Aspects of Hens' Visual Behaviour

A thesis
submitted in fulfilment
of the requirements for the degree
of
Doctor of Philosophy
at the
University of Waikato
by
RICHARD WEAVERS

University of Waikato
2000

Abstract

Five experiments were conducted to examine different aspects of hens' visual behaviour, and to assess whether hens respond to slide images in the same way as they respond to real conspecifics that those slides depict. Experiment 1 was a replication of a study by Candland (1969). Six domestic hens were trained to make simultaneous discriminations between slide images of conspecifics that differed only in combs, beaks and wattles. In further test trials these facial appendices were rearranged in all the possible combinations to determine which was the most salient. The comb appeared to be the most salient feature in both Candland's study and Experiment 1. In Experiment 2 the hens were retrained to discriminate between images of two different conspecifics, and then presented with the real object hens that the slides depicted. The subject hens did not discriminate between the real conspecifics. During Experiment 3 the same subject hens were presented with a series of different images, under the same conditions as Experiment 1. Test trials revealed that most hens discriminated between pairs of images on the basis of the uppermost feature, irrespective of whether that feature depicted part of a conspecific or a geometric shape. Backprojected sinusoidal grating patterns of varying contrast and spatial frequency were used to assess the visual resolution of four hens in Experiment 4. Contrast sensitivity functions were measured under two different viewing conditions. These two functions both spanned a range of low spatial frequencies, that is, showed that the hens had low visual acuity, and also differed in the ranges of spatial frequencies, indicating different levels of visual acuity for frontal and lateral viewing. Experiment 5 was designed to assess and demonstrate high-frequency image loss in hens. Four hens were trained to make simultaneous discriminations between two copies of one of the images used in Experiment 1. One of the copies had been blurred by removing high-frequency contrasts. During a subsequent test phase, the hens were presented with pairs of this image, with one of each pair blurred by removal of high-frequency contrasts across a range of cutoff frequencies. A mean threshold for discrimination of high-frequency image loss was measured at 2.237 cyc/° (cycles per degree of visual angle). Demonstrations of this image loss are shown in Experiment 5.

Low visual resolution was measured for the hens – at around the same levels as pigeons and six-month old humans. It was concluded that hens do not respond to slide images in the same way as they respond to real conspecifics that those slides depict, but that they might learn to do so after extensive discrimination training with both types of stimuli. Possible influences of the hens' low visual resolution on their inability to generalize responding across slide images and real conspecifics are discussed.

ACKNOWLEDGEMENTS

Several people have made significant contributions to this thesis. Grateful acknowledgements to the following:

Firstly, of course, my mentors – Assoc. Prof. Mary Foster, Dr. John Perrone and Dr. Bill Temple. John Perrone needs further acknowledgement for programming and running the image filters used in Experiment 5.

My technical guru, Rob Bakker, for all sorts of gnarly data communications programming, wiring, ever-cheerful advice and repairs, letting me take over his workshop on a number of occasions, and eking out the last vestiges of life from the film recorder with a tin of Coca-Cola.

My friends/ peer-type people, who helped with running the experiments, offered valuable advice and moral support, and performed all sorts of other innumerable helping behaviours – particularly Rebecca Sargisson, Tina McAdie, Cath Sumpter, Jenny Chandler and Steve Gallagher.

This thesis is dedicated to all the trees that died for it and Stephanie the Hen (Hen 46), without whom I might have believed Nye (1972) and given up Experiment 4 –

> Stephanie says
> That she wants to know
> Why she's given half her life
> To people she hates now
> And Stephanie says,
> When answering the 'phone
> "What country shall I say is calling
> From across the world?"
> But she's not afraid to die
> The people all call her "Alaska"
> Between worlds, so the people ask her
> 'Cos it's all in her mind.

The Velvet Underground (1984). Stephanie says. *VU.* USA: PolyGram Records.

CONTENTS

LIST OF TABLES

TABLE Page

Experiment 1

Experiment 4

Experiment 5

LIST OF FIGURES

FIGURE Page

General Introduction

Experiment 1

Experiment 2

Experiment 3

FIGURE Page

Experiment 4

Experiment 5

Studies of hens' visual perception are useful in two ways. Firstly, the results give an idea of how hens perceive their environments and might be used to enhance their welfare. Secondly, being aware of different visual systems increases understanding of vision in general. Hens make a good choice of subject for the comparative study of visual perception because their visual system is similar in some ways to that of humans, and therefore more comprehensible than visual systems of many mammals.

Animal welfare

The welfare issue is a prominent one. Poultry farming has been a large industry in many western countries for over 30 years (e.g., Wood-Gush, 1971) and most egg-laying hens are housed in small battery cages (Appleby, Hughes & Elson, 1992). Animal welfare interest groups have lobbied for the banning of battery cages, which are now illegal in Switzerland and Sweden (Tauson, 1993). A large consideration in planning alternate housing systems is how hens form and maintain stable pecking-orders (Bokkers, 1994). As visual recognition is the primary basis for the maintenance of pecking-orders (Guhl & Ortman, 1953), an understanding of hens' visual perception is important in planning, for example, the optimal size of free-range flocks (Bokkers, 1994). An understanding of hens' visual perception is also useful in planning other aspects of their environment. For example, hens will retain eggs rather than lay them in unfamiliar nesting sites, which damages the eggs and the hens (Duncan, personal communication). Knowing that hens have good colour vision, poultry farmers may colour-code nesting boxes, which reduces the time it takes hens to find their own boxes (Duncan, personal communication).

Comparative visual perception

As with other diurnal species, chickens[1] have a predominantly visual sense (McFadden, 1993). Chickens have very nearly the same spectral sensitivity as humans; that is, the same capacity for colour vision, and even evince the same sized Purkinje Shift (change in spectral sensitivity with dark adaption (Kare & Rodgers, 1976)). Chickens may be able to see a little way into the near-ultraviolet spectrum (wavelengths of light shorter than blue (Bowmaker & Knowles, 1977; Fager & Fager, 1981)).

[1] The term "chickens" is used throughout this thesis to refer to the species of domestic fowl *Gallus gallus*. "Hens" is used to refer to female chickens, "roosters" to male chickens, and "chicks" to hatchlings, up to six months old. This seems to be the dominant convention in the experimental literature (e.g., Bolhius, 1999; Bowmaker & Knowles, 1977; Candland, 1969; Hodos & Erichsen, 1990; Karakashian, Gyger & Marler, 1988), although many authors concerned with the welfare of hens refer to "hens" as a species *Gallus domesticus* (e.g., Bradshaw, 1991, Dawkins, 1996; Douglis, 1948). Experimental results in this thesis will usually be generalized to "hens", as it is the welfare of battery-farmed hens that is of concern. However, this distinction is not important for the understanding of visual perception. With the exceptions noted in Experiments 1 and 4, and some others not relevant to this thesis, it will be assumed that there are no inherent differences in the visual behaviours of "chickens", "roosters", "hens" and "chicks".

Many birds see some way into the ultraviolet spectrum, and Bennett and Cuthill (1994) suggested that ultraviolet vision may be useful to birds for navigation of the sky during flight, and in the recognition of other birds of the same species whose feathers reflect ultraviolet light. For example, snowy owls, which have a large range of ultraviolet vision, appear as uniform white to humans but probably as a whole range of different ultraviolet colours to other snowy owls (Burkhardt, 1989). Chickens, however, do not fly, and their feathers do not reflect ultraviolet light (Bennett & Cuthill, 1994).

Chickens' viewing angles

Like most non-primates, chickens' eyes are positioned laterally, which allows them a near-panoramic view. This may be difficult to identify with: whereas humans use binocular vision almost exclusively, chickens have a very limited range of binocular vision and usually fixate objects with one eye at a time (Martin, 1993). This makes for interesting differences in visual navigation. Humans can fixate on a stationary object ahead and can discern where they are going (Gibson, 1950; Perrone & Stone, 1994). Chickens cannot do this; they cannot look in the direction they are going. When a chicken moves with its beak pointing in the heading direction it can fixate only on objects to either side. To maintain stationary fixation points while moving, a chicken keeps its head stationary with respect to the fixation point as its body moves underneath, and then thrusts its head forward to form a new stable fixation point. This results in the characteristic "head-bobbing" while walking (Wallman & Letelier, 1993).

Rather than a single fovea, chickens have a foveal band in each eye, with three points of high photoreceptor (rods and cones) concentration across the band. This means that they have three different fixation angles. The most acute fixation angle can be used for binocular vision, which spans about 27° of visual angle (Andrew & Dharmaretnam, 1993). These three viewing angles are shown in Figure 0.1. "B" stands for "binocular (viewing angle or retinal fixation point)"; "ML" stands for "main lateral", and "Y" is an arbitrary designation for the mid-lateral viewing angle. Most often, a chicken's eyes are in the diverged position labeled "1" in Figure 0.1, and converge only to allow binocular fixation of close objects, as shown in Figure 0.1/panel "2" (Andrew & Dharmaretnam, 1993). The most lateral angle is used for longer-distance viewing and the inner angles are used for progressively closer fixations. Objects which are fixated at a lateral angle can then be refixated at a more acute angle once the chicken has moved close enough to focus at the new angle. Andrew and Dharmaretnam (1993) demonstrated that the fixation angles shown in Figure 0.1 are at around B = 9.5°; Y = 36.5°, and ML = 63.5° away from the centreline of the head.

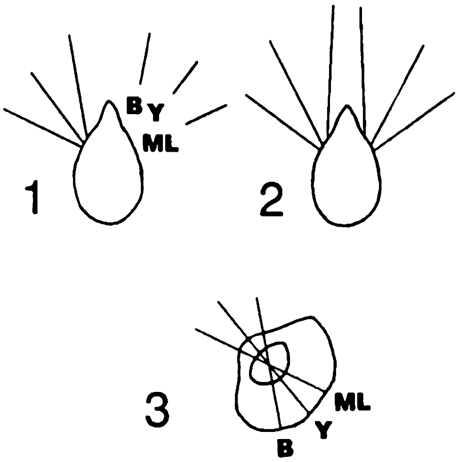


Figure 0.1. Potential lines of sight associated with the three fixation points: B, Y and ML for the primary position of gaze (1) and for convergence of the eyes to allow binocular fixation (2). The arrangement of the fixation points on the retina is shown in 3 (top view of left eye, same orientation as 1 and 2). Taken from Andrew and Dharmaretnam (1993, p.322).

Dawkins (1995, 1996) attempted to demarcate the distances that accompany these viewing angles. She gave hens the choice of feeding next to stimulus hens that were either familiar or unfamiliar to the observing hens and noted both the viewing angles used (Dawkins, 1995), and the distances at which observing hens made their choices (Dawkins 1995, 1996). Consistent preferences for feeding partners were not made at distances greater than 30 cm, or with a viewing angle greater than around 18°. Dawkins (1995, 1996) concluded that hens visually discriminate between familiar and unfamiliar hens using a frontal viewing angle, which extends no further than 30 cm. She noted that longer viewing distances were accompanied by lateral viewing angles. In the later experiments (Dawkins, 1996), she attempted to separate the effects of viewing angles from those of distances by presenting both of the stimulus hens oriented towards the observing hens, and then both stimulus hens oriented sideways (If two hens view each other at a longer, lateral viewing distance then they will be side-on to each other). Reorienting the stimulus hens had no significant effect on the observing hens' choices of feeding partners. In a further condition, Dawkins (1996) tested for the possibility that the sideways oriented stimulus hens were turning their heads towards the observing hens by replacing these stimulus hens with photographs. The observing hens did not shown any consistent preferences for photographs of either familiar or unfamiliar hens.

Dawkins's (1996) paper merits consideration and criticism. Although the stimulus hens were reoriented, this did not influence the observing hens' viewing angles. Trying to ascertain separate effects of viewing distance and angle on visual discrimination seems peculiar because both Dawkins (1995) and Andrew and Dharmaretnam (1993) demonstrated that viewing angle and distance co-vary. Dawkins (1996) considered the possible effect of reduced visibility at longer viewing distances, but discarded this as a contributing factor to the evident lack of discrimination at longer distances because "Hens, like other birds, have good visual acuity...and have no difficulty in seeing objects at different distances from the eye." (p.673). However, studies of hens' visual acuity (e.g., DeMello, Foster & Temple, 1992) have shown that it is well below that of humans'. Therefore, objects are less visible to hens than to humans at any given distance, and the distance at which visual stimuli, such as other hens, become indiscriminable is much less for hens than for the human experimenters. Increasing viewing distance has a more profound effect on stimulus visibility for hens than is evident to human observers. Knowledge of hens' ability to see objects should be an integral part of understanding their performance with visual discrimination tasks.

Two-dimensional stimuli

Dawkins (1996) also discussed the efficacy of presenting photographs as visual stimuli, in place of real hens. She did this to avoid the possible confound of the real stimulus hens reorienting themselves during the experiment, but found that the observing hens did not respond to the photographs as they had to the real hens that the photographs depicted. Two-dimensional stimuli such as photographs, slides and videos are very commonly used in place of real objects and animals in the study of animal visual discrimination (e.g., Brown & Dooling, 1992; Fersen & Lea, 1990; Vaughan & Greene, 1984). In this way, experimenters can maintain more precise control over the presentation and arrangement of visual stimuli than they can with the use of real animals or objects.

Artificial, two-dimensional stimuli can be rearranged or altered relatively easily. For example, researchers concerned with how chickens recognize each other visually have tried to isolate specific visual features of the chickens that are the most salient to chickens. Guhl and Ortman (1953) did this by altering live chicks physically and observing whether flockmates behaved differently towards these altered birds. These alterations included sewing on artificial combs and "dubbing" (removal of the comb, Guhl, 1953; cited in Guhl & Ortman, 1953). Mutilation of live animals probably has very limited appeal to most animal welfare researchers. Two-dimensional images provide a more convenient and ethically defensible medium for examining the salience of specific visual features. For example, Candland (1969) examined individual recognition by presenting roosters with slide images of conspecifics (animals of the same species), with the various facial appendices cut and pasted onto the slide images, rather than altering the real conspecifics as Guhl and Ortman (1953) had done.

Many researchers have used two-dimensional images to examine social behaviours (i.e., responses to conspecifics - e.g., Clark & Uetz, 1990; Evans & Marler, 1991; Jenssen, 1979). However, this raises the question of whether the animal subjects respond to the two-dimensional images in the same way that they do to the animals that the images supposedly represent (e.g., Dawkins, 1996). This is a complicated question. In some cases, animals have responded to two-dimensional images in the same way as to real objects. In some cases they have not. Whether they do depends partly on the objects that are depicted and the species that is responding. Inter-species differences might be explained by phylogenetic differences, or by differences in those species' visual systems. What it means to "respond in the same way" is not always well defined. If a response is defined as "pecking a response key in the presence of a stimulus", then the similarity of that response across objects and images might be easily assessed. This response similarity is more difficult to define when social behaviours are being examined. The key-pecking that Candland's (1969) roosters did in response to slide images of conspecifics, for example, was quite unlike the sorts of responses that would be expected in the presence of real conspecifics in a more natural environment.

The experiments

The purpose of these experiments was to examine aspects of hens' visual perception. "Perception" is equated with "behaviour" and the particular methods used for the experiments are from the field of behavioural "animal psychophysics" described by Blough and Blough (1977). In order to build a more general understanding, each experiment makes a different approach to the study of hens' visual behaviour. This thesis is focussed around the questions "Do hens respond to static, two-dimensional images of conspecifics as they do to the real hens that the images depict?", and therefore, "Can these images be used as a research tool to examine the social behaviours of hens?"

There are two parts to the research. Candland's (1969) study was used as a model for the first part because its design allowed the different stimulus manipulations that were made in the first three experiments. Candland arranged the combs, beaks and wattles on slide images of roosters, in all the possible different combinations, to determine which of these features was used by conspecifics for individual recognition. He concluded that the comb was the most salient feature. Experiment 1 was an attempt to replicate Candland's results with hens. In Experiment 2 the hens were presented with real conspecifics, to see whether they would respond to those conspecifics in the same way that they did to the slide images. During Experiment 3 the image features were altered to determine whether the hens' responding in Experiment 1 could be explained by properties of the image features, independent of any relation the features might have to those of real conspecifics.

For the second part of the research, some of the hens' visual capabilities were examined. The visual system necessarily limits those features of any visual stimulus which can influence behaviour, and so may be fundamental to defining what features of visual stimuli can be involved in recognition of conspecifics. In Experiment 4, measures of the hens' visual resolution were made under two different viewing conditions. Experiment 5 was an attempt to graphically demonstrate the image loss caused by the hens' low visual resolution.

EXPERIMENT 1

For several decades researchers have attempted to discover how chickens recognize each other in order to maintain dominance hierarchies (e.g., Craig, 1992; Douglis, 1948; Schjelderup-Ebbe, 1922). As discussed in the introduction to this thesis, chickens' most predominant sense is vision. Therefore, nearly all of this research has focussed on the visual aspects of chickens by which their flockmates, or other conspecifics, recognize them. Although the definition of "recognition" probably varies somewhat between different experimenters and studies, it need not imply any particular mental processes. "Recognition" here can be understood in terms of differential behavioural patterns in the presence of previously encountered conspecifics, such as pecking that conspecific, or allowing another to peck without retaliation. Duncan (1987) suggested (but did not argue for) a possibility that chickens could maintain dominance hierarchies without the need for individual recognition. That is, rather than displaying differential behavioural patterns in the presence of previously encountered conspecifics, chickens might respond, upon each encounter with a conspecific, to visual cues of the other's hormone levels, such as the size and colour of the comb. However, interactions between pairs of chickens change over the course of a number of encounters (Douglis, 1948), and dominance relationships are sometimes formed as non-transitive "pecking triangles" (Craig, 1992). Also, filial imprinting studies provide further evidence of visual recognition, which is not related to the maintenance of dominance hierarchies (e.g., Bolhuis, 1999). All these cases are evidence for individual recognition in chickens.

In an often-cited study of individual recognition, Guhl and Ortman (1953) modified the appearances of White Leghorn chicks and observed whether these modifications produced any changes in the behaviours of flockmates (mainly direction of unidirectional chicken-chicken pecking) when the chicks were re-introduced to their flocks. These modifications included removal, addition and recolouring of feathers at various different places such as the tail, trunk, neck and head, and also changes to the combs and wattles. They found that modifications of the neck and head, and especially to the comb, produced the greatest numbers of altered responses in flockmates. Modifications of the tail and trunk had little effect. Guhl and Ortman (1953) concluded that chickens use features of the head and neck regions to recognize each other.

Candland (1969) attempted to better quantify Guhl and Ortman's (1953) results by presenting slide images of conspecifics to chickens, with the facial appendices of those conspecifics cut and pasted onto the images in every possible arrangement. In this way, he hoped to isolate those facial appendices by which chickens visually discriminated between conspecifics. During a baseline phase, he trained six White Leghorn roosters to discriminate between two profiles of a previously unseen rooster of the same age and breed. The target profile included its own facial appendices, that is, the comb, beak and wattles. The non-target profile included the comb, beak and wattles photographed from another rooster. Therefore, the combs, beaks and wattles were the only visual features by which the observing chickens could learn to discriminate between the two profiles. During the test phase, subjects were required to make simultaneous discriminations between the target profile verses the same profile, but with the combs, beaks and wattles of the target and non-target profiles arranged in the six different possible combinations. The roosters made fewest errors in choosing between test combinations that included different combs, in combination with either the different beaks or wattles. Candland (1969) concluded that "the comb is the most obvious facial characteristic" (p.284) and that the size of the comb established the chicken's place in the dominance order.

Experiment 1 was an attempt to replicate Candland's results with domestic hens. Candland's procedure was followed in most details, but there were some differences, which are discussed later. An initial training phase was added to Experiment 1, before the baseline phase. For this, the hens were trained to discriminate between two different profiles of conspecifics, each with its own facial appendices. The purpose of including the initial training phase was to see whether the hens' accuracy in discriminating between the profiles would be disturbed by the move to the baseline phase, for which the non-target profile was replaced with the target profile. If it was, this might indicate that the hens had learned to discriminate between the profiles themselves, rather than any of the facial appendices that were manipulated in Candland's (1969) experiment.

There were two reasons for attempting to replicate Candland's results. First, Candland noted that the size and colour of chicken combs is affected by levels of sex hormones (mainly androgen), and therefore hen combs are smaller than those of roosters. Candland (1969) stated that for this reason, it is "unlikely that the comb is as useful for recognition among hens" (p.284). It is laying hens, and not roosters, that are kept in battery cages, and therefore for which alternative housing systems are sought (Tauson, 1993). So it would seem that it is more important to identify the individual recognition that is used to maintain dominance orders in hens, rather than roosters.

A second reason for attempting to replicate Candland's experiment was that Candland assumed that his results were indicative of real chicken-chicken interactions. This was a tenuous assumption because a generality of chickens' responses across slide images and real conspecifics had not been tested. If results similar to Candland's were to be obtained here, then these would be used as a baseline to test Candland's assumption in further experiments.

Neither of these two reasons required an exact replication of Candland's (1969) results. The current experiment might have indicated, for example, that the wattles rather than the combs, were the most discriminable features. This result would be in line with Candland's suggestion that the comb is not as useful for recognition among hens, and it would also provide a basis for testing whether there is any relation between hens' responses to slide images and their responses to real conspecifics.

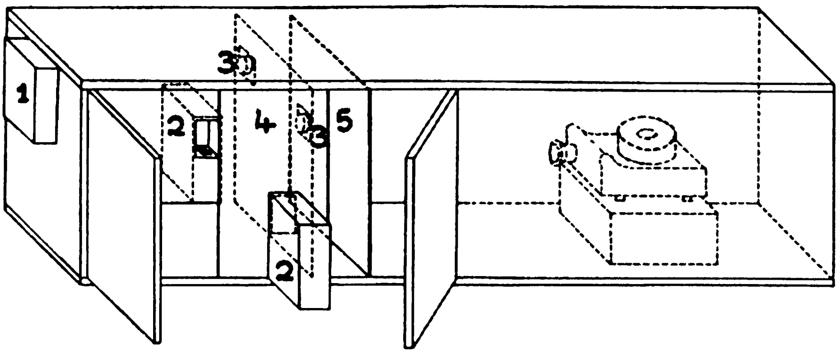
Method

Subjects

Six White Shaver domestic laying hens, numbered 71 to 76, served as subjects. They were 21 months old at the beginning of the study and had had some previous experience of key-pecking on simple schedules of reinforcement (various schedules of food presentation - see Ferster & Skinner, 1957). They were maintained at around 80 % of their free-feeding weights with supplementary feeding of commercial laying pellets. Water with vitamins was available in the home cages, and grit was provided once a week.

Apparatus

The experimental chamber was a chipboard box, painted matte black on the inside, and with internal dimensions of 500 mm wide by 500 mm high by 600 mm long. One of the end walls was 5 mm clear Perspex and held two circular Perspex response keys 32 mm in diameter, 400 mm above the floor and 70 mm from each side. These keys could each be illuminated by a 14 cd LED with peak wavelength 660 nm (red), and would close microswitches when pressed with at least 0.2-N force. On each side wall, 40 mm from the Perspex wall and 120 mm above the floor, was a hole giving access to a food hopper which dispensed wheat. The food hoppers were illuminated with a 1-W white bulb when activated. A frosted glass screen was positioned 150 mm behind the Perspex wall, onto which slide images were projected by a Kodak Ektapro 5000® random access carousel slide projector. This contained a 300-W halogen bulb which was set at 40 % of maximum intensity. The slide projector and screen were housed in a matte black tunnel the same height and width as the chamber, to exclude any light. The response keys, food hopper bulbs and projector were the only sources of light in the chamber. A fan attached to the rear wall provided air circulation and masking noise. The experimental chamber is shown in Figure 1.1. Experimental events were controlled by a Compaq 1024® 486/66 PC, remote from the chamber, operating MEDPC 1® software (later versions of MEDPC® would not drive the slide projector) and interfaced with MEDPC® programmable driver cards.



1/20 scale
1. fan housing
2. food hoppers
3. response keys
4. Perspex wall
5. projection screen

Figure 1.1. The experimental chamber.

Slides were 35 mm colour and projected as 320 mm wide by 220 mm high images on the screen, 170 mm above the chamber floor. The slides were made from professional photographs which were scanned, digitized, arranged in Adobe Photoshop 3® and recorded onto Agfachrome Professional® 100 ASA slide film with a Kodak Sayett PFR® film recorder. All the slide images were pairs of side by side profiles of hens of the same breed and age as the subject birds, and previously unseen by them. The profiles were of the neck and head regions and were projected onto the screen at about life size and height (see Figure 1.2). During initial training, the hens were trained to discriminate between two different profiles. For the baseline phase both of the profiles were of the target hen (one of the profiles was the target for one half of the subject hens, and the other profile was the target for the other half of the hens), but one of the profiles had the comb, beak and wattles of the non-target profile (see Figure 1.2B). For test sessions, the slides each depicted one target profile with its own comb, beak and wattles, and one of the same profile, but with each of the six possible combinations of its own and the non-target comb, beak and wattles – see Figure 1.2C and D. Two versions of each slide were made, one each with the target image on the left and on the right, and each version was duplicated to reduce the possibility that the hens would learn to respond to any blemishes or idiosyncrasies of particular slides.

The digitally stored versions of the images shown in Figure 1.2 were lost. Figure 1.2A was rephotographed from the projected slide image, and B, C and D were remade from this image. It can be seen in Figure 1.2A that the light is unevenly distributed across the image – the picture is brighter in the middle and darker at the bottom and right. This “hotspot” is an inherent characteristic of back-projection.

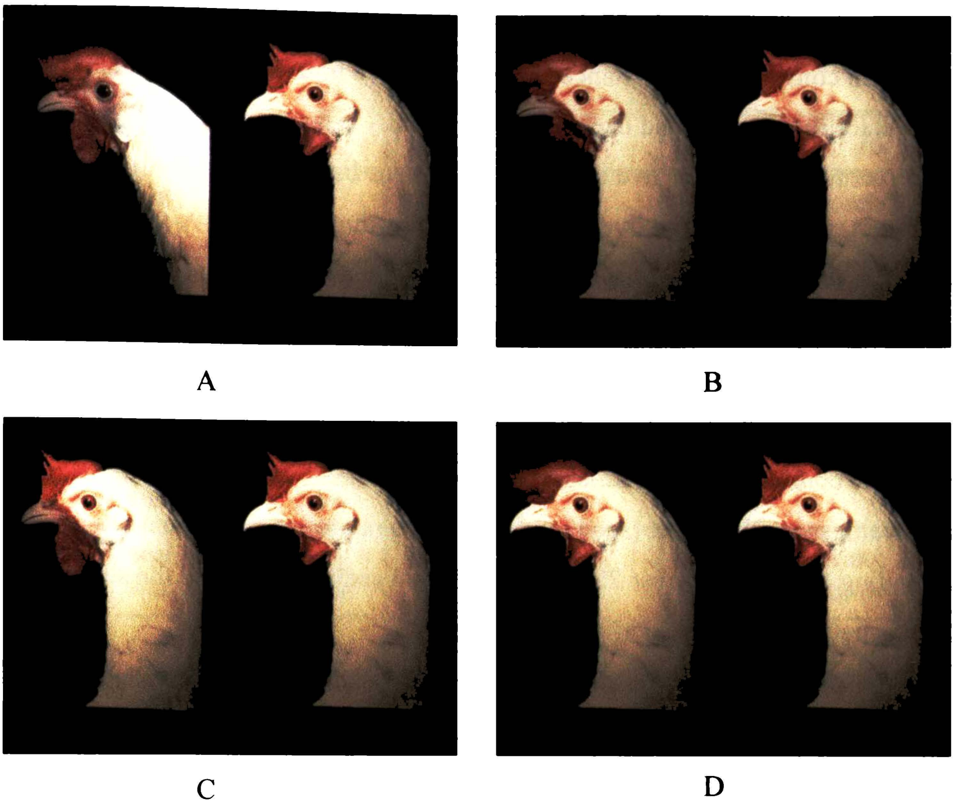


Figure 1.2. Examples of some of the slide images used. A shows two different profiles presented during the initial training phase. In B, presented during baseline, both profiles are the same, but one has the facial appendices of the non-target. C and D are test images. Profiles in C differ only in beak and wattles. The comb is the only difference in D. Target is on the right in each of these pictures.

Procedure

Sessions were conducted six or seven days each week and each session lasted for 64 trials or, during training and baseline, automatically stopped at 2400 s if all the trials had not been completed. Each trial started with the presentation of a slide showing two profiles. The target image appeared on the left or right at random (p=.5). Four seconds after the beginning of slide presentation, the two response keys were illuminated. A peck to the key in front of the target image always resulted in the raising of the same-side food hopper for 2 s. A peck to the key in front of the non-target image always resulted in 2-s blackout. Either response also resulted in the extinction of both key-lights and the projector shutter closing. There were no scheduled consequences for pecks to unlit keys. Each trial terminated with a 10-s inter-trial interval (ITI), during which all the lights were turned off.

For the initial training phase, images were of the two different profiles. Hens 71, 72 and 73 were arbitrarily assigned one of the profiles as the target, and Hens 74, 75 and 76 were assigned the other. The projection screen was 600 mm from the Perspex wall at the beginning of the training phase, but was moved to 150 mm after the first 191 sessions. This was done following the recent publication of Dawkin's (1996) paper, suggesting that hens will fail to discriminate between conspecifics at distances greater than 300 mm. The initial training phase continued until a stability criterion had been met. The stability criterion was that the median proportion of correct responses over five consecutive sessions be within 0.025 of the median proportion of correct responses of the five immediately preceding consecutive sessions, and this criterion be met five, not necessarily consecutive, times. All hens' responding had met the stability criterion 40 sessions after the screen move, that is, after 231 sessions of the initial training phase.

During the baseline phase hens had to choose between two profiles of the target hen, one of which had the comb, beak and wattles of the non-target hen. The profile with its own comb, beak and wattles was the target (see Figure 1.2B). The baseline phase continued until all hens were responding correctly on over 75 % of the trials in each session, and the stability criterion had been met. This happened after 60 sessions.

The test phase began in the session immediately following the baseline phase, and consisted of test sessions interspersed among the baseline sessions. Each test session was conducted after all hens had attained at least 75 % accuracy on the baseline sessions. Test sessions differed from baseline sessions only in the slide images that were presented. Slide images presented for the test sessions were two profiles of the target hen, one with its own comb, beak and wattles, and the other with one of the six different possible combinations of comb, beak and wattles of both the target and non-target hen. Each combination was identified by the facial appendices that differed between the two images. For example, in the "beak/ wattle" combination (shown in Figure 1.2C) the target and non-target profiles each retained their own beaks and wattles, and both profiles were appended with the target comb. The "comb" combination is shown in Figure 1.2D. There were six test sessions, each presenting one of the possible comb/ beak/ wattle combinations to each hen, arranged in the Latin-square design shown in Table 1.1. Data collected were the number of trials in each session where the target was presented to the left and right, the number of correct responses made to each, and session duration, in seconds. Only total numbers of trials and errors in each session were used for analysis.

Table 1.1. Arrangement of test sessions. The elements listed denote the differences between the two profiles. That is, in Test 1 Hen 71 was presented with two target profiles, one of which had the non-target's beak.

Test	71	72	73	74	75	76
1	beak	comb	wattles	beak/ comb	beak/ wattles	comb/ wattles
2	comb	wattles	beak/ comb	beak/ wattles	comb/ wattles	beak
3	wattles	beak/ comb	beak/ wattles	comb/ wattles	beak	comb
4	beak/ comb	beak/ wattles	comb/ wattles	beak	comb	wattles
5	beak/ wattles	comb/ wattles	beak	comb	wattles	beak/ comb
6	comb/ wattles	beak	comb	wattles	beak/ comb	beak/ wattles

Results

Proportions of correct choices of the target image for each of the 20 initial training sessions immediately before, and the 20 sessions immediately after, moving the projection screen from 600 mm to 150 mm behind the Perspex wall are shown in Figure 1.3. It can be seen from this figure that all the hens were responding with reasonably high accuracy before the move (all over .75 correct for last session). Response accuracies declined for Hens 71, 74 and 75, for several sessions after the move. Response accuracies for Hens 73 and 76 do not appear to have been affected by the move. Hen 73's responding fell to chance-level accuracy for one session, but as this was three sessions after the screen move, it is difficult to tell whether this was related to the move. The open circles in Figure 1.3 show the mean proportions of correct responses for the last five sessions of the initial training phase (sessions 227 to 231). The individual proportions for these sessions are shown in Figure 1.4.

Accuracy in choosing the target image decreased sharply for all hens with the transition from the initial training to the baseline phase. Figure 1.4 shows proportions of correct responses for the last 20 sessions of the initial training phase and the first 20 sessions of baseline phase. For the training phase, images were of two different profiles. For the baseline phase, the images were both of the target profile, but one had the comb, beak and wattles of the non-target. It can be seen in Figure 1.4 that the proportions of correct target choices decreased for all hens with this change - from around or over .8 , down to chance levels (.5) at the beginning of the new condition. For

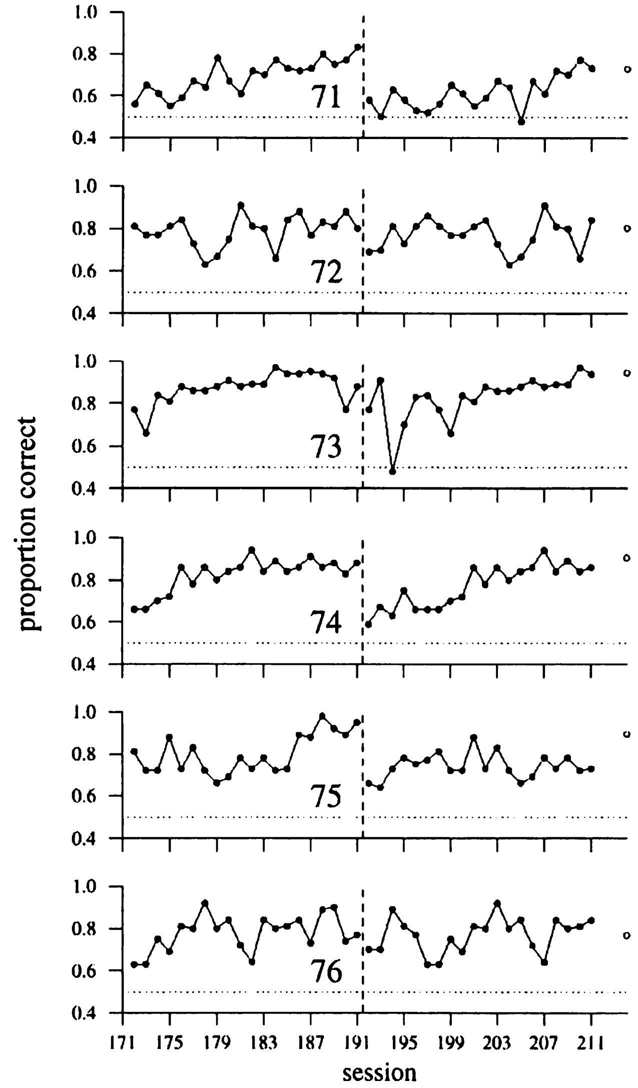


Figure 1.3. Proportions of correct responses for the 20 sessions immediately prior to moving the screen (left panels), and the 20 sessions immediately after moving the screen. Open circles show mean of last 5 initial training sessions.

Hens 72, 73, 74 and 75, proportions of correct choices increased notably within the first 20 sessions of the baseline phase. The averaged proportions of correct choices for last five sessions of the baseline phase (open circles in Figure 1.4) show that proportion of correct choices for all hens at the end of baseline phase were the same or higher than at the end of the training phase, although for Hen 74, this mean (.89) falls in the lower range of proportions of correct responses for the last 20 initial training sessions.

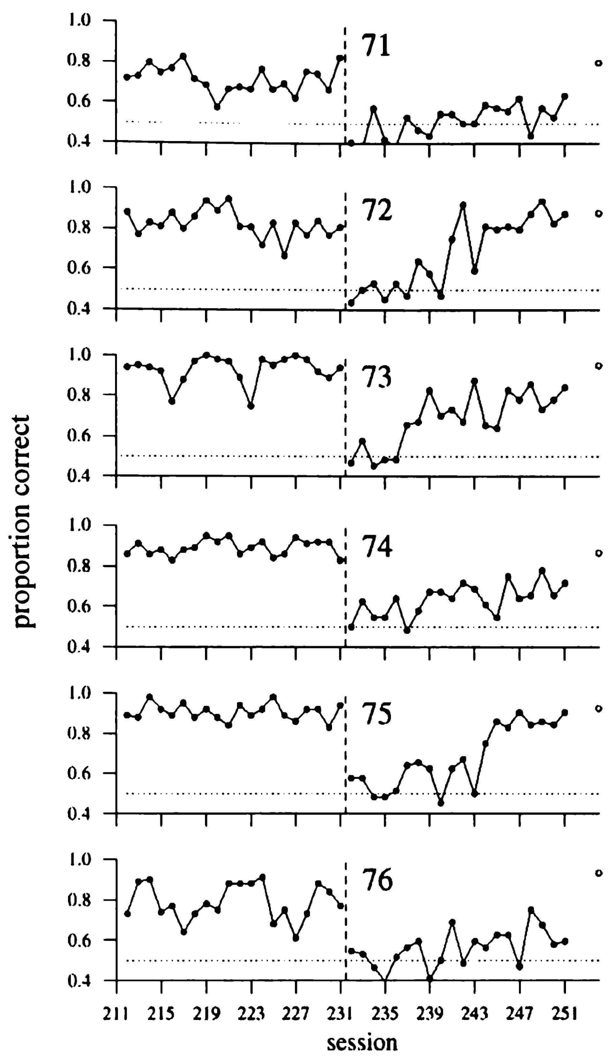


Figure 1.4. Proportions of correct responses for the last 20 sessions of initial training (left panels) and first 20 sessions of baseline condition (right panels). Open circles show mean of last 5 baseline sessions.

Numbers of errors in choosing the target image for each test session are shown in Figure 1.5. The raw data are listed in Appendix A. The test combinations are labelled with the features which differed between the two images. For example, in the “comb/beak” combination, the target image included the target comb, beak and wattles, and the non-target image included the target wattles and the non-target beak and comb. Hens 71, 73, 74, 75, and to some extent, 76, all made fewer errors in choosing between combinations which included different combs. The “comb/beak” combination and the “comb/wattles” combination did not produce fewer errors than the “comb” separately. Hen 72 made fewer errors in choosing between the two combinations which involved the beak in conjunction with either the comb or the wattles.

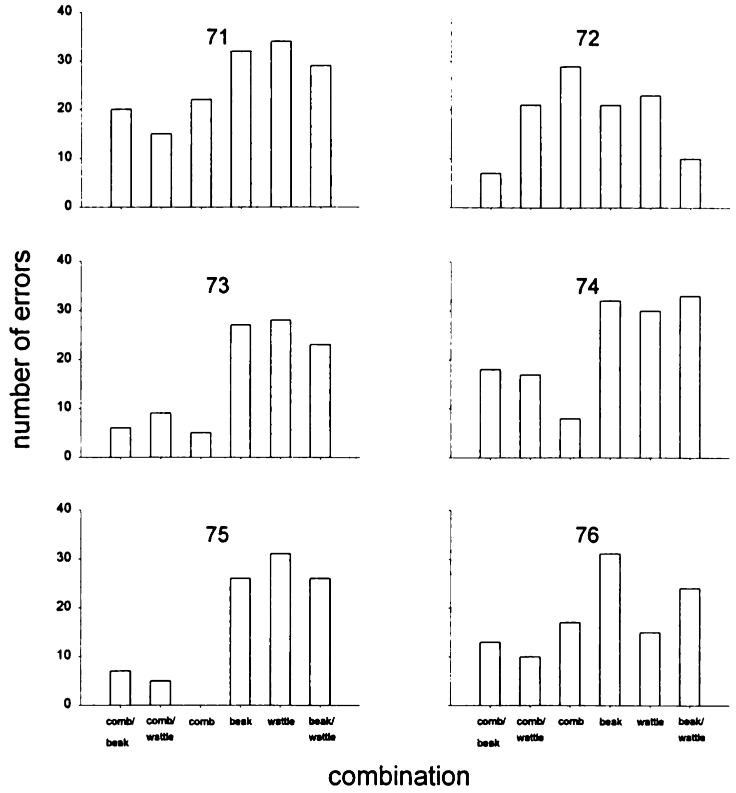


Figure 1.5. Numbers of errors made (out of 64 trials) to each combination of facial appendices.

Discussion

The procedure described in Candland's (1969) paper was followed in detail here. The most notable differences were the inclusion of the initial training phase, the use of hens rather than roosters, and the positioning of the projection screen. Candland projected slide images onto the chamber wall. In Experiment 1, the projection screen was originally positioned 600 mm behind the Perspex wall, but moved to 150 mm after 191 initial training sessions (see Figure 1.3). There was also a difference in duration of food presentation. Whereas Candland presented food for 8 s following each correct choice, the hens in this experiment were presented with food for 2 s. Food was initially presented for 3 s, but reduced in the first few sessions as the hens gained weight and failed to complete all 64 trials within each session. The food was provided to maintain, or "reinforce" (e.g., Skinner, 1981) the differential pecking, as without it the chickens presumably would not have continued to peck the keys. The 2-s food presentations in this experiment served well to maintain discriminative responding.

Figure 1.3 is included here to show the disruption to the hens' responding. No important conclusions can be made from this disruption. Images were projected at the same absolute size on the screen before and after moving the screen. So these images occupied a much greater portion of the hens' field of view at the closer distance. The hens might have responded to the screen move as a change in viewing distance. That is, they might have used a lateral fixation angle to view the images at the larger distance, and changed to a more acute fixation angle after the screen was moved closer (cf., Figure 0.1). Alternatively, the hens might have retained the same fixation angles after the move, in which case the images would have appeared to become larger. That is, the same effect would have been produced by keeping the screen at the same distance and increasing the size of the projected images. Perhaps some of the hens altered their fixation angles and some did not, and if this was the case, there might have been a correlation between changes in fixation angles and changes in response accuracy following the move. As fixation angles were not observed, no conclusions can be made about this.

Mean numbers of errors from this experiment are compared to those from Candland's in Figure 1.6. All the combinations including different combs in the current experiment show similar results, at around 12 to 14 errors on average, out of a possible 64. Notably larger numbers of errors were made in the "beak", "wattle" and "beak-wattle" combinations, with choices in the "beak" and "wattle" combinations approaching chance level (.5 correct). Whereas the mean numbers of errors from Candland's (1969) experiment steadily increase from left to right across the combinations listed in Figure 1.6, in the current experiment a fairly clear separation can be seen between those combinations which included different combs, and those which did not.

Mean numbers of errors to the tested comb/beak/wattle combinations are close to those found by Candland (1969). Although Candland noted fewest errors when the comb was presented in combination with either the beak or wattles, Figure 1.6 shows that fewest errors were made by the hens in this experiment to combinations involving the comb, irrespective of whether those combinations included beak or wattles. It can be seen from Figures 1.5 and 1.6 that the mean results are representative of each of the hens, save Hen 72, and to a smaller extent, Hen 76. Hen 72 made the fewest errors in choosing between combinations that included the beak in conjunction with either the comb or wattles. Hen 76 made fewest errors in choosing both the "wattle" combination, and all combinations that included the comb. The overall numbers of errors made to comb and non-comb combinations varied between subjects, but, as Candland (1969) noted, one should expect individual differences in abilities of chickens to discriminate aspects of other chickens. He suggested that these differences might be related to the bird's place in the dominance order. Candland also suggested that the comb would not be as useful for recognition among hens as it was for his roosters, because hen combs are notably smaller than those of roosters. However, the hens in the present experiment responded to comb images in much the same way as the roosters in Candland's experiment.

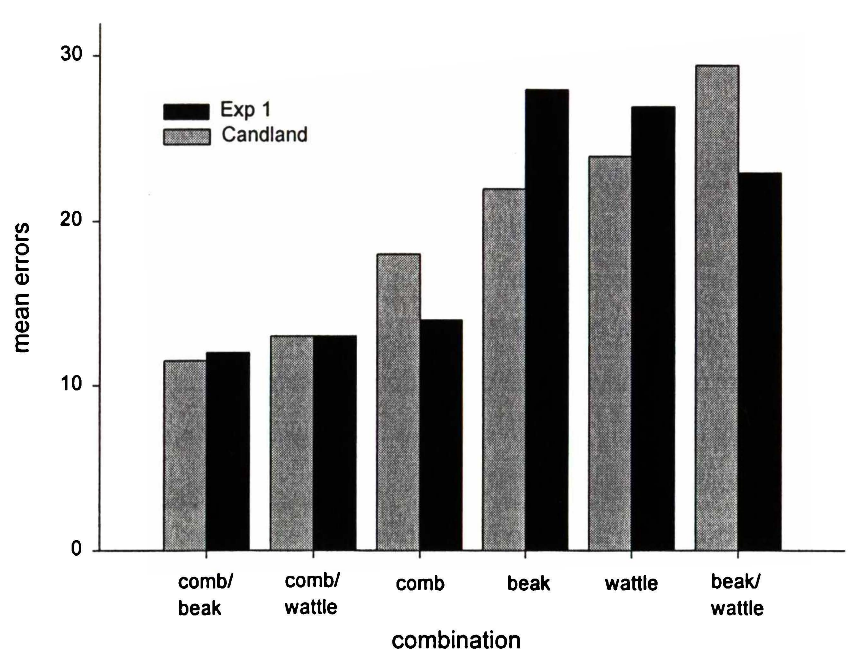


Figure 1.6. Mean errors in choosing each combination in Experiment 1, compared to those from Candland's (1969) experiment.

This result is tempered, however, by the changes in proportion of correct trials shown in Figure 1.4, when the hens moved from initial training phase to baseline phase. When the hens were presented with two images of the same profile, differing only in comb, beak and wattles at the beginning of baseline phase, they failed to discriminate as they had done with two different profiles. This means that the discriminations that were made between the two different hen profiles were not solely on the basis of any of the features which were explicitly manipulated during the tests. Either the hens learned to discriminate between the two different profiles on the basis of features other than the facial appendices, or features other than the facial appendices formed a necessary part of the discrimination. Hens might use visual cues other than, or as well as, the facial appendices to recognize each other. Many other factors might be involved in individual recognition. Guhl and Ortman (1953) found that territory was an important factor, and that a chick who was in a familiar place was more likely to be dominant than one who was not. That is, a change in pecking order shows a loss of individual recognition.

It might be that the conditions of this experiment were so different from those of hen-hen interactions that the experiment does not yield useful information about the visual cues that hens use in responding to real hens. In order to substantiate Candland's claim of ascertaining the "Discriminability of facial regions used by the domestic chicken in maintaining the social dominance order" (title, p.281), it is necessary to test, rather than assume, that chickens' responses to slide images relate in some way to those chickens' responses to real conspecifics.

EXPERIMENT 2

Candland (1969) concluded that "for the rooster, the comb is the most obvious facial characteristic..." (p.284). As the title of his paper ("Discriminability of facial regions used by the domestic chicken in maintaining the social dominance order") strongly suggests, this conclusion is about those visible aspects of chickens which are involved in individual recognition by conspecifics, or chicken-chicken interactions. Yet he examined no chicken-chicken interactions. Candland did not discuss whether the way that the chickens responded to the slide images related to the way that chickens respond to conspecifics. This relation might be difficult to define. In the experimental setting, the chickens were presented with slide images and given food, contingent upon which of two response keys they pecked. Entirely different events are expected in a natural setting. When a chicken encounters a conspecific, it might move towards or away from it, and this moving might be maintained by such consequences as unilateral pecking or access to nesting sites. The similarity between these two sets of events is open to different interpretations, and is discussed in some detail here because it is important for reasons stated later in this introduction.

The following analogy is made between the two (experimental and naturally occurring) sets of events just described, and maintaining the behaviour of a person recognizing his or her mother. Experimental events might include: presentation of photographs; the subject pressing buttons, and the consequential provision of money. In a natural setting, the person might wait at an airport terminal, view a number of people passing by, accost one of them with the expression "Hello mother", and consequently leave with that person. Behaviours in both of these settings can be said to involve "recognition", and this can be verified. At some time before both the button-pressing and the greeting, the person might say "This one is my mother. I recognize her." However, this recognition is more difficult to verify with non-verbal animals, including chickens.

A popular theory of recognition involves the supposition of unobservable "internal", "mental", or "cognitive" states (e.g., Chomsky, 1968; Piaget, 1952; Roitblat, 1982). According to this theory, animals have "internal representations" of various perceptible stimuli. If a perception of a stimulus is matched ("perception" and "matching" are also unobservable cognitive processes or states) to an internal representation, then a cognitive state of "recognition" might ensue. This recognition is presumed to mediate observable behaviours such as button pressing, greeting, or the utterance of "This is my mother. I recognize her." Although the presence of this cognitive state cannot be articulated by non-verbal animals, it is presumed to mediate observable behaviours in the same sort of way as it does for humans. (The question of how "cognitive" states can cause physical behaviours is an area of philosophical debate by itself (e.g., Smart, 1973)). The occurrence of behaviours defined by observers as "showing recognition" are taken as evidence of the mediating cognitive state.

Skinner (1953, especially p.34) objected to this cognitive theory. He argued that although it is reasonable to assume that different behaviours are mediated by different states of the behaving animal, hypothesizing about the nature of unobservable states in order to explain observable behaviours is neither parsimonious nor useful for the prediction or modification of those behaviours. For example, explaining that a chicken pecked another "because it was frustrated" gives no indication of the circumstances under which the chicken will peck, or whether it will peck on another occasion. Similarly, explaining the differential key pecking in Candland's experiment as showing that the chickens had "internal representations" or "concepts" of the chickens depicted in the slide images would give no indication of how discrimination between the slide images was learned, nor whether the chickens would show some discrimination in responding to real conspecifics. This is a complex and contentious issue (e.g., Dennett, 1987; Ryle, 1949), but the important thing here is to ascertain whether Candland's results have relevance to real chicken-chicken interactions. Theories of "cognitive representation" are not useful for this. A useful theory must specify a testable relation between the experimental and natural sets of events.

Premack (1976) gave a method for testing whether images represent real objects for animals. He made two criteria: Firstly, that the animal can respond to the image in the same way that it responds to the object, and secondly, that the animal can respond to the image differently from the way it responds to the object. The second criterion is to show that the animal can discriminate between the image and the object, else the image does not "represent" the object, but is the object for that animal. These criteria have been cited by researchers of image representation in animals (e.g., Bradshaw, 1991; Dasser, 1987; Wasserman, Kiedinger & Bhatt, 1988). However, they might not be the most effective for examining the utility of Candland's experiment. To show that Candland's results yield useful information about chicken-chicken interactions, it is not necessary to show that the chickens can discriminate between the slide images and the real chickens. The crucial factor is a demonstration of a consistent relation between the chickens' responses to the slide images and the chickens' responses to conspecifics. Such a relation might be that the hens trained to choose a slide profile of "Conspecific A" from the options "Conspecific A" and "Conspecific B" in Experiment 1, might then be seen to choose the real Conspecific A from real versions of the same options, that is -

learn to choose slide A from {A,B} → *choose real A from {A,B}*

Another useful relation might be that the hens trained to choose the slide profile of Conspecific A, might then be seen to choose real Conspecific B from the same options, that is -

learn to choose slide A from {A,B} → *choose real B from {A,B}*

So neither of Premack's (1976) criteria are necessary in demonstrating the applicability of Candland's (1969) results to real chicken interactions. Also, Premack's account of representation does not include a comprehensive definition of "responding in the same way".

Catania (1973) elucidated this issue of response similarity. Although button pushing and saying "This one is my mother" might appear as topographically different responses, they might both have the same function. In the presence of a photograph of one's mother, either response might produce the same maintaining consequence (e.g., presentation of money). Any response that is made to a particular stimulus, and which produces the same consequences, can be understood to be from the same "operant class" of behaviours (Catania, 1973) - that is, operating to produce the same consequences. The same operant class of behaviours can occur in the presence of different stimuli - for example, real mother instead of photograph. Skinner (e.g., 1974) called this occurrence of an operant class across stimuli "generalization". Thus, differentially responding to photographs in an experimental setting can be understood as a "mother recognizing behaviour", which might generalize to a topographically different form of the same behaviour when the photographs are substituted for the real mother. However, moving this behaviour from the experimental to the natural setting produces a problem for this account of behaviour similarity, because the maintaining consequences are different across the two situations. Saying "Hello mother" at the airport and pressing buttons in the experimental setting are not the same operant behaviour, according to Catania's account, if one is maintained by the company of the mother, and the other by the provision of money.

This problem can be overcome to some extent by grouping the consequences into functional categories, in the same way as the operant class of behaviours: Those which maintain the behaviour, and those which do not. The definition of "generalization" of a behaviour, from the experimental to the natural setting, is now very vague. The preceding stimulus and the topographical forms of both the behaviour and the consequence are all different. Further, maintaining consequences might differ not only in topography, but also in efficacy. For example, a person might be more or less likely to forgo a certain amount of money than to leave an airport without her or his mother. However, an experimenter can test for this generalization of a behaviour across different settings if that experimenter specifies, before the fact, exactly what topographical forms of behaviour will and will not count as generalization. This is the definition of "generalization" that is used in much human clinical psychology (e.g., Baer, Wolf & Risley, 1968; Scott, Himadi & Keane, 1983), and is also adopted here to examine the utility of Candland's results. From here onwards, the term "represent" will be used to mean that responses to the representative image will generalize to real objects that the image depicts (cf., Premack's first criterion). The contention here is that if chickens' discriminative key pecking in the presence of slide images can be shown to generalize to some discriminative behaviour in the presence of real chickens, then Candland's results are useful for the understanding of chicken-

chicken interactions, and also that the slide images represent those conspecifics to observing chickens. If no such generalization can be shown, then Candland's results are not useful for the understanding of real chicken-chicken interactions.

There are two reasons for this discussion of behaviour similarity, or generalization. First, this discussion is applicable to any study that involves the use of two-dimensional stimuli to represent real objects. There might be many studies of human visual perception employing two-dimensional images in which it would be expedient to test for, rather than assume, a generalization of behaviour to real objects. Second, there is a large amount of literature on discrimination of slide images by animals which is explained by inferences of unobservable cognitive functioning (e.g., "concept formation"), and very little which assesses the generalization of the discriminations to real objects. For example, although authors claimed to have demonstrated individual recognition of conspecifics, or same species "concepts" in macaques (Dasser, 1987), pigeons (Poole & Lander, 1971) and chickens (Ryan, 1982), none of these authors tested for generalization of their subjects' discriminations to real animals.

The theory inherent in concept formation studies is that if an animal learns to discriminate between experimenter-defined categories of objects, and then generalizes this discrimination to novel objects, then the animal must have a "concept" of those categories (Wasserman, 1993). Slide images of objects, rather than real objects, are used in most concept formation experiments (Mazur, 1997). Slide image discriminations have been used as evidence that pigeons have concepts of "people" (Herrnstein & Loveland, 1964), "trees" (Herrnstein, 1979), and "fish" (Herrnstein & de Villiers, 1980). Yet no known study has shown that pigeons can discriminate people, trees or fish from other things. The intention here is not to brand concept formation studies as "meaningless", or "irrelevant to the real world", but to evaluate the utility of claims that various animals can discriminate between other animals or objects, when no such discrimination has been demonstrated. Many studies which use the concept formation paradigm are conducted not just to demonstrate unobservable "concepts", but to examine the observable effects of arrangements of image elements on discriminations. For example, Biederman (1987) examined the visual features of complex, inanimate objects necessary for human object recognition, and Kirkpatrick-Steger, Wasserman, and Biederman (1996) examined the relations between features necessary for image discriminations in pigeons. In both of the following examples of concept formation experiments, however, the authors claimed to have demonstrated concepts of conspecifics in their subjects.

Dasser (1987) used a matching-to-sample task to train a long-tailed macaque to match colour slide images of social group members. For each trial, the macaque had to match one of two comparison images, each depicting a different group member, to a sample image which depicted another view of one of the comparison group members. During test trials, the macaque correctly matched a significantly high number of comparison images to sample images which displayed non-overlapping parts of the same animal. For example, the sample image might have been of a head, and the comparison images of lower bodies. Dasser (1987) upheld this result as unassailable evidence that the macaque had concepts of its group members, and that slides can be used to represent those group members, "because it [the result] could not have been achieved unless the subject recognized the stimulus animals." (p.71). Dasser's procedure is not clear, though. It seems that the macaque had been presented with the test slides during training trials (and possibly also during immediately preceding experiments), along with other slides showing whole-body views of the stimulus animals - which, of course, included both of the non-overlapping parts used for samples and comparisons in test trials. This aspect of the procedure might defeat Dasser's conclusions, but her description is too vague to be sure exactly what happened with the repeated slide use. Even without this procedural confound, an objection can be made that there might have been visual features common across non-overlapping body parts, such as colour, fur density, or body proportions, and therefore that the macaque responded to these features, rather than an "internal representation" of the stimulus animal. Dasser neither tested the macaque's ability to match slide images to the real animals, nor discussed the possibility of doing so. This is a peculiar omission, because a successful demonstration of this would be much stronger evidence that the slides represented the group members.

Ryan (1982) reported individual recognition of conspecifics in six bantam roosters. The roosters were trained to discriminate between two sets of slide images. Ten slides in one set showed differing views of one rooster, and ten slides in the other set showed differing views of another rooster. The subject birds generalized this discrimination to the five novel views of each of the two object roosters that were presented during test trials. Ryan (1982) claimed this result as "conclusive" evidence that the subjects formed concepts of the object roosters, and that "chickens are capable of using the information present in colour slides to discriminate between conspecifics" (p.218). Dasser (1987) was less definite about Ryan's result. She pointed out that the ten different views of the object birds used for training precluded essentially novel views, and therefore the test trials required only weak generalization. She also objected that as the real object birds had not been seen by the subjects, the generalization must have involved features common to test and training stimuli, "rather than an unconditioned association of the picture and the real object" (Dasser, 1987, p.72). Again, Ryan did not mention the possibility of testing the subjects' "individual recognition of conspecifics" for generalization to the real object birds. Ryan's stimuli were also unrealistic, in that the slide images were projected 5 cm high on the response wall.

No known study has reported that chickens' discrimination of slide or photographic images has successfully generalized to real conspecifics. Dawkins (1996), cited earlier, reported a failure of her hens to generalize their discrimination of real conspecifics to photographs. Further, Bradshaw and Dawkins (1993) reported a failure of hens to discriminate slide images of familiar conspecifics better than unfamiliar conspecifics. Following Dasser's argument above, if the hens had formed "an unconditioned association of the picture and the real object", then they should have been better able to generalize their discrimination to images of familiar, rather than unfamiliar, conspecifics. Therefore, Bradshaw and Dawkins concluded that their result was evidence that slide images do not represent real conspecifics for hens. There is only one known report that an animal's discrimination of slide images has successfully generalized to real conspecifics. Trillmich (1976) trained budgerigars to approach one of two conspecifics in a Y-maze. In subsequent tests, the budgerigars failed to show any generalization to slide images of the birds. One of the budgerigars was then trained to discriminate between slide images of two conspecifics, using ten different views of each (similar to Ryan's experiment outlined above, except that the images were life-sized and showed only head and neck regions). During the following test trials, this subject showed a significant generalization of the discrimination to the real object birds (64 correct target choices out of 95 trials).

The purpose of the following experiment was to test for generalization of hens' discrimination of conspecifics, from slide images to the real object hens. The conditions under which these discriminations were both trained and tested were kept as similar as practically possible. The visible features of the slide images and the real object hens were made as similar as possible to aid the probability of successful generalization. Response topography and maintaining consequences were constant across training and testing for the same reason, and also so that the "generalization" tested here could be easily defined.

Method

Subjects

Subjects were the same hens (71-76) used in Experiment 1, and were kept under the same conditions. Experiment 2 was started soon after the completion of Experiment 1.

Apparatus

The same apparatus was used as in Experiment 1. Slides showing profiles of two different hens, used for the initial training phase of Experiment 1, were presented again during the training phase of this experiment (see Figure 1.2A). The real hens that these slides depicted were presented for the testing phase of this experiment.

The experimental chamber was modified for the presentation of the real hens as shown in Figure 2.1. The frosted glass projection screen was replaced with a matte-black plywood wall containing a Perspex screen. The Perspex screen was 380 mm wide, 320 mm high and 150 mm from the chamber floor. In front of the plywood wall and screen was an easily removable matte-black cardboard screen, and directly behind were two matte-black cubicles, 300 mm front to back and occupying exactly a half of the width of the tunnel each (200 mm). The wall between the cubicles was a hinged doorway, allowing ready access to the cubicle more distant from the door side of the tunnel. A 180 mm long by 330 mm wide aperture was cut into the roof of the tunnel, above the cubicles and directly behind the plywood wall. A 100-W lightbulb was placed above this aperture, directly above the dividing wall, at the plywood wall end. The 100-W bulb was lit throughout the test session. A box housed the bulb and covered the aperture, which is not shown in Figure 2.1. Two lights mounted on the roof of the chamber indicated to the experimenter when to replace and remove the cardboard screen, and in which cubicles to place the target and non-target hens for the following trial. These lights were driven by the same software as the response keys and food hoppers.

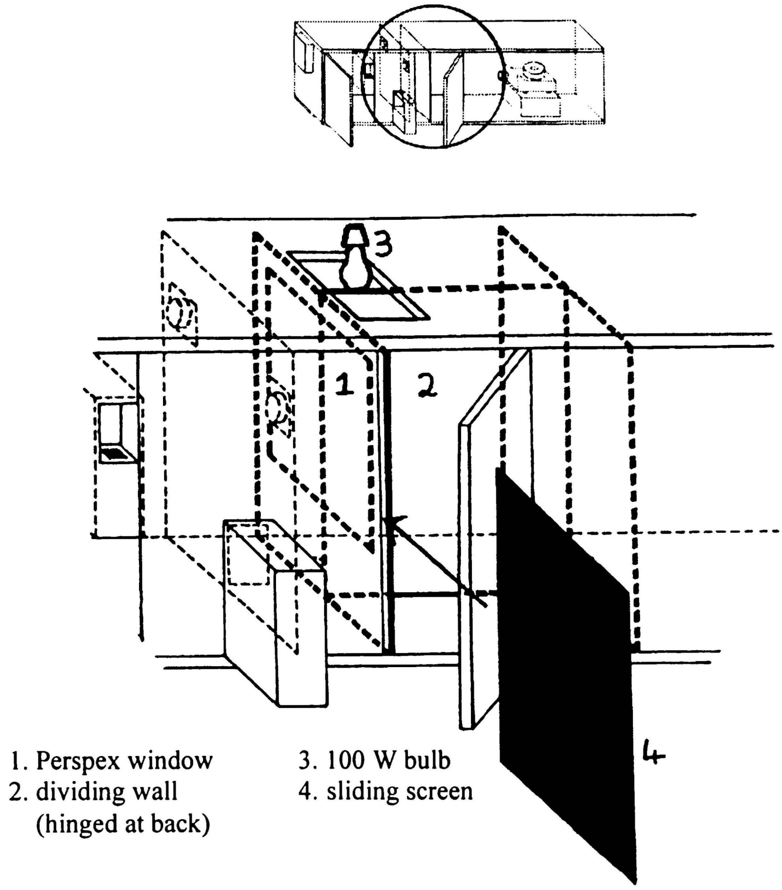


Figure 2.1. Modifications to the chamber for the presentation of real hens.

Procedure

The initial training phase used in Experiment 1 was reintroduced. The only difference here was that there were 44 trials in each session. This training phase continued until all hens had correctly chosen the target profile in at least 40 out of the 44 trials in a session, for four consecutive sessions. The test phase was conducted in the session following the 40 training sessions needed to meet this criterion.

For the test phase the projector and screen were replaced with the plywood wall and cubicles shown in Figure 2.1. The test session differed from the training sessions only in that real hens were presented instead of slide images. The object hens were those that had been photographed to produce the slide images used in the training sessions. The target test hen corresponded to the target profile for each subject hen (therefore, one test hen was the target for one half of the subjects, and the other test hen was the target for the other half of the subjects). The controlling software was programmed to drive two lights on top of the chamber, instead of the slide projector. These indicated to the experimenter when to remove and replace the cardboard screen, and in which of the two cubicles to place the target hen for the following trial. Each trial began with the cardboard screen removed, and one test hen in each cubicle. As soon as a choice response was made, one of the two lights was lit to indicate that the cardboard screen was to be manually placed in front of the plywood wall and Perspex window. This mimicked the closing of the projector shutter, and took about 0.5 s to do. The tunnel doorway and hinged dividing wall were then opened and both of the test hens removed, and then immediately put back into the cubicles, with the target test hen placed in the cubicle indicated by the sequence of lights, and the non-target placed in the other cubicle. The test hens were removed at the end of every trial, irrespective of whether they were replaced in the same order. The indicator light was extinguished at the end of the ITI, signaling that the experimenter remove the cardboard screen for the next trial. The removal and replacement of the test hens was done by two people, and practiced for some time before conducting the test session.

Results

Proportions of correct choices for the test session, along with those for the last five training sessions, are shown in Figure 2.2. Data are listed in Appendix B. All hens chose target test hens at around chance levels, ranging in proportions of correct choices from .614 for Hen 72 down to .409 for Hen 75.

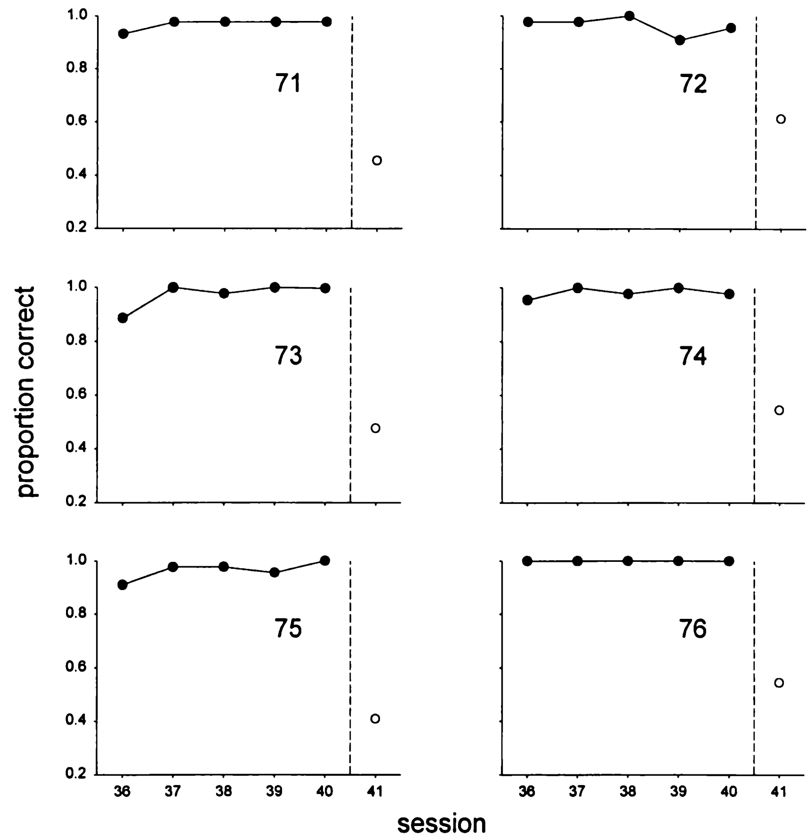


Figure 2.2. Proportions of correct choices of slide profiles for the last five training sessions (filled symbols), and of real birds in the test session (unfilled symbols).

Discussion

None of the hens generalized the discrimination that they had learnt between slide images to the real hens. The arrangement of the experimental apparatus for the presentation of the real hens (shown in Figure 2.1) was designed to minimize any differences between the training and test sessions, except for the stimuli presented. Some noticeable differences remained, however. Firstly, the Perspex window which replaced the projection screen was larger than the area over which the slides were projected. The window was made this size so that the object hens would still be visible if they moved their heads up, or to the side. Thus, there was a greater area of stimulus luminance in the test trials. Secondly, the 100-W bulb was used as it appeared to produce roughly the same overall illumination as the projected slides, when viewed from behind the wall holding the response keys. This illumination was not measured. A closer match of overall illumination would probably have been achieved if the luminance levels had been measured and adjusted. Thirdly, the object hens were not static.

These hens were observed inside the cubicles for a while before the test session was conducted, both from above and from behind the response wall. The object hens often moved their heads to either side, but sometimes remained still for varying periods - apparently fixating, and very occasionally pecking, the Perspex window (possibly looking at their own reflections).

These differences were all minimal, compared to those that would be expected outside the experimental chamber. Real hens move, so this is not a factor that should be controlled in testing for the generalization of slide discriminations to real hens. Although one effect of this movement was that the observing hens were presented with novel views of the object hens during the test trials. This effect might be at least partially addressed by training discriminations with slide images showing many different views. Illumination could have been better controlled, but Trillmich (1976) reported an unmeasured difference in illumination between slide image and real conspecific presentations with his experiment that produced successful generalization in the budgerigar. Therefore, the results of Experiment 2 indicate that hens' responses to slide images do not generalize to conspecifics, and that slide images do not represent real conspecifics, for hens.

Hens might be able to learn to generalize their discriminations from slide images to real conspecifics. Trillmich's budgerigar made this generalization only after extensive training with both the slides and the real conspecifics, so this learning was probably the crucial factor. If the testing phase of this experiment had continued for a number of sessions, the hens might have learnt to discriminate between the real conspecifics, and this discrimination might have been learnt faster than if the hens had not been exposed to the training phase (the relative speed of acquisition could be tested with a control group with no prior slide training). That is, there might have been some generalization from slides to conspecifics which was not evinced within the small number of test trials conducted. This "slow" generalization would show some relation between responses to slides and conspecifics. This relation would be less useful than the spontaneous generalization that was tested for - results such as Candland's would have to carry a stipulation like: "These results are generalizable to individual recognition of conspecifics in chickens, but only after a certain amount of discrimination training with real conspecifics." However, this relation is more useful than none. A study of relative speed of acquisition, and eventual generalization, of slide image and object discriminations would be worthwhile for establishing such relations.

Animals' abilities to generalize from one visual discrimination to another might be expected to be species specific. Chickens might learn to generalize visual discriminations at a different rate from many other species (if at all). Warren (1965) compared the results of several studies of visual discrimination tasks in different species. He noted that different species learned to generalize the requirements of the tasks at different rates: Rhesus monkeys learned to generalize relatively quickly; cats and squirrel monkeys generalized less quickly, and rats and squirrels showed very little generalization at all. Warren (1965) suggested that animals higher on the "phylogenetic scale" learned to generalize more quickly, because they were more capable of acquiring abstract information. He did not state how phylogeny was scaled. This is another example of the cognitive inference to which Skinner (1953) objected. Perhaps a comparison of specific aspects of species' visual capabilities would show a more directly observable relation with their performances on these tasks than a less well-defined "position on the phylogenetic scale". For example, rats, which have very low visual acuity (Birch & Jacobs, 1979), did poorly on these visual discrimination tasks, but have been shown to do well on similar tasks that involve olfactory (Fagan, Eichenbaum, & Cohen, 1985) and spatial stimuli (Zeldin & Olton, 1986).

As there is no evidence that the slide images in Experiment 1 represented real conspecifics, it is reasonable to assume that the salience of the comb was based on properties of the images, independent of any relation to the birds they depicted. These properties are examined in the following experiment.

EXPERIMENT 3

The extent to which particular stimuli determine whether particular behaviours will follow is often referred to as the degree of "stimulus control" (e.g., Dinsmoor, 1995; Rilling, 1977; Terrace, 1966). Complete stimulus control is evinced when a particular behaviour reliably follows the "controlling" stimulus only, that is, when a particular stimulus is discriminated from all others. At the opposite end of the scale, a behaviour which generalizes across all preceding stimuli shows no control by any particular stimulus. In general, stimuli which are more physically disparate along one or more measurable dimensions such as size or colour are more likely to be discriminated, although Dinsmoor (1995) warned that stimulus disparity might be confounded with "stimulus salience" - which he defined as the disparity between a stimulus and its background. The same absolute difference between two stimuli might be more or less discriminable, depending on the salience of those stimuli.

An animal will rarely discriminate a stimulus from its background or discriminate between two stimuli on every occasion that the stimuli are presented. In psychophysical studies, the term "threshold" is often used to describe what level of intensity (or "salience", as defined by Dinsmoor (1995)) of a stimulus, or difference in intensity between two stimuli, is necessary for discrimination to occur in a particular animal. An "absolute threshold" is usually defined as the level of stimulus intensity which will result in discriminations being made on one half of the presentations of that stimulus. That is, half way between perfect discrimination and no discrimination. Similarly, the difference in intensity necessary for an animal to discriminate between two stimuli on one half of the presentations is usually defined as the "differential threshold" (Blough & Blough, 1977).

In cases where two stimuli vary in more than one feature, such as the hen profiles presented in the last two experiments, any combination of those features could, theoretically, gain discriminative control. However, when discriminations are learned between complex stimuli, it is usually only a subset of the features that gain control over that discrimination - and often, only one. This has been demonstrated extensively with pigeons (Terrace (1966) gives some of reviews), and also with many other species including rats (e.g., Thomas, Burr & Eck, 1970) and humans (Stromer, McIlvane, Dube & Mackay, 1993). Many different factors can affect the selection of the particular discriminative feature, including the disparity or salience of the features, the particular consequences that maintain the discrimination, prior experience with the stimuli, species and individual preferences (Mackintosh, 1977).

"Blocking", "masking" and "overshadowing" are terms used to describe the ways in which particular features of complex stimuli gain discriminative control. When a discrimination between stimuli has already been learnt, an added feature is less likely to gain discriminative control. For example, if an animal learnt to choose the larger from any pair of buttons of the same colour, and then the buttons were recoloured (say - larger always red and smaller always green), the size rather than the colour will probably continue to maintain discriminative control. This precedence of discriminative control by learnt features over new features is called "blocking" (Dinsmoor, 1995). Mackintosh (1977) described processes of "masking" and "overshadowing". "Overshadowing", first described by Pavlov (1927), occurs when a feature gains discriminative control at the exclusion of another. "Masking" is a similar phenomenon, except that the dominant feature obscures the expression, rather than the acquisition, of discriminative control by the subordinate feature. This means that if the dominant ("masking") feature is held constant across the stimuli, or removed, then the subordinate feature will be observed to maintain discriminative control. For most of the hens in Experiment 1, the comb "overshadowed", rather than "blocked" or "masked", the beak and wattles. All three features were presented together throughout training, so "blocking" was not a possibility. Every possible combination of features was held constant across the two profiles for the test sessions, while the other features varied. Therefore, the same opportunity for demonstration of discriminative control was given to every possible combination of features. Yet, for four hens, only differences in the comb evinced discriminative control.

Most studies of complex stimulus control can be assigned to one of two general categories (Dinsmoor, 1995). In one category, precisely measured artificial stimuli are used, such as wavelengths of light and line orientations, to quantify the features of complex stimuli that gain discriminative control. Concept formation studies comprise the other category. Authors of these studies often claim that there are no measurably consistent differences between discriminative stimuli, so that the subjects must be matching (usually visible) images to internal representations of concepts (e.g., Dasser, 1987; Herrnstein & Loveland, 1964; Honig & Stewart, 1988). Some discrimination experiments, however, might not be easily contained within one of these categories. For example, Troje, Huber, Loidlt, Aust and Fieder (1999) trained pigeons to discriminate between images of male and female human faces, presented on a PC monitor. Rather than argue that they had demonstrated a "gender concept" in the pigeons, as many previous researchers of concept formation (cited in their paper) might have done, they carefully controlled various dimensions of the digital images to discover which were maintaining the discrimination. They found that the pigeons could generalize this discrimination to new images which had been modified so that both male and female faces had the same shape, but not to new images modified so that shape remained but average luminance was constant across the images of faces of different gender. On the basis of these results, as well as results of previous studies, Troje et al. (1999) concluded that pigeons (and possibly other birds) discriminate images on the basis of overall luminance, rather than shape. They reported that this was an unexpected result because shape, rather than luminance, differences are more discriminable by humans and easier to programme in artificial neural networks (both unpublished studies cited in Troje et al. (1999)).

Candland (1969) assumed that the reason the comb was the most "salient" feature in his experiment was that the comb represented the visible feature by which real conspecifics would be discriminated. There is no evidence that chickens respond to slide images in the same way as to real conspecifics and therefore no evidence that the slide images represented conspecifics, or that the comb images represented real combs. So there might be properties of the comb images, independent of their relation to any real comb, which make them more discriminable than the beak and wattle images.

The general aim of Experiment 3 was to examine why the comb, instead of the other facial appendices presented in the slide images in Experiment 1, gained discriminative control for most of the hens. Candland's (1969) experiment is the only known study which has attempted to isolate discriminative features of complex images for chickens. Reports of complex stimulus control in other species might be of limited relevance, in that the results might be specific to the other species examined. However, a relevance of pigeon studies, particularly Troje et al. (1999), to the visual discriminations made by hens is argued in the discussion of this experiment.

Experiment 3 was a series of six experiments, which are grouped together and labeled as "conditions" here because they share the same procedure, and in some cases, the same training phase. The purpose of Conditions 1 to 3 was to see how the hens would respond to progressively more "abstract" images. That is, the hens were presented with images which were progressively more unlike conspecifics. In the first condition, the profiles to which the combs, beaks and wattles were appended in Experiment 1, were replaced with spheres. For Condition 2, the facial appendices were presented upside-down and were not attached to anything. In all further conditions, geometric shapes were presented instead of facial appendices. If the hens continued to respond to images which clearly did not depict conspecifics, in an arguably similar way to the hen profiles in Experiment 1, then this would provide good evidence that their discriminations were controlled by features of the slide images, independent of any relation to conspecifics. If the hens' response patterns were to change with any new condition, this would indicate what properties (those changed between conditions) of the images controlled their discriminations. Conditions 4 to 6 were conducted to test for specific discriminative control properties of some of the image features.

Method

Subjects

This experiment was made up of six different conditions. For the first 5 conditions, subjects were the same as in Experiments 1 and 2 (Hens 71 to 76). However, Hen 72 died after Condition 2. Six Shaver Starcross hens were used for the final condition, numbered 81 to 86. These were ten months old at the beginning of training, and had had some experience of key-pecking on basic reinforcement schedules. Eighty percent body weights were maintained for all hens, as with the previous two experiments.

Apparatus

All apparatus and controlling software was the same as that used in Experiment 1. Different sets of slides were used. Examples are shown in Figure 3.1, and explained under each condition heading in the following procedure.

Procedure

In general, the procedure followed for each condition of this experiment was the same in every detail to that of Experiment 1, with three exceptions. First, the slide images were different (see Figure 3.1). Second, there were a maximum of 44 trials each session, as with Experiment 2. Every hen completed all 44 trials in every test session, and also in very nearly every training session. Third, there was no initial training phase in any of these conditions. Each condition started with the baseline training phase. Also, the test phase of Condition 5 was different from the test phases for Conditions 1 to 4 and 6, and the stability criterion used to decide when the test phase would begin was not used for Conditions 4 and 5. Procedural differences for these two conditions are described next. The conditions were conducted in chronological order.

Condition 1. This was a repeat of Experiment 1, with slide images of the three different facial appendices (combs, beaks and wattles) affixed to a white sphere made in Photoshop 3.0®. Two new hens, unfamiliar to the subjects and of a different breed (Ross Brown), were professionally photographed. The photographs were then digitally scanned and the facial appendices arranged onto copies of the same white sphere. All colour slides used in Conditions 1 and 2 were recorded onto Agfachrome Professional® 100 ASA slide film with a Kodak Sayett PFR® film recorder. One of the training slides is shown in Figure 3.1A. The apparent difference in shading between the two spheres shown in Figure 3.1A is caused by the uneven luminance across the projected image (the "hotspot" mentioned in Experiment 1).

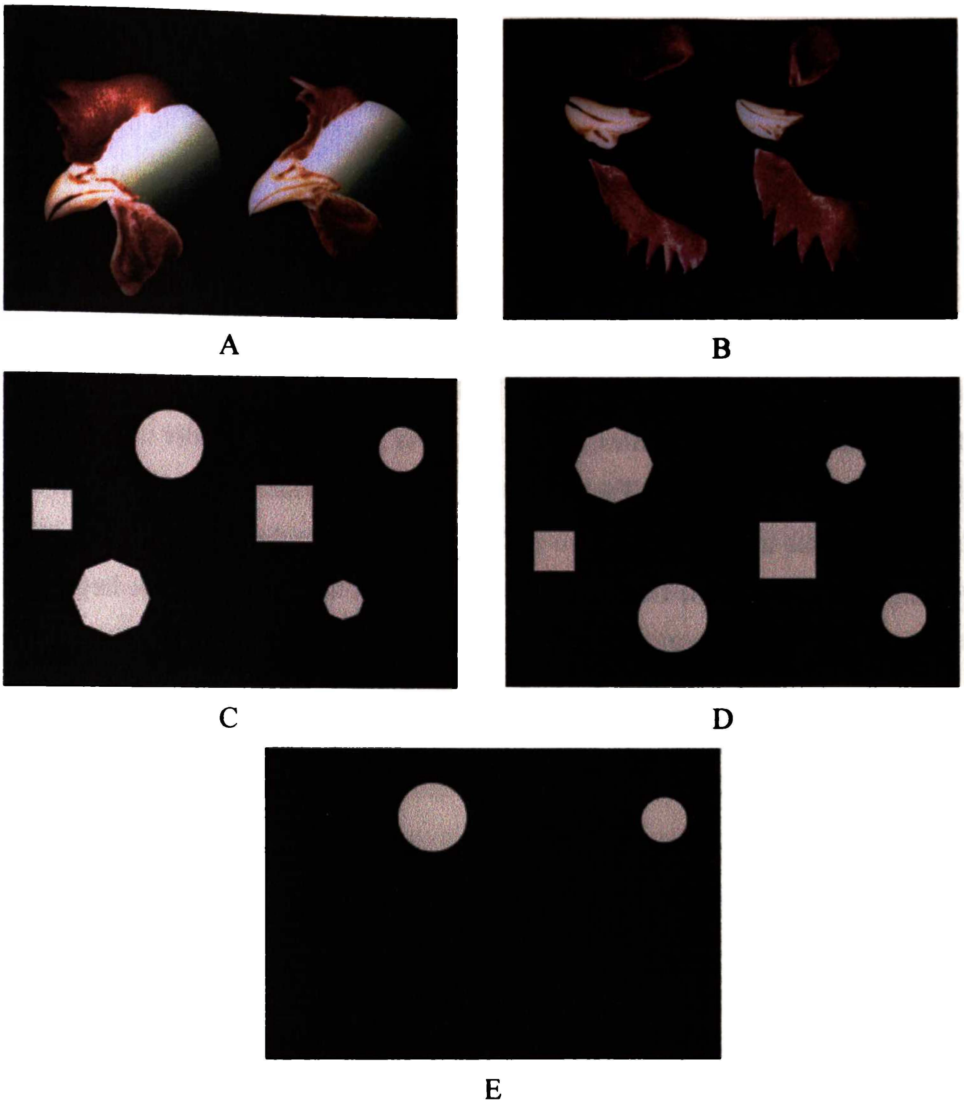


Figure 3.1. Examples of slides. A and B were training images in Conditions 1 and 2, respectively. B was a training image in Conditions 3 and 6. D is an inverted version of C, showing orientation of shapes in Condition 4. E is a test slide used in Condition 5.

Test slides showed the combs, beaks and wattles arranged on the spheres in the six combinations listed in Table 1.1. All slides were projected onto the screen at the same size as the slides in Experiment 1. Therefore, the combs, beaks and wattles were presented much larger than life size in the current experiment (compare Figure 3.1A and B with Figure 1.2). All hens' responding met the stability criterion after 85 training sessions in Condition 1.

Condition 2. Photographs of another two Ross Brown hens, unseen by the subject hens, were digitally scanned and arranged in Photoshop 3.0® to produce the images used for Condition 2. These images were of upside-down facial appendices on a dark background. One of the slides used for training is shown in Figure 3.1B. Training and testing proceeded in exactly the same way as Condition 1, and all hens' responding met the stability criterion after 137 training sessions.

Condition 3. This proceeded the same way as Conditions 1 and 2. The slides were 35 mm monochrome negatives, and depicted two sets of geometrically defined two-dimensional shapes: circles, squares and octagons (see Figure 3.1C). The shapes were made from black cardboard and photographed in all the various combinations on a sheet of white cardboard. For the Latin-square arrangement of test sessions (Table 1.1), the circle, square and octagon were matched to the comb, beak and wattles, respectively. As Hen 72 died before the test phase, the arrangements under this column of Table 1.1 were ignored. The shapes all differed in area. The circle was intermediate in area both within each of the two sets, and also in difference between corresponding shapes across the two sets. That is, in one set the square was the largest shape and the octagon was the smallest, and in the other set the octagon was the largest and the square was the smallest. Between corresponding shapes across the two sets, the octagons varied in area the most, and the squares varied the least. All hens had been trained to the stability criterion after 105 sessions.

Condition 4. The same slides that were used in Condition 3 were used again, but turned upside-down (Figure 3.1D). This condition consisted of a test phase only, which was a continuation of the Condition 3 test phase. That is, when Condition 3 had been completed, one more training session was conducted with the original slide orientation (to check 75 % correct choice levels, as was done between all test sessions), then the first test session of Condition 4 was imposed, with the slides inverted. The purpose of this test was to see whether the stimulus control exhibited by any particular shapes in Condition 3 would be retained by those shapes in their new positions.

Condition 5. Training sessions in this condition were the same as those in Condition 3. As all the hens had already met the stability criterion in that condition, stability was not reassessed for this condition. Eight more training sessions were conducted after completion of Condition 4, to check that all hens were consistently choosing target shape sets at greater than 75 % accuracy (which they did). Testing was done in one session, with the squares and octagons completely obscured in the slide images, so that the circles provided the only cues for target choices. This test was made to see whether the stimulus control exhibited by the circles in Condition 4 was retained when the other stimulus elements were removed.

Condition 6. This was a repeat of Condition 4, using six new hens. This was done to test for possible learning effects in the results of Condition 4. The stability criterion was met after 68 training sessions.

Results

Condition 1

Numbers of errors made by each hen in choosing the full target set of facial appendices attached to spheres in each test session of Condition 1 are shown in Figure 3.2. These data are presented in the same way as those from Experiment 1 and Candland's (1969) paper – that is, as absolute numbers of errors. Dotted lines on the plots mark chance responding (50 % correct), and "chance level responding" includes numbers of errors in the range 16 to 28. Numbers of errors beyond this range are significantly removed from chance (p<.05). As with Figures 1.5 and 1.6, the combinations listed at the bottom of the plots note the differences between the two images. For example, in the "beak" combination, the two images differed only in beaks, and both images showed the same comb and wattles (see Experiment 1 Method). The box plots on the left mark the mean and range for the last five sessions of the training phase. All data presented in this section are listed in Appendix C.

It can be seen that all the hens made relatively few errors in choosing between combinations in which the comb was different. All hens, except 76, chose between combinations that included the same comb ("non-comb" combinations) at around chance levels. Hen 76 responded at chance level to the combinations that differed only in beak, and well above chance accuracy to all other combinations. Hen 76 made fewer errors in responding to combinations that included different wattles, than to the combinations that did not.

In general, these results are similar to those of Experiment 1 (cf., Figure 1.5), in that most hens made few errors in choosing between combinations that included the comb, and chose between non-comb combinations at chance levels. However, there are a few differences which are noted here for later discussion. In Experiment 1, Hen 72 made fewest errors to combinations that included both the beak and either the wattles or comb. In the current condition, this hen made fewest errors to combinations that included the comb. Four hens showed a clear separation in the of numbers of errors made to comb and non-comb combinations in both experiments: 71, 73, 74 and 75. All of these hens made proportionately fewer errors to the comb combinations in this current condition. As can be seen in Figure 3.2, the smallest numbers of errors made by any hen approximately corresponded to the numbers of errors made during the last five training sessions. Hens 74 and 75 responded more

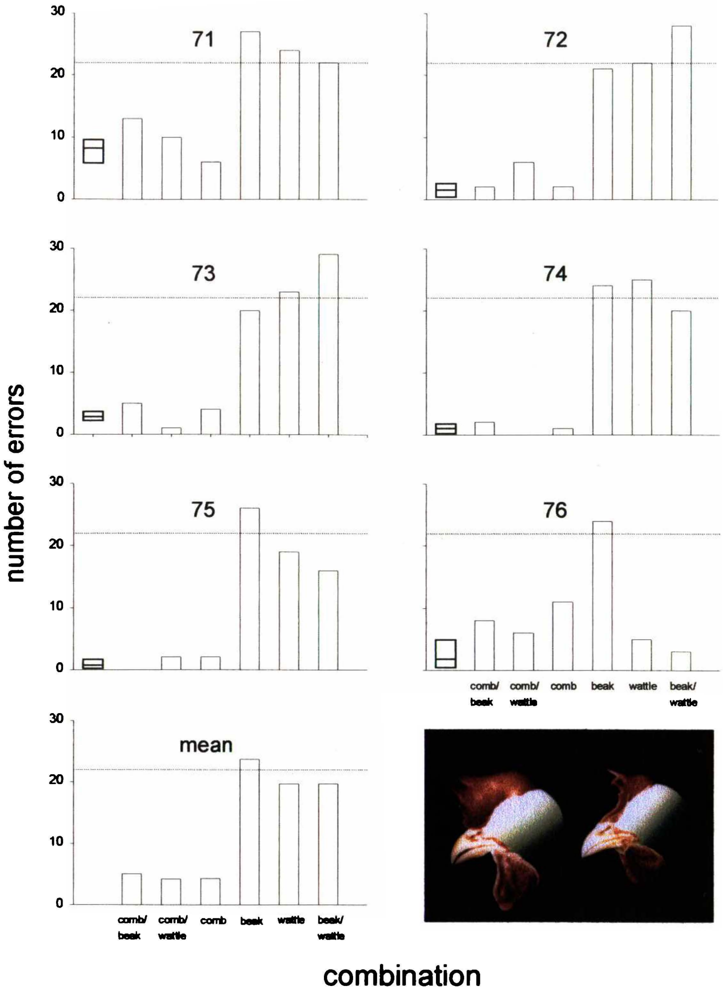


Figure 3.2. Numbers of errors made (out of 44 trials) to each combination of facial appendices attached to spheres in Condition 1. Box plots mark the mean and range of the last five sessions in the training phase.

accurately during the final five training sessions of this condition, than they did in Experiment 1 (both averaged 98 % correct in Condition 1, and 87 % and 92 % respectively in Experiment 1). Hens 71 and 73 showed the same accuracy levels over the last five training sessions of both experiments, but both made slightly fewer errors to comb combinations in the current condition: Hen 71 averaged 30 % errors across the comb combinations in Experiment 1, and 22 % in Condition 1; Hen 73 averaged 10 % in Experiment 1 and 8 % in Condition 1.

Condition 2

Figure 3.3 shows that in Condition 2 all hens made fewer errors to combinations of upside-down facial appendices that included the wattles, than to the combinations that did not. There is a clear separation in numbers of errors made to wattle and non-wattle combinations for all hens except 76. Hen 72 made no errors in the last five training sessions.

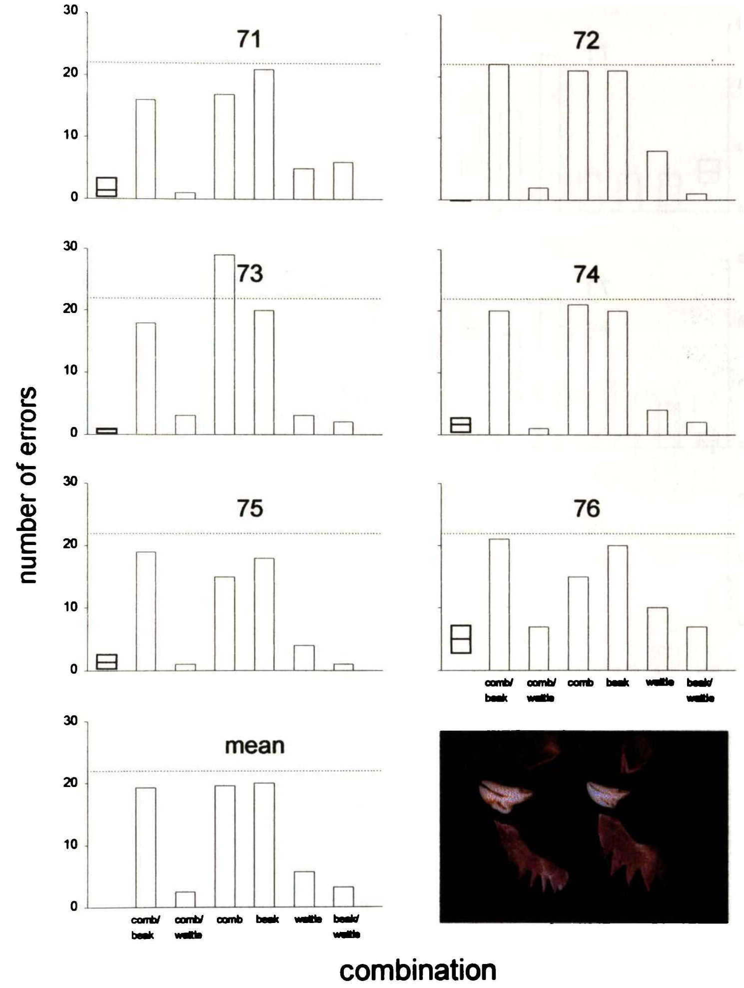


Figure 3.3. Numbers of errors made (out of 44 trials) to each combination of vertically inverted, unattached facial appendices in Condition 2.

Condition 3

It can be seen in Figure 3.4 that all five hens made fewer errors to combinations of shapes that included the circle. The combinations are labeled at the bottom of the plots in the same way as the previous two figures. For example, the "circle" combination means that the two sets of shapes differed only in circle, and both sets included the target square and octagon. There is a clear separation of numbers of errors made to circle and non-circle combinations. Hen 76 also made fewer than chance-level errors to combinations including the octagon.

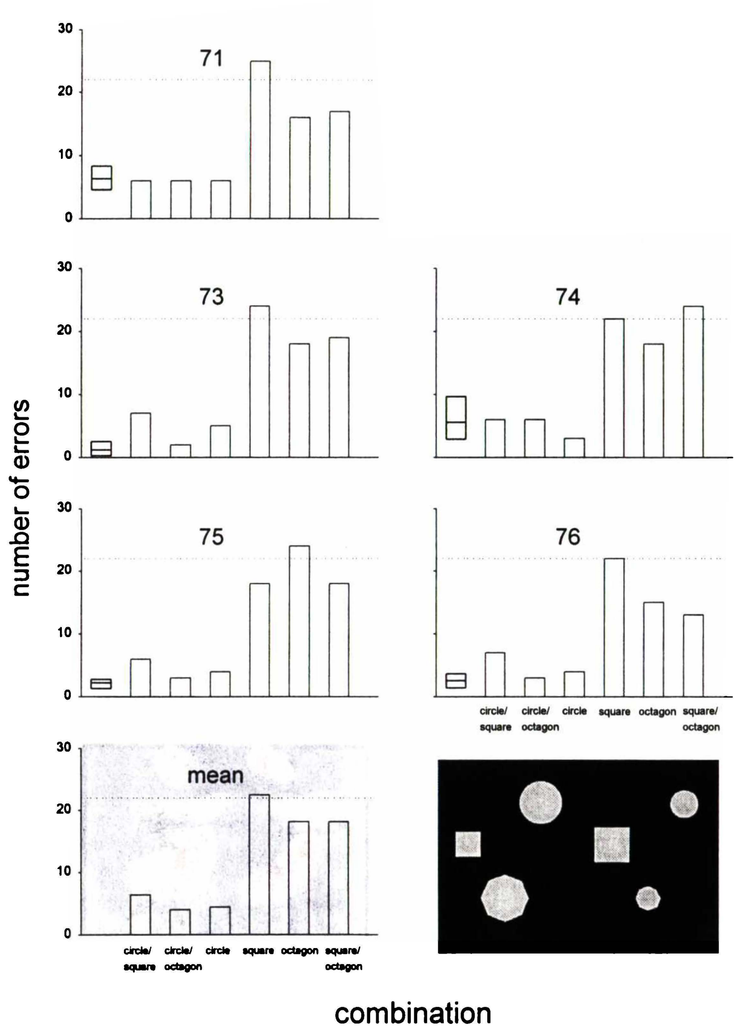


Figure 3.4. Numbers of errors made (out of 44 trials) to each combination of shapes in Condition 3.

Condition 4

Numbers of errors made to test combinations of inverted shapes in Condition 4 are shown in Figure 3.5. Hens 71 and 74 responded at around chance levels to all combinations of inverted shapes. Hen 76 made fewest errors to the "circle/ octagon" combination. Hen 73 made fewer errors to all combinations that included the circle, than to those that did not. Hen 75 made very few errors to the combinations that included both the circle and either the square or octagon, and many more errors to the other combinations.

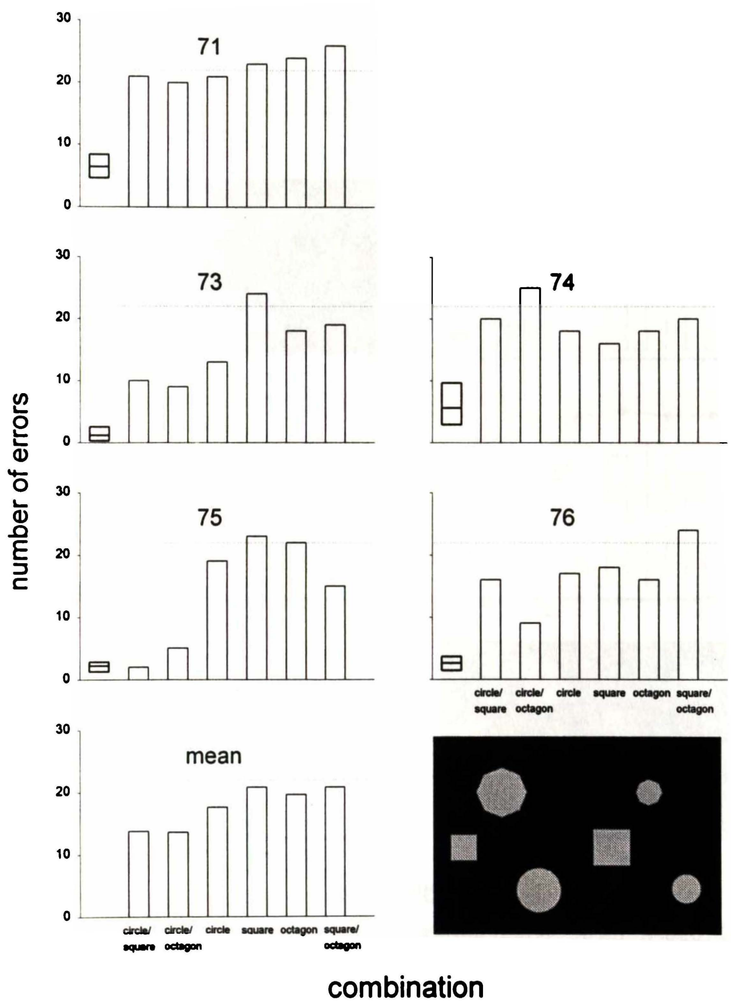


Figure 3.5. Numbers of errors made (out of 44 trials) to each combination of the vertically inverted shapes in Condition 4.

Condition 5

Proportions of correct choices of target circles (marked by unfilled circles on the plots) in Condition 5 are shown in Figure 3.6, together with the proportions of correct trials for the previous five training sessions, during which the full sets of shapes were presented. Hens 71 and 74 chose target circles at around chance levels. Hens 73, 75 and 76 all performed with consistently high accuracy on the training sessions (never more than two errors in a session) and chose target circles at around threshold levels – that is, at around 75 % correct, which is half way between no errors and chance.

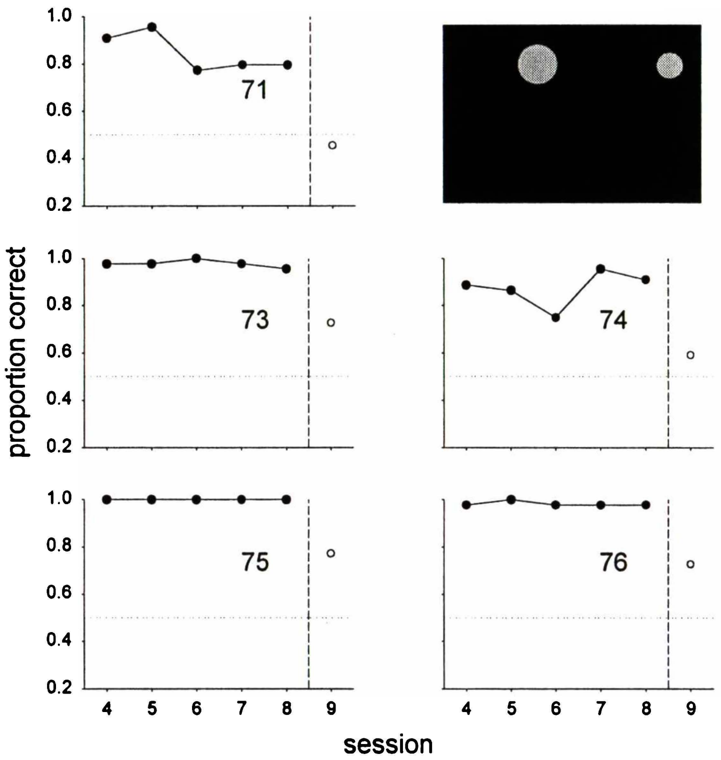


Figure 3.6. Proportions of correct choices of full sets of shapes for last 5 training sessions (filled symbols), and of target circle (unfilled symbols) in Condition 5.

Condition 6

Condition 6 was a repeat of Condition 3, with six new subject hens. As shown in Figure 3.7, all hens made very few errors to combinations of shapes that included the circle, and chose non-circle combinations at chance levels in Condition 6. Any differences between the results of this condition and Condition 3 are negligible.

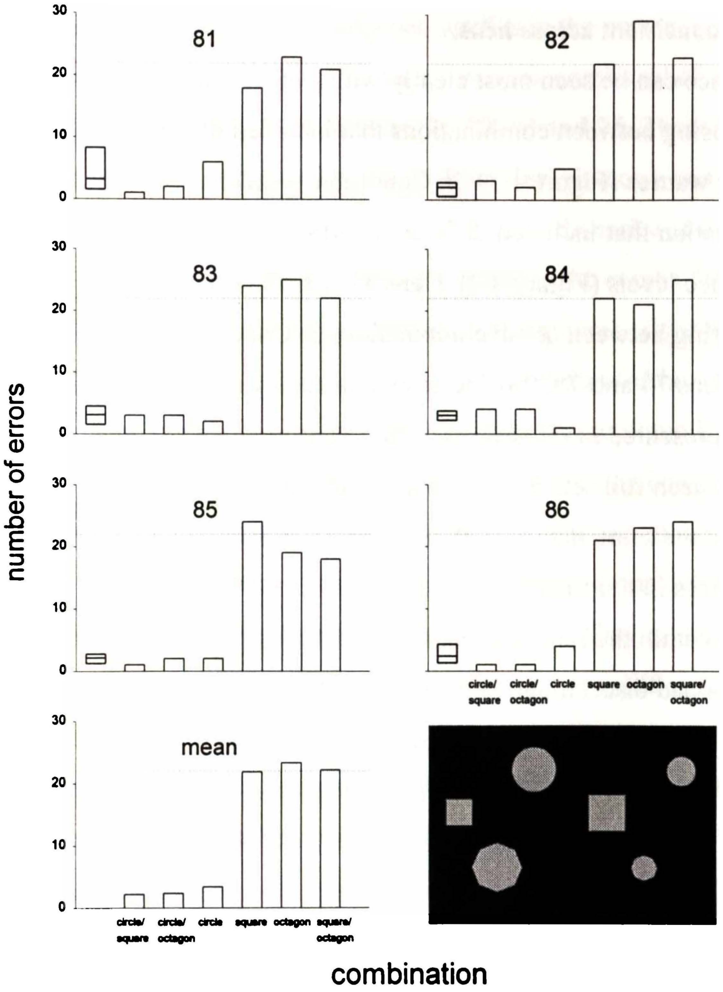


Figure 3.7. Numbers of errors made (out of 44 trials) to each combination of shapes in Condition 6.

Discussion

Condition 1

In general, the results with the combs, beaks and wattles appended to spheres in Condition 1 are similar to those of Experiment 1, in that most hens made fewer errors in choosing between combinations of facial appendices that included different combs, than between combinations that included the same comb (shown in Figures 1.5 and 3.2). These results are also a little different, however, in that most hens made proportionately fewer errors in choosing comb combinations in Condition 1 than they did in Experiment 1. This difference was generally small, but consistent across hens.

This difference can be seen most clearly with Hen 72. In Experiment 1, Hen 72 made fewest errors in choosing between combinations that included different beaks, in conjunction with either combs or wattles (Figure 1.5). In Condition 1, this hen made few errors in choosing between any combination that included different combs, and chose between non-comb combinations at chance levels (Figure 3.2). Hens 71, 73, 74 and 75 all made proportionately fewer errors in choosing between comb combinations in Condition 1 than they did in Experiment 1. For Hens 74 and 75, this increase in accuracy of discrimination between the comb combinations presented in the test sessions was accompanied by an increase in accuracy of discrimination between full sets of facial appendices during the last five training sessions. These two hens made the same numbers of errors to comb combinations as they did to the full sets of facial appendices in the final five training sessions of Condition 1 (i.e., errors to comb combinations are all within the ranges of training levels shown in Figure 3.2). This suggests that only the comb had gained discriminative control for Hens 74 and 75 – removing differences between other features had no effect on their discriminations.

The results for Hens 71 to 75, then, all show (at least slightly) greater discriminative control by the comb in Condition 1 than in Experiment 1. This might have been an effect of continued experience with a similar discrimination task. Hens can show continual improvement on a discrimination task over many months, even after stability criteria have been met (Weavers, Foster & Temple, 1998). If, however, this greater discriminative control by the comb was affected by differences in the images presented, then there are three possible reasons for it.

First, the disparity in appearance between the combs might have been greater than in Experiment 1. A greater disparity might have caused greater discriminative control by this feature (Dinsmoor, 1995). In both Experiment 1 and Condition 1 the two combs differed in size and shape (shown in Figures 1.2 and 3.1A). The sizes, shapes and colours of the combs were not measured. There appears to be a greater difference in colour for the combs in Experiment 1, but greater differences in size and shape for Condition 1. As the combs (as well as the beaks and wattles) occupied more of the slide areas in Condition 1, they were larger on the projection screen, and therefore the size differential was greater than in Experiment 1. According to the results of Troje et al. (1999), the hens were probably more sensitive to differences in size than shape (Size correlates with luminance - if two objects have the same luminance per size unit, then the larger object is more luminant overall). Troje et al.'s results are probably generalizable to hens because hens have visual acuity very similar to that of pigeons. This similarity between chicken and pigeon visual systems, and a suggestion for why lower visual acuity is accompanied by higher sensitivity to size rather than shape, are discussed in the following experiments.

Alternatively (or concurrently), the greater discriminability of the comb might have been affected by smaller disparities in the beaks and wattles in the current condition. Smaller disparities in these features would make the disparity between combs relatively larger. This is an unlikely explanation for the behaviours of Hens 71, 73, 74 and 75. These hens' discriminations were all controlled by combs only in both Experiment 1 and Condition 1 - they were not responding to the beaks or wattles at all. A change in disparity of the beaks might have affected the change in discriminative control from the beaks to the combs for Hen 72.

Second, the replacement of the hen profiles with the spheres might have contributed to the increased discriminability of the combs in the current condition. Although the profiles presented in the baseline phase of Experiment 1 and the spheres presented in Condition 1 were designed to be indiscriminable (they were both duplicates of the same images), their addition to the complex images might have affected the discriminability of those images. Redhead and Pearce (1993, 1998) found that pigeons acquired visual discriminations between two stimuli more slowly when a common feature was added to both stimuli. They argued that the addition of common features to complex stimuli makes discrimination more difficult because these features make the stimuli more similar overall. The spheres depicted less detail than the profiles in Experiment 1, so the presentation of spheres might have aided the discrimination by providing fewer features common to both target and non-target images. As the profiles and spheres formed part of the background for all the facial appendices presented in the current experiments, these might have affected the salience of those features.

Third, the enlargement of all the facial appendices across the projected image areas might have contributed to increased discriminability of the combs in Condition 1. This would have made each of the features more discretely viewable. That is, in cases where the combs gained discriminative control, it is reasonable to assume that it was the combs, rather than other parts of the images, that were being fixated. In Experiment 1, the beaks and wattles were closer to this fixation point, and therefore more likely to be within the field of view. Given Redhead and Pearce's (1993, 1998) argument above, the addition of these features within the fixated field of view are likely to have made the discrimination more difficult. The distance of the beaks and wattles from the fixation point in Condition 1 meant that they were either more removed from the central field of view, or at least (if image points other than the comb were fixated) that they were more spatially separate from the comb.

Cook, Riley and Brown (1992) reported that discriminative control in pigeons was more often gained by single features of complex visual stimuli, rather than multiple features, when those features were separated by greater distances. Although the features in Condition 1 were spatially contiguous, unlike the stimulus features in Cook et al.'s experiments, the hens would have probably had to move their heads in order to fixate each of the features presented in Condition 1.

The following measurements are given to describe the possible necessity for head movements, not to provide conclusive evidence for them. These calculations are based on the assumption that the hens fixated the centre of the combs in the slide images presented in Condition 1 from a completely perpendicular angle, which they probably did not. It is more likely that their eyes were closer to response-key level, which was about 96 mm above the centre of the combs. This would make all the angles given here slightly smaller. Lateral viewing distances were measured at around 250 mm for images presented in a similar way in the next two experiments; the measurement technique and results are described in Experiment 4. If the combs were fixated perpendicularly from 250 mm, then the beaks would have been centred at 16° below this fixation point, and the wattles at around 26° (although the position of the wattles varies between the two full sets of appendices). The maximum possible angle that a chicken can refixate by moving its eye is 15° (Turkel & Wallman, 1977). Therefore, the hens in Condition 1 would have had to move their heads to transfer fixation from the centre of the combs to the centres of the beaks or wattles. In Experiment 1, the beaks and wattle centres were all within 12° of the centre of the comb, so head movements were not necessary for fixation of these, according to these calculations.

These three possibilities for the increased discriminative control of the combs are not mutually exclusive. Any combination of these might have contributed, or it might be that none of them contributed and that this was solely an effect of continued discrimination training. Apart from this small difference in comb discriminability, the more important result of Condition 1 was that, for most hens, it was the combs rather than the beaks or wattles that gained discriminative control. This was the same general result as that found in Experiment 1, despite the replacement of hen profiles with spheres. It seems unlikely that Candland would have assumed that the images presented in Condition 1 represented real conspecifics. The facial appendices, though, were images of real conspecific features, and so it could be contended that they might have represented features of real conspecifics, even though they were not attached to hen profiles. It could also be argued that the hens learned to discriminate between real conspecific-representative combs in Experiment 1, and then generalized this discrimination to the combs in the current condition. These possibilities were addressed in some of the following conditions. One purpose of this experiment was to investigate reasons why the comb gained discriminative control as a feature which did not represent that of a real conspecifics'. This might have happened if the combs were more disparate in appearance than the beaks and wattles. Another factor might have been the position of the combs in the images.

It is possible that when the slides were presented in Condition 1 and Experiment 1 the hens fixated the combs, rather than the beaks or wattles, because they were closest to eye level and therefore required the smallest eye or head movements. It is theoretically possible that more than one feature could have gained discriminative control. However, as the combs gained high levels of discriminative control for most of the hens (few errors made in each training session), further head or eye movements necessary to refixate the beaks and wattles would have been very rarely reinforced by the provision of food. For most trials, the discriminative control gained by the uppermost feature was sufficient for the hens to obtain food. If this hypothesis is correct, then the schedule of food presentation might have influenced the discriminative control gained by the combs. In following Candland's (1969) procedure, food was presented after every correct choice in these experiments. The hens might have been encouraged to learn to discriminate more than one feature if food had been presented less often (cf., Mackintosh, 1977).

Hen 76 responded at above chance accuracy to all combinations that included either different combs or different wattles, though fewest errors were made to wattle combinations. So, both the combs and wattles gained discriminative control for this hen. This result is similar to that for Experiment 1, except that in Experiment 1 Hen 76 responded at chance level to the "beak/ wattle" combination.

Condition 2

As shown in Figure 3.3, all hens made few errors to all combinations that included different wattles when the facial appendices were presented upside-down in Condition 2, and chose between non-wattle combinations at chance levels, with one exception. Hen 76 made 15 errors to the comb combinations - one error below the range of chance responding. Hens 72 to 75 made about the same numbers of errors to wattle combinations in Condition 2 as they had to the comb combinations in Condition 1. Thus the same level of discriminative control exhibited by the combs in Condition 1 was transferred to the wattles in Condition 2. All the reasons suggested for the increased levels of discriminative control from Experiment 1 to Condition 1 are equally applicable to the same increase from the combs in Experiment 1 to the wattles in Condition 2. It seems fairly clear, however, that the disparities in size, shape and colour, between wattles presented in Condition 2 were less than those between combs in both Experiment 1 and Condition 1 (see Figures 1.2A and 3.1A and B). Therefore, the difference in proportionate numbers of errors made to the discriminative feature between Experiment 1 and Condition 2 might be accounted for by the removal of the hen profiles, the increased spread of all the features across the projection area, or a learning effect. There did not appear to be continued learning from Condition 1 to Condition 2 for Hens 72 to 75. Hen 71 made fewer errors to wattle combinations in Condition 2 than to comb combinations in Condition 1. In Condition 1, this hen made more errors to comb combinations than Hens 72 to 75, but in Condition 2, Hen 71 made around the same numbers of errors to wattle combinations as Hens 72 to 75. This might have been a learning effect.

Hen 76 responded to the comb combination at just above chance-level accuracy. In this way, Hen 76 showed some discriminative control by both comb and wattles, as this hen had also done in Experiment 1 and Condition 1. All the other hens showed a clear transfer of discriminative control from the combs in Condition 1 to the wattles in Condition 2. This strongly supports the hypothesis that the uppermost feature is most likely to gain discriminative control. It seems fairly clear from Figure 3.1A that there was a greater disparity in size between the combs than the wattles, and so it was likely to be the position, rather than the disparity, that caused the wattles to gain discriminative control in Condition 2. These two factors might not be mutually exclusive. Some disparity is necessary for discriminative control, and the disparity of the wattles in Condition 2 was large enough to allow accurate discrimination. If the wattles had not been disparate enough to allow easy discrimination, then the next uppermost feature might have gained discriminative control. The shapes presented in Condition 3 were controlled for disparities so that a clear distinction could be made between disparity and position in gaining discriminative control. If size disparity was the greater factor, then the octagons would have gained discriminative control. If position was more important, then the circles would be the most discriminative feature.

Condition 3

All the remaining hens (Hen 72 died during the training phase) showed the same patterns of responding to the sets of geometric shapes in Condition 3 as they did to the upside-down facial appendices in Condition 2 (shown in Figures 3.3 and 3.4). That is, they all made few errors in choosing between combinations that included the uppermost feature (circles) and chose between other combinations at chance levels, except Hen 76, who chose between lowermost feature (octagons) combinations at just beyond chance-level accuracy.

These results provide almost conclusive evidence for the hypothesis that it is the uppermost feature that will gain discriminative control. Only two possible objections remain. First, that circles are somehow intrinsically more discriminable than octagons (which were most disparate in size). This is very unlikely. The hens were more likely to have discriminated between size disparities, regardless of shape (c.f., Troje et al., 1999). The difference in shape between circles and octagons is clearly much less than between the combs and wattles in the previous conditions, and the uppermost feature gained discriminative control in those conditions, regardless of shape. Second, that the hens learned to discriminate the combs in Experiment 1 because, as Candland (1969) assumed, the features represented those of real conspecifics and the comb is the visual feature that gains discriminative control in interactions with real conspecifics. The hens might have generalized this discrimination of the uppermost features to those presented in Conditions 1 to 3. This possibility is addressed in Condition 6.

Condition 4

Inverting the slides for the test sessions in Condition 4 altered the relation of the shapes to each other, but not the appearance of the shapes themselves (Figure 3.1C and D), because all the shapes were symmetric about their horizontal diagonals. Condition 4 was conducted to see if the discriminative control by the circles that was learned in the training phase of Condition 3 would remain when the circles were repositioned at the bottom of the slide images. Although the circles were the only discriminable feature for four of the hens in Condition 3, the circles' relation to the other features (above them) might have formed an integral part of their discriminative control. This seemed to be the case for most hens. Hens 71 and 74 chose between all combinations of inverted shapes at chance levels (Figure 3.5). Hen 73 chose between circle combinations with above chance accuracy, but made more errors than when the circles were at the top in Condition 3 (Figure 3.4). Hen 75 accurately discriminated between combinations that included the circles in conjunction with either the squares or the octagons, and chose between all other combinations at chance levels. Hen 76 responded at above chance accuracy to the "circle/ octagon" combination only. These results all show that the circles retained some discriminative control, for some of the hens, in their new positions, but this control was greatly reduced.

Condition 5

The purpose of Condition 5 was similar to that of Condition 4 - to see whether the exclusive discriminative control exhibited by the circles in Condition 3 would be retained when the other shapes were removed. Figure 3.6 shows that this seems to depend on the level of discriminative control gained by the full sets of shapes. Hens 71 and 74, who varied in accuracy from .75 to .955 proportions of correct responses throughout the previous five training sessions, chose between circles in the test session at chance levels. Hens 73, 75 and 76, who had responded with consistently high accuracy for the previous five training sessions (never more than two errors in a session), all chose between the test circles at around .75 correct. This is the threshold level, so the difference between the circles was just barely detectable for these three hens.

Condition 6

Condition 6 was conducted to test for any learning effects that might have contributed to the results of the previous conditions. The numbers of errors made by the new hens to the various combinations of shapes are shown in Figure 3.7. All the hens made few errors to combinations that included the circles, and chose between non-circle combinations at chance levels. The numbers of errors that the new hens (Hens 81 to 86) made to circle combinations were about the same, or fewer, than those made by Hens 71 to 76 in Condition 3. These results show that both the selection of the uppermost feature for discriminative control, and the level of that discriminative control, were not influenced by learning effects.

General discussion of Experiment 3

Two general patterns emerged from Experiment 3. First, that when presented with complex slide images, the uppermost feature gained discriminative control for most of the hens, usually at the exclusion of the other features. Second, that the level of this discriminative control was slightly higher for all the images presented in Experiment 3 than in Experiment 1. Both of these results are strong evidence against Candland's assumption that the combs gained discriminative control for his chickens because they represented the combs of real conspecifics. It is more likely that Candland's (1969) chickens discriminated between the combs because they were the uppermost feature of the slide images.

This preference for the uppermost feature might be related to either the position of the response keys, or the eye heights of the chickens. Rather than response keys, Candland used 15.25 cm by 10 cm response panels, onto which the slides were projected in his experiment. Although Candland (1969) did not describe his response panels in any more detail, it seems that pecks made to any part of the panels were equally effective. Therefore, the actual placement of the response keys in the current experiment does not seem to be the crucial factor. The hypothesis that features of complex visual stimuli closer to eye level will overshadow other features could be further tested by moving the slide images higher up on a projection screen, so that other spatially distinct features are closer to eye level. The hypothesis would be supported if middle or lower features gain exclusive discriminative control when they are closer to eye level. However, this result would be fairly uninteresting. It is unlikely that researchers would want to arrange for selective discriminative control in this way. It might be more worthwhile to examine how closely visual features need to be grouped together in order to avoid this overshadowing. There might be a point (measured in degrees of visual angle) at which all spatially distinct features of a complex visual stimulus are so close to the fixation point that discriminative control by any feature is no longer influenced by the positions of those features. Whatever this visual angle might be, though, it must be smaller than that used to present life-sized images of conspecifics in both Candland's experiment and Experiment 1.

Given the results of both Experiments 2 and 3, it seems unlikely that slide images represent conspecifics for hens. As discussed in Experiment 2, hens might learn to generalize between discriminations of slide images and discriminations of real conspecifics after extensive training. This type of training was not examined. The following experiments were designed to gain some insight into what hens "can see" in the images that they were presented with, and therefore, to possibly better understand the hens' responses to those images. As many studies of chickens' visual behaviour have been reported (e.g., Candland, 1969; Dawkins, 1995, 1996; Guhl & Ortman, 1953; Ryan, 1982), it is surprising that the species-specific visual responses of chickens have not been studied as extensively as those of many other species. Knowledge of how a particular subject species responds to experimental stimuli differently from other species might be important. It might be worthwhile, for example, to understand why Troje et al.'s (1999) pigeons behaved so differently from humans in discriminating images by their luminance, rather than shape - especially here, if hens are expected to behave similarly.

EXPERIMENT 4

So far in this thesis, hens' visual behaviours have been examined in terms of factors such as those that might be involved in the maintenance of social interactions, or the positioning of the stimuli in the experimental setup. A very useful way of understanding the relation between visual stimuli and hens' responses to them might be to break it down into smaller parts. That is, it would be worthwhile to understand how the hens can respond to visual stimuli prior to analyzing the hens' responses to them. As an extreme example, if an analysis of the hen visual system suggests that a particular object is invisible to a hen, then this understanding is surely more valuable than postulations of social or stimulus control mechanisms in explaining a hen's apparent lack of response in the presence of the object. Similarly, a visual system analysis which indicates that two images "look the same" to a hen should serve as an excellent explanation for an observed lack of differential control. The value of a visual system analysis is a global approach to understanding the effects of visual stimuli; that is, an understanding of how much of any visual stimulus can be involved in influencing discriminations.

Hens' colour vision capabilities, lateral eye placement and corresponding retinal receptor distribution have already been outlined in the introduction to this thesis. Probably the most important feature of an animal's visual system is its resolution, or the animal's ability to discriminate fine detail. Visual resolution is often studied in terms of "acuity" (e.g., Jacobs, Birch & Blakeslee 1982; Schusterman & Balliet, 1970; Yarczower, Wolbarsht, Galloway, Fligsten and Malcolm, 1966). Acuity might be measured by presenting grating patterns and determining a threshold frequency grating; that is, how many lines per unit of width can be discriminated. Units of width are best expressed as the visual angle (field of view) that the grating pattern occupies, as this accounts for both the absolute size of the pattern or object, and the distance of the object from the observer. Absolute thresholds of visual acuity are usually given in cycles per degree of visual angle (cyc/°). Visual acuities have been measured for humans at 30 cyc/° (Spence, 1934); for falcons at 160 cyc/° (Fox, Lehmkuhle & Westendorf, 1976; Reymond, 1987); for gerbils at around 1.5 cyc/° (Baker & Emerson, 1983); and for hens at around 4.2 cyc/° (DeMello, Foster & Temple, 1992). Humans' visual acuity can be measured with an eye chart. The eye chart contains lines of common letters or numbers that decrease in size down the chart. The smallest line of type that can be read is taken as a measure of acuity. However, the use of acuity as a measure of visual resolution excludes an important dimension. The letters on the eye chart and the lines in the grating patterns are usually black on a white background, so that measurements are made at a uniform high contrast. A more comprehensive measure of visual resolution takes into account variations in contrast between objects and their backgrounds. If measures of absolute contrast thresholds are made at a range of spatial frequencies, a function can be fitted which indicates a "window of visibility", or a measure of what objects can be resolved by a visual system as a function of both the objects' spatial frequency and contrast. To this end, visual resolution is commonly measured as a "contrast sensitivity function" (CSF – e.g., De Valois, Morgan, & Snodderly 1974; Merigan, 1976; Northmore & Dvorak, 1979).

An illustration of this window of visibility is shown in Figure 4.1. The grating pattern increases in spatial frequency from left to right, and decreases in contrast from top to bottom.

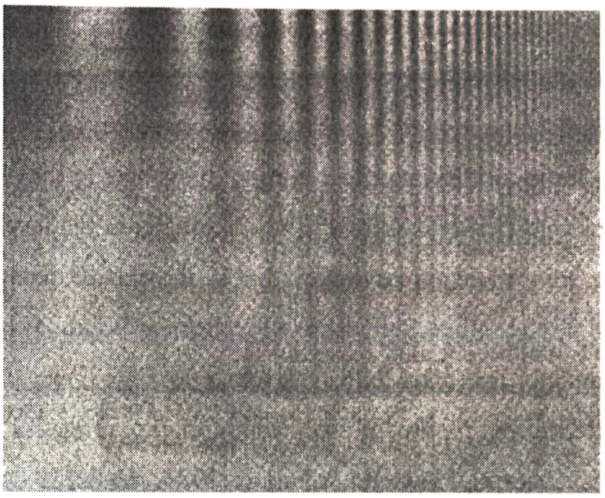


Figure 4.1. A sine-wave type function of print intensity. The wave increases in frequency from left to right and decreases in contrast from top to bottom. Adapted from Cornsweet (1970, p.343).

The print intensity in this figure varies gradually between light and dark phases. This is a sinusoidal, or "sine-wave" function. CSFs are measured using sine-wave, rather than "square-wave" (hard-edge bars) gratings because hard edges are composed of a number of different spatial frequencies. Each spatial frequency must be isolated in order to measure a contrast threshold at that frequency. The pattern in Figure 4.1 is not a true sinusoidal function as, apart from the changing frequency, the mean print intensity is higher than zero. The lowest intensity in any sine-wave grating can be no lower than the lowest possible intensity of the surface that contains it (here, the darkest possible print).

The pattern in Figure 4.1 should appear as a "U" shape because the mid-range frequencies are discernable at lower contrasts than the lower and higher frequencies. This effect is quantified by the CSF. Point estimates of "contrast sensitivity" are made by reciprocating observed absolute contrast thresholds. An inverted U-shaped function can then be fitted to these point estimates. CSFs are best described by a logarithmically scaled Gaussian function for most species, except rats (Uhlrich, Essock & Lehmkuhle, 1981).

One CSF for chicks has been reported, which was published while this experiment was being conducted. Schmid and Wildsoet (1998) constructed a CSF by measuring the optokinetic nystagmus response (eye movements in apparent response to moving gratings) of male White Leghorn-New Hampshire cross chicks at two, four and eight days since hatching. They placed the chick CSF just below that of the pigeon and noted that this should be expected as the chicken eye is very similar to that of the pigeon except for a smaller retinal receptor density in the chicken.

The purpose of this experiment was to measure the CSF for hens under two different sets of conditions. First, with the same viewing conditions as the previous experiments, so that a CSF could be obtained particular to the experimental setup. Second, with the Perspex wall removed and the projection screen moved closer to the response keys. The Perspex was removed to avoid any optically modifying effect it might have had on the projected grating stimuli. The screen was moved closer to allow the hens a greater range in viewing distance, from which to find a near point of accommodation; that is, the closest distance at which the gratings could be focused on the retina. Suggestions for the near point of accommodation for egg-laying hens range from 117 mm (DeMello, 1989) to a possible upper limit of 300 mm (Dawkins, 1995). Several different reports of the accommodation range for chickens have been made (e.g., Martin, 1993; Schaeffel, Howland & Farkas, 1986; Walls, 1942). However, the accommodation of ground-feeding birds is proportional to their height (Hodos & Erichsen, 1990), which varies greatly across different breeds of chickens. The purpose of the second condition was to produce a CSF which, if different from the first, would be more directly comparable to those of other species.

Method

Subjects

The subjects were 4 ISA brown hens, numbered 43, 44, 45 and 46, and maintained at about 80 % of free-feeding body weights with supplementary feeding of grain after each session. They were about four and a half years old at the beginning of the testing phase. Hen 43 had had some previous experience of key-pecking on basic schedules of reinforcement; the other hens were experimentally naive at the beginning of training.

Apparatus

Chamber. The experimental chamber had the same dimensions as that used for Experiment 1 (Figure 1.1). It was set up the same way, with a Kodak Ectopro 5000® carousel projector backprojecting slide images onto a screen 150 mm in front of the clear Perspex response panel. The projector, response keys, lights and food hoppers were controlled by the same PC as those in Experiment 1. There were two differences in the set-up of this chamber from that of Experiment 1. Firstly, the projection screen was 80 g/m^2 tracing paper, which could be seen through a 40-mm diameter circular aperture, centred 385 mm above the chamber floor. The aperture was cut into a wooden wall, which was painted matte black and took the place of the frosted glass used in Experiment 1. Secondly, there were three 30-mm diameter clear Perspex response keys mounted into the clear Perspex front wall of the chamber. Two side mounted keys occupied the same positions as those in Experiment 1 chamber; the third was mounted centrally, 335 mm from the chamber floor (just below the projection screen).

Stimuli. The slides were glass mounted Ilford XP2® negatives. XP2 is a 35-mm 400 ASA monochrome film. This film was chosen after trialling several monochrome films for its superior latitude of grey scale, which was measured as the range in intensity of projected maximum and minimum grey scale values, as outlined in the paragraph headed *Contrast* later in this section. The slides all depicted sinusoidal gratings of varying frequency and contrast. Examples are shown in Figure 4.2. The gratings were produced using custom software written in C®, and running on a Sun Sparc 2® workstation (Sun Microsystems®) and photographed from the 21" monitor with an SLR camera with a zoom lens. Photographing was done in a darkened room with shutter speed and aperture set at 1 s and fstop12. Sets of four copies of each specific grating used for training sessions were made. Two were oriented horizontally in the projector carousel and the other two vertically. Each orientation was doubled to reduce any possibility that the hens might learn to respond to blemishes or idiosyncrasies of the slides, rather than to orientation. For testing sessions, two copies of each specific grating were made – one for each orientation.

Frequency. To calculate grating frequencies, the visual angle that the projected gratings occupied was first calculated. This was done by mounting a video camera on the right wall of the chamber and filming the hens looking at the gratings and consequently making the correct response. Stills from these video recordings were then superimposed onto recordings of 2-mm square grids placed vertically in the centre of the chamber and filmed without moving the camera. This process yielded pictures like the one show in Figure 4.3, from which the distance from the centre of the hens' pupils to the edge of the grid could be measured. Identifying the video frames where the hens were fixating on the gratings was done by choosing sequences where a hen's head remained in a fixed position (with the right eye oriented towards the grating), while its body continued to move. These distances were then added to those from the edge of the grid to the screen, and to an estimate of the distance from

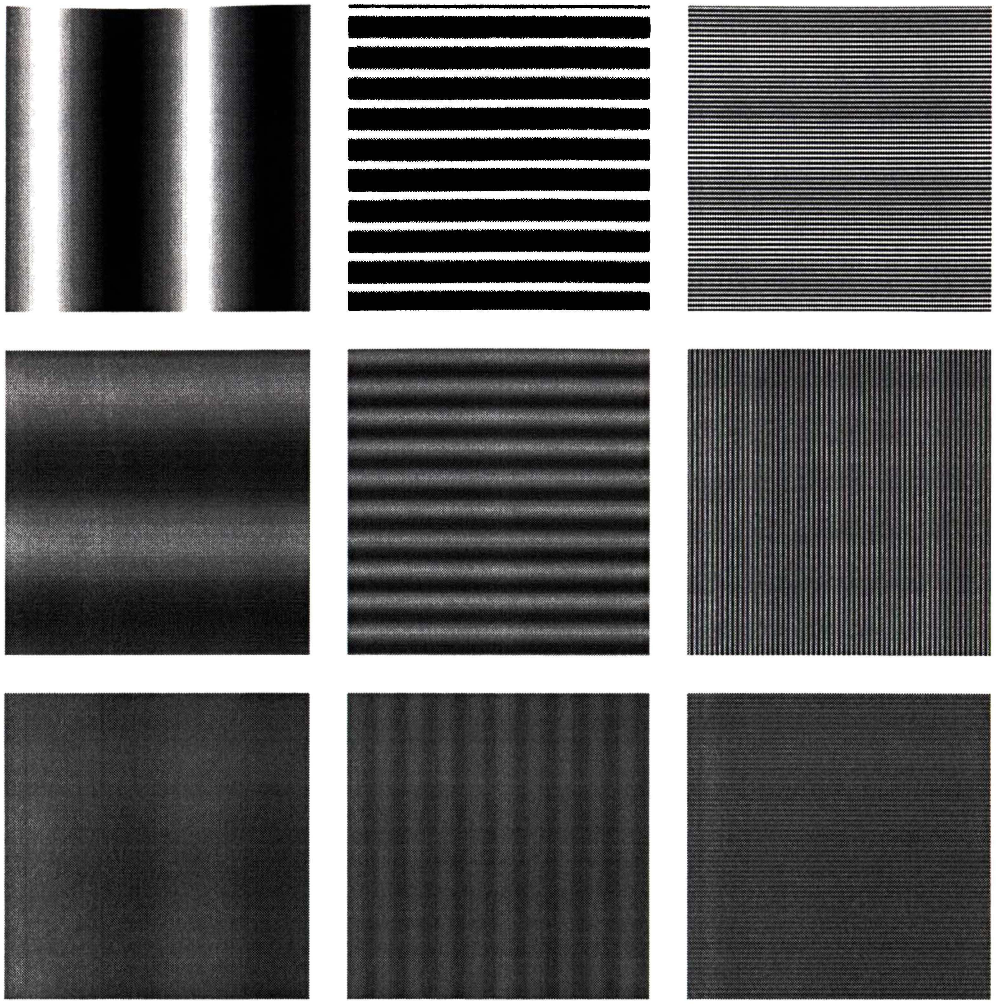


Figure 4.2. Examples of gratings used. These increase in frequency from left to right (2 cycles, 10 cycles and 60 cycles) and decrease in contrast from top to bottom. The contrast levels were specified as: 1, .5 and .1 when they were created in Photoshop®. These printed versions are largely attenuated in resolution and quality. The slide film yielded a much more even graduation of grey scale, with no discernable "graininess" (low resolution). The occasional added grey stripes in the 60 cycle gratings are caused by the halftone printing pattern (Moiree patterns), and were not in the originals. Viewed from 33 cm (normal reading distance), these gratings alternate at 0.288, 1.442 and 8.65 cyc/° of visual angle, left to right.

the centre of the pupil to the retina, following measurements given in DeMello (1989). Viewing distances obtained from this procedure are listed in Appendix D. Observations from Condition 1 showed the hens reliably turning their heads at an angle which appeared to be around 45° away from a line of sight perpendicular to the screen. For the observations in Condition 2, this angle was much more acute (possibly somewhere around 20°, see Figure 4.3 for an example), but just as constant. The mean viewing distance measured for Condition 1 was 250 mm, with a standard deviation of 1.12 mm. The mean and standard deviation of the viewing distances measured for Condition 2 were 145.63 mm and 19.68 mm. Visual angle was calculated using Equation 4.1.

$$\text{visual angle} = 2\tan^{-1}\left(\frac{0.5(\text{image width})}{\text{viewing distance}}\right) \qquad 4.1$$

Thus, a grating projected 60-mm wide on the screen in Condition 1 occupied 15.206° of visual angle, and a 10-cycle grating alternated at 0.658 cyc/° The hens were initially trained with 10-cycle gratings (Table 4.1). Grating frequencies used for testing are listed in the *Procedure.*

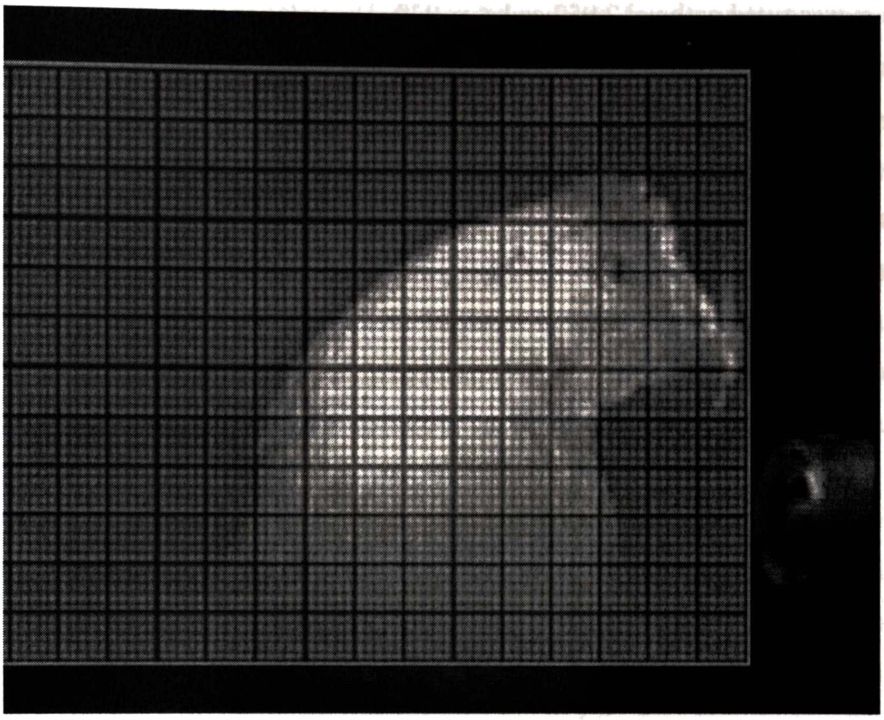


Figure 4.3. Example of image used in determining viewing distances. The grid was remade in Photoshop®, as the original was too low in resolution to be clearly seen once printed. The hen's pupil can be seen on the 5th major horizontal line from the top. This line was perpendicular to the centre of the projected grating. The pupil is centred on the 13th minor vertical line (26 mm) from the front edge of the grid. The distances measured in this way were added to the premeasured distances of front edge of grid to the screen and pupil to retina (see Appendix D).

Contrast. Grating contrasts were originally calculated using the grey scale points provided by the grating generation programme. This was nominally a 256 point scale, however, the usable range was from 1 to 254. The relation between these grey scale values and the intensities of the projected XP2 images (measured in cd/m^2) was calculated with 34 samples of photographed grey scale points, projected onto the screen and measured with a Minolta chroma meter CS-100® chromometer switched to slow speed. The function shown in Figure 4.4 is usually referred to as a “gamma function”, where “gamma” is the parameter that describes the gradient of the function. For cathode ray tube displays, gamma is the exponent of the function:

$$\textit{screen intensity} = \alpha\, \textit{frame buffer (grey scale) value}^{\gamma} + \beta$$

where α and β are fitting parameters (Wandell, 1995, p.415). For exposure properties of monochrome film, gamma is a linear gradient factor (Gonzalez & Woods, 1992). The gamma function in Figure 4.4 shows properties of both the power function and the exposure properties of the film. The asymptotic part at the highest intensities (around 500 cd/m^2) is characteristic of film exposure properties, and the rest of the function is well described by the power function. With the function inverted horizontally and the asymptotic portion (five points) removed, the power function was fitted with $\gamma = 2.952$ and $r^2 = .979$. The value of γ is a measure of the range of intensities that can be produced. Thus γ for the XP2 was higher than that of the other films that were trialled for this experiment. Contrasts were calculated as
contrast = (maximum intensity – minimum intensity)/(maximum intensity + minimum intensity). The output of the projector bulb was adjusted during the test trials so that each grating was projected with an overall luminance of 125 cd/m^2, measured with the same chromometer. These adjustments are listed in Appendix E. The “hotspot” mentioned in Experiment 1 was not discernible or measurable across the viewable portion of the projection screen in Experiment 4, probably because only the central portion of the projected images was viewable.

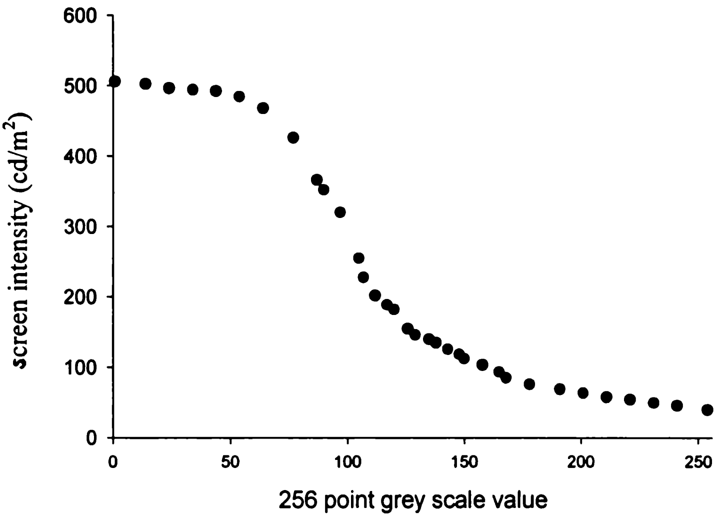


Figure 4.4. Display intensity as a function of grey-scale point value. These were recorded with one 300 W projector bulb set at .5 of maximum output. Output of the projector bulb was adjusted for presentation of each test grating (see Appendix E).

Procedure

General Procedure. Sessions were conducted six days a week. Session durations varied with each experimental phase, and are listed with each. Trials commenced with the presentation of a grating oriented either horizontally or vertically at random (p=.5). After 2 s the centre key, mounted just below the projected grating, was illuminated. Five pecks to this key caused it to be extinguished and the two side keys to be lit. A single peck to either side key resulted in the extinction of both key lights and the projector shutter closing. In cases where a grating was presented vertically, a left key-peck was assigned as "correct", and when a horizontal grating was presented, a right-side key-peck was assigned as a correct response. Pecks to correct side keys were occasionally followed by 2-s presentations of same-side food hoppers, which contained a commercially prepared pigeon food mixture. Frequency of food presentation was reduced throughout initial training (Table 4.1). There were no scheduled consequences for incorrect responses. A 10-s ITI immediately followed either food presentation, or any side key-peck which did not result in food presentation. All experimental events were remotely controlled by the same PC and software used in the previous experiments.

Initial Training. Each session lasted either until food had been presented 30 times, or until 2400 s elapsed, whichever happened first. Hens were initially trained using a single black line on a clear background in the place of the sinusoidal gratings, and by gradually increasing both the distance of the projector screen and the schedule of food presentation. These variations are listed in Table 4.1, and were made after at least three of the four hens had responded correctly on at least 90 % of the trials in the previous session. Screen distances are shown as measurements from the front Perspex wall, on which the response keys were mounted. The controlling MEDPC® software was programmed to select a number without replacement from an array of 15 at the beginning of each ITI (each session began with an ITI), and to count this number of seconds. Food was presented following a correct response only if this number of seconds had elapsed since the beginning of the previous ITI. This variable trial length (TL) contingency is defined in Table 4.1 as the mean value of the array. This contingency encourages waiting in the presence of a grating, before making a choice response. There was a portion of initial training when small increases in numbers of food presentations and decreases in the number of trials per session were noted. No such trends were noticeable in conditions following initial training. A dependency between the two side keys was also programmed throughout this experiment. This was that a particular food hopper would not be raised more than three times in succession unless a correct response had been made to the other side key. This dependency, together with the TL 25.2 s at the end of the initial training phase, resulted in the hens being presented with food following approximately one half of correct responses in each session.

Table 4.1. Initial training regime.

Stimulus	Screen (mm)	TL(s)	Sessions
1 black line	0	-	20
1 black line	0	16.3	23
4 black lines	0	16.3	15
10 cycle grating	0	16.3	66
10 cycle grating	0	19.4	27
10 cycle grating	100	19.4	16
10 cycle grating	150	19.4	64
10 cycle grating	150	23.2	12
10 cycle grating	150	25.2	9

The performance criterion was met in the final session listed in Table 4.1; that is, at least three of the four hens had correctly responded on over 90 % of the trials. Contrast threshold pilot tests were then conducted, starting from the following session. Pilot tests are described in the following paragraph, and were interspersed among 128 training sessions, each of 2400 s duration. Condition 1 immediately followed the final pilot test.

Condition 1. This consisted of interspersed training and contrast testing sessions. Training sessions were automatically stopped after 1600 s had elapsed, during which each hen completed around 50 to 60 trials. Parameters of these training sessions were the same as those listed in the final row of Table 4.1, except that the grating frequencies used were the same as those about to be tested. Data collected from training sessions included the total numbers of trials, numbers of correct trials and total number of food presentations. During training, gratings of a particular frequency were presented at maximum contrast for a number of sessions until at least three of the four hens responded correctly on over 90 % of the trials in a session. Contrast threshold testing was done in the following session using the method of constant stimuli with six sets of gratings of differing contrasts; that is, each contrast level was selected without replacement from an array of six by the controlling software and presented horizontally or vertically at random (p=.5). This procedure was repeated 10 times, so there were 60 trials for each test session. Training and testing sessions differed only in duration and the stimuli that were presented. Data collected from contrast testing sessions were the numbers of correct responses at each of the six contrast levels. In cases where a threshold could not be clearly determined from these data, owing to variability of the proportions of correct trials around the threshold level, the test session was repeated. The 0.14 cyc/° test was repeated once, and the 0.351 cyc/° test was repeated twice. Once the hens had been tested at one grating frequency, training began at the next frequency in the following session. The number of training sessions required to reach the 90 % criterion varied from one or two at the mid-range frequencies to 20 at the lowest extreme (0.132 cyc/°). The highest frequencies tested were different for each hen. All contrast levels for Hen 46 were above threshold during the 7.892 cyc/° test and so this hen was retested at a decreased grating size (8.602 cyc/°). Based on the contrast thresholds revealed at the lower frequencies, Hen 44 was tested at 5.597 cyc/°, and Hen 45 not tested above 3.946 cyc/°. The contrast levels used at each frequency are given in Appendix E. These were chosen by conducting a pilot test series (essentially a prior run of the whole of Condition 1) and selecting sets of contrast levels grouped around thresholds estimated from the pilot. Grating contrasts were originally specified in terms of the grey-scale points provided by the grating production software, and then recalculated according to the corresponding screen intensities (Figure 4.4. Each intensity that was used was directly measured from the screen). The order in which grating frequencies were tested is listed in Table 4.2.

Table 4.2. Order of testing.

	1	2	3	4	5	6	7	8	9
Condition 1							H 43	H 46	H 44
cycles	20	10	5	2	30	60	120	120	120
size (mm)	60	60	60	60	60	60	60	55	85
freq(cyc/°)	1.315	0.658	0.329	0.132	1.973	3.946	7.892	8.602	5.597
Condition 2									
cycles	20	30	60	120	10	5			
size (mm)	45	45	45	50	45	45			
freq(cyc/°)	1.025	1.537	3.074	5.544	0.512	0.256			

Condition 2. This was a repeat of Condition 1, with some modifications to the chamber. The Perspex wall between the response keys was cut away so that the hens had an uninterrupted view of the screen, and the screen was moved forward to 80 mm behind the Perspex wall. The aperture through which the gratings could be viewed was reduced to 35 mm and the width of the projected gratings was reduced to 45 mm. Several of the gratings, as well as several of the even intensity slides used to measure the gamma function in Figure 4.4, were remeasured at this new size. There were no apparent changes in screen intensity. The hens were retrained in this condition with 20 cycle gratings for 150 sessions before viewing distances were remeasured.

Results

Proportions of correct trials, out of 10, for each grating contrast, and for each hen at each grating frequency are plotted in Figures 4.5 and 4.6. Figure 4.5 shows the results from Condition 1. Each datum set was fitted with a sigmoidal curve using an iterative fitting routine. The sigmoidal function, shown below as Equation 4.2, is used to extract 75 % thresholds from psychophysical data (Treutwein, 1995):

$$y = 0.5 + \frac{0.5}{(1 + \exp 1)^{a(b-X)}} \qquad 4.2$$

This sigmoid has two free parameters, shown here as *a* and *b*, where *b* represents the 75 % threshold value of the independent variable and *a* is the gradient of the function at *b*. It can be seen in Figure 4.5 that this function is bounded at .5 and 1. In cases where proportions of correct trials in a contrast test session were too variable to be fitted with the sigmoid function, that test session was repeated and the latest datum set used. This happened for Hens 43 and 46 at 0.132 cyc/°, and for all hens at 0.329 cyc/°. These cases are noted on the plots. Numerals in the upper left corners indicate which repeat session data were used. Raw data and parameters of each sigmoidal fit are given in Appendix E. Hen 45 did not reach the 75 % threshold at any grating contrast in both the 0.132 and 0.329 cyc/° test sessions, and was not tested above 3.946 cyc/°.

The dashed vertical lines in Figure 4.5 mark the obtained 75 % threshold levels (values of *b* from Equation 4.2). Hens 43 and 45 both showed their lowest contrast thresholds at 1.315 cyc/°. The lowest contrast thresholds for Hens 44 and 46 were both at 3.946 cyc/°. The ranges of contrast thresholds across hens and grating frequencies are more clearly shown by the CSFs in Figure 4.7.

Contrast thresholds from Condition 2, for which the screen was moved closer to the response wall and the Perspex removed from between the response keys, are shown in Figure 4.6. Raw data and sigmoid fit parameters are listed in Appendix E. Hen 46 showed the lowest contrast threshold at 0.512 cyc/°. Hens 44 and 45 lowest contrast thresholds were both found at 1.537 cyc/°, and Hen 43's lowest threshold was at 0.512 cyc/°, although this hen's threshold remained almost constant at not more than ± .0057 away from .18 for the three sampled grating frequencies at 0.512, 1.025 and 1.537 cyc/°. Again, the ranges of contrast thresholds across frequencies, across hens, and also between the two conditions are more clearly discernible from Figure 4.7.

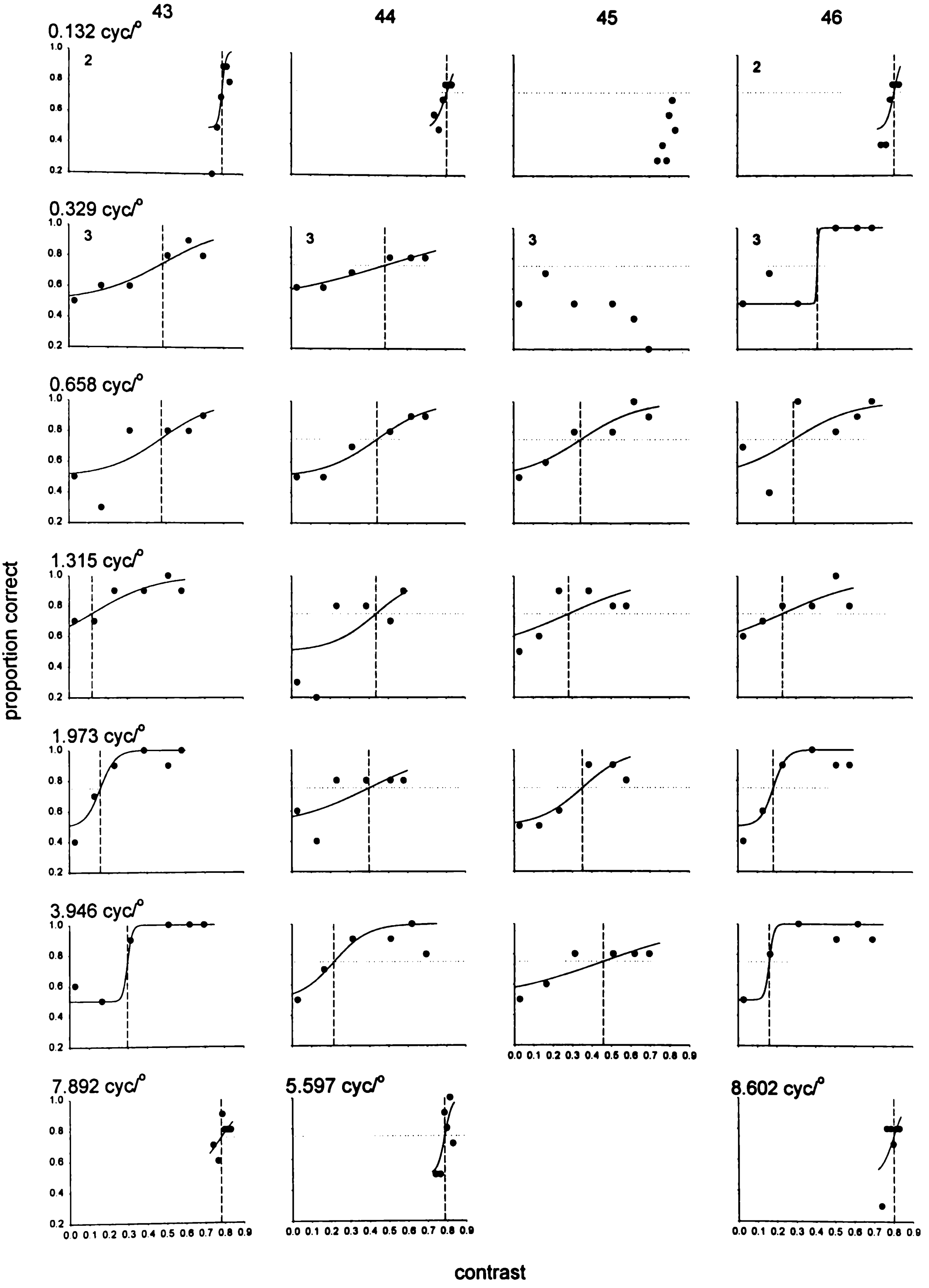


Figure 4.5. Contrast thresholds extracted from Condition 1 test results using Equation 4.2.

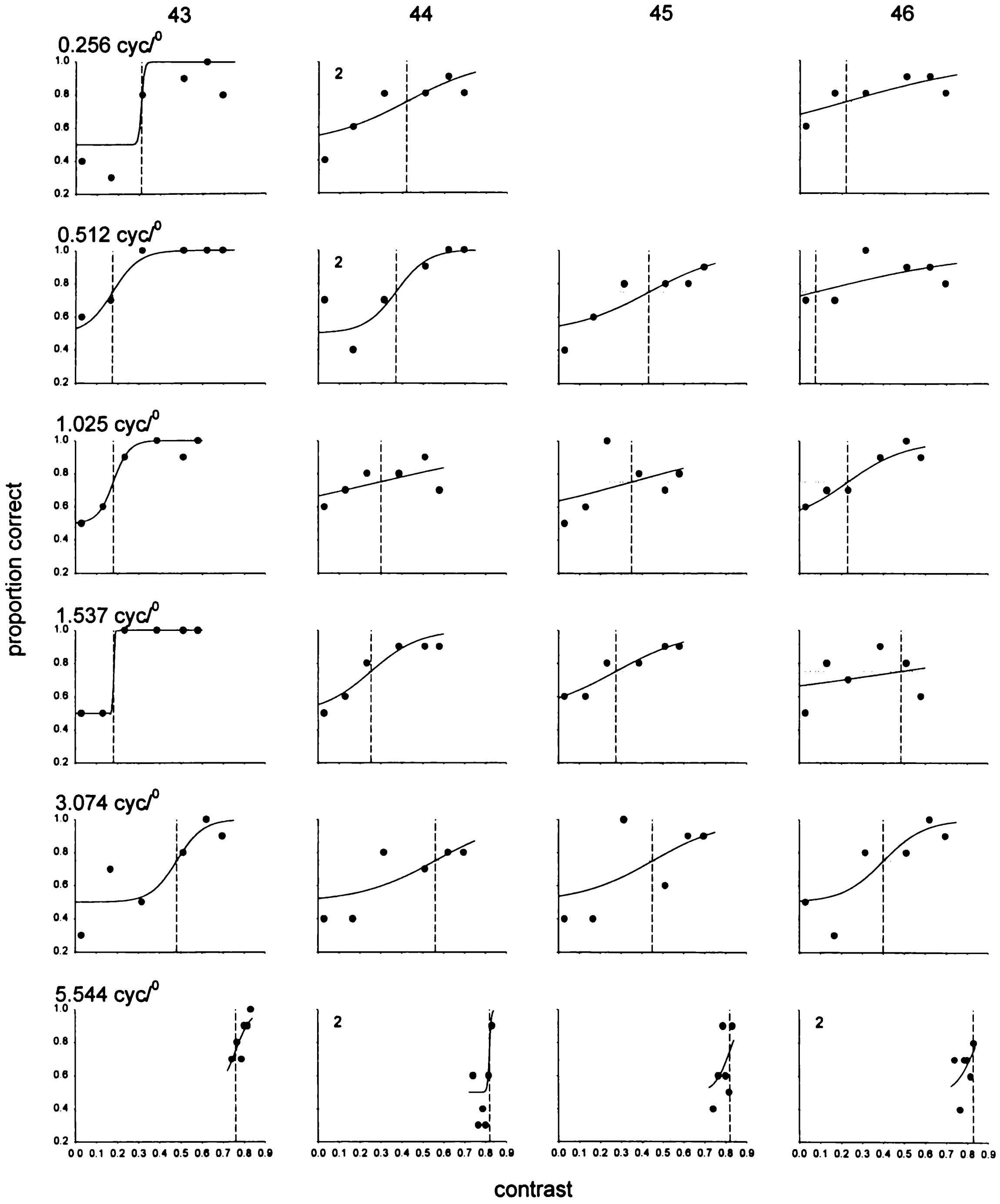


Figure 4.6. Contrast thresholds extracted from test data in Condition 2 using Equation 4.2.

The contrast thresholds extracted from the sigmoidal curve fits (Appendix E) were reciprocated to provide measures of contrast sensitivity. The resultant contrast sensitivity measures are plotted in Figure 4.7. These CSFs are logarithmic Gaussian functions which were fitted using Equation 4.3 and an iterative fitting routine.

$$y = amplitude \times \exp\left(-\left(\frac{\log X - \log \mu}{\log \sigma}\right)^2\right) \tag{4.3}$$

The three free parameters: amplitude, σ, and μ, represent the highest contrast sensitivity, the standard deviation and the mean of the curve, respectively. These parameters, as well as r^2, are listed with each plot in Figure 4.7. The curves were fitted to the original contrast sensitivity scale (1/ contrast threshold) across the ordinate axis, before the ordinate was logarithmically transformed to produce Figure 4.7.

It can be seen in Figure 4.7 that the CSFs for Hens 44 and 45 were relatively low, with peak sensitivities between 2.803 and 3.544. CSFs for Hens 43 and 46 were higher with peak sensitivities ranging from 5.433 to 13.18. Except for the one unusually high peak shown by Hen 46 at 0.512 cyc/° in Condition 2, CSFs for each hen are at about the same level for both conditions. The measure of curve fit, r^2, was always higher for the CSF fits in Condition 2. The most noteworthy result shown in Figure 4.7 is that, for three of the four hens - Hens 43, 44, and 46, the CSF fitted to Condition 1 data (at longer viewing distance) peaks at over twice the frequency of the CSF fitted to Condition 1 data. This difference failed to reach significance at $\alpha = 0.5$ with a paired t-test, however the small number of subjects precludes a statistical interpretation of this result. This result is important because it was not anticipated when the experiment was conducted and it cannot be accounted for by any possible procedural factors or by increasing age or experience of the hens (which would be shown as CSFs of differing amplitude across the same range of spatial frequencies).

CSFs of various species are plotted with those found for the hens in Figure 4.8. CSFs for the hens appear to be slightly lower and flatter than that of the pigeon. The hen CSF for the longer viewing distance is labeled "hen lateral", and for the shorter viewing distance in Condition 2, "hen front". Limitations on the absolute placement of these functions are discussed in the following section, along with very strong physiological evidence that there should be two different hen CSFs.

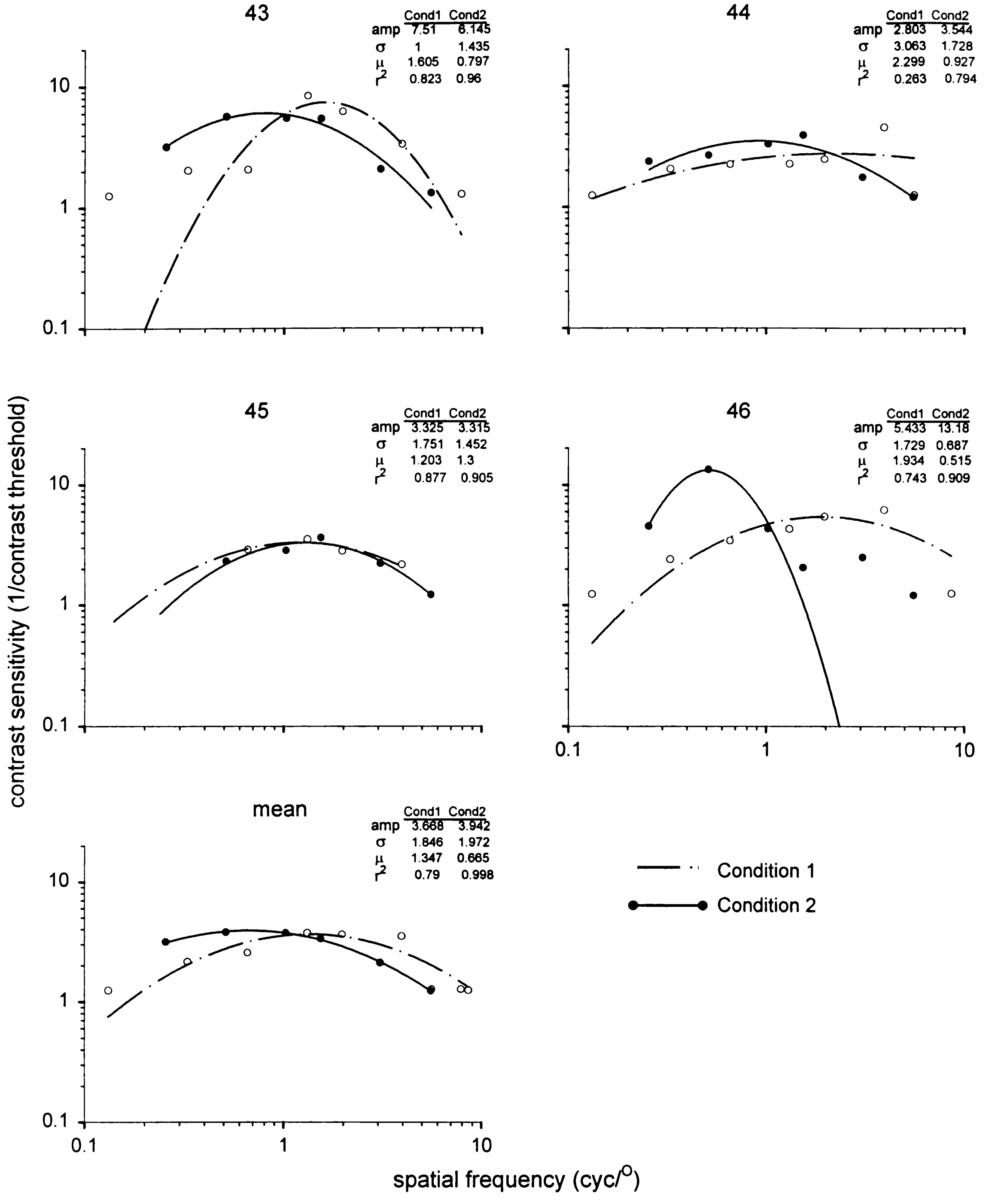


Figure 4.7. CSFs fitted from contrast thresholds found in Condition 1 (250 mm viewing through Perspex) and Condition 2 (clear 145.63 mm viewing), using Equation 4.3. Parameters for the Guassian curve fits are given to 3DP.

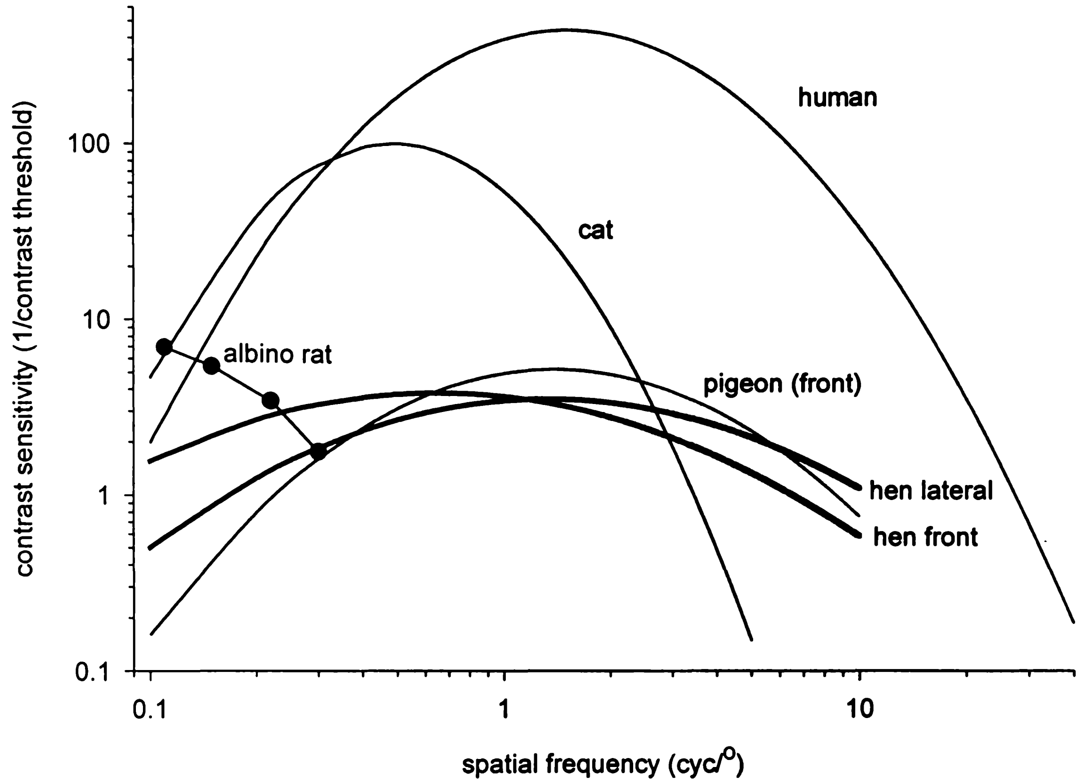


Figure 4.8. CSFs for various species, compared to those found for the hens. These have been replotted from figures in the following papers: rat and human from Birch and Jacobs (1979); cat from Blake, Cool and Crawford (1974), and pigeon from Nye (1968).

Discussion

The CSFs mapped for the hens in Figures 4.7 and 4.8 are in about the same place as the chick CSF found by Schmid and Wildsoet (1998) - just below the pigeon CSF. It is difficult to make direct comparison of Schmid and Wildsoet's CSF with others because they sampled irregularly spaced grating frequencies with the same widely spaced series of contrasts at each. Although they reported a "CSF", they did not fit a function to contrast sensitivity data. They reported peak contrast sensitivity at 1.2 cyc/°, and lesser sensitivities at the closest sampled frequencies of 0.17 and 1.7 cyc/°. Peak sensitivity on the function fitted to Condition 1 in Figure 4.7 is 1.347 cyc/°. Schmid and Wildsoet reported contrast thresholds at this peak to be around 11 %. This figure corresponds to a contrast sensitivity of about 9.1. Mean peak contrast sensitivity for the hens in the present experiment was 3.668 (contrast threshold of around 27 %) for Condition 1 and 3.942 (25 %) for Condition 2.

This difference in peak sensitivities could almost certainly be accounted for by the age difference between the hens tested in the current experiment and the chicks tested by Schmid and Wildsoet. The visual resolution of all examined species changes with age (Hodos, 1993). For most species, the highest CSF is usually found at early adulthood, after which it progressively declines (Hodos, 1993). For this reason, Hodos, Miller and Fite (1991), and Hodos (personal communication) have suggested that a standard CSF should be found at early adulthood (around 6 months for chickens). However, visual resolution in the chicken seems to detract from this pattern. The chick's visual system is often studied because of its rapid early development (e.g., Mey & Thanos, 1993) and Schmid and Wildsoet (1998) suggested that the chicken's CSF is highest a few days after hatching. There was another reason for not adopting an early adult standard CSF in the current experiment. The main purpose of generating a CSF here, particularly that of Condition 1, was to provide a measure of the visual resolution of the hens used as subjects in studies of visual behaviour; that is, comparable with those hens tested in the previous three experiments, who were of similar ages. The subjects of behavioural visual experiments are often some way beyond early adulthood, owing at least in part to the lengthy training procedures needed. Most of the papers cited in these experiments do not give the exact ages of the subjects. However, the chickens used by Candland (1969) were two years old before his experiments began, and DeMello's (1989) hens were nearly one year at the beginning of experimentation and presumably some years older at the end. So CSFs of older hens are probably better measures of the visual resolution of hens used in studies of visual behaviour.

Two CSFs are shown for the hens in Figure 4.8, labelled "hen front" and "hen lateral". The most notable difference between them is a lateral shift. The CSF from Condition 1, during which the hens viewed the gratings from a mean 250 mm, spans a range of higher frequencies than that from Condition 2, with a shorter viewing distance. Peak contrast sensitivity for the longer viewing distance was at 1.347 cyc/°, and for the shorter viewing distance at 0.665 cyc/°. Thus acuity was higher at the longer viewing distance. Although no published demonstrations of this CSF shift are apparent, it is probably a common phenomenon amongst birds, and possibly amongst all animals with laterally placed eyes. This result can be understood in terms of the arrangement of the chicken eye. Andrew and Dharmaretnam's (1993) paper, outlined in the introduction to this thesis, demonstrated that chickens use three angles of head orientation for visual fixation, and that these orientations correspond to foveal positions. More lateral angles are used at longer viewing distances. It makes sense that the part of the eye specialized for longer viewing distances should yield higher acuity. This partly compensates for the detail lost to distance. There is evidence that birds have higher acuity in the more lateral viewing positions (e.g., Hayes, Hodos, Holden & Low, 1987). This differential acuity could be caused by a number of things, including the refractive properties of the lens and cornea or the arrangement of retinal receptors. For example, human visual acuity decreases by one half at the periphery (30° from the fovea; Anstis, 1974), and this is a result of both refractive state and decreasing retinal receptor density (Hayes et al., 1987). The refractive state of the pigeon eye (and similarly, the chicken eye - Hodos & Erichsen, 1990; Schmid & Wildsoet, 1998) is not distributed differently in frontal and lateral vision (Fitzke, Hayes, Hodos, Holden & Low, 1985). This difference in acuity between frontal and lateral visual fields seems to be accounted for by differences in retinal receptor distribution (Hayes et al., 1987).

As this lateral shift of the CSF between conditions was not anticipated, head orientations during stimulus fixation were not specifically measured with an overhead camera. This was unfortunate because these figures could have been compared to those of Andrew and Dharmaretnam's (1993). However, rough estimates were manageable from the films that were taken. Figure 4.2 shows a video frame from Condition 2, where the head is clearly oriented at less than the 36.5° "Y" (mid-lateral) fixation point shown in Figure 0.1. Fixation angles used in Condition 1 appeared to be about 45°, as well as could be estimated from the video stills. This angle does not correspond exactly to any of the fixation angles reported by Andrew and Dharmaretnam, but is fairly close to the mid-lateral. This 45° angle estimated from the video stills might have been exaggerated by the wide-angle lens used for filming. It might seem odd that the hens switched from the more lateral fixation in Condition 1 to the frontal fixation angle when the screen was moved closer in Condition 2. The gratings used for the extensive (150 sessions) retraining for Condition 2 were at maximum contrast and near peak CSF frequency, as were those used for training Condition 1. Therefore, the gratings were clearly discernible from either viewing position. Probably the most important difference for the hens, in adopting the frontal viewing position during retraining, was that they were able to fixate the gratings by moving 35 mm closer to the response keys, rather than 70 mm further back. However, Nye (1972) had tremendous difficulty in training pigeons to respond to laterally placed visual stimuli. He concluded that pigeons are not neurologically disposed to peck in response to laterally placed visual stimuli. This difficulty might have influenced the lack of studies in which frontal and lateral CSFs are compared.

Those aspects of the current procedure which differed from Nye's in allowing successful measurement of the birds' lateral viewing capabilities can not be identified with certainty. Large numbers of sessions were required to train the hens to respond accurately to the laterally-viewed stimuli in Condition 1 (Table 4.1). Perhaps Nye's pigeons would have learned to respond to laterally-placed stimuli after many more training sessions. Also, Nye projected stimuli at the same distances for frontal and lateral viewing. In the present experiment, the hens altered their viewing angles after viewing distance was changed.

Schmid and Wildsoet's (1998) chick CSF is more similar to the hen CSF from Condition 1 here, where the lateral viewing position was used, rather than that of Condition 2. Schmid and Wildsoet (1998) claimed that their chicks were tested both monocularly and binocularly and that there were no differences in the two sets of data. However, their definition of "monocular" viewing was that one eye was occluded, and "binocular" viewing meant that neither eye was occluded. In no way did the lack of occlusion in the "binocular" viewing condition either necessitate or encourage binocular fixation, so the purpose of this part of their procedure is not clear. Schmid and Wildsoet's chicks viewed the gratings from 500 mm away. Given the evidence of Andrew and Dharmaretnam (1993), Dawkins (1995) and the results of the current experiment, it is highly unlikely that the chicks would have used a binocular fixation at this distance.

The Gaussian functions fitted the contrast sensitivity point estimates of Condition 2 (mean $r^2 = .998$) better than they did Condition 1 (mean $r^2 = .79$). So the Condition 1 CSF was not so well described by the logarithmic Gaussian. This result might have been affected by the Perspex viewing wall in Condition 1, which can be thought of as a flat lens. Lenses usually attenuate high frequency contrast and not low frequency contrast (Cornsweet, 1970). Thus the Perspex wall might have attenuated the contrast of gratings above a certain frequency. This would have caused the high-frequency half of the CSF to drop more steeply than the low-frequency half, resulting in a non-Gaussian distribution. The specific attenuation properties of the Perspex wall were not measured for practical and theoretical reasons. The optical properties of the Perspex probably changed as it was scratched by the hens and accumulated dust. The Perspex wall was washed before each testing session, but not to any optically measured standard. Also, the Perspex wall was included in Condition 1 so that the measured CSF would include any of its optically modifying properties. The CSF from Condition 1 was generated to be directly relevant to the viewing situation of the other four experiments, and to be comparable with other behavioural experiments in visual discrimination. Although the optical properties of viewing mediums are sometimes considered for perceptual experiments (e.g., Hodos, Rosalind & Bonbright, 1976), animal subjects more usually view stimuli through Perspex (e.g., Bradshaw, 1991; Bradshaw & Dawkins, 1993; Patterson-Kane, Nicol, Foster & Temple, 1997; Trillmich, 1976).

In general, the methods employed for Experiment 4 were successful in generating CSFs for the hens which compare well with other research (e.g., Schmid & Wildsoet, 1998). A few points of procedure might deserve explanation. First, contrast thresholds were extracted from single-session data. A problem intrinsic to animal psychophysical studies is that of providing consequences for sub-threshold responses. When a consequence such as food is provided for a response to a stimulus that the animal can not detect, this consequence can not maintain discriminative responding but might maintain some other behaviour, such as left or right key-pecking, independent of any particular stimulus-food presentation contingencies. A number of strategies might be used to reduce this effect. The strategy used here was to keep instances of sub-threshold stimuli to a minimum, and to intersperse them randomly with above-threshold stimuli. In a few cases, noted in Figures 4.5 and 4.6, these test sessions had to be repeated to obtain orderly patterns of responding. In most cases, they did not.

The second consideration is the use of the "trial length (TL)" contingency. This was designed to decrease the number of food presentations following correct responses, and to encourage waiting in the presence of the projected gratings. The purpose of decreasing the number of food presentations was, as with the first two considerations, to decrease food presentations following responses to sub-threshold stimuli. The aim of encouraging the hens to wait in the presence of the gratings was to increase the probability and duration that the hens would look at those gratings. Throughout Experiments 1 to 3, an arbitrary waiting period was enforced by lighting the response keys 4 s after the start of image presentation. Instead of enforcing an arbitrary waiting period here, the trial-length contingency was introduced and increased in duration throughout initial training (Table 4.1) based on the hens' responding. In this way, a waiting period was found that resulted in high proportions of correct responses. Based on data from 100 training sessions, sampled from all hens and from various stages of Conditions 1 and 2, the average waiting period was about 18 s per trial – 2.8 s longer than the mean food presentation time determined by the TL 25.2 s contingency.

The third procedural consideration is the use of the slide projector for presenting the gratings. The output of the projector had to be adjusted for each grating to maintain a constant overall intensity. These adjustments are listed in Appendix E. The overall intensity of each projected grating was set at 125 cd/m^2. Generally, the projector output was higher for lower contrast gratings. This suggests that the overall grating intensities were influenced more by the high intensity phases that the low. This was probably a result of the slightly unbalanced gamma function shown in Figure 4.4, and might have been influenced by unknown light-scattering properties of the projection screen. For tighter control over the grating intensities, a purpose-made oscilloscope would have been more desirable. However, this equipment was not available.

Knowledge of the properties of image display devices, such as the gamma function, might be worthwhile for studies of animal visual perception, in conjunction with knowledge of those animals' visual capabilities. For example, the gamma function of cathode ray tubes is set so that humans perceive the intensity scale as linear (Wandell, 1995). Other species' perceptions might be different.

The CSFs shown in Figure 4.8 should give some idea that the images presented in Experiments 1, 2 and 3 did not appear to the hens as they do to humans. Hens are less sensitive to contrast (subtle changes in shade are lost) and insensitive to fine detail (things appear more blurry). Hens' visual resolution is more like pigeons'. Thus hens should be expected to be able to respond to a range of visual stimuli similar to pigeons, and not to be able to respond to all that humans can see. As hens see less detail than humans, it should be possible to remove detail from images to demonstrate their lack of visual resolution more graphically. That is, humans will notice the missing detail, whereas hens will not. This demonstration is tested in the following experiment.

EXPERIMENT 5

Although measures of the bounds of visual perception such as the CSFs presented in Experiment 4 give information about what particular species should be able to detect, the impact of these limits is not usually easy to appreciate. For example, Patterson-Kane (1994) suggested that low visual acuity was probably a factor influencing her subject hens' lack of discrimination between videos of a white hen in a white box, and an empty white box. She did not report on the extent of this factor. Digital image processing can be used to provide graphic demonstrations of the impact of low resolution visual systems on making such discriminations. Brief descriptions of some of the processes involved in digital image processing (digitizing, Fourier Transformation, and filtering) are given here. Except where otherwise noted, fuller explanations of all the terms can be found in Gonzalez and Woods (1992).

Digitizing

A digital image exists only in the way that it is encoded by a machine. That is, the term "digital" relates to the binary encoding system of a digital computer. Although a digital image can be output to a monitor or printer, its "digital" sense can not be seen. Similarly, a compact disk can be used to digitally record a soundtrack, but the soundtrack can be heard only in an analogue form. An image is digitized by conversion from an analogue form, such as a photograph, into a discrete series of pixels (picture elements). The basic (uncompressed) digital image form is a bitmap, which is comprised of any number of rows and columns of pixels. Each pixel is a binary number which represents the intensity and colour of the image at that point. For example, a monochrome image might be made of 8-bit pixels. Eight bits allows a range of 256 grey-scale intensity levels. Colour images are typically encoded with 24-bit pixels – 8 bits for each primary colour intensity level. Each pixel can be altered to any specified level. To change an 8-bit monochrome pixel from black to white involves resetting the pixel value from 0 to 255.

Fourier Transformation

The Fourier Transform is used to analyze complex waveforms in terms of component pure-frequency waves. For example, the graphic equalizer on a sound system displays the magnitude of a sound signal at each of a number of sound frequencies, measured in Hz (cyc/s). Any digital image can be thought of as a composition of a number of sine-wave variations in pixel intensity (a collection of sine-wave gratings like those shown in Figure 4.2). The highest possible frequency (Nyquist) is one half the pixel width of the image - that is, where a wave alternates between high and low phases pixel by pixel. The process of converting a complex waveform into component frequencies is called "Fourier Analysis", and the opposite process of combining pure-frequency waves to reform a complex wave is called "Fourier Synthesis". Fourier Analysis is demonstrated in Figure 5.1.

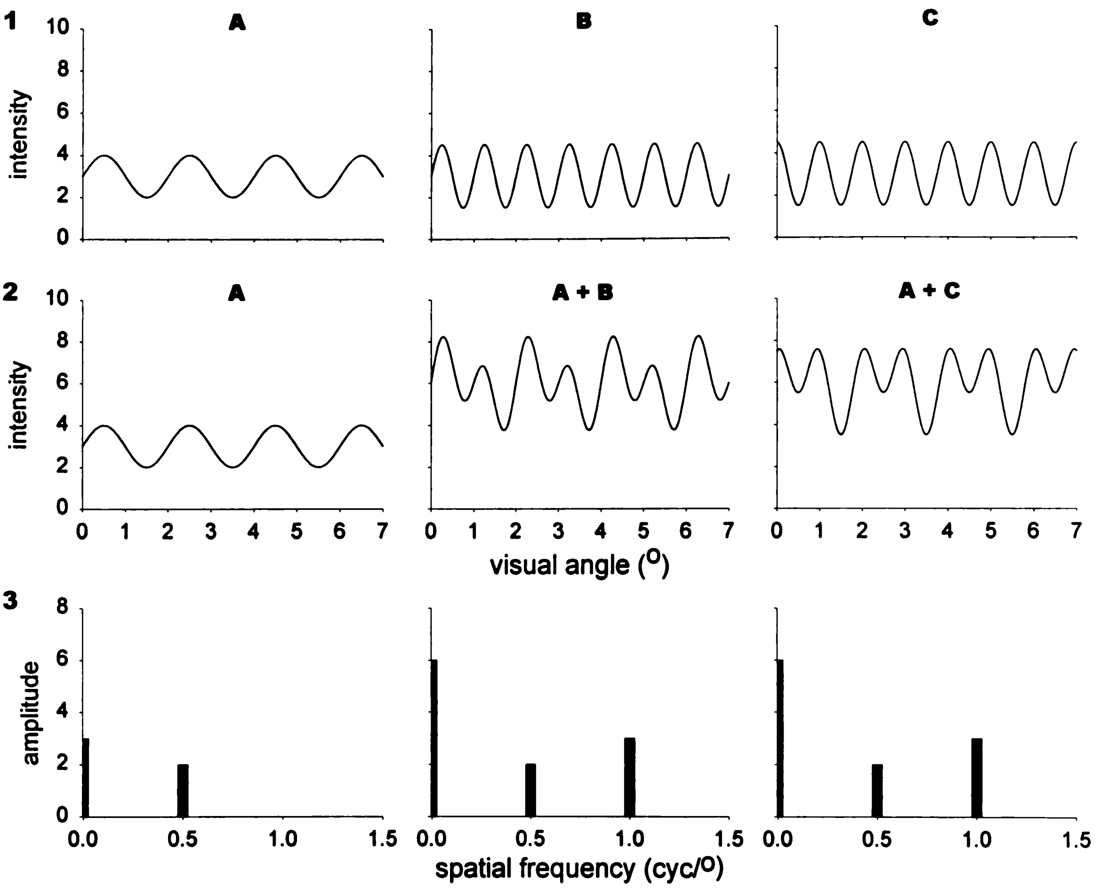


Figure 5.1. Demonstration of Fourier Analysis. Visual angles are calculated for a viewing distance of 33 cm and intensity measures are arbitary units. Row **1**: The sine wave in **A** alternates at 0.5 cyc/° and has an amplitude of 2 units. **B** alternates at twice the frequency of **A** (1 cyc/°) and has 1.5 times the amplitude. **C** is the same wave as **B**, but with phase shifted by 1/8 cycle. The waves in Row **2** are each summed from the one above and **A** (**A** is copied from Row **1**). Row **3** shows the Fourier Spectra of the waves in Row **2**.

Each bar in the Fourier Spectra of Figure 5.1 (Row 3) shows the amplitude of the component sine-wave at that frequency. In each case, the highest amplitude is at 0 cyc/°. This is the DC level (Russ, 1992), or mean wave intensity. The Fourier Spectra of the complex waveforms A+B and A+C are identical. This is because the one-dimensional spectra shown here do not include phase information. The phase information is not lost in a Fourier Analysis, but could be seen in a three-dimensional plot, by rotating the frequency axis around the intensity axis. In this case, the bar representing C would be 45° (1/8 cycle) from the bar representing B. However, this three-dimensional plot is unnecessary for understanding the filters used in this experiment. Although digital filters can be designed to differentiate between wave phases, this kind of filter is not considered here.

The wave-forms shown in Figure 5.1 are arbitrary and simple. Real images are usually much more complex. Fourier Spectra of images of natural scenes usually show contrast levels which decline across the spatial frequency scale at approximately *amplitude = 1/spatial frequency* (although this rate often varies between about *spatial frequency*$^{-0.6}$ and *spatial frequency*$^{-1.6}$ (Field & Brady, 1997)). The reason for this relation becomes evident upon examination of the composition of hard edges, which are the main structures of most natural scenes. A Fourier Analysis of a hard edge will show that it is made up of an infinite number of

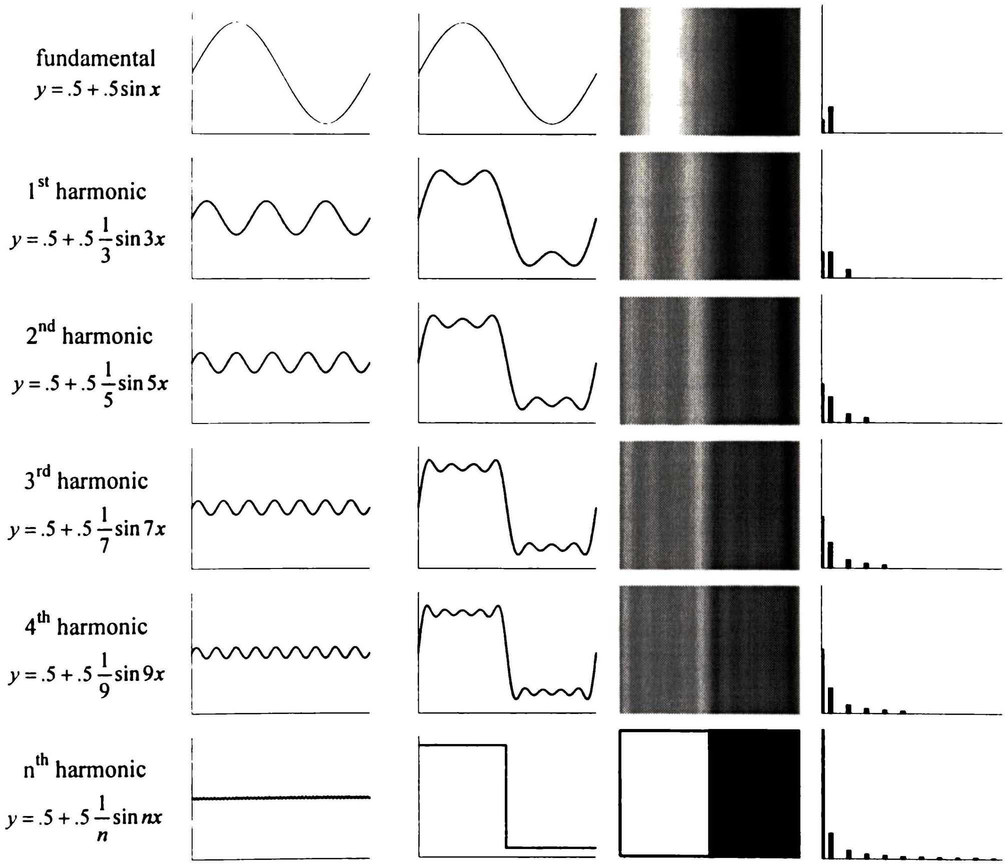


Figure 5.2. Composition of a hard edge. The fundamental and successive harmonic waveforms are listed in the first column and shown in the second. These are scaled in terms of image contrast (0 to 1). The three right-hand columns show the successive addition of the harmonic frequencies. The Fourier spectra in the final column are scaled differently from the other columns. The ordinate is scaled 0 to 5 and (as shown in Figure 5.1) the abscissa is a spatial frequency, rather than an absolute spatial, scale.

pure-frequency sine waves: a fundamental, and harmonics at 3, 5, 7,... times the frequency of the fundamental. The respective amplitudes of the harmonic frequencies are 1/3, 1/5, 1/7,...(that is: *1/frequency*, Cornsweet, 1970). The composition of a hard edge is demonstrated in Figure 5.2. Each component frequency of the hard edge has the same mean contrast, which is 0.5 in Figure 5.2. Therefore, the DC level of the Fourier Spectra shown in the far right-hand column increases by 0.5 with the addition of each harmonic. The n^th^ harmonic is an arbitrarily high one (shown as the 10th harmonic in the Fourier Spectrum).

Filtering.

Image filtering in the frequency domain (with the Fourier Spectra) is a matter of altering the contrast amplitudes at specific frequency ranges. A lowpass filter (LPF) attenuates high-frequency contrasts. That is, it allows low-frequency contrasts to "pass" unaltered. As can be seen in Figure 5.2, high-frequency components define the sharpness of detail. Therefore, the removal of high-frequency components with a LPF causes blurring in the image. Highpass filters (HPF) attenuate low-frequency contrasts. As the low-frequency components define gross detail and mean intensity of the image (DC level), these are the parts of an image which are lost when a HPF is used. A filter with both LPF and HPF functions is called a "bandpass" filter – both high and low frequencies are attenuated outside a mid-frequency band. LPF, HPF and bandpass filter functions are shown in Figure 5.3.

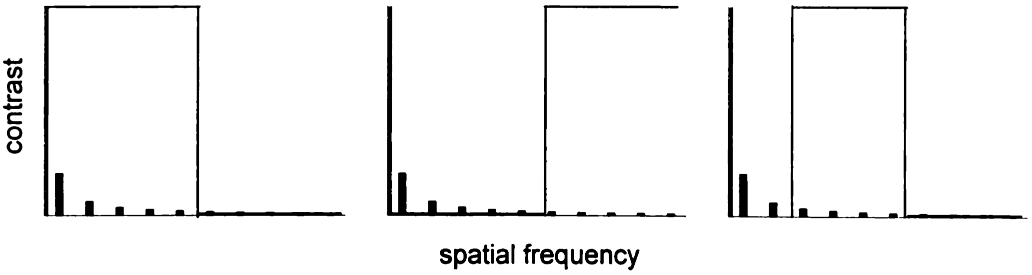


Figure 5.3. From left to right - lowpass, highpass and bandpass filter functions fitted to Fourier Spectrum of hard edge. All frequencies of the Fourier Spectrum below the function are unchanged. All frequencies above the function are removed by that filter.

The LPF and HPF functions shown in Figure 5.3 are each defined by one parameter – cutoff frequency. All contrast levels on the high-phase sides (left for LPF and right for HPF) of the cutoff frequencies are unchanged. All contrast levels on the low-phase sides are reduced to zero.

Filtering can also be done in the space domain. That is, without use of the Fourier Transform. Spatial filters do the same sorts of things as the filters just described, but without precise control over cutoff frequencies. For example, the Gaussian neighbourhood averaging filter design shown in Figure 5.4 functions like a LPF. Each little square represents one pixel. The whole square window is passed over the digital image pixel by pixel. At each location the central pixel intensity value is altered according to the summed weighting factors in the filter window. This process is called "convolution" (Gonzalez & Woods, 1992). Larger windows cause more blurring, and passing a small window over an image several times has the same effect as using a larger window.

1	2	3	2	1
2	7	11	7	2
3	11	17	11	3
2	7	11	7	2
1	2	3	2	1

Figure 5.4. Design of a Gaussian neighbourhood averaging filter with $\sigma = 0.625$ pixels. Adapted from Russ (1992, p.58).

These digital image processing methods (digitizing, Fourier Transformation, and filtering) can be used to remove those contrast levels from an image which fall outside the range of the hens' ability to detect them. As the hen CSF spans a smaller frequency range than that of humans (Figure 4.8), this kind of modification might yield an image which a hen can not differentiate from an unfiltered original, but which is clearly different to an observer with average human sensitivity to contrast. For example, the n^{th} harmonic in Figure 5.2 is shown as the one which makes the edge appear completely square. The actual value of this harmonic depends on the size and distance of the edge, and the contrast sensitivity of the observer. Viewed from 33 cm, the pictures in the second to last column of Figure 5.2 each occupy 4.165° of visual angle, side to side. Thus, the 4^{th} harmonic alternates at 2.161 cyc/° at normal reading distance. This frequency appears to be within the range of both human and hen CSFs

(Figure 4.8). Therefore, it should be expected that from 33 cm, both hens and humans can see that the picture showing the addition of the 4th harmonic is a blurry edge; that is, be able to distinguish it from a hard edge such as that shown in the bottom row. At a viewing distance of 200 cm, the 4th harmonic alternates at 13.09 cyc/°. This is within the range of the human CSF, but outside that of the hen. From 200 cm away, humans should be able to differentiate between this picture and a hard edge, but hens should not. At 600 cm, the 4th harmonic alternates at 39.27 cyc/°. This is around the upper limit of the human CSF. From 600 cm, the picture in Figure 5.2 that shows the addition of the 4th harmonic should start to appear as a hard edge. It should also be noticeable that both the dark and light phases of this picture are greyer than those in the bottom picture, showing the addition of the nth harmonic. This demonstrates the effect of the DC level – the bottom picture has a much greater overall intensity. A LPF can be used to provide an effect similar to that of moving towards this picture from more than 600 cm away. For example, if a LPF was used to remove all the harmonic frequencies above the 4th from the hard edge shown in the bottom row of Figure 5.2, then that edge would be the same as the one shown in the row above.

An ideal demonstration would involve removing all those contrast levels from an image which are beyond the hens' window of visibility (CSF). This demonstration is impractical, however, as degrading an image in this way introduces artifacts. The artifact problem is shown in Figure 5.5.

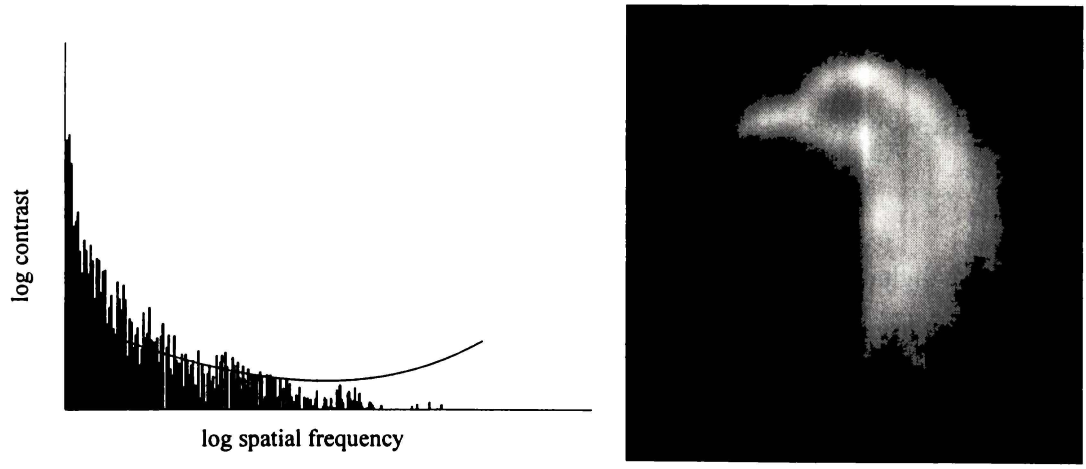


Figure 5.5. Design and result of the clipping filter.

The Fourier Spectrum on the left of Figure 5.5 is a one pixel slice through the Fourier Spectrum of the 700 pixel^2 original image (shown later in Figure 5.7. The entire Fourier Spectrum consisted in 700 horizontal by 700 vertical slices). The U-shaped function mapped onto the Fourier Spectrum is the reciprocated hen lateral CSF from Figure 4.7 ("modulation transfer function" (Cornsweet, 1970)). That is, it is a function of the original contrast thresholds, before they were converted to contrast sensitivity values. So, the contrast levels of the original image and the hens' contrast thresholds are shown together here, on the same scale. Those contrast levels of the Fourier Spectrum which fall below the hens' threshold function are invisible to the hens. Removing just these contrast levels (called "clipfiltering" here) produced the image on the right. Artifacts can clearly be seen in the image as streaks and patchiness ("ringing"). The ringing is caused by removing fundamental and lower harmonic frequencies, while leaving higher harmonics which are part of the same edge or shape. Therefore ringing is a problem intrinsic to HPF, which will be discussed later. To avoid the ringing shown in Figure 5.5, filters must pass all contrast levels within a particular range and remove all contrasts within another range, like the filter designs shown in Figure 5.3. This means that the filtered images used in this experiment will include some contrast levels which are beyond the hens' contrast threshold.

Another practical problem with demonstrating the effect of the hens' low visual resolution is the actual size of the images that are presented. An example of this problem is given in Figure 5.6.

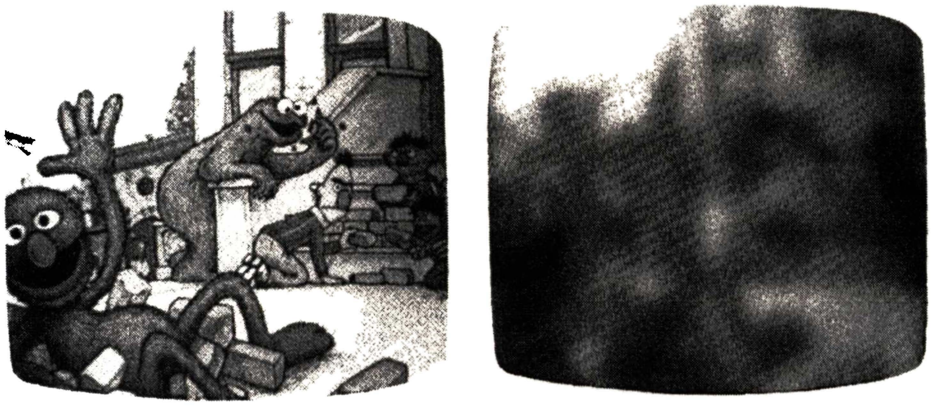


Figure 5.6. The image on the left has been filtered with a LPF to produce the image on the right. Taken from Sekular and Blake (1994, p.165), the caption read "An infant looking at these two pictures from a distance of 2 meters would be unable to tell them apart".

The images in Figure 5.6 are designed to provide the same sort of demonstration as this current experiment. The image on the right has been filtered with a LPF to show the effect of the low resolution of 6 month-old humans' visual systems (Sekular & Blake (1994) show a CSF for infants similar to the hen CSFs in Figure 4.8). From 2 m the two images in Figure 5.6 are indistinguishable to a 6 month-old infant. The images depict a television screen much smaller than life size. If the original image on the left was much larger, then more detail would remain in the filtered version on the right. That is, the details in the image would be larger and therefore more of them would remain after LPF at the same cutoff frequency. However, life-sized television pictures would not fit on the page, so a demonstration of the real effect of a 6 month-old watching television is impractical. Another approach would be to filter the image as if it were at its real size, and then invite readers to imagine that the printed images are larger than shown. This approach might demonstrate the absolute loss of detail from the life-sized object, but only in an abstract way; that is, the reader might be more inclined to regard the loss of detail as belonging to the images as they are actually presented. Sekular and Blake's (1994) method of image presentation is used for demonstrations of image loss throughout this experiment: Calculations of image losses were made for the sizes that the images are presented here.

The purpose of this experiment was to measure thresholds of high-frequency image attenuation in hens (using LPFs) and to use these measurements to produce demonstrations of the effect of hens' low visual resolution.

Method

Subjects

Four hens were used: Two White Shaver hens, numbered 72 and 75 here, which had been subjects throughout Experiments 1, 2 and 3, and were six years old when tested. Also two Shaver Starcross (brown, numbered 73 and 74) hens, which served as subjects in Condition 6 of Experiment 3, and were about two and a half years old when tested. The hens were maintained at around 80 % of free-feeding body weights, as with the previous experiments.

Apparatus

All apparatus and controlling software was the same as that used in Experiments 1 and 3. Training slides depicted two side-by-side copies of one of the hen profiles used in the initial training phase of Experiment 1. The two profiles were identical, except that one was blurred with a 10-pixel^2 Gaussian filter in Photoshop 5® (Figure 5.7). Four of these slides were used - two each of the blurred profile on either side. Each profile was projected 10 cm^2 on the screen. Therefore, the slide images were 10 cm high and 20 cm across. The test slides were similar, except that the Gaussian blurred profiles were replaced with ones which had been filtered with a series of LPFs in Matlab®. The Matlab® software used the fast Fourier Transform (FFT). The FFT algorithm is shown in Russ (1992). An example of a profile filtered with one of these LPFs is shown in Figure 5.7. Seven sets of test slides with the non-target profile filtered with a LPF were used. The cutoff frequencies for these ranged from 1 to 7 cyc/° in 1 cyc/° increments. Two versions of each test slide were made – one each with the target profile on the left and the right.

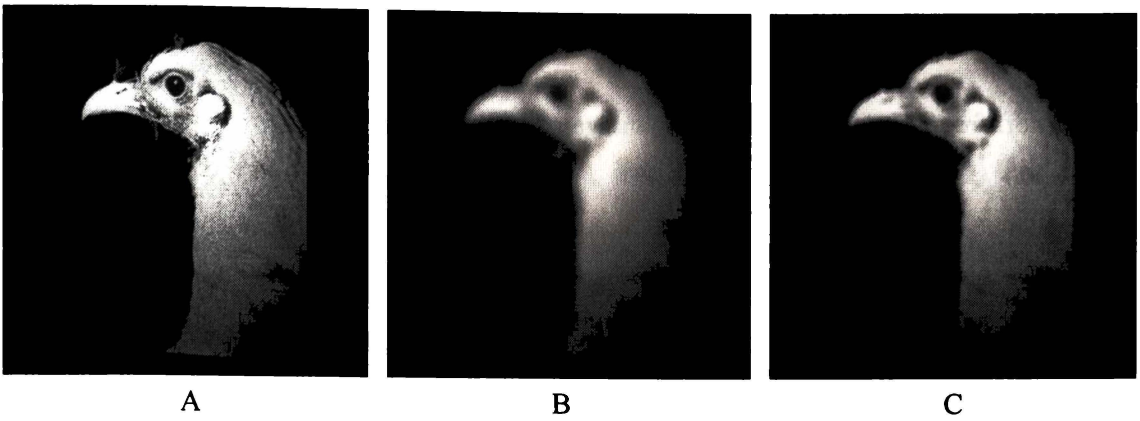


Figure 5.7. Images used in training and testing. A is the original target image. B is a copy of A, blurred with a 10-pixel^2 Gaussian filter. This was the comparison for training trials. C is an example of one of the comparisons used in testing. It is a copy of A, filtered with a LPF, with cutoff frequency represented here at about 6 cyc/°

Procedure

Training. Sessions were conducted six days a week. Each session lasted 1600 s, or until food had been presented 30 times, whichever happened first. Trials began with the presentation of a slide, with the target profile to the left or right at random (p=.5). After 4 s, the two side keys were illuminated. A single peck to either illuminated side-key resulted in the extinction of both side-keys and the projector shutter closing. A peck to the target-side key occasionally resulted in a 2-s presentation of the same-side food hopper. The side-key dependency described under *Initial Training Procedure* in Experiment 4 was used in this procedure also, and resulted in the hens being presented with food following just over one half of the correct target responses in each session. There were no scheduled consequences for non-target responses. A 10-s ITI immediately followed either food presentation, or any key-peck which did not result in food presentation. Data collected from each training session included the total number of trials and the number of correct trials, the number of food presentations, and session duration, in seconds. The criterion for moving from training to testing sessions was initially planned to be that all the hens consistently respond correctly to over 90 % of the targets in each session, but as this had not happened after 118 sessions this criterion was lowered to 81 %. Viewing distances were measured as in Experiment 4 (Figure 4.3 and Appendix D). The mean viewing distance was 249 mm, with a standard deviation of 10.94 mm. Mean viewing distance was used to calculate the size of the profiles in degrees of visual angle, using Equation 4.1.

Testing. LPF frequency cutoff thresholds were tested in two sessions using the method of constant stimuli. The differently filtered non-target profiles were selected without replacement from any array of seven by the controlling software and presented to the left or right of the target at random (p=.5). This procedure was repeated 10 times, so that each test session was comprised of 70 trials. Data collected were the numbers of correct target responses at each cutoff frequency. These data were amalgamated across the two test sessions.

Results

The proportions of correct target responses for the last five training sessions are listed in Table 5.1. These are representative of the hens' performance for a large number of previous sessions. It was hoped that all the hens would correctly respond to the target profile on over 90 % of the trials in each session. However, after 118 sessions, it was evident that this might not happen. All hens had responded correctly on over 81 % of the trials in each of the last five training sessions, and there were no discernible trends in the proportions of correct responses - any fluctuations across these sessions were representative of similar vicissitudes over many earlier training sessions.

Table 5.1. Proportions of correct responses for each of the last 5 training sessions.

session	72	73	74	75
114	.929	.912	.972	.922
115	.841	.908	.940	.812
116	.814	.877	.892	.814
117	.947	.948	.903	.855
118	.944	.957	.920	.847

Proportions of correct test trials, out of 20, for each hen at each LPF cutoff frequency are plotted in Figure 5.8. Raw data are listed in Appendix F. Each datum set was fitted with the sigmoidal function described in Equation 5.1 using an iterative fitting routine. Equation 5.1 is a slightly modified version of Equation 4.2, which is described in the Results section of Experiment 4.

$$y=0.5+\frac{0.5}{(1+\exp 1)^{1-(.1a(b-X))}} \qquad 5.1$$

The dashed vertical lines in Figure 5.8 mark the obtained LPF cutoff frequency thresholds (the value of *b* from Equation 5.1). It can be seen in Figure 5.8 that Hen 72 did not reach the 75% threshold level in discriminating between the target profile and the LPF profiles at any cutoff frequency. For the other three hens, the 75 % threshold cutoff frequencies were very similar, ranging from 2.12 to 2.38 cyc/°. The mean threshold cutoff frequency was calculated at 2.237 cyc/°.

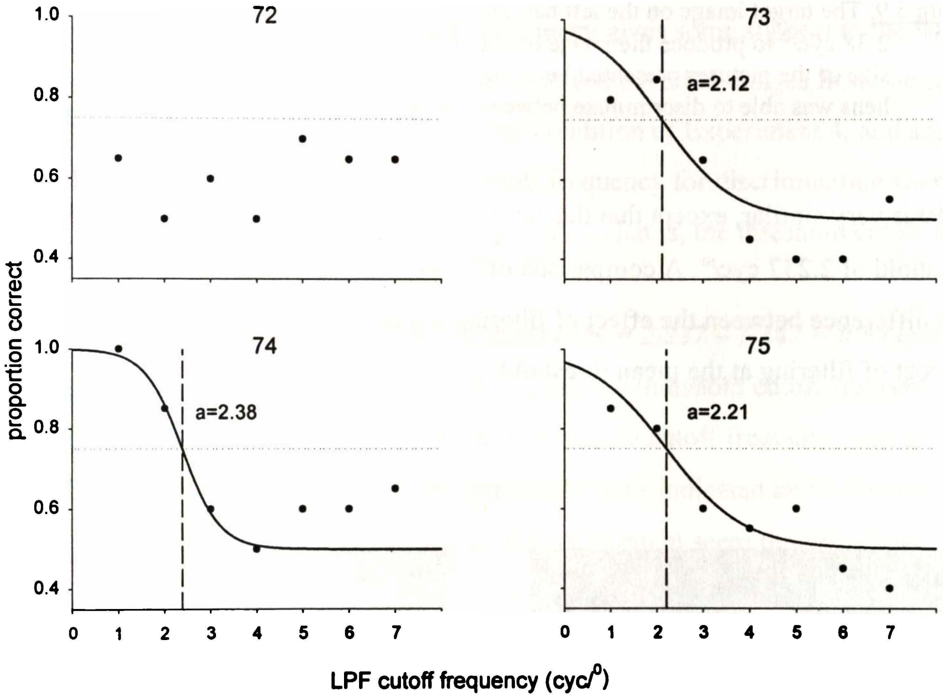


Figure 5.8. LPF cutoff frequency thresholds extracted using Equation 5.1.

These threshold values were used to filter the images in Figures 5.9 and 5.10. In Figure 5.9, the profile on the right has been filtered with a LPF with cutoff frequency set at 2.38 cyc/°, calculated with the size of the picture shown here (6 cm^2) and a normal reading distance of 33 cm. This means that if the hens viewed these profiles from 33 cm, none of them would be able to differentiate between the two.

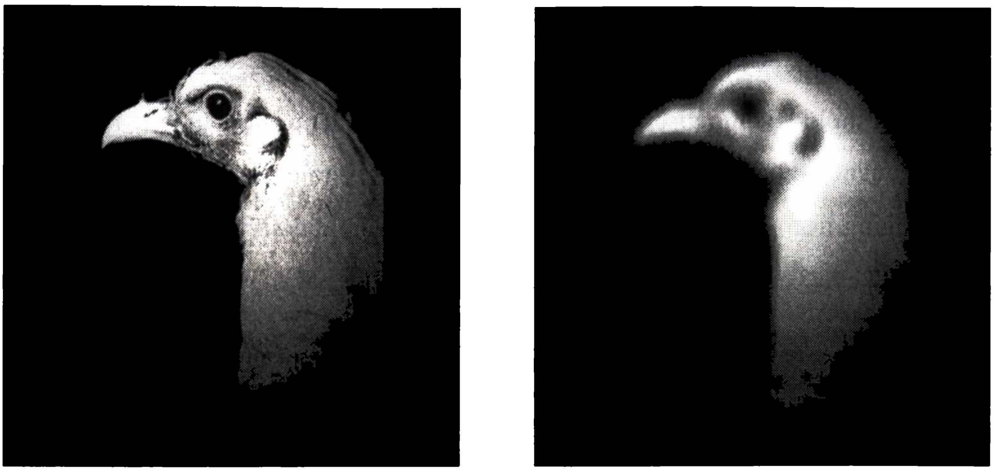


Figure 5.9. The target image on the left has been filtered with a LPF with cutoff frequency 2.38 cyc/° to produce the image on the right. These calculations are based on the size of the pictures presented here and a viewing distance of 33 cm. None of the hens was able to discriminate between the target and LPF image at this frequency.

Figure 5.10 is very similar, except that the cutoff frequency has been slightly adjusted to the mean threshold of 2.237 cyc/°. A comparison of Figures 5.9 and 5.10 shows that there is a negligible difference between the effect of filtering the image at the highest threshold frequency, and the effect of filtering at the mean threshold.

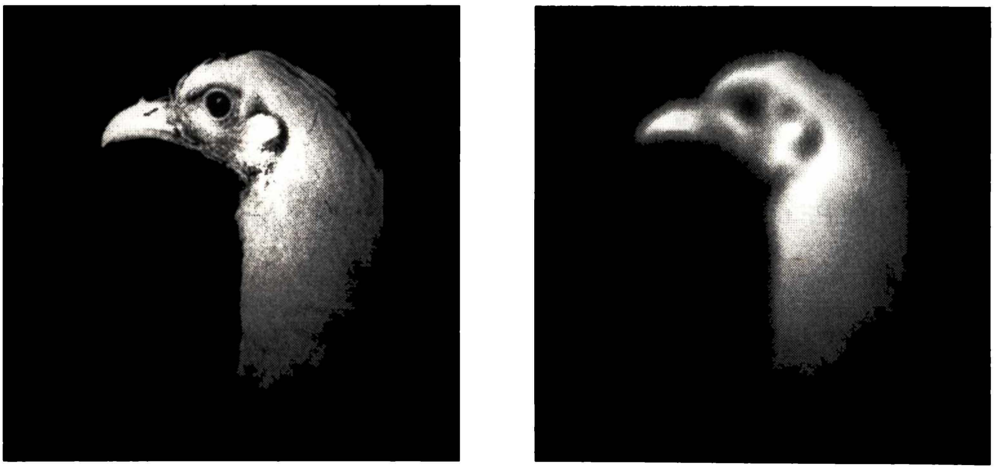


Figure 5.10. The target image on the left has been filtered with a LPF with cutoff frequency 2.237 cyc/° to produce the image on the right. These calculations are based on the size of the pictures presented here and a viewing distance of 33 cm. This was the mean threshold discrimination.

Discussion

A mean threshold cutoff frequency for the hens' ability to discriminate between an image, and that same image with high-frequency contrasts removed, was measured at 2.237 cyc/°. This suggests that, on average, the hens' were unable to detect any contrasts in the image above this frequency. Two copies of the image are shown in Figure 5.10, one with these sub-threshold contrasts removed. Thus, Figure 5.10 is designed to demonstrate the effect of hens' low sensitivity to contrast over much of the range of spatial frequencies discriminable by humans. This effect is large. It is apparent from the figure that much detail is lost when presenting visual stimuli to hens.

The value of this mean threshold cutoff frequency gives some support to the lateral CSF found in Experiment 4. The hens in this experiment viewed the slide images from the same distance (250 mm) as the hens in the lateral viewing condition of Experiment 4, and appeared to be using lateral viewing angles also. The mean cutoff frequency for discrimination found here is on the high-frequency side of the lateral CSF (Figure 4.7) That is, the threshold cutoff frequency is

mean LPF cutoff frequency – mean CSF frequency = 2.237 – 1.347 = 0.89 cyc/°

higher than the peak sensitivity shown by the CSF. Thus, the threshold cutoff frequency was found to be in the sort of place that was expected. If threshold cutoff frequency had been found at less than 1.347 cyc/° (the mean of the CSF), this might have indicated an inconsistency between the results of this experiment and Experiment 4. It might seem that the threshold cutoff frequency should be higher here because the CSF is still reasonably high at 2.237 cyc/° (Figure 4.7). However, this threshold depends not only on the hens' visual resolution shown by the CSF, but also on the actual contrast levels in the image. As the contrast levels in the image decrease at a rate of somewhere around *1/frequency* (see Fourier Spectrum shown in Figure 5.5), there was relatively little contrast at frequencies beyond 2.237 cyc/° for the hens to discriminate.

Figure 5.10 shows the effect of removing some of the contrasts that the hens could not detect. As all contrasts above a certain frequency have been removed, and all contrasts below that frequency remain, Figure 5.10 shows the effect of low visual acuity, rather than low contrast sensitivity. That is, the difference in lateral placement of the hen and human CSFs shown in Figure 4.8, rather than the difference in amplitude. The demonstration in Figure 5.10 is analogous to removing all the undetectable letters from an eye-chart, while retaining all the readable letters at full contrast. Therefore, the filtered image in Figure 5.10 does not show the full extent of image degradation caused by the hens' low sensitivity to contrast. The clipfiltered image in Figure 5.5 might give a better picture of this, except for the artifacts caused by removal of various intermediate frequency contrasts.

The purpose of this experiment was to assess and demonstrate high-frequency image loss in hens. There might also be some low-frequency image loss that was not assessed. That is, the hens could not detect contrasts above 2.237 cyc/°, and there might also be a frequency below which hens cannot detect contrasts. Low-frequency loss, however, is very difficult both to define and to demonstrate. Theoretically, a HPF would be used to demonstrate low-frequency loss in a similar way to the LPF used to create the image in Figure 5.10. A filter with both HPF and LPF components (i.e., a bandpass filter – Figure 5.3) would be used to show both low and high-frequency image loss. The effect of bandpass filtering is shown in Figure 5.11.

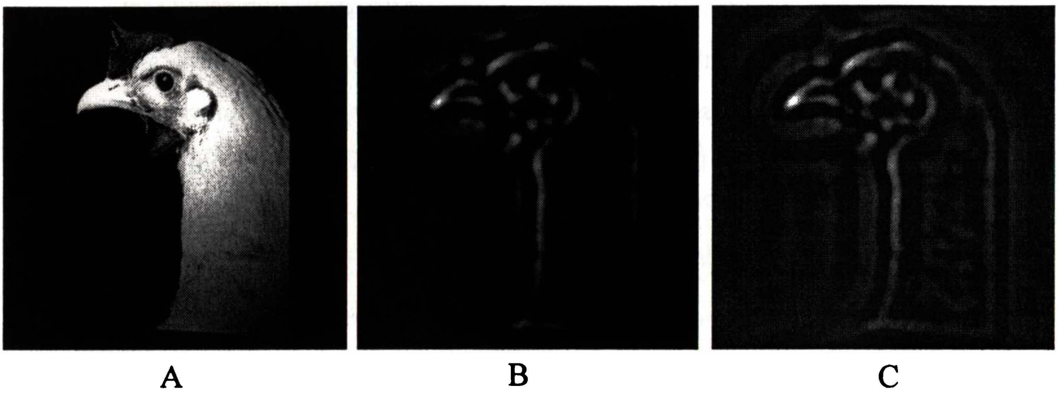


Figure 5.11. Demonstration of HPF. A is original image. This has been bandpass filtered to produce B. The DC level was then raised to its original to produce C.

The bandpass filter used to create the image in Figure 5.11B had a LPF component, with cutoff frequency set at the hens' mean threshold (2.237 cyc/°), and a HPF component, with the cutoff frequency set at the same distance below the peak of the CSF as the mean threshold was above. So the difference between Figure 5.11B and the filtered image in Figure 5.10 is caused by the addition of a HPF with cutoff frequency 0.811 cyc/°. This value is arbitrarily high. Although the CSF is symmetric, the Fourier Spectrum of the image is not. The lower-frequency contrasts of the image are higher, and more often exceed the hens' contrast thresholds, than the higher-frequency contrasts (shown in clipfilter design in Figure 5.5).

The HPF component caused both the reduction in average intensity and the ringing that can be seen in Figure 5.11B. These are undesirable artifacts, that is - alterations which might be discriminable and could be made independently of any low-frequency attenuation. Average intensity was reduced because the DC term at 0 cyc/° was (and must necessarily be) on the low-phase side of the HPF component. This was adjusted to its original level to produce

Figure 5.11C. The ringing effect could have been lessened by using a HPF function with a more gradual descent, rather than the definite cutoff function shown in Figure 5.3. Using this type of "Butterworth" filter would lessen the ringing by gradually attenuating contrasts over a range of low frequencies, but would make the actual cutoff frequency more arbitrary, instead of an definite value. Butterworth filter cutoff frequencies are conventionally defined as the point where the filter function falls to either ½ or 1/√2 of its maximum amplitude (Gonzalez & Woods, 1992). A Butterworth HPF needed to demonstrate the small amount of low-frequency image loss that might be expected for the hens (cf., clipfilter design in Figure 5.5) might not fall to 1/√2 of its maximum amplitude.

It is clear from Figure 5.10 that very little of the images presented throughout the current series of experiments was available to the hens for discriminative responding. This presentation also elucidates the results of previous studies, for example, Dawkins' (1995) finding that hens were unable to discriminate familiar from unfamiliar birds except when they were very close to them. Dawkins (1995) argued that the hens' frontal viewing angle was specialized for recognizing flockmates. It is apparent from Figure 5.10 that the frontal viewing angle is important because the close viewing distance that accompanies it is necessary for detection of fine detail.

Results from both Experiments 4 and 5 might help to explain Troje et al.'s (1999) finding that their pigeons discriminated between images on the basis of luminance, rather than shape. The borders, or edges, that define any shape are composed of contrasts at a range of spatial frequencies (shown in Figure 5.2). If some of those high-frequency contrasts are removed, then the border between a shape and its background is blurred – the shape becomes less well defined. Animals with low visual resolution, such as pigeons and chickens, are unable to detect high-frequency contrasts, and so shapes are not well defined for them. This is apparent in Figure 5.10, where the comb and wattles merge into the background of the filtered image. In Figure 5.12, the shapes that were presented to the hens in Experiment 3 have been filtered similarly.

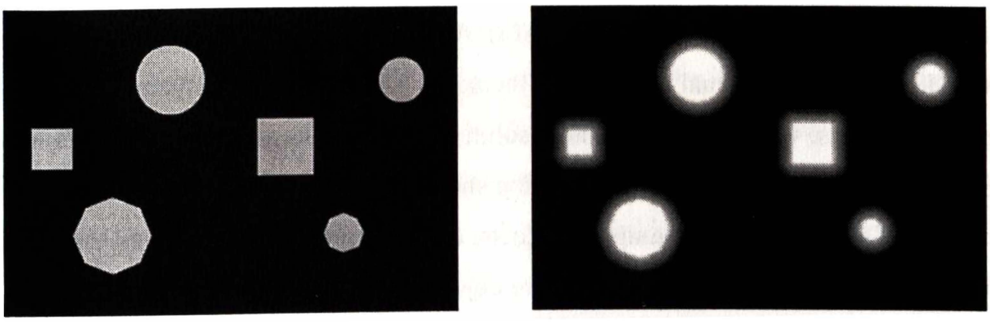


Figure 5.12. Shapes presented in Experiment 3 filtered with LPF with cutoff at 2.237 cyc/°.

The original image on the left in Figure 5.12 shows shapes with well-defined edges. This image was filtered with a LPF with cutoff frequency set at the hens' threshold, measured in this experiment at 2.237 cyc/°, to produce the image on the right. This shows a loss of shape definition. The size disparities between the shapes might also be more apparent in the right-hand image than they are in the original image. That is, this Figure 5.12 might indicate that as the shape of visible objects becomes less well-defined, the size of those objects, rather than their shape, becomes relatively more discriminable.

Hens' low visual resolution might also be involved in the failure of the hens in Experiment 2 to generalize from slide images to real conspecifics. In order to speculate about this possible connection, the discriminable features of visual stimuli might be roughly divided into four categories: gross detail; fine detail; colour, and movement (ignoring mean intensity, which will almost certainly vary between naturally observed conspecifics and their slide depictions). Assuming that humans can generalize discriminations of slide images to real conspecifics, their ability to do so might depend on their ability to detect the visible features that correspond between both types of stimuli in all four categories. That is, humans might be able to observe that gross details, fine details and colours are consistent between a slide image and a conspecific, and that only movement differs between the two stimuli. As hens cannot detect fine detail, slide images and real conspecifics might be less similar for hens than for humans. If movement is one of only three of the broadly defined features by which hens can discriminate conspecifics, then movement might be an important requisite feature for that discrimination. The absence of movement in slide images might mean that slide images appear so different from real conspecifics that hens cannot respond to them as conspecifics.

This "movement" hypothesis has two testable implications. First, that species with higher visual resolution should be better able to generalize discriminations of slide images to conspecifics than species with lower visual resolution. There are very few species for which reports of both visual resolution and slide-conspecific generalization have been published. This generalization has been demonstrated in primates (Premack, 1976), who have high visual resolution (De Valois, Morgan & Snodderly, 1974). According to the current hypothesis, falcons, who have very high visual resolution (Reymond, 1987), should easily make this generalization, and rats, who have low visual resolution (Birch & Jacobs, 1979), should not.

Second, species with low visual resolution should be better able to generalize discriminations of slide images to inanimate objects, than to animate objects. Hens have been shown to generalize discriminations of inanimate objects to videos (Patterson-Kane, Nicol, Foster & Temple, 1997). Pigeons, which have visual resolution similar to chickens (Schmid & Wildsoet, 1998; Experiment 4), have shown generalization of two-dimensional image discriminations to inanimate objects (Cabe, 1976; Lumsden, 1977).

Differences in movement can not entirely account for hens' inability to generalize discriminations across two-dimensional images and real conspecifics. Patterson-Kane et al. trained hens to discriminate between a brown hen in a white box and an empty white box, and also between a white hen in a white box and an empty white box. The brown hen/ empty box discrimination generalized to video images in further test trials: The white hen/ empty box discrimination did not. Presumably, the real white hen and the video image sequence displayed about the same amounts and types of movement. Therefore, some other factor must have been involved in this lack of generalization. Hens made target choices in Patterson-Kane et al.'s experiment by approaching the white boxes, which were placed at the ends of radial arms of a Y-maze. The arms were 90 cm long. If the hens made target choices from a viewing distance of 90 cm, then the large amount of image loss at this distance might have left very little detail for the hens to detect. That is, the high contrast of the brown hen in the white box was detectable, but the low contrast of the white hen in a white box was not detectable at the large viewing distance. Thus it is suggested that Patterson-Kane et al.'s hens would have generalized the white hen/ empty box discrimination to video images if the viewing distance had been less (possibly 30 cm, at which Dawkins (1995, 1996) found that hens discriminated between conspecifics).

SUMMARY AND CONCLUSIONS

Two-dimensional images

One consideration in planning alternate housing systems for battery-farmed hens is how those hens recognize each other in order to maintain stable dominance orders. Researchers have suggested (e.g., Bokkers, 1994) that this information can be used for planning the optimal size and arrangement of the alternate housing. Slides and photographs are sometimes used to study individual recognition in hens because these allow more precise control over the presentation of visual stimuli (e.g., Dawkins, 1996). Similarly, many researchers have used slides to study the recognition of conspecifics in many species (e.g., Brown & Dooling, 1992; Candland, 1969; Dasser, 1987; Poole & Lander, 1971). This research raises the issue of whether the animals respond to the slide images differently from the way they respond to real conspecifics.

This thesis was focussed around the research question "Do hens respond to static, two-dimensional images of conspecifics as they do to the real hens that the images depict?" The evidence indicates that they do not. Attempts to demonstrate a positive answer to this question have failed (e.g., Bradshaw & Dawkins, 1993; Dawkins, 1996, Experiment 2). The only suggestion that they do was based on a mis-use of terminology from the "concept formation" paradigm. That is, demonstration of a "concept" in the concept formation model means that an animal which has learned to discriminate between experimenter-defined categories of images will then generalize this discrimination to novel sets of images (Wasserman, 1993). This "concept" definition does not necessitate that the animal generalize the discrimination to three-dimensional objects. Ryan (1982) trained bantam roosters to discriminate between sets of slides depicting two different conspecifics and then observed that this discrimination generalized to novel slides of the same two conspecifics. One purpose of the discussion in the introduction to Experiment 2 of this thesis was to discount Ryan's (1982) result as evidence that chickens respond to slide images as they do to conspecifics.

Experiment 3 revealed that the hens were responding to the uppermost feature in the slide images, irrespective of whether that feature depicted part of a hen or a geometric shape. This result favours the argument that hens will discriminate between slide images on the basis of abstract features of those images, rather than any relation those features may have to real objects. This sort of "selective stimulus control", which was maintained by artificial contingencies (provision of food) has been demonstrated in many species, including humans (e.g., Stromer, McIlvane, Dude & Mackay, 1993). Therefore the caveat provided by this example is generalizable to other species. That is, it may be expedient to check that behaviour measured in laboratory conditions is generalizable to real-world situations for any subject species, including humans.

The results of Experiments 4 and 5, as well as much other evidence of low visual resolution in chickens, intimate that hens do not see images as humans do. Hens are able to detect much less detail. When assessing hens' responses to varying images, it is important to consider how much, or what parts, of those images the hens can detect.

All of these results indicate that two-dimensional stimuli are not a useful tool for the study of social behaviour in hens. However, different experimental procedures might facilitate the generalization of hens' responses across two-dimensional images and real objects. In Experiment 2, the hens were tested for response generalization from slide images to real conspecifics. Response generalization from conspecifics to slide images might emerge differently, although all available evidence suggests that this order of stimulus presentation is no more likely to produce successful generalization. This was the order that Dawkins (1996) presented real and two-dimensional stimuli to her hens. Trillmich (1976) has reported the only successful generalization of birds' responses across two-dimensional images and real conspecifics. He first trained two budgerigars to discriminate between conspecifics, and then tested for generalization to slide images. Neither bird generalized. It was only after extensive retraining with slide images that one of the birds later generalized from slide images to real conspecifics. Trillmich's results suggest that extensive training with both slide images and real conspecifics is important for this generalization to occur, and together with the results of Experiment 2 and Dawkins (1996), that the order of stimulus presentation is not important.

It may be possible to train hens to generalize responding across conspecifics and their two-dimensional depictions. This training would be inexpedient for many studies of social behaviour in hens, for example, in the case where Dawkins (1996) tried to control for object hen movement by replacing those hens with photographs. Successful training might be useful in other cases, such as Candland's (1969) study, in which isolation of the salient visual features of conspecifics is required, without mutilating live animals. This type of training would also be of theoretical and comparative interest, in determining whether and how it could be successful and what procedural variants might aid rapid response generalization.

If movement is an important feature of visual stimuli for hens, as tentatively suggested in the discussion of Experiment 5, then hens are more likely to generalize responses across slide images and inanimate, rather than animate, objects. Patterson-Kane, Nicol, Foster and Temple (1997) reported generalization of hens' responses across video images and inanimate objects. This generalization has also been demonstrated in pigeons (Cabe, 1976; Lumsden, 1977), which have visual resolution similar to chickens (Experiment 4; Schmid & Wildsoet, 1998). Movement cannot completely account for hens' inability to generalize across two-dimensional images and real conspecifics because Patterson-Kane et al. reported a failure of their hens to make this generalization across video images and a real conspecific.

Aspects of visual behaviour

The experiments were designed to examine various aspects of hens' visual behaviour. Some different aspects of chickens' visual behaviour are studied separately, and often reported in different journals. The present research was designed to collate knowledge and understanding of some of these aspects. For example; although ethological and welfare-oriented studies may focus on the behaviour of domestic fowl, and psychophysical studies of perception may regard laboratory behaviours as a subsidiary indication of physiological constitution, both paradigms deal with the same pattern of events: Subjects are presented with visual stimuli and resultant behaviours are assessed. This pattern of events can be well understood in terms of the learning theories proposed by Skinner (e.g., 1974). This common framework allows different types of research into the visual behaviour of hens to be cross-referenced. Issues raised in one area of research may be addressed by research in another area. Examples of some of these issues are summarized in the following three paragraphs.

Studies of chickens' visual acuity (e.g., Experiments 4 & 5; DeMello, Foster & Temple, 1992; Schmid & Wildsoet, 1998) reveal that Dawkins's (1996) contention that hens "have good visual acuity...and have no difficulty in seeing objects at different distances from the eye"(p.673) is incorrect. Patterson-Kane (1994) recognized that low visual acuity was probably frontal and lateral CSFs for pigeons and other birds, should be verified by further, different, measures such as the optokinetic nystagmus response used by Schmid and Wildsoet (1998).

References

Andrew, R.J., & Dharmaretnum, M. (1993). Lateralization and strategies of viewing in the domestic chick. In H.P. Zeigler and H.J. Bischof (Eds.) *Vision, Brain, and Behavior in Birds (pp.319-332).* Cambridge, Massachusetts and London: MIT Press.

Anstis, S.M. (1974). A chart demonstrating variations in acuity with retinal position. *Vision Research, 14,* 589-592.

Appleby, M.C., Hughes, B.O., & Elson, HA. (1992). *Poultry Production Systems: Behaviour, Management and Welfare.* Melksham, England: Redwood Press.

Baer, D.M., Wolf, M.M., & Risley, T. (1968). Current dimensions of applied behavior analysis. *Journal of Applied Behavior Analysis, 1,* 91-97.

Baker, A. G., & Emerson, V.F. (1983). Grating acuity of the Mongolian gerbil (Meriones unguiculus). *Behavioural Brain Research, 8,* 195-209.

Bennett, A.T.D., & Cuthill, I.C. (1994). Ultra-violet vision in birds: what is its function? *Vision Research, 34,* 1471-1478.

Biederman, I. (1987). Recognition-by-components: A theory of human image understanding. *Psychological Review, 94,* 115-147.

Birch, D., & Jacobs, G.H. (1979). Spatial contrast sensitivity in albino and pigmented rats. *Vision Research, 19,* 933-937.

Blake, R., Cool, S.J., & Crawford, M.L.J. (1974). Visual resolution in the cat. *Vision Research, 14,* 1211-1217.

Blough, D., & Blough, P. (1977). Animal psychophysics. In W.K. Honig and J.R. Staddon (Eds.) *Handbook of Operant Behavior (pp. 514-539).* Englewood Cliffs, NJ: Prentice-Hall.

Bokkers, E. (1994). *Operant Conditioning and Recognition in Hens.* Unpublished dissertation: Swedish University of Agricultural Sciences, Skara, Sweden.

Bolhuis, J.J. (1999). Early learning and the development of filial preferences in the chick. *Behavioural Brain Research, 98,* 245-252.

Bowmaker, J.K., & Knowles, A. (1977). The visual pigments and oil droplets of the chicken retina. *Vision Research, 17,* 755-764.

Bradshaw, R.H. (1991). Discrimination of group members by laying hens (Gallus domesticus). *Behavioural Processes, 24,* 143-151.

Bradshaw, R.H., & Dawkins, M.S. (1993). Slides of conspecifics as representatives of real animals in laying hens (*Gallus domesticus*). *Behavioural Processes, 28,* 165-172.

Brown, S.D., & Dooling, R.J. (1992). Perception of conspecific faces by budgerigars (*Melopsittacus undulatus*): I. Natural faces. *Journal of Comparative Physiology and Psychology, 106,* 203-216.

Burkhardt, D. (1989). UV vision: a bird's eye view of feathers. *Journal of Comparative Physiology A, 164*, 787-796.

Cabe, P.A. (1976). Transfer of discrimination from solid objects to pictures by pigeons: A test of theoretical models of pictorial perception. *Perception and Psychophysics, 19*, 545-550.

Candland, D.K. (1969). Discriminability of facial regions used by the domestic chicken in maintaining the social dominance order. *Journal of Comparative and Physiological Psychology, 69*, 281-285.

Catania, A.C. (1973). The concept of the operant in the analysis of behavior. *Behaviorism, 1*, 103-115.

Chomsky, N. (1968). *Language and Mind.* New York: Harcourt, Brace & World.

Clark, D.L., & Uetz, G.W. (1990). Video image recognition in the jumping spider, *Maevia inclemens* (Araneae: Salticidae). *Animal Behaviour, 40*, 884-890.

Cook, R.G., Riley, D.A., & Brown, M.F. (1992). Spatial and configural factors in compound stimulus processing by pigeons. *Animal Learning and Behavior, 20*, 41-45.

Cornsweet, T.N. (1970). *Visual Perception.* NY and London: Academic Press.

Craig, J.V. (1992). Measuring social behavior in poultry. *Poultry Science, 71*, 650-657.

Dasser, V. (1987). Slides of group members as representations of the real animals (*Macaca fascicularis*). *Ethology, 76*, 65-73.

Dawkins, M.S. (1995). How do hens view other hens? The use of lateral and binocular visual fields in social recognition. *Behaviour, 132*, 591-606.

Dawkins, M.S. (1996). Distance and social recognition in hens: Implications for the use of photographs as social stimuli. *Behaviour, 133*, 663-680.

DeMello, L.R. (1989). *The Effect of Procedural Variations on Discriminative Performance: Visual Acuity in the Domestic Hen.* University of Waikato: unpublished doctoral thesis.

DeMello, L.R., Foster, T.M., & Temple, W. (1992). Discriminative performance of the domestic hen in a visual acuity task. *Journal of the Experimental Analysis of Behavior, 58*, 147-157.

Dennett, D. (1987). *The Intentional Stance*. Cambridge, MA: MIT.

De Valois, R.L., Morgan, H., & Snodderly, D.M. (1974). Psychophysical studies of monkey vision – III. Spatial luminance contrast sensitivity tests of macaque and human observers. *Vision Research, 14*, 75-81.

Dinsmoor, J.A. (1995). Stimulus control: Part II. *The Behavior Analyst, 18*, 253-269.

Douglis, M.B. (1948). Social factors influencing the hierarchies of small flocks of the domestic hen: Interactions between resident and part-time members of organized flocks. *Physiological Zoology, 21*, 147-182.

Duncan, I.T.J. (1987). Social preference and cognition. In R. Zayan and I.J.T. Duncan (Eds.) *Cognitive Aspects of Social Behaviour in the Domestic Fowl (pp. 24-33).* New York: Elsevier.

Evans, C.S., & Marler, P. (1991). On the use of video images as social stimuli in birds: audience effects on alarm calling. *Animal Behaviour, 41,* 17-26.

Fagan, A., Eichenbaum, H., & Cohen, N. (1985). Normal learning set and facilitation of reversal learning in rats with combined fornix-amygdala lesions: Implications for preserved learning abilities in amnesia. *Annals of the New York Academy of Sciences, 444,* 510-512.

Fager, L.Y., & Fager, R.S. (1981). Chicken blue and chicken violet, short wavelength sensitive visual pigments. *Vision Research, 21,* 581-586.

Fersen, L., & Lea, S.E.G. (1990). Category discrimination by pigeons using five polymorphous features. *Journal of the Experimental Analysis of Behavior, 54,* 69-84.

Ferster, C.B., & Skinner, B.F. (1957). *Schedules of Reinforcement.* New York: Appleton-Century-Crofts.

Field, D.J., & Brady, N. (1997). Visual sensitivity, blur and the sources of variability in the amplitude spectra of natural scenes. *Vision Research, 37,* 3367-3383.

Fitzke, F.W., Hayes, B.P., Hodos, W., Holden, A.L., & Low, J.C. (1985). Refractive sectors in the visual field of the pigeon eye. *Journal of Physiology, 369,* 33-44.

Fox, R., Lehmkuhle, S.W., & Westendorf, P.D.H. (1976). Falcon visual acuity. *Science, 192,* 263-265.

Gibson, J.J. (1950). *The Perception of the Visual World.* Boston, Massachusetts: Houghton.

Gonzalez, R.C., & Woods,R.E. (1992). *Digital Image Processing.* New York: Addison-Wesley.

Guhl, A.M., & Ortman, L.L. (1953). Visual patterns in the recognition of individuals among chickens. *The Condor, 55,* 287-298.

Hayes, B.P., Hodos, W., Holden, A.L., & Low, J.C. (1987). The projection of the visual field upon the retina of the pigeon. *Vision Research, 27,* 31-40.

Herrnstein, R.J. (1979). Acquisition, generalization, and reversal of a natural concept. *Journal of Experimental Psychology: Animal Behavior Processes, 5,* 116-129.

Herrnstein, R.J., & de Villiers, P.A. (1980). Fish as a natural category for people and pigeons. In G.H. Bower (Ed.) *The Psychology of Learning and Motivation, 14.* New York: Academic Press.

Herrnstein, R.J., & Loveland, D.H. (1964). Complex visual concept in the pigeon. *Science, 146,* 549-551.

Hodos, W. (1993). The visual capabilities of birds. In H.P. Zeigler and H.J. Bischof (Eds.) *Vision, Brain, and Behavior in Birds (pp. 63-76)*. Cambridge, Massachusetts and London: MIT Press.

Hodos, W., & Erichsen, J.T. (1990). Lower-field myopia in birds: An adaption that keeps the ground in focus. *Vision research, 30,* 653-657.

Hodos, W., Leibowitz, R.W., & Bonbright, J.C. (1976). Near-field visual acuity of pigeons: Effects of head location and stimulus luminance. *Journal of the Experimental Analysis of Behavior, 25,* 129-141.

Hodos, W., Miller, R.F., & Fite, K.V. (1991). Age-dependent changes in visual acuity and retinal morphology in pigeons. *Vision Research, 31,* 669-677.

Honig, W.K., & Stewart, K.E. (1988). Pigeons can discriminate locations presented in pictures. *Journal of the Experimental Analysis of Behavior, 50,* 541-551.

Jacobs, G.H. (1977). Visual capacities of the owl monkey (*Aotus trivirgatus*) – II. Spatial contrast sensitivity. *Vision Research, 17,* 821-825.

Jacobs, G.H., Birch, D.G., & Blakeslee, B. (1982). Visual acuity and spatial contrast sensitivity in tree squirrels. *Behavioural Processes, 7,* 367-375.

Jenssen, T.A. (1970). Female response to filmed displays of Anolis nebulosus (*Sauria, Iguanidae*). *Animal Behaviour, 18,* 640-647.

Karakashian, S.J., Gyger, M., & Marler, P. (1988). Audience effects on alarm calling in chickens (*Gallus gallus*). *Journal of Comparative Psychology, 102,* 129-135.

Kare, M.R., & Rodgers, J.G. (1976). Sense organs. In P.D. Sturkie (Ed.) *Avian Physiology* (3rd ed., pp. 30-52). New York: Springer-Verlag.

Kirkpatrick-Steger, K., Wasserman, E.A., & Biederman, I. (1996). Effects of spatial rearrangement of object components on picture recognition in pigeons. *Journal of the Experimental Analysis of Behavior, 65,* 465-475.

Lumsden, E.A. (1977). Generalization of an operant response to photographs and drawings/silhouettes of a three-dimensional object at various orientations. *Bulletin of the Psychonomic Society, 10,* 405-407.

McFadden, S.A. (1993). The avian eye view. In H.P. Zeigler and H.J. Bischof (Eds.) *Vision, Brain, and Behavior in Birds (pp. 1-3)*. Cambridge, Massachusetts and London: MIT Press.

Mackintosh, N.J. (1977). Stimulus control: Attentional factors. In W.K.Honig, and J.E.R.Staddon (Eds.) *Handbook of Operant Behavior (pp.432-480)*. New Jersey: Prentice-Hall.

Martin, G.R. (1993). Producing the image. In H.P. Zeigler and H.J. Bischof (Eds.) *Vision, Brain, and Behavior in Birds (pp. 5-24)*. Cambridge, Massachusetts and London: MIT Press.

Mazur, J.E. (1997). *Learning and Behavior* (3rd ed.), New Jersey: Prentice-Hall.

Mey, J., & Thanos, S. (1993). Developmental anatomy of the chick retinotectal projection. In H.P. Zeigler and H.J. Bischof (Eds.) *Vision, Brain, and Behavior in Birds (pp. 173-194).* Cambridge, Massachusetts and London: MIT Press.

Merigan, W.H. (1976). The contrast sensitivity of the squirrel monkey (Saimiri Sciureus). *Vision Research, 16,* 375-379.

Northmore, D.P.N., & Dvorak, C.A. (1979). Contrast sensitivity and acuity of the goldfish. *Vision Research, 19,* 255-261.

Nye, P.W. (1968). The binocular acuity of the pigeon measured in terms of the modulation transfer function. *Vision Research, 8,* 1041-1053.

Nye, P.W. (1972). On the functional differences between frontal and lateral visual fields of the pigeon. *Vision Research, 13,* 559-574.

Patterson-Kane, E.G. (1994). *The Ability of Hens to Recognise Video Images as the Objects they Represent.* University of Waikato: unpublished masters thesis.

Patterson-Kane, E., Nicol, C.J., Foster, T.M., & Temple, W. (1997). Limited perception of video images by domestic hens. *Animal Behaviour, 53,* 951-963.

Pavlov, I.P. (1927). *Conditioned Reflexes.* Oxford: Oxford University Press.

Perrone, J.A., & Stone, L.S. (1994). A model of self-motion estimation within primate extrastriate visual cortex. *Vision Research, 34,* 2917-2938.

Piaget, J. (1952). *The Origins of Intelligence in Children* (2nd ed.), New York: International Universities Press.

Poole, J., & Lander, D.G. (1971). The pigeon's concept of pigeon. *Psychonomic Science, 25,* 157-158.

Premack, D. (1976). *Intelligence in Ape and Man.* New York: John Wiley & Sons.

Redhead, E.S., & Pearce, J.M. (1993). The influence of an irrelevant stimulus on two discriminations. *Journal of Experimental Psychology: Animal Behavior Processes, 19,* 180-190.

Redhead, E.S., & Pearce, J.M. (1998). Some factors that determine the influence of a stimulus that is irrelevant to a discrimination. *Journal of Experimental Psychology: Animal Behavior Processes, 24,* 123-135.

Reymond, L. (1987). Spatial visual acuity of the falcon, *Falco berigora*: a behavioural, optical and anatomical investigation. *Vision Research, 27,* 1859-1874.

Rilling, M. (1977). Stimulus control and inhibitory processes. In W.K.Honig, and J.E.R.Staddon (Eds.) *Handbook of Operant Behavior (pp.432-480).* New Jersey: Prentice-Hall.

Roitblat, H.L. (1982). The meaning of representation in animal memory. *The Behavioral and Brain Sciences, 5,* 353-406.

Russ, J.C. (1992). *The Image Processing Handbook.* London, Tokyo: CRC Press.

Ryan, C.M.E. (1982). Concept formation and individual recognition in the domestic chicken (*Gallus gallus*). *Behaviour Analysis Letters, 2,* 213-220.

Ryle, G. (1949). *The Concept of Mind.* London: Hutchinson.

Schaeffel, F., Howland, H.C., & Farkas, L. (1986). Natural accommodation in the growing chicken. *Vision Research, 26,* 1977-1993.

Schjelderup-Ebbe, T. (1922). Beitrage zur social-psychologic des haushuhns. *Zeitschrift fur Psychologic, 88,* 225-252.

Schmid, K.L., & Wildsoet, C.F. (1998). Assessment of visual acuity and contrast sensitivity in the chick using an optokinetic nystagmus paradigm. *Vision Research, 38,* 2629-2634.

Schusterman, R.J., & Balliet, R.F. (1970). Conditioned vocalizations as a technique for determining visual acuity thresholds in sea lions. *Science, 169,* 498-501.

Scott, R., Himadi, W., & Keane, T. (1983). Generalization of social skills. In M. Hersen, R. Eisler and P. Miller (Eds.) *Progress in Behavior Modification, 15, (pp. 114-172).* New York: Academic Press.

Sekuler, R., & Blake, R. (1994). *Perception* (3rd ed.), New York: McGraw-Hill.

Skinner, B.F. (1953). *Science and Human Behavior.* New York: The Free Press.

Skinner, B.F. (1974). *About Behaviorism.* New York: Alfred A Knopf, Inc.

Skinner, B.F. (1981). Selection by consequences. *Science, 213,* 501-504.

Smart, J.J.C. (1973). Sensations and brain processes. Reprinted in P. Edwards and A. Pap (Eds.) *A Modern Introduction to Philosophy* (3rd ed., pp. 241-249). New York: The Free Press.

Spence, K.W. (1934). Visual acuity and its relation to brightness in chimpanzee and man. *Journal of Comparative Psychology, 18,* 333-361.

Stromer, R., McIlvane, W.J., Dude, W.V., & Mackay, H.A. (1993). Assessing control by elements of complex stimuli in delayed matching to sample. *Journal of the Experimental Analysis of Behavior, 59,* 83-102.

Tauson, R. (1993). Productivity and performance in relation to housing systems for laying hens. Paper delivered to the 26th meeting of the standing committee of the European convention on the protection of animals kept for farming purposes, Skara, Sweden. 8-11 June.

Terrace, H.S. (1966). Stimulus control. In W.K.Honig (Ed.) *Operant Behavior: Areas of Research and Application (pp.271-344).* New Jersey: Prentice-Hall.

Thomas, D.R., Burr, D.E.S., & Eck, K.O. (1970). Stimulus selection in animal discrimination learning: An alternative interpretation. *Journal of Experimental Psychology, 86,* 53-62.

Treutwein, B. (1995). Adaptive psychophysical procedures. *Vision Research, 35,* 2503-2522.

Trillmich, F. (1976). Learning experiments on individual recognition in budgerigars (*Melopsittacusundulatus*). *Z.Tierpsychol., 41,* 372-395.

Troje, N.F., Huber, L., Loidolt, M., Aust, U., & Fieder, M. (1999). Categorical learning in pigeons: the role of texture and shape in complex static stimuli. *Vision Research, 39,* 353-366.

Turkel, J., & Wallman, J. (1977). Oscillatory eye movement with possible visual function in birds. *Neuroscience Abstracts, 3,* 158.

Uhlrich, D.J., Essock, E.A., & Lehmkuhle, S. (1981). Cross-species correspondence of spatial contrast sensitivity functions. *Behavioural Brain Research, 2,* 291-299.

Vaughan, W., & Greene, S.L. (1984). Pigeon visual memory capacity. *Journal of Experimental Psychology: Animal Behavior Processes, 10,* 256-271.

Wallman, J., & Letelier, J-C. (1993). Eye movements, head movements, and gaze stabilization in birds. In H.P. Zeigler and H.J. Bischof (Eds.) *Vision, Brain, and Behavior in Birds (pp. 245-263).* Cambridge, Massachusetts and London: MIT Press.

Walls, G.L. (1942). *The Vertibrate Eye and its Adaptive Radiation.* Bloomfield Hills, MI.: Cranbrook Institute of Science.

Wandell, B.A. (1995). *Foundations of Vision.* Massachusetts: Sinauer Associates.

Warren, J.M. (1965). Primate learning in comparative perspective. In A.M.Schrier, H.F.Harlow, and F.Stollnitz (Eds.). *Behavior of Non-Human Primates, 1.* New York: Academic Press.

Wasserman, E.A. (1993). Comparative cognition: Beginning the second century of the study of animal intelligence. *Psychological Bulletin, 113,* 211-228.

Wasserman, E.A., Kiedinger, R.E., & Bhatt, R.S. (1988). Conceptual behavior in pigeons: Categories, subcategories and pseudocategories. *Journal of Experimental Psychology: Animal Behavior Processes, 14,* 235-246.

Weavers, R., Foster, T.M., & Temple, W. (1998). Reinforcer efficacy in a delayed matching-to-sample task. *Journal of the Experimental Analysis of Behavior, 69,* 77-85.

Wood-Gush, D.G.M. (1971). *The Behaviour of Domestic Fowl.* London, England: Heinemann.

Yarczower, M., Wolbarsht, M.L., Galloway, W.D., Fligsten, K.E., & Malcolm, R. (1966). Visual acuity in a stumptail macaque. *Science, 152,* 1392-1393.

Zeldin, R.K., & Olton, D.S. (1986). Rats acquire spatial learning sets. *Journal of Experimental Psychology: Animal Behavior Processes, 12,* 412-419.

APPENDICES

Appendix A – raw data from test sessions of Experiment 1

combination	number of incorrect choices					
	71	72	73	74	75	76
comb/beak	20	7	6	18	7	13
comb/wattles	15	21	9	17	5	10
comb	22	29	5	8	0	17
beak	32	21	27	32	26	31
wattles	34	23	28	30	31	15
beak/wattles	29	10	23	33	26	24

Appendix B – proportions of correct choices for last five training sessions and test session of Experiment 2.

session	71	72	73	74	75	76
test	.455	.614	.477	.545	.409	.545
40	.932	.977	.886	.955	.909	1
39	.977	.977	1	1	.977	1
38	.977	1	.977	.977	.977	1
37	.977	.909	1	1	.955	1
36	.977	.955	.977	.977	1	1

Appendix C – data from Experiment 3.

Condition 1 – numbers of errors made to arrangements of appendices on spheres, plus last five training sessions.

	71	72	73	74	75	76	mean
85	10	1	4	1	0	1	
84	5	2	3	2	2	0	
83	9	2	3	1	1	2	
82	8	0	2	0	1	0	
81	9	3	2	1	0	6	
beak	27	21	20	24	26	24	23.67
comb	6	2	4	1	2	11	4.33
wattle	24	22	23	25	19	5	19.67
beak/wattle	22	28	29	20	16	3	19.67
comb/wattle	10	6	1	0	2	6	4.17
beak/comb	13	2	5	2	0	8	5

Condition 2 – numbers of errors made to inverted, unattached appendices, plus last five training sessions.

	71	72	73	74	75	76	mean
137	4	0	1	1	2	5	
136	0	0	1	3	0	5	
135	1	0	1	1	3	5	
134	0	0	0	0	1	8	
133	2	0	1	3	1	2	
beak	21	21	20	20	18	20	20
comb	17	21	29	21	15	15	19.67
wattle	5	8	3	4	4	10	5.67
beak/wattle	6	1	2	2	1	7	3.17
comb/wattle	1	2	3	1	1	7	2.5
beak/comb	16	22	18	20	19	21	19.33

Condition 3 – numbers of errors made to arrangements of shapes, plus last five training sessions.

	71	73	74	75	76	mean
105	9	0	4	3	2	
104	7	3	2	3	4	
103	4	1	11	1	1	
102	7	1	6	2	3	
101	5	1	5	2	3	
square	25	24	22	18	22	22.5
circle	4	5	3	4	4	4.4
octagon	16	18	18	24	15	18.2
square/circle	4	7	6	6	7	6.4
square/octagon	17	19	24	18	13	18.2
circle/octagon	4	2	6	3	3	4

Condition 4 – numbers of errors made to vertically inverted shapes.

	71	73	74	75	76	mean
square	23	24	16	23	18	20.8
circle	21	13	18	19	17	17.6
octagon	24	18	18	22	16	19.6
square/circle	21	10	20	2	16	13.8
square/octagon	26	19	20	15	24	20.8
circle/octagon	20	9	25	5	9	13.6

Condition 5 – proportions of correct choices of target circle, and previous five training sessions with full sets of shapes.

session	71	73	74	75	76
test	.455	.727	.591	.773	.727
8	.909	.977	.886	1	.977
7	.955	.977	.864	1	1
6	.773	1	.75	1	.977
5	.795	.977	.955	1	.977
4	.795	.955	.909	1	.977

Condition 6 – numbers of errors made to arrangement of shapes (replication of C4), plus last five training sessions.

	81	82	83	84	85	86	mean
68	3	2	2	3	3	1	
67	1	0	5	4	3	1	
66	10	3	1	2	1	5	
65	1	2	3	4	2	2	
64	1	3	5	2	2	3	
square	18	22	24	22	24	21	21.83
circle	6	5	2	1	2	4	3.33
octagon	23	29	25	21	19	23	23.33
square/circle	1	3	3	4	1	1	2.17
square/octagon	21	23	22	25	18	24	22.17
circle/octagon	2	2	3	4	2	1	2.33

Appendix D – viewing distances measured from videos

First CSF – Exp 4, Condition 1
(measures in mm, +176mm, edge of graph paper to screen, +10mm, pupil to retina)

43	64	
	64	
44	66	
	62	
45	64	
	65	
46	63	mean = 250mm
	64	sd = 1.12mm

fields of view calculated using Equation 4.1:

image size (mm)	field of view (degrees)
60	15.206
85	21.44
55	13.95

Second CSF – Exp 4, Condition 2
(measures in mm, +97mm, edge of graph paper to screen, +10mm, pupil to retina)

43	12	
	26	
44	57	
	41	
45	79	
	32	
46	38	mean = 145.63mm
	24	sd = 19.68mm

fields of view calculated using Equation 4.1:

image size (mm)	field of view (degrees)
45	19.517
50	21.646

Filtered profiles – Exp 5
(measures in mm, +155mm, edge of graph paper to screen, +10mm, pupil to retina)

72	82	
73	85	
	96	
74	77	
	98	mean = 249mm
75	66	sd = 10.94mm

fields of view calculated using Equation 4.1:

image size (mm)	field of view (degrees)
100	25.232

Appendix E – data from Experiment 4.

Raw data from Experiment 4. Columns are headed: cycles – grating frequency; max and min – screen intensity values in cd/m2; cont – resultant contrast calculated as max-min/(max+min); bulb – proportion of projector bulb output intensity programmed for this grating; cyc/0 – grating frequency for field of view calculated using Equation 4.1; subject numbers; mean contrast threshold (b) extracted using Equation 4.2.

					Condition 1						Condition 2					
cycles	max	min	cont	bulb	cyc/0	43	44	45	46	mean	cyc/0	43	44	45	46	mean
2	502	46	.7411	.38	0.132	.2	.6	.3	.4							
	496	50	.7664	.39		.5	.5	.4	.4							
	494	54.8	.7878	.4		.7	.7	.3	.7							
	492	58.4	.8003	.41		.9	.8	.6	.8							
	484	64	.8168	.42		.9	.8	.7	.8							
	468	69.6	.8321	.43		.8	.8	.5	.8							
					a	99.72	32.33		52							
					b	.7921	.806		.8073	.8018						
5	426	76.4	.0293	.43	.329	.5	.6	.5	.5		.256	.4	.4		.6	
	366	85.6	.1669	.44		.6	.6	.7	.7			.3	.6		.8	
	320	103.6	.3141	.45		.6	.7	.5	.5			.8	.8		.8	
	227.6	118.6	.5109	.48		.8	.8	.5	1			.9	.8		.9	
	188.8	134.8	.6209	.49		.9	.8	.4	1			1	.9		.9	
	154.8	146	.6959	.5		.8	.8	.2	1			.8	.8		.8	
					a	5.65	3.15		281.6			151.6	5.23		2.9	
					b	.4863	.4849		.4142	.4618		.31	.42		.22	.317
10	as above		.0293	.42	.658	.5	.5	.5	.7		.512	.6	.7	.4	.7	
			.1669	.44		.3	.5	.6	.4			.7	.4	.6	.7	
			.3141	.46		.8	.7	.8	1			1	.7	.8	1	
			.5109	.48		.8	.8	.8	.8			1	.9	.8	.9	
			.6209	.49		.8	.9	1	.9			1	1	.8	.9	
			.6959	.49		.9	.9	.9	1			1	1	.9	.8	
					a	7.04	7.15	6.64	6.3			15.99	13.31	5.3	2.54	
					b	.478	.4433	.3452	.2901	.3892		.1743	.371	.431	.0751	.2629
20	352	93.6	.0293	.41	1.315	.7	.3	.5	.6		1.025	.5	.6	.5	.6	
	320	103.6	.1304	.45		.7	.2	.6	.7			.6	.7	.6	.7	
	254.8	112.8	.2332	.46		.9	.8	.9	.8			.9	.8	1	.7	
	202	125.6	.3863	.47		.9	.8	.9	.8			1	.8	.8	.9	
	182	140	.5109	.47		1	.7	.8	1			.9	.9	.7	1	
	154.8	146	.5799	.48		.9	.9	.8	.8			1	.7	.8	.9	
					a	6.07	8.6	4.58	4.55			27.2	2.38	2.8	7.11	
					b	.1173	.4371	.2828	.2315	.2672		.18	.3	.35	.23	.265
30	as above		.0293	.43	1.973	.4	.6	.5	.4		1.537	.5	.5	.6	.5	
			.1304	.46		.7	.4	.5	.6			.5	.6	.6	.8	
			.2332	.47		.9	.8	.6	.9			1	.8	.8	.7	
			.3863	.48		1	.8	.9	1			1	.9	.8	.9	
			.5109	.49		1	.8	.8	.9			1	.9	.9	.6	
					a	25.48	4.92	8.96	29.7			360	8.6	5.45	1.5	
					b	.1587	.3992	.3531	.1836	.2737		.1818	.2525	.2751	.4856	.2988
60	as for		.0293	.44	3.946	.6	.5	.5	.5		3.074	.3	.4	.4	.5	
	5 & 10 cyc		.1669	.45		.5	.7	.6	.8			.7	.4	.4	.3	
			.3141	.45		.9	.9	.8	1			.5	.8	1	.8	
			.5109	.46		1	.9	.8	.9			.8	.7	.6	.8	
			.6209	.46		1	1	.8	1			1	.8	.9	1	
			.6959	.47		1	.8	.8	.9			.9	.8	.9	.9	
					a	81.75	11.29	3.64	83.04			16.29	5.52	5.7	10.18	
					b	.2971	.2164	.4595	.162	.2838		.48	.56	.45	.4	.4725
120	as for		.7411	.43	5.597/	.7	.5		.3		5.544	.7	.6	.4	.7	
	2 cyc		.7664	.43	7.892/	.6	.5		.8			.8	.3	.6	.4	
			.7878	.43	8.602	.9	.9		.8			.7	.4	.9	.7	
			.8003	.44		.8	.8		.7			.9	.3	.6	.7	
			.8168	.44		.8	1		.8			.9	.6	.5	.6	
			.8321	.44		.8	.7		.8			1	.9	.9	.8	
					a	14.62	51.72		30.97			26.6	207.5	27.95	22.23	
					b	.7808	.7884		.8013			.76	.82	.82	.83	.8075

Appendix F – Raw data from the two test sessions of Experiment 5.

1st test 21/5/99

LPF cutoff (cyc/°)	72 no. trials	72 corr	73 no. trials	73 corr	74 no. trials	74 corr	75 no. trials	75 corr
1	10	5	10	8	10	10	10	8
2	10	6	10	8	10	9	10	8
3	10	7	10	7	10	6	10	8
4	10	4	10	3	10	5	10	5
5	10	8	10	5	10	6	10	7
6	10	6	10	3	10	7	10	5
7	10	7	10	5	10	6	10	4

2nd test 23/5/99

LPF cutoff (cyc/°)	72 no. trials	72 corr	73 no. trials	73 corr	74 no. trials	74 corr	75 no. trials	75 corr
1	10	8	10	8	10	10	10	9
2	10	4	10	9	10	8	10	8
3	10	5	10	6	10	6	10	4
4	10	6	10	6	10	5	10	6
5	10	6	10	3	10	6	10	5
6	10	7	10	5	10	5	10	4
7	10	6	10	6	10	7	10	4