinforcements obtained for correct red key responses and the proportion of total reinforcements obtained for correct left key responses, plotted separately, as a function of grating spatial frequency, measured in c/mm , for all hens, for both probe series. Data points close to 0.5 indicate that the proportion of reinforcements obtained for correct responding was equal for both red and green keys, and for the left and right position of these keys. Data points at values greater than 0.5 indicate that a greater proportion of reinforcements was obtained for

Figure 2.1.9

Figure 2.1.9

The proportion of left key responses plotted as a function of grating spatial frequency measured in c/mm for both grating and grey stimulus trials for both the descending and ascending series of trials.

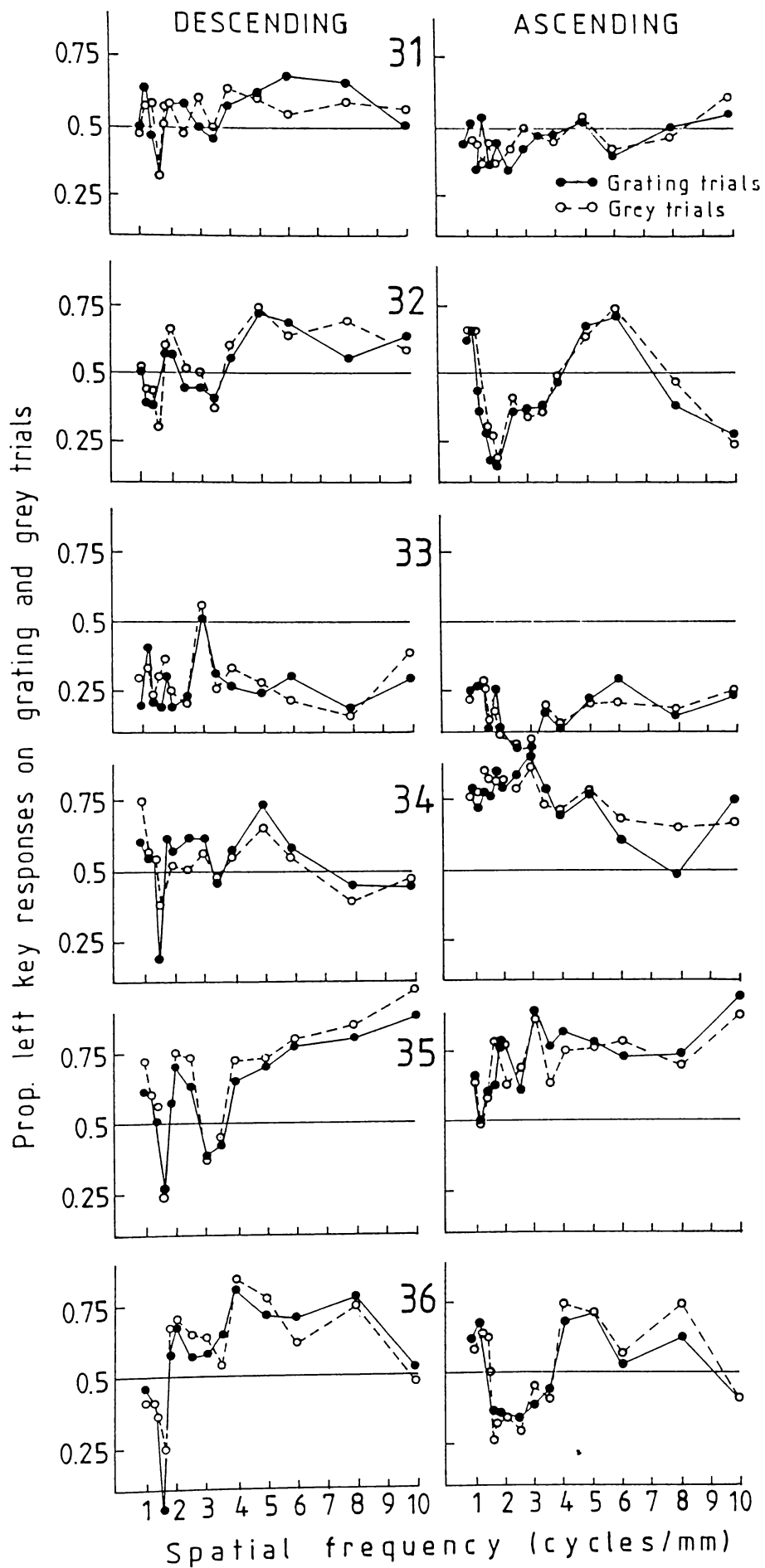
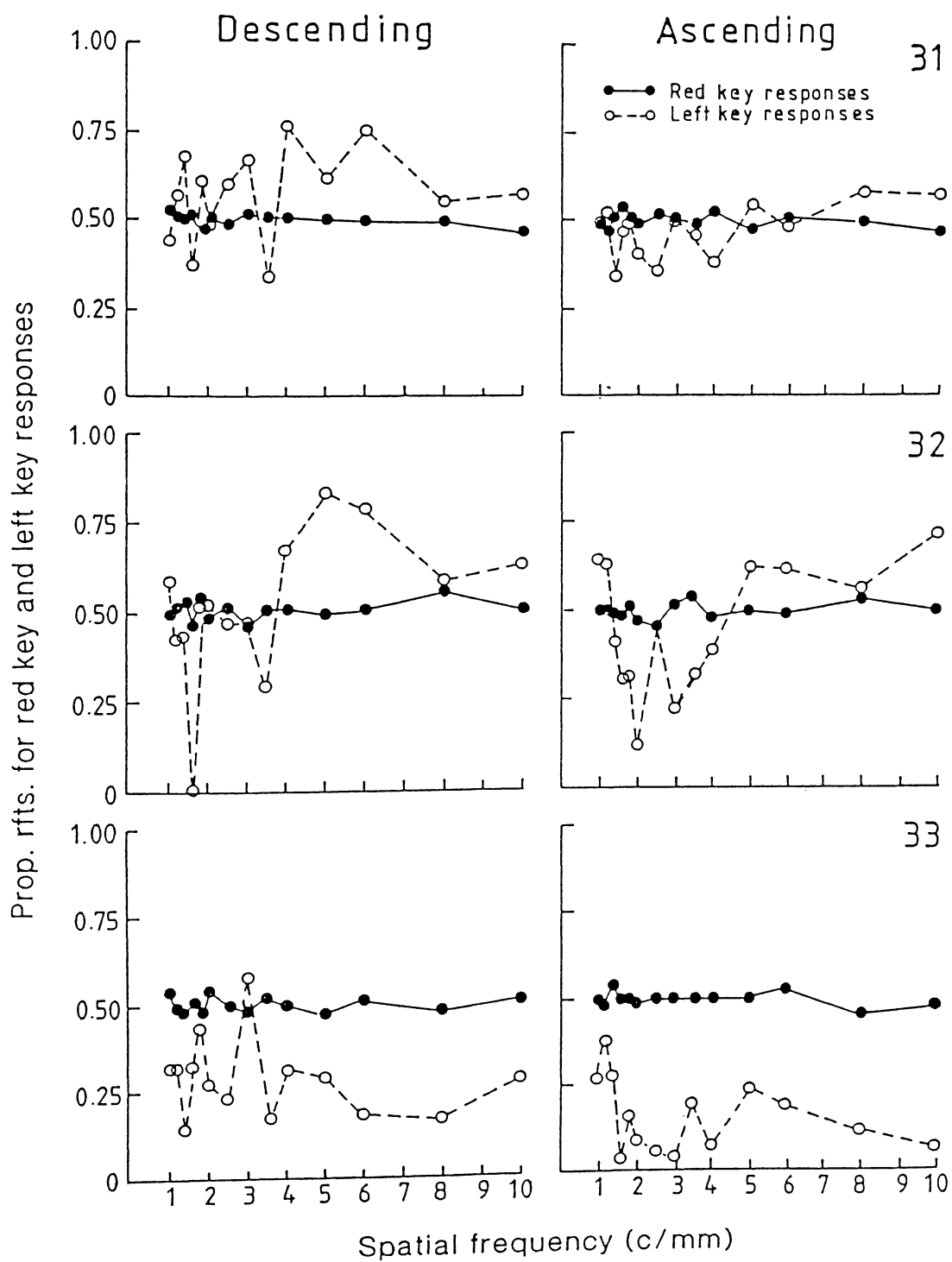


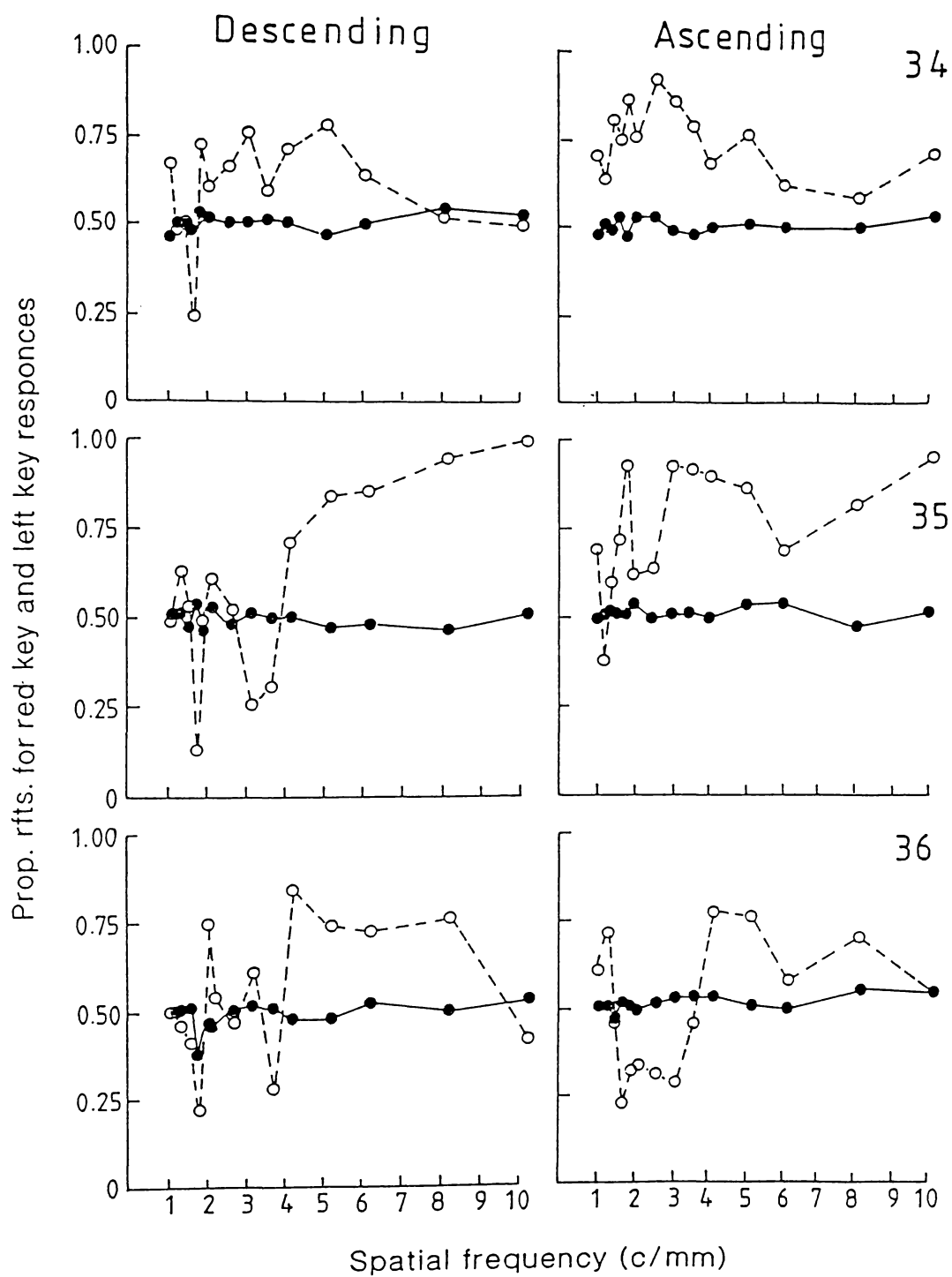
Figure 2.1.10

Figure 2.1.10

The proportion of reinforcements obtained for correct responses to the red key (filled circles joined by a solid line) and correct responses to the left key (unfilled circles joined by a broken line), plotted as a function of grating spatial frequency, measured in c/mm, for the descending and ascending series of probes.



cont.



correct responding to the red key (filled circles) or left side key (unfilled circles). The left side key may be either red or green. Data points below 0.5 indicate a greater proportion of reinforcements were obtained for correct responding to the green key (filled circles) or the right side key (open circles). The right side key may be either red or green. Reinforcements obtained at all grating values were close to equal for correct red and green key responding. Generally the proportion of total reinforcements delivered for left or right key responses varied widely and unsystematically throughout each probe series. For hen 33, the greater proportion of reinforcements was obtained for right key responses whilst for hens 34 and 35 the greater proportion of reinforcements was for correct left key responses.

Response Latencies

Response latencies to the side keys following a response to the centre sample key, measured in 0.1 s, were collected for all hens and for both probe series. These include latencies for correct responses to the red left and red right key, for incorrect responses to the green left and green right key on grating trials, for incorrect responses to the red left and right keys, and correct responses to the green left and right keys on grey stimulus trials. The data from two hens, as an example of all hens' latencies, are given in Appendix 6. The latencies varied widely from 0.9 sec to over 4 sec. For hens 31 and 32 all latencies were slightly higher for the ascending series of probes. However, there were no consistent differences in latencies for correct or incorrect responses, nor for probes at different grating values. That is, there was no clear relation between duration of time to respond on a side key after viewing the grating or grey

stimulus and correct responses, incorrect responses, key colour, key position or probe stimulus value. This finding is consistent with that for Experiment 1.1, where latencies also varied unsystematically, bearing no relation to either correct and incorrect responses, key position or probe stimulus value. Latencies for the present study, however, were generally slightly longer than those for Experiment 1.1.

Discussion 2.1

After 142 sessions (more than five months) of training in the present procedure, only one hen had reached 80% accuracy in total performance. This compares unfavorably with the discriminative performance obtained with the procedure used for Experiment 1.1 where five of six hens had obtained over 90% accuracy on the training stimuli in fewer sessions (Table 2.1.2). Because in the present study behaviour had stabilized at a level of accuracy below 80% for most hens, it was necessary to lower the accuracy criterion for commencement of probes. These results are consistent with the findings of Smith (1967) and those of Lyderson, Perkins and Chairez (1973) (cited in Lyderson & Perkins, 1974), where lower accuracy was controlled by the non-spatial, compared to the spatial discrimination task. The duration of training required, and the lower level of discriminative performance obtained at commencement of probes reflects the difficulty of learning a discrimination task where the spatial factor is present but irrelevant, and the comparison stimuli hold an arbitrary relation to the samples.

The procedures used in Experiments 1.1 to 1.5 and the present experiment, involve an exteroceptive chain of responses. The first response causes presentation of further stimuli, i.e. the lit side keys in Experiments 1.1 to 1.5, and the green and red side keys in the present experiment. While for Experiments 1.1 to 1.5 the response to these second stimuli is the same for the grating (peck left) and grey (peck right) on each discrete trial, in Experiment 2.1 the animal must determine the position of the red key following grating presentation, (either left or right) or green key following grey

stimulus presentation (either left or right). Analysis of the present procedure indicates that not one but two discriminations are required by the animal, one following the sample presentation and another following the comparison stimuli presentation. Errors in the spatial conditional discrimination are necessarily made only following presentation of the sample. However, for a non-spatial conditional discrimination where the spatial factor is present but irrelevant, as for present procedure, errors may be made either following presentation of the sample stimulus, or following presentation of the comparison stimuli. That is, an animal may clearly discriminate the grating from the grey sample stimulus, but then make an error discriminating the red side key from the green side key. Inherent position or colour preferences could further serve to confound at this point. Where, in the procedure for Experiments 1.1 to 1.5 position preferences may occur, in the present procedure, colour as well as position preferences may confound, although extreme biases may not occur simultaneously. This is because the red and green keys were programmed to appear on the left and right keys for an equal number of times within a session. If, therefore, an animal developed a position bias, it would necessarily be responding to both red and green keys. Conversely, if a colour bias developed, the animal would be responding equally to both left and right positioned keys. It is assumed that the hens in the present study are visually as capable as the hens in Experiments 1.1 to 1.5. Therefore, any differences in performance are suggested to be the result of the more complex discrimination.

Discriminative performance

The shape of the psychometric functions obtained for total discriminative performance measured either as percentages correct or

in values of $\log d$, closely replicates those functions obtained in Experiment 1.1, but at a lower level. That is, the functions are comprised of the three levels of discriminative performance as for Experiment 1.1, namely a relatively high level of accuracy at the coarsest gratings, the decreasing portion at increasingly finer gratings, and the low relatively flat portion of data at the finest grating values. However, when group data are plotted, each of these portions are at a lower level than shown for group data from Experiment 1.1 (Figure 2.1.2).

In the present study there was generally no consistent difference between discriminative performance for the descending and ascending series of probes, although the ascending series required more training sessions. A similar performance was also generated by both series of stimulus presentation for Experiment 1.1. This indicates that the better discriminative performance under the ascending probe series in Experiment 1.5 may have been due to the use of a procedure in which reinforcers to both alternatives are free to vary with behaviour (i.e. an uncontrolled reinforcement procedure). Both Blough (1971) and Terman (1970), who reported a higher discriminative performance for the descending series, used an uncontrolled reinforcement procedure, also. However, they presented several stimulus values, rather than only one, within each session. This difference in procedure may account for the different results.

Although discriminative performance in the present study generally decreased and levelled off at lower grating spatial frequencies than in Experiment 1.1, a decision was made to continue probes to the finest grating that was used for that study, for

comparison of performance.

Not only was discriminative performance at the coarsest gratings lower in the present study than in Experiment 1.1, but performance at the finer gratings decreased to a slightly lower value, 50% or $\log d$ value of 0.00. That is, generally accuracy remained slightly higher for Experiment 1.1, even at grating values assumed to be indistinguishable.

The psychometric functions in the present series of studies, generated by performance at increasingly finer gratings, bear some resemblance to those functions obtained from the delayed-matching-to-sample (DMTS) procedure (e.g. White, 1985), where discriminative performance decreases as a function of increasing delays between the offset of the sample and the onset of the comparison stimuli. White (1985) suggested that factors relating performance to the delay interval have two characteristics. Firstly, discriminability of the sample stimuli in the absence of the delay and secondly, rate of attenuation in discriminability with increasing delays.

White and McKenzie (1982) and White (1985) compared DMTS performance in pigeons for difficult and easy wavelength discriminations between sample stimuli. While initial discriminability, (the value of $\log d$ at zero delay) was higher for the easy discrimination, there was no difference in the rate of decrement of discriminability as a function of durations of the delay. That is, they found that changing the discriminability of the sample stimuli at zero delay by making it easy or difficult to discriminate,

did not affect the rate at which discriminability diminished as the duration of the delay increased.

White (1985) reported that DMTS performance was well described by a simple negative exponential function with two parameters, one describing initial discriminability at zero delay ($\log d_0$) and the other describing the rate of the decrement in discriminability with increasing delay interval duration (b). Certain parallels may be drawn between behaviour on a visual acuity task and DMTS performance. In DMTS there is the highest discriminative performance at zero delay ($\log d_0$), and in the visual acuity task there is the highest level of discriminative performance generally at the lowest spatial frequency of grating used. In the DMTS procedure, there is attenuation of discriminative performance with increasing delay between offset of the sample and presentation of the comparison stimuli, and in the visual acuity task there is attenuation of discriminative performance at increasing spatial frequency of gratings. White suggests the reduction in $\log d$ during any given interval of delay (b), is proportional to the level of $\log d_0$. If this were extended to the visual acuity task, then the rate of attenuation of discriminability of the stimuli could be proportional to the discriminability obtained at the coarsest grating stimulus. That is, the reduction of discriminability, e.g. $\log d$, as a function of increasing spatial frequency, may be proportional to $\log d$ at the coarsest grating value.

White's (1985) equation which describes discriminative performance in the DMTS procedure is as follows:

$$\log d_t = \log d_0 \cdot \exp (-bt) \quad (9)$$

where $\log d_0$ refers to $\log d$ at no delay, b is a fitted constant.

The decrement in discriminability which occurs over a small change in time from sample presentation, $-bt$, is proportional to discriminability at zero delay from sample presentation ($\log d_0$). It is immaterial whether the interval starts from zero delay or a time greater than zero delay. The constant of proportionality is b .

It may be possible, therefore, to extend this equation to describe discriminative performance on a visual acuity task, as follows:

$$\log d = \log d_0 \cdot \exp (-bsf) \quad (10)$$

where $\log d_0$ is discriminability at the lowest frequency grating (i.e. 1 c/mm) and $-bsf$ refers to the decrease in discriminability ($-b$) as a function of increasing spatial frequency (sf) of gratings. If this equation holds, then the decrement in discriminability which occurs over a small change in spatial frequency (sf), should be proportional to discriminability at the lowest spatial frequency (1 c/mm) or $\log d_0$. It is immaterial whether sf increases from 1 c/mm or a value greater or less than 1 c/mm, as behaviour measured at that point would still be known as $\log d_0$. The constant of proportionality is b (with units of $-sf$). Therefore, the parameters of the negative exponential function provide a measure of initial discriminability at the coarsest grating ($sf = 1$ c/mm or $\log d_0$) and the rate of decrement in discriminability with increasing spatial

frequency of gratings, b .

McCarthy (1981), however, suggests that DMTS performance could be better described by a rectangular-hyperbolic function according to the equation:

$$\log d_t = (h/h + t)\log d_0 \quad (11)$$

where $\log d_t$ is a measure of discriminability at time t , $\log d_0$ is the initial discriminability of the sample, $\log d$ at zero delay, and h is the "half-life", or time at which the function decreases to half of the initial value. Such a model might also be extended to account for discriminative performance in a visual acuity task, where t is replaced by sf (grating spatial frequency).

To determine their utility in describing the characteristics of discriminative performance in a visual acuity task, functions from each of these models were fitted to the mean $\log d$ values for the present study and Experiment 1.1. As the negative exponential function accounted for slightly more variance than the hyperbolic function, the former was fitted to the group data in Figure 2.1.11. Data from the descending probe series for both experiments are shown in one figure, and data from the two ascending probe series are shown in the other. The negative exponential functions (Equation 10) fitted to the data are described in the figures. The functions describe the data well, accounting for 90% or more of the data variance.

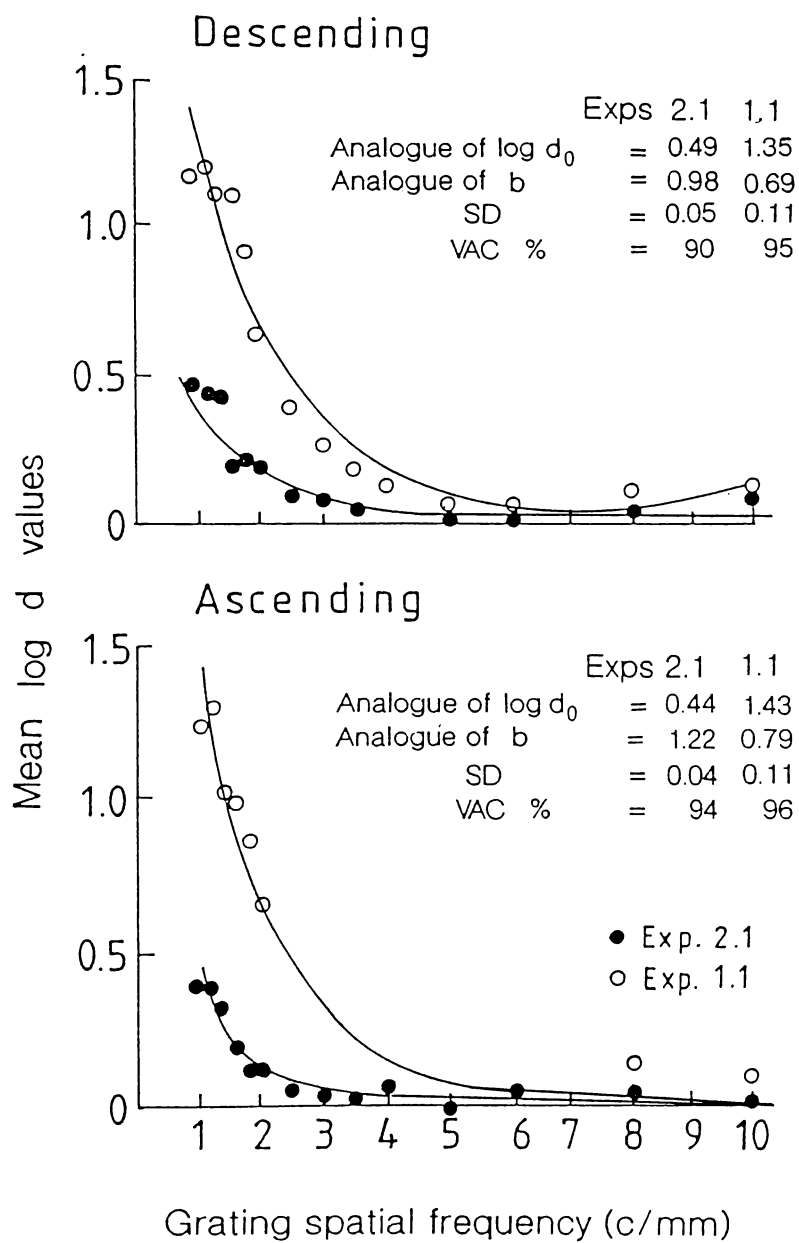
The analogue of $\log d_0$ is 0.49 and 0.44 for the descending and ascending series of probes for the present study, compared to 1.35

Figure 2.1.11

Figure 2.1.11

Mean values of $\log d$ plotted as a function of grating spatial frequency for group data from Experiments 2.1 and 1.1, for the descending and ascending series of probes. Data from Experiments 1.1 and 2.1 are shown as two separate functions in the same figure.

A negative exponential function has been fitted to the data from each experiment for each probe series. The functions and the parameter descriptions are shown in the figures.



and 1.43 for the descending and ascending series of probes from Experiment 1.1. The analogue of b , the rate of decrement of discriminative performance at increasingly finer gratings, is 0.98 and 1.2 respectively, for the descending and ascending series of probes in the present experiment, compared to 0.69 and 0.79 for the equivalent probe series from Experiment 1.1. For both probe series, the analogue of $\log d_0$ was greater for data from Experiment 1.1, and the analogue of b was less for Experiment 1.1 than the present study. That is, not only was initial discriminability (the analogue of $\log d_0$) much less for both probe series in the present study, but the rate of decrease of accuracy at increasingly finer gratings was greater.

Discriminative performance in a visual acuity task thus can be described by two parameters, discriminability at the coarsest grating and the decrement of discriminability at increasingly finer gratings. Where the use of discriminability measures which include response bias (percentage correct) and those which are assumed to be independent of response bias ($\log d$) necessarily only describe the overall discriminative performance at each stimulus value, both characteristics of performance may be quantified in terms of an analogue of the parameters of a negative exponential function ($\log d_0$ and b).

In the present study, as for Experiment 1.1, discriminative performance increased slightly for some hens at the finest grating value. In the earlier discussion it was suggested that this is either "spurious resolution" which may occur with gratings of certain frequencies which are not readily resolved (O'Neill, 1963) or the

result of detection of wavy edges of fine grating stimuli which may act as cues (Millidot, 1973). The fact that such an increase should also occur in the present study lends some support to the previous suggestion that this apparent increase in discriminability is an artefact of the finer grating stimuli rather than the actual procedure.

Response distributions

The separate response distributions for grating and grey trials in the present study were very similar to those presented in Experiment 1.1, but at a lower level of accuracy. Generally, as hens made errors on grating trials at finer gratings, they also made errors on grey trials. Although there was some slight disparity between grating and grey trial accuracy at some grating values, generally the functions are similar to that hypothetical response distribution depicted as Diagram A, in Figure 1.5.1 (Experiment 1.5), suggested to be more likely to occur with a controlled reinforcement procedure.

The grating and grey trial response distributions for both probe series were similar. The ascending and descending series of stimulus presentation have been reported to generate series effects, e.g. habituation in reporting in a certain way (Blough & Blough, 1977). However, when these probe series are separated by training sessions and a controlled reinforcement procedure is used, this does not seem to occur. If such effects did occur, they would show as a bias towards reporting that a grating was present (i.e. increase in red key responding) at finer grating values for the descending series, and as a bias towards reporting that a grey stimulus was present (i.e. increased green key responding) at coarser grating values for the

ascending series. The separate response distributions for grating and grey trials might thus show a higher percentage of correct grating than grey trials for the descending series at intermediate grating values, and a higher percentage of correct grey than grating trials for the ascending series, at intermediate grating values. However, since such response distributions were not obtained for the present study (Figure 2.1.3), habituation was not shown.

Thresholds criteria, estimates and fitted lines

By employing the same criteria and analyses it was possible to compare estimates of threshold obtained from the data for the present study, with those from Experiment 1.1. As a product of discriminative performance, those estimates from the present study generally reflected the lower accuracy obtained, compared with those of Experiment 1.1. For most hens' data, in Experiment 1.1, to estimate threshold value at the point of 50% accuracy or a log d of 0.00, it was necessary to extrapolate a line from the last 2 points on the descending portion of the data, because data did not always fall to that value. In the present study, however, accuracy generally decreased to 50%, or a log d value of 0.00. The use of a single data point to estimate the grating value which the animal can resolve on 50% of trials however, is problematic, due to random fluctuations of the data, which may be the result of other than sensory factors. For example, in some cases, performance in the present study fell to an accuracy level of 50% or log d of 0.00 at a particular grating value but, for the next few finer grating values, increased to a higher level of accuracy, prior to decreasing again. In such a case, a decision must be made, either to take the estimate from the first data point at 50% (which may have been result of random fluctuation), or

the second point, (because of evidence of discriminability following the first fall in accuracy). That is, certain assumptions must necessarily be made about the behaviour.

The present study helps clarify the problems involved in estimating thresholds from the fitted line using a value of $\log d$ of 0.00 as the criterion. That is, when a line is fitted to a descending portion of data which indicates low initial discriminability, (as was generally the case in the present study), the best fit line has very little slope and generally includes those data best described by a flat line. This problem occurred to some extent in Experiment 1.1 especially when various transformations of stimulus values resulted in a greater spread of data points comprising the descending portion, but it has been compounded in the present study, because of the generally lower level of accuracy at the coarser grating values.

Estimates of threshold from the fitted line at a $\log d$ value of 0.48 (from the data of those hens whose performance reached this level of accuracy), generally yielded values close to those from the other criteria ($\log d$ value of 0.48 and the point of 75% accuracy on total trials) regardless of the transformation of stimulus values. This is in accordance with the results for Experiment 1.1. But generally, as for Experiment 1.1, the stimulus value taken as the estimate of threshold at the point where the fitted line crossed the X-axis at a $\log d$ value of 0.00, provided a much wider range of estimates than obtained from the fitted line at the $\log d$ value of 0.48. To reiterate from Experiment 1.1, any line fitted to the descending portion of the data will tend to pivot around the point of the $\log d$

value of 0.48, as in most cases the line describes data lying both above and below this value. As a result, thresholds estimated from the point of a $\log d$ value of 0.48 would not be greatly affected by inclusion of data which did not indicate discrimination and are best described by a flat line. On the other hand, any threshold estimated from the $\log d$ value of 0.00 would be greatly affected by inclusion of these data which did not indicate discriminability. This is because the fitted line may cross the x-axis at different stimulus values, depending on the spread of these lower data points along the x axis, and this spread of data may change with various transformations of the stimulus values.

In summary, the determination of any estimate of threshold, as the best description of the discriminative performance, is beset with problems. It seems that these problems are compounded when initial discriminative performance is at a low level. Blough and Blough (1977) suggest that the inclusion of more than one data point contributes to the reliability of the threshold estimate. Perhaps then, it is more appropriate to take into account all of the descending portion of data, using a line of best fit. Terman (1970), Blough (1971) and McCarthy (1983) first excluded data points which were not a part of the descending portion of the function before fitting lines to normalized data. However, such normalized data, unlike values of $\log d$, are not independent of response bias. In the present series of studies, when several pairs of lines were generated by the method of least squares, the line chosen was that which best fitted the data (i.e. had the least standard error), but only if that data it described was clearly part of the descending portion, excluding those data best described by a flat line.

Stimulus control

Blough (1966) suggested that a procedure which generates a high level of baseline discriminative performance is more likely to maintain control over behaviour as the discrimination task becomes more difficult. The easier the discrimination task, the more likely that the animal will attain a high level of baseline discriminative performance. The present study illustrates the problem of maintenance of stimulus control at finer gratings when initial accuracy at the coarsest gratings is low. For example, it was necessary to waive hen 35's accuracy criterion for continuing probes when, following five days of intervening training sessions prior to resumption of probes, accuracy remained more than 10% below her most accurate performance in the last five days' training prior to commencement of probes. A similar change in probing criterion was made for hen 73 in Experiment 1.1. Her discriminative performance prior to commencement of the first probe series was also the least accurate of the six hens.

When stimulus control is maintained by intervening training sessions, prolonged probe sessions on indiscriminable stimulus values do not affect accuracy on coarser gratings in a simple spatial conditional discrimination procedure as Experiment 1.1. On a more difficult discrimination task such as the present procedure however, it appears that the maintenance of stimulus control may require a greater number of intervening training sessions. The use of the more difficult non-spatial discrimination procedure then, not only results in a greater number of training sessions to acquisition, but also a greater amount of training sessions between probes, compared to the more simple spatial conditional discrimination task used for

Experiments 1.1 to 1.5.

Response bias

There are some indications that pigeons peck more readily at certain colours than at others (Blough, 1966). For example, Hess (1956) found that chicks preferred to peck at orange and blue panels in preference to yellow. In addition, Pisacreta (1982) reported that, given the opportunity, pigeons will demonstrate colour matching preference. Artefactual colour preferences, then, may be a problem when the comparison stimuli are coloured keys bearing an arbitrary relation to the sample stimuli. Where color biases were evident, in the present study, there was an indication of more green key responding as gratings became finer, indicating that hens were treating gratings as grey stimuli. The controlled reinforcement procedure, though, tends to prevent the development of extreme colour preferences. Position biases, however, which were uncontrolled, varied greatly across the different levels of stimulus discriminability, for both probe series. In the present study, the relative reinforcer ratio for correct red and green key responses was controlled, while in Experiment 1.1 the relative reinforcer ratio of correct left and right key responding was controlled.

Position preferences or repeated errors to one side key which occurred in the present study, have been reported in many studies of matching (e.g. Cumming & Berryman, 1961; Farthing & Opuda 1974). The procedures in these DMTS studies, as for the present study, did not control the relative reinforcer ratio for correct responding to the left and right response alternatives. They reported that position biases were especially strong while the animals were acquiring the

task, and at increased delays. The latter would be analogous to the development of position biases at the finer gratings in present study. Some previous studies, however (e.g. Holmes, 1979) used a correction procedure to minimize these biases.

Although the hens in present study could have developed exclusive biases for position, and yet maintain equal responding to red and green keys, they did not. Instead, position biases varied across different levels of stimulus discriminability with the least amount of position biases at the coarsest grating values. This is consistent with Experiment 1.5 when an uncontrolled reinforcement procedure was used. Data in the present study then produced both iso-bias and alloio-bias functions for colour and position, respectively, consistent with the controlled and uncontrolled components of the procedure (McCarthy, 1983).

The need to minimize response bias is very important in psychophysical studies (Blough & Blough, 1977). However, it is possible that too much constraint within a procedure (i.e. controlling the relative reinforcer ratios for correct responses to both key colour and to key position) may result in too few reinforcers and a subsequent termination of responding.

Latencies

The latencies for the present study, as for those from Experiment 1.1 showed no systematic relation either between correct and incorrect responses or to different levels of stimulus discriminability. This supports the suggestion in the discussion of Experiment 1.1 (Blough, 1971) that perhaps these procedures and stimulus types are not

conducive to the generation of differential latencies. The slightly longer latencies generally found in the present study, compared to those for Experiment 1.1, are possibly due to the more complex discrimination required. Maybe, therefore, the longer latencies reflect the overall difficulty of the task, rather than difficulty within the task, that is, discrimination at finer gratings.

Conclusion

The important finding here, is that the level of discriminative performance is a function of a combination of sensory capacity and the difficulty of the discrimination task. The difficulty of a task which generates behaviour assumed to reflect the animal's sensory functions must therefore be taken into account when comparing sensory functions either between species or within a particular species. The difference in task difficulty then, may be another variable to take into account when determining the cause of disparity in estimates of sensory thresholds across different studies with the same species. For example, Bloch and Martinoya's (1982) lower threshold estimates (in c/deg) obtained for discriminative performance of pigeons in a visual acuity task, compared to those reported by Blough (1971) and Hodos, Leibowitz and Bonbright (1976), were probably a result of the short presentation time of the sample stimulus (300 ms). It is possible that this shorter presentation time would make the discrimination task more difficult. Likewise, the disparity between the estimates reported by Johnson (1914) at around 5 c/deg for hens on a visual acuity task, and those reported by Over and Moore (1981) of 1.2 c/deg for young chickens, may be a result of a more difficult discrimination task for the younger animals, rather than a difference in visual functioning, *per se*. A parallel may be drawn between the

difference in threshold estimates obtained in those two studies and the difference in estimates obtained in Experiment 1.1 and the present study.

The complexity of a task for any particular species of animal does appear to change discriminative performance, not only at coarser gratings but also at finer grating values. Discriminative performance is thus not only a product of sensory capacity but also a product of the constraints of the procedure. Comparison of discriminative performance under the two different procedures therefore aids in the understanding of the processes of such constraints. Perhaps the spatial conditional discrimination task used in Experiments 1.1 to 1.5, whilst easier than that of the present procedure, involved a more difficult discrimination for the hens than some other discrimination procedure. If this is true, then a more simple task may result in a higher level of discriminative performance, as reflected by greater estimates of threshold. However, while a simple discrimination task may provide greater estimates of threshold, thus more closely approaching the possible limits of a sensory function, a lower level of discriminative performance under a more complex procedure may be a useful source of information regarding the effects of various procedural constraints upon behaviour.

EXPERIMENT 2.2

Results of Experiment 2.1 indicated that the greater difficulty of the animals' task effectively lowered discriminative performance, compared to that for Experiment 1.1 at most grating values. Lower threshold estimates were obtained than those from Experiment 1.1, indicating less acute vision. It appears, therefore, that the complexity of a task may be an important factor to consider when attempting to test the limits of an animal's discriminative performance.

When the response requirement to the sample key was increased in Experiment 1.2, discriminative performance improved, and resulted in greater estimates of threshold than those obtained with a single response requirement. It was possible that the animals had learned to discriminate well before demonstrating this with a multiple response requirement. Discrimination decreased upon return to a single response requirement. A response requirement greater than FR1 may have therefore provided the necessary condition for the animals to demonstrate what they had already learned.

The rationale for the present study was the same as that for Experiment 1.2, namely that the FR response requirement to the sample key was increased, to determine:

- (a) whether this would improve baseline performance, and if so,
- (b) the FR response requirement at which discrimination was generally the most accurate,
- (c) whether increased accuracy was maintained upon returning to FR1, and finally,

(d) to compare these results with those obtained from Experiment 1.2 to ascertain whether, and in what manner the greater difficulty of the task affected discriminative performance.

Method 2.2

Subjects and Apparatus

The six hens serving in Experiment 2.1, numbered from 31 to 36, served. The apparatus was the same as that used for Experiment 2.1. The luminance was maintained at 3 cd/m².

Procedure

The procedure was similar to that used in Experiment 2.1. The reinforcement schedule, at VI 30 s, and the controlled reinforcement procedure, were the same. There were several variations from Experiment 2.1. There were two conditions which involved an increase in the response requirement to the sample key, to FR5 for the first condition, and to FR10 for the second. Hens were trained to an accuracy and a stability criterion, as for Experiment 2.1.

When the criteria of Experiment 2.1 had been satisfied, hens were tested with a descending series of probes, commencing with probes at gratings of the lowest spatial frequency. The number of probe stimuli were decreased from 14 to seven. However, the range of values used for probes remained the same, from 1 to 10 c/mm. Grating values used for probes were 1, 2, 3, 4, 6, 8 and 10 c/mm. The hens took 26 days to reach stability under the FR5 training condition and 15 days under the FR10 training condition. Upon completion of the series of probes with each response requirement, hens were trained for approximately five days with an FRI response requirement before the next training condition. Data were collected as for Experiment 2.1.

Results 2.2

Discrimination

Figure 2.2.1a shows the percentages of total trials correct as a function of grating spatial frequency, measured in c/mm, for all hens, for both probe series. Data from the descending probe series in Experiment 2.1, with a response requirement of FR1, are also shown for comparison. These data include those from probe stimuli not used in the present study, and are plotted in the figures as filled circles joined by a broken line. For all hens and all probe series, the percentages of total trials correct was a monotonically decreasing function of probes with gratings of increasing spatial frequency to 2 - 3 c/mm, and levelled off at approximately 50% accuracy. Higher accuracy at the coarsest grating value only, for most hens, was obtained with FR5 and FR10, compared to probes with the single response requirement.

Figure 2.2.1b presents the percentages of total trials correct as in the previous figure, but for probes at three gratings only (1, 2 and 3 c/mm), with each of the three response requirements. For three hens, 31, 32 and 34 accuracy at the coarsest grating was the same for probes with the FR5 and FR10 response requirements, although the improved performance was slightly better maintained at the 2 and 3 c/mm gratings for probes with the FR5 response requirement. For one hen only, 33, performance at the coarsest grating was most accurate for probes with FR10. For hen 36, accuracy at the first two coarsest gratings was highest for probes with FR1.

The threshold estimates for all hens and for each response

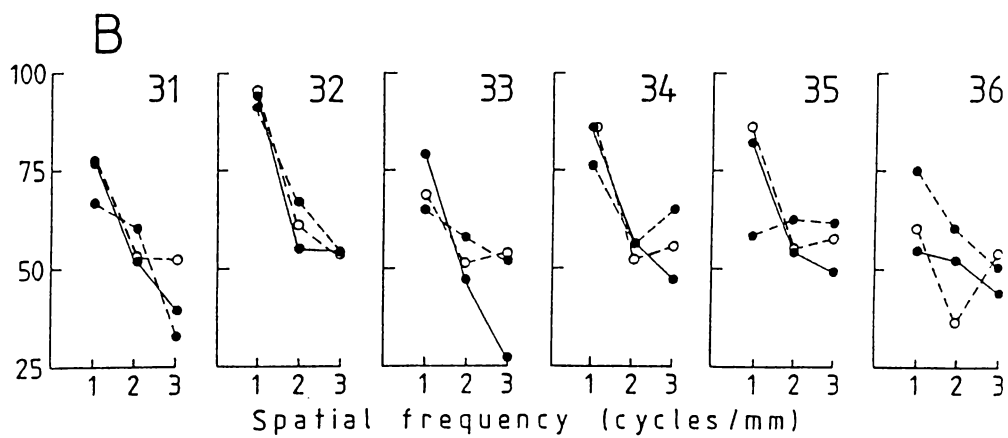
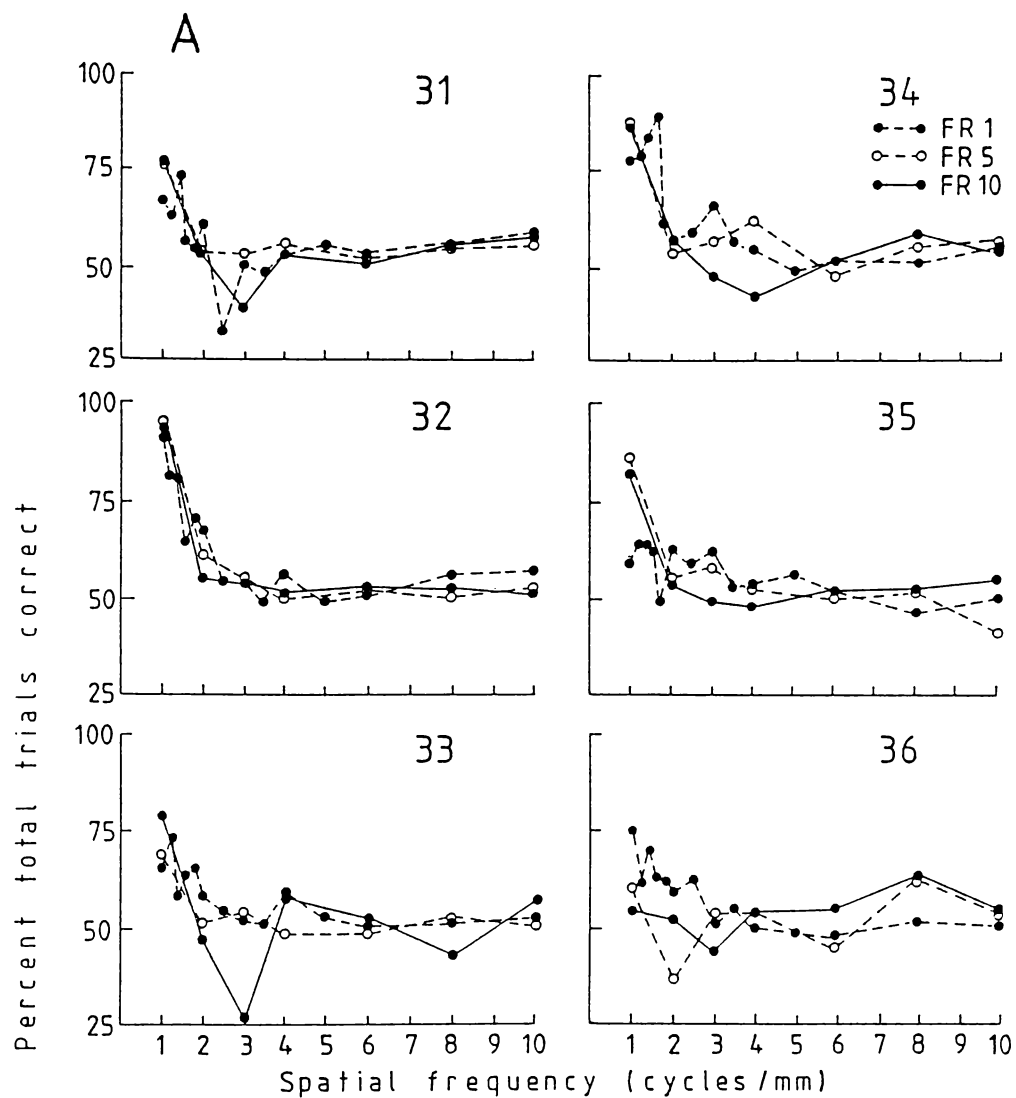
Figure 2.2.1

Figure 2.2.1a

The percentages of total trials correct plotted as a function of grating spatial frequency, measured in c/mm, for the probe series with the FR5 and FR10 response requirements. Data from the descending probe series(Experiment 2.1) are shown in the figures as filled circles joined by a broken line.

Figure 2.2.1b

The percentages of total trials correct, plotted as a function of the spatial frequency of three gratings (1,2 and 3 c/mm) for all hens, for the probe series with the FR5 and FR10 response requirements. Data for the descending probe series with the FR1 response requirement are also shown(Experiment 2.1) (filled circles joined by a broken line),



requirement were determined as that spatial frequency of the grating at which 75% of the total trials were correct. This was obtained by interpolation, as in Experiment 2.1. For some hens it was not possible to estimate thresholds, because total trial accuracy did not reach 75%. Threshold estimates (c/deg), are shown in Table 2.2.1 as Criterion 1. Those from the descending probe series with the FR1 response requirement (Experiment 2.1) are included for comparison. Estimates range from 2.2 c/deg for probes with the FR5 and FR10, to 3.4 c/deg for probes with FR1. One of the two estimates which could be compared across probes with the three response requirements was greater for probes with FR5 than for probes with either FR1 or FR10. For hen 34, the estimate from probes with FR1 was greater than those estimates from probes with either of the higher response requirements.

Figure 2.2.2 presents the mean percentages of total trials correct as a function of grating spatial frequency, measured in c/mm, for group data from the six hens in the present study and six hens in Experiment 1.2, for the series of probes with the FR5 and the FR10 response requirements. The two functions from the probe series with FR5 for the present study and Experiment 1.2 are shown in one graph and those for the probe series with FR10 are shown on the other graph, for comparison. Data from the present study show a lower discriminative performance than those from Experiment 1.2 at all grating values, for both probe series.

Figure 2.2.3 presents the mean and range of the percentage of total trials correct for:

(a) the last five days' training prior to probes with an FR1 response requirement (from Experiment 2.1),

Table 2.2.1

Table 2.2.1

Threshold estimates measured in c/deg, from the various methods of analysis and criteria, for all hens, for the probe series with the FR5 and FR10 response requirements. Estimates from the descending probe series with the FR1 response requirement (Experiment 2.1) are also shown, for comparison.

Where estimates were determined from the fitted line (Criterion 5), 95% confidence intervals are given in brackets.

Hen	Threshold Criteria	Response Requirement		
		1 (Exp 2.1)	5	10
31	1	*	2.2	*
	2	3.0	7.0	3.8
	3	2.8	*	2.4
	4	*	2.2	2.2
	5	*	2.0 (0.4)	2.0 (0.2)
32	1	3.0	3.2	2.8
	2	3.2	3.8	3.6
	3	2.8	2.8	2.8
	4	3.0	3.2	2.8
	5	3.0 (0.3)	4.6 (0.5)	4.4 (0.8)
33	1	*	*	2.2
	2	4.8	3.8	3.6
	3	2.2	*	2.6
	4	*	*	2.6
	5	*	*	1.6 (0.9)
34	1	3.4	2.6	2.6
	2	3.0	3.4	3.4
	3	2.8	2.2	2.6
	4	3.0	3.0	3.0
	5	2.6 (0.3)	3.2 (0.4)	3.0 (0.4)
35	1	*	2.8	2.4
	2	3.2	3.4	3.4
	3	2.8	2.0	2.4
	4	*	3.2	2.6
	5	*	4.0 (0.6)	2.4 (0.4)
36	1	*	*	*
	2	4.8	2.6	2.0
	3	2.2	*	*
	4	2.2	*	*
	5	0.6 (0.2)	*	*

* Estimate not calculable

Criteria: 1 = 75% total trials correct

2 = 50% grating trials correct

3 = 75% grating trials correct

4 = log d value of 0.48

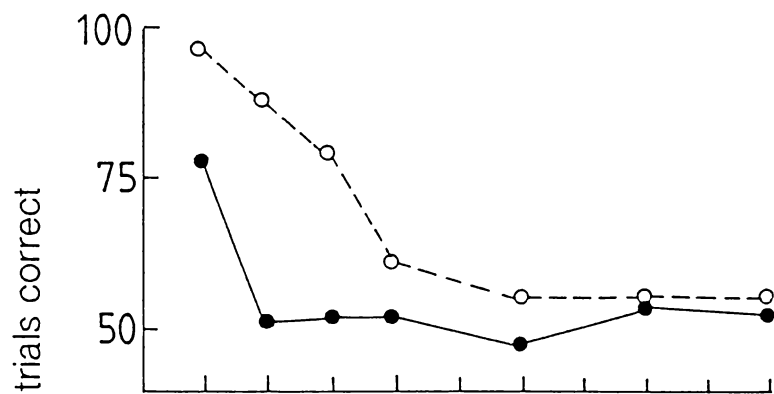
5 = determined from fitted line
at a log d value of 0.48

Figure 2.2.2

Figure 2.2.2

The mean percentages of total trials correct, plotted as a function of grating spatial frequency, measured in c/mm, for group data from the present study (filled circles) and Experiment 1.2 (unfilled circles), for the series of probes with the FR5 and the FR10 response requirements. The two functions for the probe series with FR5 are shown in one figure, and the two functions for the probe series with FR10 are shown in the other figure for comparison.

FR5



FR10

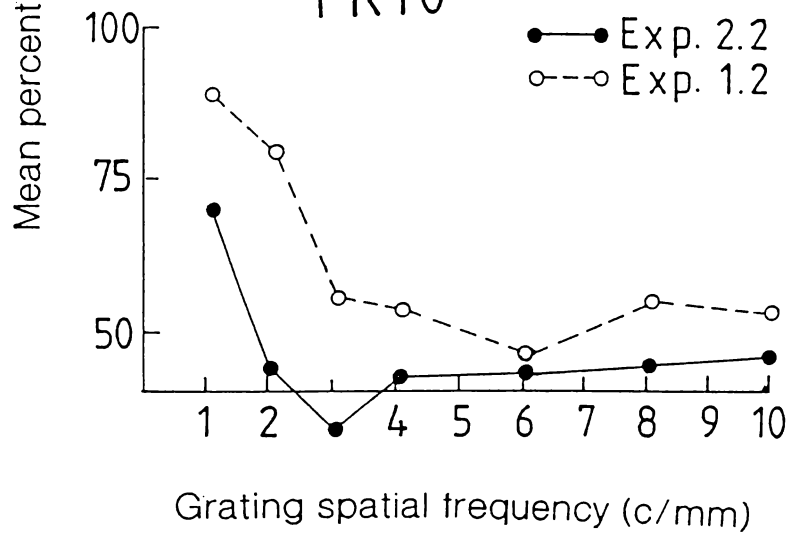
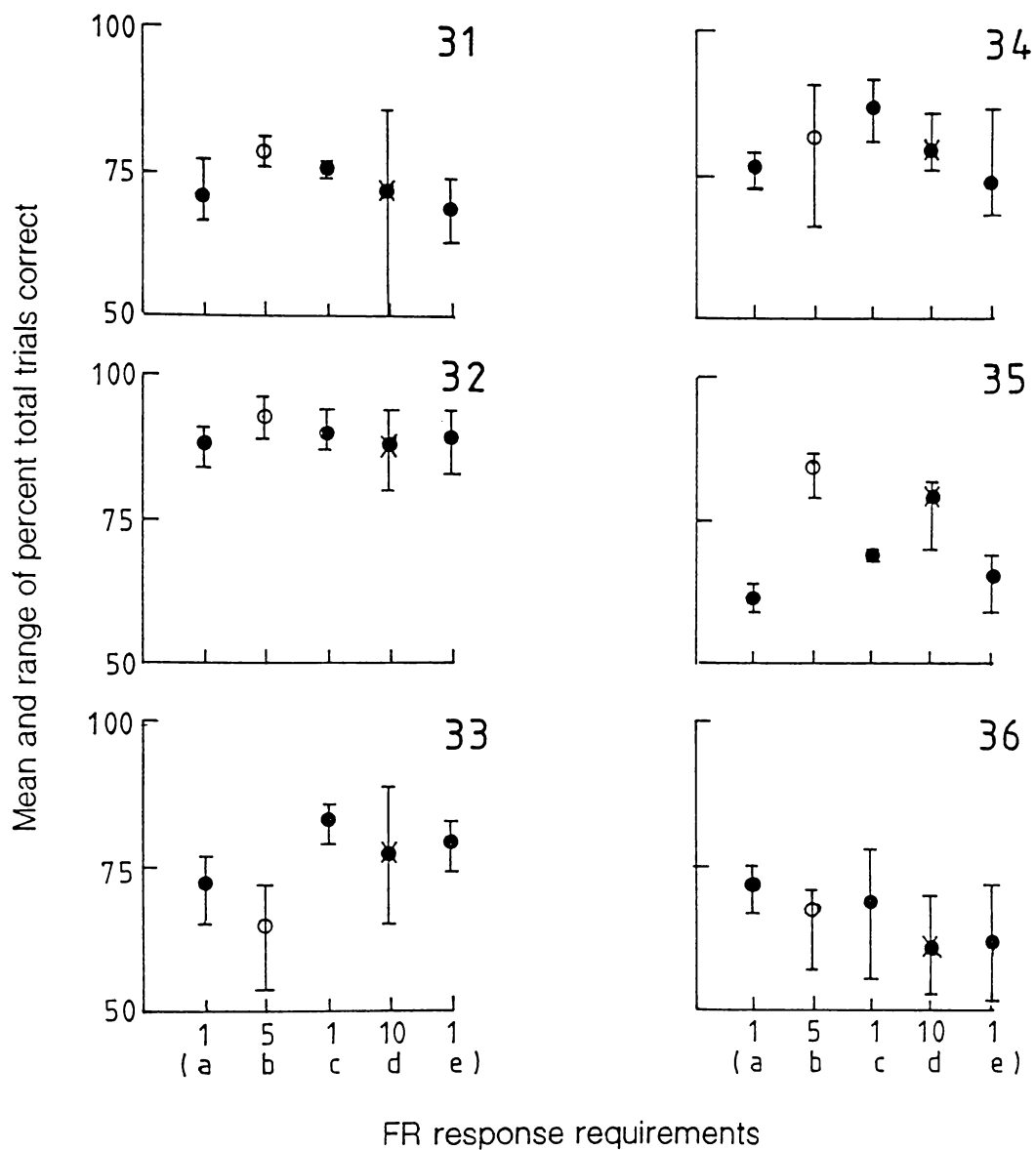


Figure 2.2.3

Figure 2.2.3

The mean and range of the percentages of total trials correct for:

- a) the last five days' training prior to probes with an FRI response requirement (Experiment 2.1)
- b) the last five days' training prior to probes with an FR5 response requirement
- c) five days' training with an FRI response requirement, following probes with the FR5 response requirement.
- d) the last five days' training with an FR10 response requirement, prior to the probe series with that response requirement.
- e) another five days' training with an FR1 response requirement, following the probe series with an FR10 response requirement.



- FR1 ○ FR5 ✕ FR10
- a last five training sessions with FR1 prior to FR1 probes
 b last five training sessions with FR5 prior to FR5 probes
 c five sessions with FR1 following FR5 probes
 d last five training sessions with FR10 prior to FR10 probes
 e five sessions with FR1 following FR10 probes

- (b) the last five days' training prior to probes with an FR5 response requirement,
- (c) five days' training with an FR1, following probes with FR5,
- (d) the last five days' training with an FR10 response requirement prior to the probe series with that response requirement, and
- (e) another five days' training with FR1, following the probe series with the FR10 response requirement.

Results indicate that, for four of six hens, accuracy was higher when training with FR5, compared to training with an FR1 response requirement. For three of six hens, 31, 32, and 35, the most accurate mean performance was obtained for training with an FR5 response requirement. Two of these hens showed a decrement in performance upon returning to training with an FR1 following the probe series with an FR5 response requirement. Only one hen's performance improved upon return to training with an FR1 response requirement. For two hens, 33 and 36, only, performance was most accurate when training with an FR1 response requirement. These two hens also show the lowest accuracy in performance for each probe series.

Figure 2.2.4a shows the percentages of correct responses made on grating trials and grey stimulus trials separately, plotted as a function of grating spatial frequency, measured in c/mm, for the two probe series with the FR5 and the FR10 response requirements. Data from the descending probe series with the FR1 response requirement (Experiment 2.1), are also presented, for comparison. Figure 2.2.4a shows that, for some hens, especially 34 and 35, the functions from the grating and grey trials become more disparate at probes with the higher response requirements compared to functions generated with a

Figure 2.2.4

Figure 2.2.4a

The percentages of correct responses made on grating and grey stimulus trials, plotted separately, as a function of grating spatial frequency, measured in c/mm, for all hens, for the probe series with the FR5 and FR10 response requirements. Data from the descending series (Experiment 2.1) with the FR1 response required are shown for comparison.

A

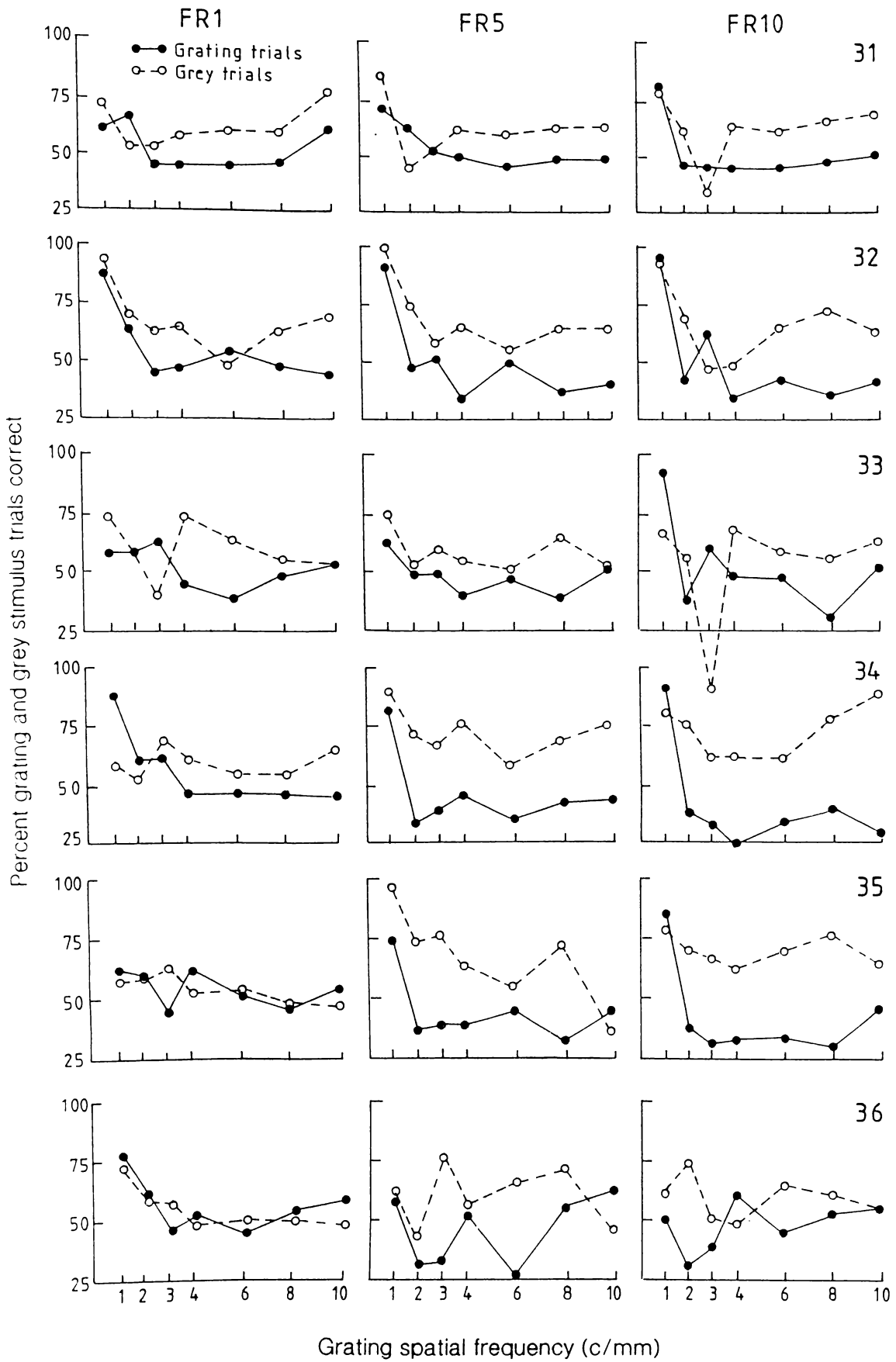
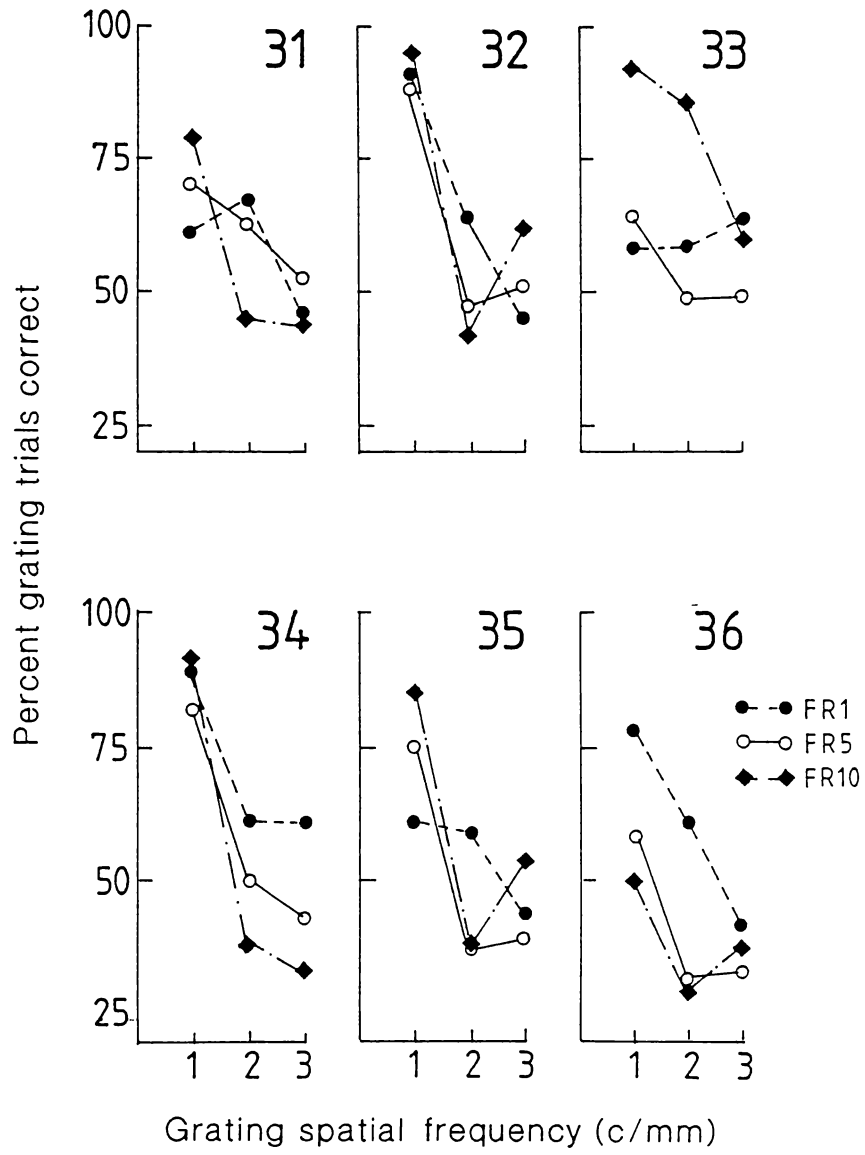


Figure 2.2.4b

The percentages of correct grating trials, plotted as a function of grating spatial frequency, measured in c/mm, for three gratings only (1, 2 and 3 c/mm), for all hens, for the series of probes with the FR5 and FR10 response requirements. Data from the descending series with the FR1 response requirement (Experiment 2.1) are also presented.

B



single response requirement. For other hens, the functions for grating and grey stimulus trials are similar across all three probe series.

Figure 2.2.4b presents the percentages of grating trials correct only, plotted as a function of the spatial frequency of three gratings (1, 2 and 3 c/mm), for all hens, for each of the three probe series with the FR1, FR5 and FR10 response requirements. The percentages of grating trials correct were higher for five hens at the coarsest grating (1 c/mm) for probes with FR10 than for probes with either the FR1 or FR5 response requirement. However, this superior performance was not maintained at all three of the coarsest gratings. These data indicate that the higher total accuracy at 1 c/mm shown for FR5 compared to probes with FR10 (Figure 2.2.1) for hens 32, 34 and 35 was the result of an increase in accuracy on grey stimulus trials rather than higher accuracy on grating trials.

The threshold estimates based on the grating trials only, were taken from the points at which the plotted functions were 50% correct, as for Experiment 2.1. These estimates are shown in Table 2.2.1 as Criterion 2. They range from 2.0 c/deg for probes with the FR10 to 7.0 c/deg for probes with the FR5 response requirement. None of the estimates taken from probes with an FR10 response requirement were greater than those obtained from probes with either FR1 or FR5. Threshold estimates taken from the points at which the plotted functions were 75% correct are also shown in Table 2.2.1 and referred to as Criterion 3. They range from 2.0 c/deg for probes with FR5, to 2.8 c/deg for probes with the FR1, FR5 and FR10 response requirements. Estimates for three hens (31, 33 and 36) could not be determined for

the FR5 probe series, and an estimate for hen 36 could not be determined for the FR10 probe series, as grating trial accuracy was less than 75%. Three threshold estimates were greater for probes with the FR1 than for probes with the FR5 or FR10 response requirements. For one hen, estimates obtained with probes at each of the three response requirements were the same.

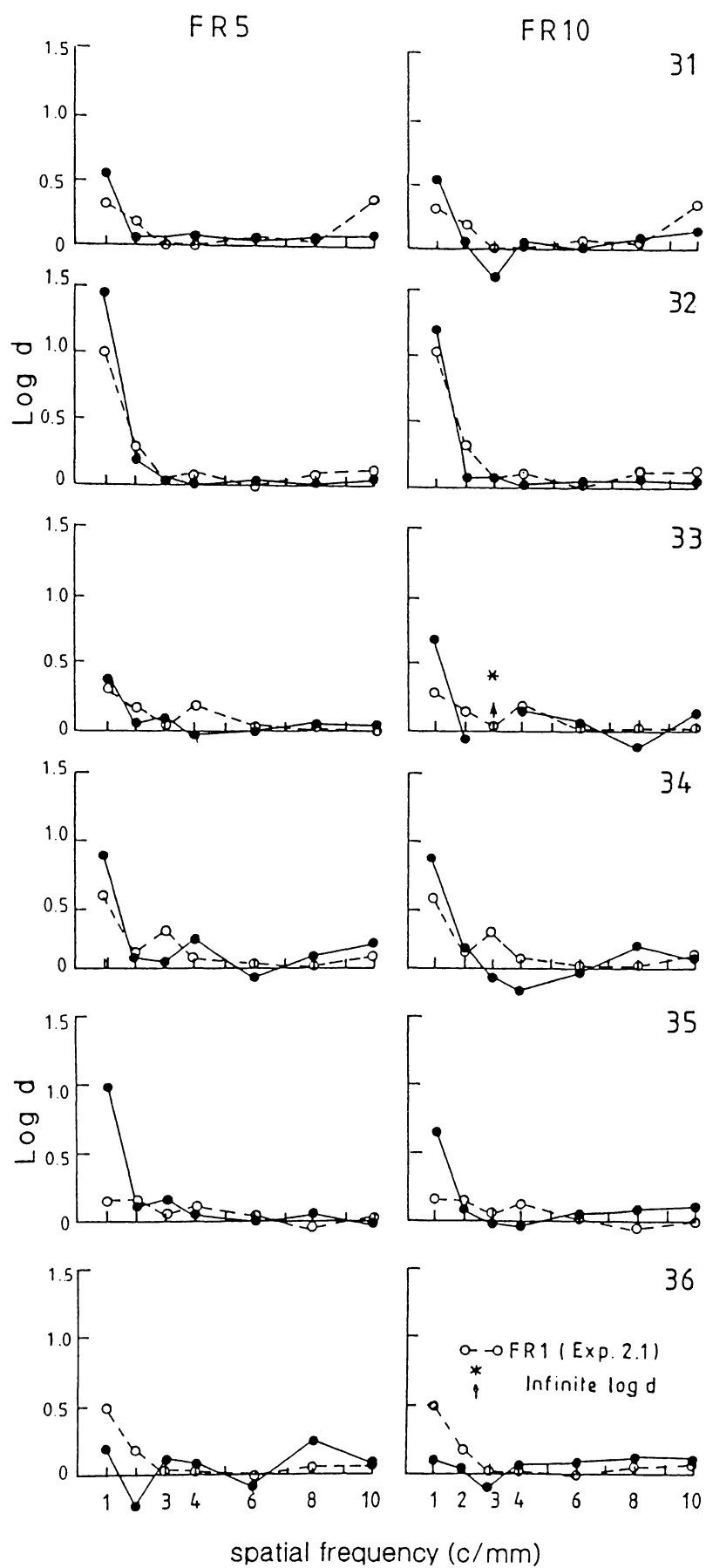
Figure 2.2.5 presents values of $\log d$ plotted as a function of the spatial frequency of gratings, measured in c/mm, for each hen and for each probe series. The data generally show a monotonically decreasing function which flattens out at the 2 - 3 c/mm grating values, and remains relatively flat at around a $\log d$ value of zero. For hen 36, however, and for probes at both of the increased response requirements, very low $\log d$ values were obtained at the coarsest grating value, and the total function is quite flat. For this hen, $\log d$ values for probes at the coarsest grating were no higher than those from probes at the finest gratings. There was no particular response requirement which resulted in higher $\log d$ values at all three coarsest gratings, over all hens, but generally, the FR5 response requirement yielded slightly higher $\log d$ values than FR10 at the coarsest gratings for most hens.

Threshold estimates were obtained by interpolation (as in Experiment 2.1) to determine the spatial frequency of grating which corresponded to a $\log d$ value of 0.48. These are shown in Table 2.2.1 as Criterion 4, and range from 2.2 c/deg for probes with FR1, FR5 and FR10, to 3.2 c/deg for probes with the FR5 response requirement. Estimates could not be determined from the data of two hens, 33 and 36, for the FR5 probe series and one hen, 36, for the FR10 probe

Figure 2.2.5

Figure 2.2.5

Values of $\log d$ plotted as a function of grating spatial frequency, measured in c/mm, for all hens, for the probe series with the FR5 and FR10 response requirements. Data from the descending probe series with the FR1 response requirement (Experiment 2.1) are shown in the figures as unfilled circles joined by a broken line.



series, as $\log d$ values for probes at the coarsest grating were less than 0.48.

The same $\log d$ values from Figure 2.2.5 are plotted in Figure 2.2.6 for hens 32 and 36 only, as an example of the most and least accurate performance, and a line has been fitted to the descending portion of the data for all hens, by the method of least squares (as in Experiment 2.1). The lines fitted to the data from hens 32 and 36 are shown in the figures. Table 2.2.2 describes the slope, intercept, the number of data points described by the fitted line, the standard error of the line fit and variance accounted for (VAC%) by each line chosen to fit the data for each hen, for the probe series with the FR5 and FR10 response requirements. Eight of the 12 fitted lines were those with the least standard error. They were the lines fitted to data from both probe series for hens 31, 32 and 35 and lines fitted to the data from the FR10 probe series for hens 34 and 36.

To determine threshold estimates, the stimulus value corresponding to a $\log d$ value of 0.48 was estimated from the fitted line (as in Experiment 2.1). Estimates could not be determined from the data of two hens, as the intercept of the fitted line crossed the Y-axis at a $\log d$ value less than 0.48. These estimates are presented in Table 2.2.1 as Criterion 5. Estimates from the descending series with the FR1 response requirement (Experiment 2.1) are included for comparison. The 95% confidence intervals, derived from the standard error of the line fit, are also presented in brackets. The estimates range from 0.6 c/deg for probes with FR1, to 4.6 c/deg for probes with the FR5 response requirement. Generally, the greatest estimates of thresholds were taken from probes with the FR5 response requirement.

Figure 2.2.6

Figure 2.2.6

Values of $\log d$ plotted as a function of grating spatial frequency, measured in c/mm, for hens 32 and 36, for the probe series with the FR5 and FR10 response requirements. A line has been fitted to the descending portion of the data from each hen by the method of least squares and is shown in the figures. Parameters of fitted lines for the data of all hens, are given in Table 2.2.2.

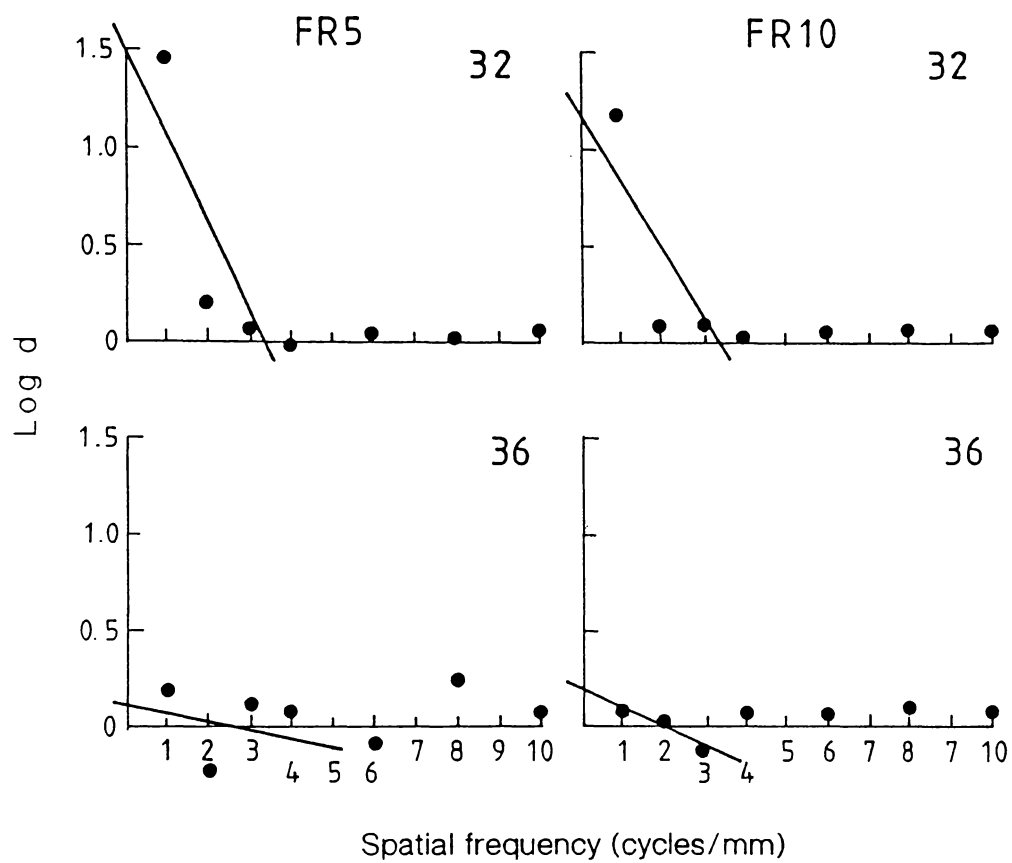


Table 2.2.2

Table 2.2.2

The slopes and the intercepts of the least-squares lines fitted to the values of $\log d$ for each hen, for the probe series with the FR5 and FR10 response requirements. The number of data points described by each line, (Data pts.), the amounts of variance accounted for by the lines (VAC%) and the standard errors of the estimates (SE) are also given.

Hen	FR5					FR10				
	Slope	Intcpt	Data Pts.	VAC%	SE	Slope	Intcpt	Data pts.	VAC%	SE
31	-0.26	0.73	3	58.2	0.19	-0.37	0.86	3	92.2	0.11
32	-0.46	1.57	4	57.9	0.45	-0.35	1.22	4	47.4	0.41
33	*-0.14	0.43	3	22.0	0.16	*-0.14	0.58	4	0.0	0.45
34	*-0.38	1.07	3	52.5	0.30	-0.43	1.16	3	81.4	0.19
35	-0.28	1.04	4	47.5	0.33	-0.34	0.91	3	68.9	0.20
36	*-0.04	0.09	3	0.0	0.31	-0.10	0.20	3	89.6	0.03

* not lowest standard error

In summary, the response requirement which most consistently generated data providing the greatest threshold estimates was FR5. However, there was no particular response requirement which generated data providing the greatest estimates across all hens, criteria and methods of analysis. For hens 31, 33 and 35 the greatest estimate was obtained from performance on the FR5 response requirement. For hens 33 and 36, performance on FR1 yielded the greatest estimate. The greatest estimate of threshold determined for hen 34, however, varied from probes with FR1 and FR5, depending on the particular criteria used.

Figure 2.2.7 presents mean values of $\log d$ plotted as a function of grating spatial frequency, measured in c/mm, for group data from the six hens in the present study and the six hens in Experiment 1.2, for the probe series with the FR5 and FR10 response requirements. The data for the present study and for Experiment 1.2 for the probe series with the FR5 response requirement are shown in one graph, and those for the probe series with FR10 are shown in the other graph, for comparison. A negative exponential function (Equation 10) has been fitted to the data from the present study and from Experiment 1.2, for each of the two probe series. These functions are described in Table 2.2.3. A description of the parameters of the negative exponential functions fitted to the data for Experiments 2.1 and 1.1 for the descending probe series with the FR1 response requirement are also presented in the table, for comparison. A decision was made to omit the data from probes at the two finest gratings, assumed to be indiscriminable (8 and 10 c/mm) for the present, and following experiments, if, by doing so, the amount of data variance accounted for

Figure 2.2.7

Figure 2.2.7

Mean values of $\log d$ plotted as a function of grating spatial frequency, measured in c/mm, for the group data from the present study and Experiment 1.2, for the probe series with the FR5 and FR10 response requirements.

A negative exponential function has been fitted to the data for each probe series. The functions are shown in the figures. The parameter descriptions are given in Table 2.2.3.

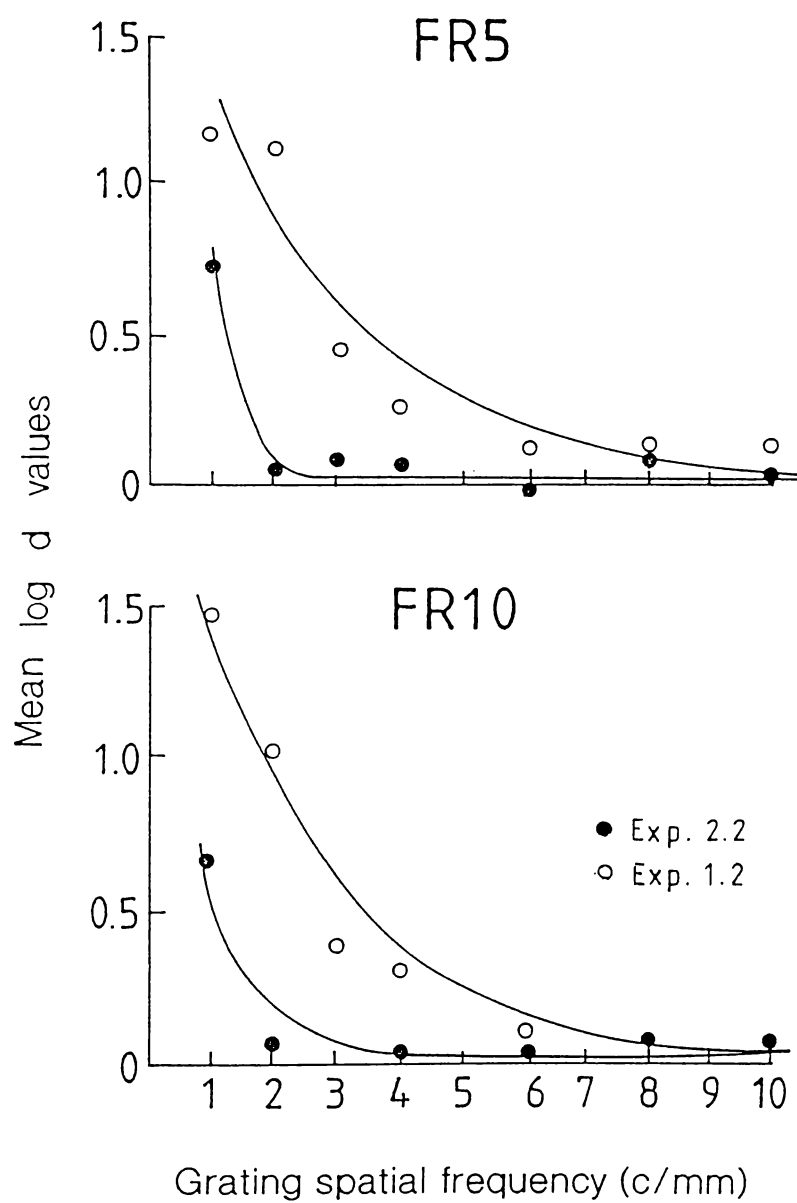


Table 2.2.3

Table 2.2.3

Parameters of the negative exponential functions fitted to the mean $\log d$ values from the probe series with the FR5 and FR10 response requirements (Experiments 2.2 and 1.2). Parameters of the negative exponential functions fitted to the mean $\log d$ values from the descending probe series with the FR1 response requirement (Experiments 2.1 and 1.1) are included, for comparison.

Exp	FR	Analogue		
		$\text{Log}d_0$	b	VAC%
2.1	1	0.49	0.98	90
2.2	5	0.73	2.68	96
2.2	10	0.66	2.69	96
1.1	1	1.35	0.69	95
1.2	5	1.28	0.41	91
1.2	10	1.50	0.44	82

by the fitted function was increased. These two data points were excluded from analysis of the FR10 probe series in Experiment 1.2. By excluding these two points the amount of data variance accounted for increased from 50% to 82%.

Although discriminative performance at the coarsest grating value in Experiment 1.2 actually increased at response requirements greater than FR1, that is not reflected in the analogue of $\log d_0$ for the FR5 probe series. Due to infinite $\log d$ values at the coarsest gratings, only the data for hens with lower accuracy could be used in the calculation of mean $\log d$ values. However, the analogue of $\log d_0$ in all cases was greater, and the analogy of b was smaller for Experiment 1.2, than for the present experiment. This indicates both higher initial discriminability and a lower rate of decrement of discriminative performance across increasingly finer gratings for Experiment 1.2. For the data from Experiment 2.2, the analogue of $\log d_0$ increased for the probe series with the FR5 compared to the FR1 response requirement, but decreased slightly for the probe series with the FR10 response requirement. However, the analogue of b increased as a function of probes with the increased response requirements. This indicates that, while initial discriminability increased, the rate of decrement of discriminative performance at increasingly finer gratings also increased.

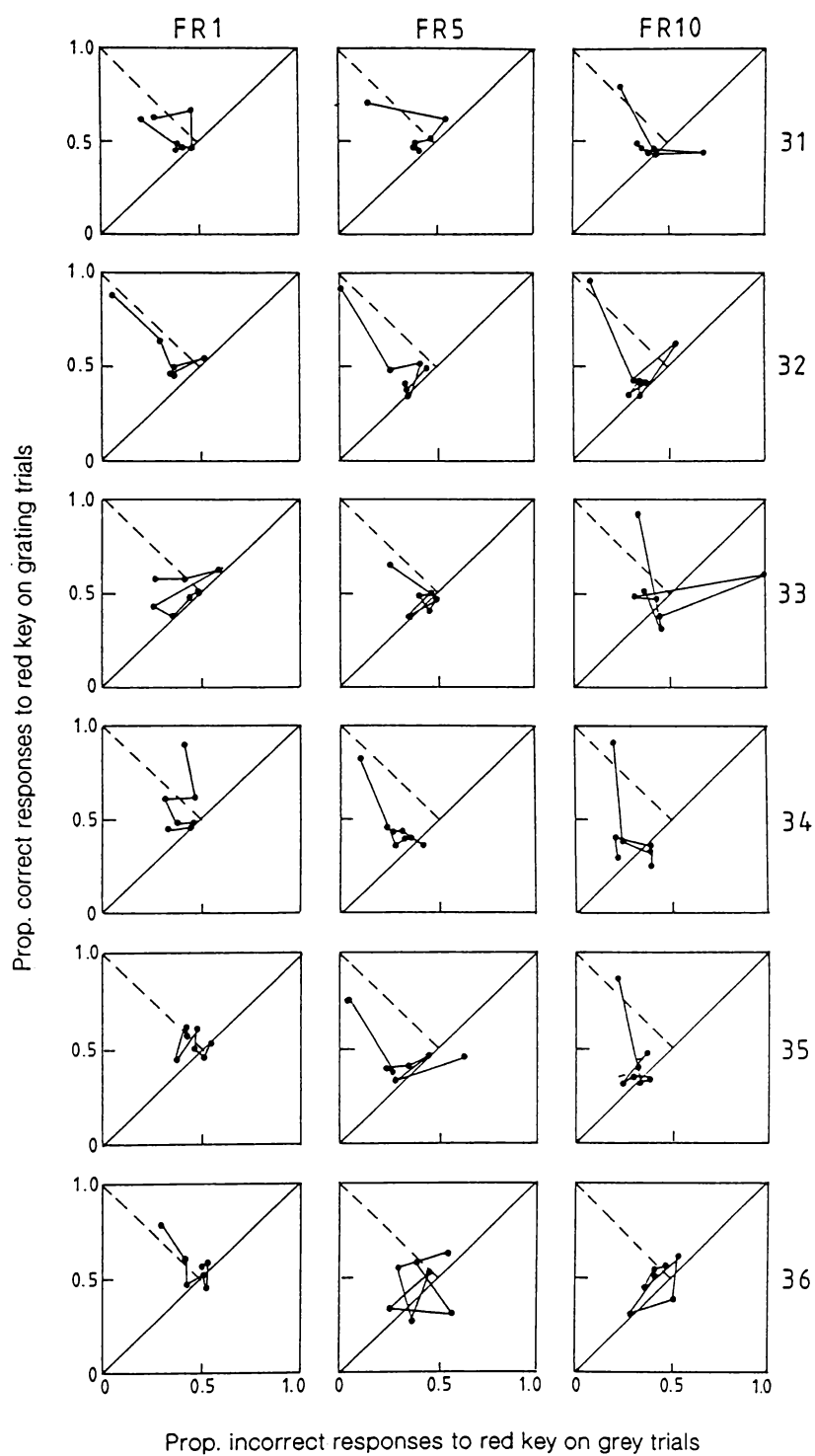
ROC plots

Figure 2.2.8 presents the proportion of correct responses to the red key on grating trials, plotted against the proportion of incorrect responses to the red key on grey stimulus trials, for probes with gratings of increasing spatial frequency. Plots for the two probe

Figure 2.2.8

Figure 2.2.8

The proportion of correct responses on grating trials plotted against the proportion of incorrect responses on grey stimulus trials for all hens, for the probe series with the FR5 and FR10 response requirements. Data from the descending probe series with the FR1 response requirement (Experiment 2.1) are also shown.



series with FR5 and FR10 response requirements are shown, and for all plots, lines join successive probes. Data from the descending probe series with the FR1 response requirement (Experiment 2.1) are also presented, for comparison. The data paths from the probe series with the FR1 and FR5 response requirements are similar. Generally data from probes at the coarsest gratings, for each probe series, are close to the minor diagonal, indicating that responses to the red and green key were close to equal. At probes with the finer gratings, the data paths for probes with the FR5 and FR10 response requirements, generally move to the left of the minor diagonal. This indicates an increase in green key responding (as though the stimulus were grey). The data paths for probes at the finest gratings, for several hens, move below the major diagonal. This indicates that the hens, for probes at these stimulus values, may have been discriminating in reverse (that is, responding to the green key following grating presentation and responding to the red key following grey stimulus presentation). This was more prevalent for probes with the FR10 response requirement.

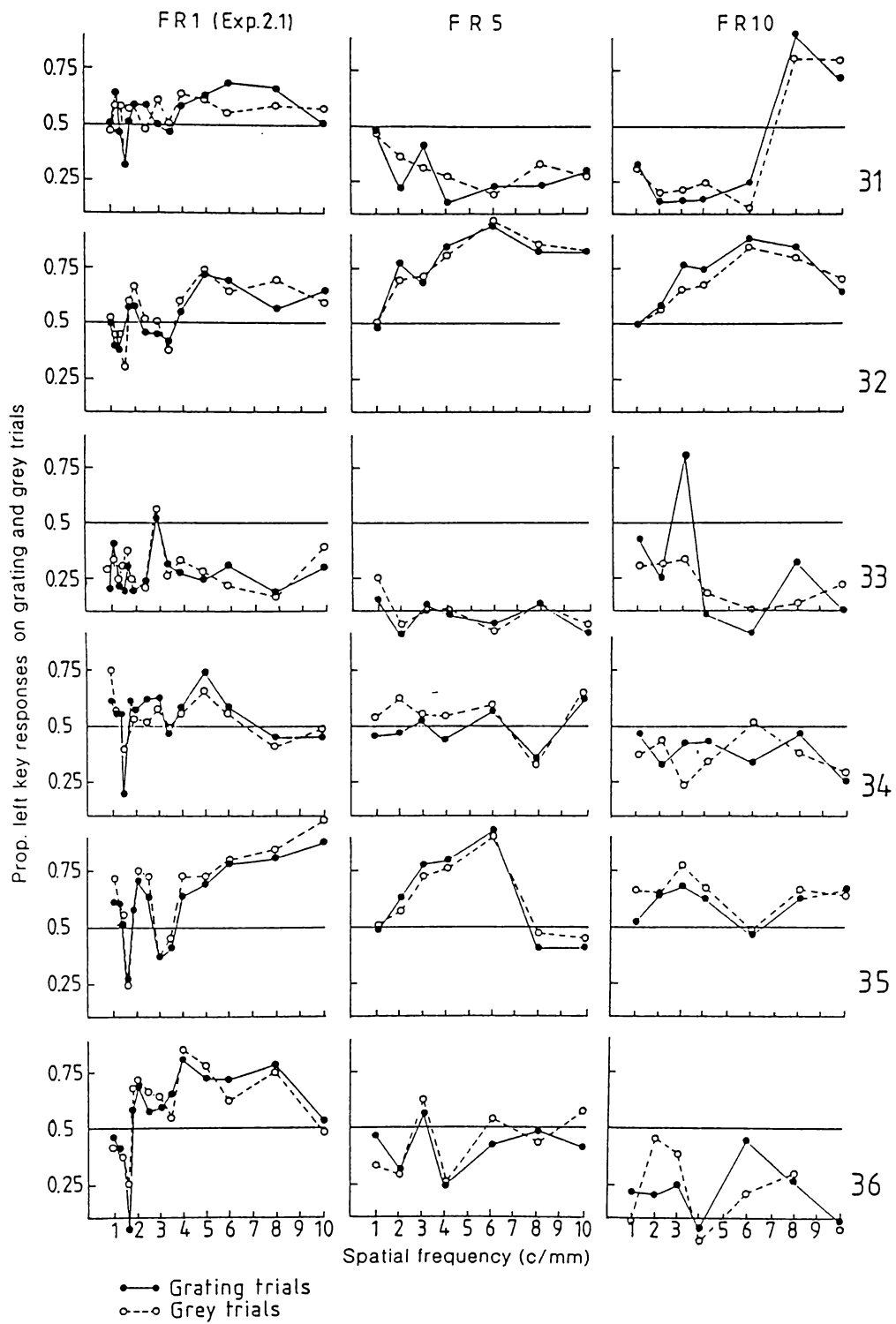
Response bias

Figure 2.2.9 presents left key responses as a proportion of total responses, plotted as a function of grating spatial frequency, measured in c/mm, for all hens, for the probe series with the FR5 and FR10 response requirements. Data from the descending series of probes with the FR1 response requirement (Experiment 2.1) are also presented for comparison. Across hens, the data varied from above 0.5 to below 0.5. This indicates that responses to the left and right key varied both across hens and across stimulus values, and stronger position biases were more prevalent at probes with the finer gratings. Four of

Figure 2.2.9

Figure 2.2.9

The proportions of left key responses plotted as a function of grating spatial frequency, measured in c/mm, for all hens, for the probe series with the FR5 and FR10 response requirements. Data from the descending probe series with the FR1 response requirement (Experiment 2.1) are also shown . Grating and grey trials are plotted separately,



six hens responded equally to left and right keys at the coarsest grating with the FR5 response requirement, but most hens responded more to one particular key at the coarsest grating, with the FR10 response requirement. That is, generally position preferences were more extreme for the probe series with the increased response requirements.

Reinforcement

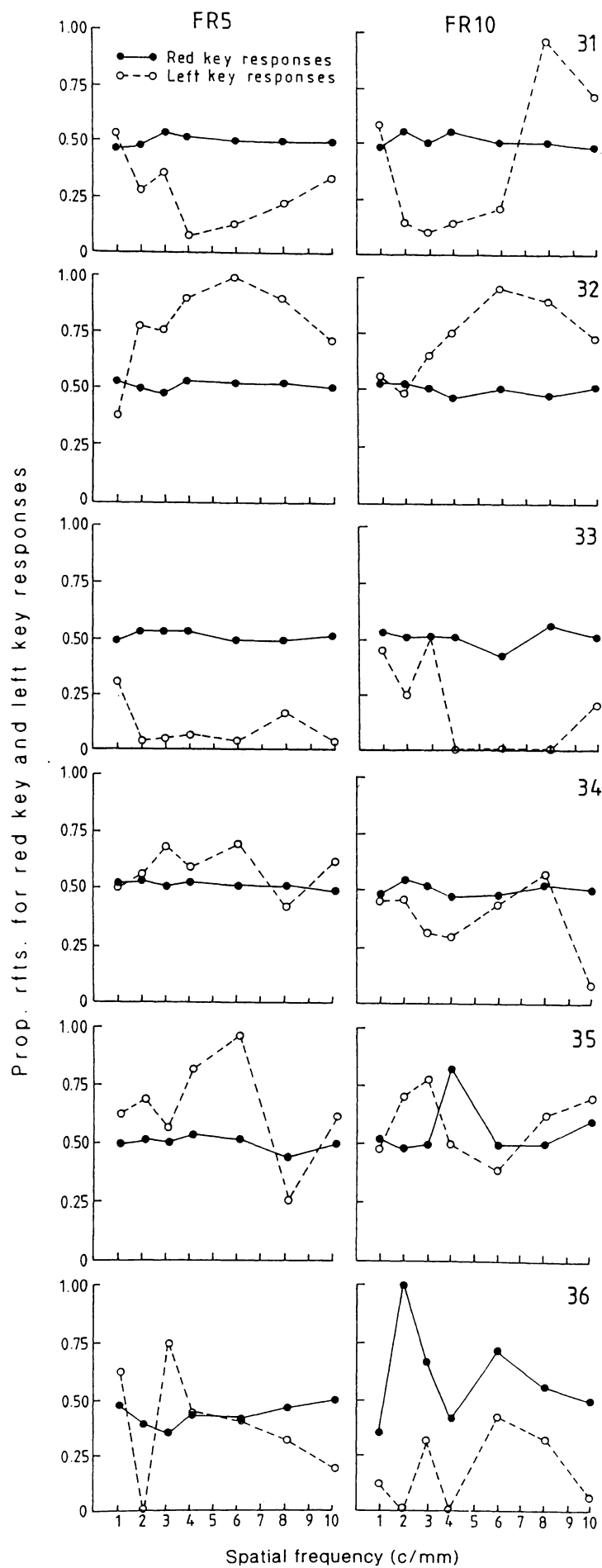
Figure 2.2.10 shows reinforcements obtained, both for correct responding to the red key, and for correct responding to the left key as a proportion of total reinforcements, for all hens for both probe series with the FR5 and FR10 response requirements. These are plotted as a function of grating spatial frequency. The proportion of reinforcements for red key responses was close to 0.5 for most hens, at all probe values, and across both probe series. For hen 36, however, a larger proportion of reinforcements was obtained for green key responses on probes with FR5, and for red key responses during most probes with the FR10 response requirement.

The proportion of reinforcements for correct responding to the left key varied across hens. Three hens obtained a greater proportion of reinforcements for right key responses, and two hens (32 and 35) received a greater proportion of reinforcements for left key responses across the two probe series. Hen 34 however, received the greater proportion of reinforcements for left key responding for probes with the FR5, and right key responses for probes with the FR10 response requirement. These data tend to reflect the various colour and position biases indicated in the previous figure.

Figure 2.2.10

Figure 2.2.10

The proportion of reinforcements obtained for correct responses to the red key (filled circles) and correct responses to the left key (open circles), plotted as a function of grating spatial frequency, measured in c/mm, for the series of probes with the FR5 and FR10 response requirements.



Discussion 2.2

The effect of increased response requirements on discriminative performance in the present study was inconsistent. That is, compared to performance with a single response requirement, performance with response requirements of FR5 and FR10 was generally more accurate at the coarsest grating value, but less accurate at the intermediate grating values (which were assumed to be discriminable), and no different at the finest gratings (assumed to be indiscriminable).

There is no reason to suspect that the hens in the present study would have different visual functioning from those serving in Experiments 1.1 to 1.5, or that their vision functioning changed between the previous study and the present one. This implies that the behaviour was affected by the procedure. That is, the decrease in accuracy at the intermediate gratings was due to the increased response requirements, rather than some change in sensory functioning.

Generally, a return to an FR1 response requirement following probes with an FR5, showed a decrease in accuracy at the coarsest grating value, further indicating that the prior improvement at this grating value was a function of the increased response requirement, rather than a practice effect. Performance for hen 36, however, actually decreased in accuracy with any increase in response requirements. Upon return to an FR1 response requirement, both her overall response rate and accuracy increased.

Such findings, with a combination of both higher and lower accuracy, compared to performance with a single response requirement

have not been reported in the literature. They are also inconsistent with those results obtained for Experiment 1.2, where accuracy generally increased with the increased response requirements and this improvement in performance extended to most grating values. Generally, the literature reports that multiple response requirements increase accuracy in tasks requiring either direct matching (Cumming & Berryman, 1961) matching to oddity (Lydersen, Perkins & Chairez, 1977) or symbolic matching to sample (Carter & Eckerman, 1975), whether the choice response to comparison stimuli is simultaneous (Spetch & Treit, 1986) or delayed (Sacks, Kamil & Mack, 1972). Increased response requirements reported to result in higher accuracy include those as low as FR2 (Wilkie & Spetch, 1978) and as high as FR40 (e.g. Rodewald, 1974; Sacks *et al.*, 1972). Sacks *et al.* found no difference in performance when increasing the response requirement to FR5, but accuracy increased at FR20.

Nevin, Cumming and Berryman's (1963) findings, however are in marked contrast to most in the literature. They used a simultaneous matching-to-sample procedure, and three possible colour sample and comparison stimuli. In their study the response requirements to the sample were increased from FR1 to FR3, FR5 and FR10. They report that any increase in the response requirement reduced accuracy in all three pigeons by 8% to 20%, with no indication of recovery of accuracy even after 43 sessions of exposure. Although they could not conclusively account for the aberrant findings, Nevin *et al.* (1963) suggest that one difference in their procedure from most other studies was the omission of a correction procedure. They suggest that the use of a correction procedure may be important since it permits the subjects to receive better than 50% reinforcement for performance which is not

based on the relation between the discriminative stimuli at all. They determined that if, for instance, a pigeon followed a pattern of responding on the right key after reinforcement and shifted to the left key if this response was followed by a blackout (for incorrect responding), two thirds of the responses would be reinforced. They state that other systematic patterns of responding may also occur, many of which may receive sufficient reinforcement to be maintained. A win-stay, lose-shift response pattern will produce the same effect if signal presentation probability (SPP) is 50% and a correction procedure is in effect. Although they stated that it was impossible to determine the effects of intermittent reinforcement on matching performance when a correction procedure is used, without a detailed trial by trial analysis, they argue that it may be important in maintaining a particular pattern of performance that may not occur in the absence of a correction procedure. That is, the increased accuracy may be an artefact of the correction procedure. However, it is unlikely that the findings of the present study resulted from the lack of a correction procedure, as none was used in Experiment 1.2 and accuracy increased with probes using increased response requirements.

As animals respond differentially to the sample stimulus in order to gain reinforcement, it is possible that any procedural manipulation which changes the reinforcement delivery may also change performance in some way. Perusal of the data from the present study show that the total number of obtained reinforcements per sessions at all grating values decreased as a function of the increased response requirements. However, it is difficult to determine whether the decreased overall reinforcement rate resulted from increased time taken with responding to the sample, or from decreased accuracy. A determination of

obtained reinforcements at the coarsest gratings however, where accuracy was generally higher at response requirements greater than FR1, showed that reinforcements per session were actually fewer with increased response requirements. That is, the decreased overall reinforcement rate was more likely to be a result of the increased time spent responding to the sample. A decreased overall reinforcement rate was also found in Experiment 1.2 at probes with increased response requirements. Therefore, the lower accuracy at probes with increased response requirements in the present study was not likely to have resulted from this.

Generally, the total number of obtained reinforcements per session differed across the present study and the equivalent study, Experiment 1.2. Although both session time and scheduled reinforcements per session were kept constant across the two procedures, the hens in Experiment 1.2 generally obtained a greater number of reinforcements per session. The difference between the obtained reinforcement rate in the two studies increased when response requirements were greater than FR1. This may have had some effect on performance, as Nevin *et al.* (1963) suggest that a high rate of reinforcement is necessary to maintain performance at difficult discriminations. However, although the obtained reinforcement rate per session was less when response requirements were increased in the present study, the probability of reinforcement increased. It might, therefore, be assumed that the effect of the increased probability of reinforcement for correct responding might have been sufficient to offset the effect of the lower overall reinforcements per session. Thus it appears that the lower accuracy in the present study, with probes at increased response requirements, may not have been the

result either of changes in the overall reinforcement rate, or changes in the reinforcement probability.

In the discussion for Experiment 1.2 it was suggested that the combination of increased effort required and the increased probability of reinforcement at increased response requirements may have provided the necessary conditions for the animals to demonstrate higher accuracy. However, despite a similar increase in the probability of reinforcement for correct responses with increased response requirements, total discriminative performance at 2 c/mm and 3 c/mm grating values for most hens actually decreased below chance, to around 40% correct at probes with increased response requirements.

It may be argued that stimulus control is more easily disrupted in animals with initially low performance. For example, the performance of hen 73 in Experiment 1.2 was initially low and was disrupted when FR40 was programmed to the sample key. However, this does not explain why the performance of hen 32 in the present study, with the highest accuracy in Experiment 2.1, was also disrupted at the intermediate grating values.

There are two more plausible explanations for the disruption of performance in the present study, at intermediate grating values. Firstly, many studies using the matching-to-sample procedure increase response requirements to the sample by small increments. For example, Roberts and Grant (1976) and Hodos and Bonbright (1972) gradually increased the response requirement by small daily increments to FR10. Perhaps in the present study, the change in the response requirement by an increment of five responses added to the difficulty of the task

at all but the coarsest grating value.

Secondly, and more likely, it is also possible that the change in stimulus value from 1 c/mm to 2 c/mm was too great for a complex discrimination task. In Experiment 2.1 the increments of spatial frequency were much smaller, with four intervening grating values presented between the 1 c/mm and 2 c/mm grating values. That is, in the present study, the probe session with the 2 c/mm grating followed the session with the 1 c/mm grating, whereas in the previous study, the probe session with 2 c/mm followed a probe session with a 1.8 c/mm grating value, an increment of only 0.2 c/mm rather than 1 c/mm. Perhaps when the task is more difficult, it is important to ensure that changes in the stimulus values are small.

Studies of DMTS performance use various delays but usually change from small to increasingly longer delays (e.g. Smith, 1967; Wilkie & Spetch, 1978). Perhaps the increase from 1 c/mm to 2 c/mm grating stimulus in the present study is analogous to making a large change in delay, rather than testing at smaller increments of delays. Large changes in stimulus value may therefore disrupt behaviour much more than small changes, when the task is difficult. In present study therefore, these large stimulus changes may have confounded with the increased response requirements to disrupt performance.

As previously discussed in Experiment 2.1, discriminative performance in a visual acuity task has two characteristics: discriminability at the coarsest grating and the rate of decrement in discriminability at increasing grating spatial frequency. In Experiment 2.1 it was shown that these two characteristics may be

quantified in terms of the parameters of a negative exponential function. As mentioned previously, White (1985) states that an important implication in DMTS studies is that these two characteristics are independent, that is changes in $\log d_0$ do not influence b . He reports that the results of his two separate experiments support this "independence" assumption. When he changed the wavelength difference between two sample stimuli $\log d_0$ also changed, but b was not affected. When b was altered by introducing a houselight during the delay between the offset of the sample stimulus and the presentation of the comparison stimuli, there was no effect on $\log d_0$. Although this latter result is trivial, (as any interference of the delay interval would not be expected to affect discriminability at zero delay), White suggests that $\log d_0$ does not necessarily need to refer to discrimination at zero delay, but may refer to discrimination at the shortest delay. White's (1985) reanalysis of Roberts' (1972) data however, suggests that changes in $\log d_0$ may not always be achieved without altering b . In Roberts' (1972) study, pigeons were trained on an easy and difficult task with an FR1, FR5 and FR15 response requirement. The easy task, in all cases, generated greater values of $\log d_0$ and smaller values of b than the difficult task. These results are consistent with those from the present and previous study in this thesis, where, in all cases, the analogue of $\log d_0$ for the spatial conditional discrimination task (Experiments 1.1 and 1.2) was greater, and the analogue of b was smaller than for the non-spatial conditional discrimination task of the present procedure. That is, there was a negative correlation between the values of the analogues of $\log d_0$ and b , for both procedures (Figure 2.1.11 & Table 2.2.3).

When Roberts (1972) increased the response requirements for both the easy and difficult tasks, $\log d_0$ increased and b decreased for both discrimination tasks as a function of the increased response requirements. Although, with the negative exponential functions fitted to group data in Experiment 1.2, the analogue of $\log d_0$ did not increase with the increase in response requirements from FR1 to FR5 (Table 2.2.3), this was a result of the number of infinite values of $\log d$ obtained at the higher response requirements. The fact that the increased response requirements generated perfect discriminative performances from several hens indicates that the analogue of $\log d_0$ should have been greater for performance with the increased FRs, consistent with Roberts' results. When response requirements were increased from FR1 to FR10, $\log d_0$ also increased. In addition, for Experiment 1.2, there was a concomitant decrease in the analogue of b with increased FR requirements from FR1 to FR5, also consistent with findings from Roberts' study. There was however, little change in b when response requirements were increased from FR5 to FR10. This lower rate of decrement of discriminative performance with FR requirements greater than FR1 was reflected in the greater threshold estimates generated by the performance in Experiment 1.2. Results from the present study, on the other hand, show a positive correlation between the analogues of values of $\log d_0$ and b when FRs were increased from FR1 to FR5 and FR10. That is, there was an increase in the rate of decrement of discriminative performance with the increased response requirements. However, as has earlier been suggested, the rate of decrement in discrimination at finer gratings (b) in the present study, may have been confounded by the concomitant greater increments of grating spatial frequency. The results from both Experiment 1.2 and the present study imply that, when used to describe discriminative

performance in a visual acuity task, the analogue of b may not be independent of $\log d_0$. Regardless of the independence or otherwise of these two parameters, the analogues of $\log d_0$ and b , it is suggested that they provide a useful description of the characteristics of performance on a visual acuity task.

Logically, however, the value of the analogue of $\log d_0$ in a visual acuity task should not be as independent of b as $\log d_0$ in a memory task. This is because, in an acuity task, there is assumed to be some theoretical point where animals can no longer discriminate, that is where the $\log d_0$ analogue reaches zero. In a memory task, however, there does not appear to be a point where there is no memory, and the negative exponential function never reaches zero. If the analogues of $\log d_0$ and b are not independent, as $\log d_0$ increases, b should also increase, so that the negative exponential function reaches close to zero at the same point, regardless of the initial discriminability ($\log d_0$). If two decaying exponentials of the function of e^{-bt} begin from different initial values, and are constrained to be the same value (close to zero) by a given spatial frequency, then the analogue of b will be greater as the analogue of $\log d_0$ increases. This corresponds with the data for the present study, where response requirements were increased from FR1 to FR5 and FR10. However, this does not correspond with the data from Experiment 1.2 where response requirements were increased from FR1 to FR10. This suggests that either the concept of some theoretical point of transition between discriminability and non-discriminability of stimuli is incorrect, or that the actual difficulty of the task affects the independence or otherwise of the analogues of $\log d_0$ and b .

Response distributions and response bias

A comparison of the grating and grey trial response distributions in the present study, to those of Experiment 1.2 shows that they were very similar. Data paths for grating and grey trial accuracy separated more at increased response requirements in a similar way to those in Experiment 1.2. Strong position biases developed at all but coarsest grating values, and performance at the finest grating values indicates a reverse discrimination for three hens with the FR5 and for four hens with the FR10 response requirement. Because this occurred at grating values which are assumed to be indiscriminable, this pattern of responding which appeared as a reverse discrimination, would necessarily be the result of random variation of responses. Where colour biases occurred they were relatively invariant across different levels of stimulus discriminability, and showed an increase in green key responding. This indicates that the hens were responding as though most stimuli were grey. This colour preference is assumed to relate to the animals' perception of the stimuli, as gratings became increasingly finer, in the same way that increased position biases in Experiment 1.2 also indicated an increase in responding as though most stimuli were grey. Position biases in the present study however, although not independent of stimulus discriminability, do not relate to stimulus values in this same way. That is, at finer grating values, position biases in Experiment 1.2 and colour biases in the present study show right position and green key biases respectively, whereas position biases in the present study vary across the different stimulus values. Because, in the present study, the reinforcement procedure was controlled for key colour but not for key position, a hen could respond exclusively to one side key and receive

reinforcement for 50% correct responding. Thus, it would be expected that position preferences would develop more readily than colour preferences in the present study.

Harnett, McCarthy and Davison (1984) using a similar procedure to the present one, studied the performance of pigeons on a light intensity discrimination task. They also programmed both a controlled and uncontrolled reinforcement procedure for colour and position, respectively, as in the present procedure. Although they reported constant-bias functions for colour biases, as for the present study, no analysis of position bias was presented. Terman (1970), however, reported marked variations in position bias at different levels of stimulus discriminability, in his study of auditory discrimination in rats. It is possible that the lower overall accuracy in the present study, compared to Experiment 1.2 may have resulted from the increased position bias at increased response requirements.

As mentioned earlier, the total performance of the hens at intermediate grating values decreased below 50% accuracy. This appears to have resulted from an extreme though not exclusive position bias, combined with occasional switching to the alternative response key, mainly when this alternative key was green, rather than red. This pattern of responding resulted in a distribution of correct responses that were actually lower than chance. Accuracy in the present study decreased more at intermediate grating values, with increased response requirements, than at probes with FR1. The effect of bias on the percentages correct is greatest at intermediate levels of detectability and diminishes to zero at the limiting cases of 100% and 50% correct (Irwin & Terman, 1970). It is possible then, that in

the present study, due to the greater complexity of the non-spatial task, biases may be more likely to occur and be more extreme, when discriminative performance is disrupted by large changes in grating spatial frequency coupled with greater effort required by multiple responses to sample stimuli.

Conclusion

Performance on any discrimination task appears to be a function not only of stimulus factors but also of response factors and of the contingencies under which choice is maintained. The present procedure then, may not be as useful in determining the limits of sensory functions as the spatial discrimination procedure in Experiment 1.2, at least for hens, as performance is more easily disrupted by variations in procedure. Such disruption in performance evidenced by increased position biases, resulted in an overall decrease in accuracy at intermediate grating values, compared with performance at a single response requirement in Experiment 2.1. The results of the present study, consistent with the findings of Nevin *et al.* (1963), indicate that changes in procedure which do not change the discriminability of the stimuli, are not necessarily consistent in their effect on discriminative performance across different discrimination tasks.

EXPERIMENT 2.3

Discriminative performance in Experiment 2.1 was generally at a lower level at most stimulus values than that for Experiment 1.1. When the response requirement to the sample was increased, in Experiment 2.2, discrimination improved for some hens only. For most hens, discrimination was lower than that obtained for Experiment 1.2, and the response requirement which produced the best performance was also lower than that required for Experiment 1.2. The difference between discriminative performance in these two studies may have been a direct result of the greater difficulty of the non-spatial discrimination task required of the hens. In Experiment 1.3, using the spatial discrimination procedure, discriminative performance changed as a function of change in luminance, even though luminance was varied within a very limited range.

The rationale for the present study was the same that as that for Experiment 1.3. That is, luminance was varied within the same limited range, to determine the effect on discriminative performance. In addition, the results were compared to those from Experiment 1.3, to ascertain whether, and in what manner the difficulty of the task in the present experiment affected the discriminative performance.

Method 2.3

Subjects and Apparatus

The six hens in the two previous studies served. The apparatus was the same as that used for the two previous studies. Two luminances were used on the sample key. They were 5.48 cd/m² and 0.28 cd/m². The changes in luminance were produced as in Experiment 1.3.

Procedure

The procedure was similar to that used in Experiment 2.2, except that five responses were required to the sample key (FR5). A single VI 30 s reinforcement schedule was used, and a controlled reinforcement procedure was programmed, as for the two previous studies. Hens were trained to a stability criterion, as for the two previous studies. There were two experimental conditions. For each, after the hens had satisfied the stability criterion, they were tested in a descending series of probes (as for Experiment 2.2) at each luminance. The luminance for the first condition was 5.48 cd/m² and the second was 0.28 cd/m². The hens took 21 sessions to reach stability under the high luminance (5.48 cd/m²) and 18 sessions under the low (0.28 cd/m²) luminance. Data were collected as for the previous two studies.

Results 2.3

Discrimination

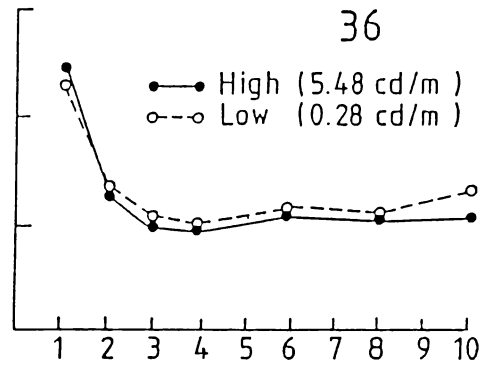
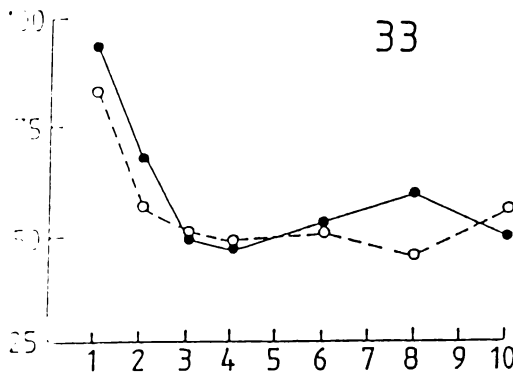
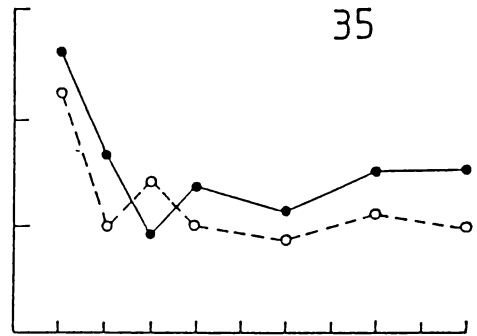
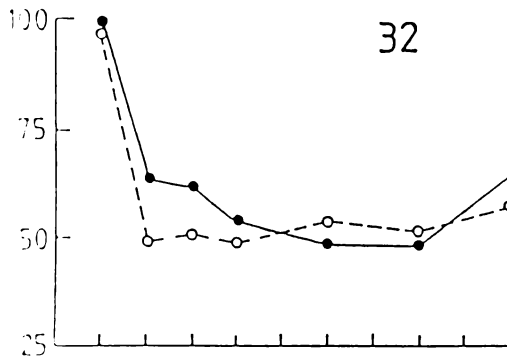
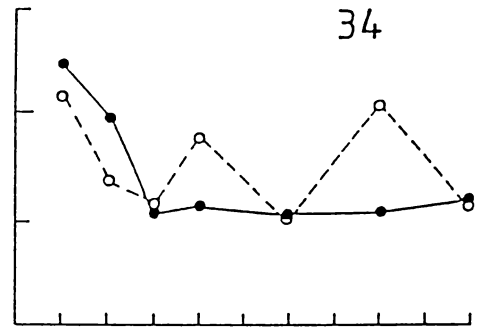
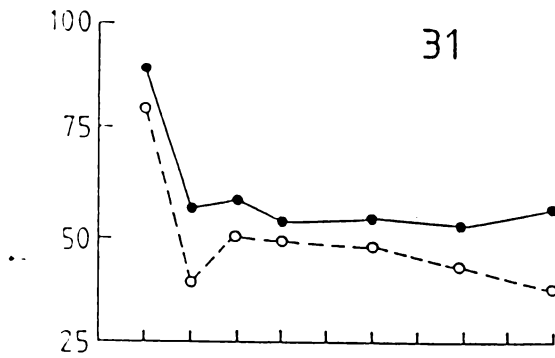
Figure 2.3.1 shows the percentages of total trials correct plotted as a function of grating spatial frequency, measured in c/mm, for all hens, for the probe series at both the high (5.48 cd/m²) and the low (0.28 cd/m²) luminance. For all hens, the percentages of total trials correct at the coarsest grating were higher for probes at the high, than the low luminance. For four of the six hens this higher accuracy extended to most of the remaining grating values. For hen 36, however, there was no difference in performance between the two probe series at all but the coarsest grating value. For some hens accuracy increased slightly at the probe with the finest grating, for both probe series. These data were compared with data from Experiment 2.2, with the same response requirement, at a luminance of 3 cd/m². Because these data did not show any consistent difference in accuracy across hens, from the data obtained at the low luminance, they have not been presented here.

Figure 2.3.2 shows the mean percentages of total trials correct, plotted as a function of grating spatial frequency, measured in c/mm, for hens in the present study and in the equivalent study, Experiment 1.3 for the probe series at the high and the low luminance. The two data functions for the probe series at the high luminance are plotted in one graph, and the two data functions from the probe series at the low luminance are plotted in the other, for comparison. Although the shape of the data functions for the present study and Experiment 1.3 is similar, the mean percentages of total trials correct for the present study were lower than those for Experiment 1.3, for both probe

Figure 2.3.1

Figure 2.3.1

The percentages of total trials correct, plotted as a function of grating spatial frequency, measured in c/mm, for all hens, for the probe series at the high (5.48 c/d/m^2) (filled circles joined by a solid line) and low (0.28 cd/m^2) (unfilled circles joined by a broken line) luminance.

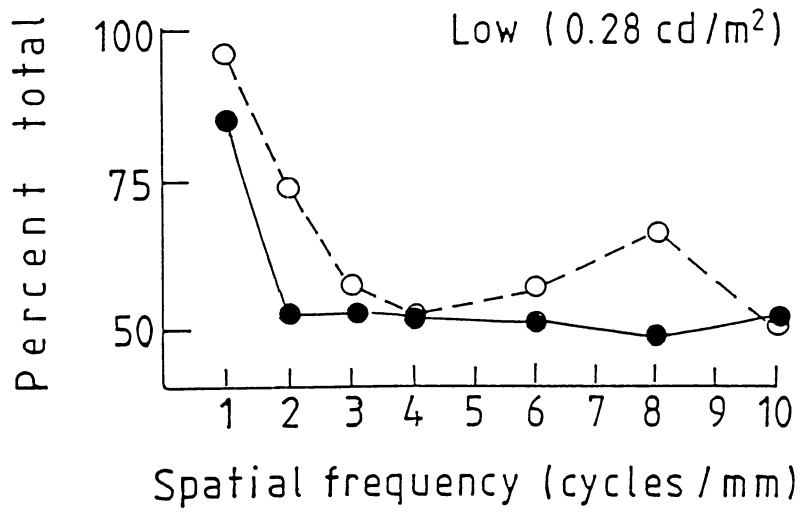
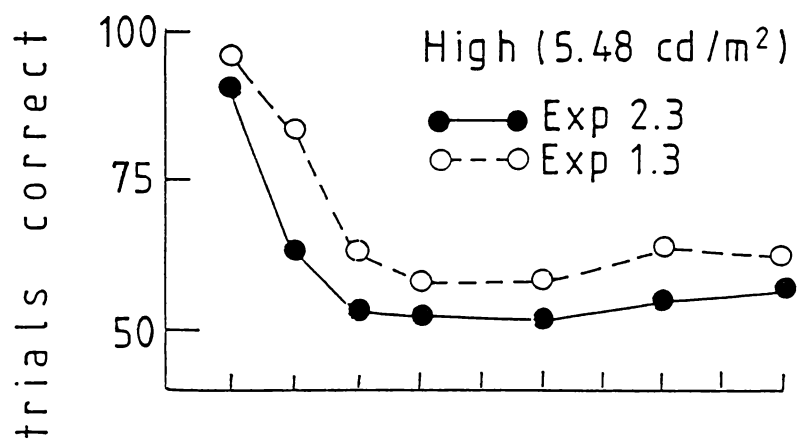


Spatial frequency (cycles/mm)

Figure 2.3.2

Figure 2.3.2

The mean percentages of total trials correct, plotted as a function of grating spatial frequency measured in c/mm, for the six hens in the present study (filled circles), and the six hens in Experiment 1.3 (unfilled circles), for the probe series at the high (5.48 cd/m^2) and low (0.28 cd/m^2) luminance. The functions for the present study and Experiment 1.3 from the probe series at the high luminance are shown in one figure, and the functions from the probe series at the low luminance are shown in the other figure.



series and across all stimulus values.

Figure 2.3.3 shows the percentages of grating and grey trials correct, plotted separately, as a function of grating spatial frequency, measured in c/mm, for all hens, for both probe series. The data from four of six hens show a flatter function for grey stimulus trials, indicating a much higher level of accuracy than on grating trials. For the other hens, where accuracy on grey stimulus trials was not as high, accuracy on grating trials generally did not decrease below 30% during probes with increasingly finer gratings.

Figure 2.3.4 presents $\log d$ values plotted as a function of grating spatial frequency, measured in c/mm, for all hens and for both probe series. $\log d$ values from probes at the coarser gratings were greater at the high, than at the low luminance. These values of $\log d$ decreased at probes with finer gratings, to a $\log d$ value around 0.00, and levelled off. For four hens, accuracy increased slightly at the finest grating. An infinite $\log d$ value obtained for the probe at the coarsest grating with the low luminance for hen 32, resulted from 100% accuracy on grey trials (see Figure 2.3.3).

The same $\log d$ values are plotted in Figure 2.3.5 for two hens only, 34 and 36, as examples of typical performance in the present study, and a line has been fitted to the data from most hens, by the method of least squares, as in Experiment 2.1. The lines chosen to describe the descending portion of the data for hens 34 and 36 are shown in the figures. It was not possible to fit a line to the data obtained at the low luminance for hen 32 because of an infinite $\log d$ value. The slope, intercept, the number of data points described by

Figure 2.3.3

Figure 2.3.3

The percentages of grating (filled circles joined by a solid line) and grey stimulus (unfilled circles joined by a broken line) trials correct, plotted separately, as a function of grating spatial frequency, measured in c/mm, for all hens, for the series of probes at the high (5.48 cd/m^2) and low (0.28 cd/m^2) luminance.

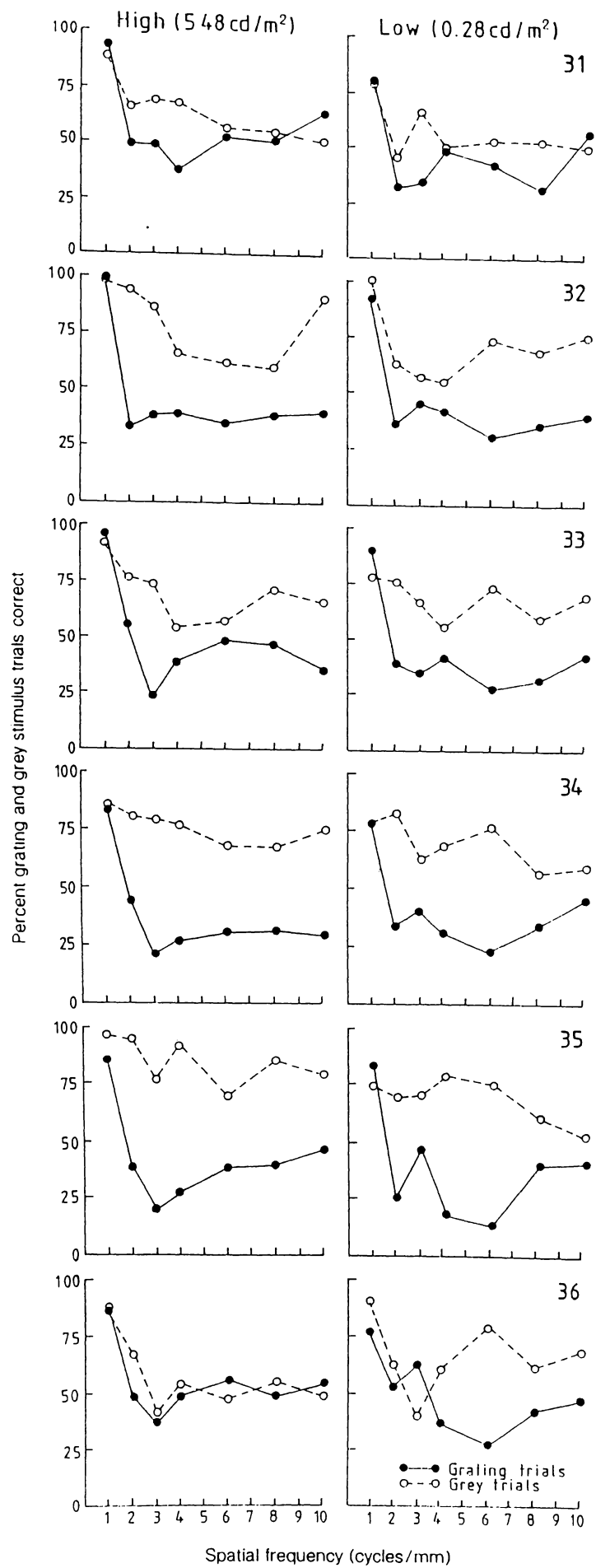


Figure 2.3.4

Figure 2.3.4

Values of $\log d$ plotted as a function of grating spatial frequency, measured in c/mm, for all hens, for the series of probes at the high (5.48 cd/m^2) (filled circles joined by a solid line) and the low (0.28 cd/m^2) (unfilled circles joined by a broken line) luminance.

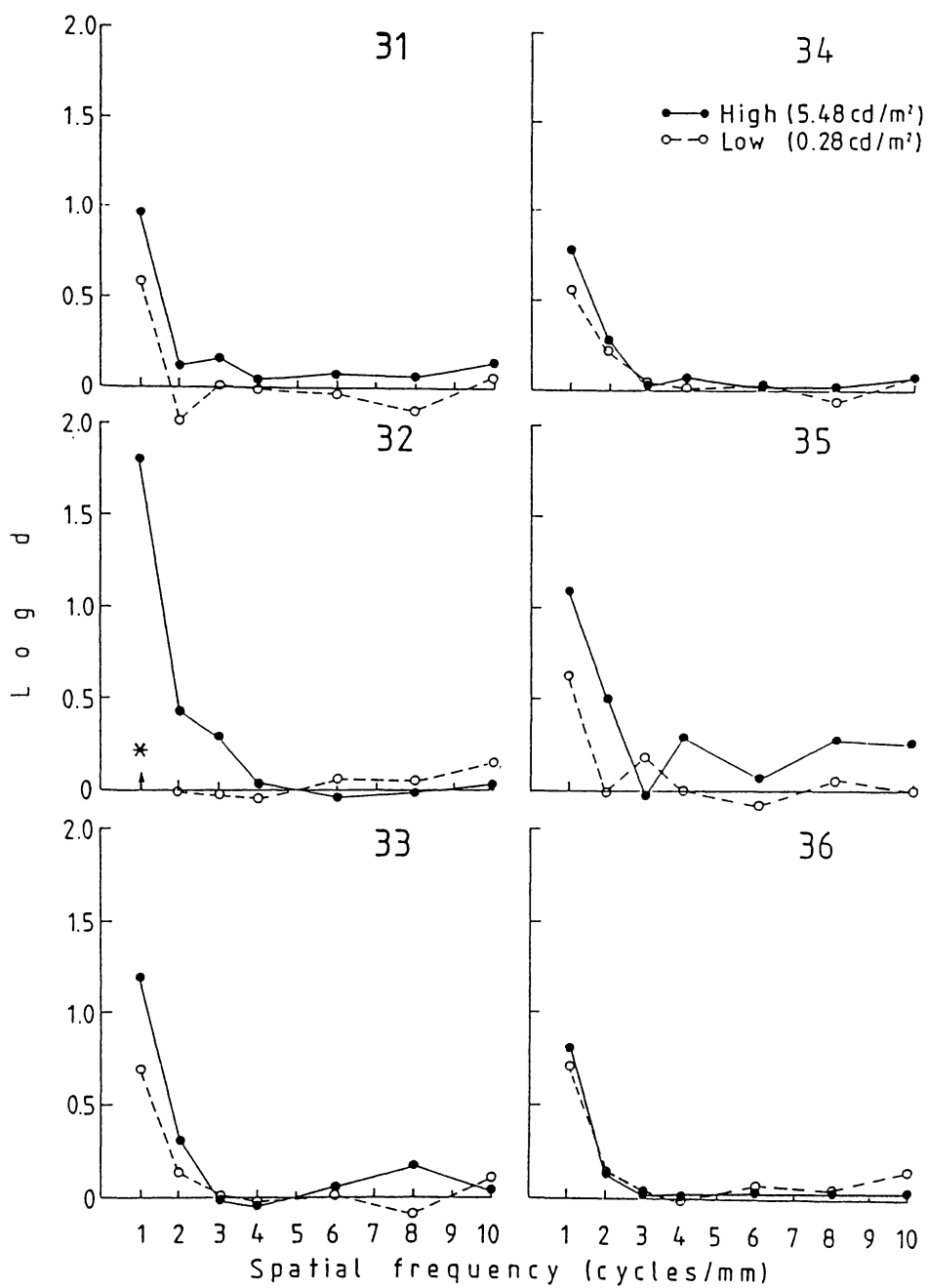
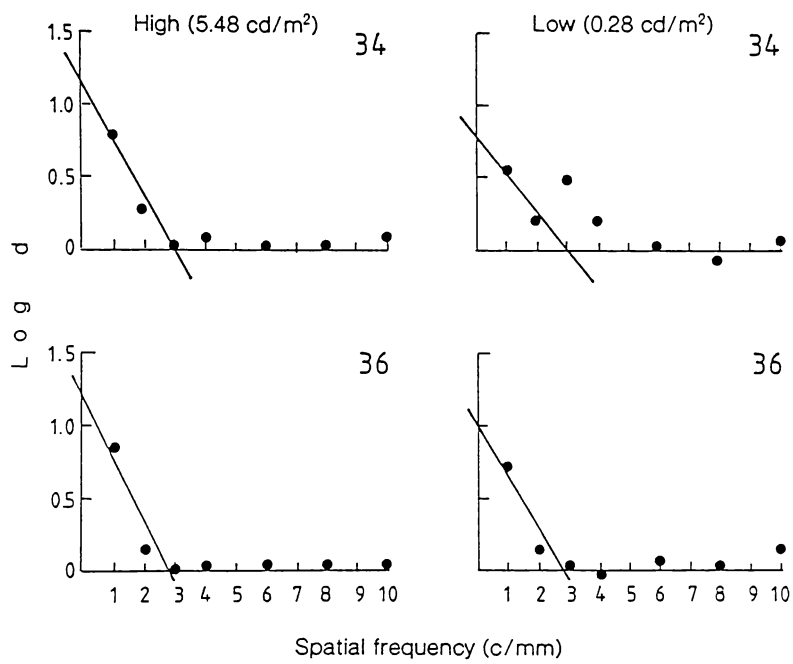


Figure 2.3.5

Figure 2.3.5

Values of $\log d$ plotted as a function of grating spatial frequency, measured in c/mm, for hens 34 and 36, for the series of probes at the high (5.48 cd/m^2) and low (0.28 cd/m^2) luminance. A line has been fitted to the descending portion of the data from each hen by the method of least squares, and is shown in the figures. Parameters of all fitted lines are given in Table 2.3.1.



the fitted line, the standard error of the estimate and variance accounted for by the lines chosen to fit the data from all hens, except 32, are shown in Table 2.3.1. All lines fitted to the data from the probe series at the high luminance were those with the least standard error. One of the five lines chosen to fit the data from the probe series at the low luminance, was that with the least standard error.

Various threshold estimates were calculated in c/deg, as for the previous studies, and are presented in Table 2.3.2. Generally, greater estimates were found for the probe series with the high luminance, regardless of the method of analysis or criteria used. The greatest estimate, at 5.6 c/deg, for data from hen 32, was determined from the fitted line at a $\log d$ value of 0.48, at probes with the high luminance, and the lowest estimate at 1.6 c/deg, for data from hen 35, also determined from the fitted line, was from probes with the low luminance. Figure 2.3.6 presents threshold estimates (c/deg) taken from the stimulus values corresponding to 75% total trial accuracy, and 50% grating trial accuracy, plotted as a function of low and high luminance, for all hens. In all cases, estimates of threshold acuity were greater at the high luminance, using the criterion of 75% total trial accuracy, and in four out of six cases, when the criterion was 50% grating trials accuracy.

Figure 2.3.7 presents mean values of $\log d$ plotted as a function of grating spatial frequency, measured in c/mm, for group data from the six hens in the present study and the six hens in Experiment 1.3, for the probe series at the high and the low luminance. The data from the present study and from Experiment 1.3 for the probe series at the

Table 2.3.1

Table 2.3.1

The slopes and the intercepts, of the least-squares lines fitted to the $\log d$ values for each hen, for the probe series at the high (5.48 cd/m²) and low (0.28 cd/m²) luminance. The numbers of data points described by each line (Data pts.), the amounts of variance accounted for by the lines (VAC%) and the standard errors of the estimates (SE) are also given.

Hen	5.48 cd/m ²					0.28 cd/m ²				
	Slope	Intcpt	Data pts.	VAC%	SE	Slope	Intcpt	Data pts.	VAC%	SE
31	-0.28	1.02	4	49.8	0.31	x-0.17	0.52	4	7.0	0.33
32	-0.54	2.01	4	67.9	0.45	*	*	*	*	*
33	-0.61	1.72	3	86.5	0.23	x-0.35	0.99	3	77.5	0.18
34	-0.38	1.14	3	93.4	0.10	-0.26	0.80	3	92.7	0.07
35	-0.54	1.60	3	100	0.00	x-0.17	0.62	4	27.1	0.25
36	-0.42	1.17	3	73.7	0.23	x-0.35	1.00	3	73.4	0.19

* line not fitted

x not least standard error

Table 2.3.2

Table 2.3.2

Threshold estimates, measured in c/deg, from the various methods of analysis and criteria, for all hens, for the probe series at the high (5.48 cd/m²) and low (0.28 cd/m²) luminance. Where estimates were determined from the fitted line (Criterion 5), 95% confidence intervals are given in brackets.

Hen	Threshold Criteria	Luminance (cd/m ²)	
		High (5.48)	Low (0.28)
31	1	2.8	2.2
	2	4.0	3.4
	3	2.8	2.4
	4	3.0	2.2
	5	4.0 (0.6)	*
32	1	3.2	2.8
	2	3.4	3.4
	3	2.8	2.6
	4	4.0	*
	5	5.6 (0.9)	*
33	1	3.4	2.6
	2	4.4	3.6
	3	3.0	2.6
	4	3.0	3.8
	5	4.2 (0.5)	3.0 (0.4)
34	1	3.8	2.4
	2	3.8	3.4
	3	2.6	2.6
	4	3.2	2.4
	5	3.4 (0.2)	2.4 (0.1)
35	1	3.2	2.4
	2	3.6	3.2
	3	2.4	2.6
	4	4.4	2.4
	5	4.2 (0.0)	1.6 (0.5)
36	1	2.8	2.6
	2	4.0	4.2
	3	2.6	2.6
	4	3.0	3.0
	5	3.2 (0.5)	3.0 (0.4)

* Estimate not calculable

CRITERIA:

= 75% total trials correct

= 50% grating trials correct

= 75% grating trials correct

log d = log d value of 0.48

= determined from the fitted line at a log d of value of 0.48

Figure 2.3.6

Figure 2.3.6

Threshold estimates for all hens, taken from the the stimulus value corresponding to 75% total trials accuracy and 50% grating trials accuracy criteria, plotted as a function of the low (0.28 cd/m^2) and high (5.48 cd/m^2) luminance.

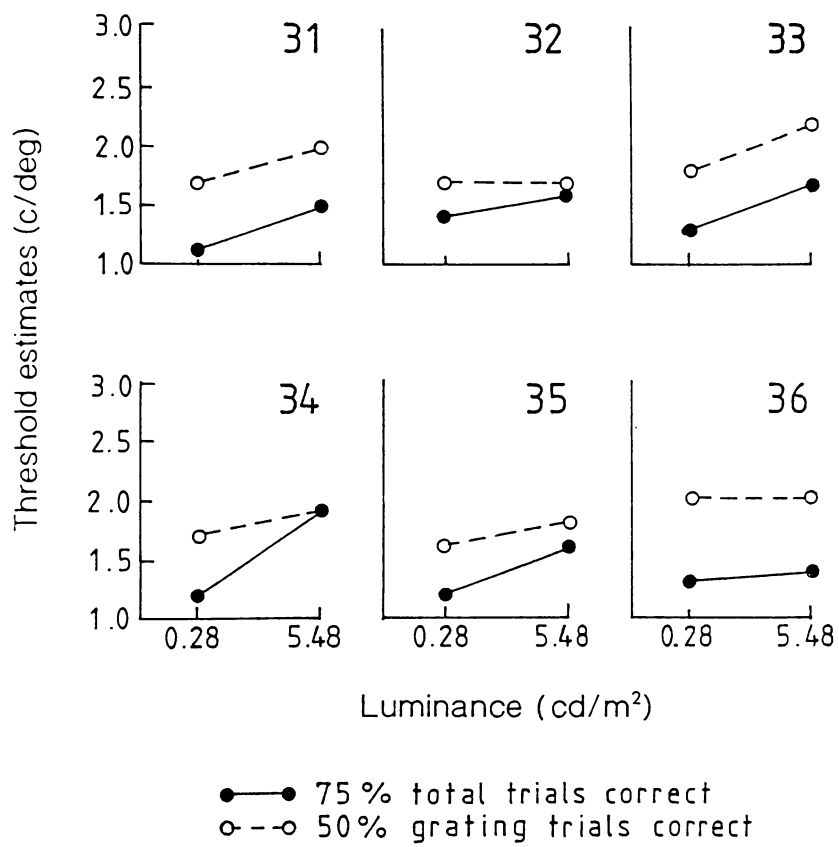
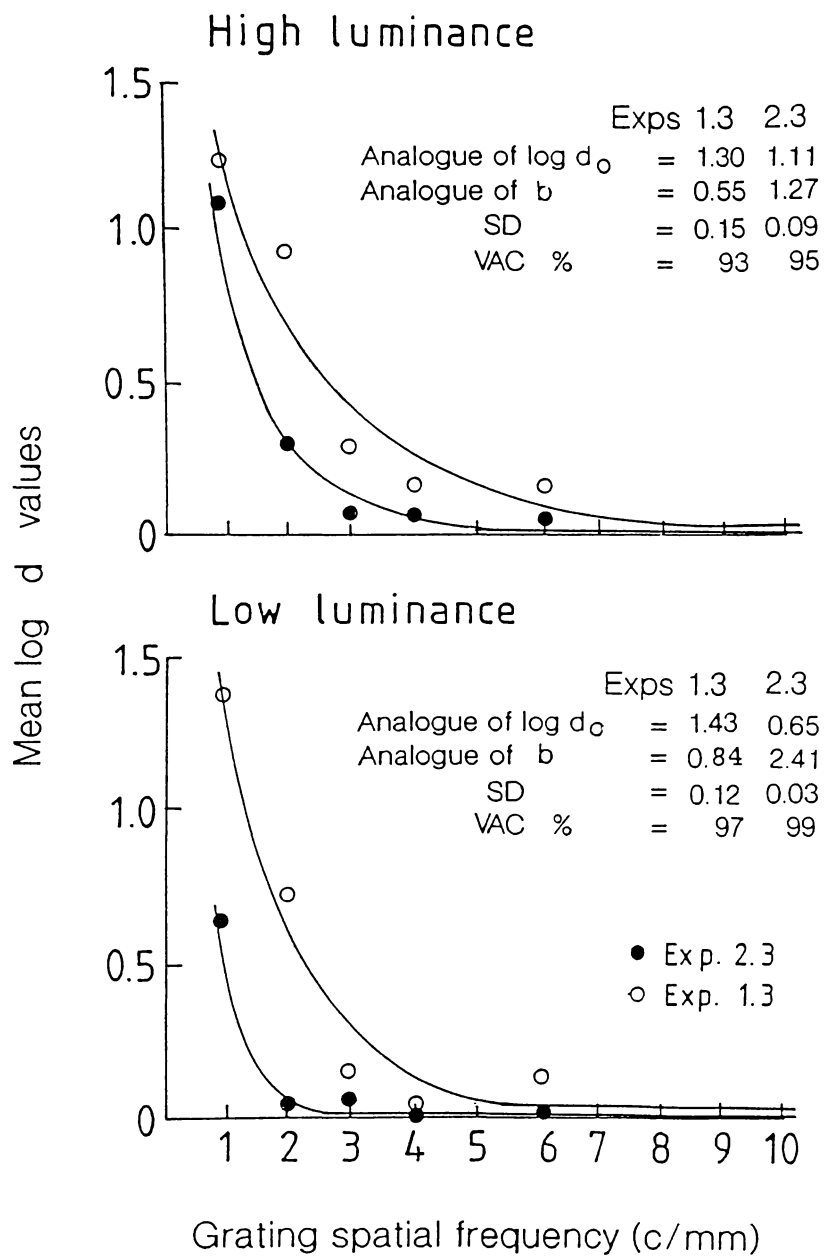


Figure 2.3.7

Figure 2.3.7

Mean values of $\log d$ plotted as a function of grating spatial frequency, measured in c/mm, for group data from Experiments 2.3 and 1.3, for the probe series at the high (5.48 cd/m^2) and low (0.38 cd/m^2) luminance.

A negative exponential function has been fitted to the data from each experiment for each probe series. The functions and the parameter descriptions are shown in the figures.



high luminance are shown in one graph, and those data from probe series at the low luminance are shown in the other. A negative exponential function (Equation 10) has been fitted to the data from the present study and Experiment 1.3, for each probe series. The data for probes at the two finest gratings (8 and 10 c/mm) assumed to be indiscriminable, were omitted from the analysis. These functions and their parameter descriptions are shown in the figures. Data variance accounted for by the fit of the functions range from 93% to 99%.

Initial discriminative performance at the coarsest grating (the analogue of $\log d_0$) was greater, and the rate of decrement in discriminative performance at finer gratings (the analogue of b) was smaller for data from Experiment 1.3 than for data from the present study, for both probe series. The functions fitting the data for the present study provide greater values of the analogue of $\log d_0$ (1.11), and smaller values of the analogue of b (1.27), for the probe series at the high luminance, compared to that at the low luminance (0.65 and 2.41, respectively). These parameters indicate that both the initial discriminative performance and the rate of decrement of discriminative performance at increasingly finer gratings appear to be affected by the luminance. Discriminative performance was not only higher at the high luminance, but decreased at a slower rate at increasingly finer gratings. For Experiment 1.3, as for Experiment 1.2, infinite values of $\log d$ at probes with the coarsest gratings resulted in the calculation of the mean $\log d$ value from data which indicated a less accurate performance. That is, although more hens provided a perfect performance at the coarsest grating at the high luminance, due to the infinite values of $\log d$, the mean value of $\log d$ for that probe series was slightly less than that for the probe

series at the low luminance. The resultant analogue of $\log d_0$ was slightly less than that for the low luminance. However, the rate of increment of discriminative performance (the analogue of b) was less for the probe series at the high luminance (0.55), compared to the probe series at the low luminance (0.84), consistent with results of the present study.

Response bias

Figure 2.3.8 presents the proportion of left key responses plotted as a function of grating spatial frequency, for all hens, for both probe series. Generally, the data show left and right position biases which were more extreme for the probe series at the low luminance, especially at finer gratings.

Reinforcements

Figure 2.3.9 shows the proportion of reinforcements obtained from red key responses, and left key responses, plotted as a function of grating spatial frequency, measured in c/mm, for all hens, for both probe series. For all hens and both probe series, the proportion of reinforcements for responses to the red key were close to equal. The proportion of reinforcements obtained for left key responses however, varied widely, and for four hens these were more extreme for probes at the low luminance. Five of six hens obtained the greater proportion of reinforcements for responding to one particular alternative, and for four of the hens this was mainly the right key.

Figure 2.3.8

Figure 2.3.8

The proportion of left key responses, plotted as a function of grating spatial frequency, measured in c/mm, for the probe series at the high (5.48 cd/m²) and low (0.28 cd/m²) luminance for both grating and grey stimulus trials.

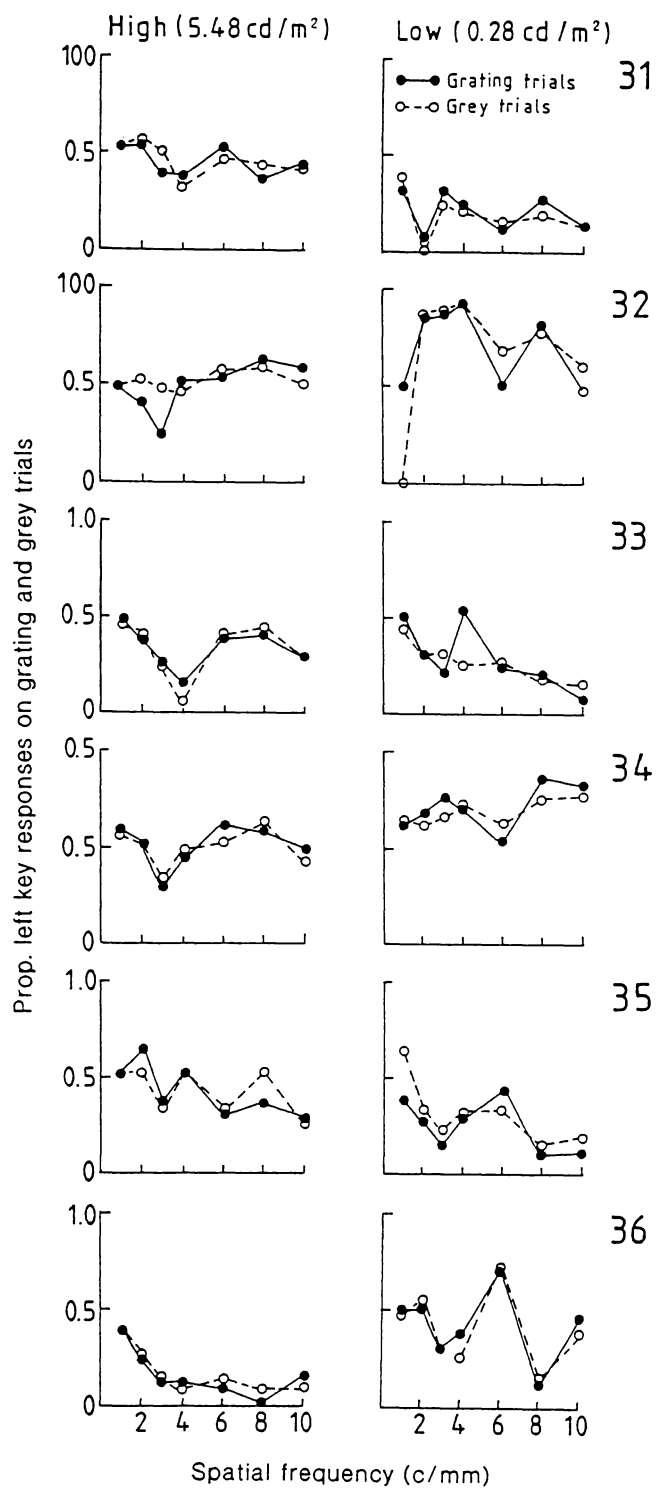
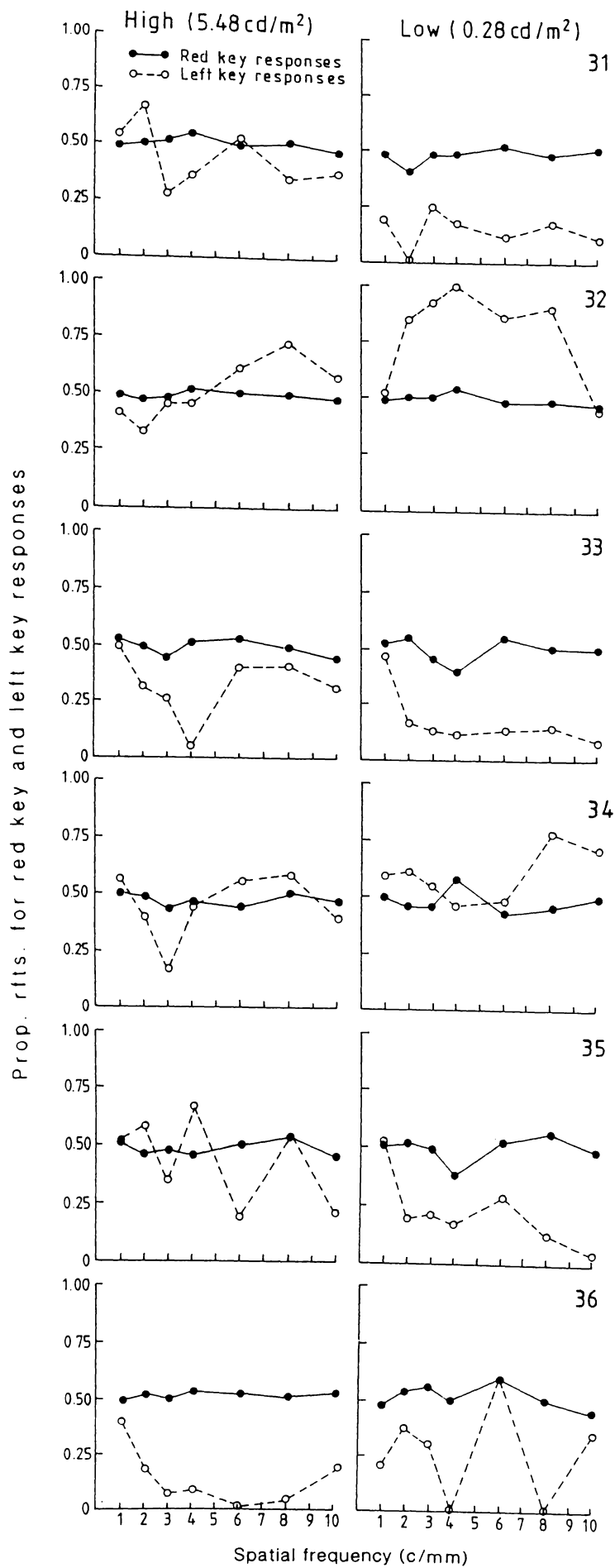


Figure 2.3.9

Figure 2.3.9

The proportion of reinforcements obtained for correct responses to the red key (filled circles) and correct responses to the left key (open circles), plotted as a function of grating spatial frequency, measured in c/mm, for the series of probes at the high (5.48 cd/m^2) and low (0.28 cd/m^2) luminance.



Discussion 2.3

Although a response requirement of FR10 was used in the equivalent study with the spatial discrimination task, Experiment 1.3, a decision was made to retain the response requirement of FR5 for the present study. This was chosen as the response requirement which overall provided greater accuracy in performance at the coarsest grating value. There was little difference between discriminative performance at the medium luminance (3 cd/m^2) from Experiment 2.2 (Table 2.3.1), and the low luminance (0.28 cd/m^2) in the present study. This finding was consistent with that for Experiment 1.3. This indicates, as for that previous study, that a greater difference in luminance is necessary to show a consistent difference in discriminative performance.

Discriminative performance

Despite the restricted range of luminances, an improvement in discriminative performance was consistent across all hens, and generally extended to most finer grating values. Because of the order of the two conditions (i.e. probes at the low luminance followed probes at the high luminance), it is possible to state that the higher accuracy obtained at the high luminance was a function of the luminance, rather than a practice effect. Estimates of threshold reflected the greater accuracy at the high luminance.

Unlike the results of the previous study, findings are very similar to those obtained in the equivalent study with the spatial discrimination task (Experiment 1.3). This implies that changes in luminance may be accompanied by changes in discriminative performance

in a similar way across procedures which use discrimination tasks of different difficulty levels. Because of the difference between performance in the previous study at the increased response requirements and that for Experiment 1.2, it was anticipated that these hens in the present procedure may require greater changes in luminance to show some difference. It appears that, whilst increased response requirements may improve discriminative performance they do not provide a consistent and predictable effect across studies (for example, Nevin *et al.*, 1963) and different procedures. The effect of changes in luminance on a visual discrimination task for animals with a duplex visual system, on the other hand, appears to be more robust.

In the discussion of Experiment 2.2, it was suggested that the value of the analogue of $\log d_0$ should possibly not be as independent of the analogue of b in a visual acuity task, as in a memory task. That is, if $\log d_0$ increases, b may also be expected to increase. Whilst for Experiment 2.2 the analogues of $\log d_0$ and b both increased with the increase of response requirements from FR1 to FR5 and FR10, for Experiment 1.2, the analogue of b decreased when the analogue of $\log d_0$ increased with increased response requirements from FR1 to FR10. In a similar manner to Experiment 1.2, the negative exponential functions fitted to the group data for the present study and Experiment 1.3 showed that increases in the value of the analogue of $\log d_0$ at the high luminance were accompanied by decreases in the value of the analogue of b . This indicates that certain factors which result in an improved discriminative performance at the coarsest grating value may also lower the rate of decrement in discriminative performance at finer grating values. It is interesting that, for the present study with the probe series at the high luminance, the

analogue of $\log d_0$ was almost twice the value, and the analogue of b was almost half the value of the same parameters for the probe series at the low luminance. Because of the limited range of luminances tested, there is scope for further investigation of this relation between the present analogues of $\log d_0$ and b , by testing at increased luminances to determine whether this would result in an even greater value of the analogue of $\log d_0$ and a concomitant smaller value of the analogue of b .

The greatest estimate of threshold obtained from the 75% total trials correct criterion for the present study was 3.8 c/deg at the high luminance of 5.48 cd/m². This was 2.6 c/deg lower than the greatest estimate taken from the same criterion at the same luminance in Experiment 1.3. It is, however, 2.6 c/deg greater than that reported by Over and Moore (1981), for young chickens, using a simultaneous discrimination task with jumping stand apparatus and a luminance of 39 cd/m².

If, as Over and Moore suggest, the hen attains its limit of visual acuity within two days' of hatching, then it is difficult to account for the difference between their findings and those of the present study. Although the jumping stand has been used with apparent success in determining the visual acuity of young animals, for example kittens (Mitchell, Giffin, Wilkinson, Anderson & Smith, 1976) there were several procedural differences between Over and Moore's study and that of Mitchell *et al.* For example, Mitchell *et al.* used a descending series of stimulus presentation, while Over and Moore used a random sequence. It has been reported (e.g. Dalland, 1970; Blough, 1971) that the descending series of stimulus presentation generates a

more accurate discriminative performance. Mitchell *et al.* increased the spatial frequency of gratings in very small steps, whilst Over and Moore used only four grating values, and the difference in the spatial frequency was relatively large. The results of the previous study (Experiment 2.2) indicate that large changes in stimulus values may disrupt discriminative performance at all but the coarsest grating value. Therefore, it is possible that procedural differences may account for the differences in results. While the jumping stand itself may not be inappropriate for the study of visual functioning of young animals, certain procedural variations may not be conducive to the generation of discriminative performance which adequately reflects the animals' actual visual capability.

Response distributions and response bias

The distributions of grating and grey trial accuracy in the previous study generally became more separate when increased response requirements were programmed on the sample key. These more separate data paths for grating and grey trial accuracy, which indicate a higher maintenance of correct responding on grey stimulus trials, generally occurred in the present study. These therefore appear to be a function of the increased response requirement, as suggested in the earlier discussion of Experiment 1.2.

Loss of accuracy in performance at the low luminance in the present study, tends to be accompanied by greater response biases, both for colour (green key responding) and for position (varying) than those at the high luminance. This is consistent with the notion that performance is under the joint control of the stimuli and the reinforcer to finer grating values, when the stimuli are more

discriminable. That is, when stimuli are less discriminable, as with a low luminance, performance becomes under the control of the reinforcer alone at a lower grating spatial frequency, than with the high luminance. There is increasing evidence in the present series of studies, that any factor which reduces discrimination is also functional in the development of extreme biases in behaviour, especially that behaviour which is not under constraint from reinforcement contingencies to maintain responding to both alternatives.

Conclusion

Changes in luminance are logically one variation in a discrimination task which should change discriminative performance and resultant threshold estimates. Where increased response requirements may, for some discrimination tasks, improve discriminative performance, any increase in accuracy is an artefact of the procedure, rather than a direct result of changes in stimulus discriminability. While both increased response requirements and increased luminance had a similar effect in terms of improving discriminative performance in Experiments 1.2 and 1.3 respectively, with the spatial discrimination task, only the increased luminance had a consistent effect in increasing accuracy across all stimulus values in the present study, with the non-spatial discrimination task.

EXPERIMENT 2.4

A comparison of performance using a controlled and an uncontrolled reinforcement procedure in Experiment 1.5 showed discrimination to be generally better with the uncontrolled procedure, whether data were analysed as percentages of total trials correct, or as values of $\log d$. However, when grating discrimination alone was compared, and estimates of threshold were obtained from grating trials only, those from the controlled descending series were greater for most hens than those from the descending series using the uncontrolled procedure. Total trial accuracy was higher with the uncontrolled procedure because of the high level of accuracy on grey stimulus trials, rather than high grating trial accuracy. Rather, the grating trial accuracy for most hens was higher for performance with the controlled procedure. That is, as the hens were less able to discriminate at finer gratings, right key responding (as though the stimuli were grey) increased, resulting in higher accuracy on grey stimulus trials, but lower accuracy on grating trials, compared to performance with the controlled procedure.

The controlled reinforcement procedure for Experiments 1.1 to 1.4 ensured that equal reinforcements were obtained for correct responding to both left and right keys. However, the controlled reinforcement procedure in Experiments 2.1 to 2.3 ensured that equal rates of reinforcement were obtained for correct responding to red and green keys, rather than to left and right keys. Because red and green were programmed to appear for an equal number of trials on each side key, an animal could respond exclusively to one side key and still obtain the scheduled number of reinforcements for correct responding. In the

three previous studies, this has resulted in an iso-bias function for responding to key colour, and an alloio-bias function for responding to key position, at increasingly finer gratings.

When performance with an uncontrolled reinforcement procedure was studied in Experiment 1.5, responses to the left and right keys were free to vary without loss of scheduled reinforcers. With an uncontrolled reinforcement procedure in the present study however, responses would be free to vary with both key colour and position. The animal though, would only be able to choose to respond more or exclusively either to one key colour, or one key position at any particular time, and not to both, simultaneously. For example, exclusive responding to the red key would require the animal to apportion responses equally to both left and right keys, and conversely, exclusive responding to one key position would require the animal to apportion responses equally to both red and green keys, as these colours presented on that one side key.

The rationale for the present study was similar to that for Experiment 1.5: to compare changes in discriminative performance and response bias under an uncontrolled reinforcement procedure. The question to be answered was: if animals had a choice to vary responses to either key colour or key position, would they choose to increase responding to a particular key colour as discrimination decreased, or would they continue responding more to key position (as for the three previous studies)? Alternatively, would they develop biases for key colour and then for key position, at different levels of discrimination, as a function of probes with increasingly finer gratings?

Method 2.4

Subjects and Apparatus

Five of the six hens serving in the previous three studies, served. These hens were numbered 31, 32, 33, 35 and 36. Hen 34 died of natural causes prior to the commencement of this study. The apparatus was the same as that used for the three previous studies. The luminance of the sample key was maintained at 5.48 cd/m².

Procedure

The procedure was similar to that used for Experiment 2.3. The response requirement to the sample key was FR5, as for Experiment 2.3. Correct responses produced wheat on a single VI 30 s schedule, as for all previous studies. There was one variation in the procedure, from that used for Experiment 2.3. An uncontrolled reinforcement schedule was programmed. That is, correct detections were reinforced on the single VI schedule and these were not scheduled to be allotted equally for correct responses to the red and green keys. Therefore, the hens were not required to respond equally to both red and green keys to obtain all scheduled reinforcements.

The hens were trained to a stability criterion as for the controlled procedure, of the previous three studies. After 29 training sessions, when the hens had satisfied the above criterion, they were tested with a descending series of probes, immediately followed by an ascending series of probes. These two probe series were conducted as for Experiment 2.1. Data were collected as for the previous three studies.

Results 2.4

Discrimination

Figure 2.4.1 shows the percentages of total trials correct plotted as a function of grating spatial frequency, measured in c/mm, for all five hens, for both series of probes with an uncontrolled reinforcement procedure. Data from the same hens, from the descending probe series with a controlled reinforcement procedure, in Experiment 2.3, at the same luminance value and with the same response requirement, are also presented, and shown as unfilled circles joined by a broken line. This allowed a comparison of both descending series of probes. For all hens, and the three probe series shown, the percentages of total trials correct decreased from 90 - 95% at the coarsest grating to approximately 50% correct at probes with grating values of 2 - 3 c/mm. A comparison of the data from the two descending probe series shows that, in general, the data paths are very similar. There were no consistent difference between the percentages of total trials correct for the two probe series with the uncontrolled procedure.

Threshold estimates for all hens for each probe series were determined as that spatial frequency of the grating at which 75% of the total trials were correct. This was obtained by interpolation, as in Experiment 2.1. These estimates are shown on Table 2.4.1 and range from 2.6 c/deg for both probe series with the uncontrolled procedure, to 4.0 c/deg for the ascending series of probes using the uncontrolled reinforcement procedure. For most hens estimates from probes with the controlled procedure were greater than those obtained for probes with the uncontrolled procedure.

Figure 2.4.1

Figure 2.4.1

The percentages of total trials correct, plotted as a function of grating spatial frequency, measured in c/mm, for all hens, for the descending and ascending series of probes with an uncontrolled reinforcement procedure. Data from the descending series of probes with a controlled reinforcement procedure (Experiment 2.3) are also presented for comparison, and are shown in the figures as unfilled circles joined by a broken line.

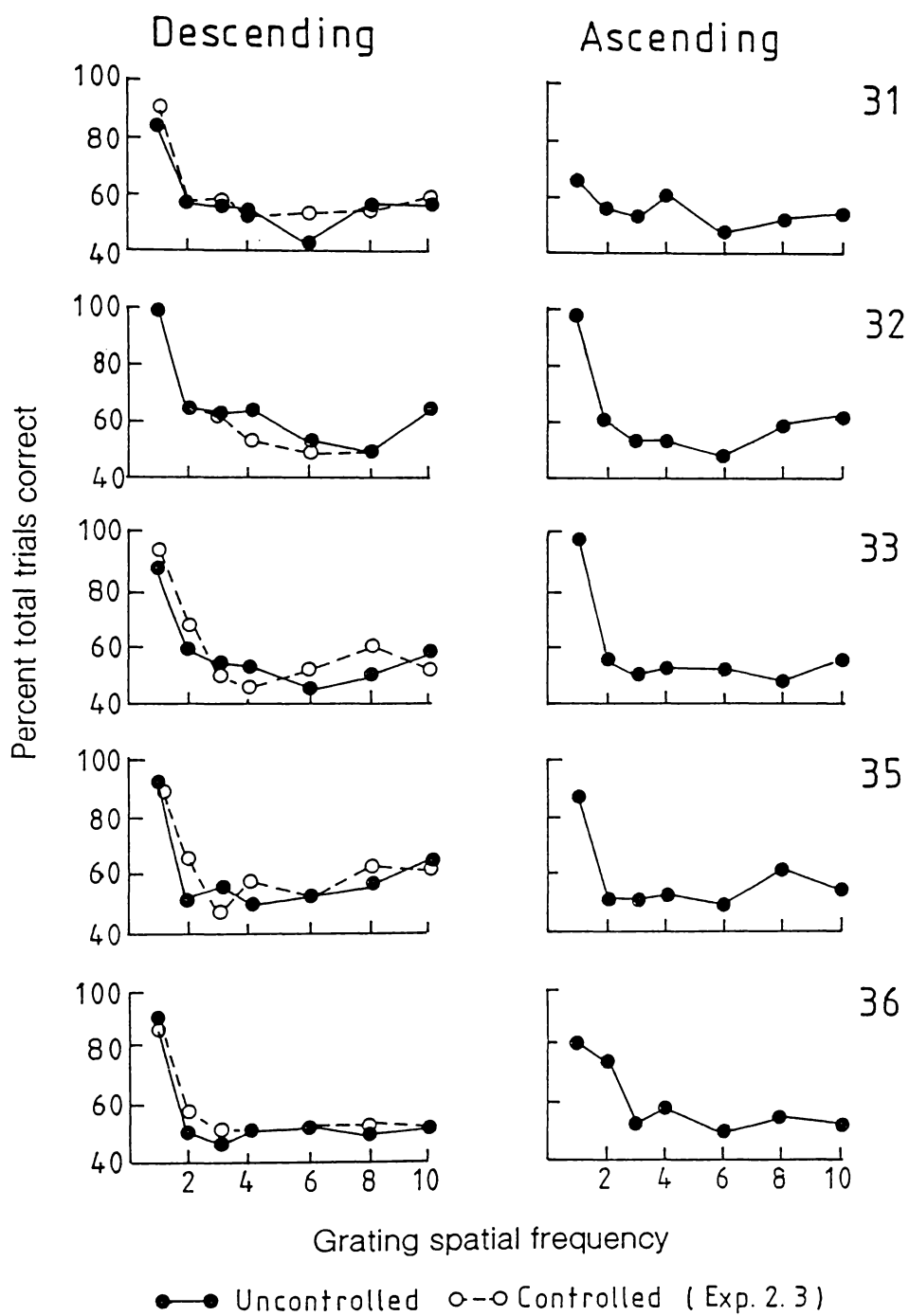


Table 2.4.1

Table 2.4.1

Threshold estimates, measured in c/deg, from the various methods of analysis and criteria, for all hens, for the descending (Desc) and ascending (Asc) series of probes with the uncontrolled reinforcement procedure. Estimates from descending probe series with the controlled reinforcement procedure (Experiment 2.3) are also shown. Where estimates were determined from the fitted line (Criterion 5), 95% confidence intervals are given in brackets.

Hen	Threshold Criteria	Reinforcement Procedure		
		Controlled (Exp. 2.3)	Uncont. (Desc)	Uncont. (Asc)
31	1	2.8	2.6	*
	2	4.0	3.4	4.4
	3	2.8	2.4	2.2
	4	3.0	3.0	*
	5	4.0 (0.6)	0.6 (0.2)	*
32	1	3.2	3.0	2.8
	2	3.4	4.0	3.8
	3	2.8	2.8	3.6
	4	4.0	*	*
	5	5.6 (0.9)	*	*
33	1	3.4	3.0	3.2
	2	4.4	3.8	3.6
	3	3.0	2.6	2.6
	4	3.0	3.2	3.0
	5	4.2 (0.5)	3.6 (0.4)	4.0 (0.6)
35	1	3.2	2.8	2.6
	2	3.6	3.2	3.6
	3	2.4	2.4	2.6
	4	4.4	3.0	3.2
	5	4.2	4.4 (0.8)	3.2 (0.6)
36	1	2.8	2.6	4.0
	2	4.0	3.6	5.6
	3	2.6	2.6	3.6
	4	3.0	3.0	6.0
	5	3.2 (0.5)	3.4 (0.8)	3.2 (0.2)

* Estimate not calculable

CRITERIA: 1 = 75% total trials correct

2 = 50% grating trials correct

3 = 75% grating trials correct

4 = log d value of 0.48

5 = determined from fitted line at a log d value of 0.48

Figure 2.4.2 presents the mean percentages of total trials correct, plotted as a function of grating spatial frequency measured in c/mm for group data from the descending and ascending series of trials with the uncontrolled reinforcement procedure in the present study, and in Experiment 1.5. Data from the descending series for both studies are shown in one graph and data from the ascending series from both studies are shown in the other, for comparison. The mean percentages of total trials correct from Experiment 1.5 for both the descending and ascending series of probes were higher than those for the present study, at all grating values.

Figure 2.4.3 shows the percentages of grating and grey trials correct, separately, plotted as a function of grating spatial frequency, measured in c/mm, for each probe series. A comparison of the data from the two descending probe series show that, for one of five hens, the grating and grey data paths are more separate for the probes with the uncontrolled procedure. That is, as accuracy on grating trials decreased as a function of increasingly finer gratings, accuracy was maintained at a higher level on grey stimulus trials over the probes with the uncontrolled reinforcement procedure. For example, for probes at 6 c/mm, the grating trial accuracy for hen 33 decreased to below 20%, while grey trial accuracy was 75%. For hen 32 however, grating and grey trial functions show more separation for probes with the controlled procedure. For other hens, grating and grey trial accuracy varied unsystematically, at times showing a wide separation of the two functions and at other times in close proximity. Differences across hens in their distribution of correct grating and grey trial responses were not reflected in their plots of percentages

Figure 2.4.2

Figure 2.4.2

The mean percentages of total trials correct, plotted as a function of grating spatial frequency measured in c/mm. for all hens in the present study (filled circles) and Experiment 1.5 (unfilled circles), for the descending and ascending series of probes with the uncontrolled reinforcement procedure. The functions for the descending series from the present study and Experiment 1.5 are shown in one figure, and the functions for the ascending series are shown in the other figure.

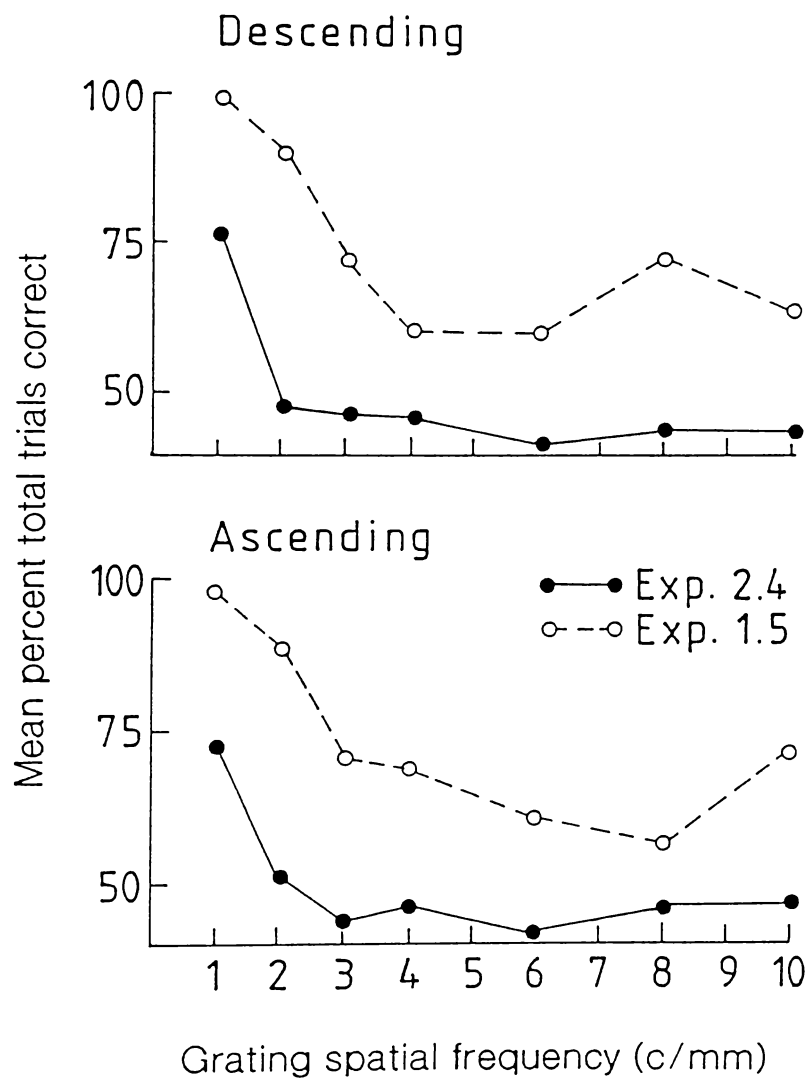
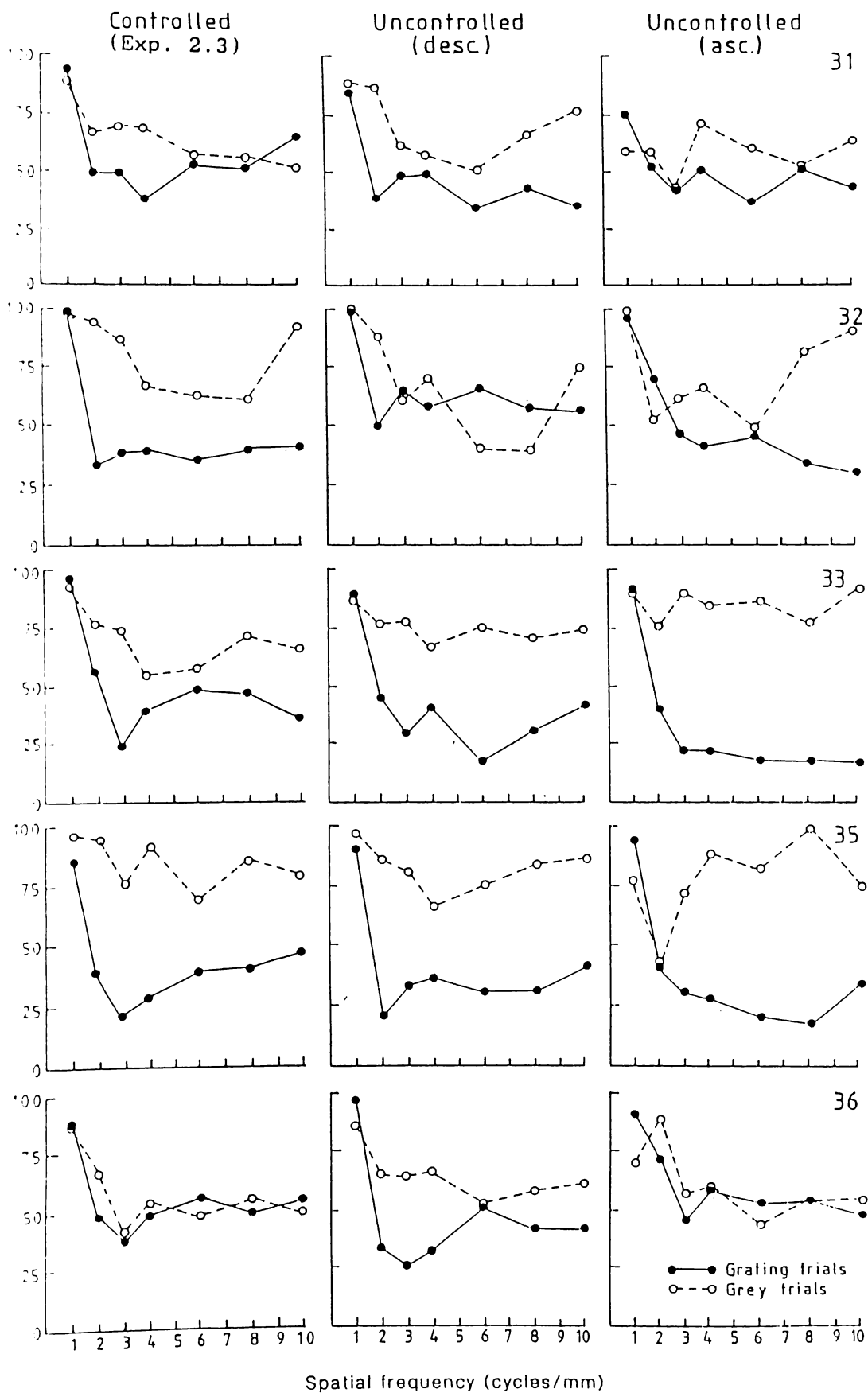


Figure 2.4.3

Figure 2.4.3

The percentages of grating (filled circles joined by a solid line) and grey stimulus trials (unfilled circles joined by a broken line) correct, plotted separately, as a function of grating spatial frequency, measured in c/mm, for all hens, for the descending and ascending series of probes with the uncontrolled reinforcement procedure. Data from the descending series with the controlled reinforcement procedure (Experiment 1.3.) are also presented.



of total trials correct. Those data which show wide separation of grating and grey trials correct, indicate that a high proportion of correct responses at finer grating values, were made following presentation of the grey stimulus. Data functions for three hens, 31, 35 and 36, are the same across the three probe series. The data from the two probe series with the uncontrolled reinforcement procedure were similar.

Threshold estimates based on the grating trials only, were taken from the point at which the plotted functions were 50% correct, as in Experiment 2.1. The estimates for all hens and the three probe series are shown in Table 2.4.1 as Criterion 2 and range from 3.2 c/deg for the descending series of probes with the uncontrolled procedure, to 5.6 c/deg for the ascending series of probes. For four of the five hens, estimates taken from probes with the controlled reinforcement procedure were greater than those obtained from the descending series with the uncontrolled reinforcement procedure. For two hens, estimates taken from the ascending series of probes were greater than from either of the descending series. Estimates taken from the points at which the plotted functions were 75% correct are also given in Table 2.4.3, and shown as Criterion 3. Both the lowest (2.2 c/deg) and the highest (3.6 c/deg) estimates were taken from the ascending probe series with the uncontrolled reinforcement procedure. An emerging pattern indicates a superior discriminative performance for probes with the controlled reinforcement procedure, although the difference between performances with the two procedures was not great.

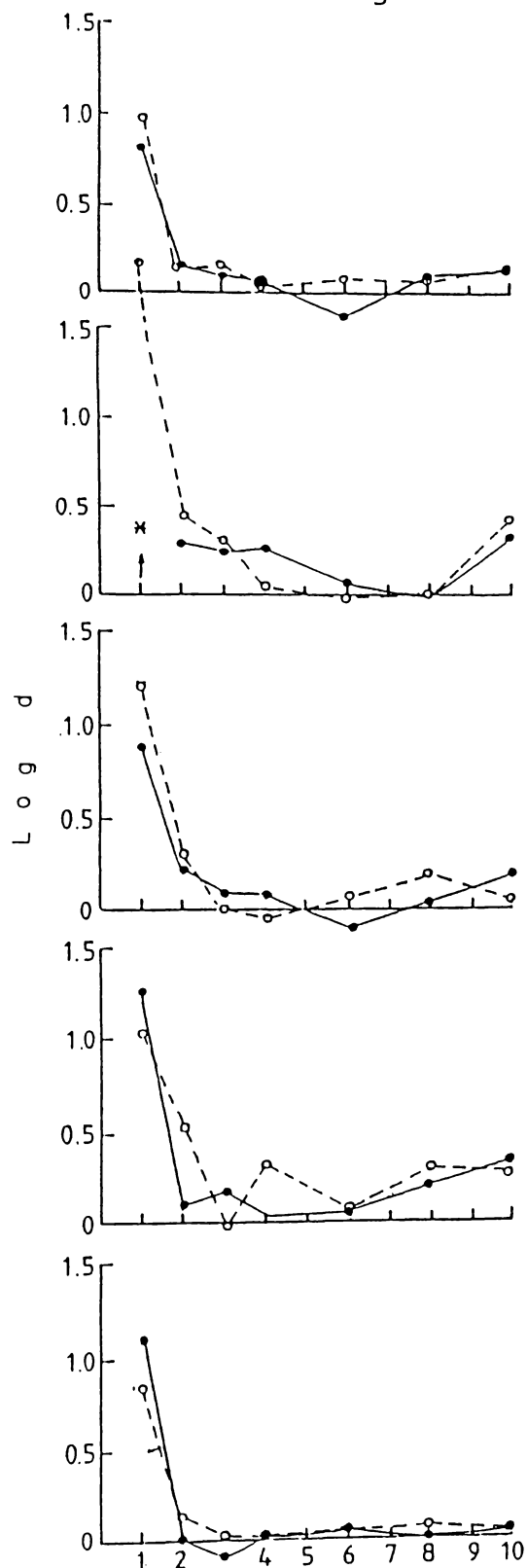
Figure 2.4.4 shows log d values plotted as a function of grating spatial frequency, measured in c/mm, for all hens and for the two

Figure 2.4.4

Figure 2.4.4

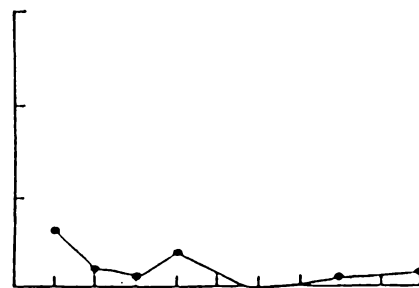
Values of $\log d$ plotted as a function of grating spatial frequency, measured in c/mm, for all hens, for the descending and ascending series of probes with the uncontrolled reinforcement procedure. Data from the descending series of probes with the controlled reinforcement procedure (Experiment 2.3) are also presented, and are shown in the figures as unfilled circles joined by a broken line.

Descending

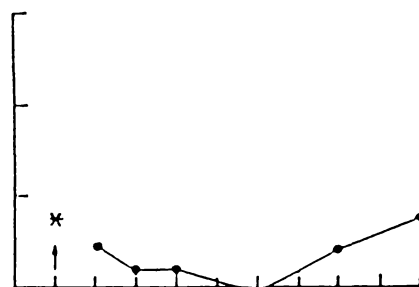


Ascending

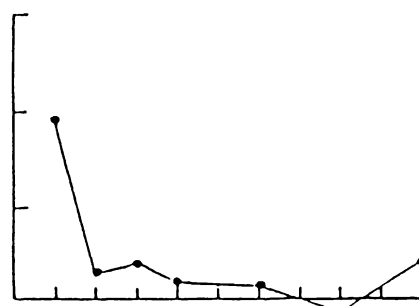
31



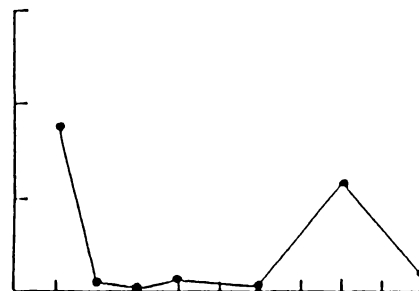
32



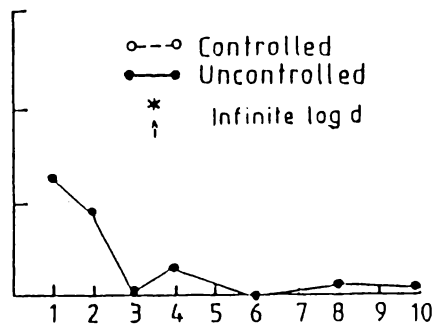
33



35



36



Grating spatial frequency (c/mm)

probe series with the uncontrolled reinforcement procedure. Data from the descending series with the controlled reinforcement procedure (Experiment 2.3) are included for comparison and are shown in the figures as unfilled circles joined by a broken line. A comparison of the two descending series shows that the $\log d$ values were not really different. Although infinite $\log d$ values for hen 32 at the coarsest grating for both descending and ascending series prevent comparison with data from the controlled procedure at that stimulus value, the data paths reflect those shown in Figure 2.4.1. The three functions are similar at probes with the finer gratings.

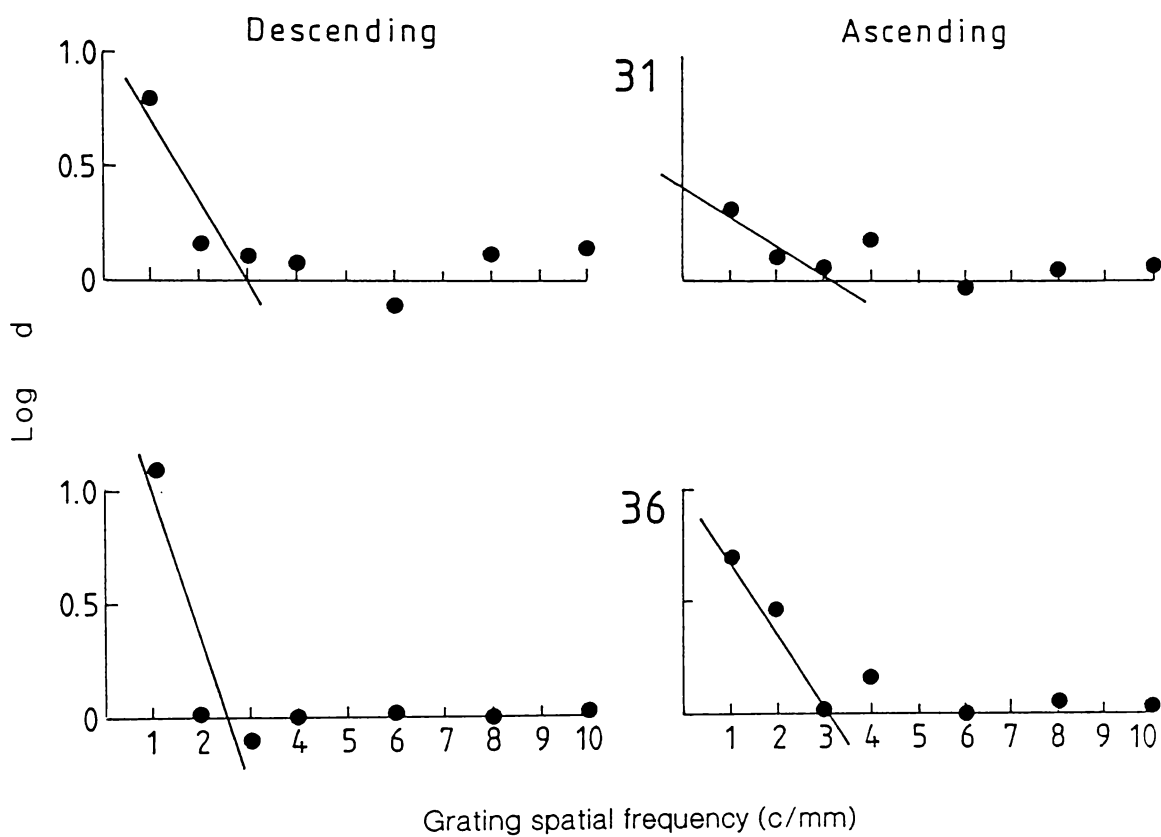
Threshold estimates were obtained by interpolation to determine the spatial frequency of grating which corresponded to a $\log d$ value of 0.48, as for Experiment 2.1. These are given in Table 2.4.1, as Criterion 4, and range from 3.0 c/deg for each probe series, to 6.0 c/deg for the ascending series of probes, with the uncontrolled reinforcement procedure. There is little difference between estimates taken from the two descending series. No estimate was taken for hen 31 for the ascending series, as the $\log d$ value at the coarsest grating was less than 0.48. No estimate was taken for hen 32 from either series of probes with the uncontrolled reinforcement procedure, due to infinite values of $\log d$. For two hens, greater estimates were obtained from the controlled procedure, and for one hen, 36, the greater estimate was obtained from the ascending series of probes with the uncontrolled reinforcement procedure.

The $\log d$ values plotted in Figure 2.4.4, from the two probe series with the uncontrolled procedure, are presented in Figure 2.4.5 for two hens only, 31 and 36. A line was fitted to the descending

Figure 2.4.5

Figure 2.4.5.

Values of $\log d$ plotted as a function of grating spatial frequency, measured in c/mm, for hens 31 and 36, for the descending and ascending series of probes with the uncontrolled reinforcement procedure. A line has been fitted to the descending portion of the data from each hen by the method of least squares, and is shown in the figures. The parameters of all fitted lines are given in Table 2.4.2.



portion of the data for four hens by the method of least squares (as in Experiment 2.1). No line could be fitted to the data for hen 32, because infinite $\log d$ values resulted in a loss of the descending portion of the data function. The lines chosen to describe the descending portion of the data for hens 31 and 36 are shown in the figures. The slopes, intercepts, the number of data points described by the fitted lines, the standard errors and variances accounted for (VAC%) by the fitted lines are given in Table 2.4.2, for both series of probes. Both lines chosen to fit the data from three of the four hens were those with the least standard error.

Threshold estimates from the stimulus value corresponding to a $\log d$ value of 0.48 were taken from the fitted lines, as in Experiment 2.1. Table 2.4.1 presents these estimates as Criterion 5. Estimates from the descending probe series with the controlled reinforcement procedure are also presented, for comparison. The 95% confidence intervals are shown in brackets. Estimates range from 0.6 c/deg for probes from the descending series with the uncontrolled procedure, to 5.6 c/deg for probes with the controlled reinforcement procedure. Again, there was little difference between estimates taken from both descending series of probes

Figure 2.4.6 presents threshold estimates taken from the various methods of analysis, plotted as a function of the various criteria, for the two probe series with the uncontrolled reinforcement procedure. Those from the previous study (Experiment 2.3) with the controlled reinforcement procedure are also presented for comparison. A comparison of estimates from the two descending probe series indicate that the 75% total trial and 50% grating trial estimates were

Table 2.4.2

Table 2.4.2

The slopes and the intercepts of the least-squares lines fitted to the values of $\log d$ for all hens, for the descending and ascending series of probes with the uncontrolled reinforcement procedure. The number of data points described by each line (Data pts.), the amounts of variance accounted for by the lines (VAC%) and the standard error of the estimates (SE) are also given.

Hen	Descending					Ascending				
	Slope	Intcpt	Data pts.	VAC%	SE	Slope	Intcpt	Data pts.	VAC%	SE
31	x-0.36	1.07	3	63.3	0.24	-0.13	0.42	3	69.5	0.08
32	*	*		*	*	*	*		*	*
33	-0.40	1.19	3	73.6	0.22	-0.26	0.99	4	48.3	0.30
35	-0.36	1.29	4	45.9	0.43	-0.25	0.87	4	37.7	0.33
36	-0.60	1.53	3	61.2	0.41	-0.32	1.02	3	88.7	0.11

* line not fitted

x not least standard error

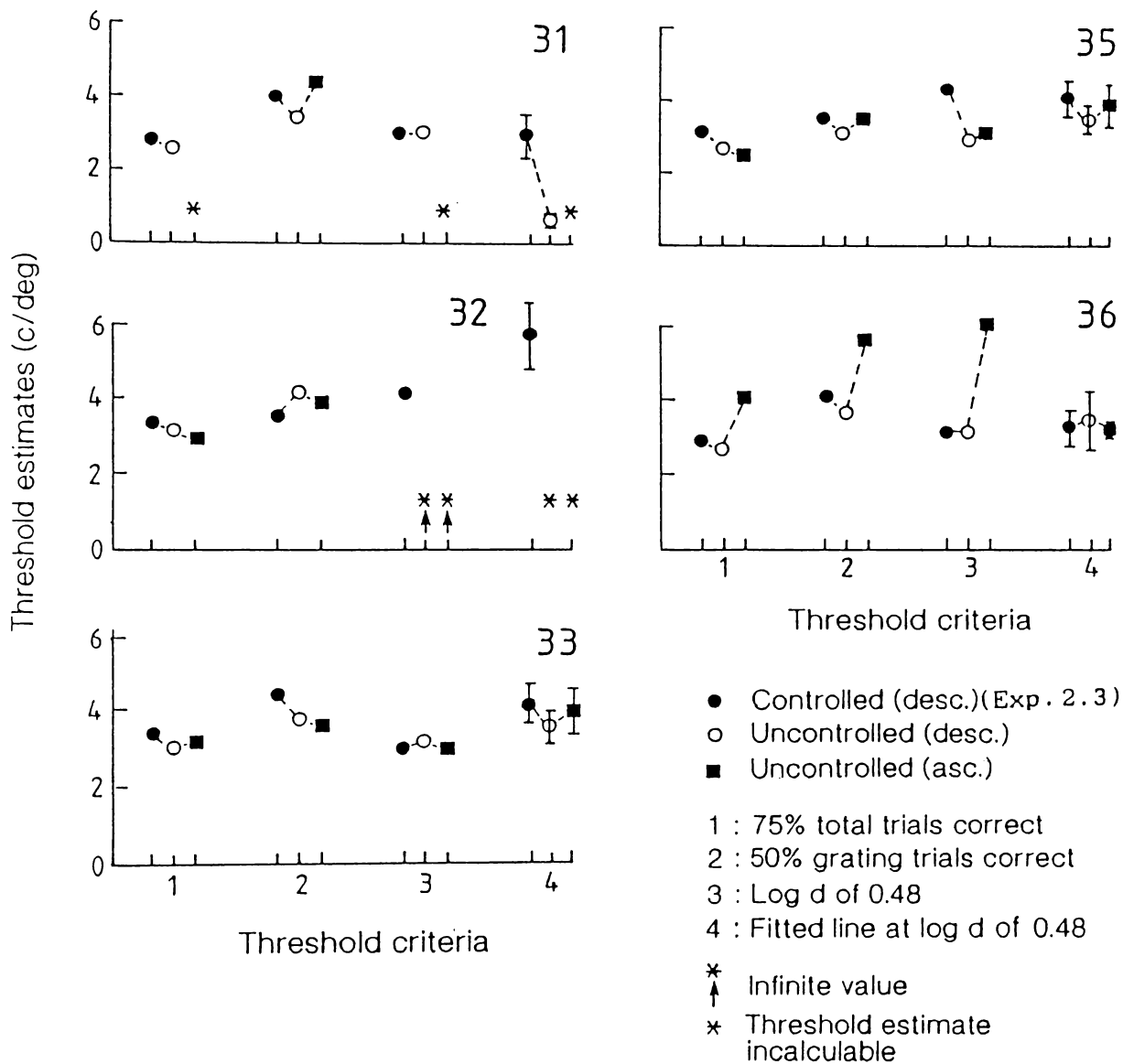
Figure 2.4.6

Figure 2.4.6

Threshold estimates from the various methods of analysis. These estimates were taken from the stimulus value corresponding to:

1. 75% total trial accuracy
2. 50% grating trial accuracy
3. a $\log d$ value of 0.48
4. a $\log d$ value of 0.48, determined from the fitted line.

The 95% confidence intervals, determined from the standard error of the line fit, are shown for estimates from the fitted line.



generally greater from the probe series under the controlled reinforcement procedure. Estimates taken from 75% grating trial accuracy and a $\log d$ value of 0.48 (either with, or without the fitted line) however, were not very different across both reinforcement procedures. There was no consistent difference between those taken from the two probe series with the uncontrolled reinforcement procedure.

Figure 2.4.7 presents mean values of $\log d$ plotted as a function of grating spatial frequency measured in c/mm, for group data from both series of probes with the uncontrolled reinforcement procedure, for the present study and for Experiment 1.5. Data for the two finest grating values (8 and 10 c/mm), assumed to be indiscriminable, were omitted from analysis. Data from the two descending series are shown in one graph, and data from the two ascending series are shown in the other, for comparison. A negative exponential function has been fitted to the data for each probe series from the present study and Experiment 1.5. These functions and their parameters are shown in the figures. Data variance accounted for by the fitted function ranged from 95% to 98%. Table 2.4.3 presents the parameters and includes those from the negative exponential functions fitted to the descending series of probes with the controlled procedure (Figure 1.3.3 in Experiment 1.3 and Figure 2.3.4 in Experiment 2.3). The figures show that, for both probe series with the uncontrolled reinforcement procedure, the analogue of $\log d_0$ was greater, and the analogue of b was smaller, for the data from Experiment 1.5, compared with those for the present study.

A comparison of both descending probe series for the present

Figure 2.4.7

Figure 2.4.7

Mean values of $\log d$ plotted as a function of grating spatial frequency, measured in c/mm, for group data from the present study and from Experiment 1.5, for the descending and ascending series of probes with the uncontrolled reinforcement procedure. A negative exponential function has been fitted to the data from each probe series. The functions are shown in the figures, and the parameter descriptions are given in the figures and in Table 2.4.3.

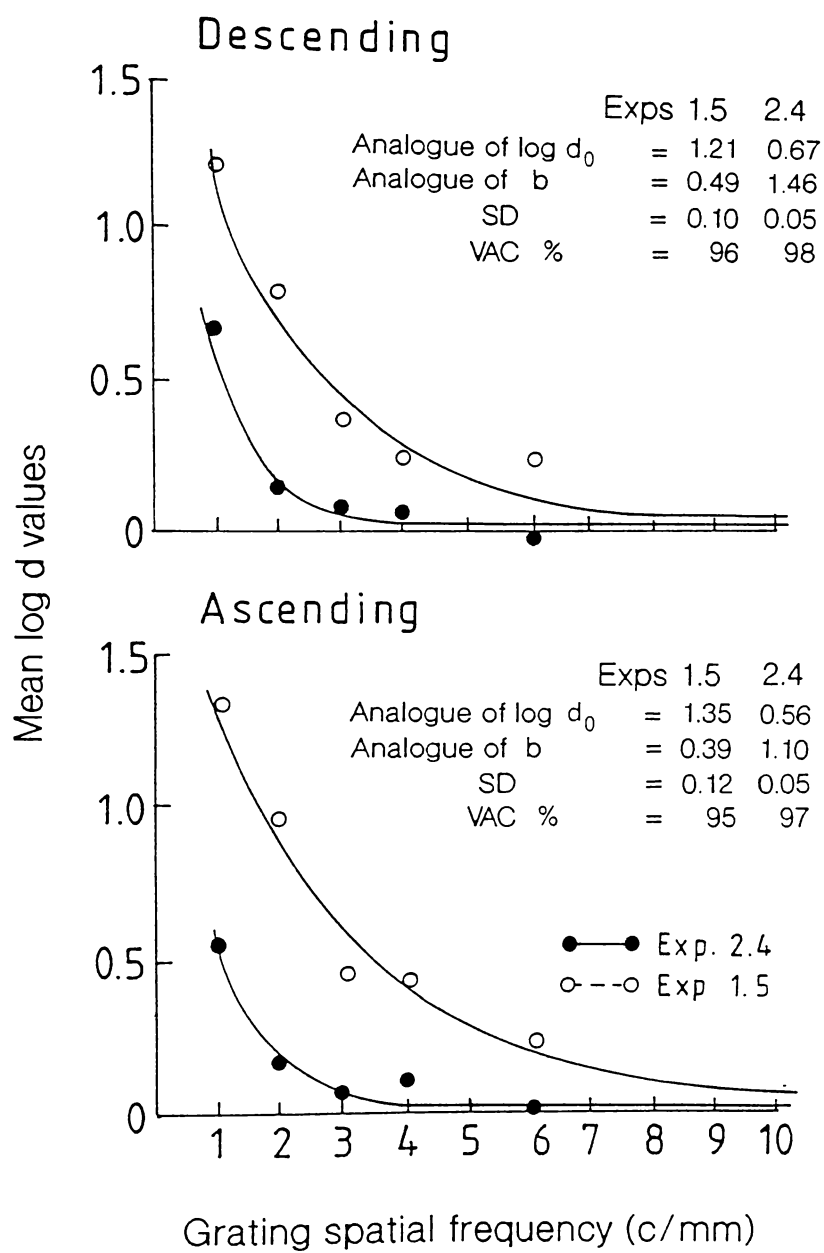


Table 2.4.3

Table 2.4.3

Parameters of the negative exponential functions fitted to the mean $\log d$ values from the descending and ascending probe series (Experiments 2.4 and 1.5) with the uncontrolled reinforcement procedure. Parameters of the negative exponential functions fitted to the mean $\log d$ values from the descending probe series (Experiments 2.3 and 1.3) with the controlled reinforcement procedure are included, for comparison.

Exp	Probe Series	Rft proc	Analogue		VAC%
			$\log d_0$	b	
2.3	desc	contr	1.11	1.27	95
2.4	desc	unc	0.67	1.46	98
2.4	asc	unc	0.56	1.10	97
1.3	desc	contr	1.30	0.55	93
1.5	desc	unc	1.21	0.49	96
1.5	asc	unc	1.35	0.39	95

study and Experiment 2.3 (Table 2.4.3) shows that the analogue of $\log d_0$ was greater and the analogue of b was smaller, for data from the controlled, compared to the data from the uncontrolled reinforcement procedure. This indicates that, for the present study, initial accuracy was higher and the rate of decrement of discriminative performance was lower for the probe series with the controlled reinforcement procedure. A comparison of the two probe series with the uncontrolled reinforcement procedure shows that analogues of $\log d_0$ and b were lower for the ascending probe series with the uncontrolled procedure. That is, both initial accuracy and the rate of decrement of accuracy with probes at increasingly finer gratings were lower for that probe series.

For Experiment 1.5 the analogues of both $\log d_0$ and b were greater for the descending series with the controlled reinforcement procedure. However, for the ascending series of probes with the uncontrolled reinforcement procedure, in Experiment 1.5, the analogue of $\log d_0$ was greater and the analogue of b was lower than for either of the two descending series of probes. This indicates both higher accuracy at the coarsest grating value and a slower rate of decrement in discriminative performance at increasingly finer grating values for the ascending series of probes with the uncontrolled reinforcement procedure, compared to either of the two descending series of probes. The analogue of $\log d_0$ and the analogue of b thus reflect the general findings for that study, that is, higher accuracy and greater threshold estimates for the ascending series with the uncontrolled reinforcement procedure, in contrast to the results of the present study.

ROC plots

Figure 2.4.8 shows the proportion of correct responses to the red key on grating trials, plotted against the proportion of incorrect red key responses on grey stimulus trials, for all hens for the two probe series with the uncontrolled reinforcement procedure. Lines join successive probes. Data from the descending series with the controlled reinforcement procedure (Experiment 2.3) are included for comparison. For all hens and all probe series, the data path is closest to the minor diagonal at the coarsest grating values, then moves toward the left of the minor diagonal at probes with finer gratings. This indicates that responding to red and green keys was close to equal for the probes at the coarsest gratings, but for probes at finer gratings, more green key responding occurred (as though the gratings were grey). Generally there was no difference in this pattern of responding across both descending probe series, nor across both reinforcement procedures.

Response bias

Figure 2.4.9 shows the proportion of left key responses plotted as a function of grating spatial frequency, for the three probe series. Generally, the data were closest to 0.5 at probes with the coarsest grating, indicating equal left and right key responding. Data moved below and above 0.5 at probes with increasingly finer gratings. This indicates the development of extreme position biases as discriminability of the stimuli presumably decreased. Three of the five hens, 31, 33 and 36, showed extreme right key biases. Generally, position biases were somewhat greater for the probe series with the uncontrolled reinforcement procedure.

Figure 2.4.8

Figure 2.4.8

The proportion of correct responses to the red key on grating trials, plotted against the proportion of incorrect responses to the red key on grey stimulus trials, for all hens, for the descending and ascending series of probes with the uncontrolled reinforcement procedure. Data from the descending series of probes with the controlled reinforcement procedure (Experiment 2.3) are also presented.

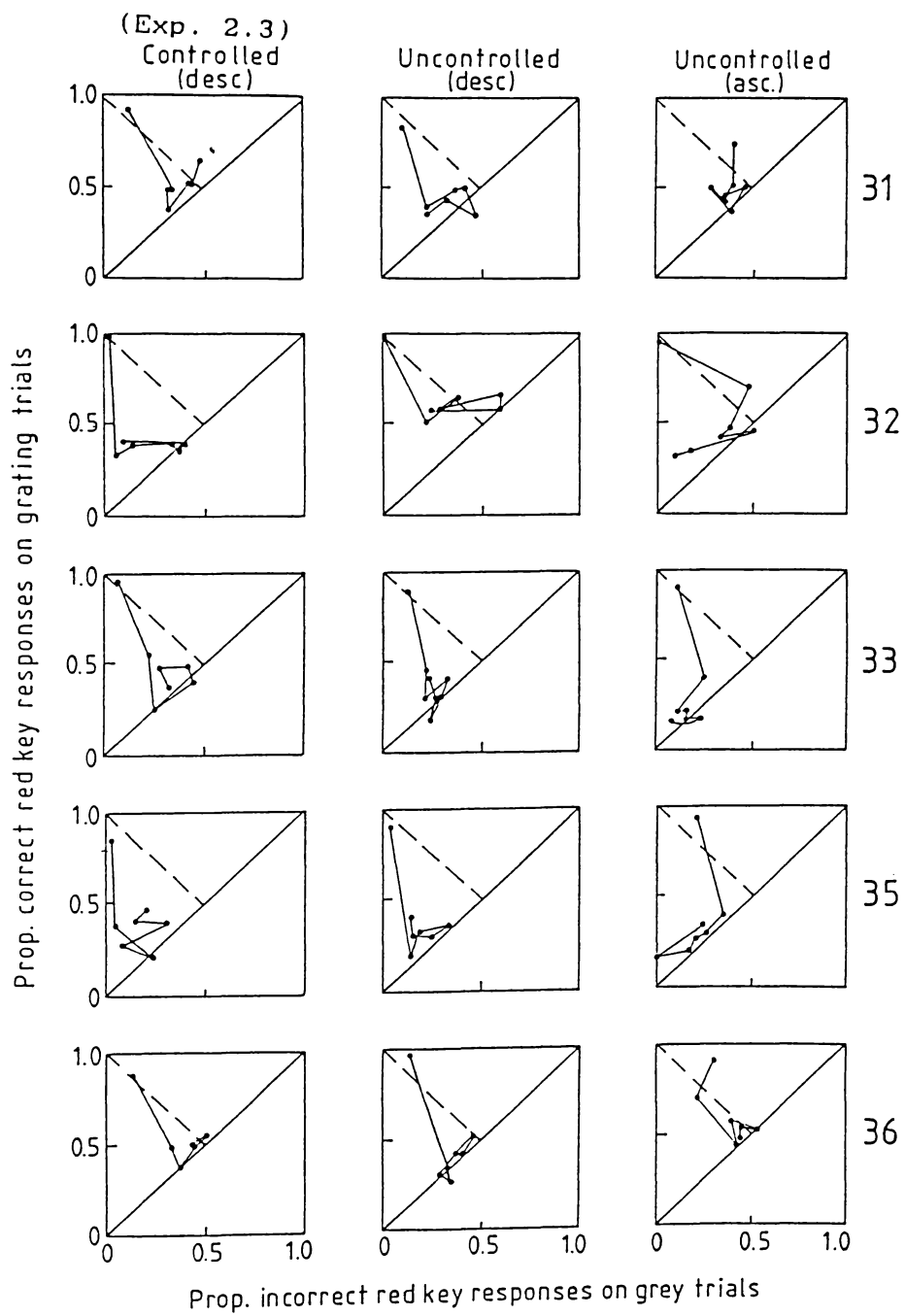
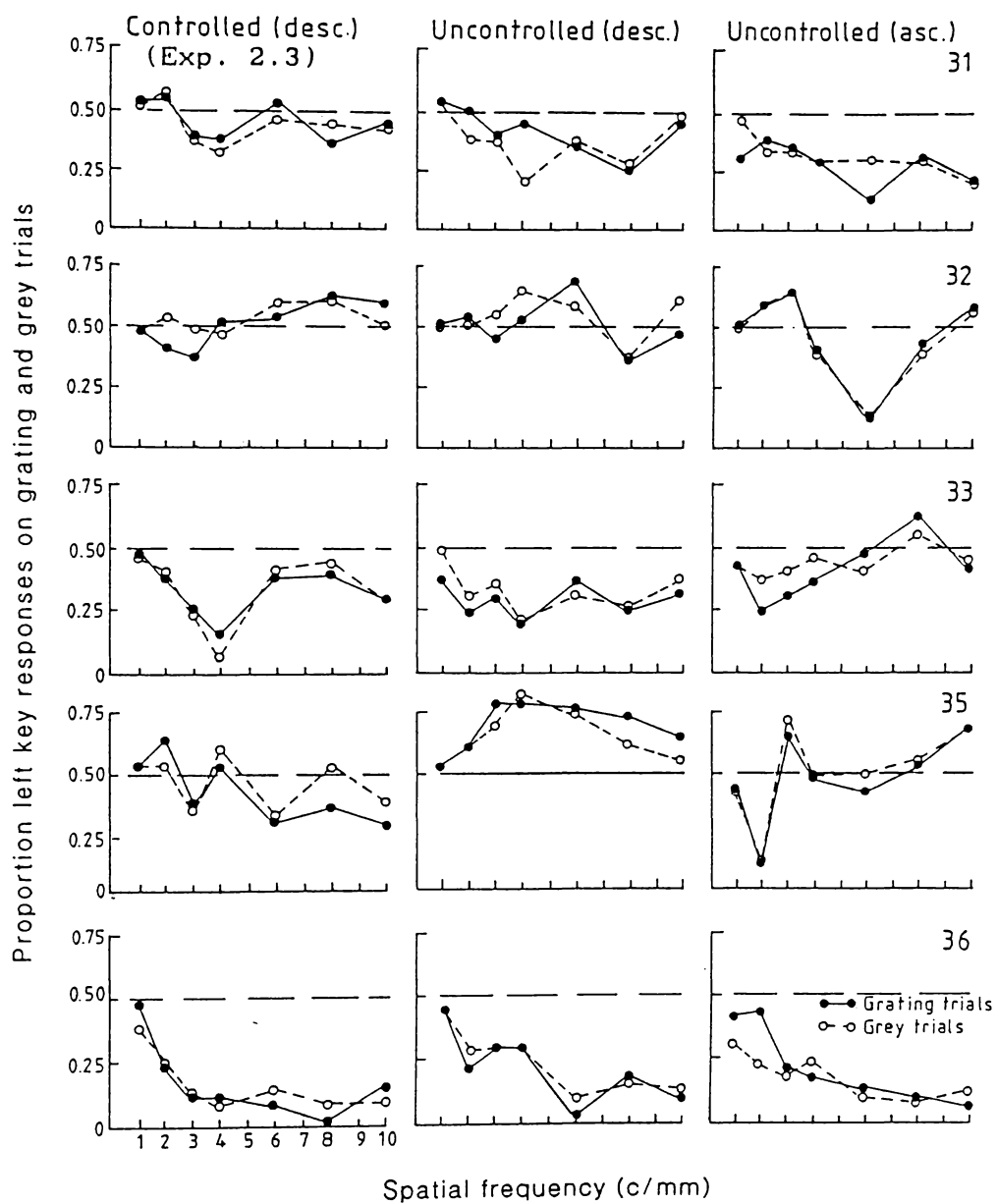


Figure 2.4.9

Figure 2.4.9

The proportion of left key responses plotted as a function of grating spatial frequency, measured in c/mm, for all hens, for the descending and ascending series of probes with the uncontrolled reinforcement procedure. Data for the descending probe series with the controlled procedure (Experiment 2.3) are also presented. Grating and grey trials are plotted separately.



Reinforcements

Figure 2.4.10 presents the proportion of reinforcements delivered for correct responses to the red key, and correct responses to the left key, plotted as a function of grating spatial frequency, measured in c/mm, for all hens, for the descending and ascending series of probes with the uncontrolled reinforcement procedure. Data from the previous study, (Experiment 2.3) with the controlled reinforcement procedure are included, for comparison. Proportions below 0.5 indicate that a larger proportion of reinforcement was obtained for correct responses to the green key following grey stimulus presentation, and proportions above 0.5 indicate that a larger proportion of reinforcements were obtained for correct responses to the red key following grating presentation.

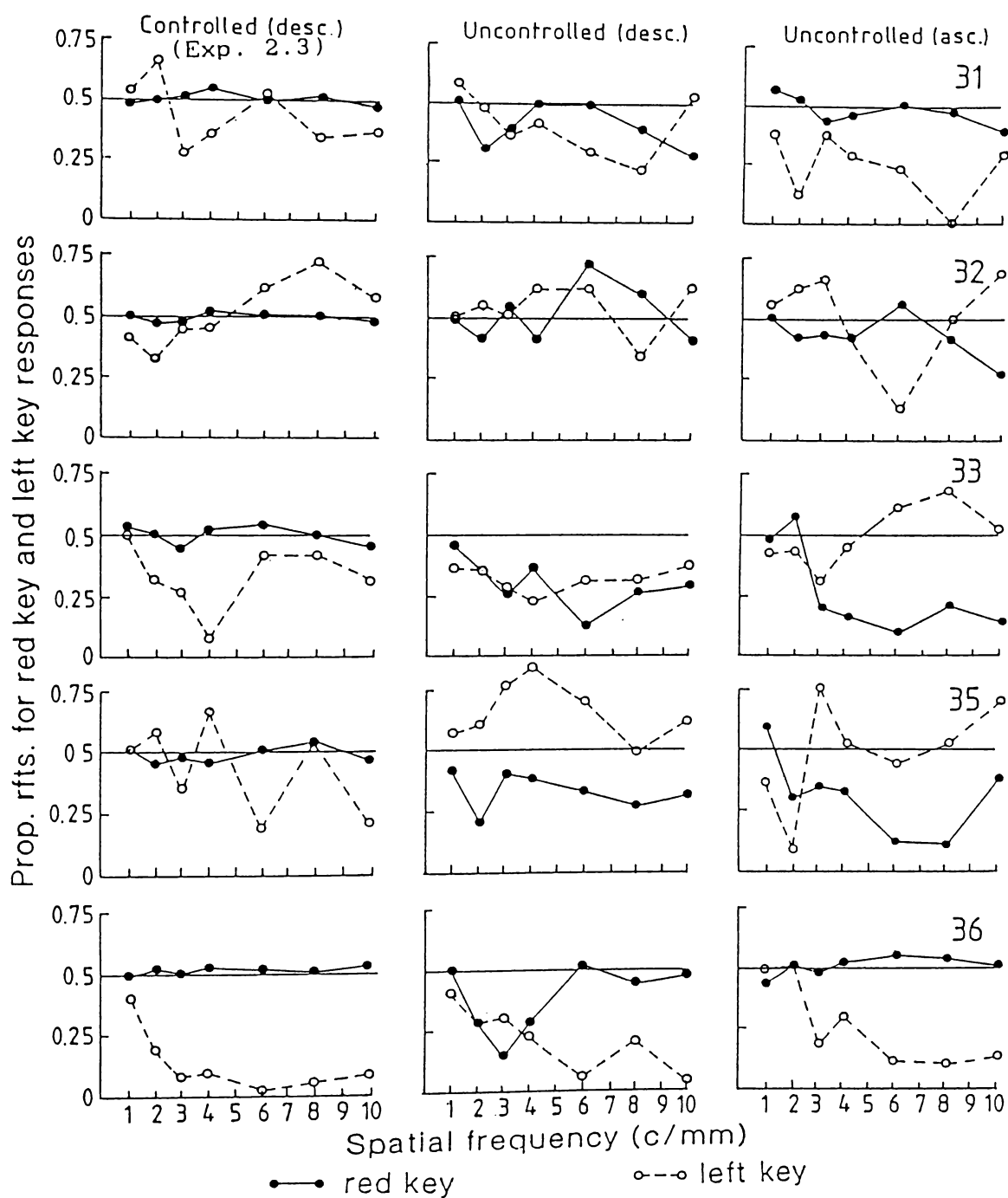
Data show that the proportion of reinforcements for correct responses to the red key, (shown as filled circles and solid lines) was close to equal for probes with the controlled reinforcement procedure. However, for both probe series using the uncontrolled procedure, the proportion of reinforcements for responses to the red key varied. For two hens, 33 and 35, a greater proportion of reinforcements were obtained for green key responding following presentation of the grey stimulus.

For the proportion of correct responses to the left key, (shown as unfilled circles and broken lines) values greater than 0.5 indicate a greater proportion of reinforcements for correct left key responding. These proportions varied across hens, and the variation was similar across all probe series. Reinforcements for correct responding to left and right keys were generally closest to equal

Figure 2.4.10

Figure 2.4.10

The proportion of reinforcements for correct responses to the red key (filled circles and solid lines) and correct responses to the left key (open circles and broken lines), plotted as a function of grating spatial frequency, for the descending and ascending series of probes with the uncontrolled reinforcement procedure. Data from the descending series of probes with the controlled reinforcement procedure (Experiment 2.3) are also presented.



at the coarsest grating values. At finer grating values, reinforcements allotted for correct responding to left and right keys varied. For two hens, 31 and 36, reinforcements were mainly obtained from right key responses across all probe series. Reinforcement at the 8 c/mm grating value for the ascending series of probes, for hen 31, was obtained exclusively from responses to the right key. Generally, for probes at finer grating values, the proportion of obtained reinforcements varied unsystematically, reflecting the colour and position biases which had developed.

Discussion 2.4

Discriminative performance

The findings of the present study in some ways differ from those of the equivalent study with the spatial discrimination task, Experiment 1.5. Results from that study indicated a more accurate discriminative performance with the uncontrolled, compared to the controlled reinforcement procedure. However, in the present study, estimates of threshold (taken from 75% total accuracy) reflecting discriminative performance, were generally greater for performance with the controlled reinforcement procedure. The parameters of the negative exponential functions fitted to the group data reflect these findings. That is, comparison of the two descending probe series with the present procedure showed that the controlled reinforcement procedure generated the better discriminative performance, measured both by higher accuracy at the coarsest grating and the lower rate of decrement in discriminative performance at increasingly finer gratings. These results, however, are consistent with those of McCarthy and Davison (1980a) and McCarthy (1983), who also reported greater estimates of discriminability with a controlled than an uncontrolled reinforcement procedure, when training pigeons in discrimination tasks. Both of their studies involved a spatial discrimination task, similar to that employed for Experiments 1.1 to 1.5.

McCarthy and Davison (1980a) suggested that the difference in discriminative performance between the two reinforcement procedures may have been a result of the differences in the number of responses emitted per reinforcers obtained. That is, responses per reinforcer

were fewer for the controlled procedure. However, McCarthy and Davison (1982) later discounted this suggestion when they demonstrated that changing the number of responses per reinforcer did not affect discriminability measures.

Perusal of the data in the present study shows that the number of correct responses per reinforcer was actually fewer for the uncontrolled reinforcement procedure, a finding consistent with that of Experiment 1.5. The higher probability of reinforcement with the uncontrolled procedure was suggested, in Experiment 1.5, as a possible reason for the better discriminative performance. The present findings then, are not consistent with that suggestion. However, it may be that the difference in the findings of the present study compared to those of Experiment 1.5, is related in some way to the difference between the two discrimination tasks. It is difficult to come to a definite conclusion on the basis of the present findings.

Response distributions and response bias

Generally, when the uncontrolled procedure was used in Experiment 1.5, the grating and grey trial response distributions showed greater separation than those response distributions when a controlled procedure was used. However, in the present study there was a greater separation in the data paths of grating and grey trial accuracy for only two hens, when the uncontrolled procedure was used. These plots looked similar to Diagram B, Figure 1.5.1, from Experiment 1.5, the extreme hypothetical response distribution suggested to be more likely to occur with an uncontrolled reinforcement procedure. Response distributions of grating and grey trial accuracy, however, for the remaining three hens using the uncontrolled procedure, were similar to

those obtained using the controlled procedure. The data show that when accuracy decreased on grating trials as a function of grating spatial frequency, accuracy also decreased to some extent on grey stimulus trials. These response distributions were more similar to those of Diagram A, Figure 1.5.1, from Experiment 1.5, suggested to be more likely to occur with the controlled reinforcement procedure. Therefore, generally the hens in the present study did not consistently respond in the predicted manner, for performance under an uncontrolled reinforcement procedure.

In the present study, with the uncontrolled procedure, reinforcer frequency for both the correct key colour and correct key position was free to vary with the hens' behaviour. Accordingly, response biases could develop for either key colour or position without total loss of reinforcement. Although there was some increase in colour bias for performance under the uncontrolled procedure, this was not as extreme as the increase in position biases. Throughout this series of nine experiments, there is evidence that any decrease in stimulus discriminability or increase in the effort required to obtain reinforcement (e.g. increased response requirements) results in a concomitant increase in response biases. These findings are consistent with those of many studies which report development of strong shifts in response biases correlated with a decrease in discriminability (e.g. Stubbs, 1968; Terman & Terman, 1972; Hodos & Bonbright, 1972; McCarthy & Davison, 1980a).

It is interesting that, under the uncontrolled procedure in the present study, position biases should become more extreme than under the controlled reinforcement procedure, which also allowed the ratio

of reinforcers for responding to the left or right keys to vary with the animals' behaviour. Perhaps position biases are more likely to occur than colour biases in a procedure in which either may develop, though not simultaneously. The following points may help in speculating why this could be so.

Firstly, Davison and Tustin (1978) suggest that, when stimuli are indiscriminable, in such a procedure as the present one, performance becomes analogous to performance under concurrent schedules of reinforcement. It is likely, then, that in a discrete trial discrimination task, where fine gratings and grey stimuli look the same, the hens may tend to repeat the previous response which was reinforced. However, in such a procedure as the present one, there are two ways in which the "previous trial" could be defined. For example, if a hen was delivered a reinforcer for pecking a red key on the left, the reinforced response could be defined either as the "red key" response or the "left key" response. It could, of course, also be defined as the "red left key" response. However, the red key might not appear on the left in the following trial, but on each trial there would always be a red key and a left positioned key. Therefore, it is possible that to the hen the reinforced response would be effectively defined in terms of colour or position, but not both.

Secondly, it seems that animals perform in such a way as to maximize the density of reinforcers per session for the least effort (Irwin & Terman, 1970). For example animals will, when given the opportunity, choose to make those responses which require the least effort, to obtain reinforcement (e.g. Pisacreta, 1982). Clearly, it would require less effort on the part of the animal to move to a

particular position following sample key responses, than to make an additional discrimination between comparison keys, then choose the key of a particular colour and move to the position of that key.

Thus, firstly, when the hens cannot discriminate between gratings and grey stimuli they are possibly more likely to repeat the previously reinforced response. Secondly, because they are possibly more likely to respond to key position than key colour, they would repeat the previous left or right key response that was reinforced.

Assuming that effort required to respond to both response alternatives is equal, the probability of left or right position biases might possibly be determined by the position of the first response reinforced in a particular session. This may explain why position biases in the present study changed across different levels of stimulus discriminability (i.e sessions with different gratings values).

Colour biases in Experiments 2.1 to 2.4 are assumed to be related to the hens' perception of the stimuli and are thus predictable as discriminability of the stimuli decreases (i.e. increased green key responding, as though all stimuli are grey). However, left or right position preferences which occur at different levels of stimulus discriminability are not predictable in the same way. That is, position biases do not appear to be related in any way to the hens' perception of the stimulus. In a similar way to colour biases, however, position biases appear to be related to stimulus discriminability. That is, colour and position biases predictably increase at lower levels of stimulus discriminability.

However, it could be possible, with a trial by trial analysis, to determine the position of the first reinforced response to the comparison stimulus in an experimental session, at the finer grating stimuli (assumed to be indiscriminable), to test the above hypothesis regarding the development of left or right position biases. Such data were not available for analysis in the present series of experiments. *De facto* in most concurrent schedule research, it is assumed that bias is constant across conditions. The present results however, suggest that biases move very sharply across sessions. Thus, there is a need for further research into the development of position biases in non-spatial discrimination procedures.

GENERAL DISCUSSION

The aims of the present series of studies were threefold: to investigate the effect of procedural manipulations on discriminative performance under two different procedures, to evaluate the utility of various methods of analysis and threshold criteria and to estimate the visual acuity of the domestic hen.

This thesis has examined the effects of several variables on discriminative performance. The strength and consistency of the effects of these factors varied across and within procedures. The relation of discriminative performance to the spatial frequency of gratings was found to vary according to the complexity of the actual procedure. The non-spatial discrimination procedure appeared to result in lower accuracy than the spatial procedure. It seems therefore, that one variable which possibly has the most important effect on the level of discriminative performance is the basic requirements of the actual procedure. The difficulty of the task could be measured in terms of the chain of responses required to obtain reinforcement. The non-spatial task represents a more complex chain of responses, providing more opportunity for error. Not only does an easier task appear to control a faster rate of acquisition, and a higher level of accuracy across increasingly finer gratings, but performance is less likely to be disrupted across changes in procedure. For example, where increased response requirements were accompanied by an increase in the increment of spatial frequency of gratings, accuracy was not increased in the non-spatial procedure, whilst accuracy improved in the spatial discrimination task.

Certain factors change visual discriminative performance in a consistent way, despite differences in task difficulty. Luminance is one such variable which appears to have a consistent effect even when changed within a limited range. The effect of increased FR response requirements, in contrast, in the present series of studies, appears in part to depend on the difficulty of the discrimination task. When the increase in grating spatial frequency was changed by greater increments concomitant with the change in FR response requirements in Experiment 2.2, it was not anticipated that performance might be disrupted. Otherwise this change would have been made prior to increasing the response requirements. However, the findings are useful in that they indicate that discriminative performance in difficult procedures may be more easily disrupted.

The effect of controlled and uncontrolled reinforcement delivery on discriminative performance does not appear to be consistent across different procedures, nor even across similar procedures. For example, McCarthy and Davison (1980a) and McCarthy (1983) reported different findings for two separate studies, even though both studies employed a spatial discrimination procedure. In the easier spatial discrimination task, in the present series of experiments, discriminative performance was slightly more accurate under an uncontrolled procedure, but with the more difficult non-spatial discrimination task, the controlled procedure generated a slightly more accurate performance.

Animals reliably develop response biases in procedures where relative reinforcer ratios are free to vary with the animals'

behaviour and such biases are related to the decrease in discriminability of the stimuli. Certain biases may be directly related to the stimulus types used, for example, a constant and a variable stimulus. Such biases, in the present series of experiments, appear to be related to the animals supposed perception of the stimuli and are thus predictable and consistent. That is, at less discriminable gratings, the hens consistently responded as though stimuli were grey, regardless of whether a spatial or non-spatial discrimination procedure was used.

It appears that position bias may override colour bias. That is, when the reinforcement procedure was uncontrolled for both colour and position, position biases increased. This may be explained by the hens' attempt to maximize the number of reinforcements obtained for the least effort. Colour biases which occurred in Experiments 2.1 to 2.4, indicate that the animals were treating assumedly indiscriminable grating stimuli as grey. However, position biases in these same experiments appeared in no way related to the animals' perception of the grating stimuli. It was suggested earlier, that these shifting position biases may be related to the position of the first reinforced response of the experimental session. In contrast to common assumptions in concurrent schedule research, position biases at less discriminable stimulus values shift sharply across sessions. Further research involving trial-by-trial analyses is required to test this hypothesis.

The types of stimuli employed in visual acuity studies are likely to affect the animals' distribution of responses. Millidot (1973) suggested that visual acuity tasks should use two variable gratings.

The constant and variable stimuli as in the present study may encourage development of response biases at lower levels of stimulus discriminability. Generally, visual acuity studies using both constant and variable stimuli do not analyse the two component response distributions to determine the patterns of responding which contribute to resultant estimates of threshold. On the basis of the present results it is concluded that pairs of variable gratings differing in orientation, although they may not ensure bias free performance, at least may be less likely to encourage them. Terman's study (1970) of auditory discrimination in rats is one of the few which provides a comprehensive analysis of both total performance and separate component distributions of responses on constant and variable stimulus trials. Such analyses in the present series of experiments have provided useful information on performance on both trial types (gratings and grey), and thus clarification of the contribution of each trial type to the overall performance. It is suggested that when future research requires the use of two stimulus types, that such separate analysis of the contribution of each trial type to overall performance, is an important requirement.

It was found that a one session probe at various stimulus values provided an adequate description of stable performance once the hens had acquired the task. Prolonged practice at finer gratings did not result in better accuracy. This has important implications for studies which invest a great amount of time spent in training to stability for each change of stimulus.

Threshold estimates provide a useful measure of changes in discriminative performance when they are taken from intermediate

performance, half-way between perfect performance and chance. Because this is one level of performance which was strongly affected by response bias, it is important to use a procedure which minimizes such biases. This may be accomplished to some degree by the use of a controlled reinforcement procedure and possibly, by using two variable grating stimuli. If, as is apparent in the present series of experiments, a controlled reinforcement procedure generates a more bias-free performance, it should be employed, regardless of whether or not the resultant performance is more or less accurate, using a bias-free measure, than performance under an uncontrolled procedure.

Animal studies of visual acuity traditionally analyse performance as percentages correct. This is a measure that is confounded by response biases, especially at intermediate levels of stimulus discriminability. Because estimates of threshold are generally determined from the stimulus value corresponding to 75% total performance, this criterion perhaps more than the 50% correct is more likely to be confounded by response biases. An unbiased estimate of discriminability, $\log d$, on the other hand, provides a useful measure. Because of the problem of infinite $\log d$ values at perfect discriminative performance levels, however, it is probably necessary to retain the percentage correct, as a supplementary measure.

Estimates of threshold were used here to reflect changes in the discriminative performance. Those taken from 75% total trial accuracy may not be comparable with those taken from 50% grating accuracy, especially when constant and variable stimuli are used, yet this has not been discussed in the literature. Estimates of threshold, as a product of behaviour, have been taken as a reflection of

discriminative performance, shown as a single value. It is important, therefore, that this single value is the most valid reflection possible, of the discriminative performance. Lines fitted to data transformed from percent correct, to determine threshold, still retain response biases. Lines fitted to bias free estimates of discriminability, for example, $\log d$ however, describing the decreasing discriminative function of the data perhaps, then, provide the best description of the performance. Estimates of threshold determined from least-squares lines fitted to $\log d$ values at some intermediate point such as a $\log d$ value of 0.48 may be more reliable, not only in providing a bias-free estimate, but in taking into account more of the available data than estimates based on a single data point.

Where point estimates of log response bias are used, (for example, estimates of $\log c$) there is also the problem with infinite values, and their calculation assumes an equal distribution of reinforcers to both response alternatives. To use such response bias estimates, therefore, requires a procedure which controls equal reinforcer ratios to both alternatives. The use of the signal detection analysis, for example ROC plots, however does not, and provides a useful indication of response bias changes.

The two parameters of the negative exponential function provide a useful description of the initial discriminability at the coarsest grating and the decrement in discriminability at increasingly finer gratings. Although, in the present series of experiments, the negative exponential functions were used to compare performance across

equivalent studies with the spatial and non-spatial discrimination task, threshold estimates could have been determined from negative exponential fits to single subject data, at a log d value of 0.48, in the same way as the use of straight line fits.

Visual acuity of the hen

Visual acuity depends not only on ganglion cell density, but also on optical factors, the grain of the photo-receptor mosaic, and the resolving power of the neural system (Hughes, 1977). Knowledge of these factors alone, however, is not sufficient to determine the ability of any species to resolve fine detail. What has been found in this series of studies is that discriminative performance is affected by procedural manipulations and that performance is probably more the result of the constraints of non-sensory variables within the procedure rather than of actual sensory functioning.

Levels of visual acuity obtained in the present study are similar to those obtained by Johnson (1914) around 5 or 6 c/deg, and greater than those obtained by Over and Moore (1981). It is suggested that the latter study did not tap the limits of the acuity of the chickens under study. It is possible that greater estimates of threshold than those obtained in the present series of experiments may be generated at higher luminances. Visual acuity, as measured in the present studies, is similar to that reported for the cat (Mitchell, Giffin, Wilkinson, Anderson & Smith, 1976) dolphin and sea lion (Schusterman & Balliet, 1971) and lower than the pigeon (Hodos, Leibowitz & Bonbright, 1976). As predicted, it is lower than that reported for such flying predators such as the eagle, (Reynolds, 1985) and falcon (Fox, Lehmkuhle & Westendorf, 1976) and about four times lower than

that of humans and primates (Spence, 1934).

Visual acuity measures depend on the type of analysis and the criteria employed. Rather than attempt to determine the limits of visual functioning in the hen, the present studies have attempted to determine the effect of procedural manipulations. It is suggested that the limits of visual resolution in the hen have not been approached by these procedures, either in the use of sufficient luminance or possibly in the simplicity of the task. Perhaps we are measuring only the constraints of the procedure rather than the visual functioning *per se*. It is more likely that behavioural procedures will underestimate sensory capacities due to the effect of non-sensory variables. Consistent with Woodworth and Schlosberg's (1954) suggestion, it appears that estimates of threshold for the same sensory functions and species do reflect variation in the difficulty of the discrimination task, differences in threshold criteria and data analyses employed.

Conclusion

This thesis was undertaken to determine the effects of some procedural variation on discriminative performance and attempted to determine the "true" threshold of visual acuity for the domestic hen. When performance varies as a function of variations in procedure, distinct from variations in stimulus discriminability (e.g grating spatial frequency and luminance), as evidenced in the present series of experiments, the concept of a distinct point of transition between discriminability and non-discriminability of stimuli, such as threshold, becomes somewhat vague. The threshold estimate may provide useful information of the changes in discriminative performance, but

there appears to be no specific point at which discrimination ceases, unaffected by non-sensory procedural variation and the method by which the discriminative performance is analysed.

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Appendix 1

The hen number, the grating value (Gtg), the number of correct responses to the left key (CorL) and incorrect responses to the right (IncR) key on grating trials, the number of incorrect responses to the left key (IncL) and correct responses to the right (CorR) key on grey stimulus trials and the number of reinforcements for correct left (L) key and right (R) key responses. Headings are shown for each experiment and for conditions within each experiment. Data for the last five days of training prior to each probe series are also shown.

Hen	Grating			Grey		L	R
	Gtg	CorL	IncR	IncL	CorR		
Experiment 1.1							
Descending series							
71	1.0	143	6	9	141	24	20
71	1.0	142	8	10	141	22	20
71	1.0	149	7	12	143	21	22
71	1.0	147	6	14	140	20	23
71	1.0	136	15	3	146	22	23
71	1.2	137	15	5	145	21	22
71	1.0	143	8	3	148	20	23
71	1.4	142	6	2	146	20	22
71	1.0	128	4	2	129	19	18
71	1.6	101	32	4	128	18	19
71	1.0	137	12	1	149	22	21
71	1.8	68	20	6	83	14	15
71	1.0	126	7	8	125	19	19
71	2.0	104	48	15	135	22	20
71	1.0	140	7	14	134	20	21
71	2.5	66	73	31	110	19	18
71	1.0	68	3	10	158	14	10
71	1.0	126	7	8	123	17	22
71	3.0	77	70	48	98	17	19
71	1.0	139	12	12	135	21	22
71	1.0	137	10	7	140	22	22
71	3.5	34	50	19	64	12	12
71	1.0	116	20	6	128	20	20
71	1.0	133	20	6	146	23	20
71	1.0	123	4	13	114	17	16
71	1.0	157	4	8	152	22	21
71	4.0	72	79	41	111	18	20
71	1.0	154	5	9	147	23	21
71	5.0	78	59	59	79	19	16
71	1.0	123	2	34	94	17	18
71	1.0	110	6	23	93	16	16
71	6.0	71	81	60	89	19	18
71	1.0	159	1	45	117	20	22
71	8.0	108	54	79	81	21	20
71	1.0	155	8	38	126	20	20
71	1.0	156	1	54	101	21	23
71	1.0	156	6	22	141	22	21
71	10.0	87	73	61	100	21	20

Ascending series

71	1.0	154	7	54	107	20	21
71	1.0	153	8	36	125	20	22
71	1.0	158	0	39	119	21	23
71	10.0	67	77	52	91	17	19
71	1.0	149	4	27	126	24	21
71	1.0	156	2	36	121	21	22
71	8.0	92	61	64	88	19	19
71	1.0	152	7	41	117	22	21
71	1.0	153	3	41	116	21	22
71	6.0	80	65	84	61	16	18
71	1.0	152	1	32	122	23	22
71	1.0	142	5	36	112	20	22
71	5.0	83	70	73	80	19	18
71	1.0	148	2	20	127	21	22
71	1.0	148	5	20	131	22	21
71	1.0	154	3	25	132	22	21
71	4.0	100	50	52	100	21	19
71	1.0	155	4	26	132	24	21
71	3.5	111	45	77	80	20	19
71	1.0	160	1	38	124	20	23
71	3.0	109	52	72	88	20	19
71	1.0	162	0	22	139	21	20
71	2.5	108	40	59	90	19	21
71	1.0	158	6	20	143	22	23
71	2.0	140	19	43	114	20	20
71	1.0	160	0	13	147	22	21
71	1.8	141	17	32	127	21	20
71	1.0	160	1	8	152	22	22
71	1.6	153	7	24	136	22	22
71	1.0	158	2	5	154	23	22
71	1.0	160	0	8	150	21	23
71	1.4	147	4	18	133	21	23
71	1.0	153	4	16	142	22	21
71	1.0	155	1	8	147	22	22
71	1.0	149	2	10	141	22	20
71	1.2	155	4	6	151	23	21
71	1.0	163	3	4	159	22	23

Experiment 1.2

FR5

71	1.0	107	0	3	105	19	20
71	1.0	108	0	1	109	21	22
71	1.0	109	1	0	109	19	20
71	1.0	107	0	1	104	22	20
71	1.0	101	0	1	101	19	19
71	2.0	90	10	2	97	18	20
71	3.0	60	42	18	83	19	16
71	4.0	48	47	17	77	17	19
71	6.0	38	52	11	81	15	15
71	8.0	33	55	34	54	14	16
71	10.0	35	46	28	53	16	13

Return to FR1

71	1.0	150	5	11	145	21	23
71	1.0	160	4	9	153	23	21

71	1.0	155	1	8	149	21	22
71	1.0	151	2	6	149	24	21
71	1.0	153	2	2	154	21	23
FR10							
71	1.0	69	0	0	67	19	19
71	1.0	61	1	0	60	19	18
71	1.0	61	8	1	61	18	18
71	1.0	60	0	0	61	18	18
71	1.0	74	2	0	74	17	20
71	2.0	68	10	2	75	20	18
71	3.0	31	47	16	62	13	13
71	4.0	45	29	22	54	15	15
71	6.0	38	32	19	51	14	14
71	8.0	33	39	9	64	11	14
71	10.0	44	31	21	53	16	15
Return to FR1							
71	1.0	141	3	8	135	21	23
71	1.0	136	9	14	130	22	23
71	1.0	146	1	4	142	23	21
71	1.0	144	1	4	140	22	22
71	1.0	148	0	2	149	21	21
FR15							
71	1.0	51	0	0	55	16	15
71	1.0	51	0	0	54	15	16
71	1.0	50	0	1	51	17	16
71	1.0	56	1	2	56	17	16
71	1.0	51	0	0	52	16	16
71	2.0	51	5	3	50	16	17
71	3.0	31	25	6	49	10	12
71	4.0	24	27	10	44	13	14
71	6.0	18	32	13	39	9	9
71	8.0	24	21	5	42	11	14
71	10.0	23	25	7	38	11	11
Return to FR1							
71	1.0	146	7	2	151	21	23
71	1.0	139	5	0	144	23	21
71	1.0	138	5	6	138	23	22
71	1.0	130	8	9	128	21	23
71	1.0	140	2	3	140	22	23
FR25							
71	1.0	27	0	0	27	13	11
71	1.0	32	0	0	33	12	13
71	1.0	34	0	0	83	13	12
71	1.0	34	0	0	33	14	13
71	1.0	32	0	1	32	15	15
71	2.0	24	5	1	27	13	13
71	3.0	13	20	5	27	8	9
71	4.0	8	26	3	31	6	9
71	6.0	15	20	11	24	8	8
71	8.0	13	23	10	26	6	7
71	10.0	15	14	4	26	9	11
Return to FR1							
71	1.0	142	5	1	146	21	23
71	1.0	137	6	0	144	21	24
71	1.0	137	8	2	145	21	23

71	1.0	140	3	4	139	21	22
71	1.0	132	9	3	140	21	21
FR40							
71	1.0	19	0	0	19	11	9
71	1.0	19	0	0	19	10	9
71	1.0	21	0	0	21	10	8
71	1.0	14	0	1	15	10	8
71	1.0	16	0	0	16	12	14
71	2.0	19	2	0	21	9	12
71	3.0	1	11	0	9	1	5
71	4.0	7	14	5	15	4	7
71	6.0	2	6	0	8	2	2
71	8.0	9	15	3	18	5	7
71	10.0	10	13	1	21	6	5
Return to FR1							
71	1.0	138	1	0	136	21	21
71	1.0	131	2	1	136	22	22
71	1.0	136	4	3	137	20	22
71	1.0	143	1	1	143	19	23
71	1.0	141	2	2	139	21	23
FR1							
71	1.0	139	2	5	134	22	21
71	1.0	142	2	4	139	22	22
71	1.0	126	3	6	125	21	21
71	1.0	130	4	7	127	21	23
71	1.0	128	3	4	127	22	21
71	2.0	101	34	12	122	22	20
71	3.0	90	51	21	119	21	20
71	4.0	79	57	46	89	18	19
71	6.0	80	67	44	101	17	21
71	8.0	90	52	41	99	20	19
71	10.0	84	58	52	90	18	20

Experiment 1.3

Medium luminance

71	1.0	60	1	1	62	17	17
71	1.0	63	2	3	61	17	17
71	1.0	59	2	1	62	17	16
71	1.0	57	1	0	56	16	17
71	1.0	59	3	0	62	16	17
71	2.0	65	2	2	62	16	16
71	3.0	36	27	27	36	12	13
71	4.0	33	29	25	35	15	10
71	6.0	50	20	29	44	14	15
71	8.0	51	10	17	46	16	16
71	10.0	45	13	15	41	17	16

High luminance

71	1.0	68	0	0	69	16	16
71	1.0	61	0	3	59	17	17
71	1.0	59	0	2	58	19	19
71	1.0	63	0	0	63	16	15
71	1.0	63	0	3	61	17	16
71	2.0	65	0	10	54	20	17
71	3.0	39	25	30	36	13	14
71	4.0	34	26	28	31	15	15

71	6.0	47	22	24	43	13	16
71	8.0	30	30	5	53	14	15
71	10.0	41	22	16	48	16	16
Low luminance							
71	1.0	58	0	4	54	18	16
71	1.0	48	1	3	46	16	16
71	1.0	59	0	0	58	17	17
71	1.0	64	0	0	66	19	17
71	1.0	61	0	2	61	18	16
71	2.0	63	4	2	63	18	17
71	3.0	48	26	19	50	15	16
71	4.0	24	42	16	52	12	13
71	6.0	33	34	23	43	11	14
71	8.0	43	20	3	61	16	17
71	10.0	37	26	13	50	15	14

Experiment 1.4

71	2.0	64	0	1	62	19	19
71	2.0	59	1	2	56	16	19
71	2.0	59	0	4	57	19	17
71	2.0	70	0	6	63	17	17
71	2.0	69	0	2	66	19	17
71	1.0	62	0	2	62	17	17
71	2.0	62	5	1	66	17	16
71	3.0	38	26	9	56	16	15
71	4.0	39	29	13	58	12	13
71	6.0	35	28	21	41	14	14
71	8.0	40	19	2	55	14	15
71	10.0	45	15	12	45	16	15

Experiment 1.5

Descending series

71	1.0	58	0	1	57	25	19
71	1.0	57	0	0	57	21	22
71	1.0	57	0	0	58	21	22
71	1.0	55	0	0	58	24	19
71	1.0	56	0	0	55	26	16
71	2.0	67	0	3	65	26	19
71	3.0	14	15	0	61	10	22
71	4.0	24	34	8	50	10	28
71	6.0	23	31	12	43	10	22
71	8.0	46	17	3	59	16	25
71	10.0	46	46	7	53	17	23

Ascending series

71	1.0	53	0	0	52	21	23
71	2.0	51	1	3	48	21	20
71	3.0	44	12	13	42	19	22
71	4.0	28	30	4	56	12	29
71	6.0	30	28	12	45	16	23
71	8.0	40	12	5	47	15	25
71	10.0	47	12	11	48	22	20

Experiment 1.1

Descending series

72	1.0	134	11	14	132	22	21
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72	1.0	145	1	9	139	24	21
72	1.0	143	0	23	120	23	20
72	1.0	144	0	26	116	20	23
72	1.0	138	5	24	117	21	22
72	1.2	145	1	15	134	21	21
72	1.0	102	5	6	101	16	17
72	1.4	146	0	21	126	22	21
72	1.0	134	6	13	125	20	18
72	1.6	144	4	22	127	23	21
72	1.0	149	3	19	134	21	22
72	1.8	136	17	30	120	20	21
72	1.0	153	1	22	129	22	20
72	2.0	110	42	27	126	23	21
72	1.0	146	3	31	120	22	21
72	2.5	90	58	54	94	19	20
72	1.0	144	4	36	111	22	23
72	1.0	146	5	35	116	20	23
72	3.0	89	63	53	100	20	21
72	1.0	136	10	38	106	20	22
72	1.0	149	1	27	126	21	21
72	3.5	81	78	61	96	20	18
72	1.0	140	9	42	106	20	23
72	1.0	88	16	26	76	15	13
72	1.0	131	19	32	119	23	21
72	1.0	144	5	26	122	22	21
72	4.0	78	82	55	103	17	18
72	1.0	144	4	25	123	23	21
72	5.0	71	83	70	84	20	18
72	1.0	144	6	40	109	23	19
72	1.0	146	3	35	115	20	23
72	6.0	56	102	61	95	18	19
72	1.0	142	6	19	130	21	21
72	8.0	67	86	52	103	18	22
72	1.0	131	12	5	137	20	22
72	1.0	141	2	33	111	22	21
72	1.0	146	0	32	115	21	22
72	10.0	75	77	57	96	19	18
Ascending series							
72	1.0	124	21	28	117	20	22
72	1.0	131	18	24	125	21	22
72	1.0	137	8	18	127	22	20
72	10.0	58	96	55	98	19	21
72	1.0	142	3	26	118	22	20
72	1.0	139	6	15	129	22	22
72	8.0	56	98	56	97	18	16
72	1.0	126	12	12	124	23	21
72	1.0	127	10	8	129	20	22
72	6.0	68	83	71	79	18	17
72	1.0	126	14	12	125	22	20
72	1.0	132	16	15	133	20	20
72	5.0	50	101	49	103	16	19
72	1.0	121	21	14	128	23	20
72	1.0	137	13	14	135	21	20
72	1.0	140	5	5	140	22	21
72	4.0	68	82	53	99	20	18

72	1.0	128	16	20	124	21	21
72	3.5	71	80	37	117	19	19
72	1.0	137	16	22	132	22	22
72	3.0	73	75	36	113	20	19
72	1.0	120	30	7	142	21	22
72	2.5	91	65	24	132	22	19
72	1.0	134	14	4	142	21	21
72	2.0	117	37	14	137	23	21
72	1.0	137	13	0	151	23	22
72	1.8	111	39	2	146	21	22
72	1.0	143	10	0	151	22	23
72	1.6	134	18	5	144	22	23
72	1.0	135	20	2	150	22	22
72	1.0	135	21	5	152	23	21
72	1.4	133	17	0	150	23	19
72	1.0	129	20	2	148	20	21
72	1.0	128	19	0	147	23	22
72	1.0	130	21	1	148	22	22
72	1.2	135	10	1	145	20	23
72	1.0	139	9	1	147	22	23

Experiment 1.2

FR5

72	1.0	91	2	1	90	20	19
72	1.0	94	0	1	93	22	19
72	1.0	89	2	5	84	19	21
72	1.0	90	2	0	92	19	21
72	1.0	92	1	0	90	20	19
72	2.0	94	8	0	103	18	18
72	3.0	53	47	13	89	17	16
72	4.0	44	47	16	74	18	17
72	6.0	41	64	34	69	16	15
72	8.0	52	38	32	55	15	15
72	10.0	45	50	31	64	17	16

Return to FR1

72	1.0	123	16	14	127	21	22
72	1.0	138	11	8	134	22	20
72	1.0	128	19	2	143	19	22
72	1.0	141	11	7	144	22	23
72	1.0	139	8	8	139	20	23

FR10

72	1.0	53	4	0	54	15	14
72	1.0	54	0	0	55	16	15
72	1.0	59	2	0	61	15	15
72	1.0	59	3	1	62	17	18
72	1.0	58	1	3	58	14	16
72	2.0	67	4	1	73	18	19
72	3.0	30	34	8	55	15	15
72	4.0	33	37	11	58	14	14
72	6.0	22	46	12	58	11	12
72	8.0	35	35	20	54	14	15
72	10.0	21	45	22	44	11	11

Return to Fr1

72	1.0	115	22	8	131	22	21
72	1.0	131	14	5	139	22	20

72	1.0	128	22	1	150	21	22
72	1.0	134	22	4	149	20	21
72	1.0	138	9	2	148	22	21
FR15							
72	1.0	41	6	1	46	16	16
72	1.0	30	18	4	44	12	12
72	1.0	25	15	3	38	11	12
72	1.0	32	7	0	39	15	13
72	1.0	42	6	2	47	16	16
72	2.0	36	8	4	41	15	15
72	3.0	19	38	7	47	9	6
72	4.0	21	30	9	42	11	10
72	6.0	7	46	13	44	6	8
72	8.0	19	37	11	44	10	10
72	10.0	22	30	20	32	12	11
Return to FR1							
72	1.0	125	14	5	136	22	21
72	1.0	137	15	9	142	20	21
72	1.0	142	5	4	144	21	23
72	1.0	146	6	5	146	23	21
72	1.0	144	6	8	141	21	20
FR25							
72	1.0	20	1	0	20	11	6
72	1.0	29	0	0	27	1	12
72	1.0	25	0	0	24	8	10
72	1.0	26	3	0	28	9	12
72	1.0	24	2	0	28	11	11
72	2.0	25	0	0	29	13	13
72	3.0	16	12	3	25	11	9
72	4.0	18	14	6	27	10	10
72	6.0	14	16	11	18	7	7
72	8.0	12	13	6	21	8	6
72	10.0	8	13	4	17	5	5
Return to FR1							
72	1.0	139	6	5	141	21	22
72	1.0	126	10	13	121	21	19
72	1.0	132	7	10	130	20	22
72	1.0	138	5	3	138	21	22
72	1.0	142	6	5	142	21	20
FR40							
72	1.0	16	0	0	14	10	8
72	1.0	14	1	0	13	8	4
72	1.0	14	3	0	16	9	10
72	1.0	15	1	0	16	8	10
72	1.0	15	0	0	16	7	8
72	2.0	17	1	0	18	9	10
72	3.0	12	3	0	13	6	7
72	4.0	7	4	7	6	5	4
72	6.0	6	5	4	7	1	5
72	8.0	7	6	1	11	5	5
72	10.0	7	8	10	5	4	4
Return to FR1							
72	1.0	152	5	8	148	22	22
72	1.0	137	4	7	136	20	22
72	1.0	141	6	0	149	22	23

72	1.0	139	8	4	143	22	20
72	1.0	147	5	4	148	22	20
FR1							
72	1.0	134	12	2	145	21	21
72	1.0	139	14	5	150	21	22
72	1.0	142	11	4	148	21	23
72	1.0	132	20	9	146	20	21
72	1.0	134	11	14	132	22	21
72	1.0	133	16	1	148	20	21
72	2.0	120	35	19	134	20	22
72	3.0	83	77	27	133	20	21
72	4.0	73	89	44	119	21	20
72	6.0	71	93	60	103	18	19
72	8.0	72	88	37	123	19	17
72	10.0	70	91	36	125	21	20

Experiment 1.3

Medium luminance

72	1.0	67	1	0	69	18	16
72	1.0	67	0	0	64	19	16
72	1.0	57	0	2	57	17	17
72	1.0	61	1	0	64	15	16
72	1.0	67	1	0	68	17	17
72	2.0	18	2	1	17	6	6
72	3.0	47	19	2	63	16	17
72	4.0	17	55	2	69	13	13
72	6.0	19	60	10	67	13	12
72	8.0	21	47	9	60	10	13
72	10.0	28	32	17	14	13	12

High luminance

72	1.0	66	1	1	68	17	17
72	1.0	64	0	4	57	18	18
72	1.0	68	0	5	64	17	19
72	1.0	62	0	2	62	19	17
72	1.0	62	1	2	59	19	16
72	2.0	67	1	3	64	19	18
72	3.0	53	13	16	53	16	14
72	4.0	28	35	16	45	11	12
72	6.0	26	42	18	50	11	13
72	8.0	27	26	11	39	13	13
72	10.0	27	42	20	47	13	13

Low luminance

72	1.0	59	0	1	59	17	18
72	1.0	58	1	0	60	19	19
72	1.0	55	2	0	57	16	16
72	1.0	65	0	1	64	17	17
72	1.0	64	2	1	64	18	18
72	2.0	61	8	2	64	18	18
72	3.0	27	40	4	64	13	16
72	4.0	25	47	16	57	13	13
72	6.0	28	40	14	53	16	15
72	8.0	34	33	6	59	15	16
72	10.0	30	40	13	57	14	16

Experiment 1.4

72	2.0	52	10	16	47	19	16
72	2.0	61	3	17	45	16	16
72	2.0	59	9	18	50	16	16
72	2.0	62	6	24	43	16	16
72	1.0	71	1	7	63	17	18
72	2.0	66	4	6	68	18	19
72	3.0	37	31	14	53	15	16
72	4.0	28	43	17	52	11	9
72	6.0	31	32	16	42	13	13
72	8.0	49	13	4	59	17	17
72	10.0	45	27	16	56	16	17

Experiment 1.5

Descending series

72	1.0	74	0	0	77	18	27
72	1.0	67	0	1	65	23	21
72	1.0	66	0	0	67	23	22
72	1.0	53	0	3	55	13	24
72	1.0	66	0	1	64	16	28
72	2.0	67	2	0	67	19	24
72	3.0	16	6	4	18	7	10
72	4.0	21	39	6	54	12	25
72	6.0	29	28	12	49	14	22
72	8.0	30	16	2	42	12	18
72	10.0	2	5	1	6	1	4

Ascending series

72	1.0	51	0	0	51	22	20
72	2.0	59	2	2	59	16	27
72	3.0	54	9	14	48	24	18
72	4.0	45	15	10	51	16	25
72	6.0	26	41	17	50	16	21
72	8.0	0	7	0	5	0	3
72	10.0	15	49	6	59	10	25

Experiment 1.1

Descending series

73	1.0	105	44	57	94	19	19
73	1.0	123	33	60	98	20	22
73	1.0	96	44	60	81	18	18
73	1.0	103	46	73	80	19	20
73	1.0	117	39	57	99	23	20
73	1.0	117	39	57	99	23	20
73	1.2	99	50	71	75	17	18
73	1.0	96	52	29	119	20	20
73	1.4	77	66	35	108	21	19
73	1.0	21	14	12	27	4	6
73	1.6	79	68	45	100	20	19
73	1.0	91	48	42	97	20	19
73	1.8	78	62	49	91	17	18
73	1.0	95	36	55	76	18	20
73	2.0	101	53	74	81	19	16
73	1.0	112	42	41	114	23	21
73	2.5	79	82	69	90	19	21
73	1.0	94	52	44	100	18	22

73	1.0	118	22	45	97	20	18
73	3.0	69	78	81	65	17	17
73	1.0	120	29	67	80	20	19
73	1.0	116	37	49	103	20	21
73	3.5	67	42	66	43	15	15
73	1.0	102	26	67	61	17	17
73	1.0	99	19	55	65	18	17
73	1.0	111	45	46	107	21	18
73	1.0	104	46	25	127	21	19
73	4.0	62	101	63	100	16	16
73	1.0	121	32	42	112	23	21
73	5.0	74	83	58	99	20	19
73	1.0	77	27	47	57	15	14
73	1.0	117	21	29	105	21	19
73	6.0	58	72	56	74	16	14
73	1.0	99	34	33	97	17	18
73	8.0	50	37	41	44	10	9
73	1.0	130	12	44	98	20	19
73	1.0	119	18	46	90	21	20
73	1.0	111	13	87	86	17	19
73	10.0	30	29	37	24	7	6
Ascending series							
73	1.0	120	30	47	107	21	18
73	1.0	117	28	42	105	20	18
73	1.0	108	25	35	96	20	20
73	10.0	69	69	54	85	18	16
73	1.0	111	24	46	91	18	22
73	1.0	53	11	25	37	12	11
73	8.0	59	65	51	73	16	16
73	1.0	89	36	31	95	21	17
73	1.0	81	42	39	86	18	19
73	6.0	23	21	23	22	4	6
73	1.0	15	2	9	9	2	2
73	1.0	71	10	27	54	13	13
73	5.0	57	70	59	68	18	17
73	1.0	44	20	28	36	11	9
73	1.0	86	30	49	66	16	16
73	1.0	66	18	17	67	14	13
73	4.0	37	33	30	41	13	13
73	1.0	60	18	25	54	13	15
73	3.5	46	32	46	31	12	12
73	1.0	79	14	35	59	12	12
73	3.0	56	45	43	58	13	15
73	1.0	86	28	52	64	18	18
73	2.5	51	53	47	57	15	16
73	1.0	102	23	37	88	17	19
73	2.0	85	51	74	61	19	18
73	1.0	107	31	4	91	19	19
73	1.8	75	63	47	92	19	17
73	1.0	111	38	30	120	22	20
73	1.6	102	48	43	107	19	20
73	1.0	124	30	24	131	22	21
73	1.0	106	37	35	108	21	21
73	1.4	80	48	40	87	19	19
73	1.0	109	36	28	122	20	19

73	1.0	117	31	32	117	21	22
73	1.0	77	13	36	54	12	13
73	1.2	126	26	27	121	20	23
73	1.0	115	26	37	104	18	22

Experiment 1.2

FR5

73	1.0	83	5	9	80	17	19
73	1.0	87	6	9	85	18	19
73	1.0	90	5	8	87	21	22
73	1.0	81	5	4	80	20	18
73	1.0	60	3	5	58	14	14
73	2.0	63	33	11	82	19	17
73	3.0	35	39	25	49	13	14
73	4.0	46	45	41	48	16	14
73	6.0	43	58	37	66	14	16
73	8.0	28	14	24	19	6	5
73	10.0	44	38	39	44	13	12

return to FR1

73	1.0	97	37	26	109	18	21
73	1.0	93	26	16	109	18	18
73	1.0	53	29	20	62	11	13
73	1.0	110	29	29	106	18	21
73	1.0	104	36	27	113	20	21

FR10

73	1.0	78	3	2	80	17	22
73	1.0	69	9	1	74	20	19
73	1.0	78	2	0	79	20	18
73	1.0	54	2	5	49	14	13
73	1.0	76	2	4	74	21	17
73	2.0	41	19	17	42	11	11
73	3.0	23	15	17	25	7	7
73	4.0	15	17	7	26	7	6
73	6.0	13	14	11	14	6	3
73	8.0	28	17	9	38	11	8
73	10.0	6	6	3	6	2	2

Return to FR1

73	1.0	104	40	29	114	20	22
73	1.0	98	42	25	115	19	22
73	1.0	101	46	23	125	21	19
73	1.0	103	39	30	114	20	22
73	1.0	126	25	24	131	21	21

FR15

73	1.0	39	6	2	4	14	11
73	1.0	23	4	3	26	8	7
73	1.0	21	5	6	17	9	9
73	1.0	11	0	6	5	2	3
73	1.0	42	4	4	42	14	4
73	2.0	6	5	4	8	3	3
73	3.0	18	32	15	36	8	12
73	4.0	8	12	9	12	3	2
73	6.0	7	21	4	22	3	5
73	8.0	20	19	13	29	12	10
73	10.0	23	25	16	31	10	9

Return to FR1

73	1.0	130	18	16	132	20	22
73	1.0	115	34	15	134	22	21
73	1.0	112	41	10	143	22	19
73	1.0	95	49	23	123	19	21
73	1.0	120	31	7	147	21	22

FR25

73	1.0	6	4	1	7	3	3
73	1.0	21	7	1	26	12	12
73	1.0	8	7	0	11	4	4
73	1.0	13	3	3	13	4	5
73	1.0	16	6	3	16	5	6
73	2.0	2	1	1	3	0	2
73	3.0	0	1	0	3	0	2
73	4.0	2	8	2	6	2	1
73	6.0	5	10	1	12	3	6
73	8.0	10	9	4	19	7	6
73	10.0	2	2	3	2	2	1

Return to FR1

73	1.0	107	32	14	125	20	21
73	1.0	83	46	11	117	20	20
73	1.0	100	40	22	119	21	19
73	1.0	89	49	10	127	20	19
73	1.0	102	45	11	134	21	19

FR1

73	1.0	98	46	28	115	20	21
73	1.0	102	42	11	131	20	21
73	1.0	84	60	31	116	19	20
73	1.0	93	49	28	114	19	20
73	1.0	106	46	23	125	19	18
73	2.0	71	79	44	105	21	19
73	3.0	68	82	64	85	18	17
73	4.0	65	86	58	92	18	19
73	6.0	64	88	56	94	19	20
73	8.0	74	68	50	93	20	20
73	10.0	62	86	58	90	18	18

Experiment 1.3

Medium luminance

73	1.0	60	12	9	61	15	15
73	1.0	58	12	3	64	19	16
73	1.0	56	9	7	59	17	16
73	1.0	48	12	11	47	15	15
73	1.0	59	11	12	55	18	17
73	2.0	30	30	22	39	15	10
73	3.0	31	36	27	43	13	14
73	4.0	25	23	17	31	12	11
73	6.0	37	36	35	37	13	13
73	8.0	19	24	22	23	6	7
73	10.0	5	3	4	7	2	3

High luminance

73	1.0	63	10	13	60	16	15
73	1.0	59	4	9	53	14	14
73	1.0	67	10	14	61	17	17
73	1.0	59	10	12	53	16	14

73	1.0	62	3	18	46	16	14
73	2.0	54	21	25	51	16	16
73	3.0	41	34	25	47	12	15
73	4.0	37	17	23	30	15	11
73	6.0	31	38	28	43	*	*
73	8.0	29	26	23	31	10	9
73	10.0	32	23	20	34	14	13
Low luminance							
73	1.0	65	6	10	64	17	19
73	1.0	28	6	6	28	9	9
73	1.0	31	11	4	36	8	8
73	1.0	52	4	7	49	15	11
73	1.0	69	6	6	65	17	20
73	2.0	24	26	19	32	9	10
73	3.0	25	24	20	31	12	12
73	4.0	35	37	37	34	13	12
73	6.0	24	36	20	40	11	10
73	8.0	30	31	24	38	14	12
73	10.0	27	27	22	30	10	9

Experiment 1.4

73	2.0	64	14	34	40	15	16
73	2.0	53	21	28	48	16	16
73	2.0	54	18	24	48	16	15
73	2.0	51	20	10	60	16	17
73	1.0	68	4	3	70	19	19
73	2.0	52	20	11	61	16	16
73	3.0	33	33	18	51	14	16
73	4.0	28	24	13	40	9	9
73	6.0	29	36	19	47	14	13
73	8.0	45	22	28	37	14	14
73	10.0	13	16	14	14	4	4

Experiment 1.5

Descending series

73	1.0	97	2	1	59	17	24
73	1.0	58	1	1	57	19	24
73	1.0	51	7	0	56	17	24
73	1.0	44	1	2	43	18	22
73	1.0	47	2	4	44	19	20
73	2.0	28	25	10	43	12	24
73	3.0	10	22	4	28	7	13
73	4.0	2	14	1	15	1	9
73	6.0	11	33	5	40	6	23
73	8.0	2	5	1	5	1	4
73	10.0	0	4	1	6	0	4

Ascending series

73	1.0	38	0	4	34	15	16
73	2.0	40	10	8	41	22	20
73	3.0	30	25	11	43	9	23
73	4.0	33	21	11	40	14	19
73	6.0	38	20	26	32	19	17
73	8.0	0	2	1	2	0	1
73	10.0	30	31	7	57	8	30

Experiment 1.1

Descending series

74	1.0	153	4	11	146	21	24
74	1.0	154	3	24	134	22	21
74	1.0	151	7	28	132	21	21
74	1.0	153	4	38	119	21	22
74	1.0	146	11	18	140	21	23
74	1.0	146	11	18	140	21	23
74	1.2	134	15	5	148	21	22
74	1.0	133	11	2	144	21	22
74	1.4	130	11	2	140	22	21
74	1.0	120	22	0	142	21	23
74	1.6	124	16	1	140	22	23
74	1.0	113	42	2	149	21	22
74	1.8	104	42	6	139	20	20
74	1.0	132	16	0	150	22	21
74	2.0	120	33	6	147	21	22
74	1.0	135	13	5	141	22	20
74	2.5	101	45	41	104	21	18
74	1.0	151	7	6	151	20	23
74	1.0	144	7	18	133	20	20
74	3.0	59	54	35	77	14	15
74	1.0	120	3	27	96	16	16
74	1.0	146	12	37	123	20	22
74	3.5	65	63	42	86	15	15
74	1.0	97	9	20	85	16	14
74	1.0	131	1	29	103	20	18
74	1.0	120	2	25	99	18	18
74	4.0	88	77	58	105	20	21
74	1.0	121	3	18	105	17	17
74	5.0	43	61	47	56	11	11
74	1.0	99	14	51	63	16	16
74	1.0	138	5	19	125	22	22
74	6.0	63	71	52	81	16	16
74	1.0	134	6	33	107	20	18
74	8.0	81	83	64	103	19	21
74	1.0	153	6	28	130	22	22
74	1.0	154	0	32	118	22	20
74	1.0	158	1	32	128	21	22
74	10.0	81	72	86	69	17	17

Ascending series

74	1.0	146	9	48	106	19	21
74	1.0	149	12	47	115	21	21
74	1.0	138	4	26	113	22	19
74	10.0	87	63	49	103	20	19
74	1.0	134	5	21	120	21	21
74	1.0	149	4	32	117	22	20
74	8.0	46	40	31	55	12	10
74	1.0	142	2	18	124	22	20
74	1.0	121	4	31	95	20	22
74	6.0	79	69	72	76	19	20
74	1.0	120	4	42	83	18	18
74	1.0	46	6	1	51	7	10
74	1.0	66	3	9	59	11	11
74	5.0	62	82	64	78	16	17

74	1.0	71	4	25	49	11	11
74	1.0	113	3	27	91	18	18
74	4.0	44	32	25	50	10	9
74	1.0	99	9	13	98	14	16
74	3.5	81	64	59	86	18	18
74	1.0	118	10	25	103	17	18
74	3.0	69	67	61	75	20	19
74	1.0	75	5	14	68	11	11
74	2.5	78	62	60	79	20	17
74	1.0	164	3	27	138	22	20
74	2.0	184	22	22	136	24	21
74	1.0	156	2	22	135	21	22
74	1.8	140	22	43	119	21	20
74	1.0	159	5	20	142	22	21
74	1.6	144	17	43	118	21	22
74	1.0	152	1	48	105	21	22
74	1.0	153	4	32	127	21	20
74	1.4	98	11	38	71	15	13
74	1.0	144	6	52	99	21	23
74	1.0	104	6	30	82	16	19
74	1.0	116	17	31	103	20	17
74	1.0	129	7	11	121	21	18
74	1.2	151	3	12	140	21	22
74	1.0	148	5	25	128	21	20

Experiment 1.2

FR5

74	1.0	46	5	1	49	11	13
74	1.0	71	5	2	71	17	16
74	1.0	82	6	0	90	18	20
74	1.0	82	6	0	89	20	18
74	1.0	44	5	0	50	9	11
74	2.0	62	28	2	87	16	17
74	3.0	33	39	15	59	11	13
74	4.0	21	39	10	48	10	11
74	6.0	42	41	32	51	13	15
74	8.0	28	42	14	53	11	12
74	10.0	22	26	12	33	8	6

Return to FR1

74	1.0	131	8	43	97	20	19
74	1.0	118	4	31	92	17	17
74	1.0	83	2	13	71	15	12
74	1.0	101	2	17	88	15	15
74	1.0	138	3	10	132	23	20

FR10

74	1.0	54	1	0	56	17	18
74	1.0	36	1	0	38	12	11
74	1.0	43	3	1	42	13	13
74	1.0	8	0	1	8	2	2
74	1.0	29	1	0	31	9	8
74	2.0	36	6	4	39	12	12
74	3.0	11	22	9	24	6	5
74	4.0	6	11	1	18	4	2
74	6.0	5	8	4	9	2	1
74	8.0	3	19	1	18	2	4

74	10.0	7	7	1	12	4	4
Return to FR1							
74	1.0	70	27	5	91	16	16
74	1.0	110	19	25	106	20	20
74	1.0	128	12	30	110	20	22
74	1.0	84	16	13	86	16	13
74	1.0	117	8	13	114	19	19
FR15							
74	1.0	46	1	1	45	14	15
74	1.0	45	2	0	48	15	14
74	1.0	50	0	1	47	16	16
74	1.0	42	2	0	45	14	15
74	1.0	29	12	0	42	13	15
74	2.0	8	27	5	30	7	6
74	3.0	28	23	17	34	11	11
74	4.0	15	25	12	29	8	8
74	6.0	16	17	9	25	7	8
74	8.0	10	18	2	26	7	8
74	10.0	16	21	2	39	10	9
Return to FR1							
74	1.0	105	18	17	104	19	19
74	1.0	112	25	14	123	21	22
74	1.0	130	14	10	134	22	19
74	1.0	122	11	35	96	19	20
74	1.0	134	7	14	127	21	21
FR25							
74	1.0	22	3	2	25	11	9
74	1.0	9	4	0	11	4	4
74	1.0	20	4	1	25	10	9
74	1.0	10	5	1	15	7	4
74	1.0	13	10	6	17	8	10
74	2.0	0	8	0	7	0	2
74	3.0	4	5	3	7	3	3
74	4.0	7	9	7	10	4	4
74	6.0	7	15	5	15	4	3
74	8.0	10	7	6	12	2	4
74	10.0	5	8	7	6	2	3
Return to FR1							
74	1.0	125	13	7	130	19	22
74	1.0	94	4	5	93	14	16
74	1.0	143	3	16	132	22	21
74	1.0	130	5	25	112	20	19
74	1.0	129	8	34	102	21	19
FR40							
74	1.0	12	1	0	10	7	5
74	1.0	3	3	0	6	3	0
74	1.0	12	4	1	16	7	9
74	1.0	7	3	0	10	6	4
74	1.0	12	0	5	10	7	7
74	2.0	5	10	3	12	4	4
74	3.0	3	11	2	12	1	2
74	4.0	0	7	2	2	0	0
74	6.0	7	14	7	13	4	3
74	8.0	4	8	3	7	2	3
74	10.0	7	7	5	10	3	3

Return to FR1

74	1.0	133	9	9	132	22	21
74	1.0	60	12	0	69	12	9
74	1.0	123	9	10	122	20	23
74	1.0	121	9	13	119	19	20
74	1.0	138	5	23	120	22	19

FR1

74	1.0	152	3	27	124	22	21
74	1.0	149	6	23	131	21	22
74	1.0	142	8	39	109	21	23
74	1.0	141	8	39	109	21	22
74	1.0	139	12	40	110	21	19
74	2.0	79	76	66	90	17	22
74	3.0	67	61	58	70	16	17
74	4.0	95	56	73	78	17	19
74	6.0	90	68	75	83	19	18
74	8.0	107	50	96	61	20	17
74	10.0	93	66	83	73	18	18

Experiment 1.3

Medium luminance

74	1.0	54	0	0	54	17	16
74	1.0	50	0	0	52	15	16
74	1.0	51	1	0	52	17	17
74	1.0	36	0	0	36	11	10
74	1.0	50	1	2	48	16	16
74	2.0	22	20	9	32	10	8
74	3.0	25	16	23	18	12	9
74	4.0	28	28	18	39	14	13
74	6.0	23	33	29	28	10	9
74	8.0	26	30	14	42	12	12
74	10.0	17	15	8	21	9	6

High luminance

74	1.0	51	0	0	51	17	17
74	1.0	46	0	0	47	16	17
74	1.0	52	0	3	51	16	17
74	1.0	40	1	0	40	14	16
74	1.0	50	0	0	52	15	16
74	2.0	22	33	9	45	13	12
74	3.0	26	26	15	36	11	13
74	4.0	26	28	15	40	11	11
74	6.0	31	28	18	38	13	14
74	8.0	28	22	16	33	14	11
74	10.0	32	23	7	49	15	15

Low luminance

74	1.0	52	4	5	53	15	16
74	1.0	47	6	4	47	17	16
74	1.0	52	4	5	50	18	16
74	1.0	43	4	1	42	15	14
74	1.0	53	2	1	53	16	16
74	2.0	28	33	25	38	13	14
74	3.0	25	28	28	25	10	11
74	4.0	20	40	22	39	12	11
74	6.0	39	25	15	47	14	15
74	8.0	23	37	22	36	10	11

74	10.0	20	38	20	40	10	9
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Experiment 1.4

74	2.0	55	8	7	52	16	17
74	2.0	58	5	14	49	16	16
74	2.0	62	2	16	48	16	16
74	2.0	53	2	18	36	16	15
74	1.0	60	0	5	56	16	17
74	2.0	50	8	4	57	17	17
74	3.0	29	27	21	39	13	12
74	4.0	42	23	29	36	13	13
74	6.0	37	22	27	32	13	12
74	8.0	23	13	18	19	10	11
74	10.0	37	22	17	43	13	14

Experiment 1.5

Descending series

74	1.0	58	0	0	54	24	20
74	1.0	50	1	1	47	23	20
74	1.0	56	0	0	57	22	22
74	1.0	45	0	7	38	22	18
74	1.0	57	0	0	58	27	17
74	2.0	36	18	0	55	17	23
74	3.0	21	20	10	33	8	20
74	4.0	24	20	6	37	17	19
74	6.0	21	27	12	36	11	20
74	8.0	24	38	1	60	12	27
74	10.0	12	2	5	11	6	7

Ascending series

74	1.0	40	6	2	42	15	20
74	2.0	42	7	8	41	21	15
74	3.0	21	28	9	39	13	21
74	4.0	21	33	6	52	12	27
74	6.0	28	34	22	41	16	19
74	8.0	0	6	0	7	0	4
74	10.0	32	23	4	54	11	27

Experiment 1.1

Descending series

75	1.0	137	21	6	150	22	23
75	1.0	149	12	6	157	21	22
75	1.0	154	5	8	152	21	22
75	1.0	153	3	6	150	22	22
75	1.0	161	7	5	162	22	21
75	1.2	158	3	7	154	23	22
75	1.0	154	9	7	157	22	23
75	1.4	154	6	4	157	23	22
75	1.0	149	9	8	151	22	23
75	1.6	152	6	8	151	22	21
75	1.0	154	6	7	150	21	23
75	1.8	155	4	3	156	22	23
75	1.0	155	5	5	155	22	22
75	2.0	145	9	0	153	22	23
75	1.0	156	1	2	155	22	23
75	2.5	130	26	12	145	20	22

75	1.0	157	3	4	155	21	24
75	1.0	156	3	2	156	23	21
75	3.0	110	49	30	130	19	23
75	1.0	157	2	10	149	20	23
75	1.0	161	1	4	159	21	22
75	3.5	100	64	59	103	18	18
75	1.0	148	0	23	126	21	21
75	1.0	159	0	32	128	22	23
75	1.0	161	3	23	142	22	22
75	4.0	89	73	74	87	17	20
75	1.0	153	2	16	140	22	21
75	5.0	79	82	65	96	19	18
75	1.0	152	3	22	134	21	23
75	1.0	158	2	13	147	23	21
75	6.0	69	92	69	94	18	17
75	1.0	156	1	7	147	21	22
75	8.0	74	84	56	103	19	19
75	1.0	164	0	7	160	22	23
75	1.0	163	0	17	145	22	21
75	1.0	159	3	20	146	21	22
75	10.0	89	66	63	90	20	18
Ascending series							
75	1.0	152	9	26	136	21	23
75	1.0	140	17	30	127	20	21
75	1.0	157	0	8	151	23	22
75	10.0	60	89	46	108	19	22
75	1.0	156	0	9	146	24	21
75	1.0	153	1	3	149	21	23
75	8.0	57	53	28	83	15	15
75	1.0	152	0	10	140	20	21
75	1.0	153	0	22	131	21	22
75	6.0	71	84	66	90	18	17
75	1.0	156	0	7	150	22	21
75	1.0	50	0	4	45	7	8
75	1.0	40	0	6	33	6	6
75	5.0	75	80	70	83	18	19
75	1.0	148	3	11	142	22	20
75	1.0	152	4	5	149	21	23
75	4.0	93	53	57	92	20	20
75	1.0	123	0	2	122	16	17
75	3.5	98	58	77	79	19	19
75	1.0	161	0	17	144	21	23
75	3.0	102	48	51	108	18	22
75	1.0	151	1	12	140	21	22
75	2.5	123	29	40	112	22	22
75	1.0	155	2	8	148	22	23
75	2.0	145	8	23	130	22	22
75	1.0	152	1	11	145	21	23
75	1.8	157	3	13	144	21	23
75	1.0	155	4	12	145	21	24
75	1.6	163	1	11	154	23	21
75	1.0	159	4	5	157	21	23
75	1.0	163	2	15	148	21	22
75	1.4	155	4	7	151	20	22
75	1.0	157	4	3	159	22	21

75	1.0	162	0	13	149	22	23
75	1.0	154	6	16	145	22	21
75	1.2	155	3	10	144	21	22
75	1.0	154	4	16	142	20	22

Experiment 1.2

FR5

75	1.0	101	2	13	90	21	20
75	1.0	102	1	4	99	21	19
75	1.0	91	2	1	90	20	20
75	1.0	82	1	3	80	20	19
75	1.0	87	0	2	82	21	19
75	2.0	79	2	4	78	18	19
75	3.0	66	7	7	67	17	19
75	4.0	53	23	19	55	16	16
75	6.0	57	42	44	54	16	16
75	8.0	39	55	20	73	15	14
75	10.0	41	61	39	60	14	16

Return to FR1

75	1.0	152	2	24	132	20	22
75	1.0	153	5	1	156	23	21
75	1.0	159	0	4	153	22	21
75	1.0	155	0	13	142	22	22
75	1.0	162	1	10	154	23	22

FR10

75	1.0	57	7	0	65	19	17
75	1.0	52	9	0	60	16	18
75	1.0	53	3	1	59	16	18
75	1.0	54	7	0	61	17	17
75	1.0	63	1	0	65	19	18
75	2.0	51	9	2	59	16	17
75	3.0	35	20	1	53	14	14
75	4.0	15	37	8	45	6	7
75	6.0	24	33	24	35	12	10
75	8.0	33	18	16	35	13	15
75	10.0	35	22	16	40	13	16

Return to FR1

75	1.0	143	9	12	137	21	20
75	1.0	154	3	7	153	22	23
75	1.0	159	1	5	154	22	23
75	1.0	162	2	4	159	21	23
75	1.0	165	1	9	156	22	22

FR15

75	1.0	53	0	1	57	16	17
75	1.0	56	0	0	57	16	16
75	1.0	50	3	0	50	18	16
75	1.0	46	4	0	49	15	13
75	1.0	55	1	1	53	16	16
75	2.0	38	6	1	45	15	14
75	3.0	14	31	2	43	7	8
75	4.0	7	23	1	25	5	6
75	6.0	4	10	5	11	3	3
75	8.0	19	21	10	30	10	10
75	10.0	32	19	19	31	15	13

Return to FR1

75	1.0	148	9	8	148	20	23
75	1.0	155	2	3	153	23	20
75	1.0	158	0	5	151	22	23
75	1.0	158	2	5	155	21	22
75	1.0	160	0	3	157	22	23

FR25

75	1.0	22	0	1	19	13	10
75	1.0	6	0	0	10	3	4
75	1.0	27	0	0	25	13	12
75	1.0	23	0	0	23	12	12
75	1.0	19	0	0	18	7	9
75	2.0	7	4	1	9	3	4
75	3.0	8	6	1	12	6	6
75	4.0	9	7	3	13	5	5
75	6.0	7	8	4	11	3	5
75	8.0	11	5	3	13	6	6
75	10.0	7	6	4	9	3	3

Return to FR1

75	1.0	162	0	2	161	23	21
75	1.0	83	0	0	83	12	11
75	1.0	159	1	6	155	21	23
75	1.0	160	0	1	154	22	21
75	1.0	150	4	10	142	22	23

FR40

75	1.0	6	0	2	5	2	3
75	1.0	9	0	1	7	2	4
75	1.0	4	1	0	7	3	2
75	1.0	10	0	0	7	4	4
75	1.0	10	0	0	7	2	6
75	2.0	8	2	1	8	6	3
75	3.0	2	4	0	8	2	6
75	4.0	3	5	5	4	3	4
75	6.0	2	3	1	4	0	1
75	8.0	1	1	1	3	0	1
75	10.0	8	4	1	12	6	4

Return to FR1

75	1.0	161	0	6	155	22	23
75	1.0	160	0	7	152	21	23
75	1.0	156	2	0	158	23	22
75	1.0	162	3	0	158	22	22
75	1.0	163	0	2	159	23	22

FR1

75	1.0	162	0	1	159	23	21
75	1.0	161	0	6	154	21	22
75	1.0	152	0	5	145	22	22
75	1.0	162	1	4	157	22	22
75	1.0	157	1	6	153	21	21
75	2.0	131	33	18	145	21	22
75	3.0	85	78	26	139	20	20
75	4.0	75	82	58	97	19	17
75	6.0	75	83	53	102	20	19
75	8.0	78	84	40	121	19	19
75	10.0	73	87	56	104	19	18

Experiment 1.3

Medium luminance

75	1.0	57	3	1	58	19	17
75	1.0	49	3	0	52	18	18
75	1.0	59	3	0	64	19	18
75	1.0	51	2	0	51	16	16
75	1.0	64	0	1	62	19	17
75	2.0	53	3	0	58	17	18
75	3.0	23	11	5	28	12	10
75	4.0	11	32	4	38	9	10
75	6.0	18	31	9	42	13	12
75	8.0	31	36	10	57	13	15
75	10.0	33	18	12	39	12	12

High luminance

75	1.0	58	3	0	62	16	17
75	1.0	59	0	0	60	17	19
75	1.0	61	4	0	70	16	17
75	1.0	59	1	1	61	19	18
75	1.0	68	1	0	70	19	19
75	2.0	65	4	1	68	19	18
75	3.0	34	25	11	52	15	15
75	4.0	24	40	8	54	12	13
75	6.0	20	40	7	51	14	13
75	8.0	30	39	1	67	16	16
75	10.0	24	44	19	51	15	14

Low luminance

75	1.0	61	0	0	62	17	18
75	1.0	53	8	2	61	17	17
75	1.0	61	6	2	66	19	17
75	1.0	62	5	1	65	17	17
75	1.0	69	0	1	69	19	18
75	2.0	52	22	4	70	17	18
75	3.0	34	44	28	50	13	13
75	4.0	21	52	20	53	12	12
75	6.0	30	43	20	55	11	12
75	8.0	40	26	3	64	18	17

Experiment 1.4

75	2.0	72	3	0	74	17	20
75	2.0	72	6	0	77	20	19
75	2.0	75	2	0	77	20	19
75	2.0	72	4	0	73	19	17
75	1.0	71	0	0	69	18	21
75	2.0	65	0	0	66	19	17
75	3.0	44	25	0	68	15	5
75	4.0	9	12	4	18	6	5
75	6.0	17	34	2	49	11	11
75	8.0	24	27	8	46	15	12
75	10.0	20	26	7	39	9	12

Experiment 1.5

Descending series

75	1.0	69	4	0	72	26	18
75	1.0	57	1	0	57	19	24
75	1.0	48	0	0	48	22	19

75	1.0	62	0	0	61	27	17
75	1.0	66	0	0	67	25	19
75	2.0	79	0	0	76	25	20
75	3.0	28	8	3	31	14	16
75	4.0	19	37	7	47	9	23
75	6.0	25	26	10	40	14	15
75	8.0	39	36	1	73	16	28
75	10.0	33	29	18	44	18	18
Ascending							
75	1.0	63	2	1	65	24	21
75	2.0	36	3	6	32	18	10
75	3.0	45	19	4	62	18	25
75	4.0	20	17	1	33	13	13
75	6.0	32	36	4	64	9	31
75	8.0	19	35	8	44	12	24
75	10.0	29	19	10	38	14	17

Experiment 1.1

Descending series

76	1.0	154	14	3	167	23	21
76	1.0	161	3	1	161	22	22
76	1.0	153	9	1	165	23	21
76	1.0	155	6	3	158	22	23
76	1.0	152	8	1	159	22	23
76	1.2	152	10	2	162	23	22
76	1.0	157	7	1	165	23	21
76	1.4	154	14	8	166	22	22
76	1.0	163	6	2	166	22	23
76	1.6	149	13	3	162	23	22
76	1.0	168	1		168	24	21
76	1.8	144	27	6	167	22	23
76	1.0	160	12	1	171	23	21
76	2.0	117	52	8	162	21	20
76	1.0	151	13	3	161	23	20
76	2.5	101	68	16	156	21	19
76	1.0	166	3	7	163	21	23
76	1.0	168	1	3	166	21	24
76	3.0	104	62	27	139	20	20
76	1.0	162	5	4	164	21	22
76	1.0	164	5	4	164	21	22
76	1.0	149	4	7	150	22	20
76	3.5	87	80	29	139	21	20
76	1.0	150	6	7	151	21	21
76	1.0	157	8	3	160	23	22
76	1.0	153	15	5	163	23	22
76	4.0	72	101	41	149	19	19
76	1.0	148	2	10	140	23	21
76	5.0	74	61	66	69	16	15
76	1.0	155	4	10	150	21	21
76	1.0	155	2	11	124	20	22
76	6.0	62	98	41	119	17	19
76	1.0	62	0	9	154	23	22
76	8.0	71	90	45	120	19	19
76	1.0	160	5	11	156	22	23
76	1.0	167	1	17	151	22	19

76	1.0	142	20	9	153	21	22
76	10.0	74	90	61	103	20	18

Ascending series

76	1.0	147	18	22	143	21	22
76	1.0	148	14	33	130	20	21
76	1.0	152	6	6	152	22	20
76	10.0	74	82	48	108	19	20
76	1.0	152	11	7	158	21	22
76	1.0	159	0	15	141	21	23
76	8.0	87	73	49	111	20	20
76	1.0	149	10	12	146	19	23
76	1.0	127	14	7	134	22	21
76	6.0	62	80	56	87	16	18
76	1.0	157	0	9	149	22	23
76	1.0	147	13	11	149	21	22
76	1.0	110	16	10	113	18	17
76	5.0	54	109	63	103	18	16
76	1.0	157	3	14	145	23	22
76	1.0	137	10	7	142	22	20
76	4.0	74	83	45	109	19	18
76	1.0	154	5	14	141	22	21
76	3.5	71	90	54	107	17	18
76	1.0	150	10	9	152	22	22
76	3.0	94	72	48	116	17	21
76	1.0	146	10	11	144	23	22
76	2.5	94	62	27	128	22	20
76	1.0	152	11	8	157	20	23
76	2.0	112	54	9	155	23	20
76	1.0	158	2	5	154	22	23
76	1.8	143	19	5	156	21	22
76	1.0	158	2	1	161	21	23
76	1.6	148	15	9	154	22	23
76	1.0	110	8	2	115	16	16
76	1.0	153	4	1	158	23	22
76	1.0	158	6	2	162	21	23
76	1.4	149	16	1	166	21	23
76	1.0	151	8	1	159	23	22
76	1.0	149	9	7	151	23	20
76	1.0	161	5	1	163	23	21
76	1.2	142	18	2	159	23	20
76	1.0	149	15	4	163	21	23

Experiment 1.2

FR5

76	1.0	117	0	0	115	20	20
76	1.0	119	0	0	117	19	20
76	1.0	115	0	0	116	22	19
76	1.0	115	0	0	114	21	20
76	1.0	111	1	0	112	20	20
76	2.0	89	25	1	114	20	21
76	3.0	45	70	7	106	18	17
76	4.0	42	71	18	97	16	17
76	6.0	17	97	18	95	10	9
76	8.0	42	69	34	76	16	15
76	10.0	63	50	32	82	18	17

Return to FR1

76	1.0	152	4	7	151	22	20
76	1.0	157	3	5	158	22	23
76	1.0	145	10	5	148	23	22
76	1.0	152	8	2	160	22	22
76	1.0	161	5	3	161	21	23

FR10

76	1.0	75	2	7	69	18	18
76	1.0	75	1	0	78	20	20
76	1.0	78	1	1	78	19	18
76	1.0	83	0	4	78	19	19
76	1.0	84	1	0	84	18	19
76	2.0	80	4	0	87	20	20
76	3.0	47	40	11	74	16	16
76	4.0	43	46	24	67	16	16
76	6.0	41	51	42	49	16	19
76	8.0	45	36	16	66	17	17
76	10.0	49	36	27	57	16	16

Return to FR1

76	1.0	146	10	4	150	21	23
76	1.0	149	16	5	159	21	24
76	1.0	159	9	9	159	20	23
76	1.0	159	6	5	159	21	23
76	1.0	165	3	6	162	21	23

FR15

76	1.0	60	7	0	65	17	17
76	1.0	57	0	0	55	17	16
76	1.0	57	2	4	55	18	17
76	1.0	58	0	0	60	15	16
76	1.0	58	1	0	59	19	17
76	2.0	47	11	1	56	19	13
76	3.0	30	31	11	50	15	12
76	4.0	21	38	7	53	12	15
76	6.0	19	34	22	30	9	9
76	8.0	30	27	16	39	13	13
76	10.0	40	24	20	41	15	14

Return to FR1

76	1.0	143	12	10	147	23	21
76	1.0	140	14	7	148	21	22
76	1.0	138	19	3	154	24	21
76	1.0	148	13	4	157	23	21
76	1.0	156	7	4	158	21	23

FR25

76	1.0	29	0	0	31	13	13
76	1.0	27	1	0	26	12	12
76	1.0	29	0	0	28	12	10
76	1.0	30	0	1	27	13	12
76	1.0	26	1	0	27	14	11
76	2.0	11	14	1	26	8	9
76	3.0	8	17	6	19	3	0
76	4.0	16	16	12	20	5	7
76	6.0	32	0	1	33	13	13
76	8.0	16	7	4	20	7	10
76	10.0	15	6	9	13	8	6

Return to FR1

76	1.0	138	13	4	146	22	21
76	1.0	138	13	0	151	23	20
76	1.0	137	17	1	154	23	22
76	1.0	133	26	3	154	20	21
76	1.0	135	20	1	153	22	23

FR40

76	1.0	19	0	0	18	9	11
76	1.0	15	0	0	15	11	8
76	1.0	18	0	2	16	9	7
76	1.0	20	0	0	20	8	7
76	1.0	18	0	1	17	7	8
76	2.0	20	2	1	20	10	7
76	3.0	2	16	2	14	2	0
76	4.0	8	7	8	5	1	0
76	6.0	4	9	4	11	3	3
76	8.0	10	9	2	18	7	10
76	10.0	17	6	12	10	6	6

Return to FR1

76	1.0	129	22	3	148	22	19
76	1.0	142	18	3	157	22	22
76	1.0	140	16	5	148	22	21
76	1.0	143	18	6	157	20	23
76	1.0	152	12	0	166	23	22

FR1

76	1.0	131	39	1	168	20	22
76	1.0	147	24	1	168	23	21
76	1.0	135	35	2	170	22	22
76	1.0	137	31	5	161	22	23
76	1.0	142	31	1	169	22	21
76	2.0	91	82	21	149	21	21
76	3.0	61	108	29	140	19	16
76	4.0	50	123	34	141	19	19
76	6.0	56	120	51	126	19	18
76	8.0	76	94	32	140	20	20
76	10.0	76	100	36	140	20	20

Experiment 1.3

Medium luminance

76	1.0	75	0	1	72	18	21
76	1.0	71	0	1	69	18	20
76	1.0	72	0	2	68	19	18
76	1.0	70	0	1	70	17	17
76	1.0	77	1	2	73	17	19
76	2.0	71	16	4	83	19	19
76	3.0	69	1	66	3	2	0
76	4.0	24	49	17	58	14	13
76	6.0	39	42	24	58	16	16
76	8.0	45	30	19	55	16	16
76	10.0	49	17	24	40	15	13

High luminance

76	1.0	71	0	0	70	18	17
76	1.0	75	0	0	74	19	18
76	1.0	73	0	0	73	19	17
76	1.0	72	0	0	73	18	22

76	1.0	72	0	0	75	17	17
76	2.0	69	12	7	75	17	16
76	3.0	42	38	15	65	16	15
76	4.0	39	50	37	50	15	13
76	6.0	43	37	35	43	13	12
76	8.0	36	38	15	58	15	16
76	10.0	45	31	19	55	17	18

Low luminance

76	1.0	77	3	2	78	19	18
76	1.0	76	3	1	79	17	21
76	1.0	80	2	0	81	18	19
76	1.0	75	10	0	85	18	19
76	1.0	81	8	2	86	19	19
76	2.0	41	35	22	55	15	15
76	3.0	29	51	28	50	14	16
76	4.0	33	51	31	53	15	14
76	6.0	37	46	40	43	15	14
76	8.0	45	30	15	59	14	13
76	10.0	44	35	17	59	15	16

Experiment 1.4

76	2.0	51	24	9	67	17	16
76	2.0	54	28	6	77	17	18
76	2.0	68	10	4	75	16	18
76	2.0	68	11	4	71	19	17
76	1.0	77	0	1	77	19	10
76	2.0	64	9	0	74	19	17
76	3.0	33	43	16	59	16	16
76	4.0	28	14	19	25	9	7
76	6.0	26	44	16	57	15	13
76	8.0	52	13	4	60	16	15
76	10.0	46	24	16	54	16	14

Experiment 1.5

Descending series

76	1.0	71	0	0	73	18	27
76	1.0	63	1	0	62	22	23
76	1.0	66	0	0	65	20	25
76	1.0	60	1	0	59	20	23
76	1.0	66	0	0	67	18	26
76	2.0	60	16	1	74	22	23
76	3.0	7	14	2	21	3	13
76	4.0	2	62	2	62	1	36
76	6.0	0	58	0	57	0	32
76	8.0	35	34	1	66	14	27
76	10.0	19	49	1	67	9	29

Ascending series

76	1.0	74	0	0	70	20	25
76	2.0	39	13	8	43	12	19
76	3.0	4	76	2	79	1	38
76	4.0	9	65	11	62	3	33
76	6.0	23	51	20	54	14	21
76	8.0	18	47	3	61	10	28
76	10.0	37	33	4	67	14	24

* missing values

Appendix 2

The hen number, the grating value (Gtg) and the latencies of correct responses to the left key (CorL) and incorrect responses to the right key (IncR) on grating trials and incorrect responses to the left key (IncL) and correct responses to the right key (CorR) on grey stimulus trials, for the last five days of training and for all training and probe sessions for Experiment 1.1.

Hen	Grating		Grey	
	Gtg	CorL IncR	IncL CorR	
Descending series				
71	1.0	1760 90	126 1678	
71	1.0	1786 85	112 1472	
71	1.0	1810 82	110 1601	
71	1.0	1640 88	150 1633	
71	1.0	1583 148	19 1605	
71	1.2	1749 167	46 1613	
71	1.0	1734 95	19 1703	
71	1.4	1793 72	54 1542	
71	1.0	1673 38	32 1356	
71	1.6	1219 387	56 1369	
71	1.0	1721 146	19 1517	
71	1.8	887 448	70 1047	
71	1.0	1507 70	88 1502	
71	2.0	1351 550	201 1554	
71	1.0	1619 60	144 1539	
71	2.5	984 856	432 1279	
71	1.0	3494 59	173 780	
71	1.0	1439 115	103 1403	
71	3.0	915 931	646 1307	
71	1.0	1565 139	125 1569	
71	1.0	1605 124	72 1590	
71	3.5	493 705	288 805	
71	1.0	1901 214	66 1497	
71	1.0	1922 204	93 1599	
71	1.0	1398 42	121 1090	
71	1.0	1629 37	81 1522	
71	4.0	833 790	453 1174	
71	1.0	1942 49	112 1438	
71	5.0	825 569	814 758	
71	1.0	1392 19	308 902	
71	1.0	1224 61	217 887	
71	6.0	826 806	660 888	
71	1.0	1386 9	408 1130	
71	8.0	1019 573	821 828	
71	1.0	1231 97	320 1199	
71	1.0	1723 8	498 954	
71	1.0	1473 56	184 1358	
71	10.0	776 697	654 1010	
Ascending series				
71	1.0	1738 56	483 968	
71	1.0	1750 66	330 1164	
71	1.0	1612 0	310 1022	
71	10.0	737 1035	849 915	

71	1.0	1611	37	253	1137
71	1.0	1430	20	280	1061
71	8.0	951	532	622	798
71	1.0	1284	59	314	981
71	1.0	1436	32	334	986
71	6.0	837	650	869	637
71	1.0	1524	7	262	1044
71	1.0	1501	56	311	1204
71	5.0	777	585	624	677
71	1.0	1470	21	164	1087
71	1.0	1361	49	166	1158
71	1.0	1393	25	170	1132
71	4.0	1000	462	602	886
71	1.0	1464	33	207	1033
71	3.5	1014	449	742	735
71	1.0	1511	9	306	1058
71	3.0	1044	433	583	763
71	1.0	1446	0	211	1139
71	2.5	1049	381	571	859
71	1.0	1796	56	197	1256
71	2.0	1455	194	442	1071
71	1.0	1507	0	138	1180
71	1.8	1439	146	291	1020
71	1.0	1621	9	84	1218
71	1.6	1552	75	212	1135
71	1.0	1456	16	36	1413
71	1.0	1610	0	89	1330
71	1.4	1634	57	249	1289
71	1.0	1489	39	140	1262
71	1.0	1717	11	81	1349
71	1.0	1472	17	95	1372
71	1.2	1372	41	53	1225
71	1.0	1381	33	32	1401

Descending series

72	1.0	1953	99	210	1291
72	1.0	1986	31	153	1180
72	1.0	1950	0	350	1070
72	1.0	2054	0	341	1173
72	1.0	2041	62	355	1185
72	1.2	1908	15	202	1328
72	1.0	1483	55	74	961
72	1.4	2060	0	301	1257
72	1.0	1796	62	197	1234
72	1.6	2003	38	261	1213
72	1.0	1854	31	341	1229
72	1.8	1744	181	426	1217
72	1.0	1905	12	266	1178
72	2.0	1335	413	317	1327
72	1.0	1829	25	416	1315
72	2.5	1207	588	665	920
72	1.0	1781	52	456	1005
72	1.0	1834	47	406	1149
72	3.0	1261	581	684	920
72	1.0	1823	146	480	1262

72	1.0	1927	17	294	1187
72	3.5	994	855	749	989
72	1.0	2010	89	593	1085
72	1.0	1179	187	270	903
72	1.0	1753	176	401	1252
72	1.0	1822	126	325	1258
72	4.0	1028	694	627	922
72	1.0	2162	40	280	1318
72	5.0	845	854	977	781
72	1.0	1961	62	521	1016
72	1.0	1779	23	418	1025
72	6.0	677	943	718	854
72	1.0	2062	83	233	1174
72	8.0	1040	736	750	901
72	1.0	1990	152	48	1187
72	1.0	2297	27	514	1114
72	1.0	2509	0	461	1089
72	10.0	1201	730	917	930
72	1.0	1799	168	286	1051
72	1.0	2017	160	265	1070
72	1.0	1941	75	248	1173
Ascending series					
72	10.0	771	851	825	885
72	1.0	2287	27	351	1048
72	1.0	1996	63	225	1124
72	8.0	757	823	829	837
72	1.0	2212	140	160	1140
72	1.0	2090	92	118	1249
72	6.0	841	812	925	725
72	1.0	1926	141	145	1208
72	1.0	1882	175	179	1182
72	5.0	759	887	808	917
72	1.0	1745	193	203	1233
72	1.0	1973	115	190	1141
72	1.0	2222	46	63	1257
72	4.0	967	697	747	884
72	1.0	1823	141	294	1155
72	3.5	962	638	553	1018
72	1.0	1782	108	268	1129
72	3.0	1199	632	547	937
72	1.0	1630	248	64	1180
72	2.5	1264	678	268	1128
72	1.0	1933	124	39	1250
72	2.0	1504	343	170	1303
72	1.0	1933	111	0	1190
72	1.8	1767	316	40	1264
72	1.0	1716	76	0	1303
72	1.6	1843	147	61	1245
72	1.0	1899	204	30	1263
72	1.0	1913	166	72	1201
72	1.4	1966	154	0	1170
72	1.0	1977	168	29	1144
72	1.0	1903	146	0	1222
72	1.0	1914	184	38	1184
72	1.2	1958	69	9	1125

72	1.0	1975	107	12	1144
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Descending series

73	1.0	1427	598	620	1199
73	1.0	1631	404	725	1214
73	1.0	1290	739	832	1157
73	1.0	1280	728	876	982
73	1.0	1468	475	642	1038
73	1.2	1181	616	917	1023
73	1.0	1355	678	438	1580
73	1.4	1243	829	501	1494
73	1.0	262	347	171	561
73	1.6	1153	892	615	1206
73	1.0	1310	568	642	1238
73	1.8	1146	754	880	1229
73	1.0	1361	572	872	1189
73	2.0	1182	711	872	1192
73	1.0	1504	564	549	1500
73	2.5	1196	1087	898	1125
73	1.0	1459	737	571	1465
73	1.0	1477	739	658	1350
73	3.0	971	1127	946	954
73	1.0	1362	424	832	1264
73	1.0	1554	583	557	1440
73	3.5	894	825	1075	889
73	1.0	1476	549	1013	1051
73	1.0	1630	375	839	1242
73	1.0	1430	670	572	1443
73	1.0	1454	749	373	1668
73	4.0	827	1179	736	1126
73	1.0	1794	424	477	1498
73	5.0	999	1074	848	1270
73	1.0	1085	575	592	959
73	1.0	1717	290	391	1383
73	6.0	853	1070	968	1045
73	1.0	1787	440	554	1513
73	8.0	1296	510	521	581
73	1.0	1767	175	671	1515
73	1.0	1736	316	916	1508
73	1.0	1819	189	892	1558
73	10.0	439	513	525	391
73	1.0	1650	470	597	1461
73	1.0	1683	446	543	1447
73	1.0	1580	462	611	1549

Ascending series

73	10.0	989	903	656	1284
73	1.0	1843	416	630	1347
73	1.0	1277	533	495	1000
73	8.0	1080	1065	706	1142
73	1.0	1506	518	396	1585
73	1.0	1157	893	696	1489
73	6.0	295	310	6235	273
73	1.0	366	54	189	220
73	1.0	1032	167	523	922
73	5.0	914	1155	944	1287

73	1.0	750	608	634	866
73	1.0	1251	530	692	1191
73	1.0	1069	426	456	1081
73	4.0	535	724	714	1180
73	1.0	1034	743	360	1212
73	3.5	1088	814	836	841
73	1.0	1138	209	426	940
73	3.0	829	789	687	940
73	1.0	1333	760	948	1402
73	2.5	731	902	1529	1095
73	1.0	1317	401	513	1515
73	2.0	1218	931	986	911
73	1.0	1481	550	658	1269
73	1.8	1066	874	756	1126
73	1.0	1315	510	363	1660
73	1.6	1376	654	555	1499
73	1.0	1592	391	230	1596
73	1.0	1362	569	457	1512
73	1.4	1003	819	515	1089
73	1.0	1296	556	385	1669
73	1.0	1401	462	370	1595
73	1.0	1254	222	478	990
73	1.2	1365	290	277	1615
73	1.0	1265	439	511	1682

Descending series

74	1.0	1814	35	113	1572
74	1.0	1859	26	304	1420
74	1.0	1802	70	294	1361
74	1.0	1867	76	450	1190
74	1.0	1780	104	180	1265
74	1.2	1880	167	48	1501
74	1.0	1827	153	27	1588
74	1.4	1903	100	23	1586
74	1.0	2064	208	0	1402
74	1.6	1827	159	14	1422
74	1.0	1709	337	53	1417
74	1.8	1671	332	83	1467
74	1.0	1909	144	0	1591
74	2.0	1799	249	102	1539
74	1.0	1898	104	89	1700
74	2.5	1481	443	582	1154
74	1.0	1765	50	80	1725
74	1.0	1835	46	261	1590
74	3.0	940	602	474	852
74	1.0	1530	118	308	1105
74	1.0	1568	112	331	1189
74	3.5	777	684	626	938
74	1.0	1291	201	208	875
74	1.0	1604	29	315	1040
74	1.0	1500	15	316	1061
74	4.0	1067	723	659	960
74	1.0	1417	24	193	1113
74	5.0	589	545	593	480
74	1.0	1047	119	634	662

74	1.0	1686	44	239	1090
74	6.0	812	634	625	779
74	1.0	1522	48	409	859
74	8.0	880	620	602	825
74	1.0	1514	47	254	1087
74	1.0	1521	0	370	1131
74	1.0	1518	6	351	1051
74	10.0	836	759	911	751
74	1.0	1452	77	487	918
74	1.0	1389	119	50	1032
74	1.0	1455	35	239	1109

Ascending series

74	10.0	1034	543	522	943
74	1.0	1465	30	221	1171
74	1.0	1535	50	298	1065
74	8.0	525	353	327	485
74	1.0	1472	18	142	1006
74	1.0	1367	54	314	1041
74	6.0	878	621	809	680
74	1.0	1437	37	525	1124
74	1.0	690	72	14	462
74	1.0	754	37	117	557
74	5.0	606	713	747	697
74	1.0	882	39	326	579
74	1.0	1300	29	284	1031
74	4.0	543	314	346	570
74	1.0	1221	107	157	816
74	3.5	818	667	621	782
74	1.0	1274	77	256	1039
74	3.0	847	607	818	689
74	1.0	1039	58	208	549
74	2.5	897	552	695	764
74	1.0	1513	18	244	1128
74	2.0	1352	186	196	1162
74	1.0	1583	9	214	1142
74	1.8	1412	194	414	934
74	1.0	1650	31	202	1253
74	1.6	1563	177	443	1234
74	1.0	1637	28	489	1061
74	1.0	1597	37	311	1310
74	1.4	1277	104	396	874
74	1.0	1541	53	586	1096
74	1.0	1254	59	352	909
74	1.-	1445	196	355	1105
74	1.0	1390	79	90	1036
74	1.2	1585	28	124	1107
74	1.0	1626	46	235	1102

Descending series

75	1.0	1813	216	73	1833
75	1.0	1711	95	67	1765
75	1.0	1853	48	114	1879
75	1.0	1616	28	57	1681
75	1.0	1549	77	43	1775
75	1.2	1807	35	95	1456

75	1.0	1592	80	85	1776
75	1.4	1783	52	73	1769
74	1.0	1777	93	79	1813
75	1.6	1895	68	100	2033
75	1.0	1687	61	88	2013
75	1.8	1839	26	19	1940
75	1.0	1879	52	45	1917
75	2.0	1777	111	0	1973
75	1.0	1718	8	15	1976
75	2.5	1655	325	128	1973
75	1.0	1597	27	44	2021
75	1.0	1643	21	20	2271
75	3.0	1142	605	332	1743
75	1.0	1674	22	107	2003
75	1.0	1757	4	54	2165
75	3.5	1185	810	708	1271
75	1.0	1873	0	280	2016
75	1.0	1781	0	426	1770
75	1.0	1750	39	243	1706
75	4.0	1005	956	784	1151
75	1.0	2005	18	213	1986
75	5.0	925	1045	747	1210
75	1.0	1717	35	316	1964
75	1.0	1715	17	151	1434
75	6.0	805	959	890	1017
75	1.0	1818	9	54	1893
75	8.0	882	937	626	1256
75	1.0	1691	0	79	1843
75	1.0	1734	0	222	1735
75	1.0	1815	22	183	1606
75	10.0	1050	780	768	1160
75	1.0	1830	111	295	1633
75	1.0	1729	202	378	1650
75	1.0	1968	0	83	1686
Ascending series					
75	10.0	806	1108	592	1401
75	1.0	1829	0	94	1607
75	1.0	1972	10	33	1669
75	8.0	793	524	373	900
75	1.0	1749	0	167	2005
75	1.0	1752	0	254	1729
75	6.0	887	989	887	1091
75	1.0	2235	0	95	1680
75	1.0	620	0	48	570
75	1.0	464	0	72	738
75	5.0	1078	1027	996	1057
75	1.0	1905	28	128	1956
75	1.0	1773	30	77	1781
75	4.0	1498	670	805	1410
75	1.0	1551	0	31	1318
75	3.5	1311	778	969	1125
75	1.0	2007	0	202	1719
75	3.0	1368	612	689	1304
75	1.0	2292	9	127	1897
75	2.5	2104	329	563	1457

75	1.0	2085	11	84	1911
75	2.0	2158	94	267	1562
75	1.0	2130	11	133	1767
75	1.8	2171	25	118	1507
75	1.0	1772	49	127	1724
75	1.6	2106	4	134	1642
75	1.0	2022	35	42	1757
75	1.0	2020	17	184	1726
75	1.4	1954	87	132	1976
75	1.0	2075	27	34	1989
75	1.0	2157	0	153	1806
75	1.0	1722	49	210	1655
75	1.2	1760	24	103	1710
75	1.0	1849	47	158	1725

Descending series

76	1.0	1655	96	33	1257
76	1.0	1667	25	10	1409
76	1.0	1638	68	5	1324
76	1.0	1564	47	26	1278
76	1.0	1512	58	14	1258
76	1.2	1454	81	15	1380
76	1.0	1474	52	10	1315
76	1.4	1528	121	0	1340
76	1.0	1565	48	26	1329
76	1.6	1459	102	34	1417
76	1.0	1467	23	8	1345
76	1.8	1289	210	60	1374
76	1.0	1321	95	8	1351
76	2.0	1114	427	71	1357
76	1.0	1465	102	24	1442
76	2.5	981	575	169	1306
76	1.0	1406	24	61	1343
76	1.0	1533	7	26	1311
76	3.0	1044	508	276	1135
76	1.0	1369	55	29	1386
76	1.0	1229	68	51	1507
76	3.5	900	640	272	1193
76	1.0	1550	67	63	1516
76	1.0	1397	61	25	1262
76	1.0	1235	110	52	1237
76	4.0	716	784	406	1013
76	1.0	1414	13	99	1159
76	5.0	1045	861	807	809
76	1.0	1469	49	93	1326
76	1.0	1237	12	182	1225
76	6.0	639	761	415	918
76	1.0	1478	0	92	1126
76	8.0	680	689	415	936
76	1.0	1385	39	93	1138
76	1.0	1335	5	132	1185
76	1.0	1297	158	73	1093
76	10.0	719	770	561	844
76	1.0	1313	155	208	1108
76	1.0	1347	112	293	1059

76	1.0	1347	47	54	1151
Ascending series					
76	10.0	752	732	451	909
76	1.0	1382	89	61	1206
76	1.0	1484	0	138	1163
76	8.0	837	589	444	909
76	1.0	1292	69	105	1134
76	1.0	1241	122	68	1353
76	6.0	589	778	533	875
76	1.0	1363	0	83	1259
76	1.0	1237	115	91	1163
76	1.0	991	159	107	834
76	5.0	529	814	544	779
76	1.0	1317	27	115	1173
76	1.0	1290	91	64	1153
76	4.0	735	690	417	898
76	1.0	1318	54	120	1173
76	3.5	737	717	485	855
76	1.0	1305	93	84	1213
76	3.0	958	552	472	982
76	1.0	1265	76	99	1175
76	2.5	958	521	277	1089
76	1.0	1529	104	79	1332
76	2.0	1067	450	75	1218
76	1.0	1306	15	46	1200
76	1.8	1274	152	48	1196
76	1.0	1378	14	16	1235
76	1.6	1409	113	101	1228
76	1.0	957	68	21	905
76	1.0	1519	32	21	1448
76	1.0	1432	49	21	1336
76	1.4	1365	146	9	1330
76	1.0	1300	81	10	1296
76	1.0	1374	70	56	1240
76	1.0	1242	48	5	1128
76	1.2	1140	137	14	1163
76	1.0	1180	126	41	1240

Appendix 3

Latencies of correct responses to the left key (CorL) and incorrect responses to the right key on a grating trial (IncR), incorrect responses to the left key (IncL) and correct responses to the right key on a grey stimulus trial (CorR), measured in 0.10 sec, for all hens, for the descending and ascending series of probes for Experiment 1.1.

Descending series					Ascending series			
Probe	CorL	IncR	IncL	CorR	CorL	IncR	IncL	CorR
Hen 71								
1.0	12	10	6	11	8	11	8	9
1.2	13	11	9	11	9	10	9	8
1.4	13	12	27	11	11	14	14	10
1.6	12	12	14	11	10	11	9	8
1.8	13	22	12	13	10	9	9	8
2.0	12	11	13	12	10	10	10	9
2.5	15	12	14	12	10	10	10	10
3.0	12	14	14	14	10	8	8	9
3.5	15	14	15	13	9	10	10	9
4.0	12	10	11	11	10	9	12	9
5.0	11	10	14	10	9	8	9	8
6.0	12	10	11	10	10	10	10	10
8.0	9	11	10	10	10	9	10	9
10.0	11	10	11	10	11	13	16	10
Hen 72								
1.0	15	12	15	10	14	12	12	8
1.2	13	15	13	10	15	7	9	8
1.4	14	*	14	10	15	9	*	8
1.6	14	10	12	10	14	8	12	9
1.8	13	11	14	10	16	8	20	9
2.0	12	10	12	11	13	9	12	10
2.5	13	10	12	10	14	10	11	9
3.0	14	9	13	9	16	8	15	8
3.5	12	11	12	10	14	8	15	9
4.0	13	8	11	9	14	9	14	9
5.0	12	10	14	9	15	9	16	9
6.0	12	9	12	9	12	10	13	9
8.0	16	9	14	9	14	8	15	9
10.0	16	9	16	10	13	9	15	9

* no responses

Appendix 3 cont...

Probe	Descending series				Ascending series			
	CorL	IncR	IncL	CorR	CorL	IncR	IncL	CorR
Hen 73								
1.0	13	12	11	10	11	17	14	16
1.2	12	12	13	14	11	11	10	13
1.4	16	13	14	14	12	17	13	13
1.6	15	13	14	12	13	14	13	14
1.8	15	12	18	14	14	14	16	12
2.0	12	14	12	15	14	18	13	15
2.5	15	13	13	13	14	17	33	19
3.0	14	14	12	15	15	18	16	16
3.5	13	20	16	21	24	25	18	27
4.0	13	12	12	11	14	22	24	29
5.0	14	13	15	13	16	17	16	19
6.0	15	15	17	14	13	15	271	12
8.0	26	14	13	13	18	16	14	16
10.0	15	18	14	16	14	13	12	15
Hen 74								
1.0	12	9	10	9	11	9	9	9
1.2	14	11	10	10	10	9	10	8
1.4	15	9	12	11	13	9	10	12
1.6	15	9	14	10	11	10	10	10
1.8	16	8	14	11	10	9	10	8
2.0	15	8	17	10	7	8	9	9
2.5	15	10	14	11	12	9	12	10
3.0	16	11	14	11	12	9	13	9
3.5	12	11	15	11	10	10	11	9
4.0	12	9	11	9	12	10	14	11
5.0	14	9	13	9	10	9	12	9
6.0	13	9	12	10	11	9	11	9
8.0	11	7	9	8	11	9	11	9
10.0	10	11	11	11	12	9	11	9
Hen 75								
1.0	10	11	9	11	12	12	10	12
1.2	11	12	14	13	11	8	10	12
1.4	12	9	18	11	13	22	19	13
1.6	12	11	13	13	13	4	12	11
1.8	12	7	6	12	14	8	9	10
2.0	12	12	*	13	15	12	12	12
2.5	13	13	11	14	17	11	14	13
3.0	10	12	11	13	13	13	14	12
3.5	12	13	12	12	13	13	13	14
4.0	11	13	11	13	16	13	14	15
5.0	12	13	11	13	14	13	14	13
6.0	12	10	13	11	12	12	13	12
8.0	12	11	11	12	14	10	13	11
10.0	12	11	12	13	13	12	13	13

Appendix 3 cont...

Probe	Descending series				Ascending series			
	CorL	IncR	IncL	CorR	CorL	IncR	IncL	CorR
Hen 76								
1.0	10	7	14	8	8	8	10	8
1.2	10	8	8	9	8	9	7	7
1.4	10	9	0	8	9	9	9	8
1.6	10	8	11	9	10	8	11	8
1.8	9	8	10	8	9	8	10	8
2.0	10	8	9	8	10	8	8	8
2.5	10	8	11	8	10	8	10	9
3.0	10	8	10	8	10	8	10	8
3.5	10	8	9	9	10	8	9	8
4.0	10	8	10	7	10	8	9	8
5.0	14	4	12	12	10	7	9	8
6.0	10	8	10	8	10	10	10	10
8.0	10	8	9	8	10	8	9	8
10.0	10	9	9	8	10	9	9	8

Appendix 4

The hen number, the grating value (Gtg), the number of correct left (CLR) and correct right (CRR) responses to the red key on grating trials, incorrect left (INLG) and right (INRG) responses to the green key on grating trials, incorrect left (INLR) and right (INRR) responses to the red key on grey stimulus trials, and correct left (CLG) and right (CRG) responses to the green key on grey stimulus trials, the number of reinforcements for responses to the red (R) and green (G) keys, and the number of reinforcements for responses to the left (L) and right (R) keys. Headings are shown for each experiment and for conditions within each experiment. Data for the last five days of training prior to each probe series are also shown.

Hen	Gtg	Grating Trials				Grey Trials				R	G	L	R
		Red	Green	Red	Green	Red	Green	Red	Green				
CLR	CRR	INLG	INRG	INLR	INRR	CLG	CRR						
Experiment 2.1													
Descending series													
31	1.0	60	58	18	14	14	23	52	62	20	22	16	26
31	1.0	58	44	31	15	11	19	55	61	21	19	27	13
31	1.0	6	17	5	17	6	14	9	17	5	8	4	9
31	1.0	49	44	26	18	15	20	48	54	21	21	20	22
31	1.0	41	42	27	26	18	21	48	51	19	17	16	20
31	1.2	53	34	32	13	30	21	43	35	19	18	21	16
31	1.0	47	45	26	23	16	20	51	55	22	21	24	19
31	1.4	41	45	19	22	19	9	55	45	20	20	27	13
31	1.0	42	38	25	22	15	20	44	49	21	22	19	24
31	1.0	42	41	22	22	13	20	44	50	19	19	19	19
31	1.6	13	31	18	35	8	26	24	41	14	13	10	17
31	1.0	48	34	31	19	27	9	56	39	19	20	16	23
31	1.0	54	36	28	9	28	18	45	36	20	19	20	19
31	1.8	32	31	33	31	31	22	40	32	18	20	23	15
31	1.0	54	39	29	12	22	25	42	45	20	17	20	17
31	2.0	56	45	31	19	41	28	47	34	18	17	17	18
31	1.0	57	52	19	13	18	17	53	52	22	21	18	25
31	2.5	39	28	42	30	26	31	41	45	17	18	21	14
31	1.0	50	46	21	16	13	17	49	53	18	20	17	21
31	3.0	32	32	37	38	40	25	45	30	17	16	22	11
31	1.0	50	44	23	20	21	20	48	48	19	19	22	16
31	3.5	25	31	40	46	31	30	40	40	18	17	12	23
31	1.0	45	41	28	23	22	30	39	47	21	20	24	17
31	1.0	40	48	21	28	18	17	42	51	20	19	19	20
31	1.0	47	37	30	18	32	16	49	35	20	22	26	16
31	1.0	52	32	32	13	22	19	46	43	19	20	22	17
31	1.0	51	46	21	14	13	22	44	51	20	20	19	21
31	4.0	36	26	42	31	37	19	50	31	18	17	27	8
31	1.0	57	42	23	10	20	14	51	46	21	18	28	11
31	5.0	41	23	47	28	35	20	49	34	17	17	21	13
31	1.0	41	37	19	15	14	12	43	42	19	18	17	20
31	6.0	40	17	46	22	28	22	42	35	17	17	26	8
31	1.0	52	36	28	13	26	17	48	39	19	21	25	15
31	8.0	42	20	46	23	32	21	46	33	17	17	19	15
31	1.0	47	42	25	22	16	24	44	51	19	19	21	17
31	1.0	41	42	25	24	15	16	50	51	19	20	21	18

31	1.0	39	39	23	23	20	22	41	43	17	17	15	19
31	1.0	44	45	23	23	14	16	54	55	20	20	22	18
31	1.0	43	40	26	28	19	10	54	46	20	20	23	17
31	10.0	37	27	44	37	17	20	51	54	18	20	22	16
Ascending series													
31	1.0	35	52	15	33	16	15	52	52	19	18	16	21
31	1.0	44	39	26	21	26	18	46	38	22	19	27	14
31	1.0	32	47	17	33	13	18	47	52	19	19	16	22
31	1.0	41	35	29	25	17	22	44	49	19	17	16	20
31	1.0	48	39	28	20	14	24	43	54	19	19	20	18
31	1.0	46	30	33	17	24	17	47	40	20	20	26	14
31	10.0	36	28	33	26	32	18	44	29	17	19	21	15
31	1.0	54	34	30	10	23	25	39	41	19	19	25	13
31	1.0	40	35	23	20	18	13	45	41	19	19	21	17
31	1.0	35	37	24	28	26	19	43	36	19	18	24	13
31	8.0	28	28	35	36	19	22	41	45	17	17	20	14
31	1.0	47	35	33	20	23	25	41	44	20	19	27	12
31	1.0	37	43	24	29	19	26	42	47	18	21	22	17
31	1.0	49	39	26	15	23	23	41	41	20	20	21	19
31	1.0	50	43	25	20	16	27	42	52	20	20	10	24
31	1.0	44	42	24	21	25	15	50	39	21	20	25	16
31	6.0	21	32	21	30	19	26	25	34	15	16	12	19
31	1.0	35	39	21	23	14	25	33	46	19	18	18	19
31	1.0	40	50	9	18	15	24	35	44	19	16	20	15
31	1.0	41	45	21	24	15	26	40	51	19	19	19	19
31	5.0	39	36	31	27	37	32	37	30	16	17	18	15
31	1.0	48	48	16	16	26	31	33	38	20	21	20	21
31	1.0	60	46	20	8	31	19	47	35	19	19	28	10
31	1.0	56	38	24	4	22	16	47	39	19	20	23	16
31	1.0	58	39	26	6	21	29	35	43	20	19	18	21
31	4.0	31	35	34	39	24	32	37	44	18	16	13	21
31	1.0	40	49	19	28	16	32	35	53	18	16	15	19
31	1.0	37	46	20	30	12	30	36	54	19	17	17	19
31	1.0	37	54	8	22	10	27	33	50	20	20	17	23
31	1.0	44	40	22	18	20	33	29	42	19	19	19	19
31	1.0	39	50	12	23	15	25	34	47	19	17	16	20
31	3.5	32	35	22	27	27	32	29	31	17	18	16	19
31	1.0	37	51	15	28	27	28	38	38	18	19	17	20
31	1.0	25	43	20	37	20	34	27	42	18	16	12	22
31	1.0	33	43	16	27	13	25	33	46	19	19	17	21
31	1.0	40	42	21	23	8	29	34	55	18	21	14	25
31	3.0	26	37	28	38	21	22	44	43	18	17	18	17
31	1.0	38	49	12	25	9	30	32	54	19	18	14	23
31	1.0	29	44	13	29	11	39	20	47	17	18	12	23
31	1.0	39	50	13	24	10	37	27	53	19	20	19	20
31	1.0	29	56	7	33	10	35	28	5	18	18	11	25
31	1.0	34	38	16	20	20	29	26	34	19	18	19	18
31	2.5	24	44	19	39	24	33	29	40	17	16	12	21
31	1.0	46	50	14	18	23	37	27	41	18	19	17	20
31	1.0	51	44	20	14	22	37	27	43	19	19	16	22
31	1.0	41	49	14	22	13	34	28	50	20	18	15	23
31	1.0	40	54	9	23	12	25	37	50	19	19	16	22
31	1.0	42	50	12	18	14	18	44	48	20	19	19	20
31	2.0	26	27	25	37	19	37	27	43	17	18	14	21
31	1.0	36	48	9	21	7	19	38	49	19	21	15	25

31	1.0	36	40	18	25	11	15	45	50	18	17	14	21
31	1.8	23	40	21	39	15	22	39	47	19	18	18	19
31	1.0	34	49	13	25	10	24	36	15	19	22	15	26
31	1.0	45	46	17	19	16	25	38	48	21	17	20	18
31	1.0	37	47	16	25	20	18	45	43	20	21	15	26
31	1.6	42	37	31	25	19	37	30	50	21	18	18	21
31	1.0	51	56	6	12	19	17	44	44	22	18	21	19
31	1.0	40	46	11	17	7	25	32	49	17	17	11	23
31	1.0	45	48	10	15	7	18	40	53	22	19	17	24
31	1.4	36	54	9	28	24	32	31	39	18	17	12	23
31	1.0	42	38	17	12	16	23	31	39	19	20	19	20
31	1.0	39	45	13	19	15	23	35	44	20	20	17	23
31	1.0	48	52	12	16	12	25	39	51	19	19	12	26
31	1.0	40	47	15	23	22	40	42	31	18	19	18	19
31	1.2	46	44	22	21	23	30	35	42	18	20	20	18
31	1.0	40	47	15	23	22	40	42	41	18	19	18	19

Experiment 2.2

FR5

31	1.0	25	36	8	19	2	6	37	43	18	17	13	22
31	1.0	29	35	9	17	7	10	34	37	18	21	16	23
31	1.0	25	39	4	17	3	9	35	39	19	16	11	24
31	1.0	26	37	4	14	4	16	24	36	16	16	8	24
31	1.0	28	30	12	13	5	8	33	37	16	18	18	16
31	2.0	11	31	4	22	14	23	10	20	12	13	7	18
31	3.0	11	23	16	16	11	26	13	27	15	13	10	18
31	4.0	6	29	5	31	6	22	13	30	13	12	2	23
31	6.0	8	37	14	41	5	36	14	45	16	16	4	28
31	8.0	11	39	13	42	11	29	24	41	16	16	7	25
31	10.0	15	36	17	37	8	31	20	44	16	16	11	21

FR1

31	1.0	55	61	16	23	17	19	56	60	19	21	18	22
31	1.0	58	59	19	17	24	17	60	53	21	20	22	19
31	1.0	50	63	14	24	18	14	62	59	21	21	20	22
31	1.0	50	63	10	25	13	21	53	60	21	22	22	21
31	1.0	42	64	10	31	14	23	52	59	20	21	19	22

FR10

31	1.0	21	25	2	4	3	6	19	24	15	16	12	19
31	1.0	15	22	2	9	8	9	15	16	13	13	10	16
31	1.0	1	7	1	6	1	6	1	5	3	3	0	6
31	1.0	17	22	5	9	5	5	22	23	13	14	13	14
31	1.0	15	23	1	9	1	11	14	23	14	15	11	18
31	2.0	3	17	4	20	3	16	6	21	12	10	3	19
31	3.0	1	10	3	11	5	11	0	8	5	5	1	9
31	4.0	3	21	6	24	4	18	10	24	12	10	3	19
31	6.0	6	22	10	26	1	25	7	30	14	14	6	22
31	8.0	24	1	26	3	18	1	25	9	11	11	22	1
31	10.0	13	6	15	5	13	0	19	8	10	11	15	6

FR1

31	1.0	40	63	4	25	22	34	32	43	19	18	13	24
31	1.0	36	51	12	28	24	31	33	40	19	19	18	20
31	1.0	45	54	7	18	14	24	37	47	19	20	15	24
31	1.0	35	61	7	34	15	33	36	53	20	19	21	18
31	1.0	51	59	7	14	25	25	41	42	17	18	11	24
31	1.0	43	60	1	16	28	33	29	32	21	17	11	26

Experiment 2.3

High luminance

31	1.0	28	37	5	15	3	5	36	40	19	18	19	18
31	1.0	30	38	5	12	1	3	38	41	19	21	15	25
31	1.0	33	41	3	9	3	4	40	40	19	19	16	22
31	1.0	37	27	15	4	12	1	40	30	19	19	18	20
31	1.0	46	44	5	2	7	5	44	43	20	21	22	19
31	2.0	21	17	21	19	16	11	29	23	12	12	16	8
31	3.0	16	25	17	26	8	17	23	33	15	14	8	21
31	4.0	8	16	16	24	5	16	16	20	12	10	8	14
31	6.0	27	25	25	22	20	22	26	30	16	16	17	15
31	8.0	20	33	18	31	19	30	31	32	16	15	11	20
31	10.0	28	32	13	19	19	25	20	27	14	15	11	18

Low luminance

31	1.0	12	22	6	16	2	5	22	27	15	14	9	2
31	1.0	24	37	4	17	2	9	32	39	19	17	12	24
31	1.0	20	29	4	14	1	9	24	32	19	18	14	23
31	1.0	23	36	2	13	3	10	28	36	18	19	16	21
31	1.0	26	40	0	15	5	12	28	37	16	17	6	27
31	2.0	0	4	1	7	0	7	0	6	2	3	0	5
31	3.0	5	16	14	25	3	17	13	27	10	11	5	16
31	4.0	9	26	9	28	8	29	9	29	11	12	4	19
31	6.0	2	38	8	45	5	37	10	40	14	13	3	24
31	8.0	6	25	21	41	7	38	14	39	14	15	5	24
31	10.0	9	37	3	30	6	33	6	34	15	15	3	27

Experiment 2.4

Descending series

31	1.0	33	36	8	9	8	11	31	35	19	23	25	17
31	1.0	40	36	9	5	7	7	36	36	21	24	26	19
31	1.0	38	32	11	5	11	4	40	32	21	24	27	18
31	1.0	43	36	7	3	16	2	42	28	28	17	29	16
31	1.0	13	14	18	21	6	5	28	27	9	26	18	17
31	1.0	35	32	8	5	6	3	38	35	23	21	26	18
31	2.0	14	13	21	22	4	11	22	29	13	28	20	21
13	3.0	17	27	19	26	12	23	23	34	16	24	15	25
31	4.0	5	6	5	6	1	9	4	10	6	6	5	7
31	6.0	3	5	5	10	4	6	4	7	5	5	3	7
31	8.0	8	28	13	33	4	23	19	37	13	28	9	32
31	10.0	10	14	19	23	7	8	24	25	10	25	19	16

Ascending series

31	1.0	9	15	1	7	6	7	9	10	12	9	8	13
31	2.0	6	10	6	9	4	9	7	12	9	8	2	15
31	3.0	11	22	17	28	8	19	18	31	16	21	14	23
31	4.0	12	28	12	27	4	19	20	35	16	19	10	25
31	6.0	1	19	7	27	6	15	10	21	15	15	7	23
31	8.0	12	26	12	24	10	25	13	27	17	19	0	26
31	10.0	5	27	11	30	2	25	13	35	15	23	11	27

Experiment 2.1

Descending series

32	1.0	63	56	20	10	10	0	73	65	21	20	23	18
32	1.0	69	62	12	4	16	2	70	57	23	21	23	21
32	1.0	67	58	13	4	12	5	67	59	21	23	20	24
32	1.0	67	55	17	5	11	2	70	61	21	22	22	21

32	1.0	64	64	9	8	6	3	70	66	21	22	19	14
32	1.2	50	65	6	21	2	10	60	69	22	21	18	25
32	1.0	51	72	4	23	2	7	68	73	23	19	18	24
32	1.4	46	64	8	25	8	16	56	64	22	20	18	24
32	1.0	43	67	3	24	1	6	64	68	20	22	12	30
32	1.0	51	67	1	15	4	4	62	64	20	23	19	24
32	1.6	5	54	8	58	0	24	38	63	17	20	0	28
32	1.0	2	57	8	65	0	8	58	65	19	18	11	26
32	1.0	59	63	2	8	9	6	61	58	20	22	21	21
32	1.8	54	44	32	22	26	11	64	50	22	19	21	20
32	1.0	65	63	7	5	18	5	65	52	22	23	23	22
32	2.0	52	42	32	22	33	10	62	40	20	22	25	17
32	1.0	69	71	3	5	11	7	67	63	22	21	21	22
32	2.5	35	41	35	44	32	31	47	45	18	17	16	19
32	1.0	63	67	2	7	11	8	59	58	21	19	23	17
32	3.0	31	38	37	46	28	28	48	47	17	20	18	19
32	1.0	50	64	0	12	11	15	48	52	21	21	18	24
32	3.5	20	35	42	56	20	40	38	57	17	17	10	24
32	1.0	64	70	2	8	5	20	52	67	22	19	17	24
32	1.0	61	68	2	11	3	12	59	69	22	20	15	27
32	1.0	60	70	2	13	3	8	66	70	23	21	18	26
32	1.0	64	72	0	8	7	5	67	65	21	20	20	21
32	1.0	61	70	4	12	2	3	70	73	23	21	19	25
32	4.0	38	32	44	36	35	18	56	42	18	18	24	12
32	1.0	68	70	5	9	10	4	72	67	20	24	21	23
32	5.0	43	10	62	29	47	11	62	27	17	18	29	6
32	1.0	71	73	5	5	25	9	66	52	22	20	23	19
32	6.0	55	26	49	20	50	28	46	25	17	17	27	7
32	1.0	64	69	2	5	14	8	60	56	21	22	21	22
32	8.0	40	31	43	33	40	13	60	32	22	18	23	17
32	1.0	66	73	1	10	9	7	67	64	21	24	20	25
32	1.0	70	70	3	4	31	14	59	42	21	21	19	23
32	1.0	63	65	5	5	23	20	49	46	20	19	17	22
32	1.0	60	68	4	12	12	8	64	59	22	22	19	25
32	1.0	67	72	6	12	13	6	72	66	22	21	23	20
32	10.0	44	23	52	31	31	16	60	46	19	19	24	14
Ascending series													
32	1.0	68	58	15	6	19	6	70	55	22	22	26	18
32	1.0	66	69	5	6	20	3	69	53	22	20	23	19
32	1.01	64	58	10	6	20	2	67	47	20	21	25	16
32	1.0	65	62	9	7	16	8	64	55	21	21	19	23
32	1.0	61	56	15	10	10	0	71	59	22	22	21	23
32	1.0	63	57	13	6	13	5	62	56	20	20	18	22
32	1.0	67	61	11	5	11	1	70	60	22	22	27	17
32	10.0	56	40	49	15	58	19	49	12	16	16	23	9
32	1.0	60	55	9	4	20	3	62	44	20	23	24	19
32	1.0	67	61	4	1	9	6	61	56	22	20	15	27
32	1.0	68	60	9	3	15	6	62	55	21	20	21	20
32	8.0	20	36	38	53	26	28	45	48	18	16	19	15
32	1.0	71	68	4	2	13	11	61	61	23	20	17	26
32	1.0	61	62	7	8	11	14	55	59	19	21	19	21
32	1.0	63	73	0	9	10	10	63	64	21	21	16	26
32	1.0	64	67	5	8	12	8	65	60	23	20	25	18
32	1.0	68	63	6	2	10	2	65	58	20	23	22	21
32	6.0	56	23	49	17	52	17	57	21	19	20	24	15

32	1.0	59	55	12	8	19	4	64	50	20	20	20	20
32	1.0	70	61	7	0	18	1	68	51	22	21	21	22
32	1.0	62	59	6	5	23	4	63	44	22	21	22	21
32	5.0	52	26	50	21	50	29	46	25	17	17	21	13
32	1.0	69	68	4	1	22	4	65	48	23	21	21	23
32	1.0	65	68	2	3	29	11	59	41	22	21	24	19
32	1.0	64	60	5	1	11	5	59	53	21	20	22	19
32	1.0	55	59	4	9	14	12	52	49	20	20	20	20
32	4.0	29	31	36	39	20	23	46	46	16	17	13	20
32	1.0	57	68	1	9	6	4	65	63	22	22	15	29
32	1.0	57	61	9	12	8	2	67	61	21	22	26	17
32	1.0	55	64	2	14	7	4	63	62	19	20	13	26
32	1.0	55	64	6	12	9	8	61	61	21	22	18	25
32	1.0	51	64	5	17	4	3	67	64	22	22	18	26
32	3.5	16	32	34	50	8	25	39	57	20	17	12	25
32	1.0	60	64	4	8	5	10	59	63	20	22	24	18
32	1.0	49	67	4	20	4	7	60	66	20	22	18	24
32	1.0	52	67	3	19	2	11	60	68	21	22	13	30
32	1.0	47	61	6	20	8	6	62	59	22	22	23	21
32	3.0	22	40	30	45	14	36	33	55	19	18	8	29
32	1.0	33	42	3	14	3	11	34	41	13	12	6	19
32	1.0	54	63	5	16	4	26	43	65	21	20	18	23
32	1.0	42	56	4	16	10	17	41	49	19	17	16	20
32	1.0	46	56	15	26	5	16	56	66	21	20	20	21
32	1.0	48	60	7	21	7	20	47	61	21	18	16	23
32	2.5	24	42	28	46	20	31	37	51	17	21	17	21
32	1.0	51	57	13	17	5	18	49	64	21	20	17	24
32	1.0	49	61	4	17	4	18	49	62	20	21	15	26
32	1.0	45	55	10	21	7	17	50	58	20	21	20	21
32	1.0	50	60	3	19	7	24	42	59	18	20	13	25
32	1.0	52	64	6	16	5	17	51	64	20	20	16	24
32	1.0	47	53	12	20	3	9	57	62	21	21	18	24
32	2.0	13	48	6	42	3	36	18	51	16	18	4	30
32	1.0	46	63	2	20	6	29	38	59	18	21	14	25
32	1.0	48	56	6	11	6	14	48	56	20	21	17	24
32	1.8	19	61	6	47	12	43	24	55	20	19	12	27
32	1.0	50	61	5	16	4	11	54	63	21	23	21	23
32	1.0	47	62	6	20	5	8	58	61	19	22	19	22
32	1.0	50	62	5	15	1	15	50	65	21	21	13	29
32	1.6	23	52	16	45	1	28	39	67	19	21	12	28
32	1.0	36	55	7	27	2	12	50	61	19	20	16	23
32	1.0	42	52	13	22	2	14	52	62	20	20	13	27
32	1.0	42	51	7	18	5	10	51	54	19	20	12	27
32	1.4	34	50	6	22	3	10	47	53	20	21	17	24
32	1.0	46	40	16	10	11	5	51	45	20	17	17	20
32	1.0	46	46	9	8	7	13	42	49	18	21	15	24
32	1.0	47	43	13	8	10	8	48	46	19	17	18	18
32	1.2	57	38	22	5	17	1	61	43	20	20	25	15
32	1.0	60	44	16	2	18	1	61	42	21	21	27	15

Experiment 2.2

FR

32	1.0	39	35	3	1	2	0	39	37	18	21	21	18
32	1.0	37	3	9	5	2	2	0	41	20	17	15	22
32	1.0	37	37	5	5	1	1	40	40	19	19	21	17

32	1.0	40	34	7	1	9	0	40	31	18	19	24	13
32	1.0	36	38	3	4	1	0	40	41	18	16	13	21
32	2.0	29	7	30	10	18	2	36	21	16	16	25	7
32	3.0	28	13	28	12	26	9	33	15	14	15	22	7
32	4.0	32	0	47	14	31	2	44	16	16	14	27	3
32	6.0	44	2	44	3	41	0	47	4	15	14	29	0
32	8.0	31	2	42	14	31	0	43	12	15	14	26	3
32	10.0	32	4	41	12	31	1	44	14	16	16	23	9
Return to FR1													
32	1.0	67	70	6	8	3	2	73	73	21	23	19	25
32	1.0	68	68	9	9	4	5	73	74	22	22	15	29
32	1.0	66	63	17	13	3	4	75	76	22	22	20	24
32	1.0	68	64	13	9	4	7	70	73	22	23	21	24
32	1.0	66	64	14	10	8	6	71	70	22	22	22	22
FR10													
32	1.0	24	26	5	7	5	0	30	27	14	16	15	15
32	1.0	24	28	2	7	5	0	31	26	16	17	17	16
32	1.0	30	29	1	0	8	1	30	23	15	15	15	15
32	1.0	20	23	8	10	2	4	24	28	17	16	12	21
32	1.0	30	30	1	2	2	3	28	30	17	16	18	15
32	2.0	13	9	18	13	11	7	21	17	11	10	11	10
32	3.0	21	8	15	3	16	9	15	7	10	10	13	7
32	4.0	16	3	26	11	14	4	24	14	11	13	18	6
32	6.0	23	0	26	6	19	0	26	8	11	11	21	1
32	8.0	16	0	23	7	13	0	23	9	9	10	17	2
32	10.0	17	8	22	14	18	5	25	13	11	11	16	6
Return to FR1													
32	1.0	76	65	16	6	3	7	74	78	22	22	19	25
32	1.0	58	68	14	23	7	11	71	74	21	22	20	23
32	1.0	77	79	3	3	6	8	73	75	23	20	17	26
32	1.0	72	71	12	9	12	9	74	72	21	22	20	23
32	1.0	72	73	7	8	6	4	75	74	21	24	28	17
Experiment 2.3													
High luminance													
32	1.0	41	44	0	1	0	0	43	43	19	19	18	20
32	1.0	40	42	1	3	1	0	43	41	18	19	15	22
32	1.0	48	47	1	0	0	0	48	48	20	22	19	23
32	1.0	44	44	0	1	4	1	42	39	19	17	18	18
32	1.0	48	40	0	1	0	2	47	48	20	21	17	24
32	2.0	12	21	29	37	5	1	47	45	14	16	10	20
32	3.0	12	24	23	36	6	7	41	42	14	15	13	16
32	4.0	18	17	29	26	14	17	29	32	15	14	13	16
32	6.0	19	15	33	29	22	14	34	25	14	14	17	11
32	8.0	25	13	37	23	25	14	34	24	15	15	22	8
32	10.0	25	15	34	25	5	4	44	43	15	16	18	13
Low luminance													
32	1.0	43	42	4	1	1	0	43	45	19	21	18	22
32	1.0	48	43	7	2	1	0	52	48	21	19	23	17
32	1.0	43	41	9	5	1	0	48	47	19	19	16	22
32	1.0	42	36	10	4	3	1	43	44	20	20	16	24
32	1.0	43	43	4	3	0	0	48	47	21	22	22	20
23	2.0	33	0	45	13	33	0	45	11	16	16	29	5
32	3.0	33	1	36	6	32	1	37	7	15	15	28	2
32	4.0	31	0	38	5	35	0	39	4	13	11	24	0

32	6.0	24	5	41	23	21	3	43	26	14	15	25	4
32	8.0	31	1	43	15	26	1	43	18	14	15	26	3
32	10.0	17	21	27	30	17	6	42	31	17	19	16	20

Experiment 2.4

Descending series

32	1.0	35	31	3	0	0	0	37	35	20	25	22	23
32	1.0	36	35	2	0	0	0	36	37	20	25	21	24
32	1.0	35	37	0	0	1	1	36	35	23	22	25	20
32	1.0	35	37	1	3	0	1	34	37	26	19	21	24
32	1.0	38	38	1	0	0	0	39	39	22	23	23	22
32	2.0	21	18	21	18	9	8	30	31	18	25	24	19
32	3.0	22	26	11	15	16	13	25	21	21	17	20	18
32	4.0	22	20	16	14	16	5	29	19	16	23	24	15
32	6.0	34	19	21	6	27	20	19	12	27	10	23	14
32	8.0	18	30	12	23	20	30	11	22	24	16	14	26
32	10.0	23	20	17	15	13	6	33	24	17	24	26	15

Ascending series

32	1.0	39	38	2	1	0	0	39	40	22	23	25	20
32	2.0	17	13	8	5	12	9	14	10	11	15	16	10
32	3.0	23	12	25	15	19	9	28	18	16	21	24	13
32	4.0	12	22	20	27	8	18	22	32	16	23	16	23
32	6.0	2	21	4	23	3	23	4	22	18	15	4	29
32	8.0	9	14	19	23	2	10	24	30	15	22	18	19
32	10.0	14	8	27	22	5	1	37	32	10	28	26	12

Experiment 2.1

Descending series

33	1.0	50	38	26	15	25	20	44	30	17	21	20	18
33	1.0	49	52	14	17	9	22	44	58	19	19	11	27
33	1.0	43	38	17	11	22	12	43	31	16	16	19	13
33	1.0	43	61	9	28	6	32	39	65	20	20	13	27
33	1.0	45	61	6	25	3	35	35	64	19	20	7	32
33	1.0	19	59	8	48	4	33	35	63	19	17	11	25
33	1.2	52	67	6	20	14	38	34	60	20	22	13	29
33	1.0	38	65	9	35	7	40	34	65	19	19	6	32
33	1.4	26	71	6	49	16	57	21	61	17	19	5	31
33	1.0	40	64	2	27	10	53	16	57	23	20	10	33
33	1.0	30	72	0	40	4	48	23	67	22	19	7	34
33	1.6	21	63	9	61	6	35	38	66	19	19	12	26
33	1.0	5	66	2	62	1	49	18	66	19	17	4	32
33	1.0	28	58	5	36	5	34	29	58	19	20	15	24
33	1.8	23	48	13	38	9	24	35	50	18	19	16	21
33	1.0	36	65	1	32	4	43	25	63	20	19	6	33
33	2.0	17	54	6	45	10	41	21	50	16	14	8	22
33	1.0	53	69	1	18	8	39	31	63	22	20	15	27
33	2.5	15	53	19	58	7	50	23	65	17	18	8	27
33	1.0	48	50	5	8	9	21	33	47	16	18	16	18
33	3.0	44	40	26	24	43	35	31	22	14	16	17	3
33	1.0	49	63	5	17	10	28	39	58	21	21	17	25
33	3.5	10	54	21	64	13	49	27	62	18	17	6	29
33	1.0	60	60	4	5	18	23	44	48	20	23	21	22
33	1.0	30	55	5	28	11	23	35	48	17	17	9	25
33	1.0	42	66	4	29	7	34	37	62	20	23	11	32
33	1.0	49	65	4	19	8	24	47	61	19	23	16	26

33	1.0	52	53	10	11	16	21	40	47	19	20	17	22
33	4.0	13	46	23	53	6	29	38	61	17	18	11	24
33	1.0	52	57	7	11	8	26	38	56	21	20	13	28
33	5.0	11	44	21	55	9	40	28	56	16	19	10	25
33	1.0	50	56	8	14	8	26	38	56	18	21	16	23
33	6.0	11	36	26	52	5	41	22	56	17	17	6	28
33	1.0	48	56	8	14	13	30	33	50	22	17	16	23
33	8.0	12	52	14	56	8	51	14	57	17	19	6	30
33	1.0	46	52	6	11	19	30	28	39	20	19	16	23
33	1.0	56	64	2	12	24	36	28	41	20	20	17	23
33	1.0	51	58	4	11	23	29	23	38	20	19	14	25
33	1.0	64	56	14	3	39	17	52	30	18	20	27	11
33	1.0	60	62	9	11	27	25	47	43	19	21	12	28
33	10.0	23	50	19	47	25	40	28	44	16	16	9	23
Ascending series													
33	1.0	51	56	8	13	20	26	38	44	20	22	14	28
33	1.0	44	61	3	19	23	23	40	41	20	20	16	24
33	1.0	28	62	7	40	10	25	41	57	21	17	12	26
33	1.0	38	50	8	20	16	31	27	42	20	20	16	24
33	1.0	50	58	8	17	13	17	49	54	21	20	20	21
33	1.0	37	65	4	29	16	24	42	52	22	19	12	29
33	1.0	3	62	67	15	15	23	44	54	19	21	19	21
33	10.0	16	53	18	55	18	51	19	52	16	17	3	30
33	1.0	47	57	4	15	15	19	42	47	18	20	20	18
33	1.0	51	54	9	11	18	12	51	45	19	21	21	19
33	1.0	50	58	4	13	17	21	41	45	19	21	16	24
33	8.0	9	55	15	61	8	50	18	61	17	20	5	32
33	1.0	45	60	3	18	15	34	29	49	19	20	13	26
33	1.0	45	62	1	17	11	29	34	51	20	20	13	17
33	1.0	43	60	1	18	16	24	16	24	19	19	13	25
33	1.0	47	61	6	22	16	30	37	52	21	20	17	24
33	1.0	35	59	4	28	14	27	35	49	18	20	12	26
33	6.0	21	49	21	49	9	49	21	62	18	16	7	27
33	1.0	43	66	0	23	9	35	31	57	21	22	11	32
33	1.0	53	66	0	11	13	23	42	52	20	21	15	26
33	1.0	41	60	1	20	5	12	47	55	21	18	18	21
33	5.0	8	42	20	56	7	44	20	56	16	16	8	24
33	1.0	49	32	0	11	10	19	42	51	20	21	21	20
33	1.0	40	56	1	17	23	20	39	33	19	19	19	19
33	1.0	45	56	1	11	16	11	45	40	22	20	20	22
33	1.0	48	60	1	13	15	22	39	46	20	19	16	23
33	4.0	3	56	12	68	11	64	7	58	17	17	3	31
33	1.0	51	62	2	13	13	23	41	51	20	20	15	25
33	1.0	54	54	7	7	20	21	38	41	20	19	20	19
33	1.0	30	58	6	34	10	34	31	54	19	17	9	27
33	1.0	34	52	2	20	19	17	38	35	18	19	17	20
33	1.0	33	58	5	29	10	18	45	53	22	20	17	25
33	3.5	6	40	13	48	7	39	14	46	17	17	7	27
33	1.0	24	56	0	32	7	34	22	51	19	19	9	29
33	1.0	33	58	1	28	14	34	28	47	18	18	11	25
33	1.0	19	55	3	39	6	38	20	52	18	18	8	28
33	1.0	14	41	1	27	3	30	12	37	13	14	9	18
33	3.0	2	55	4	56	3	52	6	57	16	16	2	30
33	1.0	25	60	1	38	9	47	15	53	17	19	12	24
33	1.0	29	65	0	35	2	48	18	63	17	19	9	27

33	1.0	42	50	6	14	12	26	30	44	17	18	18	17
33	1.0	21	56	6	39	5	35	27	57	19	20	7	32
33	1.0	10	63	0	51	1	54	8	61	17	21	2	36
33	2.5	1	62	5	67	3	65	2	64	18	18	3	33
33	1.0	24	52	1	30	10	35	17	43	16	16	10	22
33	1.0	28	41	7	21	7	31	17	41	17	17	11	23
33	1.0	30	44	4	19	3	31	18	46	16	15	9	22
33	1.0	50	63	3	19	7	24	42	59	18	20	13	25
33	1.0	25	51	5	31	2	33	21	53	19	17	7	29
33	1.0	36	57	3	24	4	39	22	56	20	17	8	29
33	2.0	9	63	9	64	4	61	11	68	17	18	4	31
33	1.0	37	62	2	27	8	27	38	57	18	19	15	22
33	1.0	43	54	5	18	14	23	37	47	20	19	19	20
33	1.8	18	48	15	46	9	51	14	55	17	17	5	28
33	1.0	25	53	2	28	12	29	22	42	16	16	10	22
33	1.0	25	48	3	24	12	34	16	37	16	15	8	23
33	1.0	26	44	1	19	4	20	24	41	16	15	12	19
33	1.6	6	45	6	44	5	42	9	46	14	14	1	21
33	1.0	36	48	4	17	14	22	31	39	19	19	15	23
33	1.0	21	45	2	27	6	29	18	40	19	16	8	27
33	1.0	29	47	3	21	9	23	29	42	17	17	13	21
33	1.4	13	30	5	20	5	19	14	28	13	11	7	17
33	1.0	15	31	2	19	8	20	14	26	10	13	10	13
33	1.0	23	43	3	24	6	33	14	41	14	13	2	25
33	1.0	14	38	1	24	7	24	13	31	11	14	7	18
33	1.2	18	33	0	16	4	19	14	30	11	12	9	14
33	1.0	13	28	2	15	3	20	11	28	9	9	5	13

Experiment 2.2

FR5

33	1.0	10	30	0	21	0	20	12	30	14	14	7	21
33	1.0	6	32	1	27	0	20	12	33	13	12	3	22
33	1.0	3	32	0	30	4	27	7	29	12	13	3	22
33	1.0	18	34	0	16	2	20	13	32	15	14	8	21
33	1.0	9	28	0	21	0	15	15	29	13	14	8	19
33	2.0	0	33	0	34	1	31	2	34	13	12	1	24
33	3.0	2	19	3	19	0	17	4	21	11	10	1	20
33	4.0	0	31	7	39	1	35	7	37	14	13	2	25
33	6.0	0	3	4	35	0	35	1	35	13	14	1	26
33	8.0	1	29	10	38	0	27	11	40	12	13	4	21
33	10.0	0	34	1	33	1	32	2	34	13	13	1	25

Return to FR1

33	1.0	52	61	3	12	5	16	48	59	20	22	17	25
33	1.0	47	56	3	10	9	21	36	49	19	20	16	23
33	1.0	53	54	4	4	11	15	43	46	19	20	22	17
33	1.0	48	50	6	8	4	14	42	50	19	19	23	15
33	1.0	42	47	2	20	7	22	39	54	17	20	19	18

FR10

33	1.0	14	15	0	1	5	1	14	11	12	12	13	11
33	1.0	7	12	0	3	2	4	7	10	7	7	7	7
33	1.0	5	9	0	4	0	6	4	8	5	7	3	9
33	1.0	5	9	1	4	3	5	4	6	3	5	3	5
33	1.0	15	18	0	3	2	11	10	17	13	12	11	14
33	2.0	1	5	3	7	2	5	3	6	4	4	2	6
33	3.0	2	1	2	0	2	4	0	0	0	0	0	0

33	4.0	1	15	2	15	0	11	6	17	7	7	0	14
33	6.0	0	14	0	16	0	13	3	15	5	7	0	12
33	8.0	1	10	8	18	1	17	4	18	6	5	0	11
33	10.0	3	18	1	19	1	14	8	18	10	10	4	16
Return to FR1													
33	1.0	57	54	11	7	19	12	52	45	22	18	24	16
33	1.0	44	51	5	12	16	14	42	40	19	20	17	22
33	1.0	48	55	4	10	13	22	38	46	18	20	16	22
33	1.0	42	45	17	18	14	15	49	49	20	17	16	21
33	1.0	58	52	13	8	15	8	56	50	19	20	25	14

Experiment 2.3
High luminance

33	1.0	20	26	0	5	2	7	17	23	12	12	8	16
33	1.0	17	28	0	10	2	6	21	26	14	15	16	13
33	1.0	34	35	0	4	5	3	35	31	20	17	19	18
33	1.0	27	32	0	6	2	11	24	32	19	16	11	22
33	1.0	35	35	0	3	1	5	32	34	20	18	19	19
33	2.0	18	16	5	22	6	13	28	36	17	17	11	23
33	3.0	1	18	19	37	1	19	18	38	10	12	6	16
33	4.0	3	31	11	41	1	36	5	40	14	13	2	25
33	6.0	13	21	14	22	12	17	17	23	13	11	10	14
33	8.0	15	24	17	25	10	13	27	32	18	18	15	21
33	10.0	7	23	17	34	6	21	19	36	10	12	7	15

Low luminance

33	1.0	23	17	7	2	10	1	24	14	13	10	9	14
33	1.0	25	25	4	5	8	5	23	22	13	16	14	15
33	1.0	22	22	2	2	9	5	19	16	13	14	11	16
33	1.0	23	24	5	5	3	3	26	26	14	14	13	15
33	1.0	20	19	3	2	4	6	16	18	10	9	9	10
33	2.0	3	8	6	11	1	6	8	13	6	5	2	9
33	3.0	1	12	7	17	3	11	10	17	6	7	2	11
33	4.0	1	13	4	15	4	11	5	13	6	9	2	13
33	6.0	1	15	13	29	1	15	16	28	11	9	3	17
33	8.0	1	20	13	32	4	23	9	30	9	9	3	15
33	10.0	0	39	7	44	0	28	15	46	15	15	3	27

Experiment 2.4

Descending series

33	1.0	24	27	3	3	3	6	23	26	14	19	15	18
33	1.0	27	29	3	3	3	6	25	27	22	21	21	22
33	1.0	24	32	3	9	4	9	25	29	22	19	15	26
33	1.0	21	29	1	10	4	11	19	28	18	21	14	25
33	1.0	21	30	0	6	3	4	24	24	18	20	14	24
33	2.0	5	17	7	20	1	10	14	23	9	16	9	16
33	3.0	4	17	17	31	3	12	21	31	9	26	10	25
33	4.0	3	21	9	26	1	19	12	28	13	22	8	27
33	6.0	1	8	18	24	2	11	14	24	3	22	8	17
33	8.0	1	15	12	24	2	13	12	25	8	22	10	20
33	10.0	5	11	7	15	2	8	13	17	7	16	9	14

Ascending series

33	1.0	29	35	1	5	2	6	28	34	20	22	18	24
33	2.0	1	3	1	5	0	2	3	3	4	3	3	4
33	3.0	0	8	11	17	0	4	15	18	4	16	6	14
33	4.0	2	8	15	21	3	4	18	20	4	21	11	14

33	6.0	4	4	17	19	1	5	17	21	2	21	14	9
33	8.0	7	1	22	15	7	4	20	17	5	20	17	8
33	10.0	2	4	13	17	0	3	18	18	3	20	12	11

Experiment 2.1

Descending series

34	1.0	66	48	18	2	42	9	57	25	21	20	22	19
34	1.0	64	55	12	4	30	11	58	37	21	19	20	20
34	1.0	67	53	19	4	39	8	64	33	21	21	29	13
34	1.0	67	47	24	4	25	7	63	46	22	20	18	24
34	1.0	70	54	16	0	34	14	55	35	17	21	25	13
34	1.2	67	61	10	3	30	20	52	41	21	22	20	23
34	1.0	68	64	10	6	22	14	59	52	21	20	19	22
34	1.4	63	56	14	7	16	10	60	54	22	22	22	22
34	1.0	57	55	11	10	17	8	59	49	21	22	21	22
34	1.0	57	59	6	7	15	7	59	51	21	21	21	21
34	1.6	1	35	20	54	0	13	43	53	14	15	7	22
34	1.0	0	43	29	72	0	10	62	72	16	16	7	25
34	1.0	68	58	15	7	26	12	64	48	22	22	27	17
34	1.8	53	37	34	17	39	21	47	32	19	17	2 6	10
34	1.0	64	59	13	8	31	19	53	41	22	21	24	19
34	2.0	49	39	34	23	37	31	41	37	18	17	21	14
34	1.0	64	65	9	9	27	23	49	46	19	23	23	19
34	2.5	47	28	43	28	34	31	36	36	19	19	25	13
34	1.0	64	57	15	6	15	23	48	57	19	20	20	19
34	3.0	49	20	22	23	27	17	55	45	17	17	26	8
34	1.0	64	54	16	5	21	27	43	49	21	20	18	23
34	3.5	35	42	35	39	28	31	44	48	19	18	22	15
34	1.0	67	45	25	4	29	17	54	43	20	19	27	12
34	1.0	58	54	12	7	22	9	56	44	19	21	21	19
34	1.0	57	55	15	13	20	23	47	49	20	19	21	18
34	1.0	62	51	18	8	18	20	50	52	21	20	23	18
34	1.0	53	43	21	11	23	14	50	41	20	19	22	17
34	4.0	37	27	41	30	30	22	45	37	17	17	24	10
34	1.0	55	40	22	7	27	12	50	35	20	19	26	13
34	5.0	46	15	54	21	43	22	46	24	18	19	29	8
34	1.0	67	38	28	1	32	8	58	34	19	22	25	16
34	6.0	39	26	43	31	35	27	42	34	18	18	23	13
34	1.0	44	55	11	20	12	23	42	53	18	20	17	21
34	8.0	26	32	31	37	23	34	28	39	16	13	15	14
34	1.0	58	52	13	6	19	27	37	46	22	18	20	20
34	1.0	59	45	22	7	36	17	51	31	19	18	23	14
34	1.0	58	50	15	6	22	14	50	43	20	21	23	18
34	1.0	57	51	12	6	13	14	50	51	21	19	20	20
34	1.0	55	38	26	9	23	4	60	43	19	20	24	15
34	10.0	27	33	34	40	23	25	44	44	19	17	18	18

Ascending series

34	1.0	62	48	19	7	21	15	53	48	20	20	27	13
34	1.0	53	37	24	5	32	9	51	28	19	18	23	14
34	1.0	48	46	17	14	21	3	59	41	18	20	22	16
34	1.0	58	48	15	5	22	12	52	42	23	20	23	20
34	1.0	43	51	14	21	10	10	54	54	20	19	18	21
34	1.0	52	55	13	18	17	21	47	51	19	22	17	24
34	1.0	50	54	7	9	12	8	51	47	21	20	16	25
34	10.0	39	15	37	11	38	20	30	13	15	13	20	8

34	1.0	56	46	16	4	24	18	44	38	19	18	21	16
34	1.0	59	43	20	3	28	10	54	36	19	20	24	15
34	1.0	60	52	17	11	35	8	60	35	19	21	21	19
34	8.0	26	27	39	40	38	16	50	29	16	16	19	13
34	1.0	59	47	17	5	28	4	60	37	20	20	24	16
34	1.0	60	37	28	7	25	10	58	41	21	19	28	12
34	1.0	66	30	37	3	50	6	60	18	18	19	29	8
34	1.0	64	46	23	4	29	11	56	40	20	19	26	13
34	1.0	61	45	25	7	36	12	55	33	19	17	22	14
34	6.0	38	23	44	30	36	13	56	31	17	17	21	13
34	1.0	62	44	20	3	32	8	58	33	20	20	27	13
34	1.0	50	50	12	12	28	5	58	35	19	21	17	21
34	1.0	58	43	23	10	19	8	56	46	18	21	17	22
34	5.0	49	12	58	20	51	12	59	19	18	17	27	8
34	1.0	57	41	22	6	34	12	52	29	18	19	27	10
34	1.0	53	35	27	7	30	10	51	32	18	19	19	18
34	1.0	58	40	27	10	33	4	62	34	19	19	26	12
34	1.0	60	42	26	5	26	8	57	41	20	20	23	17
34	4.0	41	17	46	22	33	8	55	29	17	17	23	11
34	1.0	57	39	27	7	32	4	61	34	20	20	29	11
34	1.0	59	27	36	4	43	7	55	20	16	19	27	8
34	1.0	65	38	30	5	37	6	63	30	19	20	29	10
34	1.0	58	29	32	2	41	3	60	20	22	18	29	11
34	1.0	61	42	22	5	24	2	63	41	22	20	26	18
34	1.0	48	12	52	17	42	11	55	24	16	17	26	7
34	1.0	66	32	37	0	34	6	62	34	20	20	23	17
34	1.0	63	29	37	4	38	1	66	29	18	19	24	13
34	1.0	58	34	27	5	17	1	61	46	19	20	23	16
34	1.0	66	22	43	1	44	1	65	22	20	18	30	18
34	3.0	57	2	69	11	52	1	68	18	18	19	32	5
34	1.0	69	19	53	3	55	1	70	17	19	19	31	7
34	1.0	64	20	49	2	46	5	64	22	21	19	31	9
34	1.0	62	23	42	3	44	6	60	22	18	19	26	11
34	1.0	70	38	35	2	35	3	71	38	21	18	27	12
34	2.5	56	9	63	16	50	10	62	22	18	16	31	3
34	1.0	64	32	35	2	48	4	63	17	21	19	31	9
34	1.0	75	24	52	2	63	2	75	12	19	20	33	6
34	1.0	53	17	38	2	39	5	51	17	16	16	24	8
34	1.0	64	32	34	3	49	5	60	18	18	19	26	11
34	1.0	69	25	44	0	48	5	63	20	19	20	33	7
34	1.0	63	28	41	3	40	1	66	29	19	21	29	11
34	2.0	45	12	44	12	37	3	54	20	19	17	27	9
34	1.0	60	29	32	1	37	3	56	22	20	19	28	11
34	1.0	67	37	29	2	28	8	59	41	19	19	22	16
34	1.8	52	7	59	14	47	4	61	19	18	19	32	5
34	1.0	52	16	38	1	31	0	53	22	19	17	30	6
34	1.0	64	25	41	1	47	2	63	18	18	17	20	15
34	1.0	54	37	20	2	31	3	55	26	18	17	18	17
34	1.6	62	30	37	3	49	7	59	18	18	16	25	9
34	1.0	62	32	32	0	36	9	54	27	20	18	26	12
34	1.0	56	31	31	6	34	7	55	28	17	20	24	13
34	1.0	48	18	38	9	29	2	54	27	19	19	27	11
34	1.4	57	23	39	6	44	0	60	18	17	18	28	7
34	1.0	58	19	43	2	34	0	61	27	22	17	28	11
34	1.0	58	20	36	1	39	6	51	18	17	18	26	9

34	1.0	59	28	31	3	32	4	56	28	18	19	23	14
34	1.2	51	28	28	4	30	1	55	26	18	17	22	13
34	1.0	53	22	31	2	28	2	52	25	16	17	23	10

Experiment 2.2
FR5

34	1.0	53	22	31	2	28	2	52	25	16	17	23	1
34	1.0	31	37	2	9	1	3	37	38	16	17	16	17
34	1.0	27	38	4	14	5	5	38	37	18	20	17	21
34	1.0	31	33	7	10	3	2	39	37	17	19	19	17
34	1.0	35	31	11	6	4	3	38	39	19	20	19	20
34	1.0	32	36	6	9	6	2	39	36	18	17	17	18
34	2.0	13	15	26	28	16	7	36	24	15	14	16	13
34	3.0	17	15	27	24	17	11	31	26	15	15	20	10
34	4.0	17	22	21	24	12	8	34	29	16	15	18	13
34	6.0	21	13	35	27	25	15	33	23	14	14	19	9
34	8.0	13	27	20	35	7	23	24	39	17	17	14	20
34	10.0	23	13	29	19	17	4	38	25	15	16	19	12

Return to FR1

34	1.0	61	59	13	13	10	19	54	64	22	21	22	21
34	1.0	68	71	6	9	6	21	57	71	23	21	14	30
34	1.0	74	70	5	4	1	16	61	75	21	22	24	19
34	1.0	64	59	11	4	12	1	66	57	22	22	26	18
34	1.0	71	60	19	7	17	3	76	61	22	21	25	18

FR10

34	1.0	26	26	6	6	4	15	18	29	14	14	14	14
34	1.0	25	22	10	7	3	12	19	27	16	14	15	15
34	1.0	25	19	12	7	5	4	28	26	15	16	14	17
34	1.0	26	30	4	8	4	10	23	29	16	14	13	17
34	1.0	30	32	2	4	3	10	22	30	16	17	15	18
34	2.0	7	16	13	24	5	9	20	23	13	11	11	13
34	3.0	8	13	19	23	4	20	11	27	13	12	6	19
34	4.0	5	10	22	26	7	17	14	23	7	8	3	12
34	6.0	8	15	18	26	13	12	20	19	12	13	11	14
34	8.0	11	12	17	19	3	11	20	26	12	11	13	10
34	10.0	2	17	15	32	1	14	19	33	11	11	2	20

Return to FR1

34	1.0	58	57	23	22	16	31	48	64	19	21	22	18
34	1.0	60	65	15	20	8	35	45	72	20	20	13	27
34	1.0	66	58	22	14	26	27	53	53	21	21	23	19
34	1.0	59	49	31	21	14	30	49	66	21	20	21	20
34	1.0	62	53	26	16	15	25	55	64	22	19	22	19

Experiment 2.3
High luminance

34	1.0	36	50	4	15	0	15	38	52	19	19	10	28
34	1.0	34	41	4	12	1	7	38	45	19	19	19	18
34	1.0	41	49	5	14	4	13	41	49	18	21	16	23
34	1.0	43	45	7	9	5	9	44	46	17	20	17	20
34	1.0	44	37	11	3	9	3	44	38	18	17	20	15
34	2.0	26	24	32	30	10	9	46	45	16	16	13	19
34	3.0	0	21	27	48	1	18	31	48	10	12	4	18
34	4.0	11	17	33	39	10	11	38	39	15	16	14	17
34	6.0	21	10	38	27	16	13	35	32	13	15	16	12
34	8.0	18	10	31	25	18	7	35	23	13	12	15	10

34	10.0	11	14	26	30	7	12	28	34	14	15	12	17
Low luminance													
34	1.0	36	25	14	3	1	3	35	38	17	19	20	16
34	1.0	32	24	10	0	5	0	33	28	17	16	18	15
34	1.0	38	31	8	2	6	6	33	33	20	17	19	18
34	1.0	29	30	7	5	8	2	32	29	16	16	14	18
34	1.0	34	25	12	4	13	3	35	24	17	16	20	13
34	2.0	20	6	32	19	11	1	37	28	13	14	17	10
34	3.0	12	6	17	9	12	4	18	11	11	12	13	10
34	4.0	12	3	21	11	13	1	22	11	9	6	12	13
34	6.0	9	7	27	24	12	3	31	21	10	12	11	11
34	8.0	25	0	36	10	24	5	29	11	12	13	20	5
34	10.0	37	7	39	10	30	5	40	15	17	16	24	9

Experiment 2.1
Descending series

35	1.0	44	29	32	18	30	11	51	32	19	19	21	17
35	1.0	46	26	34	12	31	8	50	28	20	20	20	20
35	1.0	44	31	28	15	38	6	52	21	19	18	23	14
35	1.0	44	15	36	9	31	9	43	21	18	18	26	10
35	1.0	44	30	32	16	40	13	48	22	20	19	19	20
35	1.2	50	37	28	14	32	19	45	32	21	20	26	15
35	1.0	49	45	22	19	38	22	45	30	17	18	17	18
35	1.4	41	40	25	23	27	19	46	38	18	20	20	18
35	1.0	43	32	30	16	32	9	52	28	20	18	20	18
35	1.0	49	25	37	14	28	15	46	33	19	18	20	17
35	1.6	3	27	27	53	2	33	23	53	13	11	3	21
35	1.0	1	48	15	61	1	27	34	61	18	17	3	32
35	1.0	42	33	28	20	24	9	52	38	18	21	21	18
35	1.8	42	33	33	23	26	15	50	39	18	21	19	20
35	1.0	48	36	28	14	36	12	51	27	18	21	24	15
35	2.0	56	27	44	13	47	12	59	23	19	17	22	14
35	1.0	46	35	32	19	40	12	54	27	18	20	22	16
35	2.5	28	14	32	20	29	7	40	19	13	14	14	13
35	1.0	19	17	11	7	19	7	19	8	9	8	9	8
35	3.0	20	34	27	42	15	31	29	45	18	17	9	26
35	1.0	31	34	27	31	21	22	39	40	18	20	16	22
35	3.5	24	35	29	38	21	28	35	41	16	16	10	22
35	1.0	33	41	18	26	19	25	32	40	16	15	11	20
35	1.0	39	31	29	23	24	23	39	37	19	16	19	16
35	1.0	27	34	12	17	17	21	25	27	14	13	12	15
35	1.0	34	36	30	31	31	32	33	36	17	18	13	22
35	1.0	43	29	35	23	37	20	46	29	18	19	24	13
35	4.0	43	26	31	14	40	14	42	17	17	17	24	10
35	1.0	31	29	25	20	26	22	31	28	16	16	20	12
35	5.0	39	14	44	21	35	9	48	22	18	19	31	6
35	1.0	52	15	47	11	44	9	53	19	19	18	31	6
35	6.0	52	14	53	14	51	11	55	16	16	17	28	5
35	1.0	52	11	48	6	46	3	56	13	17	19	32	4
35	8.0	51	9	57	16	57	11	54	8	18	19	35	2
35	1.0	61	12	53	5	57	7	59	9	17	17	29	5
35	1.0	61	4	61	6	59	7	60	7	16	17	31	2
35	1.0	37	8	38	8	35	7	39	10	14	14	23	5
35	1.0	66	7	62	3	65	5	66	4	18	19	35	2
35	1.0	61	8	57	3	62	5	59	4	18	21	37	2

35	1.0	63	8	58	6	50	9	58	16	20	18	31	7
35	10.0	66	10	61	5	71	3	66	0	20	19	39	0
Ascending series													
35	1.0	64	13	56	5	66	8	61	4	18	17	32	3
35	1.0	68	4	64	1	66	9	59	3	18	17	35	0
35	1.0	67	4	64	2	62	4	63	5	18	19	35	2
35	1.0	65	8	62	4	66	7	63	3	19	19	37	1
35	1.0	60	4	57	2	55	4	58	7	18	19	36	1
35	1.0	64	4	64	5	59	4	65	8	18	19	34	3
35	1.0	65	9	62	5	59	3	66	11	19	17	35	1
35	10.0	65	3	66	6	58	5	65	11	19	18	35	2
35	1.0	59	7	57	5	46	10	53	18	19	19	31	7
35	1.0	45	19	46	22	43	21	46	23	18	16	22	12
35	1.0	52	22	46	14	47	12	54	20	19	18	27	10
35	8.0	45	14	50	20	47	21	44	19	18	19	30	7
35	1.0	49	14	51	15	43	15	51	22	16	18	27	7
35	1.0	57	8	56	7	42	15	49	22	17	19	32	4
35	1.0	58	13	60	14	56	11	61	17	18	18	32	4
35	1.0	59	8	63	10	58	5	66	13	21	19	36	4
35	1.0	57	10	57	11	50	12	54	17	19	18	31	6
35	6.0	49	18	49	18	54	17	51	12	18	16	23	11
35	1.0	64	10	60	7	55	17	51	16	16	16	29	3
35	1.0	47	32	40	24	45	28	43	25	17	16	24	9
35	1.0	63	29	43	9	58	17	53	14	19	19	30	8
35	5.0	55	15	57	17	55	18	54	17	19	17	31	5
35	1.0	59	13	55	10	55	11	58	14	19	19	32	6
35	1.0	57	15	56	12	57	10	58	13	18	18	32	4
35	1.0	54	10	57	14	49	7	59	18	18	18	33	3
35	1.0	59	17	55	13	43	11	61	27	20	19	31	8
35	4.0	61	14	63	14	62	24	51	14	17	18	31	4
35	1.0	63	16	56	11	63	9	65	11	19	17	34	2
35	1.0	58	14	58	14	49	19	53	22	18	19	32	5
35	1.0	59	23	49	13	57	20	52	16	18	16	30	4
35	1.0	58	25	47	14	51	23	49	21	17	18	28	7
35	1.0	51	30	38	18	36	22	45	31	17	19	27	9
35	3.5	53	16	59	20	55	35	40	20	16	16	29	3
35	1.0	56	23	46	12	50	15	55	19	19	19	31	7
35	1.0	58	21	51	14	56	15	57	15	21	17	36	2
35	1.0	51	9	45	5	41	6	49	14	13	15	26	2
35	1.0	67	17	58	7	61	21	54	13	21	18	33	6
35	3.0	60	5	65	11	62	11	60	10	19	19	35	3
35	1.0	63	13	58	7	58	12	56	12	20	19	34	5
35	1.0	57	32	40	15	49	20	52	24	18	19	24	13
35	1.0	55	26	43	15	44	20	48	25	18	18	25	11
35	1.0	55	31	38	15	38	20	48	31	18	19	30	7
35	1.0	54	31	42	18	50	21	52	24	18	18	28	8
35	2.5	45	29	41	26	45	18	52	25	17	18	22	13
35	1.0	44	32	37	23	41	15	54	28	19	18	26	11
35	1.0	53	34	39	19	40	13	59	32	18	17	25	10
35	1.0	59	26	43	12	59	13	58	13	21	17	31	7
35	1.0	62	25	48	10	50	15	57	22	19	16	29	6
35	1.0	57	35	38	17	40	16	57	34	20	20	25	15
35	1.0	55	43	32	18	33	20	54	41	21	20	24	17
35	2.0	49	40	33	23	40	23	49	32	20	18	23	15
35	1.0	63	50	24	10	46	21	53	27	19	19	20	10

35	1.0	56	39	34	17	43	14	59	29	20	20	32	8
35	1.8	62	18	56	15	51	11	63	23	19	19	35	3
35	1.0	67	25	49	6	58	15	57	15	17	20	31	6
35	1.0	59	42	30	13	54	17	56	18	18	19	27	10
35	1.0	57	50	26	16	44	21	53	31	20	19	25	14
35	1.6	61	42	30	13	52	12	60	20	19	19	27	11
35	1.0	61	39	31	10	42	13	56	29	22	19	32	9
35	1.0	63	43	28	7	46	16	54	24	20	20	30	10
35	1.0	57	36	34	14	45	14	55	24	17	19	25	11
35	1.4	53	39	33	19	33	22	51	39	20	19	23	16
35	1.0	62	52	20	9	37	20	51	34	19	22	29	12
35	1.0	48	49	20	19	37	16	54	31	19	18	21	16
35	1.0	57	43	26	14	38	15	55	33	20	19	25	14
35	1.2	49	49	23	23	29	30	42	43	19	19	14	24
35	1.0	58	35	34	13	40	20	49	31	19	21	27	13

Experiment 2.2

FR5

35	1.0	32	28	8	4	16	3	34	20	16	17	22	1
35	1.0	28	32	3	8	4	2	34	31	17	17	19	15
35	1.0	36	36	5	6	6	9	31	35	20	17	18	19
35	1.0	31	35	3	6	8	3	36	30	19	16	20	15
35	1.0	26	26	8	9	1	1	34	34	17	17	15	9
35	2.0	19	9	28	19	12	7	29	24	15	14	20	9
35	3.0	22	4	30	11	16	0	34	19	18	17	20	15
35	4.0	27	4	36	12	24	3	36	16	15	13	23	5
35	6.0	35	1	39	5	34	2	38	6	15	14	28	1
35	8.0	9	16	23	30	10	11	26	30	12	15	7	20
35	10.0	14	20	17	24	17	24	12	12	13	13	16	10

Return to FR1

35	1.0	40	45	19	24	24	19	44	40	22	19	20	21
25	1.0	49	56	13	18	29	26	43	38	19	18	17	20
35	1.0	49	47	15	14	35	16	46	26	18	19	19	18
35	1.0	53	51	17	12	29	23	42	38	19	19	20	18
35	1.0	40	48	19	29	17	17	52	50	21	20	20	21

FR10

35	1.0	19	19	1	4	9	2	21	13	13	14	13	14
35	1.0	14	15	4	4	13	2	17	7	12	10	11	11
35	1.0	13	16	1	3	6	2	16	11	10	12	10	12
35	1.0	17	18	1	1	8	3	16	10	14	12	12	14
35	1.0	18	16	3	3	8	1	20	13	15	14	14	15
35	2.0	12	5	17	11	11	3	19	13	10	11	15	6
35	3.0	11	2	18	11	11	2	19	8	9	9	14	4
35	4.0	5	3	10	6	7	2	9	6	5	1	3	3
35	6.0	6	7	12	13	5	6	13	13	9	9	7	11
35	8.0	9	3	16	12	8	1	18	12	8	8	10	6
35	10.0	8	3	8	5	6	2	9	6	6	4	7	3

Return to FR1

35	1.0	40	25	28	14	28	9	45	25	18	19	25	12
35	1.0	31	17	33	18	28	3	47	21	17	17	25	9
35	1.0	41	34	15	8	32	5	43	17	16	18	18	16
35	1.0	40	22	27	9	19	6	42	29	18	16	21	13
35	1.0	35	22	27	14	24	6	42	24	16	18	24	10

Experiment 2.3

High luminance

35	1.0	29	38	4	12	3	7	35	38	18	19	15	22
35	1.0	22	29	8	16	4	3	34	33	16	16	16	16
35	1.0	34	37	3	6	4	0	38	36	19	19	18	20
35	1.0	37	30	5	1	7	0	36	28	19	19	19	19
35	1.0	32	29	6	5	3	0	36	34	19	18	19	18
35	2.0	19	8	26	17	3	1	34	32	12	14	15	11
35	3.0	4	11	23	33	3	13	21	31	11	12	8	15
35	4.0	12	10	30	28	4	3	37	36	11	13	16	8
35	6.0	6	21	15	28	5	17	18	30	13	13	5	21
35	8.0	9	20	18	26	7	4	33	31	15	13	15	13
35	10.0	8	21	10	23	2	11	21	29	11	13	5	19

Low luminance

35	1.0	27	32	6	10	4	2	35	34	19	19	17	21
35	1.0	33	31	7	6	9	4	35	29	17	18	19	16
35	1.0	20	22	14	14	8	5	32	28	15	16	14	17
35	1.0	27	30	7	8	2	4	34	34	18	18	17	19
35	1.0	25	33	2	8	16	0	34	17	17	17	18	16
35	2.0	2	17	17	31	4	16	19	29	11	10	4	17
35	3.0	5	29	6	30	1	18	15	34	12	12	5	19
35	4.0	0	13	18	30	1	11	18	29	7	11	3	15
35	6.0	4	7	26	28	3	12	21	30	9	8	5	12
35	8.0	1	25	5	29	0	22	9	29	13	10	3	20
35	10.0	2	27	6	31	4	24	8	28	11	11	1	21

Experiment 2.4

Descending series

35	1.0	37	36	4	2	6	0	40	34	23	22	17	28
35	1.0	36	36	8	3	7	2	37	30	24	20	24	20
35	1.0	37	34	6	2	4	1	38	36	20	24	20	24
35	1.0	38	32	9	3	4	1	39	36	17	28	25	20
35	1.0	36	35	5	3	2	0	39	36	19	26	26	19
35	2.0	11	3	31	25	9	1	34	26	8	30	23	15
35	3.0	22	2	34	14	14	0	37	22	16	24	31	9
35	4.0	24	1	34	10	23	0	33	12	15	23	32	6
35	6.0	19	2	34	15	18	0	35	19	13	25	27	11
35	8.0	21	3	35	18	11	1	37	28	10	26	18	19
35	10.0	18	8	23	14	6	3	29	26	12	26	24	14

Ascending series

35	1.0	30	35	0	4	5	11	26	31	26	17	16	27
35	2.0	1	16	5	20	0	15	6	20	7	16	2	21
35	3.0	17	5	32	20	19	2	34	19	13	24	28	9
35	4.0	8	9	23	24	6	8	24	25	12	24	19	17
35	6.0	4	8	22	27	6	5	24	25	4	29	15	18
35	8.0	6	4	25	23	0	1	39	30	4	34	20	18
35	10.0	17	5	27	15	14	2	30	18	14	23	26	11

Experiment 2.1

Descending series

36	1.0	42	47	7	12	19	16	39	36	19	20	24	15
36	1.0	43	30	15	4	29	7	39	17	17	17	24	10
36	1.0	31	37	6	13	17	16	27	27	15	14	13	16
36	1.0	50	46	16	11	35	20	42	27	20	20	21	19
36	1.0	17	19	4	6	5	7	13	18	7	7	7	7

36	1.2	41	51	15	25	21	37	29	36	20	19	18	21
36	1.0	53	55	15	18	26	23	49	45	19	19	18	20
36	1.4	45	55	12	21	15	33	34	52	21	20	17	24
36	1.0	48	64	5	18	18	21	45	50	21	18	16	23
36	1.0	54	45	17	10	25	14	49	38	21	20	26	15
36	1.6	1	23	1	21	0	11	11	22	5	8	3	10
36	1.0	8	52	13	57	4	8	57	62	19	19	15	23
36	1.0	51	44	11	4	31	8	48	25	18	19	25	12
36	1.8	50	39	30	20	41	15	54	29	17	19	27	9
36	1.0	61	49	16	3	37	12	53	27	20	20	24	16
36	2.0	51	28	37	13	41	14	52	24	17	20	20	17
36	1.0	63	60	5	1	26	13	52	38	22	20	22	20
36	2.5	43	36	23	14	34	16	42	24	17	17	16	18
36	1.0	42	40	11	7	29	15	36	22	16	16	17	15
36	3.0	30	21	35	26	32	16	40	24	16	15	19	12
36	1.0	30	37	13	10	15	9	31	25	16	13	14	15
36	3.5	40	23	35	18	29	25	36	30	19	18	22	15
36	1.0	42	36	12	5	31	7	40	16	16	15	22	9
36	1.0	45	29	18	1	36	8	36	10	14	14	19	9
36	1.0	25	26	2	4	13	9	20	16	*	*	*	*
36	1.0	42	30	12	2	26	6	36	16	14	12	16	10
36	1.0	59	29	28	1	39	7	53	19	20	17	23	14
36	4.0	37	10	36	7	40	8	39	6	15	16	26	5
36	1.0	55	33	26	3	46	7	53	14	17	21	28	10
36	5.0	35	12	41	17	40	10	43	13	15	16	23	8
36	1.0	54	37	22	6	35	13	45	25	21	18	22	17
36	6.0	33	12	38	17	31	20	32	19	15	14	21	8
36	1.0	43	34	19	7	28	12	38	24	17	17	20	14
36	8.0	49	16	45	10	46	15	46	15	17	17	26	8
36	1.0	52	36	21	5	34	10	48	24	19	19	23	15
36	1.0	51	35	21	6	39	21	37	17	18	19	22	15
36	1.0	58	37	22	4	44	15	45	17	20	20	28	12
36	1.0	50	51	12	13	29	9	52	35	18	20	19	19
36	1.0	51	47	17	14	32	23	41	32	21	18	23	16
36	10.0	35	40	34	21	33	35	30	32	19	17	15	21
Ascending series													
36	1.0	55	45	22	11	35	14	51	32	19	20	21	18
36	1.0	57	47	17	7	44	20	44	20	16	19	19	16
36	1.0	49	50	17	19	35	35	32	33	16	19	20	15
36	1.0	36	51	11	25	18	37	25	44	21	19	11	29
36	1.0	51	37	26	12	37	16	47	24	18	19	24	13
36	1.0	48	40	25	19	38	22	44	28	18	19	20	17
36	1.0	48	42	11	6	22	15	38	31	16	17	19	14
36	10.0	26	38	19	30	19	29	27	37	18	16	18	16
36	1.0	29	36	19	24	24	19	35	30	17	17	16	18
36	1.0	45	30	26	11	29	16	40	26	18	19	25	12
36	1.0	41	49	12	22	24	25	37	38	20	18	21	17
36	8.0	33	17	16	12	31	9	34	14	14	12	18	8
36	1.0	45	47	13	13	27	22	36	32	20	17	17	20
36	1.0	41	37	20	16	26	23	34	30	19	19	20	18
36	1.0	35	37	17	16	26	22	30	26	16	17	16	17
36	1.0	42	37	16	12	25	14	39	28	16	17	19	14
36	1.0	49	40	22	11	18	20	39	43	20	18	22	16
36	6.0	32	30	29	27	31	24	34	28	17	18	20	15
36	1.0	15	16	3	4	11	10	8	8	5	5	3	7

36	1.0	19	21	5	7	10	14	11	16	12	9	11	10
36	1.0	29	24	11	8	19	8	27	18	13	13	13	13
36	5.0	43	19	36	13	39	15	40	17	16	16	24	8
36	1.0	47	23	27	5	35	8	41	15	17	20	29	8
36	1.0	42	21	23	3	34	8	38	11	14	16	21	9
36	1.0	54	45	19	10	24	11	52	39	19	20	21	18
36	1.0	42	28	23	12	25	7	45	26	17	18	21	14
36	4.0	33	15	32	15	30	7	40	17	17	16	25	8
36	1.0	49	28	27	7	31	11	43	24	17	19	28	8
36	1.0	44	30	21	5	26	6	44	25	18	19	27	10
36	1.0	41	46	11	15	13	17	40	43	18	17	14	21
36	1.0	44	48	8	12	26	15	41	30	19	19	15	23
36	1.0	50	50	8	11	16	25	34	42	21	20	23	18
36	3.5	14	21	33	39	15	25	31	40	15	14	13	16
36	1.0	30	51	5	23	15	25	29	405	18	17	12	23
36	1.0	39	51	5	17	9	28	28	47	19	19	17	21
36	1.0	29	44	6	22	12	28	21	39	18	17	12	23
36	1.0	40	60	2	24	7	31	32	56	17	21	12	26
36	3.0	16	25	20	31	20	25	22	27	16	15	9	22
36	1.0	26	58	4	37	6	39	22	57	20	19	8	31
36	1.0	33	53	5	28	6	26	31	52	19	18	15	22
36	1.0	22	51	3	32	7	27	27	48	17	17	7	27
36	1.0	36	52	7	22	9	22	38	51	20	17	14	23
36	1.0	34	42	7	16	9	18	33	40	20	20	19	21
36	2.5	18	35	16	31	10	31	19	39	18	17	11	24
36	1.0	45	54	4	15	10	29	29	48	21	20	18	23
36	1.0	38	51	8	20	19	29	29	41	17	19	12	24
36	1.0	40	41	12	14	9	10	44	43	18	20	19	19
36	1.0	27	48	11	30	15	26	34	43	20	19	13	26
36	1.0	30	54	5	31	21	6	40	53	20	21	14	27
36	1.0	42	63	2	23	12	19	45	53	23	21	15	29
36	2.0	17	35	21	39	10	28	28	47	17	18	12	23
36	1.0	40	55	3	18	2	28	32	56	20	20	13	27
36	1.0	32	55	4	25	8	24	34	50	19	19	14	24
36	1.8	22	51	11	41	13	34	29	51	19	19	12	26
36	1.0	38	52	1	14	4	23	28	49	19	18	12	25
36	1.0	38	62	0	24	6	36	28	57	19	20	11	28
36	1.0	38	64	1	28	6	32	34	60	20	22	12	30
36	1.6	28	57	5	35	11	42	19	50	18	17	8	27
36	1.0	37	33	7	2	15	10	30	23	16	15	17	14
36	1.0	58	61	8	10	18	19	50	51	23	21	26	18
36	1.0	53	40	18	6	28	18	39	30	19	17	22	14
36	1.4	18	18	6	6	13	7	16	10	6	7	6	7
36	1.0	65	43	26	4	27	16	52	42	20	25	14	31
36	1.0	61	42	23	4	35	15	49	29	18	20	18	20
36	1.0	53	47	17	11	23	17	47	41	19	19	18	20
36	1.2	65	41	29	4	33	13	57	37	20	20	28	12
36	1.0	63	48	18	2	27	16	48	38	20	20	24	16

Experiment 2.2

FR5

36	1.0	18	15	4	3	3	6	16	18	16	14	7	23
36	1.0	14	16	4	6	5	7	12	16	12	11	9	14
36	1.0	22	21	9	8	11	13	17	20	10	9	5	14
36	1.0	11	19	5	13	7	16	8	17	13	15	15	13

36	1.0	14	17	11	11	6	14	11	21	14	15	12	17
36	2.0	1	4	4	7	2	6	2	4	2	3	0	5
36	3.0	7	5	13	11	6	2	15	11	5	9	9	3
36	4.0	4	13	4	12	3	11	5	13	7	9	7	9
36	6.0	4	6	12	16	7	6	13	11	5	7	5	7
36	8.0	8	9	7	7	3	5	9	11	7	8	5	10
36	10.0	9	12	5	8	11	8	9	7	7	7	3	11
Return to FR1													
36	1.0	25	39	9	20	7	26	20	39	16	19	13	22
36	1.0	29	35	8	13	4	20	24	39	18	17	16	19
36	1.0	24	37	7	21	6	20	25	39	17	16	12	21
36	1.0	13	19	0	7	2	8	12	17	10	6	9	7
36	1.0	24	36	5	17	6	21	21	36	16	16	15	17
FR10													
36	1.0	2	2	4	5	2	0	6	6	3	2	1	4
36	1.0	5	4	2	3	0	4	3	7	3	7	3	7
36	1.0	2	1	2	3	0	2	1	4	2	2	2	2
36	1.0	3	1	1	2	1	0	3	1	0	2	2	0
36	1.0	3	9	2	10	0	10	2	13	5	9	2	12
36	2.0	0	3	2	5	1	2	4	4	2	0	0	2
36	3.0	1	2	1	4	2	2	1	3	2	1	1	2
36	4.0	1	11	0	8	0	11	0	10	5	7	0	12
36	6.0	3	4	4	5	1	4	2	7	5	2	3	4
36	8.0	3	9	3	8	2	6	4	8	5	4	3	6
36	10.0	1	11	1	9	0	10	1	11	6	6	1	11
FR1													
36	1.0	13	41	4	33	4	20	24	40	16	16	8	24
36	1.0	6	48	0	43	2	36	13	48	15	16	2	29
36	1.0	13	56	0	25	8	29	27	48	22	17	12	27
36	1.0	5	50	1	49	2	48	4	50	16	16	1	31
36	1.0	19	55	0	36	9	42	13	45	18	18	10	26
Experiment 2.3													
High luminance													
36	1.0	21	30	2	9	2	6	25	29	17	17	15	19
36	1.0	28	27	0	3	0	11	21	32	16	14	10	20
36	1.0	24	27	0	5	2	0	29	25	16	16	17	15
36	1.0	29	29	0	1	3	11	19	27	17	17	16	18
36	1.0	27	34	0	8	1	8	25	32	17	18	14	21
36	2.0	6	23	8	22	3	16	11	27	14	13	5	22
36	3.0	0	30	9	39	0	29	11	37	12	12	2	22
36	4.0	4	33	5	34	2	33	5	36	16	14	3	27
36	6.0	6	39	1	34	7	36	5	34	15	14	1	28
36	8.0	0	42	2	42	2	36	6	41	16	16	2	30
36	10.0	7	31	4	27	4	31	3	30	14	13	5	22
Low luminance													
36	1.0	16	22	3	11	1	8	19	25	14	16	10	20
36	1.0	30	29	3	2	10	13	19	22	15	15	13	17
36	1.0	24	21	4	3	4	5	24	22	1	15	13	15
36	1.0	24	29	1	6	7	5	25	23	16	15	12	19
36	1.0	26	25	8	7	3	4	30	30	16	17	15	18
36	2.0	17	16	15	14	13	10	22	18	14	12	16	10
36	3.0	10	19	4	13	9	17	5	13	9	7	5	11
36	4.0	3	5	5	8	1	8	5	9	2	2	0	4
36	6.0	3	1	7	3	3	0	7	4	3	2	3	2

36	8.0	1	20	5	23	1	18	6	25	9	9	0	18
36	10.0	16	13	12	19	5	10	14	20	9	11	7	13

Experiment 2.4

Descending series

36	1.0	32	34	0	1	2	20	13	33	25	17	18	24
36	1.0	36	36	0	0	7	15	22	28	26	18	20	24
36	1.0	29	30	0	2	3	10	19	26	19	24	22	21
36	1.0	23	31	0	9	3	10	20	28	15	25	21	19
36	1.0	24	29	0	2	3	5	22	26	19	19	16	22
36	2.0	1	9	5	14	2	8	6	13	5	12	5	12
36	3.0	1	12	13	23	4	14	11	22	6	23	9	20
36	4.0	2	10	8	16	2	10	8	16	6	15	5	16
36	6.0	1	30	0	30	2	25	3	28	17	16	2	31
36	8.0	2	20	7	23	1	20	6	24	15	18	7	26
36	10.0	0	14	3	16	0	13	4	17	12	13	1	24

Ascending series

36	1.0	24	29	0	6	3	14	14	25	18	23	20	21
36	2.0	3	2	0	2	0	2	2	5	3	3	3	3
36	3.0	5	24	8	27	3	25	8	29	15	16	6	25
36	4.0	6	24	3	19	3	18	9	23	17	16	10	23
36	6.0	4	27	3	25	4	26	1	25	18	15	4	29
36	8.0	3	26	2	23	1	25	3	27	19	16	4	31
36	10.0	1	30	2	31	2	27	5	30	16	16	4	28

* missing values

Appendix 5

The hen number, the grating value (Gtg), the latencies of correct responses to the left red key (CLR) and correct responses to the right red key (CRR) on grating trials, incorrect responses to the left green key (INLG) and the right green key (INRG) on grating trials, incorrect responses to the left red key (INLR) and the right red key (INRR) on grey stimulus trials, and latencies of correct responses to the left green key (CLG) and the right green key (CRG) on grey stimulus trials for the last five days of training and for all training and probe sessions for Experiment 2.1.

Hen	Gtg	Grating trials				Grey trials			
		Red		Green		Red		Green	
		CLR	CRR	InLG	InRG	InLR	InRR	CLG	CRG
31	1.0	947	1117	300	258	150	339	1011	1302
31	1.0	1019	798	633	295	145	245	1143	1267
31	1.0	148	410	114	390	89	381	327	436
31	1.0	950	1066	515	423	242	345	1166	1226
31	1.0	707	916	625	413	278	381	1168	1225
31	1.2	1065	794	666	346	580	359	943	981
31	1.0	953	975	550	529	247	344	1087	1396
31	1.4	912	996	382	595	338	157	1310	1255
31	1.0	871	911	563	678	258	383	984	1314
31	1.0	930	966	535	648	242	403	1042	1404
31	1.6	362	873	548	993	813	737	814	1036
31	1.0	1064	825	657	521	491	242	1130	1103
31	1.0	1018	818	491	385	560	394	955	1246
31	1.8	690	792	684	887	580	404	968	867
31	1.0	1032	821	638	233	446	498	926	1267
31	2.0	981	718	587	536	604	419	961	816
31	1.0	1053	952	378	402	303	303	1147	1190
31	2.5	616	636	862	714	394	693	930	1064
31	1.0	978	821	386	370	219	357	1076	1476
31	3.0	649	621	808	850	804	540	885	628
31	1.0	931	868	456	420	693	643	1018	899
31	3.5	407	629	701	910	628	513	750	821
31	1.0	928	909	544	413	438	514	655	972
31	1.0	858	1082	399	645	328	561	864	1248
31	1.0	1027	891	664	373	595	335	897	969
31	1.0	1078	681	504	359	397	444	904	1099
31	1.0	1074	1158	357	361	259	567	802	1286
31	4.0	786	614	731	727	699	324	992	800
31	1.0	1225	841	438	313	643	297	889	1299
31	5.0	827	485	924	746	654	421	849	1049
31	1.0	1057	1286	484	701	299	514	978	1583
31	6.0	798	410	935	574	732	635	828	1270
31	1.0	1066	898	565	352	604	303	912	1036
31	8.0	907	573	870	608	698	434	887	924
31	1.0	990	917	427	549	357	536	786	1080
31	1.0	873	965	562	601	359	343	1001	1320
31	1.0	861	1163	539	625	399	690	931	1213
31	1.0	109	1086	481	586	287	394	1115	1219
31	1.0	1011	947	534	721	404	289	1081	1072

31	10.0	642	651	764	830	414	414	870	1245
Ascending series									
31	1.0	828	1295	233	917	327	399	1026	1192
31	1.0	1058	961	515	468	581	368	1011	1001
31	1.0	863	975	282	940	330	315	1112	1326
31	1.0	1115	861	638	647	382	497	935	1053
31	1.0	1179	766	614	363	233	434	902	1094
31	1.0	1102	802	648	367	547	376	1055	964
31	10.0	866	660	832	554	718	353	997	765
31	1.0	1236	846	637	238	475	504	765	1012
31	1.0	1101	688	555	632	407	186	922	953
31	1.0	951	759	587	688	670	410	1046	899
31	1.0	663	616	712	741	529	357	1126	1130
31	1.0	1197	650	758	394	605	567	907	866
31	1.0	860	860	447	579	431	454	916	1236
31	1.0	1103	1008	466	399	575	451	966	987
31	1.0	1116	794	568	500	312	460	687	1183
31	1.0	1313	823	501	520	544	285	1022	935
31	6.0	844	1051	575	1248	535	782	657	1388
31	1.0	815	844	484	551	314	586	656	1184
31	1.0	1260	1176	224	623	395	870	819	1085
31	1.0	1110	1056	358	528	279	482	857	1082
31	5.0	835	740	590	702	830	655	668	635
31	1.0	1273	924	287	280	636	534	649	1196
31	1.0	1597	847	368	148	638	309	903	923
31	1.0	146	778	50	187	444	284	946	1312
31	1.0	1462	910	569	268	467	689	665	1047
31	4.0	750	802	618	950	565	554	677	1066
31	1.0	908	973	539	631	326	898	844	1120
31	1.0	954	993	368	636	269	750	439	1357
31	1.0	1336	1283	160	589	288	679	944	1365
31	1.0	1292	1169	432	443	407	894	636	1123
31	1.0	1041	1201	213	641	430	751	894	1045
31	3.5	876	988	458	714	629	928	701	1008
31	1.0	1021	1095	346	656	663	724	794	881
31	1.0	747	1230	396	1043	561	947	602	1032
31	1.0	956	1051	359	519	274	837	970	1292
31	1.0	1169	1021	440	554	214	741	737	1312
31	3.0	717	914	603	825	648	481	972	915
31	1.0	1097	1207	277	680	294	701	843	1325
31	1.0	1090	1242	222	763	456	1326	576	1289
31	1.0	1315	1125	306	616	365	978	737	1062
31	1.0	963	1164	105	846	233	884	740	1360
31	1.0	956	1417	270	556	669	975	812	961
31	2.5	623	1222	436	825	557	906	703	1236
31	1.0	1143	1261	253	454	476	941	840	993
31	1.0	1378	962	341	336	641	688	739	1128
31	1.0	1045	817	234	428	329	559	866	1177
31	1.0	1035	1426	226	498	349	503	949	1183
31	1.0	1016	1318	389	372	300	466	1421	1135
31	2.0	663	922	665	1108	522	941	787	880
31	1.0	1008	1373	393	443	178	676	1347	1232
31	1.0	1065	1055	544	653	363	293	1366	1375
31	1.8	552	931	640	1028	525	709	1168	1144
31	1.0	896	1000	293	494	461	509	1060	920

31	1.0	1217	1136	409	587	369	541	919	951
31	1.0	985	1005	422	527	487	402	1029	947
31	1.6	936	685	514	489	442	778	728	986
31	1.0	1340	1256	148	235	561	402	1262	1039
31	1.0	1075	946	281	339	158	451	793	1104
31	1.0	1338	1213	387	378	447	345	1216	1338
31	1.4	1005	1360	306	702	463	722	1025	1158
31	1.0	1191	1247	640	227	554	603	142	1059
31	1.0	1162	1371	529	478	603	576	1139	1181
31	1.0	1139	1536	276	370	291	528	1180	1158
31	1.2	1039	1056	618	457	543	485	928	986
31	1.0	1069	1209	478	682	533	434	1225	1122

Experiment 2.1

Descending series

32	1.0	1191	887	298	272	230	0	1144	834
32	1.0	1055	940	161	43	261	19	1301	765
32	1.0	1130	848	190	91	316	60	1122	847
32	1.0	984	910	319	69	188	21	1226	866
32	1.0	952	1028	138	138	120	37	1428	874
32	1.2	889	1080	79	348	33	179	1214	856
32	1.0	873	1148	56	365	30	195	1430	865
32	1.4	846	921	102	373	226	341	1137	872
32	1.0	706	923	51	411	21	102	1144	851
32	1.0	900	985	17	299	64	89	1045	861
32	1.6	234	840	183	1726	0	453	800	1073
32	1.0	24	858	112	1880	0	114	803	1010
32	1.0	1060	920	42	136	258	80	1027	740
32	1.8	775	605	698	403	333	154	938	655
32	1.0	898	780	122	74	246	75	1026	694
32	2.1	724	761	533	321	627	190	1118	521
32	1.0	1012	862	61	105	236	159	1196	883
32	2.5	558	615	581	587	563	448	792	520
32	1.0	1056	924	69	99	187	171	1182	797
32	3.0	530	510	519	564	396	545	913	593
32	1.0	1124	971	0	404	206	305	888	699
32	3.5	308	436	711	627	400	468	649	682
32	1.0	1049	785	22	131	103	275	917	838
32	1.0	964	811	38	145	65	199	1024	913
32	1.0	893	848	41	161	113	103	1297	788
32	1.0	1208	858	0	127	127	94	1259	743
32	1.0	853	848	117	176	31	44	1329	845
32	4.0	559	533	733	418	606	312	949	503
32	1.0	1059	836	54	108	154	107	1242	766
32	5.0	648	152	1098	384	780	152	915	305
32	1.0	994	870	120	66	382	114	1161	562
32	6.0	853	365	817	239	810	446	749	321
32	1.0	1064	866	22	89	283	101	1188	687
32	8.0	684	425	664	401	656	173	968	347
32	1.0	1132	864	16	126	216	83	1203	825
32	1.0	1155	925	56	51	522	193	1026	559
32	1.0	1162	956	74	98	411	378	1037	544
32	1.0	961	903	73	151	206	116	1089	729
32	1.0	1023	948	100	175	241	83	1166	788
32	10.0	717	346	790	370	510	231	951	648

32	1.0	1052	790	278	106	393	117	1195	672
32	1.0	1148	996	105	68	316	35	1172	711
32	1.0	1219	864	231	130	347	34	1250	637
32	1.0	1107	872	162	108	235	131	1146	773
32	1.0	962	904	284	142	163	0	1117	872
32	1.0	1139	866	203	91	248	93	1180	80
32	1.0	1123	855	152	79	233	18	1460	823
32	10.0	949	358	706	271	913	316	892	204
32	1.0	1100	833	222	94	342	47	1132	644
32	1.0	1155	849	87	13	142	92	1162	886
32	1.0	989	877	174	43	299	90	1265	881
32	8.0	321	473	721	659	391	384	842	672
32	1.0	1063	978	42	25	230	199	1132	834
32	1.0	1070	908	160	132	170	189	1086	904
32	1.0	965	936	0	141	156	170	1187	821
32	1.0	1045	899	97	101	182	97	1105	802
32	1.0	1109	876	171	27	171	22	1026	1036
32	6.0	789	338	678	261	829	257	980	345
32	1.0	947	844	222	142	340	67	998	860
32	1.0	904	898	112	0	315	11	1175	880
32	1.0	1016	834	86	101	458	56	994	893
32	5.0	786	373	743	287	699	392	631	358
32	1.0	989	886	90	15	320	50	1150	663
32	1.0	1033	892	30	44	430	206	1080	664
32	1.0	1045	810	92	11	145	86	1152	796
32	1.0	921	824	111	187	263	181	960	843
32	4.0	486	467	586	538	347	300	705	693
32	1.0	793	885	12	130	82	64	1039	904
32	1.0	976	868	220	200	170	24	1171	981
32	1.0	848	895	39	355	141	59	1017	915
32	1.0	791	906	115	161	197	96	1011	892
32	1.0	765	857	87	238	63	49	1146	1054
32	3.5	263	521	638	691	118	383	726	787
32	1.0	1054	846	93	115	94	150	1096	953
32	1.0	845	997	86	271	53	95	1030	911
32	1.0	817	919	64	280	71	164	938	965
32	1.0	778	816	105	234	96	82	1116	777
32	3.0	379	563	528	670	267	601	577	761
32	1.0	536	587	56	207	60	147	690	552
32	1.0	884	1495	91	213	60	397	810	827
32	1.0	741	864	64	281	121	259	819	665
32	1.0	729	783	340	470	77	271	956	860
32	1.0	1150	865	164	378	141	320	892	859
32	2.5	468	743	533	637	314	472	825	794
32	1.0	859	946	238	305	87	298	852	910
32	1.0	857	948	84	235	171	300	966	862
32	1.0	835	861	239	381	125	336	979	808
32	1.0	972	918	44	262	165	400	875	825
32	1.0	834	957	86	215	64	330	833	879
32	1.0	838	950	194	316	71	133	1021	860
32	2.0	301	843	126	776	90	685	414	838
32	1.0	814	877	30	290	136	469	713	904
32	1.0	934	928	152	166	198	258	979	946
32	1.8	394	1034	104	713	221	671	537	896
32	1.0	887	942	84	243	54	180	968	962

32	1.0	929	1015	118	313	150	119	1067	986
32	1.0	857	1067	168	237	20	255	977	962
32	1.6	475	846	281	670	24	419	715	983
32	1.0	845	1017	152	419	27	218	963	960
32	1.0	849	911	253	316	45	236	976	910
32	1.0	835	1007	134	298	130	163	1221	905
32	1.4	643	949	135	444	77	216	1088	893
32	1.0	967	819	369	183	274	102	1090	848
32	1.0	1011	893	205	127	121	258	850	897
32	1.0	889	796	267	134	247	140	1016	842
32	1.2	1068	805	413	88	358	17	1159	728
32	1.0	1133	848	369	38	438	25	1199	724

Experiment 2.1

Descending

33	1.0	1589	571	525	287	669	283	959	605
33	1.0	1298	839	389	239	210	340	1414	821
33	1.0	1189	499	286	144	648	179	1217	435
33	1.0	1282	846	186	388	97	405	1086	890
33	1.0	1393	841	167	403	61	472	1167	799
33	1.0	549	887	440	821	161	650	1152	1005
33	1.2	1511	925	160	298	327	505	843	875
33	1.0	971	1034	354	493	125	615	910	1020
33	1.4	749	1039	145	667	421	760	749	807
33	1.0	1532	803	175	429	263	675	704	835
33	1.0	1255	1054	0	565	122	686	737	890
33	1.6	840	942	307	765	256	493	1179	993
33	1.0	130	950	31	1621	26	723	735	936
33	1.0	1224	914	273	527	200	457	1187	767
33	1.8	928	851	413	496	383	543	1353	768
33	1.0	1026	879	10	425	154	699	873	889
33	2.0	744	622	209	683	882	553	706	722
33	1.0	1400	1049	36	213	266	481	976	857
33	2.5	540	724	606	836	278	722	622	960
33	1.0	1584	744	227	109	270	282	1302	689
33	3.0	828	538	402	381	761	547	532	398
33	1.0	1410	873	120	229	256	454	1603	763
33	3.5	315	626	594	801	450	601	749	783
33	1.0	1524	874	96	66	561	336	1539	789
33	1.0	1090	785	304	539	413	372	1535	706
33	1.0	1146	827	100	380	275	446	1359	866
33	1.0	1384	863	130	247	187	298	1535	884
33	1.0	1482	784	383	162	547	385	1268	776
33	4.0	297	695	700	706	222	528	1335	910
33	1.0	1532	935	188	151	212	319	1220	904
33	5.0	513	631	611	827	370	583	1074	878
33	1.0	1618	850	392	223	267	401	1368	982
33	6.0	469	581	1057	842	191	898	834	969
33	1.0	1525	874	310	204	398	406	1346	852
33	8.0	323	748	573	879	247	769	639	925
33	1.0	1372	901	144	201	696	550	1284	704
33	1.0	1499	924	45	216	730	498	928	699
33	1.0	1523	944	139	186	792	612	897	744
33	1.0	1365	646	384	39	887	249	1172	404
33	1.0	1419	757	265	139	563	315	1416	603

33	10.0	640	715	517	681	781	524	1093	568
Ascending series									
33	1.0	1321	947	293	176	540	455	1540	713
33	1.0	1399	860	151	295	717	333	1792	626
33	1.0	775	945	206	540	355	321	1755	778
33	1.0	1247	820	425	330	477	537	1132	759
33	1.0	1430	845	446	223	281	209	863	748
33	1.0	914	1022	187	407	367	294	1443	782
33	1.0	1019	947	275	218	308	313	1309	761
33	10.0	308	691	716	785	424	721	579	765
33	1.0	1132	978	143	220	347	317	1535	711
33	1.0	1479	901	239	164	418	191	1822	646
33	1.0	1338	983	266	167	481	284	1799	731
33	8.0	293	767	605	782	207	740	673	881
33	1.0	1248	916	156	253	520	503	1224	798
33	1.0	1283	960	22	233	407	443	1239	790
33	1.0	1094	885	61	218	444	366	1675	622
33	1.0	1304	894	176	265	438	412	1434	736
33	1.0	1062	922	151	389	338	433	1369	691
33	6.0	601	642	683	672	191	604	882	862
33	1.0	1136	911	0	349	271	529	1201	814
33	1.0	1354	838	0	176	342	312	1686	813
33	1.0	1405	838	17	300	98	128	1599	785
33	5.0	239	545	956	734	218	580	1080	805
33	1.0	1578	868	0	138	276	322	1926	726
33	1.0	1278	807	15	238	825	295	2101	429
33	1.0	1869	849	47	152	538	140	2520	579
33	1.0	1767	843	17	189	387	302	1921	634
33	4.0	142	735	420	841	372	852	287	749
33	1.0	1214	813	65	153	325	272	1670	652
33	1.0	1604	776	283	76	595	385	1098	604
33	1.0	932	855	279	468	358	469	1173	741
33	1.0	1298	803	119	295	757	345	2340	557
33	1.0	804	899	256	419	245	302	2008	705
33	3.5	229	973	444	668	256	673	716	729
33	1.0	984	921	0	496	205	780	1507	672
33	1.0	1162	827	69	524	633	892	1379	674
33	1.0	1062	891	124	583	154	742	1557	735
33	1.0	759	680	115	822	101	560	930	497
33	3.0	38	1491	386	621	87	1576	506	644
33	1.0	1401	811	69	586	307	726	1120	640
33	1.0	1048	1058	0	463	49	589	1110	746
33	1.0	1069	577	436	168	319	382	1333	586
33	1.0	784	789	181	449	166	649	963	704
33	1.0	375	1033	0	755	37	919	376	869
33	2.5	16	959	255	890	110	901	64	803
33	1.0	1134	816	102	424	439	715	1355	652
33	1.0	1300	654	397	523	181	1146	1374	745
33	1.0	1142	795	106	267	82	643	926	602
33	1.0	972	918	44	262	165	400	875	825
33	1.0	1045	752	117	468	136	1278	873	750
33	1.0	1127	901	127	355	68	1321	1345	824
33	2.0	366	972	312	921	86	1043	295	980
33	1.0	1070	848	75	340	267	338	1970	841
33	1.0	1501	805	263	260	358	409	1622	731

33	1.8	602	771	785	618	260	853	720	718
33	1.0	799	792	53	384	569	622	1056	794
33	1.0	828	860	204	869	416	787	1055	510
33	1.0	1131	825	64	320	81	373	1151	626
33	1.6	529	674	265	566	466	703	688	564
33	1.0	1023	843	111	427	417	492	1511	618
33	1.0	716	935	72	470	213	493	1031	731
33	1.0	1006	845	128	349	247	719	1780	632
33	1.4	381	575	266	325	239	358	760	416
33	1.0	676	576	95	523	535	558	604	714
33	1.0	995	769	127	708	679	924	899	736
33	1.0	534	862	17	626	381	835	913	595
33	1.2	715	528	0	323	129	393	645	716
33	1.0	600	450	20	302	48	2665	591	595

Experiment 2.1

Descending series

34	1.0	1124	1389	156	129	428	186	1079	1165
34	1.0	1405	971	388	24	817	206	1203	774
34	1.0	1200	1193	268	96	604	215	1237	943
34	1.0	1213	1030	414	101	656	164	1234	780
34	1.0	1358	949	487	108	411	124	1237	1104
34	1.0	1288	1229	369	0	617	328	1121	870
34	1.2	1201	1071	198	70	544	560	959	1094
34	1.0	1222	1200	173	201	348	262	1066	1266
34	1.4	1195	1156	259	226	298	225	1199	1506
34	1.0	1209	1101	219	348	335	228	1205	1218
34	1.0	1123	1234	118	235	338	156	1459	1438
34	1.6	13	630	401	1464	0	231	843	3446
34	1.0	0	729	460	1610	0	138	944	1755
34	1.0	1015	1066	234	155	357	155	1047	1001
34	1.8	971	797	699	403	671	622	1042	708
34	1.0	1036	1226	179	197	482	454	995	915
34	2.0	1063	668	539	450	873	587	780	695
34	1.0	1121	1106	147	176	359	439	910	822
34	2.5	911	565	754	527	746	669	568	891
34	1.0	1088	1121	266	188	222	570	853	1137
34	3.0	737	494	770	512	406	381	861	1001
34	1.0	1111	1100	269	199	305	610	831	1158
34	3.5	541	781	532	679	366	626	718	831
34	1.0	1166	1053	469	97	463	376	981	867
34	1.0	1221	1117	245	156	482	207	1245	1038
34	1.0	995	1091	287	391	304	557	916	1015
34	1.0	1271	973	276	188	299	369	928	1191
34	1.0	1145	977	468	367	546	307	1002	934
34	4.0	752	558	919	763	652	576	799	916
34	1.0	1339	1007	410	218	521	298	1133	983
34	5.0	826	502	957	493	776	441	869	565
34	1.0	1230	814	477	44	651	216	961	745
34	6.0	686	533	831	666	610	574	753	695
34	1.0	944	1153	191	563	208	552	906	1128
34	8.0	640	710	647	899	420	1047	579	888
34	1.0	1075	1094	243	156	300	710	969	1084
34	1.0	1058	1063	364	222	629	455	993	658
34	1.0	1055	1157	228	159	335	412	950	1134

34	1.0	1045	1116	181	173	321	329	849	1275
34	1.0	1033	974	428	261	338	150	1247	1022
34	10.0	481	870	645	887	467	492	797	872
Ascending series									
34	1.0	1068	1098	286	198	300	259	945	1092
34	1.0	871	959	411	207	755	307	943	636
34	1.0	939	1276	343	381	346	88	1303	1012
34	1.0	1008	905	312	116	335	335	918	987
34	1.0	673	1632	242	565	187	227	1117	1167
34	1.0	1087	1057	207	405	320	414	870	1002
34	1.0	1012	1496	173	256	232	191	1199	1146
34	10.0	1257	733	1296	391	1206	917	1030	460
34	1.0	996	1208	363	101	467	468	789	895
34	1.0	1031	1381	416	96	509	288	269	1037
34	1.0	787	1520	307	263	482	174	976	822
34	8.0	514	701	836	951	684	374	978	829
34	1.0	1107	1454	372	192	550	85	1296	847
34	1.0	1135	910	599	202	606	211	1192	1154
34	1.0	1217	1234	569	77	862	141	1071	479
34	1.0	983	1221	392	86	529	291	1114	885
34	1.0	1083	1018	429	174	557	310	1067	818
34	6.0	542	522	725	664	613	376	1068	898
34	1.0	1114	1002	365	66	568	170	1005	904
34	1.0	888	1535	215	363	512	148	1042	870
34	1.0	941	1050	375	265	371	200	1018	1266
34	5.0	874	264	1009	487	562	357	932	412
34	1.0	1187	1022	451	165	602	388	888	726
34	1.0	1098	1042	524	184	674	316	1117	983
34	1.0	1079	1163	437	272	611	98	1151	840
34	1.0	1078	926	554	113	547	182	1092	1155
34	4.0	1028	577	954	572	764	232	1051	814
34	1.0	959	838	567	238	567	129	1087	893
34	1.0	1268	772	770	114	888	216	1053	544
34	1.0	1126	803	588	87	787	133	1139	719
34	1.0	1341	826	789	57	992	70	1312	574
34	1.0	1036	1111	422	154	473	36	1061	1154
34	1.0	891	298	1166	515	864	298	1134	777
34	1.0	1146	768	728	0	694	192	1149	1018
34	1.0	1074	794	776	141	814	42	1315	791
34	1.0	1126	853	514	184	433	22	932	1364
34	1.0	1272	585	796	12	851	31	1023	693
34	3.0	1024	59	1105	320	939	10	1131	548
34	1.0	1146	629	961	79	941	9	1145	455
34	1.0	1089	589	882	49	810	212	1043	638
34	1.0	1179	840	696	222	791	256	1247	641
34	1.0	939	850	538	37	520	81	1218	1080
34	2.5	911	262	1070	421	878	297	1014	538
34	1.0	1085	821	574	42	864	127	961	672
34	1.0	1085	674	767	66	931	96	1176	413
34	1.0	965	459	566	40	727	172	970	514
34	1.0	1219	1238	525	79	960	116	1055	617
34	1.0	1111	842	749	0	835	185	1077	555
34	1.0	1099	903	656	111	797	36	1114	887
34	2.0	902	559	825	385	754	78	1077	676
34	1.0	1290	1078	812	43	773	159	1252	705

34	1.0	1065	1202	480	58	416	232	1095	1410
34	1.8	905	257	1105	492	905	107	1096	631
34	1.0	1347	452	977	42	770	0	1281	1020
34	1.0	1017	1220	699	64	831	49	1013	934
34	1.0	1086	1310	359	57	679	241	1049	983
34	1.6	976	950	634	83	858	216	1169	582
34	1.0	1153	1235	713	0	746	262	1098	988
34	1.0	1125	889	627	227	764	151	1174	983
34	1.0	1005	544	904	307	630	57	1169	1081
34	1.4	1186	821	803	254	954	0	1327	560
34	1.0	1370	711	836	54	699	0	1209	992
34	1.0	1114	1032	585	78	638	87	1142	1043
34	1.0	1209	847	629	124	759	52	1073	864
34	1.2	1033	1165	609	157	661	49	1304	917
34	1.0	1456	825	884	11	865	188	1028	722

Experiment 2.1

Descending series

35	1.0	1221	484	696	193	638	210	823	412
35	1.0	1109	524	840	226	714	168	1474	638
35	1.0	1151	489	814	255	698	102	1513	575
35	1.0	1081	547	678	304	1064	92	1644	424
35	1.0	1511	333	1143	236	904	145	1196	607
35	1.0	1127	525	703	261	1124	248	1065	472
35	1.2	1196	636	445	227	645	237	1105	619
35	1.0	1107	569	490	331	834	327	1010	393
35	1.4	1353	635	639	321	652	313	994	623
35	1.0	1041	540	686	234	749	117	1405	449
35	1.0	1027	439	954	241	736	334	1191	498
35	1.6	232	462	784	1762	34	580	751	1473
35	1.0	24	704	477	1619	10	344	900	1587
35	1.0	1075	743	755	262	728	116	141	573
35	1.8	918	695	779	306	604	216	1283	624
35	1.0	1361	655	702	224	935	187	1453	410
35	2.0	1049	374	1123	200	1025	147	1327	462
35	1.0	1007	551	655	252	1045	171	1376	440
35	2.5	806	215	738	333	641	113	1025	307
35	1.0	526	332	495	122	583	108	807	123
35	3.0	634	590	1239	730	359	459	1063	827
35	1.0	740	666	897	417	648	316	1670	649
35	3.5	577	546	1196	470	562	433	1294	593
35	1.0	850	737	849	475	595	349	887	596
35	1.0	1331	616	846	269	783	361	1150	573
35	1.0	832	794	333	209	554	336	874	420
35	1.0	1049	761	748	382	855	458	950	507
35	1.0	1074	443	992	321	928	289	1195	414
35	4.0	1364	568	757	186	1330	232	1544	282
35	1.0	1261	724	865	278	1044	480	1464	566
35	5.0	1404	285	1490	317	1108	175	1538	287
35	1.0	1356	327	1166	198	989	135	1580	265
35	6.0	1244	236	1127	219	1145	129	1270	191
35	1.0	1380	264	1123	101	1220	50	1553	201
35	8.0	1218	192	1082	279	1295	164	1312	144
35	1.0	1294	199	1375	87	1178	91	1492	132
35	1.0	1226	80	1646	74	1334	85	1436	88

35	1.0	1034	213	1356	147	1011	127	1084	177
35	1.0	1119	138	1331	42	1051	63	1573	55
35	1.0	1190	142	1332	55	1232	92	1451	74
35	1.0	1317	130	1327	120	1018	149	1167	312
35	10.0	1108	169	1384	80	1180	36	1233	0
Ascending series									
35	1.0	1244	310	1071	58	1234	146	1249	81
35	1.0	1268	103	1355	16	1209	150	1226	60
35	1.0	1274	73	1416	45	1392	45	1162	73
35	1.0	1186	196	1198	58	1160	112	1188	42
35	1.0	1227	80	1269	29	1171	63	1414	122
35	1.0	1163	71	1254	52	1210	72	1194	151
35	1.0	1349	181	1268	60	1120	53	1042	153
35	10.0	1161	66	1354	99	1270	83	1196	205
35	1.0	1143	171	1350	74	1071	219	1051	303
35	1.0	1023	351	966	375	1012	429	1243	390
35	1.0	1053	452	983	207	946	240	1173	399
35	8.0	1099	262	1257	460	1007	370	991	289
35	1.0	936	268	962	226	866	282	1289	359
35	1.0	1155	146	1070	88	846	277	1001	283
35	1.0	1068	179	1041	150	1054	197	972	228
35	1.0	1118	109	1102	117	1170	64	1144	206
35	1.0	1201	168	1071	150	1176	229	1016	231
35	6.0	1242	391	1342	354	1211	277	1197	150
35	1.0	1266	170	1148	98	1289	259	927	182
35	1.0	1097	715	844	352	995	443	863	310
35	1.0	1261	463	818	106	1305	317	914	210
35	5.0	1155	213	873	246	1168	231	1169	187
35	1.0	1243	296	868	94	1310	150	973	296
35	1.0	1271	311	997	151	1220	164	1010	181
35	1.0	1202	257	1162	188	1266	108	1121	235
35	1.0	1177	340	913	121	876	160	1148	401
35	4.0	1054	202	1035	187	979	320	945	162
35	1.0	1192	247	1009	116	1200	112	1048	267
35	1.0	1310	250	1077	147	935	210	1089	207
35	1.0	1194	387	864	176	1040	280	1060	184
35	1.0	1107	488	788	164	1108	341	916	241
35	1.0	1092	572	733	242	832	397	897	473
35	3.5	1043	238	1071	335	1082	440	657	229
35	1.0	1268	341	939	147	1147	198	1132	291
35	1.0	1113	342	888	182	1160	231	1059	187
35	1.0	1042	116	794	74	779	57	892	211
35	1.0	1162	299	877	81	1237	321	938	202
35	3.0	1304	74	1053	123	1360	144	979	144
35	1.0	1322	224	1102	73	1199	180	984	136
35	1.0	1118	681	618	196	971	280	870	377
35	1.0	1194	515	713	229	882	283	964	502
35	1.0	1163	581	698	232	929	240	848	605
35	1.0	1208	676	686	213	1007	356	896	386
35	2.5	986	582	693	311	1066	383	1040	449
35	1.0	1020	715	744	369	958	191	988	399
35	1.0	1045	670	735	267	760	202	1014	551
35	1.0	1117	729	807	149	1337	137	1048	208
35	1.0	1168	522	808	163	1014	244	1016	358
35	1.0	1095	699	600	229	799	224	952	539

35	1.0	1212	603	535	279	713	315	961	648
35	2.0	1236	696	590	282	845	320	939	408
35	1.0	1378	749	478	87	974	280	579	480
35	1.0	1066	760	660	190	837	141	1381	322
35	1.8	1281	318	1034	176	977	109	1250	230
35	1.0	1298	535	855	65	1071	72	1182	156
35	1.0	1306	858	582	146	1208	294	1115	252
35	1.0	1204	801	506	176	959	320	977	438
35	1.6	1350	797	526	157	1145	1001	1236	217
35	1.0	1577	626	593	111	1064	132	1051	381
35	1.0	1525	794	507	88	1033	189	1094	314
35	1.0	1391	676	671	192	1057	208	1177	354
35	1.4	1433	708	707	262	730	261	997	565
35	1.0	1357	734	448	118	880	177	1004	544
35	1.0	1210	956	446	296	938	147	1171	528
35	1.0	1289	620	679	148	924	176	1125	546
35	1.2	1046	785	454	230	784	360	909	616
35	1.0	1392	626	530	253	981	15	1292	528

Experiment 2.1

Descending series

36	1.0	489	686	22	431	424	426	1274	714
36	1.0	1114	1090	157	290	564	610	1581	960
36	1.0	1348	912	417	124	1139	203	1046	552
36	1.0	732	810	158	268	489	367	756	659
36	1.0	1142	1168	402	246	842	450	957	788
36	1.0	369	442	94	152	116	141	329	372
36	1.2	962	1184	245	543	474	870	518	902
36	1.0	1028	1218	258	348	493	445	880	913
36	1.4	945	1284	231	430	362	730	680	1092
36	1.0	965	1593	80	342	421	499	999	1188
36	1.0	1269	1123	366	269	697	349	1087	830
36	1.6	20	567	19	514	0	243	343	569
36	1.0	207	1275	231	1948	87	182	1193	1369
36	1.0	1153	1094	255	102	873	217	1347	734
36	1.8	948	1001	516	475	821	354	990	682
36	1.0	1371	1344	298	59	819	334	1042	702
36	2.0	1081	900	697	368	872	471	1033	642
36	1.0	1420	1446	103	21	495	338	1163	938
36	2.5	1013	1046	601	344	899	428	963	733
36	1.0	1216	1188	276	164	884	572	872	510
36	3.0	760	729	805	630	880	547	889	578
36	1.0	1218	1147	78	262	500	821	924	622
36	3.5	1031	807	858	429	699	617	982	791
36	1.0	971	930	258	81	834	163	988	459
36	1.0	1101	2943	555	24	820	253	967	317
36	1.0	618	697	206	164	474	362	*	*
36	1.0	979	916	317	34	681	165	821	425
36	1.0	1324	932	968	54	983	256	1421	512
36	4.0	1420	376	1456	226	1428	299	1389	284
36	1.0	1228	972	825	82	1110	162	1609	381
36	5.0	1197	442	1112	494	1162	253	1111	409
36	1.0	1406	1000	579	186	855	408	1141	690
36	6.0	1009	321	1087	442	830	863	773	521
36	1.0	1155	988	437	149	695	334	1051	699

36	8.0	1204	437	1129	237	1094	429	1212	421
36	1.0	1341	1052	517	144	769	289	1384	600
36	1.0	1491	942	520	124	967	598	1265	394
36	1.0	1329	996	766	97	965	343	1349	354
36	1.0	1110	1196	314	295	675	155	1553	715
36	1.0	1159	1220	405	257	651	517	1081	653
36	10.0	715	851	640	619	739	782	833	712
Ascending series									
36	1.0	1041	1176	519	265	806	353	1200	760
36	1.0	1297	1120	515	175	1159	425	1430	717
36	1.0	1119	1102	431	378	658	776	814	709
36	1.0	912	1374	302	509	361	858	613	1009
36	1.0	1154	714	781	238	968	327	1297	546
36	1.0	1048	940	586	405	822	555	1006	651
36	1.0	1229	987	433	129	557	490	1213	728
36	10.0	1556	924	589	1003	563	713	957	754
36	1.0	881	966	623	566	747	442	1109	882
36	1.0	1281	777	892	283	981	430	1366	564
36	1.0	978	1028	401	473	723	530	1399	899
36	8.0	808	479	783	273	940	223	962	338
36	1.0	1168	1155	347	268	772	508	1344	716
36	1.0	1137	883	755	350	644	602	1175	700
36	1.0	1269	1023	813	356	863	725	1207	603
36	1.0	1048	942	431	288	668	294	1162	673
36	1.0	1447	1010	552	248	528	474	1143	950
36	6.0	839	683	862	686	837	570	1238	599
36	1.0	346	410	98	82	383	208	222	238
36	1.0	597	684	153	218	454	400	401	482
36	1.0	781	690	321	236	615	270	792	448
36	5.0	1280	495	1229	290	1118	416	1329	457
36	1.0	1716	666	820	135	1379	241	1743	419
36	1.0	1639	632	691	81	1086	184	1221	296
36	1.0	1208	1042	372	258	604	282	1122	946
36	1.0	1494	833	590	390	772	219	1399	812
36	4.0	1520	453	1076	463	1152	228	1387	475
36	1.0	1413	760	743	156	1022	289	1334	619
36	1.0	2143	806	800	128	1340	148	1540	602
36	1.0	1558	1011	514	287	884	351	1442	968
36	1.0	1620	1234	175	250	955	416	1292	809
36	1.0	1745	1016	340	254	641	562	1264	946
36	3.5	735	548	1309	971	842	620	1230	902
36	1.0	1525	1175	629	562	667	618	1339	925
36	1.0	1699	1044	324	362	609	634	1114	1094
36	1.0	1434	1383	251	476	693	559	815	975
36	1.0	1126	1293	89	589	275	698	987	1290
36	3.0	748	762	631	884	880	645	855	788
36	1.0	689	1408	72	813	136	810	620	1241
36	1.0	1254	1229	102	601	249	576	990	1149
36	1.0	892	1175	133	773	260	569	832	1101
36	1.0	1230	1160	260	456	416	434	1240	1131
36	1.0	1260	1001	343	353	487	555	1407	999
36	2.5	1027	818	483	613	493	658	747	829
36	1.0	1621	1175	91	366	326	573	818	989
36	1.0	1252	1168	180	379	585	663	856	883
36	1.0	1708	1082	353	358	414	289	1217	1056

36	1.0	751	1232	257	668	526	668	904	993
36	1.0	1093	1233	293	655	165	454	1259	994
36	1.0	1085	1330	36	432	317	350	1050	1140
36	2.0	508	1056	695	753	524	602	930	908
36	1.0	1327	1234	83	382	44	691	1292	1063
36	1.0	1402	1148	121	477	312	477	1049	969
36	1.8	881	1049	338	745	341	862	833	997
36	1.0	2647	1104	27	263	198	470	1377	1080
36	1.0	1462	1128	0	469	157	645	716	1098
36	1.0	973	1224	31	546	154	707	1240	1163
36	1.6	912	1276	133	718	373	970	595	1158
36	1.0	1116	920	282	65	833	287	912	670
36	1.0	1443	1091	394	156	661	403	868	713
36	1.4	399	531	116	132	264	188	357	269
36	1.0	1061	536	103	662	359	1056	1031	19
36	1.0	1257	1080	505	113	759	416	1081	672
36	1.0	1247	1052	383	254	586	467	1033	948
36	1.2	1226	940	589	70	626	267	1216	764
36	1.0	1299	1084	492	65	560	330	1049	869

Appendix 6

Latencies of correct responses to the left red key (CLR) and the right red key (CRR) and incorrect responses to the left green key (InLG) and the right green key (InRG) on grating trials, incorrect responses to the left red key (InLR) and the right red key (InRR) and correct responses to the left green key (CLG) and the right green key (CRG) on grey trials, measured in 0.10 sec, for two hens, for the descending and ascending series of probes for Experiment 2.1.

Grating trials					Grey trials			
Probe	CLR	CRR	InLG	InRG	InLR	InRR	CLG	CRG
Hen 31								
Descending series								
1.0	17	22	23	16	15	18	24	24
1.2	20	23	21	27	19	17	22	28
1.4	22	22	20	27	18	17	24	28
1.6	28	28	31	28	102	28	34	25
1.8	22	26	21	29	18	18	24	27
2.0	18	16	19	28	15	15	20	24
2.5	16	23	21	24	15	22	23	24
3.0	20	19	22	22	20	22	20	21
3.5	16	20	18	20	20	17	19	21
4.0	22	24	17	23	19	17	20	26
5.0	20	21	20	27	19	21	17	31
6.0	19	24	20	26	26	29	20	36
8.0	22	29	19	26	22	21	19	28
10.0	15	16	29	32	22	41	16	27
Ascending series								
1.0	27	26	32	30	24	11	29	27
1.2	23	24	28	22	24	16	27	23
1.4	28	25	34	25	19	23	33	30
1.6	22	19	17	20	23	21	24	20
1.8	24	23	30	26	35	32	30	24
2.0	26	34	27	30	27	25	29	20
2.5	26	28	23	21	23	27	24	31
3.0	28	25	22	22	31	22	22	21
3.5	27	28	21	26	23	29	24	33
4.0	24	23	18	24	24	17	18	24
5.0	21	21	19	26	22	20	18	21
6.0	39	26	23	18	17	23	26	35
8.0	24	22	20	21	28	16	27	25
10.0	24	24	25	21	22	20	23	26

Appendix 6 cont ...

Grating trials					Grey trials			
Probe	CLR	CRR	InLG	InRG	InLR	InRR	CLG	CRG
Hen 32								
Descending series								
1.0	15	16	15	17	20	12	20	13
1.2	18	17	13	16	17	18	20	12
1.4	18	14	13	15	28	21	20	14
1.6	47	16	23	30	*	19	21	17
1.8	14	14	22	18	13	14	15	13
2.0	14	18	17	15	19	19	18	13
2.5	16	15	17	13	18	14	17	12
3.0	17	13	14	12	14	19	19	13
3.5	15	12	17	11	20	12	17	12
4.0	15	17	17	12	17	17	17	12
5.0	15	15	18	13	17	14	15	11
6.0	16	14	17	12	16	16	16	13
8.0	17	14	15	12	16	13	16	11
10.0	16	15	15	12	16	14	16	14
Ascending series								
1.0	19	19	23	19	24	25	20	17
1.2	19	21	19	18	21	17	19	17
1.4	19	19	23	20	26	22	23	17
1.6	21	16	18	15	24	15	18	15
1.8	21	17	17	15	18	16	22	16
2.0	23	18	21	18	30	19	23	16
2.5	20	18	19	14	16	15	22	16
3.0	17	14	18	15	19	17	17	14
3.5	16	16	19	14	15	15	19	14
4.0	17	15	16	14	17	13	15	15
5.0	15	14	15	14	14	14	14	14
6.0	14	15	14	15	16	15	17	16
8.0	16	13	19	12	15	14	19	14
10.0	*	17	9	14	18	16	17	18

* No responses