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ASSESSING PSYCHOPHYSICAL ABILITIES IN BRUSHTAIL POSSUMS.

A thesis
submitted in partial fulfilment of the requirements
for the degree
of
Doctor of Philosophy in Psychology
at the
University of Waikato

by

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2002

Abstract

In Experiment 1, 6 brushtail possums were trained, using food, to perform a conditional discrimination between flickering (5.00 Hz) and steady lights. A block-wise method of limits procedure was then used to increase flicker speed over five steps to 50.00 Hz and percentages correct decreased to near or below 75 %. In Experiment 2 further flicker speeds were presented but percentages correct did not decrease as flicker speed increased. In Experiment 3 flicker speeds ranging from 16.67 Hz to 71.42 Hz were presented in either 5 or 10 steps. Percentages correct remained high at all flicker speeds regardless of the speed of stimulus change, suggesting that an extraneous variable had come to control behaviour. In Experiment 4, auditory cues, background lighting and relative luminance cues were examined using the 10 step stimulus change series. Once the relative luminance of the lights were equalised percentage correct dropped as flicker speed increased beyond 20.00 Hz. Flicker speeds between 20.00 and 25.00 Hz (equal luminance) were presented in Experiment 5 and gave all-or-none functions which fell abruptly at 24 .00 Hz. In Experiment 6 a simultaneous stimulus discrimination task was trained and CFF was tested over several ranges. The threshold functions were very similar to those from the conditional discrimination experiments. These experiments suggest that the CFF of possums is 24.00 Hz (at an average luminance of $2.1 \log \text{ cd/m}^2$). The implications of this for possums' visual abilities are discussed. In Experiment 7 six new possums learned a conditional discrimination between the presence and absence of a tone (at 880 Hz) using methodology similar to Experiment 1. Possums learnt the task quickly. Tone intensity (dBA) was reduced from 80 dBA in 8 dBA steps until percentages correct fell below 50 %. Threshold functions did not resemble those found in Experiments 5 and 6. There were response biases here but not in the previous flicker experiments and possible implications of this on threshold measures are discussed. In Experiment 9 six possums were trained on a conditional discrimination using dim and bright stimuli. Difficulties with producing appropriate stimuli meant only 2 possums learned the task. During threshold sessions the luminance of the bright stimulus was reduced in five steps using a blockwise method of limits. The threshold functions found were gradual resembling those of Experiment 7, suggesting that the step function found in the flicker experiments may be unique to possums and CFF determinations. These experiments show that it is possible to train possums to perform visually-based and auditory-based conditional discriminations, but suggest that caution is needed when comparing threshold estimates across experiments.

Acknowledgements

My thanks and appreciation go to Drs Mary Foster and Bill Temple for their support, encouragement and advice throughout this thesis. My thanks also go to the other students at both the animal and human operant labs, your support and well wishes meant a lot as this was coming together. Special thanks go to the other 'possum' people, Angela Bron and Jo Martin, who helped with the day-to-day data collection over the years. Extra special thanks go to Jenny Chandler who made sure that the possums kept working despite fire, flood and disease.

Dedication

This thesis is dedicated to my parents, Sonia and Ian Signal, who helped in the process of this thesis from building possum rooms and locating lost possums to supplying support and chocolate when they were most needed. Special thanks go to my mother for all the weekends spent feeding and weighing possums.

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Trichosurus vulpecula, otherwise known as the Brushtail possum, was first introduced into New Zealand around the 1840's (Pracy, 1974). According to Pracy (1974) the main reason for the introduction of this Australian native was the establishment of a fur industry, with some animals also being brought into the country as pets. Acclimatisation societies bred and released possums around the country with the support of the New Zealand Government between 1846 and 1912 (Pracy, 1974). Possums were generally seen as a "valuable and harmless animal" (Annual Report Auckland Acclimatisation Society 1916-17, cited in Pracy, 1974, p.6). In 1911, an act was passed which made it illegal to trap or destroy possums. Due to the profits available from trapping these animals, however, this act was removed in 1912 but was later re-instated in some parts of the country (Pracy, 1974).

According to Morgan (1990) earlier liberations and the natural dispersal of the possum has led to this animal occupying approximately 90% of the country. Recent estimates suggest that possums now number between 60 and 70 million and occupy approximately 98% of the country (Montague, 2000). The negative effect that this occupation has had on native flora and fauna is evident and extensive (Batchelor, 1983; Rose, Pekelharing, Platt & Woolmore, 1993). The possum has also been identified as a vector of infection in bovine tuberculosis (Ekdahl, Smith & Money, 1970; Department of Conservation, 1996; Morgan, 1990, Montague, 2000).

Brockie, Fitzgerald, Green, Morris and Pearson (1984) conducted a survey of all existing and on-going possum research in New Zealand and Australia for the New Zealand Wildlife Research Liaison Group. They identified several key areas where research was lacking. While some of these areas have subsequently been addressed, one of their recommendations has remained relatively ignored. Brockie et al. (1984) suggested that "...more information is required on basic possum behaviour, sensory perception and food preferences if lures, baits and poisons are to be used more effectively..." (p.3). Since this report, there have been studies on general possum behaviour (e.g., social behaviour, Hickling & Reddiex, 1996) and their food preferences (Hudson, 1996). However, there is still very little information available on the possums' learning and sensory abilities (Clout & Sarre, 1997; Wynne & McLean, 1999).

It has been suggested that to understand an organism's sensory abilities anatomical, physiological and behavioural data must be combined (Blough & Blough, 1977). While the physiology and anatomy of brushtail possums has been extensively studied (e.g., Aitkin & Kenyon, 1981; Freeman & Tancred, 1978; Gilmore, 1985; Harman, 1994; Haynes, 1995; Jackson & Morris, 1996; Jolly, Eason, & Frampton, 1993; Oldham, 1986) there have been only two behavioural, laboratory based, investigations into the sensory abilities of brushtail possums.

Behavioural studies of possum's sensory abilities to date

Kirkby and Williams (1979) and Webster (1975) both examined possum's ability to discriminate between visual stimuli. Webster (1975) reported no difficulty in training possums to press a bar for a food reward, although he had difficulty training a visual discrimination. He reported that initially their ability to discriminate between horizontal and vertical lines never increased much beyond chance levels. He eventually combined the stimulus, reward and manipulandum into one object, namely "...a vertical piece of carrot..." (p.44), after which the animals gained the required orientation discrimination.

Kirkby and Williams (1979) measured errors made on successive reversals of two discrimination tasks by possums. They found that when the discrimination was based on position each possum made few errors over 19 reversals. However when possums were faced with a visually based discrimination (relative brightness), only two learned the task to a criterion of 90% correct within 25 sessions. Another possum learned the task after approximately 300 more sessions, and the final possum never reached criterion after more than 700 sessions. Of the two possums that did learn the original task, neither reached the criterion level of performance after 25 sessions at the first reversal.

Webster's (1975) difficulty in training a visual discrimination may have been due, at least in part, to the experimental conditions, as all sessions were run under full light conditions during the day. As possums are a nocturnal animal (Clout & Sarre, 1997), these experimental sessions would have been held during the animals' normal sleep time. However, Kirkby and Williams (1979) also had trouble training a visual discrimination (and its reversal) under red light and reverse day/night conditions. One possible argument for the lack of a light versus dark discrimination developing (for two of the possums) and failure to learn the reversal (for the other two) would be that the light stimulus was aversive. The procedure required the possum to approach and interact with the 'bright' stimulus (a block lit by a 15-W bulb). If that stimulus was 'too' bright it may have been aversive for animals with eyes adapted for nocturnal vision, thus leading to the possums avoiding approaching the light. One would expect any such aversive control to be readily apparent however, and Kirkby and Williams (1979) state that no such preference or avoidance behaviour was noticeable during training.

These two studies suggest that it is difficult (and in some cases may be impossible) to teach brushtail possums a solely visual-based discrimination. However, it is hard to form a firm conclusion from only two pieces of research. Further investigation into the abilities of brushtail possums to perform visual and other discriminations, while experimental variables such as background illumination and stimulus type are controlled for, is needed.

Several factors seem to be important when training and testing these animals. As they are a nocturnal species, testing during their active periods (i.e., when it is dark) would

seem sensible. Secondly, both Kirkby and Williams (1979), and Webster (1975) used manipulandum that could only be used for one trial before being manually re-set. Kirkby and Williams (1979) used wood blocks which needed to be placed back in position after every trial, while Webster (1975) presented pieces of carrot, one of which needed to be replaced after every trial as the possums were required to reach for and remove one of the carrot sticks. Both of these would have required a lot of human intervention within an experimental session, potentially disrupting behaviour and limiting the range of stimuli that could be presented. Developing remotely controlled experimental apparatus that is capable of presenting stimuli automatically would enable a wider range of abilities to be investigated with fewer interruptions during an experimental session.

Hudson, Foster and Temple (1999) developed an operant response panel for use with possums. While they successfully trained four possums to respond on a key (with a horizontal bite bar attached), problems were encountered when the panel was moved from individual to individual. They suggested that in future experiments the use of individual response panels would reduce the amount of time possums spent scent marking rather than responding within a session. Hudson et al. (1999) also reported that the topography of one possum's responding changed as the response requirement increased, thus designing operant equipment that would result in a more defined response (that does not change over time) would also be useful for future research where rate of responding is considered.

As so little is known about possums' sensory abilities from a behavioural perspective, information from physiological studies is useful to help determine whether a possum is physically capable of detecting the stimulus being presented. Physiological findings suggest that the brushtail possum has a well developed visual system similar to the cat and other mammals (Crewther, Crewther & Sanderson, 1984; Freeman & Tancred, 1978) with both rods and cones in their retina (Harman, Sanderson & Beazley, 1992), thus the possum should be physically capable of detecting and responding to visual stimuli. The auditory abilities of possums have also been studied physiologically (e.g., Aitkin, Gates & Kenyon, 1979; Gates & Aitkin, 1982) and the results from these studies suggest that possums should also be able to detect and respond to a range of auditory stimuli.

Within the broad field of psychophysics certain theoretical positions entail particular experimental procedures and methods of data analysis. These theoretical positions can be divided into: traditional psychophysical methods; methods based around the theory of Signal Detection and methods based around Behavioural Detection theory.

Traditional psychophysics as a means to study sensory abilities

Stebbins (1970) defined traditional psychophysics as a "...methodology for presenting stimuli to an organism to determine the limits and dimensions of its sensory experience..." (p.2). He points out that the aim of psychophysics has traditionally been to

estimate the minimum level of a stimulus that an organism can detect, commonly termed an absolute threshold (e.g., the point at which a tone is just too quiet to hear), or the minimum detectable difference between two stimuli, commonly termed a difference threshold. In order to estimate an either threshold, an organism's responses to varying intensities of the chosen stimulus dimension, or levels of disparity between stimuli, are examined, and the threshold is taken to be the intensity at which some pre-defined accuracy is reached (Blough & Blough, 1977). While the following coverage will focus on absolute thresholds, difference threshold can be assessed using the same procedures.

Regardless of how stimulus intensity is manipulated in a psychophysical experiment, the traditional view of the threshold was that the organism (generally human) would either be able to detect the stimulus or not. Thus the data from such experiments should result in a function similar to that shown in Figure 0.1a (Engen, 1972), that is, a step-like function which moves from no detection to 100% detection at a 'threshold' value. While some researchers reportedly found this all-or-none pattern after extended observer training (e.g., von Bekesy, 1930, cited Engen, 1972), generally a more ogival function was found, thought to be due to variability in observer reports (Engen, 1972). This ogival function (a cumulation of the normal distribution) became the theoretical psychophysical function and the threshold was taken to be the stimulus value that resulted in 50 % detection (Woodworth & Schlosberg, 1955). A typical, stylised version of this is shown in Figure 0.1b.

With the development of two-stimulus psychophysical procedures (which will be discussed further later in this Introduction) alternative threshold criteria have been adopted. Madigan and Williams (1987) and Treutwein (1995) both advocate the use of differing threshold criteria depending on the method of stimulus presentation. That is, they suggest that a 50 % criterion should be used when two stimuli are presented successively, and a 75 % criterion when stimuli are presented simultaneously. However, the majority of psychophysical investigations present the stimulus intensity that results in 75 % overall correct performance as the threshold intensity value regardless of the method of stimulus presentation (e.g., Georgeson & Georgeson, 1985; Grossetete & Moss, 1998; Hodos & Bonbright, 1972; Irwin & Terman, 1970; Spong & White, 1971) as it is said to give the "...least stimulus value at which there is clear perception..." (DeMello, 1989).

Psychophysical experiments with animals

Psychophysical methods fall into three general categories; those that use a pre-existing behaviour, those that use Classical Conditioning to establish stimulus control of an existing behaviour, and those that use Operant Conditioning to establish stimulus control of a new (trained) behaviour. In all psychophysical experiments, an organism is required to respond in some manner that differs when it does or does not detect the stimulus. If

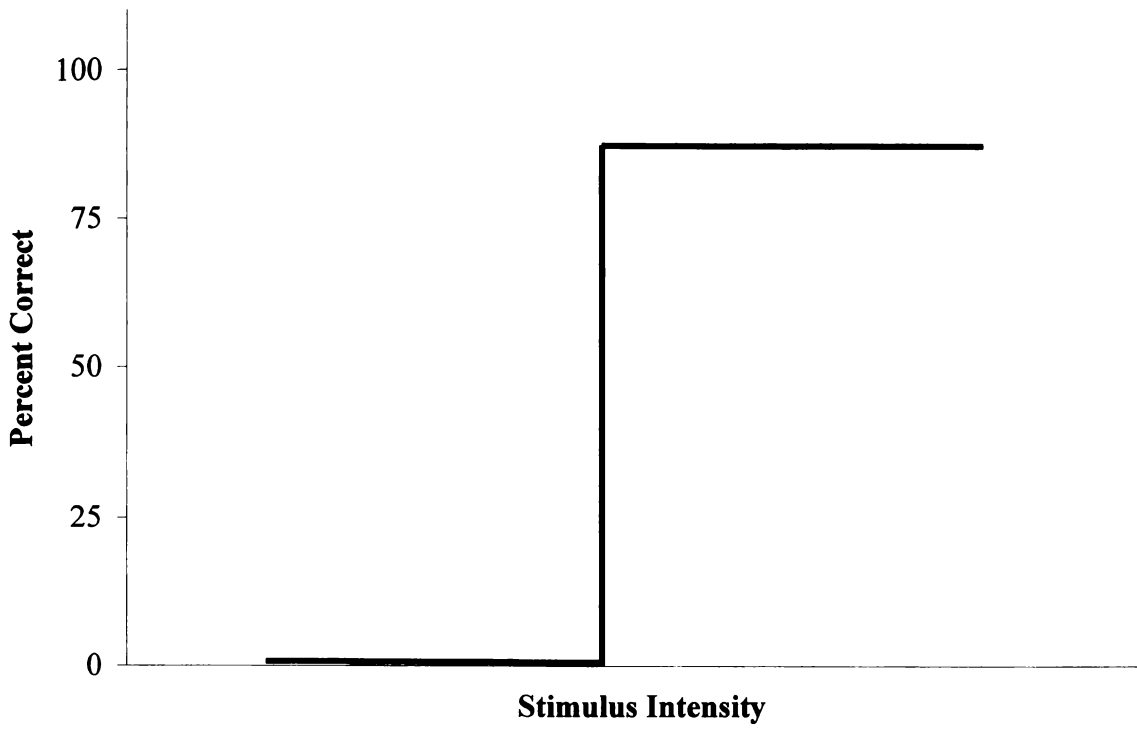


Figure 0.1a Theoretical accuracy function for one stimulus experiments.

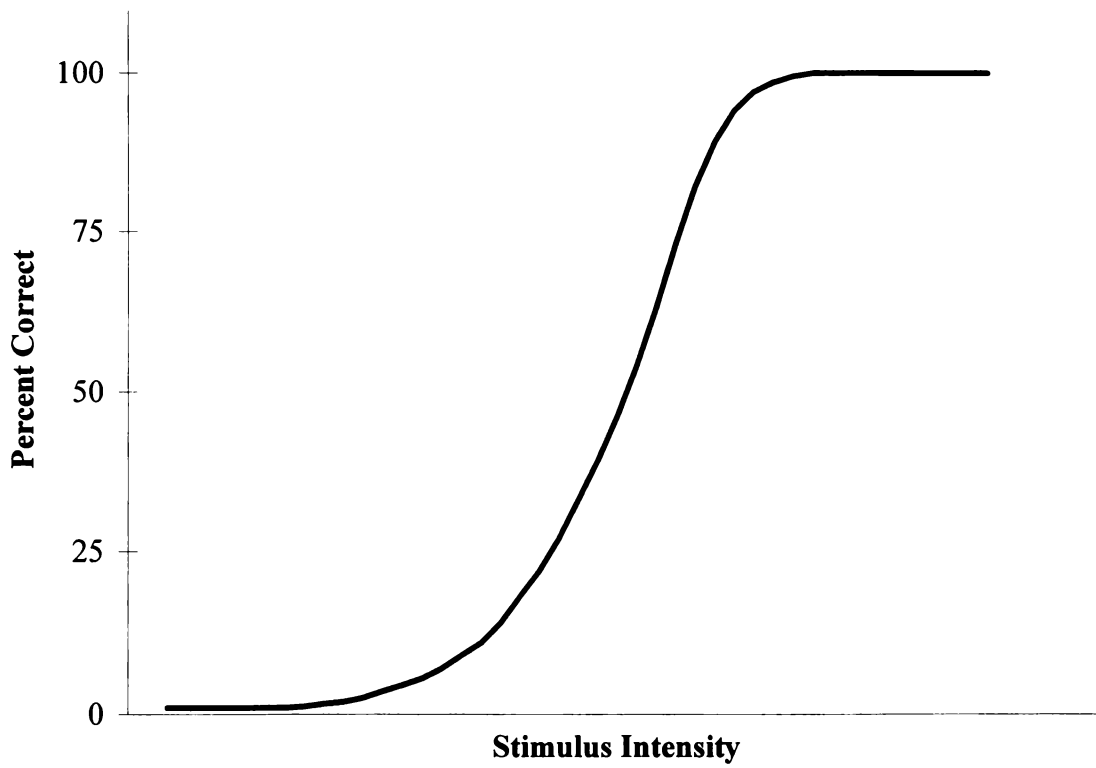


Figure 0.1b Obtained accuracy function for one stimulus experiments.

behaviour occurs in the presence of a certain stimulus and not in its absence, that stimulus can be defined as a discriminative stimulus for that behaviour.

Some psychophysical experiments have utilised untrained, innate behaviours that occur differentially in the presence of a certain stimulus. For example Cronly-Dillon (1966) measured the light sensitivity of scallops by using their response to sudden changes in light levels (they close their shells when light levels abruptly reduce). He shone different coloured lights (of varying luminance) at groups of scallops and counted how many scallops closed their shells when he turned the light off. The threshold value for each coloured light was taken to be the brightness which resulted in two thirds of the scallops shutting their shells. More recently, Clark and Uetz (1990) used the stereotypical response of a jumping spider (e.g., jumping towards prey) to measure the spider's ability to perceive and respond to video images. This approach however seriously limits the scope of possible investigations, as it is dependent upon an innate response pre-existing in the modality being examined (Stebbins, 1970).

Pavlovian or Classical Conditioning where an unconditioned stimulus (e.g., puff of air into eyes) is paired by repeated presentation with a conditioned stimulus (e.g., a tone) and this conditioned stimulus comes to elicit the same response (e.g., blinking) as previously occurred following the unconditioned stimulus, has also been used to establish differential behaviours in the presence of a particular stimulus. Dalton (1967, cited in Stebbins, 1970), for example, used Classical Conditioning techniques to derive an audiogram for the rhesus monkey. He paired tones with electric shocks and measured the subsequent Galvanic Skin Response (GSR) of the monkeys whenever a tone was played. If the GSR did not change following a particular intensity of tone he concluded that the monkey could not detect that intensity. This approach is however also limited by problems with habituation, adaptation and the loss of the trained behaviour (Stebbins, 1970).

Operant Conditioning techniques where a certain behaviour (e.g., a lever press) is made more likely in the presence of particular stimuli (e.g., a tone) due to its consequences. With non-human subjects, this consequence is often access to food and is termed reinforcement. Operant Conditioning allows the training of an essentially unlimited array of behaviours in the presence (or absence) of an equally diverse range of stimuli, limited only by the physical capabilities of the organism. Various methods have been developed using Operant techniques. For example; Conditioned Suppression, Go/No Go and Two-Alternative Forced-Choice, all of which present the stimulus on every trial, other methods will be covered later in this Introduction.

Within Conditioned Suppression methods an organism is trained to perform a specific behaviour (e.g., press a lever or lick a water spout) maintained by access to food or water, a stimulus is presented and an aversive event (e.g., electric shock) paired with that

stimulus. The stimulus becomes a signal for the aversive event and in the presence of the stimuli behaviour is suppressed. Thus, the change in the organism's rate of responding indicates detection of the stimulus under this procedure. Conditioned Suppression techniques have been used to study hearing in a wide range of animals (e.g., Dalton, 1967 (Pigeon); Heffner, Heffner & Masterton, 1971 (Guinea Pig); Heffner, Ravizza & Masterton, 1969 (Tree Shrew); Ravizza, Heffner & Masterton, 1969 (Opossum)).

In Go/No Go procedures, an animal is trained to respond in the presence of a stimulus and not in its absence, again maintained by some reinforcing event (e.g., access to food). For example, Awbrey, Thomas and Kastelein (1988) trained Belugas to swim to an underwater testing station and wait for a tone. If they heard the tone, they were required to back out of the testing station within 2 s and swim to the trainer where they received "...a fish reward..." (p.2274). If the animals did not respond within 2 s, the intensity of the tone was increased and it was played again. Similar techniques have been used to assess absolute thresholds in a wide range of species (e.g., Barton, Bailey & Gatehouse, 1984 (Quail); Ginsburg & Nilsson, 1971 (Budgerigar); Heffner & Heffner, 1983b (Horse and Cattle)).

In Two-Alternative Forced-Choice procedures, two stimuli are presented simultaneously in each trial, but only one stimulus is designated as the target to which the animal must respond. For example, when presented with a flickering and a steady light, Loop, Petuchowski and Smith's (1980) cats were required to respond on the lever below the flickering light and not on the lever below the steady light. In subsequent trials the position of the target stimuli changed randomly. In this example, threshold was taken to be the point at which the cats' performance fell to 70%, although no rationale for this criterion was given. Again, this procedure has been used in the assessment of thresholds in a wide variety of species (e.g., Gerstein, Gerstein, Forsythe & Blue, 1999 (Manatee); Grossetete & Moss, 1998 (Bats); Schwabl & Delius, 1984 (Pigeon)).

Alternative procedures to those outlined above that involve the successive presentation of two stimuli (compared to the simultaneous presentation in Two-Alternative Forced-Choice procedures), have also been developed and used extensively with human and non-human subjects (e.g., DeMello, Foster & Temple, 1992 (Hen); Georgeson & Georgeson, 1985 (Human); Irwin & Terman, 1970 (Rat); Spong & White, 1971 (Dolphin)). While Blough and Blough (1977) state that such procedures were designed specifically to increase stimulus control in psychophysical studies with non-human subjects, successive presentation, two-stimulus procedures appear to have a lot in common with Signal Detection procedures and will be examined in further detail later in this Introduction.

Presenting stimuli in psychophysical studies

Various psychophysical methods have been used to present and change stimuli when determining threshold values once an organism is responding differentially to a

discriminative stimulus (regardless of how, or whether, that response was trained). Two main methods are; the Method of Constant Stimuli and the Method of Limits.

When using the Method of Constant Stimuli, a fixed set of stimulus values (normally five to seven (Stebbins, 1970)) are presented in mixed or random order to the subject. The set is picked so that, at one extreme, the subject will always detect the stimulus (which will result in close to 100% correct responding) and, at the other extreme, it will never detect the stimulus (Stebbins, 1970). This is a commonly used method (e.g., Klump & Maier, 1990; Okanoya & Dooling, 1990), however, one problem with this method is that the stimulus values must be chosen before the threshold is measured. Some of the values chosen may prove to be redundant once the threshold is found so this method can be quite inefficient. Curran and Wattis (1998) state that this method is time consuming and inappropriate for subjects where lengthy testing sessions would prove difficult.

The Method of Limits involves initially presenting a stimulus at an intensity where it is either always detected or never detected. In each succeeding trial the stimulus intensity (or its difference from a standard stimulus) is either increased or decreased (depending on the starting point) until the subject's pattern of responding changes. While this method may be more efficient than the Method of Constant Stimuli (in that all of the stimulus intensity values are not pre-chosen and thus redundant extreme intensities are not as likely to be encountered), there are problems with possible order effects. With the method of limits, the initial intensity of the stimulus and rate of change of intensity are pre-set by the experimenter (Stebbins, 1970). As a result, a subject may be presented with a series of trials with apparently similar stimuli to which they respond identically until the intensity of the stimulus changes sufficiently for the subject to detect that change. It is possible that a subject may persist in responding in the same manner beyond the point where the stimulus has changed. This can happen regardless of the direction of the intensity change. As such, ascending and descending series are often presented successively, and the average stimulus intensity at which responding changed on both series is defined as the threshold to counteract any such order effects. De Weerd, Vandenbussche and Orban (1991), using cats' performance on an orientation difference task, compared thresholds obtained by the Method of Constant Stimuli and a Method of Limits based adaptive (where the change in stimulus intensity depends on the organisms responses) procedure. They found that the Method of Limits procedure was more efficient and more robust against various manipulations (e.g., amount of training and initial stimulus disparity) than the Method of Constant Stimuli, but that the threshold estimates were very similar.

Variations of the Method of Limits have been developed (e.g., the staircase method (Levitt, 1971), Parameter Estimation by Sequential Testing or PEST (Findlay, 1978) and Best PEST (Pentland, 1980)). These variations have been designed to increase efficiency

and to overcome sequential effects by making the direction (and size) of any stimulus change dependent on the subject's responses rather than predetermined by the experimenter (Levitt, 1971; Stebbins, 1970). According to Blough and Blough (1977) adaptive or tracking methods reduce the number of 'redundant' trials, keeping the subject responding to stimulus intensity values around the point of threshold. However, this kind of threshold determination may require longer training than non-adaptive methods and requires the subject to make repeated judgements about stimuli which are close to their threshold (Blough & Blough, 1977; Stebbins, 1970). It has also been found that these adaptive procedures have led to threshold estimates both higher and lower than those obtained using non-adjusting procedures (e.g., Frazier & Elliot, 1963; Hesse, 1986; Sargisson, 1998).

The 'block trial' procedure is another variation of the Method of Limits which has been developed and used widely (e.g., Georgeson & Georgeson, 1985; Hodos & Bonbright, 1972; Irwin & Terman, 1970; Kelly, Kavanagh & Dalton, 1986; Loop & Frey, 1982; Loop et al., 1980). In this procedure the difference in stimulus intensity across stimuli are generally larger than in the standard method of limits experiment, and each stimulus intensity is presented to the subjects for a 'block' of trials before changing to the next intensity. This change is normally contingent upon some measure of performance (e.g., percent correct across the previous block of trials). According to Blough and Blough (1977), this method has been found to be particularly useful with non-human subjects as performance can change over trials and average performance over several trials may be a more reliable indicator of the ability to detect the presence or absence of a stimulus.

In all of the psychophysical techniques covered to this point, the limits and dimensions of an organism's sensory experience are measured through the use of percent correct analysis and based on the concept of a fixed sensory threshold. There are alternative paradigms to this traditional approach and these include Signal Detection and Behavioural Detection Theories.

Signal Detection Theory

Signal Detection Theory (SDT) is one approach to measuring sensory abilities which proposes that an organism's performance will depend on contextual factors rather than a fixed sensory threshold (Macmillan & Creelman, 1991; Stanislaw & Todorov, 1999; White & Wixted, 1999). SDT is based on the idea that an observer receives an 'input' and that the observer must then make a decision as to whether that input was caused by a 'noise + signal' ($n+s$) event (e.g., stimulus-present) or a 'noise' alone (n) event (e.g., stimulus-absent) (Sorkin, 1999) where 'noise' is the background level of stimulation that is always present. These environmental events are regarded as having two separate underlying normal probability distributions with equal variance, one when n alone trials occur and one, displaced along the x axis, when $n+s$ trials occur. The further apart the means of these two

probability distributions the easier the signal is to detect. Whether the subject responds as if that event was $n+s$ or n is said to depend on the subject's decision criterion (e.g., Macmillan & Creelman, 1991; Sorkin, 1999; Stanislaw & Todorov, 1999). This decision criterion is determined by the subject's past experience of such things as prior occurrences of each stimulus and the relative 'payoff' for the various responses (Green & Swets, 1966; Sorkin, 1999; White & Wixted, 1999).

The concept of a fixed threshold above which a signal can always be detected does not fit within a SDT framework. In SDT, the measure d' is used to describe the subject's sensitivity to the difference between n and $n+s$ events, d' is said to be unaffected by response bias (where response bias is shown by the subject making one type of response more frequently than the other) assuming two conditions are met. These are that the two distributions underlying $n+s$ and n are normal and that these distributions have equal standard deviations. Unfortunately neither of these assumptions can be tested within standard signal detection (SD) experiments (Stanislaw & Todorov, 1999).

Typical SD experiments involve training a subject to make one response (e.g., a left-lever press) in the presence of one stimulus say a tone (termed a tone-on or $n+s$ trial), and a different response (e.g., a right-lever press) in the presence of another stimulus, say no-tone (e.g., termed a tone-off or n trial, Macmillan & Creelman, 1991). Stimulus presentation in this type of procedure is successive, that is, only one stimulus is presented to the subject at a time. In the Two-Alternative Forced-Choice procedure outlined earlier the two stimuli are presented simultaneously and this does not constitute a SD task. Some authors assert that successive discrimination tasks are harder than simultaneous discrimination tasks (e.g., Bushnell, 1999; McLean & White, 1982) as the subject is required to learn a conditional discrimination, (e.g., if the tone is on press left, if the tone is off press right) rather than to just respond toward the target stimulus. This successive two-stimulus conditional discrimination (CD) procedure is also termed a Yes/No procedure where the two separate responses (left and right lever presses in the above example) take the place of verbal 'Yes' and 'No' responses (McCarthy & Davison, 1980b).

A stimulus response matrix can be drawn for such a CD or SD task. The four possible outcomes of the SD task are shown in Figure 0.2. The two top quadrants (W and X) present the respective number of times the subject responded either Yes or No when a $n+s$ trial occurred. As the subject has to make one of these two possible responses, given that a $n+s$ or stimulus-present trial has occurred, the probabilities of the two responses occurring must add to one (i.e., $P(\text{Yes}/(n+s)) + P(\text{No}/(n+s)) = 1$). For example, if the probability of saying Yes to a $n+s$ trial was 0.8, then the probability of saying No on the same type of trial would be 0.2. The two bottom quadrants (Y and Z) represent the number of times the subject

	YES	NO
NOISE + SIGNAL	<div>W</div> <div>CORRECT</div> <div>(HIT)</div>	<div>X</div> <div>INCORRECT</div> <div>(MISS)</div>
NOISE	<div>Y</div> <div>INCORRECT</div> <div>(FALSE ALARM)</div>	<div>Z</div> <div>CORRECT</div> <div>(CORRECT REJECTION)</div>

Figure 0.2 Stimulus response matrix for Signal Detection and Log *d* analysis where stimuli are presented successively.

responded Yes or No respectively, given that a n alone or stimulus-absent trial occurred. The probability of these two responses occurring must also add to one.

As mentioned earlier, the probability of each response occurring is dependent on the subject's decision criterion, which is a result of experience of the stimuli and the relative payoff (likelihood of reinforcement) of subsequent responses. The two correct responses, that is, correctly identifying a stimulus-present trial (W or $Yes/(n+s)$) or a stimulus-absent trial (Z or $No/(n)$), are termed Hits and Correct Rejections, respectively. If a stimulus-present ($n+s$) trial occurs which does not exceed the subject's decision criterion and is therefore treated as a stimulus-absent (n) trial, a Miss is said to have occurred (X or $No/(n+s)$). A False Alarm is counted when the subject incorrectly responds as if a stimulus were present (Y or $Yes/(n)$). The discriminability measure d' , is calculated by subtracting the z score corresponding to the proportion of False Alarms from the z score corresponding to the proportion of Hits (assuming equal distributions). Thus, although the concept of a fixed threshold is not part of SDT, an organism's sensory abilities can be assessed by d' . When d' equals zero, the organism is making an equal number of Hits and False Alarms and is unable to distinguish the difference between stimulus-absent (n) and stimulus-present ($n+s$) trials, this would equate to the absolute threshold (or 50 % accuracy) discussed earlier.

Data from the stimulus response matrix can also be plotted onto a Receiver Operating Characteristic (ROC). The ROC curve summarises all of the possible responses of a subject when performing a discrimination task. By plotting data on ROC axes the control exerted by "...experimenter-specified stimuli..." (Sidman, 1992, p.174) can be analysed. Figure 0.3 presents a ROC diagram. ROC plots present $P(Yes/n+s)$ (proportion of correct stimulus-present trials) as a function of $P(Yes/n)$ (proportion of incorrect stimulus-absent trials), the major diagonal (b) is the 'chance' line, where $P(Yes/n+s) = P(Yes/n)$. Data falling along this line indicate that the subject cannot discriminate between the two stimuli (McCarthy & Davison, 1984; Sidman, 1992). Data that fall on the minor diagonal (a) where the $P(Yes/n+s) = 1 - P(Yes/n)$, show no response bias (McCarthy & Davison, 1984). Position (c) indicates perfect accuracy (100 % correct responding), and the closer to (c) the data on the ROC plot falls, the higher the accuracy of responding (Sidman, 1992) and the larger d' becomes. A bias towards the Yes response is indicated by data falling in Area 2, while a No response bias would result in data falling in Area 1 (Sidman, 1992). Generally data points do not fall below the major diagonal, as this would indicate that the subject was responding at a level below 50 % correct.

Response bias can be altered by manipulating the relative 'pay-off' or consequence of each response, and/or by changing the relative occurrence of each stimulus (Tanner & Swets, 1954). Hume and Irwin (1974) found that animal subjects responded similarly to human subjects when faced with these kind of manipulations, in that the relative

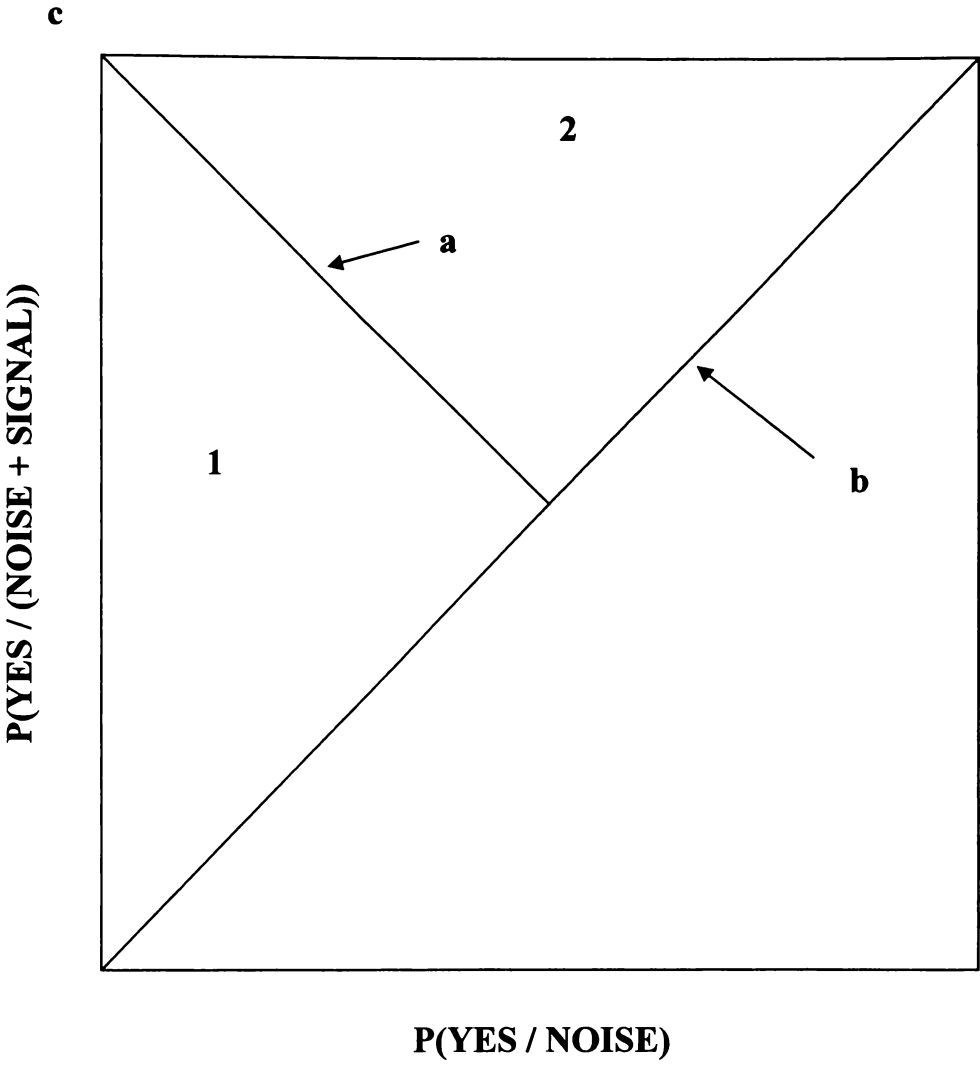


Figure 0.3 Receiver Operating Characteristic (ROC) graph

reinforcement rate (or 'pay-off') of each response type biased behaviour. In a controlled reinforcement procedure, where relative reinforcement rate is kept equal across responses, response bias is said to remain constant. This results in iso-bias curves when data are plotted in ROC space with data points falling along the minor diagonal (McCarthy, 1983).

McCarthy (1983) argued that changing or alloio-bias occurs with uncontrolled reinforcement procedures and is seen in ROC plots when data points trend away from the minor diagonal. Signal presentation probability, or the relative occurrence of each stimulus, can also affect behaviour if relative reinforcement rate is not kept equal (McCarthy & Davison, 1984). If one particular stimulus occurs more frequently, one type of correct response will potentially receive more reinforcement and will lead to response bias (McCarthy & Davison, 1984), this would also be seen in ROC space by data points falling away from the minor diagonal. Thus, ROC plots provide a useful description of performance on a SD task.

Behavioural Detection Theory

Another approach to the measurement of an organism's ability to discriminate between two stimuli is through the use of a measure termed $\log d$ (Davison & Tustin, 1978; White & Wixted, 1999). $\log d$ is said to be equivalent to the measure of discriminability d' , from Signal Detection Theory (Davison & Tustin, 1978; White, 1985; White & Wixted, 1999) and has been used to analyse data from SD experiments. In fact, the same procedure as described for SDT (i.e., two stimuli presented successively and two responses) is used in this approach and is termed a conditional discrimination.

Davison and Tustin (1978) describe how the Generalised Matching Law (GML) is used to derive $\log d$. Simply put, the GML states that the ratio of responses (e.g., left or right lever presses) made to two concurrently available alternatives is a function of the ratio of reinforcement gained from the two alternatives (Baum, 1974). Under a two-choice conditional-discrimination procedure there are two stimuli and two possible responses, of which only one is deemed correct given the presence of a particular stimulus. The two by two matrix derived for this situation is identical to that of SDT (Figure 0.2). Given that reinforcers are delivered for correct responses, the ratios of responses in the Hit and Correct Rejection quadrants (W and Z) to the number of responses in the Miss and False Alarm quadrants (X and Y) reflect the biasing effect of the discriminability of the two stimuli. In a situation where reinforcement is received for only two responses (i.e., W and Z), the GML predicts that organisms will allocate responses proportionally to the reinforcement gained for making the two responses. The more discriminable the stimuli, the more likely it is that the animal will respond appropriately if parameters such as reinforcement rate and signal presentation probability are controlled.

$\log d$ is a derived measure that reflects this stimulus discriminability. Presented below is the equation derived for calculating a point estimate of $\log d$ using the stimulus-response matrix in Figure 0.2, when the reinforcement rates on both alternatives are equal:

$$\log d = 0.5(\log(W/X) - \log(Y/Z)) \quad (1)$$

where W is the number of correct stimulus-present ($n+s$) trials or hits, X is the number of incorrect stimulus-present ($n+s$) trials or misses, Y is the number of incorrect stimulus-absent (n) trials or false alarms and Z is the number of correct stimulus absent (n) trials or correct rejections. As $\log d$ is the measure of the bias in responding due to stimulus discriminability, a higher ratio of correct (W and Z) to incorrect (X and Y) responses can be attributed to the biasing effect of the stimuli alone, independent of inherent biases (e.g., a tendency to press left regardless of consequences, Davison & Tustin, 1978; McCarthy & Davison, 1979, 1980b).

In contrast, $\log c$, also derived from the GML, measures bias due to response preference independently of stimulus discriminability (or inherent bias). The equation below gives a point estimate of this bias, and like Equation 1, refers to the stimulus response matrix in Figure 0.2, with parameters as defined for Equation 1.

$$\log c = 0.5(\log(W/X) + \log(Y/Z)) \quad (2)$$

As stimulus discriminability decreases so does $\log d$ (Davison & Tustin, 1978), while $\log c$ should remain constant assuming reinforcement and any other sources of bias are controlled. Again, while a fixed detection threshold is not inherent in behavioural analyses, when $\log d$ equals zero the organism is not discriminating between the stimuli and this could be taken as the organism's absolute threshold for that stimulus dimension.

McCarthy and Davison (1980, 1984) have studied the effects of controlled and uncontrolled reinforcement rates in discrimination experiments and have concluded that, in order to minimise response bias (and increase stimulus control), obtained reinforcement ratios for both response types must be controlled. One method for controlling relative reinforcement rate (dependent scheduling) has been developed from concurrent-schedule research (McCarthy & Davison, 1984). A two-choice conditional discrimination experiment can be thought of as analogous to two successively available concurrent schedules, where reinforcement for the two concurrently available responses (e.g., left and right lever presses) is scheduled according to which stimuli are present (Davison & Tustin, 1978). By making reinforcer delivery dependent (i.e., once a reinforcer is scheduled for one type of correct response a reinforcer cannot be obtained for any other response), the animal is forced to

continue responding on both alternatives in order to maximise reinforcement. Exclusive responding on one alternative would not result in reinforcement and such exclusive responding would therefore decrease in frequency (i.e., undergo extinction).

Conclusion

As indicated earlier apart from physiological evidence, very little is known about the brushtail possums' sensory abilities. This lack of information has been highlighted in various reviews (e.g., Aitkin, 1995; Clout & Sarre, 1997; Wynne & McLean, 1999) along with an acknowledgement of the paucity of information about the abilities of marsupials in general (Aitkin, 1995). Brushtail possums have been shown to survive well in captivity (Day & O'Connor, 2000) and are prolific and easily obtained in New Zealand making them an ideal laboratory animal. Developing methods to study the sensory abilities of possums may have the added benefit of serving as a model for the study of sensory abilities in other marsupial species. As mentioned earlier, possums have proved difficult to train in sensory experiments (Kirkby & Williams, 1979; Webster, 1975) and therefore careful choice of method and stimulus is required here. Stimuli from two sensory modalities will be examined in this thesis, the first will be visual, the second auditory. Since both of these modalities have been covered extensively in the physiological literature they provide a sensible starting point for a behavioural investigation, as we can be certain that the possums are, at least physically, capable of detecting the stimulus presented to them. The aim of the first experiment in each of the modalities (Experiment 1 – vision and Experiment 7 – auditory) was to teach the possums to perform a standard SD or CD task with the respective stimuli.

Experiment 1

Critical flicker fusion frequency (CFF) has been extensively studied in humans (e.g., Ali & Amir, 1991; Baer, 1965; Hale & Pinninti, 1995; Landis, 1954; Smith & Misiak, 1973) and a variety of other species such as the dog (Coile, Pollitz & Smith, 1989), budgerigar (Ginsburg & Nilsson, 1971), cat (Loop et al., 1980), and pigeon (Ploog & Williams, 1995). CFF can be defined as the lowest frequency at which a flickering light is reported to be steady. Alternatively it can be defined as the frequency of a flickering light source that is required to produce the same sensations as are produced by a continuous stimulus (Bartley, 1939).

Loop et al. (1980) described the ability to discriminate light fluctuations as a “... fundamental operating characteristic of the visual system ...” (p.49). In support of this, Ali and Klyne (1985) suggest that an organism’s CFF is a good predictor of its visual system’s ability to follow movement. Honigfeld and Turner (1970) suggest that flicker fusion thresholds can measure the nervous system’s ability to cope with intermittent stimuli. According to Ali and Klyne (1985) fast moving animals tend to have a faster CFF than slower moving animals. Since the ability to detect flickering (moving) stimuli is so fundamental to an animal’s visual perception it is safe to assume that an animal will be able to discriminate between flickering and steady stimuli at some rate of flicker. If a subject were unable to discriminate between steady and flickering stimuli, this would indicate that their visual system is incapable of following movement, a serious disadvantage for prey and predator species alike. Thus, possums should be able to learn a flicker vs. steady light discrimination. It would be safe to assume that any failure to discriminate must be due to the methodology rather than to the possums’ visual system.

Traditionally, in studying CFF, subjects (both human and animals) were trained to observe a flickering stimulus created by rotating a disk with clear (or white) and black (or opaque) segments, back lit by a strong light source (e.g., a car headlight, Bartley & Nelson, 1960). Increasing the rotation speed of the disk altered the flicker rate. Alternatively, the stimulus could be created by an intermittent light source such as a stroboscope (e.g., McNemar, 1951). Subjects (generally human) were asked to fixate on the flickering stimulus as the disk rotation speed or intermittent flash rate was increased, and to indicate when the flickering stimulus appeared steady. This continuous presentation of a flickering stimulus, changing to an apparently steady light (when the rotation speed was increased) was termed an ascending series. The reverse procedure, termed a descending series, occurred when the frequency of the flicker was reduced (from the point the stimulus

appeared steady) until the subject reported seeing the stimulus flickering (e.g., Dillon, 1959).

Factors which influence CFF

Estimates of CFF thresholds can be influenced by the procedure used. Both Knox (1945) and Landis (1954) found, in particular, that whether an ascending (flicker to fusion) or descending series (fusion to flicker) was used could alter the obtained thresholds. Such order effects are not restricted to CFF investigations. Ginsburg (1967) argued that it was the subject's adaptation to the flickering stimulus in ascending trials which led to these differences. That is, the perception that the stimulus was flickering persisted longer in an ascending series. Generally threshold estimates from both ascending and descending series were determined and the average of these taken as the CFF value (e.g., Dillon, 1959).

During continuous stimulus presentations subjects are required to focus on the stimuli for long periods of time while the flash rate is gradually increased or decreased. Ricciuti and Misiak (1954) state that such continuous presentations, requiring long concentration periods, are inappropriate when assessing CFF with children, and the mentally disturbed [sic]. Those using non-human subjects and this type of procedure have generally overcome the problem of long fixation periods by restraining the animal's head (or eyes) in some manner to ensure continued attention (e.g., Granit & Riddell, 1934; Lennox, 1956; Loop & Berkley, 1975; Loop & Frey, 1982).

However, Ricciuti and Misiak (1954) point out that long exposure to bright stimuli is likely to result in visual fatigue and this would affect any estimation of CFF thresholds. Several authors have suggested that presenting brief or discrete trials with stimuli flickering at different speeds should overcome the temporal adaptation and fixation problems (Curran & Wattis, 1998; Ricciuti & Misiak, 1954). Ricciuti and Misiak (1954) report lower individual variation in CFF estimates with human subjects when they used discrete trials (that is, brief presentations of stimuli at different flicker speeds) and the method of constant stimuli rather than continuous stimulus presentation and the method of limits. In the following experiment discrete trials were used to avoid fixation and adaptation problems.

Another variable found to alter CFF is the light to dark ratio of the flickering stimulus, that is, how long the on/off periods are in each cycle. Bartley and Nelson (1960) reported, in particular, that changing the length of the light portion of the cycle altered the CFF threshold found with human subjects. They used stimuli with various light:dark ratios and found a uniform relation between the length of the light portion and the threshold estimate reached. Crozier and Wolf (1944) found that when the light portion occupied more than 75% of the total cycle the CFF threshold was elevated, while Lloyd and Landis (1960) found that the CFF threshold increased, nearly linearly, when the duration of the dark

interval increased. Lovekin (1968) commented on the wide range of findings when the light:dark ratio was manipulated and suggested that the light:dark ratio may not be independent of flicker rate when certain stimulus presentation methods are used. In procedures where the light portion is set to a constant value, any "...increase in speed occurs at the expense of the dark portion..." (Lovekin, 1968, p.308). Thus when the flicker rate is increased, the light:dark ratio will necessarily change, potentially affecting CFF estimates. Most commonly (where the light:dark ratio is mentioned), a one to one ratio is used which is said to keep average luminance constant, or "...independent of frequency..." (Brown, 1965, p.265). Thus, a one to one light:dark ratio was used in the current experiment.

One of the most important variables in CFF determinations is the light intensity or luminance of the stimulus (McNemar, 1951). However, the exact effect of light intensity on CFF is not clear. Goldzband and Clark (1955) using rats as subjects, found that the CFF threshold was a function, not only of the actual flicker rate, but also of the intensity of the light. Bartley and Nelson (1960) and Lloyd and Landis (1960) both varied the intensity of the light stimulus at the same time as changing the light:dark ratio, and both found a systematic change in threshold (although in opposite directions) depending on the intensity of the light. Both Ginsburg and Nilsson (1971) and Bernholz and Matthews (1975) found a linear increase in CFF estimation as stimulus intensity increased. When Wilkinson (1957) investigated light intensity however he failed to find any effect at all.

Loop et al.'s (1980) study of CFF with cats as subjects, presented discrete trials with both a flickering and a steady stimulus using a blockwise, ascending (i.e., from flicker to fusion), method of limits. As discussed earlier, this method of stimulus presentation is said to be particularly useful when presenting stimuli to animal subjects (Blough & Blough, 1977). Although other discrete trial, Conditional Discrimination studies of CFF in animals exist, all involve adaptive threshold techniques for CFF estimation (e.g., Bernholz & Matthews, 1975 (Harp seals); Ginsburg & Nilsson, 1971 (Budgerigars); Nuboer, Coemans & Vos, 1992 (Hens)). Given that adaptive techniques (such as PEST) have been said to give rise to longer training times (Blough & Blough, 1977; Stebbins, 1970), and that the brushtail possum has proved difficult to train in the past, a method similar to Loop et al.'s was selected here.

Loop et al. (1980) trained three cats (with previous colour-discrimination training) to press keys with their noses while they were in a restraining box with their heads in a confined chamber. The cats were then presented with two side-by-side lights and were trained to press the key on the side of the lit stimulus, which side was lit was changed pseudo-randomly. Once this initial discrimination was learnt, the stimuli were changed with

both lights lit and one flickering and the cats were trained to press the key on the side associated with the flickering stimulus (which side the flickering stimulus appeared on was decided pseudo-randomly). This flicker vs. steady training procedure (at a single average luminance) continued until each animal's performance over four consecutive sessions was greater than or equal to 90 % correct, this was defined as the criterion level of performance. Once this level had been reached testing sessions were initiated. Testing sessions began with a block of 40 trials with the stimulus light at the training flicker speed. The flicker frequency of the light was then increased by 7 Hz and another 40 trials were conducted. This pattern was continued until a flicker frequency was reached where the animal's performance over a block of 40 trials fell to 64 % or less. A final 40 trials at the original flicker speed (that is, the training speed) ended the session. Loop et al. (1980) suggested that if percentage correct over these final trials did not fall below 80 %, any decrease in accuracy during the session could not be attributed to fatigue or satiation. This type of 'performance check' is fairly common in psychophysical experiments (e.g., Gerstein et al., 1999).

Loop et al. (1980) calculated CFF thresholds from a daily graph of percentage correct (as a function of flicker frequency) and the frequency at which the data path crossed 70 % was deemed to be the threshold, although no reason was given for the use of this particular threshold criterion. Ten test sessions at a single average luminance level ($2.4 \log \text{cd/m}^2$) were presented to the cats and the procedure was then repeated under varying conditions. In the initial study (single luminance) the estimated CFF thresholds were found to range from 53.6 to 56.9 Hz (Loop et al., 1980).

Given the considerations covered above, a method similar to Loop et al.'s was used in the present experiment, that is, a 'block trial' ascending variation of the Method of Limits with successive presentations of discrete flickering and steady trials. One further reason for using a method similar to Loop et al. (1980) was that their subjects were cats. As mentioned earlier, possums have been found to have a well-developed visual system (Hayhow, 1967; Sanderson, Pearson & Dixon, 1978) similar to that of the domestic cat and other mammals (Crewther et al., 1984; Freeman & Tancred, 1978). A methodology, which allowed estimation of CFF thresholds for cats, seemed a good starting point for CFF determination with possums. The aims of this experiment were three-fold. Firstly, to develop equipment and establish a method for training brushtail possums within an operant framework, secondly, to see if flickering stimuli could be used to establish a visual discrimination, and if so, thirdly, to estimate the CFF of the brushtail possum at a single luminance level (approximately $2.2 \log \text{cd/m}^2$).

Method

Subjects

Six intact, experimentally naïve, adult brushtail possums served as subjects. The 4 female (named Ratty, Bodwyn, D3 and Silver) and 2 male (named Zeek and Max) subjects were captured as pouch young (with their mothers) and removed to a communal room once they were weaned. The possums were touched and hand-fed treats (e.g., sultanas) every day, and remained in this room until they were sexually mature or weighed 2 kg (whichever was sooner). At this time they were moved to individual cages with water available at all times. The possums' room (containing 12 possums) was maintained on a 12:12 hr reversed light/dark cycle. Initially there were no dietary restrictions, however, as each possum started experimental sessions (approximately one year from weaning) supplemental feed (dock (broadleaf pasture plant), apples and pellets) was restricted to a level where they would work for food reinforcers, but that did not result in weight loss (as measured by weekly weighing). Any supplementary food was given at least one hour after the end of an experimental session. If any individuals lost weight during the week their supplemental food would be increased and vice versa. D3 was put on a stricter diet, as recommended by the Veterinary adviser, due to obesity problems.

Apparatus

A response panel was attached to the home cage of each possum and remained attached at all times. In the initial training sessions the panels contained one central amber key light (small 'grain' 24-W bulb with plastic amber cover which reduced any changes in light colour due to temperature) and a hole below this, through which a removable response lever could be inserted. The lever was a heavy-duty micro-switch which was cut so that approximately 25 mm of lever protruded from the panel once inserted. A central magazine hole was cut below this, which allowed access to the food hopper.

In subsequent conditions two amber lights and two round holes through which levers could be inserted were placed in the panel directly below the lights and the original central light and lever were removed. Figure 1.1 shows the dimensions of the final response panel. The levers were removed after each session to prevent damage.

A mix of steam-flaked barley and carob chips (at a 15:1 ratio by volume, chips ranging from 2 to 5 mm in length) was accessible through the magazine hole when the food hopper was raised for 2 s. While the food magazine was operating the amber lights were dark and no responses on the levers were registered. A computer controlled all the experimental events and recorded data using the MED/PC system.

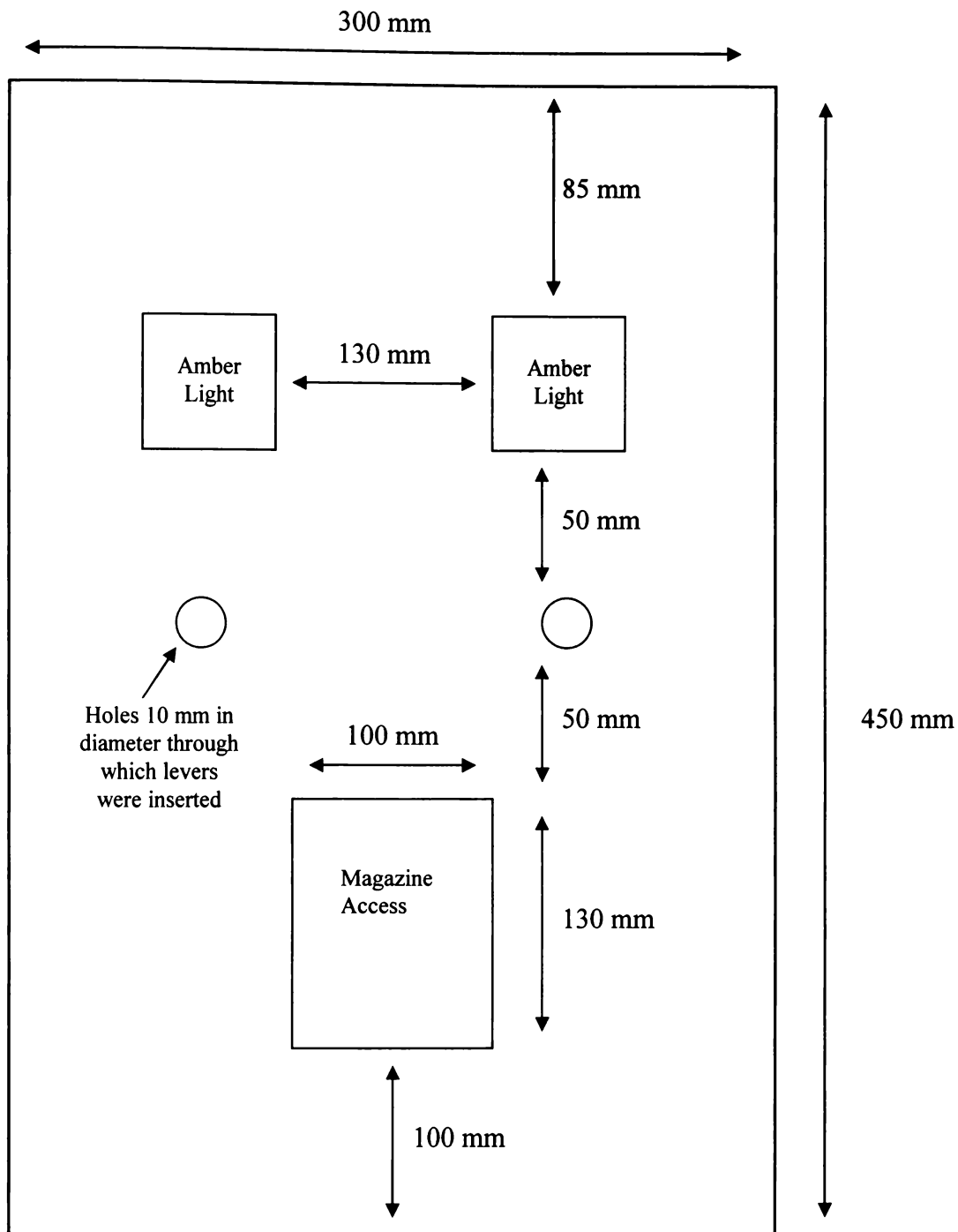


Figure 1.1. Dimensions of the final possum response panel for the flicker vs. steady discrimination task.

Procedure

Each session began with the levers being inserted through the holes in the response panels. Daily sessions started approximately one hour into the dark phase of the light/dark cycle. During the 12-hr dark phase of the cycle no lights were on in the housing room, except during experimental sessions when three red light bulbs (60 W) were on. For the light phase (also 12 hr) three standard 100-W white bulbs were used to illuminate the room.

Lever press training. Initially, possums were trained to eat from the magazine when it operated. Following this, each possum was manually trained through successive approximations to operate the central lever. Any response was acceptable as long as enough pressure (> 0.25 N) was applied to operate the microswitch making an effective lever press, whenever this occurred, a brief feedback beep (0.05 s) sounded from a speaker located behind the panel. As soon as the possum was reliably responding on the single lever, a variable interval (VI) 7.5-s schedule was introduced. Under this schedule, a reinforcer was available for the first response made after an average of 7.5 s had elapsed since the previous reinforcer was delivered. The intervals between reinforcers were determined from an arithmetic series of 15 intervals with an average of 7.5 s. This was extended to a VI 15-s schedule once each possum was obtaining more than 80 reinforcers in their 40-min sessions. Sessions were terminated after either 40 min had elapsed or 100 reinforcers had been obtained. They also terminated if a period of 5 min with no lever pressing occurred. The number of reinforcers gained each session was graphed. When the number of reinforcers was greater than 80 and no longer trending, the next stage of training began. The center amber light and lever were removed and amber lights and levers were attached to each side of the response panel as shown in Figure 1.1.

Flicker training. During this phase trials began with one of the side lights being lit, right light for flickering trials and left light for steady trials. The right light flickered at 5.00 Hz with the light lit for 0.1 s then off for 0.1 s resulting in a 1:1 light:dark ratio. A response on the lever beneath the lit light resulted in 2-s access to the magazine and a beep followed by a 3-s inter-trial interval (ITI). Responding on the other lever resulted in a 2-s blackout period followed by a 3-s ITI. Flicker (right light lit and right lever correct) and steady (left light lit and left lever correct) trials were pseudo-randomly scheduled using a version of the Gellerman (1933) series. This ensured that there would be no more than three consecutive trials of the same type and that the number of each type of trial would be approximately equal within a session. Training with only the correct side light lit on each trial continued for each possum until accuracy of responding was above 90 % correct. Once this occurred the next phase began.

Successive trials with continuous reinforcement. In this phase all trials began with both lights lit. That is, both lights were simultaneously flickering (at 5.00 Hz) or steady, whether a trial presented flickering or steady lights was scheduled pseudo-randomly as in the previous phase. The consequences for correct and incorrect responding remained the same as previously. For five of the six subjects, this procedure continued until responding was above 90 % correct (typically three sessions). For one subject (D3), accuracy of responding remained below 60 % and she was placed into the next phase after six sessions.

Successive trials with intermittent reinforcement. The only change in this phase was that reinforcement was made intermittent meaning that not every correct response resulted in access to food. A correct response was always followed by a short beep however, and an incorrect response by a 2-s blackout period. After each reinforcer was delivered, which type of correct response (i.e., left or right correct) would next result in reinforcer delivery was decided pseudo-randomly, using a version of the Gellerman (1933) series. This was done to ensure each type of response was reinforced equally. Threshold sessions were started once the animals achieved the criterion of five consecutive sessions with percentage correct responding at 90 % or better.

Threshold determination. Each threshold-trial session began with a block of 20 trials using the training flicker frequency (5.00 Hz). Approximately equal numbers of flickering and steady trials occurred within each block of trials, arranged pseudo-randomly using a version of the Gellerman (1933) series. The flicker rate was then increased along the following series from the training speed 5.55 Hz, 7.14 Hz, 10.00 Hz, 16.67 Hz, 50.00 Hz with blocks of 40 trials at each frequency. It was assumed that 50 Hz would be well above the possum CFF and thus no further speeds were programmed. Throughout the series, a 1:1 light:dark ratio was in effect. If the percentage of correct responses at the completion of a set of 40 trials was 64 % or above, the next flicker rate in the series was introduced. As soon as the percentage of responses correct fell to below 64 % for a set of 40 trials, the ascending series was stopped and a further 20 trials at the training flicker frequency (5.00 Hz) were presented. After this, the session was terminated, threshold sessions had no time limit for completion. Correct responses continued to be reinforced on an intermittent basis as in the previous phase at all of the flicker frequencies, a beep always sounded after a correct response and a blackout period followed all incorrect responses.

Each threshold-trial session was followed by a session where only the training flicker rate was presented. If an animal's percentage correct for this session was 90 % or greater the next session would be a threshold-trial session. If percentage correct responding fell below this criterion level non-threshold sessions would continue for this animal until percentage correct responding was again greater than or equal to 90 %. Threshold sessions

continued until each animal had completed a total of 10 threshold sessions (with a return to 80 % correct responding on the final block of training speed trials), with the exception of one animal (Silver) who completed only seven sessions to this criterion.

Results

Figure 1.2 presents the overall percentage correct for the training sessions with one lever (One Lever), the training sessions with two levers, flickering and steady lights and continuous reinforcement (Two Levers - CRF) and the training sessions with two levers and intermittent reinforcement (Two Levers – Intermittent Rft) as a function of session number, for each possum. Over the initial (One lever) training there was a steep increase in percentage correct over relatively few sessions. All six possums show a similar pattern, initially responding at close to chance level (50 %) followed by percentage correct increasing rapidly to 100 % correct. By the end of this training all possums were responding between 90 and 100 % correct.

During the second phase of training (Two levers – CRF) percentage correct initially decreased for all subjects relative to the first phase of training. Gaps in the data line indicate sessions where a possum did not respond at all. For five of the six possums, percentage correct responding returned quickly to the same high level of accuracy as seen at the end of the initial flicker training. D3, however, failed to show any increase in percentage correct responses over six sessions, with performance remaining at chance (50%) levels. After intermittent reinforcement was introduced for correct responses, percentage correct remained high for five possums and for D3 it showed a steady, but slow, increase until it was as high as that of the others.

Figure 1.3 presents the percentage correct for each stimulus value presented for each of the 10 threshold sessions and for each possum. Successive threshold sessions are presented down the figure. Percentages correct at each flicker speed are shown plotted against the log of the flicker rate (measured in Hz). The open circles on each graph mark the percentage correct for the final re-presentations of the first flicker speed (5.00 Hz) for each session, where this circle is not visible, percentage correct gained during the re-presentation was identical to that gained in the first presentation. The horizontal lines mark 64 and 75 % correct. Four possums successfully completed all 10 threshold sessions (i.e., continued responding throughout the session and reached criterion on the second block of training speed trials). Max required an extra six sessions (due to him ceasing responding during threshold sessions) while Silver was presented with a total of 19 threshold sessions and of these she continued responding to the end of the session in only seven. The failed sessions for both Max and Silver occurred in no discernable pattern. Generally the

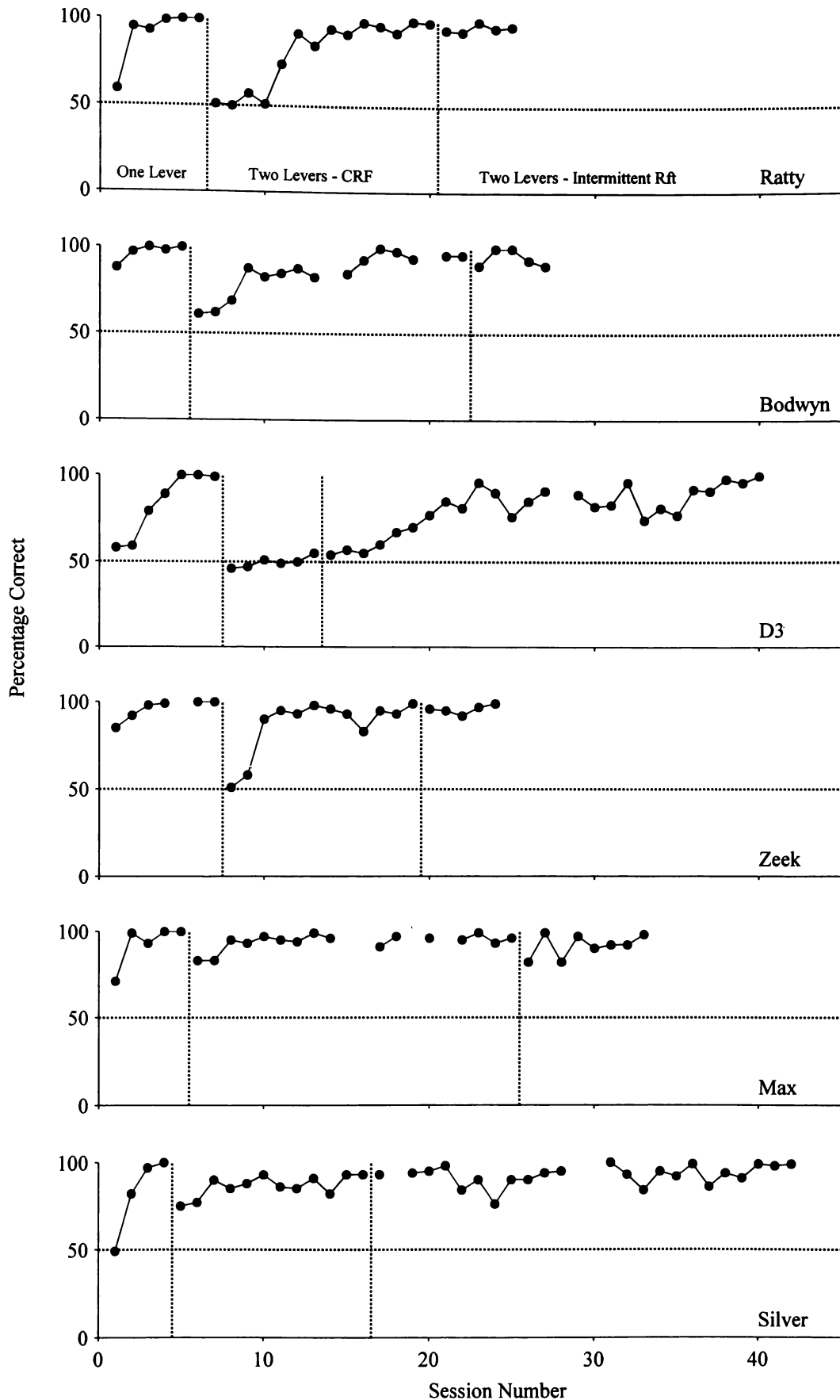


Figure 1.2. Percentage correct gained in each training session over three conditions.

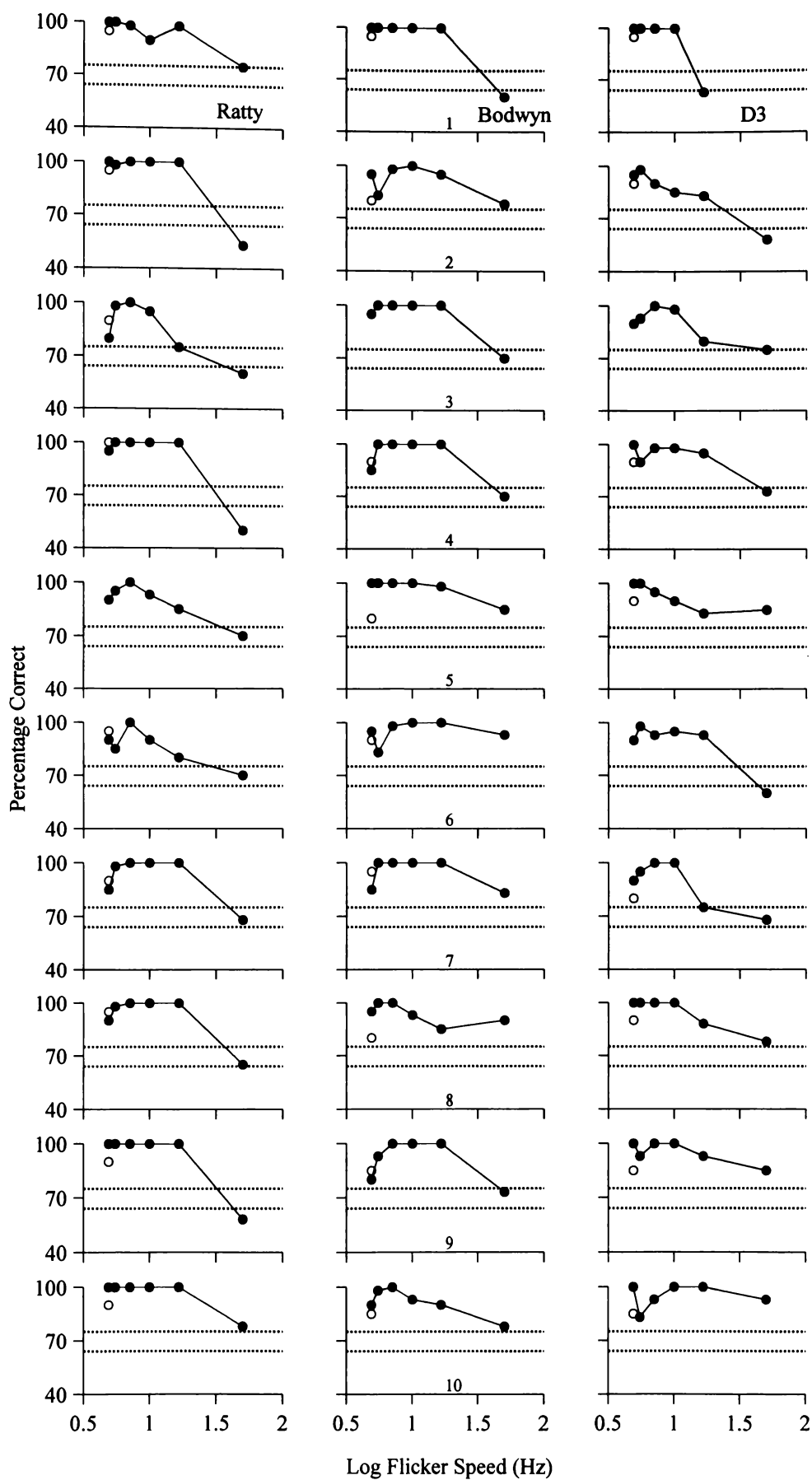


Figure 1.3. Percentage correct in each threshold session as a function of the log of the flicker speed.

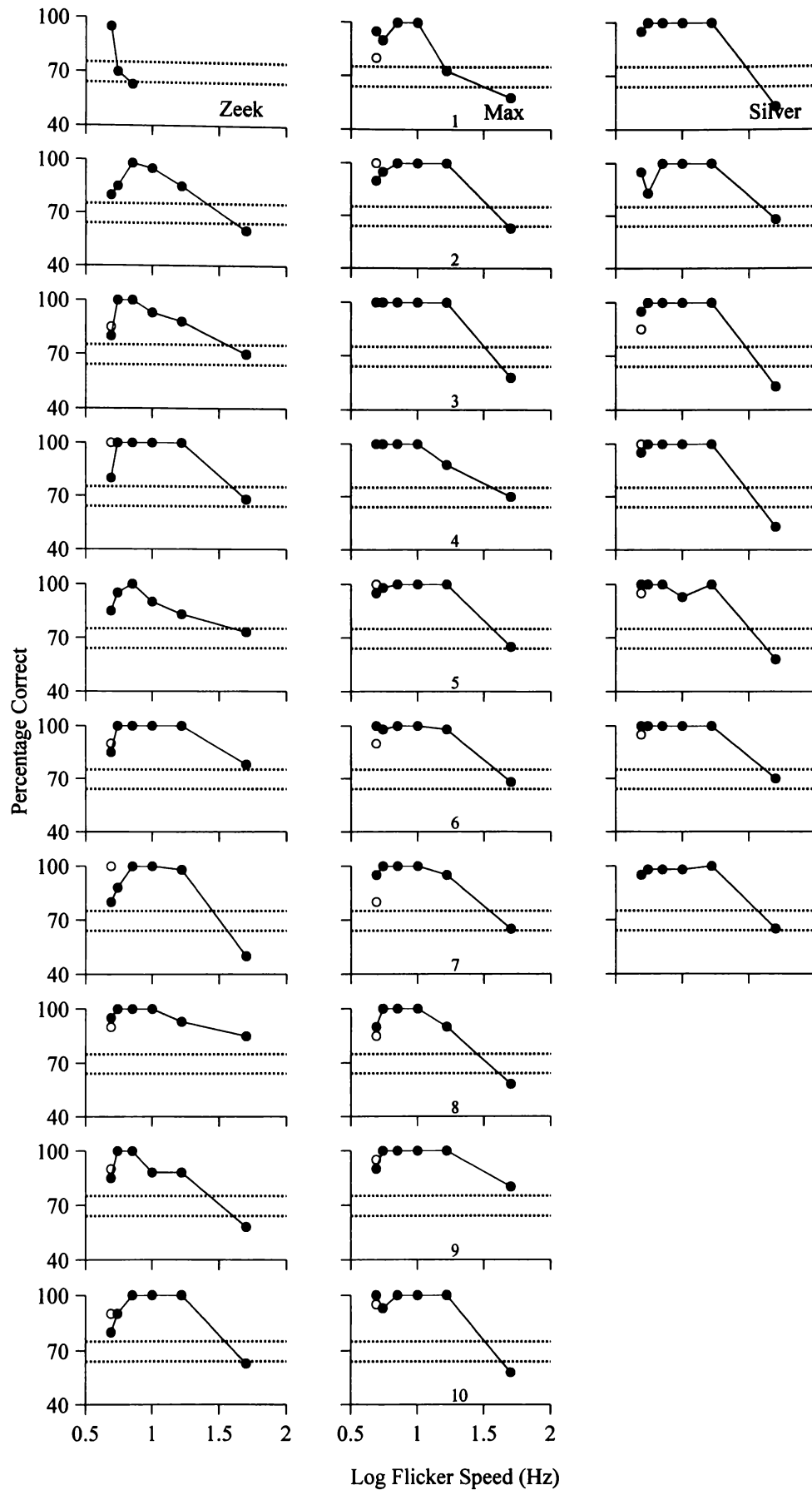


Figure 1.3 cont. Percentage correct in each threshold session as a function of the log of the flicker speed.

individual session data follow a similar pattern for all six possums, with accuracy generally remaining high until the final flicker speed (50.00 Hz) on which accuracy dropped. In 49 of the 57 data paths, accuracy on the final flicker speed presented was at or below 75 %, while responding at previous speeds remained above this value. All scheduled flicker speeds were presented to the subjects in each of these completed threshold sessions bar two (one each for D3 and Zeek). There are no consistent changes in the form of the functions across threshold sessions for any subject.

The average percentage correct at each flicker speed over the 10 threshold sessions (with the exception of Silver) are plotted as a function of the log of the flicker speed for each possum in Figure 1.4. The horizontal dotted lines are at 75 % and 64 % correct and the unfilled circle on each graph represents the average percentage correct value of the final block of training trials at the end of each threshold session (this circle is not apparent in Ratty's graph as the average value of the final block of trials was equal to that of the first block). The vertical lines at each data point indicate ± 1 standard error either side of the average value. These averages represent the individual session data well as indicated by the small standard errors. All of the functions are similar in shape, and there are no consistent differences across the 6 possums' data, however Bodwyn's average data path does not fall below 75 %. Percentage correct responding remained high overall except at the final flicker speed. The initial increase in percentage correct that can be seen over the first three flicker speeds is common to all 6 possums. Linear interpolation from these average data paths result in the following estimates of CFF using 75 % as threshold criterion: Ratty 38.1 Hz, D3 44.6 Hz, Zeek 39.8 Hz, Max 38.2 Hz and Silver 37.3 Hz.

The left panel of Figure 1.5 presents the average log d estimate as a function of the log of the flicker speed. As there were cells in the response matrix (see Figure 0.1) which equalled zero (e.g., no false alarms) resulting in incalculable log d values, the Hautus (1995) correction was used in all log d calculations. The Hautus correction (which involves adding 0.5 to all cells) has been suggested as being the most appropriate way to deal with this type of situation (Davison & Nevin, 1999; Hautus, 1995). The log d value for the re-presentation of the original flicker speed (5.00 Hz) at the end of each session is also shown (represented by an unfilled circle). The data paths for all 6 possums are similar. Log d was generally highest at the third flicker speed presented (7.14 Hz). This resulted in a bi-tonic function with log d values typically falling on either side of 7.14 Hz. The fastest flicker speed (50.00 Hz) is associated with the smallest log d value. The data presented in the right panel of Figure 1.5 are ROC plots of the averaged data joined in order of presentation with the points at the top left of the diagram being presented earlier where proportion correct on flicker trials is plotted as a function of the proportion incorrect on steady trials. It can be seen that

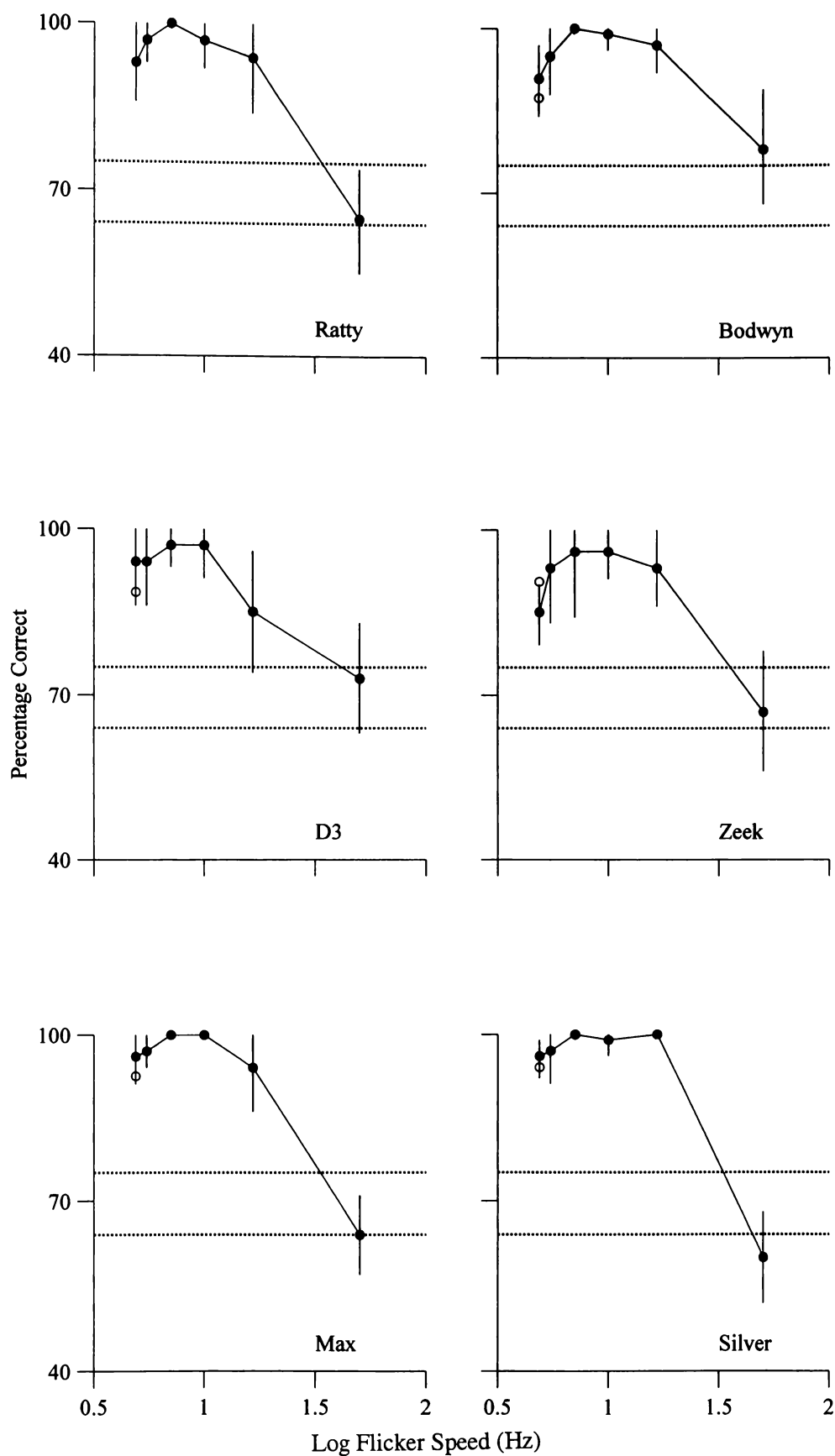


Figure 1.4. Average percentage correct gained over all threshold sessions as a function of the log of the flicker speed.

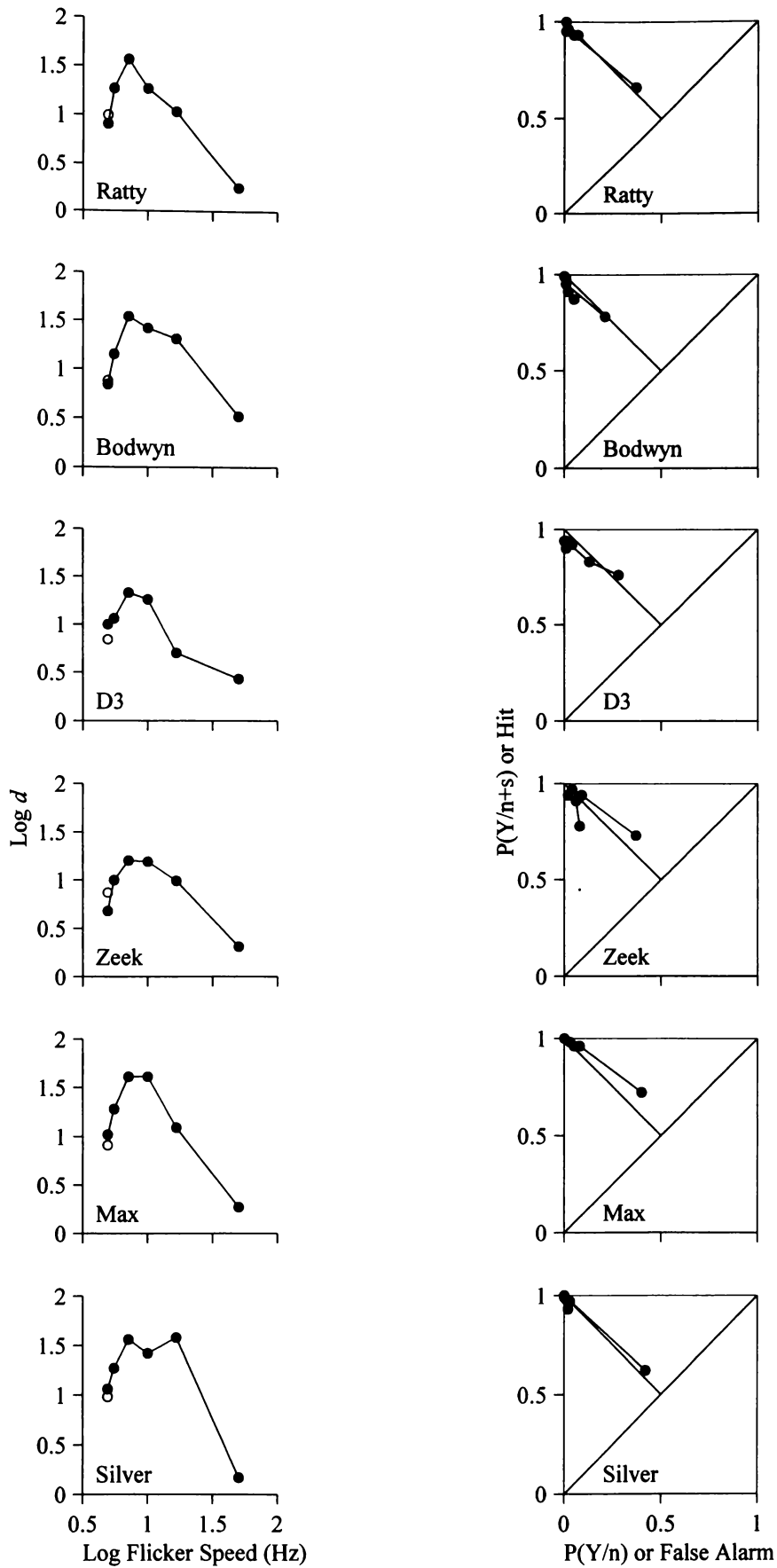


Figure 1.5. Log d and ROC plots of data averaged over all threshold sessions.

data points for all 6 possums generally fall on, or close to, the minor diagonal, indicating little or no response bias.

Discussion

All three of the aims for this study were met. That is, the current equipment and methodology proved successful in establishing a visually-based conditional discrimination in the brushtail possum, it was also possible to estimate a CFF threshold.

Equipment and methodology

The present results show that the lever used here worked as a suitable manipulandum for the possum, which could be remotely controlled and reduced the level of human intervention to nil during experimental sessions. All 6 subjects readily learnt to depress the lever with sufficient force. There was no sign of the behavioural topography changing once the initial response was trained unlike the findings of Hudson et al. (1999). Thus, the lever used in the current study would appear to be a superior manipulandum for use with the possum to the bite bar/key used by Hudson et al. (1999) because topography of responding was more stable. Another problem encountered by Hudson et al. (1999) was the amount of time lost within each experimental session to scent marking as their equipment was moved between possums. Having individual operant panels which were permanently attached to each possums' home cage eliminated this problem entirely.

Establishing a visual-discrimination

These results show that it is possible to establish a visually-based conditional discrimination with brushtail possums. The possums quickly learned to discriminate between the two visually different stimuli. The ease with which this discrimination was learned is in contrast to the findings of Webster (1975) and Kirkby and Williams (1979). As mentioned previously, there are several possible factors that may have contributed to the difficulties experienced by these researchers that were avoided in this study (particularly background lighting levels). All sessions here were run under a reverse day/night cycle and low background illumination in order to optimize the experimental conditions for the possums.

Determining a CFF threshold

The final aim of this experiment was to estimate the CFF of the possums (at a luminance of $\approx 2.2 \log \text{cd/m}^2$) given that the initial flicker discrimination had been successfully learnt. By manipulating the speed of the flickering stimulus the accuracy of all 6 possums' responding decreased in a similar manner. Interpolation from the average data paths resulted in individual percentage correct threshold (at 75 % correct) estimates for

flicker ranging from 37.3 to 44.6 Hz with an average value of 39.6 Hz ($s_x = 2.9$) at the current level of luminance. Although average accuracy over the final flicker speed block of trials for Bodwyn was lower than that of the slower flicker speeds, accuracy did not fall below 75 % (accuracy on final block was 78 %) and so her data was not included in the overall average value.

Loop et al.'s (1980) analysis used a threshold value of 70 % and derived CFF estimates of 53.6 to 56.9 Hz for cats at a similar luminance level to that here. To allow comparison between the current data and Loop et al.'s, CFF values using a 70 % threshold value were extrapolated from the average data paths and the average of these was 46.7 Hz ($s_x = 6.6$). This CFF value is lower than that found by Loop et al. (1980).

Analysis of the data using SDT and Behavioural Detection measures confirm that the fastest flicker speed was the hardest to discriminate for the possums (lowest log d values and data points falling closest to the major diagonal in ROC plots). It is also apparent from the ROC plots that there was little or no response bias present in the current data. Interestingly, the training flicker speed of 5.00 Hz was not the flicker speed that was most easily discriminated, as shown by higher log d values at other speeds. Flicker speeds between 7.14 and 16.67 Hz proved to be more readily discriminable than the training flicker speed.

It is tempting to attribute the low accuracy values at 5.00 Hz to variability within the 20 trials presented at the training flicker speed. All other flicker speeds were presented within a block of 40 trials, thus one error in the 20 training speed trials would have a greater effect on overall accuracy for that block than one error in 40 trials over one of the subsequent blocks of trials. However, this argument cannot explain why accuracy continued to increase between the second and third block of trials (both containing 40 trials).

Determining whether this initial increase in percentage correct is common in other CFF threshold functions is difficult. Most studies present an overall CFF function at various luminance levels rather than at a single luminance level as here. The studies that do present a single function (with the exception of Loop et al., (1980)) use conditioned suppression techniques (e.g., Coile et al., 1989; Loop & Berkley, 1975; Williams, Pollitz, Smith & Williams, 1985). It is unclear what effect this would have on the pattern of data obtained. Blough and Blough (1977) comment that the extent to which thresholds determined by conditioned suppression methods will differ from thresholds determined in other manners is unknown. They go on to say that while there is some evidence that methodological differences may not result in large changes in threshold estimate (e.g.,

Mentzer, 1966, Wier, Jesteadt, & Green, 1976) any comparisons that are made are difficult to interpret due to other confounding factors.

A search of the literature did not discover any published comparisons between threshold functions determined using conditioned suppression methods and conditional discrimination methods. Heffner & Heffner (1986a) did compare thresholds obtained from conditioned avoidance (similar to conditioned-suppression except that ceasing responding avoids the aversive event) and conditioned suppression methods with macaques and made no mention of any significant differences. A further study also failed to find any difference between sound localization ability in the horse using either a two-choice procedure or a conditioned avoidance procedure (Heffner & Heffner, 1986b). Thus, while it is unclear as to the exact nature of any differences in threshold functions derived using different methods there appears to be no reason to assume that there will be any major differences.

Another methodological difference between the current study and other CFF determinations was the possums' ability to move around during experimental sessions. Due to this it was not possible to determine exactly where each possum was positioned at the beginning of a trial. Therefore performance on any given trial could be the result of the possum detecting the stimulus with a single eye (monocular) or having the image of the stimulus falling on any part of the retina. Both of these factors could alter the ability to detect the stimulus. Ali and Amir (1991) for example, found that the average CFF threshold under monocular conditions was significantly lower than for binocular vision (with human subjects). CFF thresholds have also been found to be affected by the region of the retina exposed, particularly as the ratio of rods to cones alters (e.g., Bernholz & Matthews, 1975; Brown, 1965). However due to the similarities in the CFF estimates across possums it seems likely that the position of each possum was consistent across threshold sessions and similar to the other possums.

The overall pattern of performance, common to all possums was an initial increase in accuracy until the third block of trials (7.14 Hz) then a relatively abrupt drop in accuracy between the fifth and sixth block of trials (16.67 and 50.00 Hz). This pattern of relatively high, accurate, responding with an abrupt drop in performance may be due to the relatively large difference in flicker speed between the two final blocks of trials. In the current experiment the final change in flicker speed was 33.33 Hz compared to Loop et al., (1980) who increased flicker speed by 7 Hz. Thus, while the current experiment showed that possums could be taught to perform a conditional discrimination between flickering and steady visual stimuli flicker speeds between 16.67 and 50.00 Hz need to be presented in order to determine more precisely the CFF of these possums.

Experiment 2

For 5 of the 6 possums in Experiment 1, accuracy on the flicker vs steady task fell to, or below, 75 % between the two fastest flicker speeds (16.67 and 50.00 Hz) at an average value across possums of 39.60 Hz. The biggest drop in accuracy for all 6 possums was also between these flicker speeds. To study the relation between percentage correct and flicker speed between 16.67 and 50.00 Hz, the following experiment presented flicker speeds between these two frequencies.

Method

Subjects

The same subjects served as for Experiment 1.

Apparatus

The same apparatus was used as in Experiment 1.

Procedure

Each session began when the two levers were placed in the response panels.

Threshold determination. Threshold sessions were similar to those in Experiment 1. They began once a possum had reached the criterion performance level at the training flicker speed (that is, five consecutive sessions at or above 90 % correct). Each threshold session started with 20 trials at the training flicker frequency (5.00 Hz). The flicker speed was then increased along the following steps 16.67, 20.00, 25.00, 33.33 and 50.00 Hz with blocks of 40 trials (with approximately equal numbers of flickering and steady trials) at each frequency. If the percentage of correct responses at the completion of a set of 40 trials was 64 % or above, the following block of trials used the next flicker speed in the series. As soon as percentage correct fell to below 64 % for a block of trials, the ascending series was stopped and a further block of 20 trials with the original training frequency (5.00 Hz) were presented and then the session terminated. Threshold sessions had no time limit for completion. In the event that a subject completed 40 trials at 50.00 Hz (the fastest flicker speed) and their percentage of correct responses did not fall below 64 % the session was terminated following a further 20 trials at the original flicker speed. Correct responses continued to be reinforced intermittently as in the training phase of Experiment 1 and a beep always sounded after a correct response.

Each threshold session was followed by a session where only the training flicker speed was presented. If the possum's percentage correct for this session was 90 % or greater the next session would be a threshold session. If the possum's percentage correct fell below this criterion level, training continued until percentage correct responding was greater than

or equal to 90 %. Threshold sessions were conducted for each possum until that possum had successfully completed 10 of these sessions.

Results

Figure 2.1 presents the data from every threshold session for each possum. Percentage correct is plotted as a function of the log of the flicker rate (Hz) and the horizontal dotted lines indicate 64 and 75 % correct. The unfilled circle on each graph is the percentage correct gained on the final re-presentation of the training flicker speed (5.00 Hz) in that session. For the majority of the data paths accuracy on the first two or three flicker speeds was high (around 100 %) and then decreased sharply at some point as flicker speed increased. In contrast to Experiment 1 there is no consistent increase in percentage correct across the initial flicker speeds. For 40 of the 57 data paths accuracy on the fastest flicker speed (50.00 Hz) was at or above 75 % correct. Both Ratty and Bodwyn successfully completed ten threshold sessions in the minimum number of sessions. D3, Zeek and Max required extra sessions (two, four and one respectively) due to accuracy of performance not reaching 80 % on the final block of trials, and Silver required one extra session due to her ceasing responding before the end of the session. As in Experiment 1 there was no pattern to when the unsuccessful sessions occurred.

The averaged data from all these threshold sessions are presented in Figure 2.2. The vertical lines show one standard error either side of the data point and the open circle depicts the average accuracy gained on the final block of trials at the training speed. Accuracy decreased at some point as flicker speed increased for every possum, however, the point at which this occurred was not consistent and only one possums' data path fell below 75 % (Max).

Log d estimates (calculated using the Hautus correction, as discussed in Experiment 1) are presented in Figure 2.3. On the left, log d estimates are plotted as a function of the log of the flicker rate with the open circles indicating the log d value of the final block of training speed trials. All the data paths show some decrease in accuracy as the flicker speed increased. Also shown in Figure 2.3 are the ROC plots of the data. These show there was little or no response bias with the data falling close to the minor diagonal. The data points, joined in order of presentation with the points at the top left of the diagram being presented earlier, are all clustered towards the upper left corner of the ROC graphs (away from the major diagonal) indicating that all of the stimuli presented were relatively easy to discriminate.

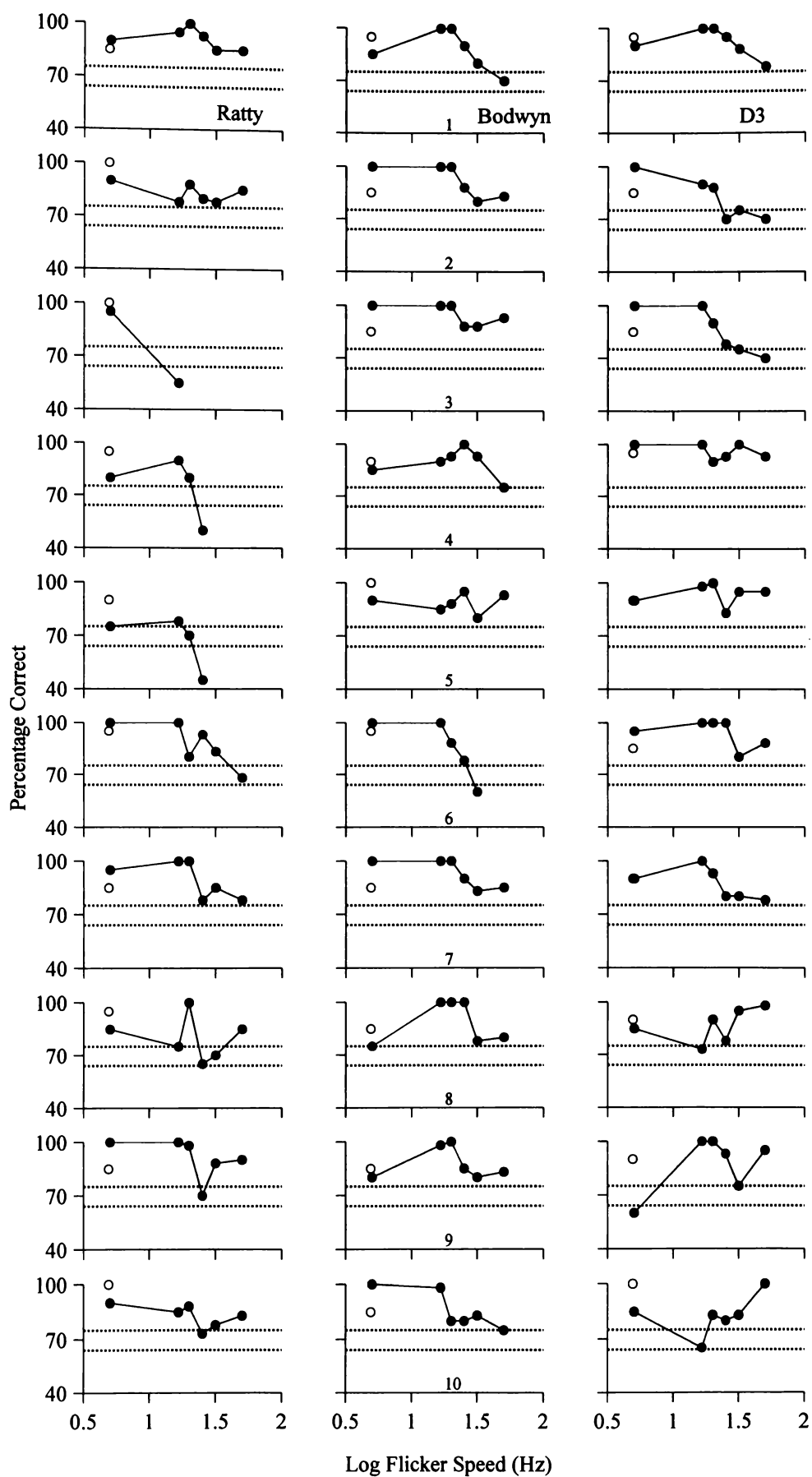


Figure 2.1. Percentage correct gained each threshold session as a function of the log of the flicker speed.

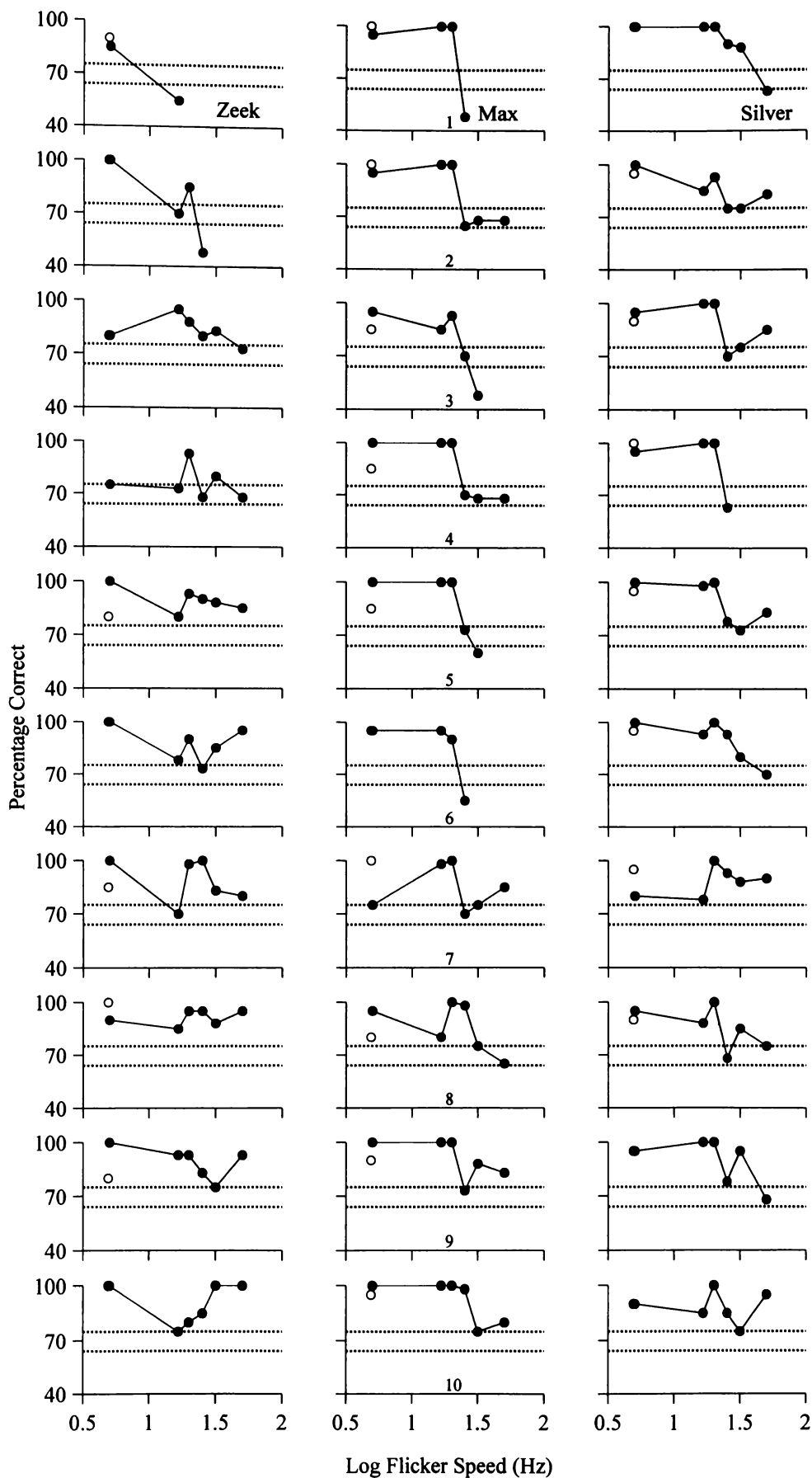


Figure 2.1 cont. Percentage correct gained each threshold session as a function of the log of the flicker speed.

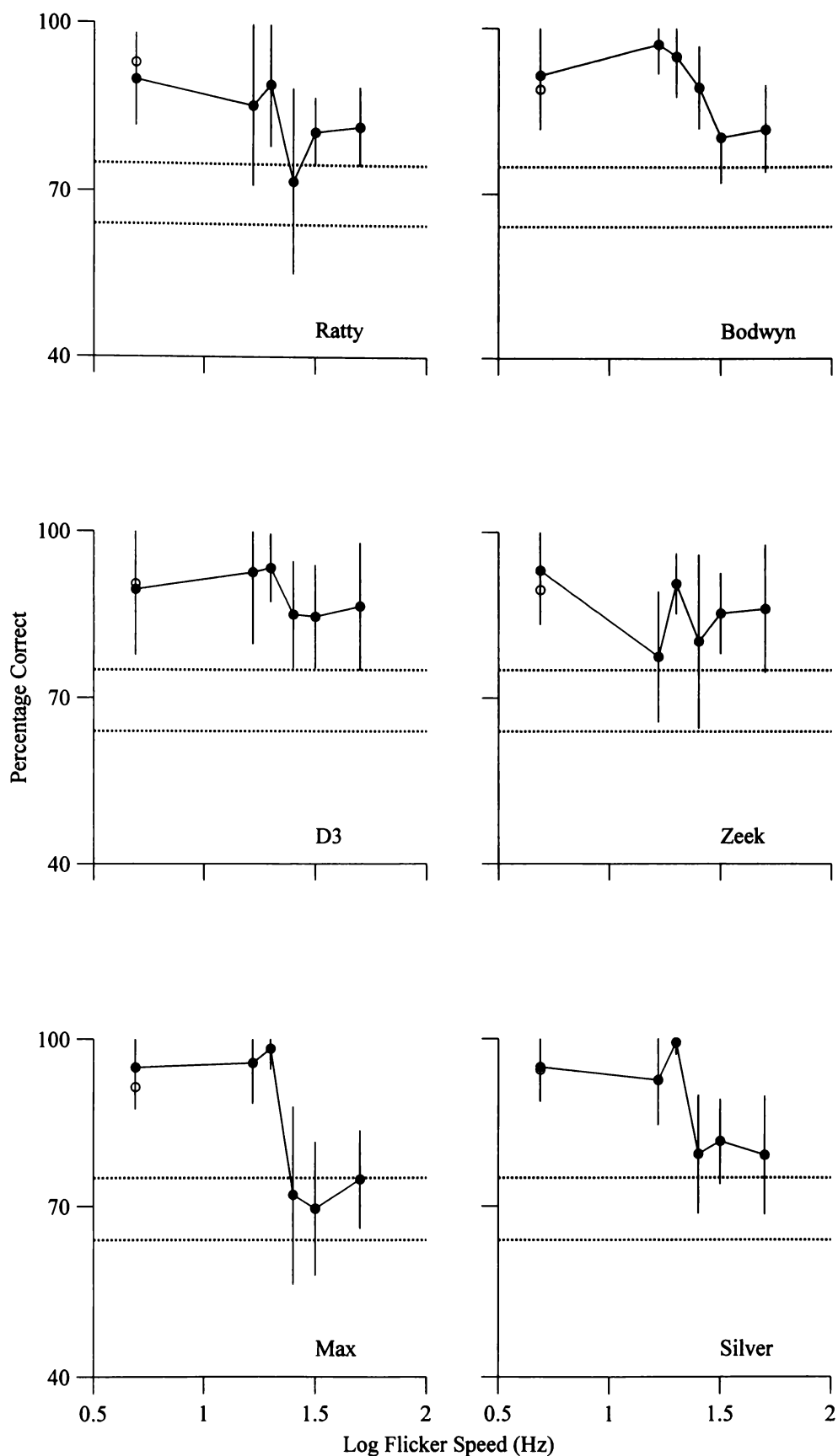


Figure 2.2. Average percentage correct gained over 10 threshold sessions as a function of the log of the flicker speed.

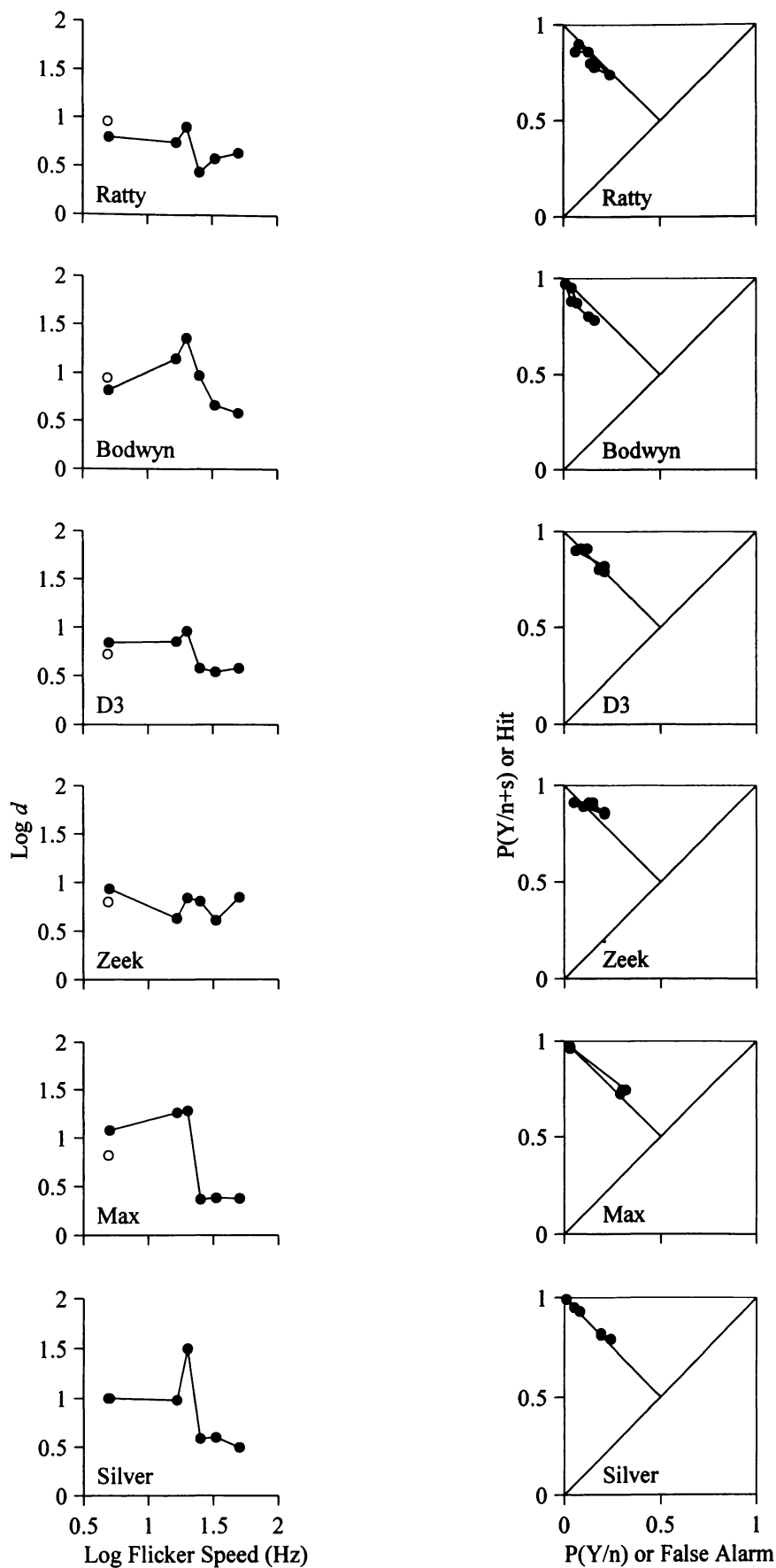


Figure 2.3. Log d and ROC plots of data averaged over 10 threshold sessions.

Discussion

The data from Experiment 1 suggested that the average CFF for possums fell between the two fastest flicker speeds presented at approximately 39.60 Hz. The aim of this experiment was to define the CFF more precisely by presenting stimuli between the two fastest flicker speeds. This aim was not achieved.

The data obtained in Experiment 1 were very orderly, with all threshold sessions resulting in similar data paths for each subject. This was not the case in the current experiment. The increase in percentage correct seen over the initial flicker speeds in Experiment 1 was also no longer present. It would seem likely that this was due to the intervening flicker speeds being omitted as there were no flicker speeds presented between 5.00 Hz and 16.67 Hz in the current experiment.

Figure 2.4 presents the data from Experiment 1 (filled circles) and the present experiment (crosses) for comparison. The data shown are those from Figures 1.4 and 2.2. Three of the flicker speeds were presented in both threshold series, the training flicker speed (5.00 Hz, first data point), 16.67 Hz (fifth data point across) and 50.00 Hz (last data point). The average percentage correct gained at these speeds is presented in Table 2.1 for ease of comparison. From the table and figure it is clear that average percentage correct at the training speed (at the beginning of each threshold session) was essentially unchanged from one experiment to the next. However for the other two speeds there are differences. At 16.67 Hz there was no consistent difference, with four data paths showing lower percentage correct and two higher in the current experiment. However all six possums responded with greater accuracy at 50.00 Hz in the current experiment than in Experiment 1.

It is unlikely that this increased level of accuracy at the higher flicker speeds is due to some type of learning effect common to CFF studies. Various authors have examined the stability of CFF thresholds (generally with human subjects) and all have found no learning effect and high test re-test reliability for repeated CFF measurements (e.g., Levander, 1982; McNemar, 1951; Parkin, Kerr & Hindmarch, 1997). Figure 2.5 presents a comparison between the average percentage correct gained at 5.00, 16.67 and 50 Hz over the first and last three threshold sessions in the current experiment. If an increase in percentage correct at the faster flicker speeds (resulting in the flatter functions seen here) occurred over repeated threshold sessions, the average value for the last three sessions (represented by a plus) should be above the average value for the first three sessions (represented by a filled circle). For all except 1 possum (Bodwyn), percentage correct at 50 Hz was higher in the last three sessions than in the first three. However, for Ratty and Silver this difference was minimal. The data suggests that there may have been some general increase in performance across the 10 threshold sessions.

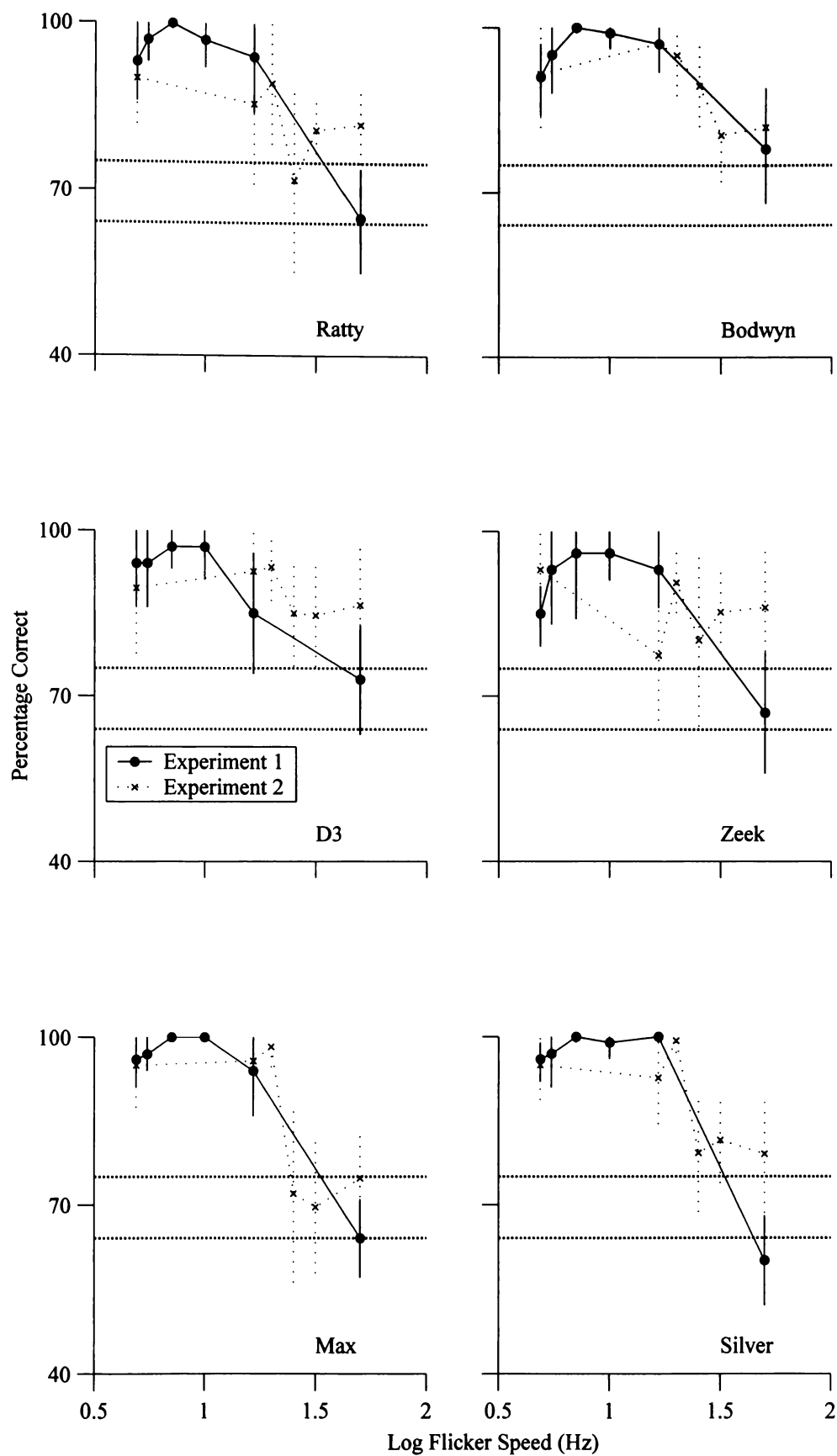


Figure 2.4. Comparison of average percentage correct gained over threshold sessions in Experiment 1 and 2 as a function of the log of the flicker speed.

Table 2.1
Percentage Correct at 5.00, 16.67 and 50.00 Hz from Experiments 1 and 2.

Possum	5.00 Hz		16.67 Hz		50.00 Hz	
	Experiment	Experiment	Experiment	Experiment	Experiment	Experiment
	1	2	1	2	1	2
Ratty	93.0	89.5	93.8	86.6	64.6	81.6
Bodwyn	90.5	90.0	97.0	95.5	78.3	80.8
D3	94.0	92.0	85.3	90.6	73.0	78.4
Zeek	84.5	93.3	92.8	82.0	67.2	89.6
Max	95.5	96.5	94.4	97.1	64.3	71.8
Silver	95.7	95.0	100.0	92.7	59.5	79.1

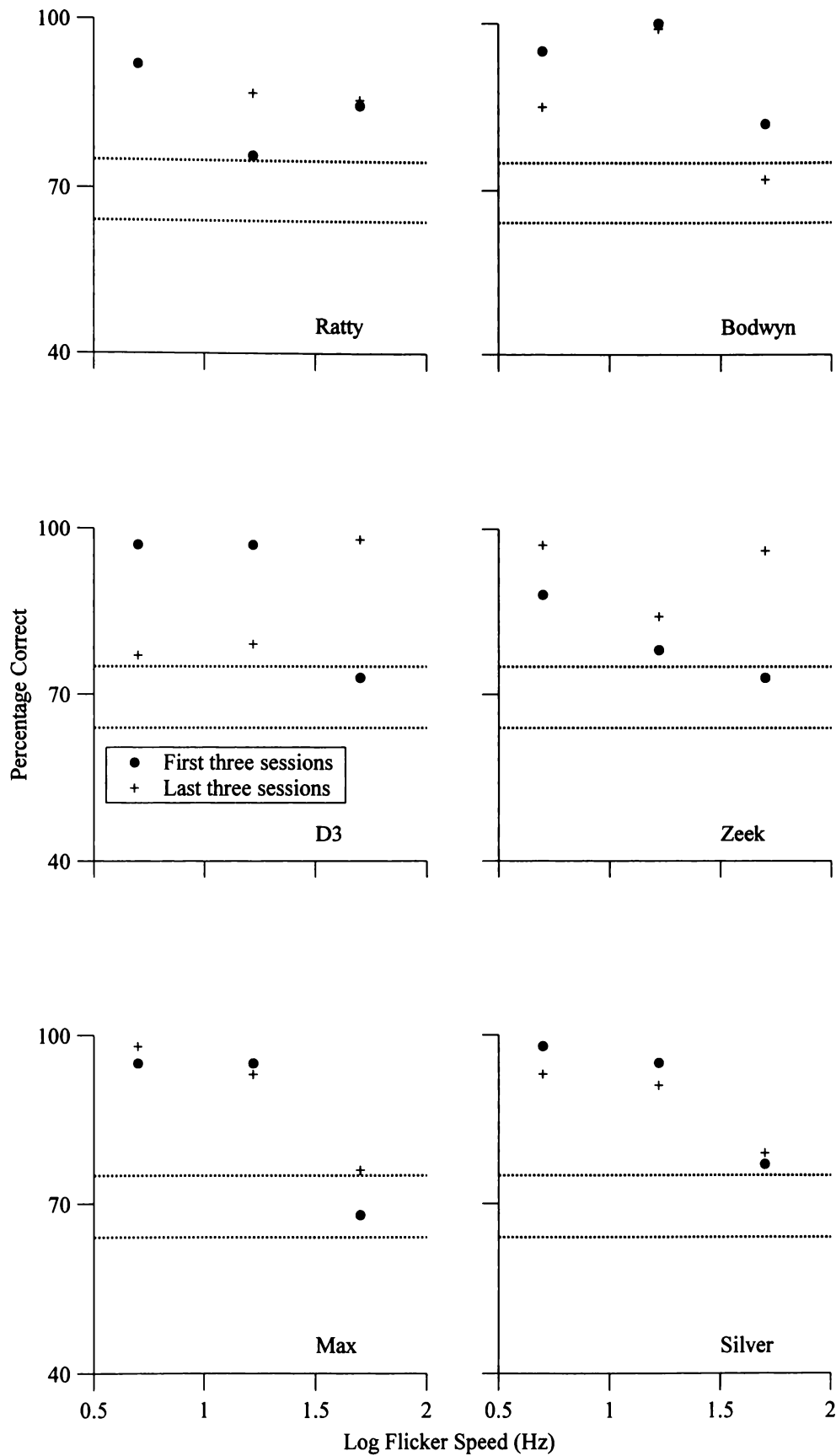


Figure 2.5. Percentage correct gained at 5.55, 16.67 and 50.00 Hz averaged over the first and last three threshold sessions in Experiment 2.

It is also possible that the increase in accuracy at the faster flicker speeds shown here (in comparison to that found in Experiment 1) is due to the degree of stimulus change used in the current experiment. The rate at which stimulus change occurs has been shown to have a reliable effect on traditional, continuous, CFF determinations (Dillon, 1959; Lovekin, 1968; Mahneke, 1957), in that CFF estimates generally tend to be higher as the rate of stimulus change increases. This effect has not been examined with discrete trial methods of stimulus presentation.

In discrete trials it would seem that the step size (that is, the size of the change in frequency between blocks of trials) maybe analogous to the rate of stimulus change in continuous trials. The larger the step size in discrete trials, the faster the CFF threshold is reached. In the present experiment, there was a larger difference between the training speed (5.55 Hz) and the first threshold speed presented (16.66 Hz) than was present in Experiment 1 (i.e., 5.55 Hz to 7.14 Hz). During the first experiment, 16.66 Hz was the fastest flicker speed that still resulted in above threshold accuracy for 5 of the possums. By presenting this flicker speed directly after the block of training speed flicker trials it is possible that threshold (or CFF) was reached faster in the current experiment than in Experiment 1 (where two other speeds were presented between the training speed and 16.66 Hz). Thus resulting in a higher rate of stimulus change than previously and this may have contributed to the higher degree of accuracy seen here. This increase in percentage correct may reflect that the CFF has been shifted beyond 50 Hz by the increase in the rate of stimulus change. To look at this possibility, different degrees of change in test stimuli could be used.

The cut-off accuracy for presenting faster flicker speeds in a threshold session in both the current and previous experiments was 64 % as used by Loop et al. (1980). It is possible that this is too high and that the lack of any decrement in accuracy seen here may be due in part to the possums not encountering threshold level flicker speeds. The cut-off accuracy in the next experiment was dropped to 50 %.

One logical follow-on from the present experiment would be to reassess thresholds while manipulating the rate of change of the flicker speed between blocks and scheduling faster flicker speeds in case CFF is beyond 50 Hz.

Experiment 3

The aim of the following experiment was to manipulate the rate of stimulus change in the presentation of the flickering stimulus. To do this, two threshold series were presented. Both started at the same flicker speeds, but one series involved smaller stimulus changes between blocks of trials than the other. The series with a smaller degree of stimulus change effectively had a slower rate of change than the series with large changes in stimulus speed. As mentioned in Experiment 2, there was a disproportionate change between the training flicker speed and the next flicker speed presented in the threshold determinations in that experiment. To avoid this in the current experiment, a training speed of 16.67 Hz was used, resulting in a smaller change from the training speed to the first threshold test speed. In both previous experiments, each test stimulus speed was presented to the possums pseudo-randomly within a block of 40 trials. However, due to the increased number of blocks likely to be needed, each new flicker speed was presented within a block of 20 trials in this experiment. This was done to restrict the number of reinforcers that a possum could potentially receive in a threshold session and so avoid possible satiation effects. To minimise differences between the two series this restriction on trial numbers applied to both series.

If the rate of stimulus change does affect CFF determinations, then the thresholds obtained from the two threshold series should be different. Faster flicker speeds than previously scheduled in Experiments 1 and 2 were available for presentation in this experiment (up to 71.42 Hz) in case CFF had been shifted beyond 50 Hz due to the effect of the rate of stimulus change. One further change was made for this experiment. In Experiments 1 and 2, threshold series were presented until each possum had successfully completed 10 threshold sessions (except with Silver in Experiment 1). Following analysis of the data from Experiments 1 and 2 using the first three, five and all 10 sessions, it was concluded that the number of threshold sessions could be reduced without coming to any different conclusions. Thus, in this experiment each series was presented for five sessions.

Method

Subjects

The subjects were the same as those used in Experiment 1.

Apparatus

The apparatus was the same as that used in Experiment 1.

Procedure

As before each session began with levers being placed into the response panels.

Training sessions. Training sessions were the same as in Experiment 2, except that the training flicker speed was changed to 16.67 Hz (0.03 s light on and a 1:1 light:dark ratio). These training sessions continued for each possum until each had re-gained criterion level of performance (five consecutive sessions at or above 90 % correct over all trials).

Threshold determination. Two different threshold series were used in alternating threshold sessions. Both threshold series involved flicker speeds ranging from 16.67 Hz (the training flicker speed) to 71.42 Hz. The only difference between the two threshold series was the number of flicker speeds presented within this range. During the threshold series with smaller differences between consecutive blocks of trials, 10 different flicker speeds were available to cover this range. In the other series five flicker speeds were available. The flicker speeds available in each of the threshold series are listed in Table 3.1.

All threshold sessions began with 20 trials at the training flicker frequency (16.67 Hz). The flicker rate was then increased as shown in Table 3.1. In this experiment, if the percentage correct at the completion of a set of 20 trials was 50 % or above the next flicker rate was introduced. As soon as percentage of responses correct fell to below 50 % for a block of trials, the series was stopped and there was a further 20 trials at the training flicker frequency (16.67 Hz). After this, the session was terminated. Correct responses continued to be reinforced on an intermittent basis as in training sessions for all of the flicker frequencies, and a beep always sounded after a correct response. Incorrect responses were always followed by a 2-s blackout.

Each threshold session was followed by at least one training session to maintain criterion level of responding (accuracy at or above 90 % correct). The two threshold series were alternated. Each possum experienced five threshold sessions with each series and only sessions that were successfully completed were used in the data analysis. A successful session was one in which the percentage correct from the final 20 trials of the training speed was 80 % or greater.

Results

Bodwyn, Max and Silver, showed no decrease in percentage correct when the new training speed was introduced at the beginning of this experiment. Ratty and Zeek required a few extra sessions to re-gain criterion level of performance while D3 took 22 sessions to reach criterion at the new training flicker speed.

Figure 3.1 presents overall percentage correct as a function of the log of the flicker speed for each threshold session for both of the threshold series. Data from successive threshold sessions are presented down the page, with the small stimulus change series presented to the left of the large stimulus change series for each possum. The horizontal lines on each graph are at 50 % and 75 %. The unfilled circles show the overall percentage

Table 3.1

Flicker speeds presented during small and large stimulus change threshold series (all flicker rates on a 1:1 light:dark ratio)

Flicker Speed (Hz)	Light on (s)	Small stimulus change series	Large stimulus change series
16.67	0.0300	✓	✓
20.00	0.0250	✓	
25.00	0.0200	✓	✓
33.00	0.0150	✓	
50.00	0.0100	✓	✓
52.60	0.0095	✓	
55.60	0.0090	✓	✓
58.80	0.0085	✓	
62.50	0.0080	✓	✓
66.67	0.0075	✓	
71.42	0.0070	✓	✓

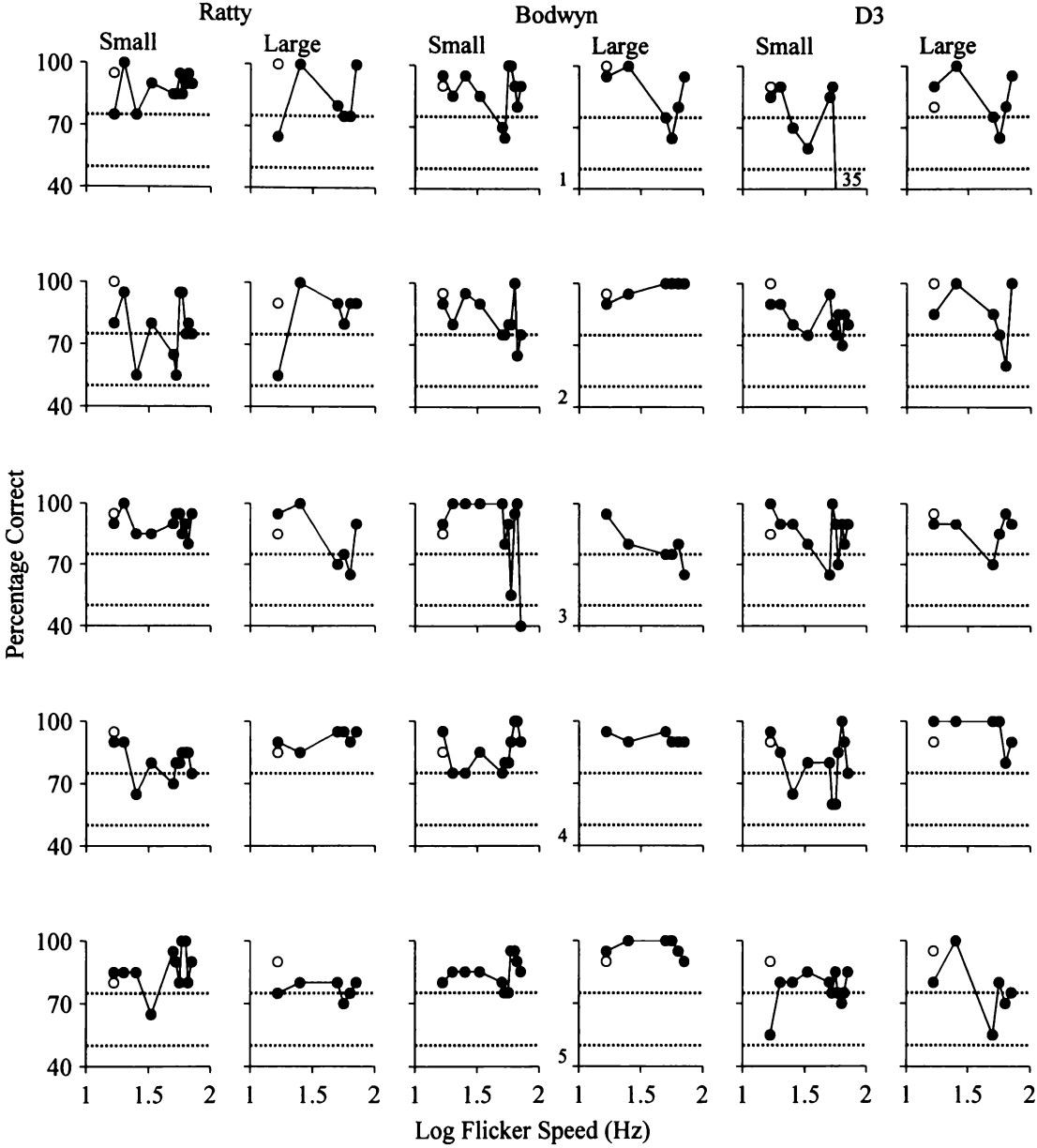


Figure 3.1. Percentage correct gained each threshold session as a function of the log of the flicker speed for both small and large stimulus change series.

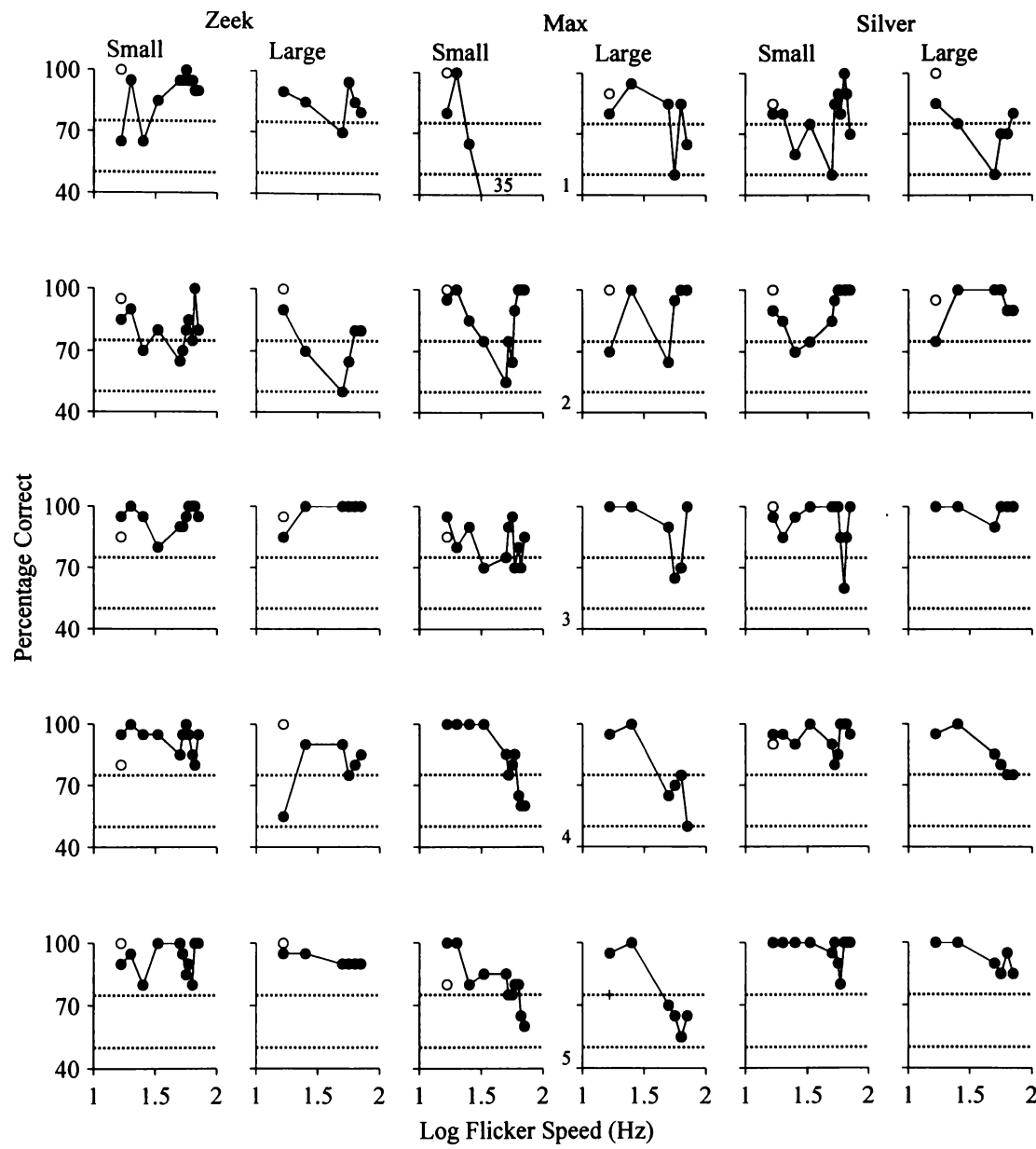


Figure 3.1 cont. Percentage correct gained each threshold session as a function of the log of the flicker speed for both small and large stimulus change series.

correct obtained during the final re-presentation of the training flicker speed. Accuracy on the final block of trials for Max's fifth threshold session of the large stimulus change series failed to reach criterion (80 % correct) and this is indicated by the + symbol. However, despite accuracy on this final block only being 75 %, the data from this 'unsuccessful' session does not look different to the earlier 'successful' sessions. Data from this session was not included in any subsequent analyses. The graphs show that the data paths are relatively flat for both of the series with percentage correct generally remaining high across all flicker speeds (with the possible exception of Max). In only one case (Max's first session on the small increment series) did percentage correct fall to the 50 % cut off before the fastest flicker speed was presented, in all other sessions all of the available flicker speeds were presented.

Figure 3.2 shows the percentage correct for each flicker speed averaged over the five threshold sessions for both the small (represented by a cross) and the large (represented by a filled circle) stimulus change series for each possum. This figure highlights the similarities between the data from the two threshold series. There are no consistent differences between the data paths from the two threshold series or across possums, and neither data paths cross the 75 % line in an orderly pattern.

Log d and ROC plots are presented in Figure 3.3. As could be seen in Figure 3.2, there is little difference between the data from the two threshold series and the data do not decrease as flicker speed increased in any systematic way. Log d conclusions therefore do not differ from percentage correct analysis. ROC analysis (last two columns) also serves to highlight the similarities between the data from the two threshold series. It can also be seen from the ROC graphs that all of the stimuli presented in the two series were being readily discriminated by the possums, as is shown by the data points, joined in order of presentation with the points at the top left of the diagram being presented earlier, clustering on the minor diagonal away from the major diagonal and not trending towards either side.

Discussion

Two threshold series were presented in this experiment to investigate the effect of the rate of stimulus (flicker) change on subsequent CFF estimates. The data from these two determinations are remarkably similar, indicating that, at least in the current situation, altering the rate of change of the flickering stimulus from block to block of trials has had little effect. This is in contrast to what is found when continuous stimulus presentation methods are used when determining CFF thresholds (e.g., Dillon, 1959; Lovekin, 1968; Mahneke, 1957). However, what was most apparent in the current data was the lack of any real decrement in percentage correct as flicker speed increased.

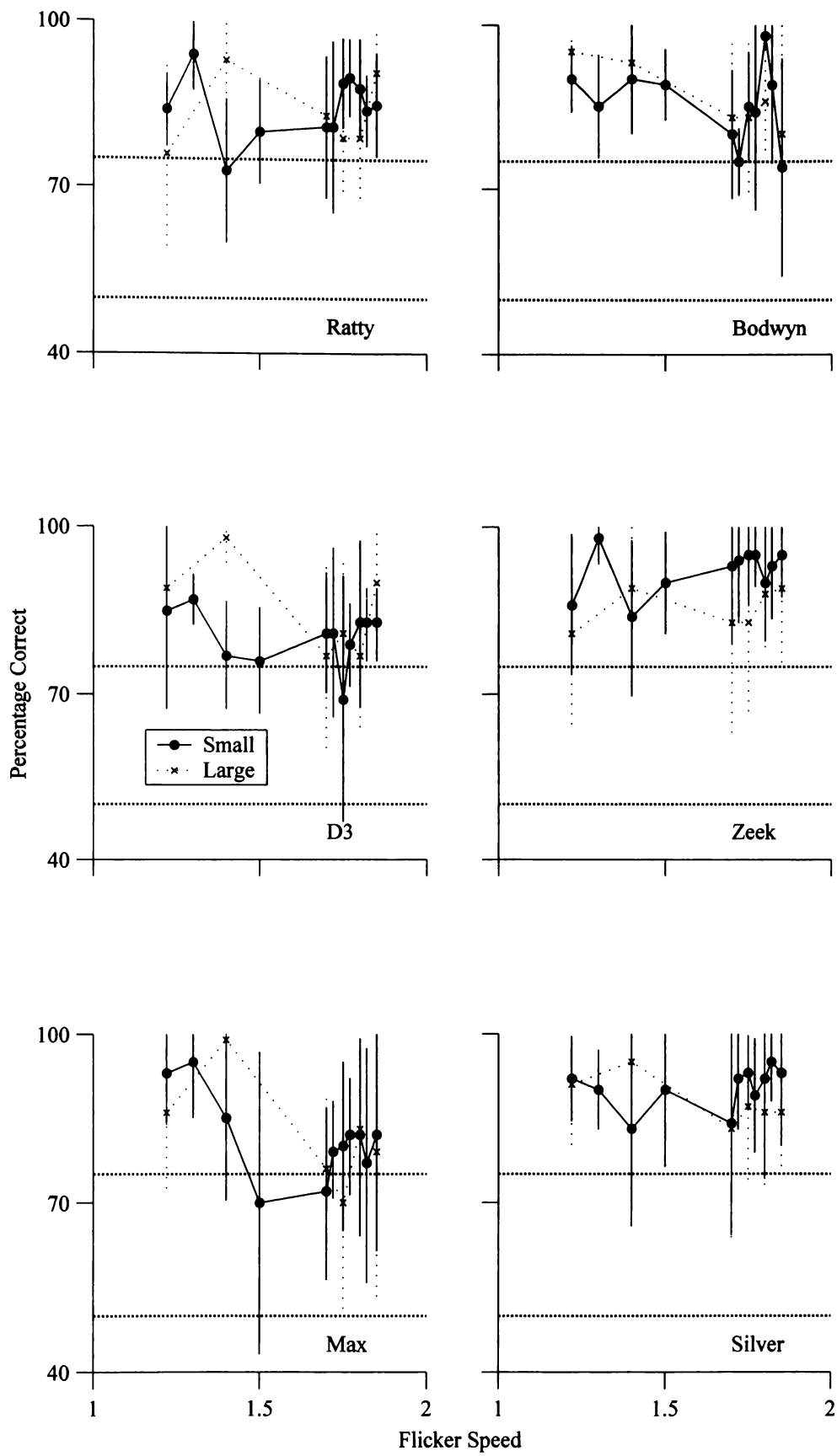


Figure 3.2. Comparison of average percentage correct gained over threshold sessions in both the small and large stimulus change series.

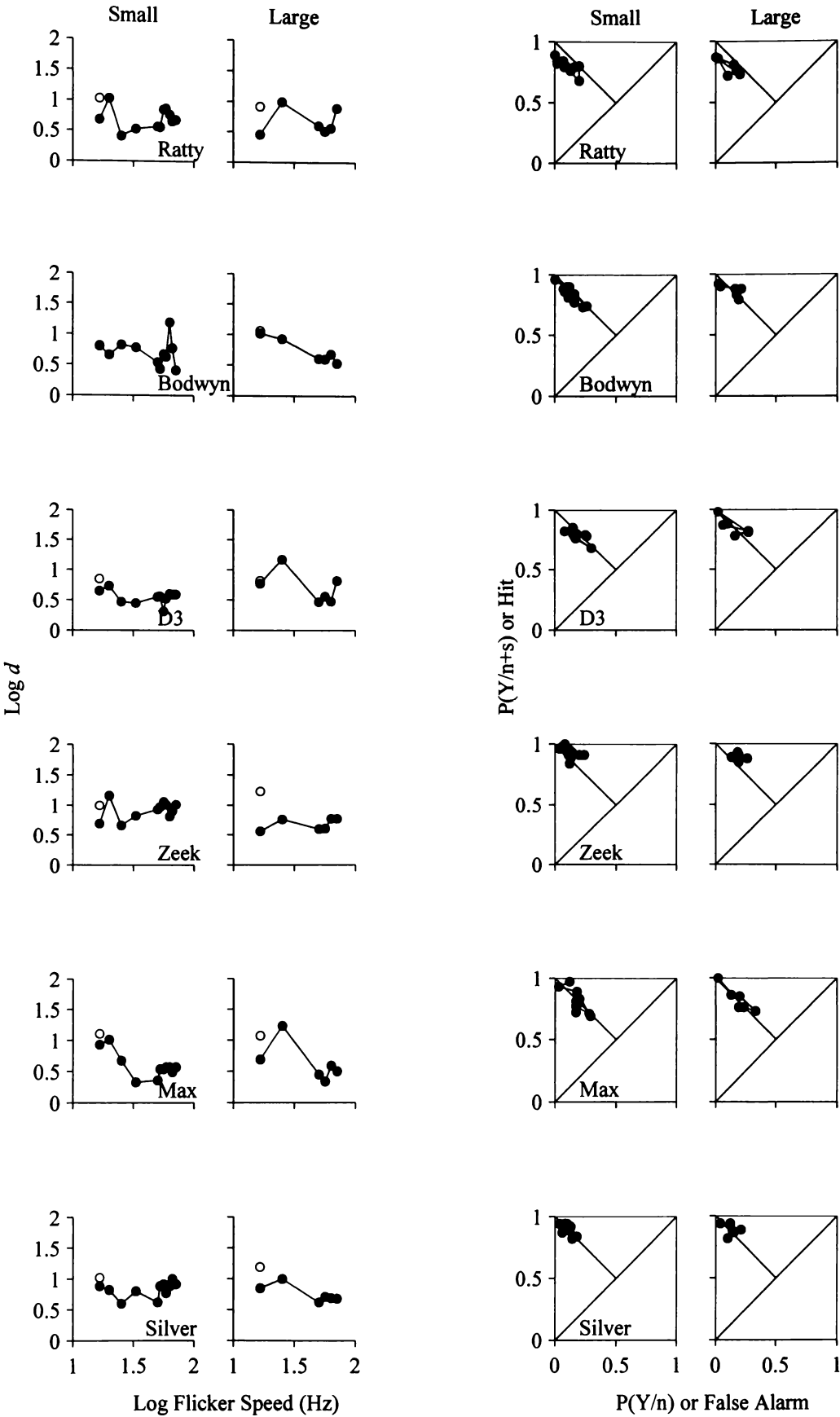


Figure 3.3. Average Log d and ROC plots for both small and large stimulus change series.

In Experiment 1, both Silver and Max required several extra sessions in order to complete the required number of 'successful' sessions. A successful session was deemed to be one where the possum continued to respond throughout the session and gained 80 % correct (or higher) on the final block of training trials, which ended each session. In the current experiment, each possum was presented with five sessions at each of the two threshold series and of the six possums, only Max failed to complete both sets of five sessions successfully. This unsuccessful session was due to accuracy on the final block of trials not reaching the 80 % criterion rather than the possum ceasing responding at some point in the session as in Experiment 1. Examination of the data path from this 'unsuccessful' session indicates that performance throughout the session was essentially identical to the previous 'successful' sessions. Thus even if the failure to gain 80 % was due to fatigue or satiation it did not effect performance at the earlier stimulus values.

In this experiment flicker speeds of up to 71.42 Hz were presented. As Loop et al. (1980) found the CFF for cats to be between 50 and 60 Hz (at a similar luminance level), this, in conjunction with the results of Experiment 1, made it seem likely that 71.42 Hz should have been well above the CFF of possums. However, in this experiment all of the subjects continued to respond differentially to flickering and steady stimuli well above the 16.66 to 50 Hz range identified in Experiment 1. One extreme example is Silver who was apparently able to detect stimuli flickering at 71.42 Hz close to 100 % of the time by the last threshold session. While it is possible that possums do have very high CFF thresholds and that the increase in percentage correct seen over the past experiments was due to the possums learning the task, an alternative explanation seems more likely. That is, that the possums learnt to discriminate on the basis of another stimulus which varied concurrently with the flickering or steady stimuli. Thus, the experimental procedures were re-examined for possible stimulus changes that might correlate with the flickering and steady stimuli.

A very faint (barely audible to a human observer) 'buzz' noise was detected from the speaker which produced the feedback beep when the lights were flickering at the higher flicker speeds and mainly for three sets of equipment, those of Ratty, Max and Silver. This audible cue could explain why the possums (especially Silver) were able to discriminate so accurately at the higher flicker speeds.

Another source of potential confound was the amber filtered panel lights, which were chosen so as not to be too bright. It was possible that the red overhead illumination may somehow change the appearance of the lights at higher flicker speeds, or that the inherent cycling of the power of the overhead lights may have been interacting with the stimuli. Simonson and Brozek (1952) and Foley (1961) have both shown that background and surround luminance can alter subsequent CFF estimations. CFF has generally been

found to decrease as environmental illumination increases, turning the red overhead lights off may result in an increase in CFF for the possum.

A third possible source of an extraneous cue was a small difference in luminance between the stimulus lights when they were flickering and steady. With the use of a Minolta CS100 Chromametre this difference was measured for each set of equipment. The difference in luminance between the flickering and steady light across individual panels ranged from 0.5 to 0.8 log cd/m². Since Kirkby and Williams (1979) had found that possums did not readily learn a brightness discrimination, this suggested that the possums would have had difficulty learning to discriminate on the basis of such a small difference in relative luminance as that found between flickering and steady lights in the current series of experiments and so brightness was not varied here. This may however be the source of the current problem.

As most CFF investigations utilise continuous presentation methods, any disparity between flickering and steady luminance has not been widely commented on. Brown (1965) in fact asserts that if the light to dark ratio is kept equal (i.e., 1:1) the "...average luminous energy reaching the eye per unit time also remains constant, independent of frequency..." (p.265). Loop et al. (1980) kept the luminance of the flickering trials constant (2.4 log cd/m²) while the luminance of steady trials was randomly varied between three levels (2.45, 2.38 and 2.27 log cd/m²). This was apparently done to eliminate any possibility of the cats learning to discriminate on the basis of luminance. However, if the luminance of the flickering trials was indeed kept at a constant luminance this should not have been a problem. Ginsburg and Nilsson (1971) studied CFF in the budgerigar using discrete, randomly presented steady and flickering trials (using a glow modulator tube). The bird's responding on the key when it was lit with a steady light was reinforced, but responding on the flickering key was not and the luminance of the light was reported to be a steady 17.1 cd/m². At no point is the relative luminance of the steady and flickering stimuli mentioned. Ploog and Williams (1995) used an incandescent bulb to produce their flickering stimulus, and again no mention is made of any differences in luminance.

These three (noise, background luminance and relative luminance) possible sources of extraneous stimuli were tested in the next study by replicating threshold sessions with appropriate controls.

Experiment 4[†]

It was apparent from the results of Experiments 2 and 3 that the possums were continuing to respond accurately to high flicker rates (above 50 Hz). These flicker speeds were far above those one might expect them to be able to discriminate, especially given the findings of Experiment 1. Thus, it seemed likely that the subjects had learned a discrimination other than one based exclusively on flicker, which allowed them to continue to respond accurately at these fast flicker speeds. Three possible sources of extraneous, controlling stimuli were identified and investigated in this experiment.

Method

Subjects

The same subjects served as in the previous experiments.

Apparatus

The apparatus was the same as in Experiment 1, with the exception of that of Ratty, Max and Silver. For these three, the speaker which produced the feedback beep was removed and replaced with a relay. Whenever a correct response was made the relay produced an audible 'click'.

Procedure

The procedure was identical to that of the small increment threshold series in Experiment 3 except that three variables were manipulated across subsequent conditions. Five threshold sessions were performed for each condition. A new condition began only after criterion performance (five consecutive sessions at or above 90 % correct) was reached at the completion of the previous condition.

Relay condition. Relays replaced the speaker when providing feedback on correct trials for Ratty, Max and Silver. The relay made no audible noise when the lights were flickering at any speed and remained in place for the remainder of the conditions in this experiment.

Red-light condition. The overhead red lights were turned off during all training and threshold sessions. Threshold sessions occurred once criterion performance was regained with the overhead lights turned off. After five threshold sessions the red lights were turned back on.

Equal-luminance condition. The luminance of the lights when steady (i.e., on continuously) was equalised to the luminance of the lights when at the training flicker speed (16.66 Hz) with the aid of a Minolta CS100 Chromametre. Each possums' lights were

[†]Part of this experiment has been published in the following: Signal, T. D., Temple, W., & Foster, T. M. (2001). Visual discrimination in the brushtail possum. *Australian Journal of Psychology*, 53(3), 152-154.

equalised to their training flicker speed luminance. This resulted in a range of luminance averaging $\log 2.1 \text{ cd/m}^2$ (when measuring the brightest part of the light from a distance of 200 mm). The lights remained equalised from this point on. During this condition a RI 10-s (Random Interval) schedule was added to randomise reinforcer delivery further. This meant that although a reinforcer was scheduled, for example, for the next correct flicker response, it would not be available until the scheduled interval (randomly arranged by the computer with an average of 10 s) had also elapsed. Once the scheduled interval had elapsed, another interval did not begin counting down until the scheduled reinforcer had been delivered.

Results

Presented in Figure 4.1 are the data from threshold sessions for the three possums in the Relay condition. Percentage correct is plotted as a function of the log of the flicker speed, the horizontal lines are at 50 % and 75 % correct and each successive threshold session is presented below the preceding session. The data paths are generally flat although they do cross the 75 % line occasionally (and repeatedly in some cases). The unfilled circles on each graph represent the accuracy gained during the final block of trials in a threshold session (at the training speed of 16.67 Hz). With few exceptions, the accuracy of this final block is higher than, or equal to, that of the first block at 16.67 Hz.

The data paths from the Red-light condition are presented in Figure 4.2 as in Figure 4.1. While initial data paths are fairly flat across flicker speeds for most possums (Ratty, Bodwyn, D3 and Silver), there was a tendency for accuracy to decrease as flicker speeds increased over successive threshold presentations (with the possible exceptions of Bodwyn and Silver). As in the previous graph, accuracy on the final block of training speed trials is indicated by an unfilled circle, in situations where accuracy over this final block of trials did not reach criterion (80 % or greater) a '+' symbol indicates the accuracy reached, and where the value of a data point falls below 40 %, this value is written on the graph. Ratty (second session), D3 (fourth and fifth session) and Zeek (fifth session) all had sessions in which they failed to reach criterion in the final block of trials. However, none of these 'unsuccessful' sessions appear to have resulted in data paths different from those of the successful sessions. In contrast to Figure 4.1, all of the 26 data paths from successful sessions presented in this figure fall below 75 %, and in the majority of cases accuracy over subsequent flicker speeds fluctuates around 75 % correct.

Figure 4.3 presents the data from the Equal-luminance condition as in the previous two figures. All six possums successfully completed the five threshold sessions presented in this condition. The data paths are similar across repeated threshold sessions and individuals, with accuracy dropping as flicker speed increased. In this condition, most of the possums were not presented with all of the available flicker speeds (the exceptions being Zeek, twice,

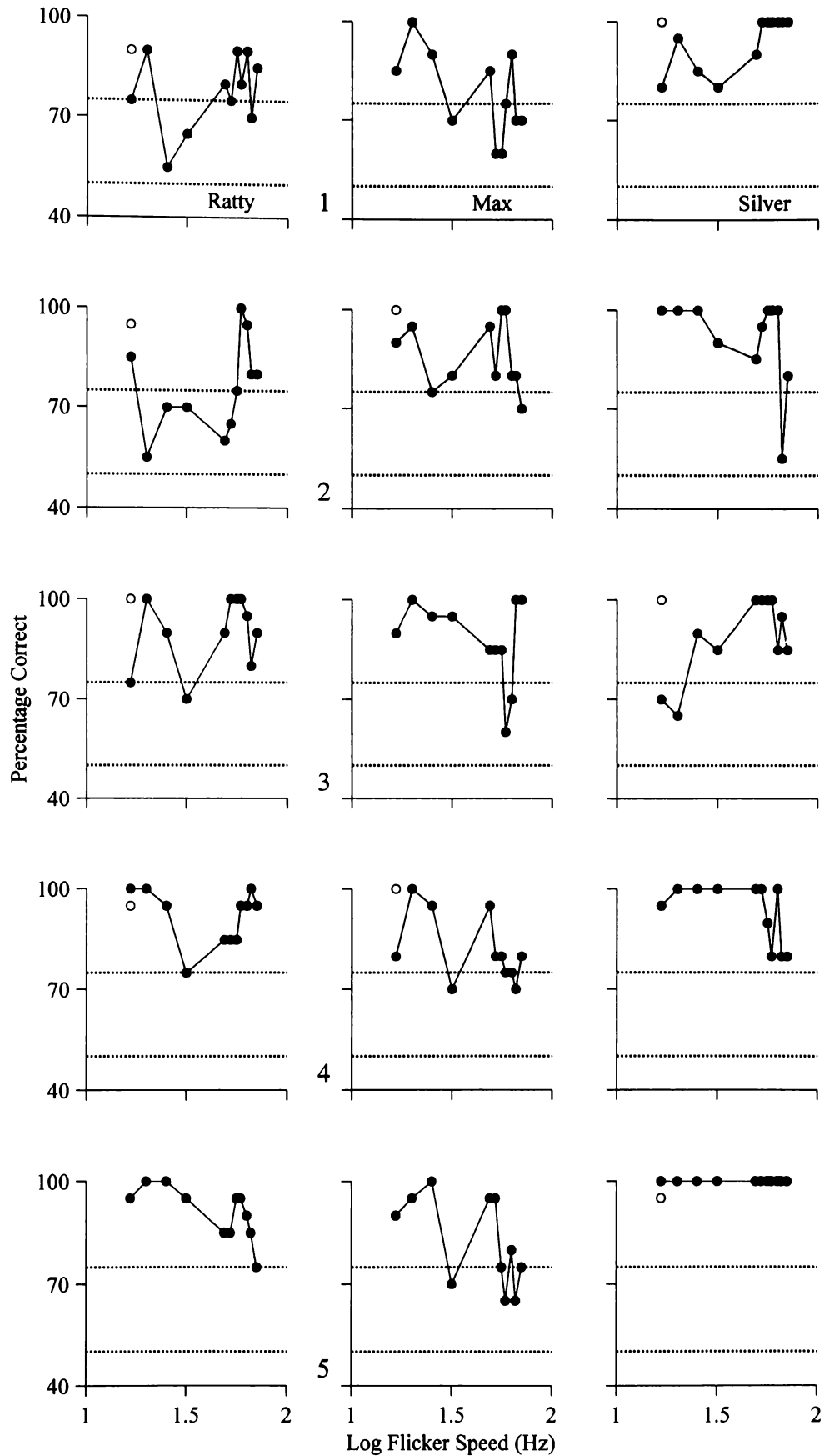


Figure 4.1. Percentage correct gained each threshold session as a function of the log of the flicker speed (Relay condition).

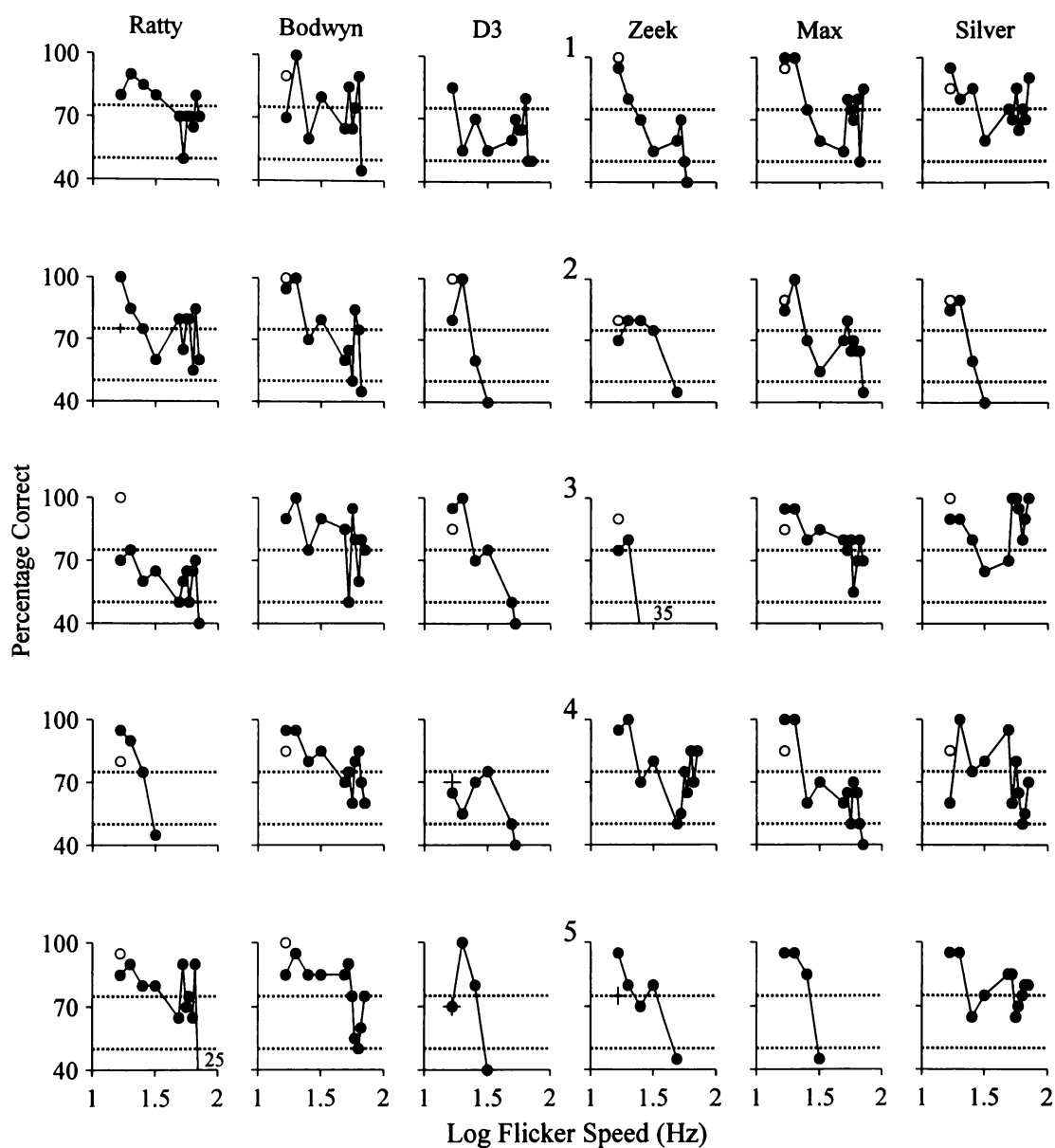


Figure 4.2. Percentage correct gained each threshold session as a function of the log of the flicker speed (Red-light condition).

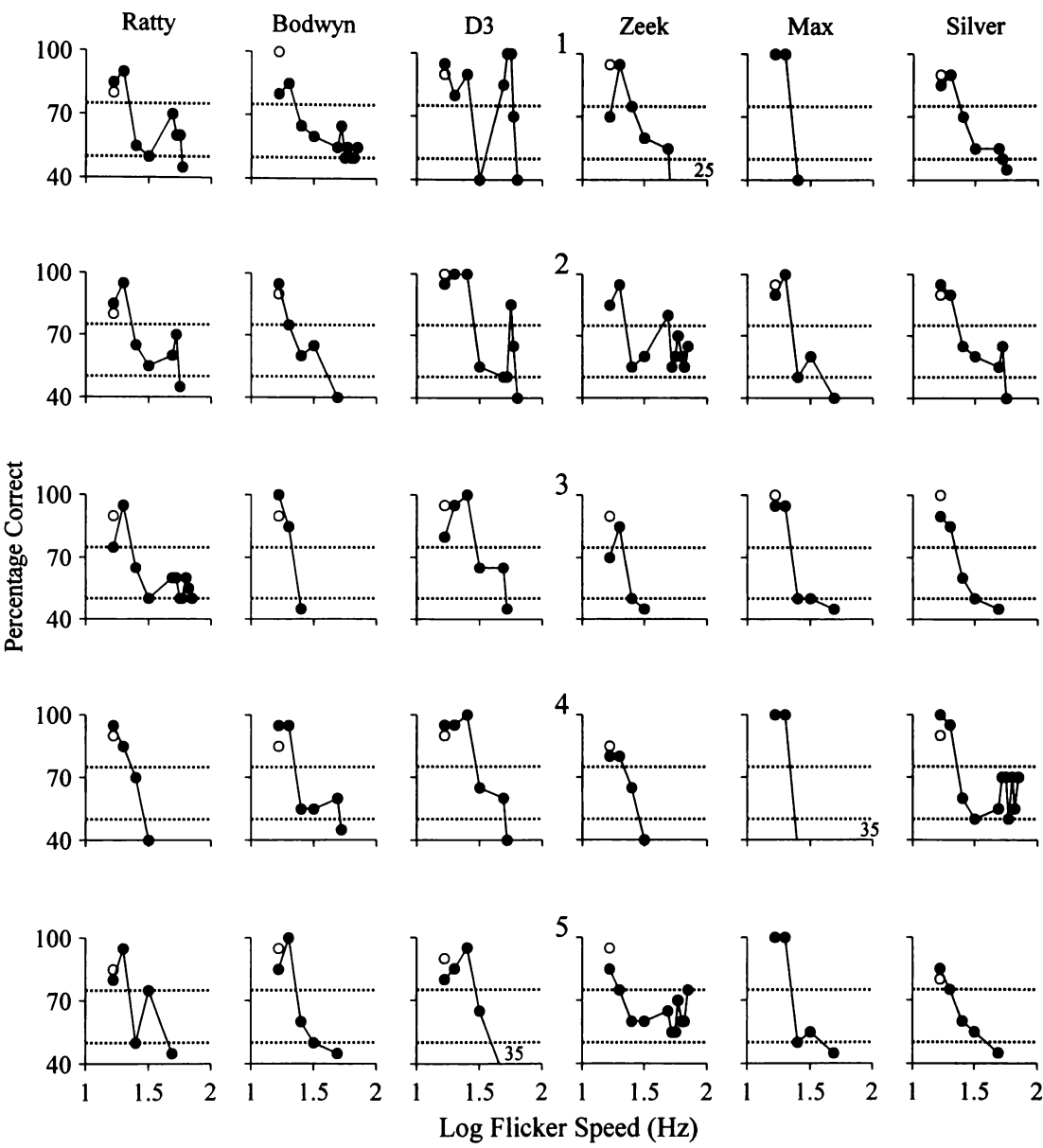


Figure 4.3. Percentage correct gained each threshold session as a function of the log of the flicker speed (Equal-luminance condition).

and Silver, once) meaning that accuracy fell below 50 % at some speed before all 11 available speeds had been presented. In both of the previous conditions it was more common for all 11 speeds to be presented than not.

The average data paths from each condition and for each possum are presented in Figure 4.4 with the data from each condition in separate columns across the page. The vertical lines at each data point indicate a range of one standard error each side of these averages, the unfilled circle indicates average value gained on the final block of trials and the horizontal lines are at 50 % and 75 % correct. A change in the pattern of percentage correct over the three conditions is apparent, particularly between the Relay and Red-light conditions. In the first panel (Relay), average percentage correct remained high across all of the presented flicker speeds. In the second panel (Red-light), the data paths for all possums show a general decrease in accuracy over successive flicker speeds with performance fluctuating around 75 % correct at the higher flicker speeds. The data paths presented in the third column (Equal-luminance) are more orderly (as shown by smaller standard error lines at each average data point with the possible exception of D3) than in either the Relay or Red-light conditions. In the Equal-luminance condition percentage correct decreased below 75 % between the second and third flicker speed in all of the data paths. Interpolating from these points, an overall average flicker speed of 22.4 Hz ($s_x = 0.27$) at 75 % correct was derived for this condition (individual estimates: Ratty, 22.7; Bodwyn, 22.1; D3, 22.8; Zeek, 22.2; Max, 22.2 and Silver, 22.5 Hz).

Log d (Figure 4.5) and ROC (Figure 4.6) analyses on the data from all three conditions followed the same path as the percentage correct analysis indicating little bias. The changing pattern of responding across the three conditions is also apparent in the log d and ROC analyses. In Figure 4.5 log d values near zero (indicating low discriminative performance) were consistently apparent only during the Equal-luminance condition. ROC plots (Figure 4.6), with data points joined in order of presentation with the points at the top left of the diagram being presented earlier, indicate that the stimuli presented in the Relay condition were all readily discriminable (as indicated by data points all clustered in the top left of the ROC plot). However, the stimuli presented in the Red-light and Equal-luminance conditions resulted in data points ranging from the top left of the minor diagonal down to the major diagonal.

Discussion

Following Experiment 3, it was suggested that there might be an extraneous variable which had come to control the possums' behaviour. The aim of the current experiment was to identify this extraneous stimulus. This aim appeared to be achieved when the luminance of the flickering and steady stimuli was equalised. That is, following the removal of the

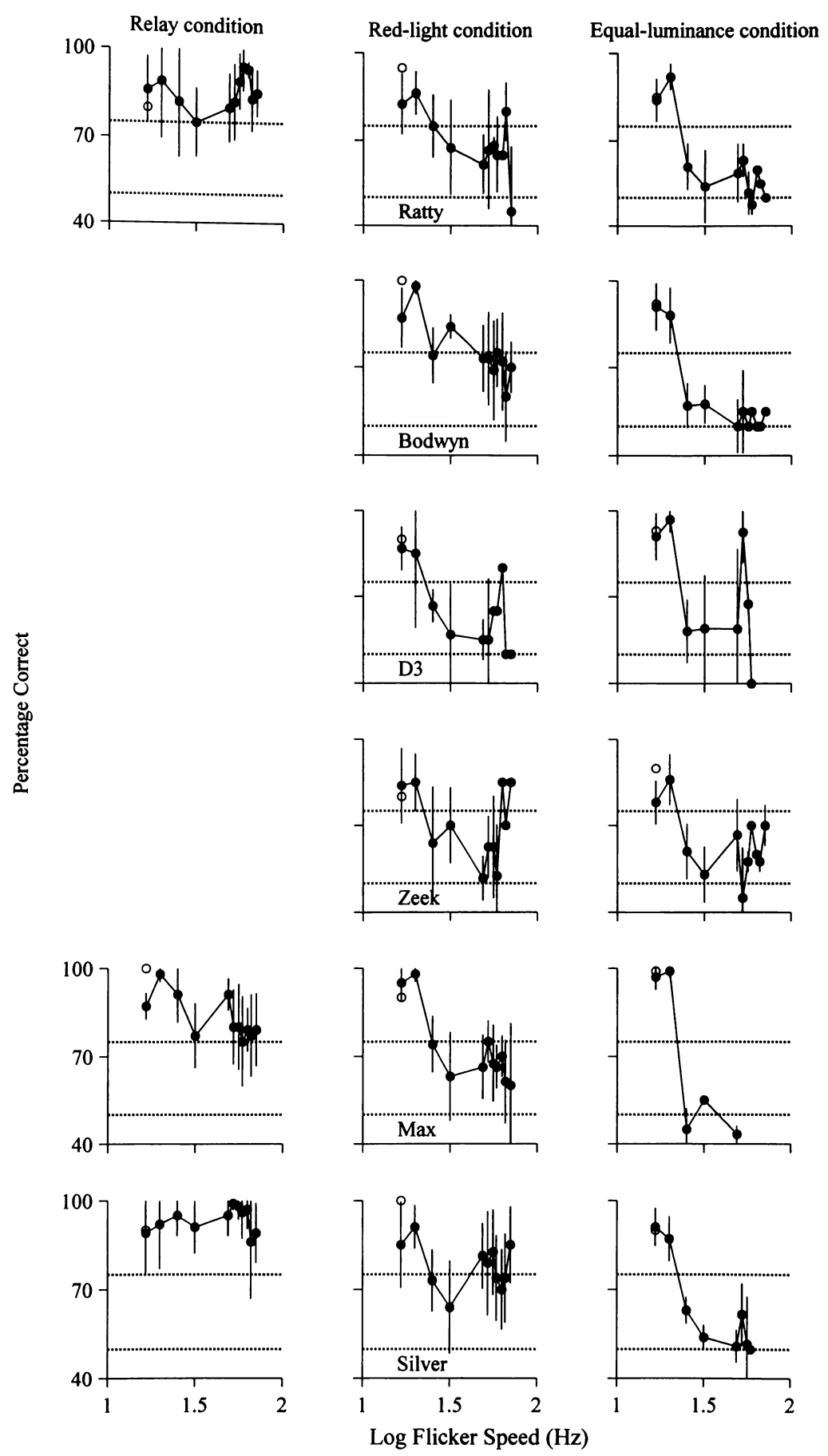


Figure 4.4. Percentage correct gained averaged over threshold sessions as a function of the log of the flicker speed for all three conditions.

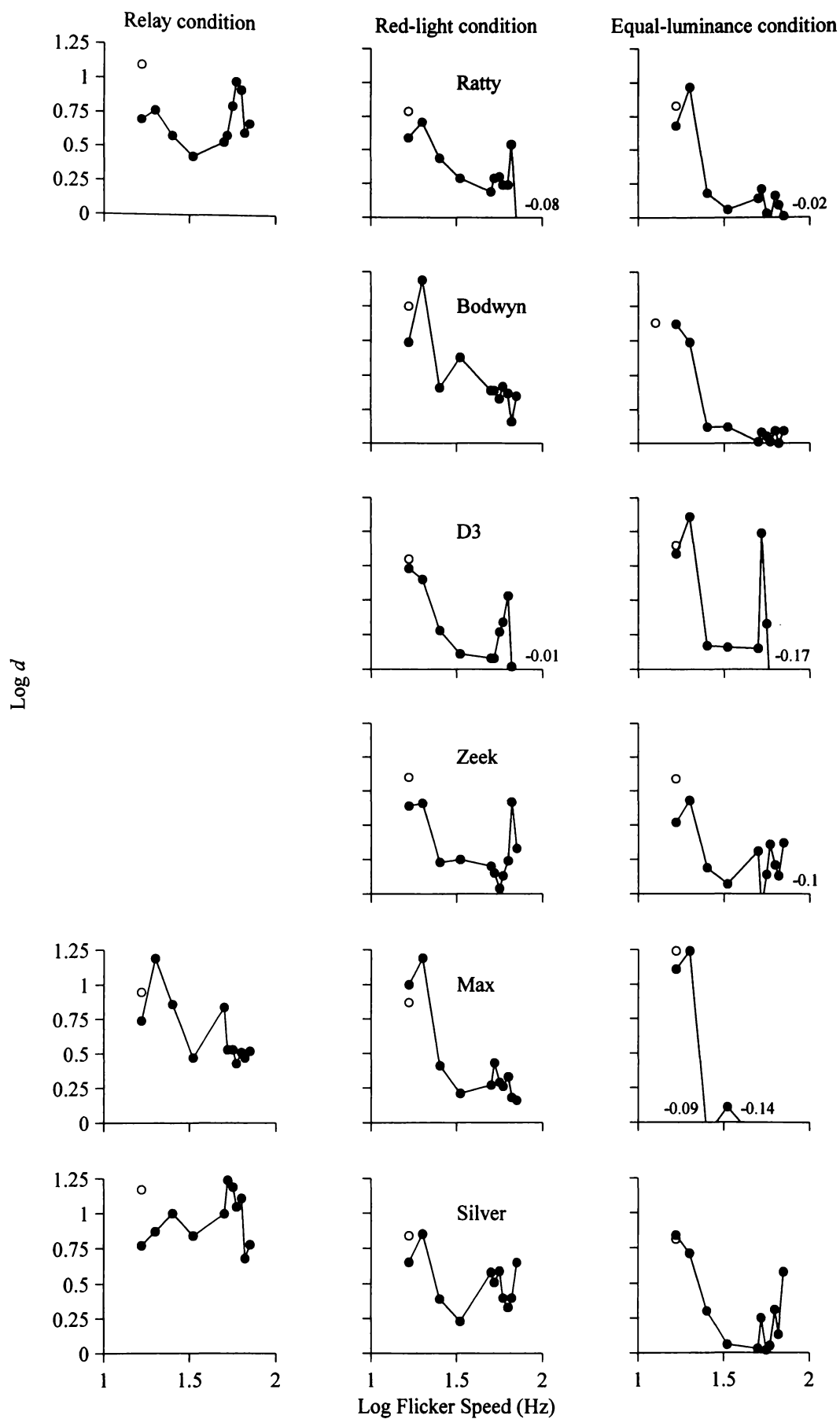


Figure 4.5. Log d plots of averaged data from all three conditions as a function of the log of the flicker speed.

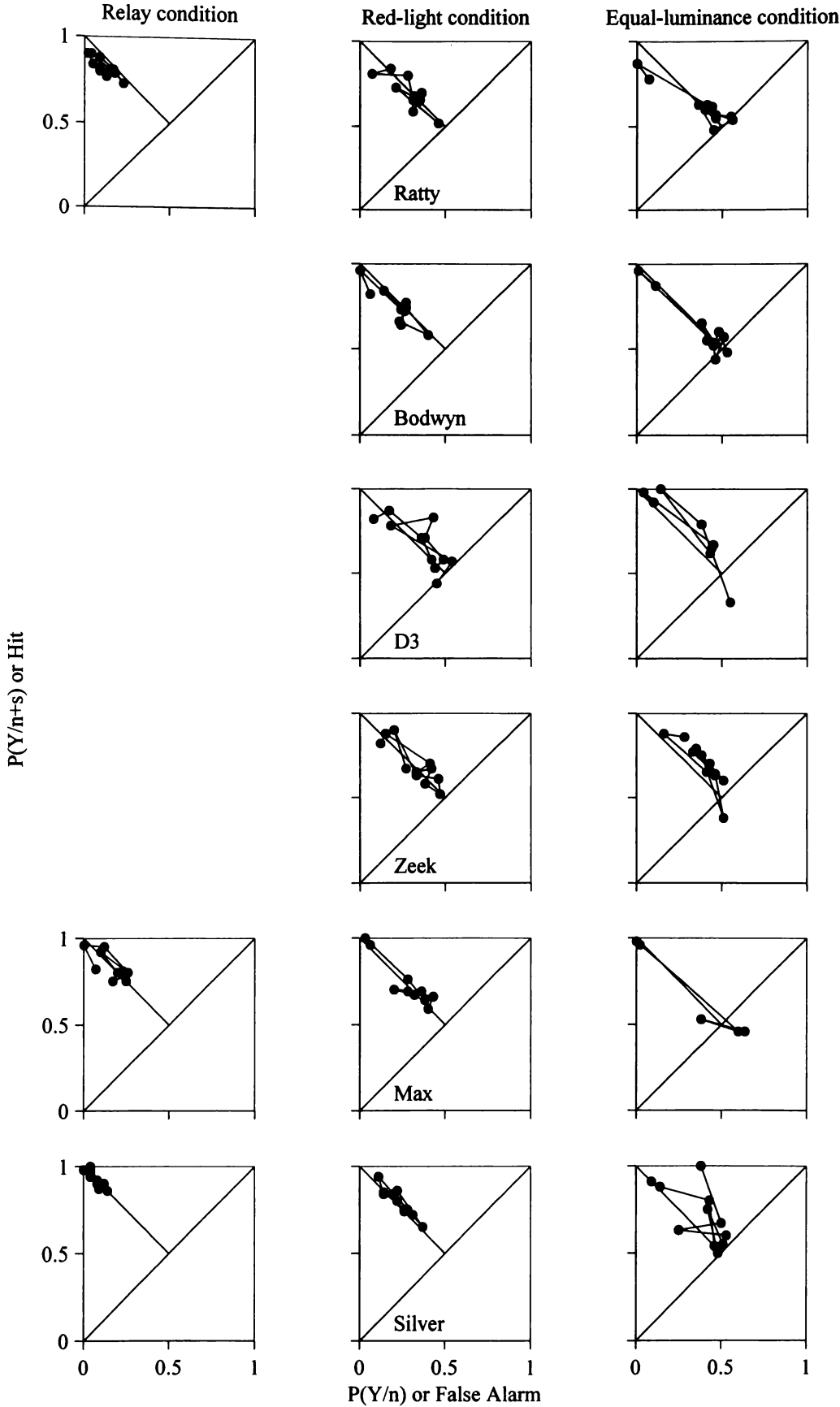


Figure 4.6. ROC plots of the averaged data from all three conditions.

possible brightness cue, percentage correct again fell as the flicker speed was increased. Manipulation of a possible auditory cue (Relay condition) resulted in little or no change in behaviour compared to that seen in Experiment 3. Manipulation of environmental lighting (Red-light condition) however, did appear to have some effect on behaviour with a general decrease in accuracy as flicker speed increased. Although this decrease was present, accuracy did not fall much below 75 % and it is likely that this change was due to some interaction between background illumination and the luminance difference between the flickering and steady lights. Interestingly, based on previous research (e.g., Foley, 1961; Simonson & Brozek, 1952), it would have been expected that such a decrease in background illumination would lead to an increase in CFF which would result in increased accuracy at the higher flicker speeds rather than the decrease seen here.

As mentioned previously, the difference between the luminance of the flickering and steady stimuli was slight, but measurable (difference ranging from 0.5 to 0.8 log cd/m²), nevertheless, as is evident from the data, once relative luminance was equalised accuracy at the higher flicker speeds dropped markedly. Thus the disparity in luminance does seem to have come to control discriminative behaviour. However, as this relative disparity was not deliberately manipulated here, it is possible that other variables such as the length of training also contributed to the effect, although, if another source of extraneous control was still present it would be expected that the threshold function would have remained relatively flat. The shape of the function in the final condition suggests that an extraneous cue which had previously controlled behaviour had indeed been removed. Interestingly, control by relative luminance (or a combination of variables including luminance) may have been what led to the increase in accuracy seen at the higher flicker speeds in Experiment 2 (for 5 possums).

While some CFF investigations do mention that the 'steady' stimulus was kept at the same average luminance as the flickering stimulus (e.g., Coile et al., 1989; Ginsburg & Nilsson, 1971) others do not (e.g., Ploog & Williams, 1995). The control of average luminance across the two stimulus types seems essential (in hindsight) to discrete trial CFF investigations even though it is not mentioned as one of the main variables which affect CFF measures (e.g., Curran & Wattis, 1998).

A comparison of the current results from Equal-luminance condition (represented by filled circles) and the average data for each possum from Experiment 1 (represented by x's) is presented in Figure 4.7 with percentage correct shown as a function of the log of the flicker speed and ± 1 standard error bars at each data point. This figure suggests that even in

Experiment 1 the disparity in relative luminance may have been affecting discriminative performance at the higher flicker speeds to some extent. This is indicated by accuracy at the higher flicker speeds being lower (with a few exceptions) in the current data (filled circles) than in Experiment 1 (crosses). It seems likely that as the flicker vs. steady

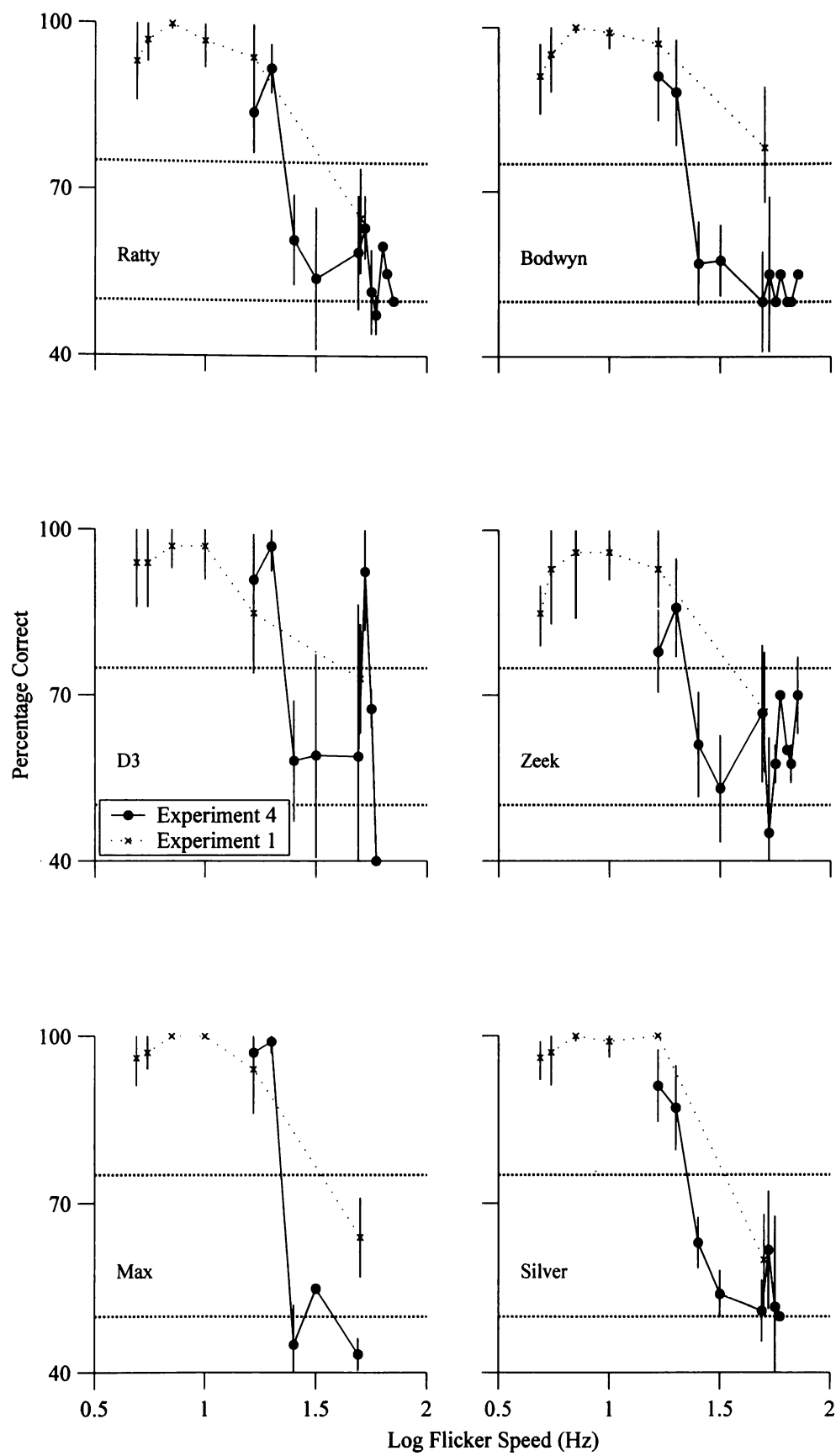


Figure 4.7. Comparison of average percentage correct gained over threshold sessions in Experiments 1 & 4 (Equal-luminance condition) as a function of the log of the flicker speed.

task grew progressively harder (Experiments 2 and 3), the relatively easier luminance discrimination came to control behaviour. Most studies of CFF do not involve the kind of repeated testing used in the current series of experiments. It is possible that, in situations where relative luminance was not controlled (e.g., Ploog & Williams, 1995), that control of behaviour by relative luminance may not have arisen as repeated presentation of near-threshold stimuli did not occur.

With the current step size it is possible to say that the possums' CFF falls between the second and third flicker speed for all 6 possums (Ratty 22.74 Hz; Bodwyn 22.10 Hz; D3 22.82 Hz; Zeek 22.20 Hz, Max 22.22 Hz; Silver 22.50 Hz) with an interpolated average value of 22.43 Hz ($s_x = 0.30$). In all cases, the drop from fairly accurate behaviour (at 20.00 Hz) to below threshold (25.00 Hz) accuracy is steep, suggesting that a further experiment presenting smaller steps within this range (while keeping average luminance equal) would define the CFF even more precisely.

Experiment 5

Once relative luminance had been removed as source of extraneous control (Experiment 4) percentage correct generally fell at the fastest flicker speeds in the threshold sessions. These results suggested that the CFF of brushtail possums lies between 20.00 and 25.00 Hz (with an average of the individual interpolated values of 22.43 0 Hz). This estimate is somewhat slower than the 39.60 Hz derived from the average data paths in Experiment 1. However, as discussed in Experiment 4, it is likely that luminance cues may have affected responding to some degree in all of the earlier experiments. Given that percentage correct in the final condition of Experiment 4 fell below 75 % before 25 Hz, it was decided to focus on flicker speeds around this value rather than present speeds as fast as those used in Experiment 1. In the following experiment, luminance was equalised, smaller increments in flicker speed were used and only flicker speeds within the 20 to 25 Hz range were presented. It was expected that this would allow a precise determination of the threshold.

Method

Subjects

The same subjects served as in the previous experiments.

Apparatus

The apparatus was the same as in Experiment 1.

Procedure

The procedure was identical to that of the third condition in Experiment 4 (i.e., with stimulus luminance equalised), except that the flicker speeds presented were; 16.67 (training speed), 20.00, 21.00, 22.00, 23.00, 24.00, and 25.00 Hz. Each threshold session was followed by at least one training session to maintain criterion level of responding (at or above 90 % correct). Each possum was presented with, and successfully completed, four threshold-testing sessions.

Results

Data from each successive threshold session are presented in Figure 5.1 with each panel presenting one possums' data from the four threshold sessions. Percentage correct is plotted as a function of the log of the flicker speed, the horizontal lines are at 50 % and 75 % and the unfilled circles represent accuracy on the final block of 16.67 Hz trials. As in previous experiments in situations where this circle is not present, percentage correct over the final block of trials was equal to percentage correct over the first block of trials. Generally, percentage correct remained high over the first six flicker speeds then decreased

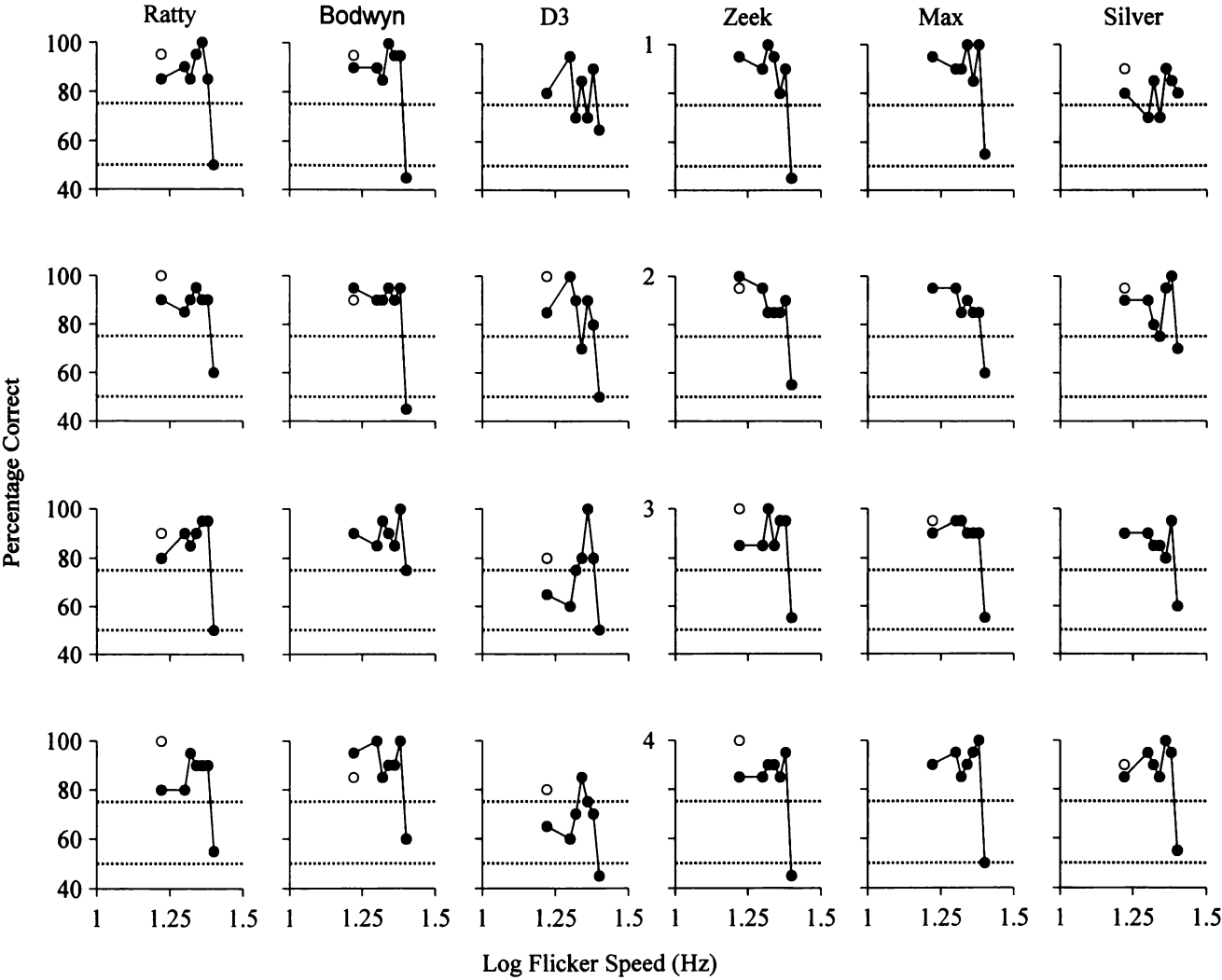


Figure 5.1. Percentage correct gained in each threshold session as a function of the log of the flicker speed.

at the final flicker speed (25 Hz). Although D3's data paths are not as orderly as this generalisation suggests, accuracy gained during the 25 Hz block of trials was lower, in all cases, than at any of the other flicker speeds. This is also true for all of the other data paths (with the exception of Silver's first session). For 4 of the 6 subjects, overall percentage correct decreased to 75 % or below on the final block of trials (25 Hz) only, resulting in a relatively flat line followed by a sharp decrease in accuracy.

This pattern is clearly seen in Figure 5.2 which presents the average percentage correct gained at each flicker speed from the four threshold sessions for each possum, together with the standard error. The large standard error bars at each data point indicate the variability in D3's data. In contrast, Ratty, Zeek and Max's data were relatively similar across threshold sessions. The stimulus value that resulted in 75 % correct was interpolated from these average data paths for each possum. They were; Ratty, 24.2 Hz; Bodwyn, 24.5 Hz; D3, 24.2 Hz; Zeek, 24.4 Hz; Max, 24.5 Hz and Silver, 24.7 Hz. The overall average across possums was 24.5 Hz ($s_x = 0.16$).

Log d and ROC analysis are presented in Figure 5.3. On the left, log d (calculated using the Hautus correction) is plotted as a function of the log of the flicker speed. The unfilled circles indicate the log d estimate for the final block of trials in each session at the training flicker speed. In four cases (Ratty, Bodwyn, D3 and Zeek) the log d estimate at 25.00 Hz is close to zero. ROC plots are presented on the right of Figure 5.3, where the probability of being correct on a flicker trial is plotted as a function of the probability of being incorrect on a steady trial and the data points joined in order of presentation with the points at the top left of the diagram being presented earlier. In all cases (except Silver), there is a cluster of data points towards the top left corner of the ROC space with the final data point (25.00 Hz) being noticeably separate from the other data points. The data points all fall close to the minor diagonal indicating little response bias.

Discussion

The aim of this experiment was to define the threshold CFF for the brushtail possum more precisely than in Experiment 4. This was achieved with all six average data paths falling below 75 % beyond 24 Hz. The average CFF value was interpolated from the data paths and found to be 24.5 Hz with very little difference across possums (Ratty 24.41 Hz, Bodwyn 24.55 Hz, D3 24.18 Hz, Zeek 24.41 Hz, Max 24.48 Hz, Silver 24.68 Hz, $s_x = 0.17$). However, the abrupt change in accuracy between the 24.00 and 25.00 Hz block of trials was not expected.

The presence of an abrupt, all-or-none, change in discriminative performance is unusual as a more ogival shape is generally found in psychophysical studies (Engen, 1972). The pattern seen in the current experiment between 24.00 and 25.00 Hz is similar to that

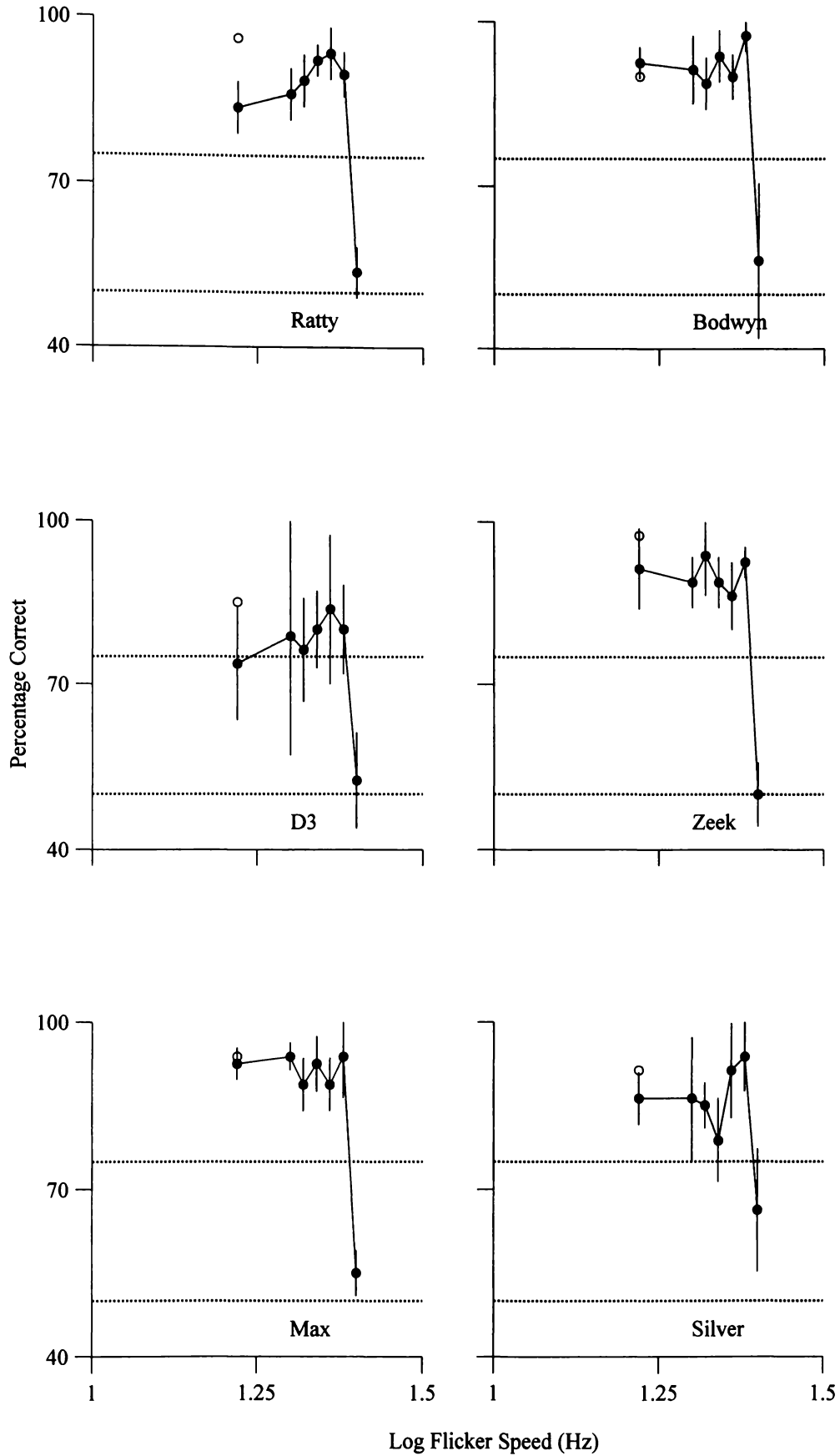


Figure 5.2. Average percentage correct gained over four threshold sessions as a function of the log of the flicker speed.

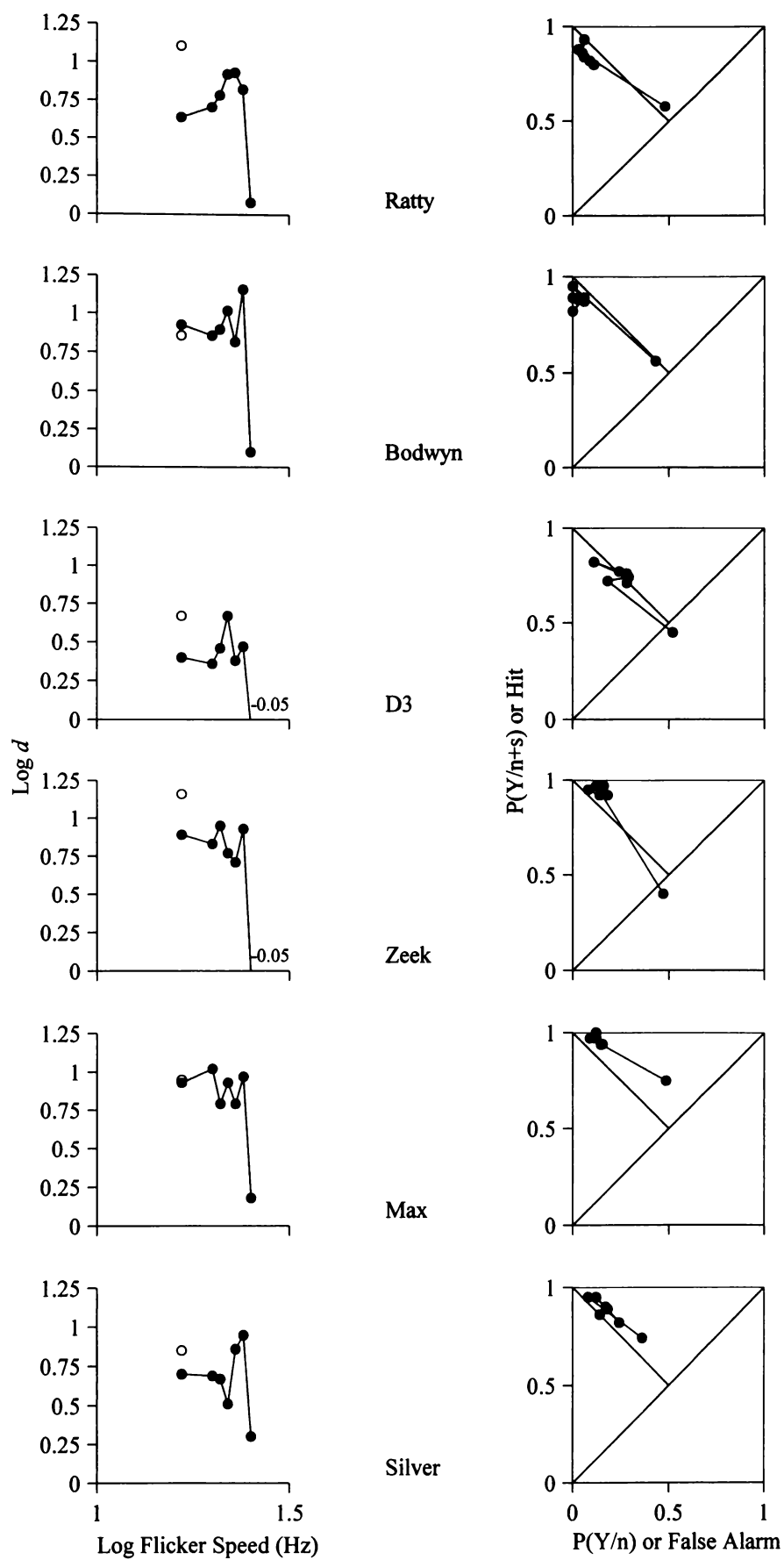


Figure 5.3. Log d and ROC plots averaged over four threshold sessions.

seen in the final condition of Experiment 4 between 20.00 and 25.00 Hz. There are several possible sources of this unexpected pattern of responding. These include the procedure and size of stimulus change; the flicker vs. steady task; or the possums themselves.

Size of stimulus change

Such a large change in percentage correct from one stimulus to the next might suggest that the stimulus change was too large. However, the 1 Hz change in the flickering stimuli in the current experiment is smaller than that used in all other, discrete trial, CFF determinations found in the literature (e.g., Bernholz & Matthews, 1975 (2 Hz), Loop & Berkley, 1975 (5 Hz); Loop et al., 1980 (7 Hz); Williams et. al., 1985 (2 Hz)). As none of these studies mention the type of change in percentage correct seen here it does not seem likely that it arose from too large a stimulus change. Two of the studies above (Loop & Berkley, 1975; Williams et al., 1985) present a function depicting performance at a single luminance over a range of flicker speeds using a conditioned suppression paradigm. None of the functions presented show any sign of a rapid change in performance as the flicker speed was increased. In fact Loop and Berkley (1975) state that the cat's behaviour was not "...all-or-none, but rather ... a graded response showing progressive changes in flicker detection..." (p.558). This would suggest that the sudden change seen in the current results is not common to CFF detection experiments with other species when conditioned suppression techniques are used.

Stimulus presentation method

One difference between the current study and Loop et al.'s (1980) study (on which the current methodology is loosely based), is the way in which the discriminative task was presented. Here stimuli were presented successively in contrast to Loop et al.'s simultaneous presentation.

The effect of simultaneous and successive presentation of stimuli on performance has been widely debated (e.g., Bushnell, 1999; Milosevic, 1993; Parasuraman & Mouloua, 1987; Thomas, Cook, & Terrones, 1990). McLean and White (1982) state that it is a well known, but little understood, fact that successive discriminations are harder than simultaneous discriminations. Various studies have found performance to be more accurate and more stable over time on simultaneous tasks compared to successive discrimination tasks (e.g., Bushnell, 1999; Milosevic, 1993; Parasuraman & Mouloua, 1987). In at least one case however, this conclusion may be confounded by order effects (e.g., Bushnell, 1999). There are also studies which suggest that successive stimulus presentation leads to more accurate responding compared to simultaneous tasks (e.g., Gonzalez & Shepp, 1961), while other studies have found evidence that the method of stimulus presentation has little or no effect on subsequent performance (e.g., Shelton, Picardi & Green, 1982).

Thus while many authors agree that successive and simultaneous presentations of stimuli have different effects on subsequent discriminative behaviour, exactly what those effects are is still being debated. Interestingly, both of the previous behavioural studies with the brushtail possum presented stimuli simultaneously and reported difficulty establishing a visual discrimination (Kirkby & Williams, 1979; Webster, 1975), while the current study (with successive presentations of stimuli) encountered little difficulty.

A further study using simultaneous stimulus presentation and the current stimuli would be of interest because, if the current abrupt change in performance is due in some way to the method of stimulus presentation, training the possums to perform a simultaneous flicker discrimination may result in a more gradual decrease in percentage correct as flicker speed increases.

CFF as cause of abrupt change in performance

As mentioned previously, several CFF investigations using conditioned suppression paradigms have not found such an abrupt change in performance. Loop and Frey (1982), while not presenting CFF data at a single luminance, make no mention of any such change in performance. Nuboer et al. (1992) trained two hens to perform a conditional discrimination between a flickering and steady light and then varied the flicker rate to determine the CFF of the hens. While they used a tracking procedure rather than a block-wise design, they did use discrete trials and an equal number of flickering and steady trials. It is apparent from the average function they present at a single luminance that accuracy of responding decreased gradually as flicker speed was increased. Given that CFF determinations with other species using various methods do not seem to result in an all-or-none function, it seems unlikely that the flicker vs. steady discrimination task itself is causing the pattern of responding seen in the current experiment.

Species effect

The shape of the data function seen in the current experiment is also not common when other modalities are tested using conditional discrimination procedures. Auditory thresholds have been widely determined in a range of species, for example; beluga (Awbrey et al., 1988), cat (Heffner & Heffner, 1985b), ferret (Kelly et al., 1986) and manatee (Gerstein et al., 1999). Commonly these give a gradual drop in percentage correct as stimuli become less discriminable. Threshold testing with another modality (such as auditory) using the same method as used here with the brushtail possum, would serve to test the hypothesis that the drop seen here is somehow a product of CFF determinations with the possum rather than of the method or of the task itself.

CFF and the brushtail possum

While most CFF investigations do not present threshold values at individual luminance levels as are presented here, it is possible to get an idea of approximate CFF

values, at a similar luminance, from overall CFF functions. Coile et al. (1989) present a figure showing CFF functions over a range of luminance values for several species. However, the functions presented in their graph were derived from experiments using a conditioned suppression paradigm and a threshold criterion of 33 % suppression in responding. This criterion is commonly used within condition suppression experiments (e.g., Coile et al., 1989; Loop & Berkley, 1975) but, as discussed previously, it is not immediately obvious how to compare the current findings to their results. Keeping in mind this complication, a straight comparison of the CFF functions presented by Coile et al. (1989) to the current data indicate that, at the current stimulus luminance level, the current CFF thresholds found for possums are similar to that of rats, but lower than dogs, cats and monkeys.

A search of the literature resulted in only one CFF determination where a threshold estimate was reported for a single luminance using a method similar to that used in the current series of experiments (i.e., Loop et al., 1980). As mentioned in Experiment 1, Loop et al. (1980) reported a CFF of between 53 and 56 Hz for cats at luminance of $2.4 \log \text{ cd/m}^2$ using a two-alternative forced-choice procedure. The threshold criterion used by Loop et al. (1980) was 70 % correct. Using this criterion, an average CFF value of 24.60 Hz ($s_x = 0.17$, average luminance of $\log 2.2 \text{ cd/m}^2$) was interpolated from the individual average data paths (Ratty 24.55 Hz, Bodwyn 24.67 Hz, D3 24.36 Hz, Zeek 24.53 Hz, Max 24.61 Hz, Silver 24.86 Hz). Given that CFF estimates have been found to increase with stimulus luminance (Gortelmeyer & Zimmerman, 1982, cited Curran & Wattis, 1998), some of the difference between the CFF estimates reported for the cat, and those found here, may be due to the higher luminance of Loop et al.'s (1980) stimulus. Replicating the current experiment with stimuli of the same average luminance as Loop et al. would serve to identify how much of the difference in CFF estimates is due to the difference in luminance.

The 24.60 Hz CFF found with the current data (using a 70 % threshold criterion) would suggest that possums are not as good at detecting movement at this light level as the cat. This is not surprising as it has been found previously that the CFF values tend to be related to the environment and normal behaviours of the organism (Frank, 1999). Thus, one would expect a fast moving predator like the cat to have a visual system with better temporal resolution, as shown by higher CFF values, than an animal that is mainly herbivorous (Clout & Sarre, 1997; McArthur, Goodwin & Turner, 2000) like the brushtail possum. However, the identified similarities between the possums' visual system and that of the cat means that the cat still remains one of the most appropriate animals available for comparison. There appear to be very few CFF determinations with other herbivorous species, the one found (with guinea pigs) presents an overall CFF function and makes no mention of any individual luminance functions. However, the authors (Dodt & Wirth, 1953) mention that the guinea

pig's retina is made up almost solely of rods, thus the visual system of the possum is likely to have more in common with the cat than the guinea pig.

The current experiment succeeded in determining more precisely the CFF of the brushtail possum at a single luminance. However, the rapid change in accuracy from above to below threshold was unexpected and several possible sources of unusual pattern have been presented. A further experiment using the same range of flicker speeds with a simultaneous presentation method has been suggested, as well as comparing the pattern of responding in the current series of experiments to possums discriminating another modality (e.g., auditory intensity) and the same training and threshold determination methods as here.

Experiment 6

It was suggested in Experiment 5 that the method used (i.e., successive presentation of stimuli) to examine CFF in the previous experiments may have contributed in some manner to the shape of the threshold functions found. In the following experiment the flicker vs. steady discrimination was presented simultaneously with one stimulus light flickering while the other remained steady. Which side of the response panel each stimulus was presented on varied pseudo-randomly from trial to trial. Possums were required to press the lever below the flickering light. Once percentage correct reached the criterion level threshold sessions began, initially using the same range of flicker speeds as in Experiment 4. A second series of threshold sessions then presented flicker speeds between 20 and 25 Hz (as in Experiment 5), and in a third series flicker speeds beyond 25 Hz were presented to 3 possums.

Method

Subjects

Seven possum were trained for this experiment. Four experienced possums (Ratty, Bodwyn, D3 and Zeek) and 2 naïve possums (Mickey (male) and Gizmo (female) both between one and two years of age) completed the first condition. Zeek and Bodwyn died before completion of the second condition. The 2 naïve possums began training and experimental sessions once their weight had stabilised and they were adjusted to the cage environment. Thus, these 2 possums began the first threshold condition later than the 4 experienced possums. Both of the naïve possums took a long time to train and test due to one (Mickey) not adjusting well to the cage environment and human presence, and the other (Gizmo) not maintaining responding throughout a session. Despite several changes in the food consequence (described further in the procedure section) and dietary restrictions, this problem continued for this possum. Gilbert (hand-reared male, approximately one-year old at the beginning of training) participated only in the second condition.

Apparatus

The apparatus was the same as in Experiment 1.

Procedure

Each session began with the levers being inserted through the holes in the response panels. Environmental conditions remained the same as in the previous experiments (i.e., overhead lighting, temperature, start time). As in Experiment 5, the relative luminance of the flickering and steady lights were equalised.

Simultaneous discrimination training. During this phase, each possum was trained to press the lever below the flickering light (at 16.67 Hz and a 1:1 light:dark ratio). During

this training phase both lights were lit and the computer controlled pseudo-randomly which light would flicker, using a version of the Gellerman (1933) series. This ensured that there would be no more than three consecutive trials with the flickering stimuli on the same side, and that the number of times the flickering stimulus appeared on each side would be approximately equal within a session. A beep and 2-s access to food followed every correct response while a 2-s blackout followed every incorrect response, a 3-s ITI followed every trial. After two sessions with continuous reinforcement a RI 4-s schedule was instituted. This schedule was gradually increased to RI 10 s.

Training sessions continued until each possum reached criterion level of performance. Criterion performance, as in all previous experiments, was initially set at five consecutive sessions at or above 90 % correct, however after lengthy training (50 sessions or more) this criterion was dropped to five consecutive sessions at or above 85 % correct for 4 possums (Ratty, Bodwyn, D3 and Zeek). Early in the training 3 possums (D3, Gizmo and Zeek) ceased to respond for the barley and carob mix used previously. After checking equipment, and trying various reinforcers (e.g., Cocopops™ mixed with commercial possum pellets, Toasted Museli and Banana Vitacrunch™) D3 reliably responded for Banana Vitacrunch while Zeek and Gizmo (initially) responded for a 1:3 (by volume) Cocopops™ and possum pellet mix. D3 and Zeek continued to respond for these reinforcers throughout the condition they experienced, but Gizmo eventually stopped responding for the Cocopop™ mix. At this point Banana Vitacrunch™ was found to maintain her behaviour and was used for the remainder of the sessions in the current experiment. Once performance reached the appropriate criterion threshold sessions began.

Threshold sessions. All threshold sessions began with 20 trials of the training flicker frequency (16.67 Hz). The flicker rate was then increased along the steps in Table 6.1 depending on the condition currently in effect. If the percentage correct at the completion of a set of 20 trials was 50 % or above, the next flicker rate was introduced. As soon as percentage correct fell below 50 % for a block of trials a further 20 trials at the training flicker frequency (16.66 Hz) were presented and the session terminated. Correct responses continued to be reinforced intermittently as in training sessions at all flicker frequencies. Each threshold session was followed by at least one training session to maintain criterion level of responding (percentage correct at or above 90). At the completion of a threshold condition (five successful sessions), each possum was presented with training sessions until five consecutive sessions were completed at or above the appropriate criterion (i.e., 85 or 90 %).

Table 6.1

Flicker speeds (Hz) scheduled for each of the three threshold condition in Experiment 6

Condition 1	Condition 2	Condition 3
16.67	16.67	16.67
20.00	20.00	20.00
25.00	21.00	21.00
33.00	22.00	22.00
50.00	23.00	23.00
52.60	24.00	24.00
55.60	25.00	25.00
58.80		26.00
62.50		27.00
66.70		28.00
71.40		29.00
		30.00

Condition 1 (20-71 Hz). The flicker speeds scheduled during this condition were identical to those in Experiment 4 (first column, Table 6.1). In this condition each possum was presented with threshold sessions until five had been completed successfully (i.e., responding throughout the session and re-gaining 80 % correct or better on the final block of trials).

Condition 2 (20-25 Hz). The flicker speeds scheduled during this condition were identical to those of Experiment 5 (second column, Table 6.1). Four possums successfully completed five sessions in this condition (Ratty, Gilbert, D3 and Mickey) while Gizmo completed only three sessions successfully out of the 11 presented to her.

Condition 3 (20-30 Hz). The flicker speeds presented during this condition were similar to those of the previous condition except that additional, faster, speeds were also scheduled (third column, Table 6.1). Only 3 possums were presented with this condition. Ratty and D3 successfully completed five sessions while Mickey completed three out of eight sessions.

Table 6.2 presents that number of, and reason for, unsuccessful sessions in all three conditions.

Results

Table 6.3 shows the number of training sessions required for each possum to reach criterion level of performance. The 4 possums who had extensive experience with successive flicker presentation (Experiments 1 to 5) required more sessions to meet a reduced criterion (85 %) than the 3 naïve possums (Gilbert, Gizmo and Mickey).

Data from successful threshold sessions for each possum from the first condition are presented in Figure 6.1. Percentage correct is plotted as a function of the log of the flicker speed, the horizontal lines are at 50 % and 75 % and the unfilled circles depict the percentage correct gained during the final representation of the training flicker speed. In situations where this circle is not apparent, accuracy over the final block of trials was identical to accuracy on the first block of trials. Data from successive sessions are presented down the page, where data points fell below 40 % the percentage correct gained at that stimulus is presented on the graph. Percentage correct generally decreased as the flicker speed increased for all possums. The majority (20 out of 30) of the data paths cross the 75 % line between the second and third flicker speed (20.00 and 25.00 Hz).

Figure 6.2 presents the data from the Condition 2 (20.00-25.00 Hz) as in Figure 6.1. Patterns of responding are more varied under this threshold condition. Generally, percentage correct remained high and relatively stable over the initial flicker speeds and decreased at the fastest flicker speed. For 3 possums (Ratty, Gilbert and Mickey) accuracy fell to, or below, 75 % (with one exception for Mickey) at the fastest flicker speed. While a similar pattern

Table 6.2

Number of unsuccessful sessions in each of the three conditions for individual possums due to either, failing to reach 80 % or greater accuracy on the final block of trials (< 80 % column) or stopping responding before the end of the sessions (stopped column).

Possum	Condition 1		Condition 2		Condition 3	
	< 80 %	stopped	< 80 %	stopped	< 80 %	stopped
Ratty	2	0	0	0	0	1
Bodwyn	0	3	-	-	-	-
Gilbert	-	-	0	1	-	-
D3	1	3	1	0	2	1
Zeek	0	0	-	-	-	-
Gizmo	2	1	0	8	-	-
Mickey	0	1	0	2	0	5

Table 6.3

Number of training sessions required to reach criterion performance (five consecutive sessions at or above criterion value) in a simultaneous flicker discrimination

Possum	Number of Sessions	Criterion Value
Ratty	60	85 %
Bodwyn	50	85 %
Gilbert	21	90 %
D3	95	85 %
Zeek	55	85 %
Gizmo	15	90 %
Mickey	34	90 %

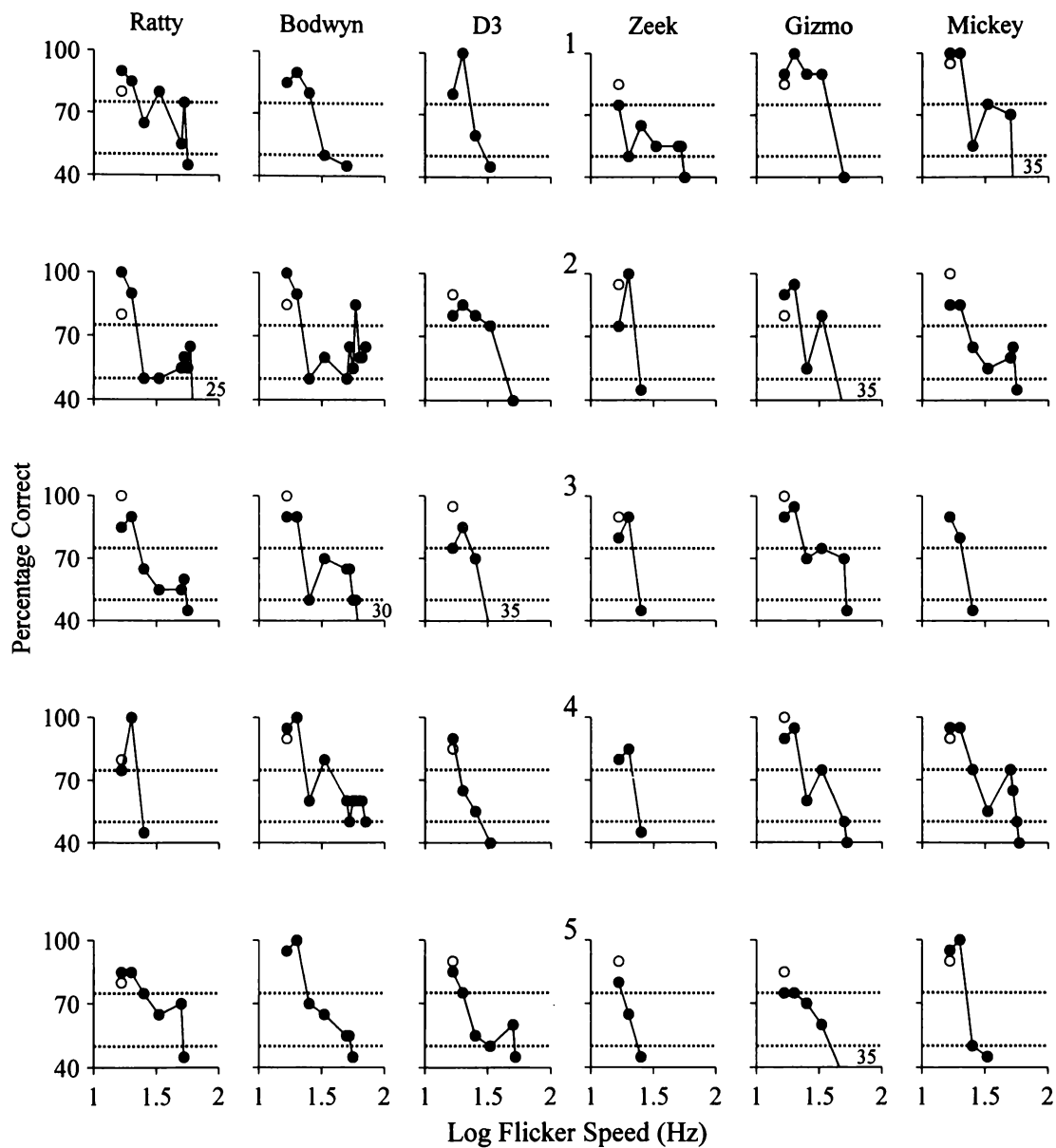


Figure 6.1. Percentage correct gained in each threshold session as a function of the log of the flicker speed (Series 1).

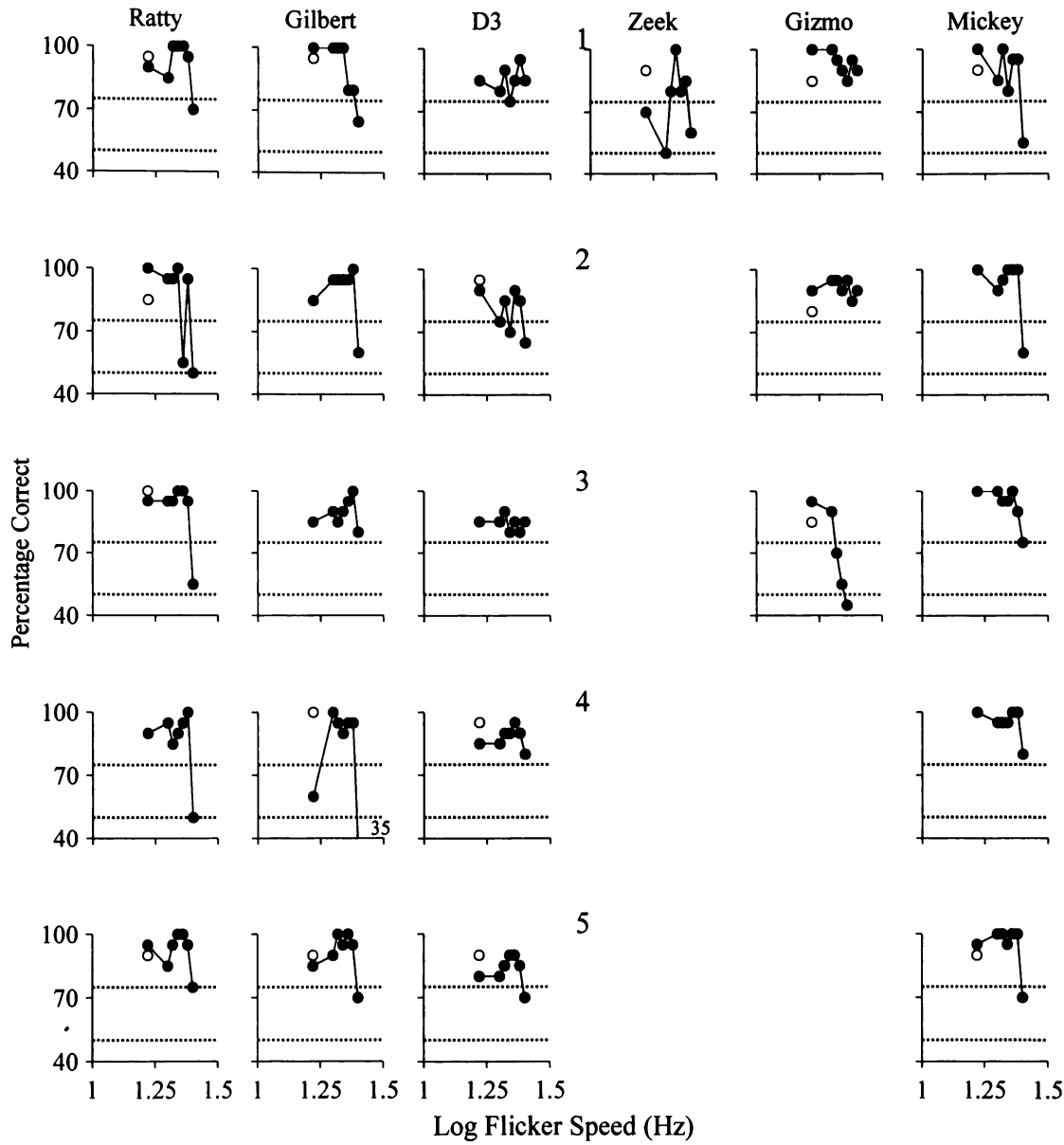


Figure 6.2. Percentage correct gained in each threshold session as a function of the log of the flicker speed (Series 2).

can be seen in the majority of D3 and Gizmo's data paths, accuracy at the final flicker speed rarely fell below 75 %.

The data from Condition 3 (20.00-30.00 Hz) are presented in Figure 6.3 as in the previous figures. Nine of the 13 data paths begin with a high percentage correct for the first five or six data points followed by a rapid decrease in percentage correct. The steepest drop occurs (and the 75 % line is crossed) between the sixth and seventh flicker speed (24.00 and 25.00 Hz) for eight of these data paths, while one crosses the line between the seventh and eighth flicker speed (25.00 and 26.00 Hz; fourth threshold session for Ratty). Ratty encountered all of the scheduled flicker speeds once (out of five successful threshold sessions), while D3 and Mickey encountered all of the scheduled speeds in all of the threshold sessions presented.

Average data from the three conditions are presented in Figure 6.4 as a function of the log of the flicker speed. The horizontal lines are at 50 % and 75 % and the vertical lines at each data point represent one standard error either side of the mean value. The average data are representative of the individual sessions as indicated by the relatively small standard errors. Four of the possums participated in more than one condition and a comparison of the average functions from these conditions (minus the standard error bars) are presented in the fourth panel of graphs. As can be seen from the comparison graphs, with the possible exception of D3, the data paths from each of the conditions are very similar and show a general decrease in percentage correct as flicker speed increased. D3's data for the first condition (represented by unfilled circles) showed an overall pattern of decreasing accuracy as flicker speed was increased, however the data paths from Condition 2 (represented by pluses) and 3 (represented by crosses) are clearly different with accuracy remaining much higher over all of the flicker speeds than seen in Condition 1. Presented in Table 6.4 for ease of comparison are the 75 % threshold estimates interpolated from the average data paths for each possum in all three conditions. From the table the similarities between the threshold conditions is again apparent.

Unlike the previous experiments, log d and ROC plots cannot be used here as there is only one trial type (i.e., stimulus is present on every trial). Thus, the presence or absence of response bias and its potential effect on percentage correct analysis cannot be determined as previously. By calculating the percentage of responses made to one side (e.g., left), a general indication of bias can be obtained. As the number of left and right correct trials and the reinforcement ratio was kept approximately equal within a session, the percentage of responses made to one side should be approximately 50 % if there is no response bias. Figure 6.5 presents the percentage of left responses averaged over the individual sessions for each threshold condition as a function of the flicker speed, the vertical lines at each data point represent one standard error either side of the mean value and the horizontal line is at

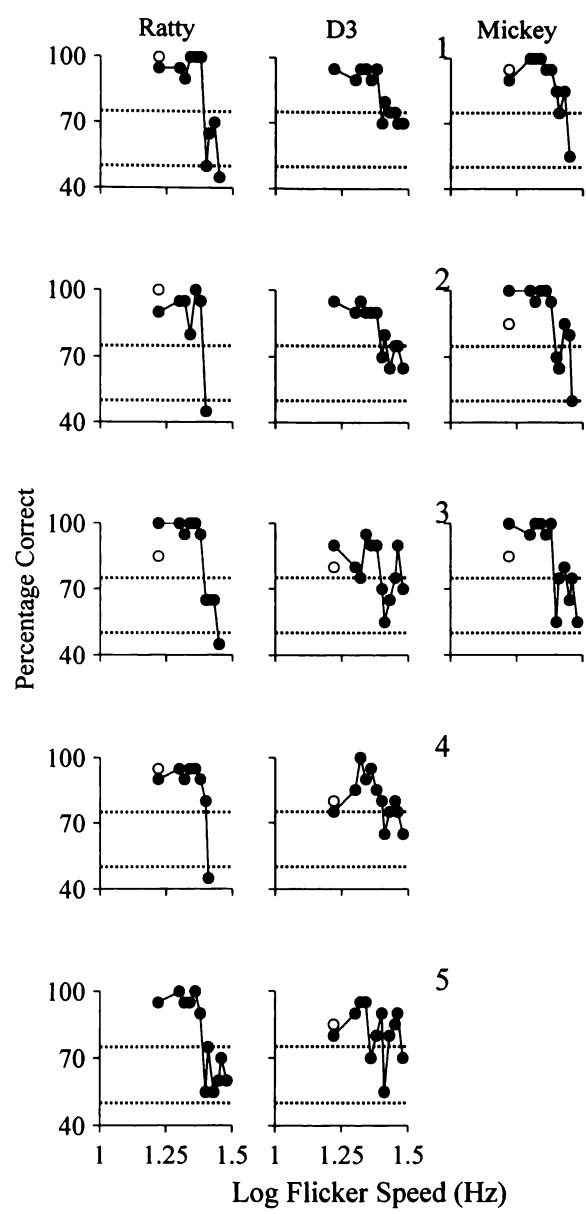


Figure 6.3. Percentage correct gained in each threshold session as a function of the log of the flicker speed (Series 3).

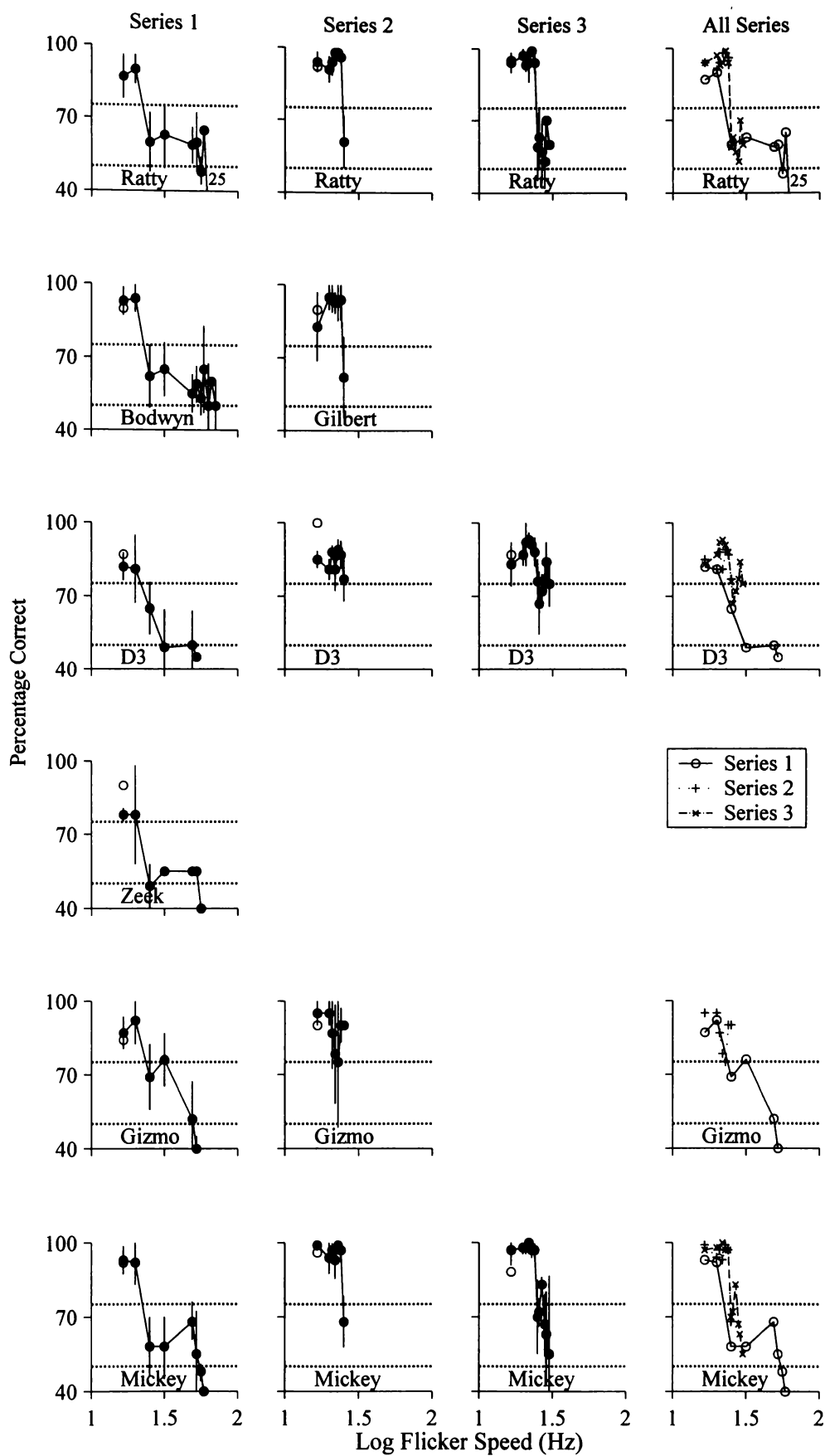


Figure 6.4. Average percentage correct gained in each condition as a function of the log of the flicker speed and a comparison between series for 4 possums.

Table 6.4
CFF estimates (Hz) using 75 % threshold criterion for all possums in each threshold condition.

	Condition 1	Condition 2	Condition 3
	20 - 71 Hz	20 - 25 Hz	20 - 30 Hz
Ratty	22.50	24.60	24.54
Bodwyn	22.97	-	-
D3	21.88	25.20	25.11
Zeek	20.52	-	-
Gizmo	23.70	23.00	-
Mickey	22.50	24.76	24.81
Average	22.35	24.39	24.82
St Dev	1.08	0.96	0.29

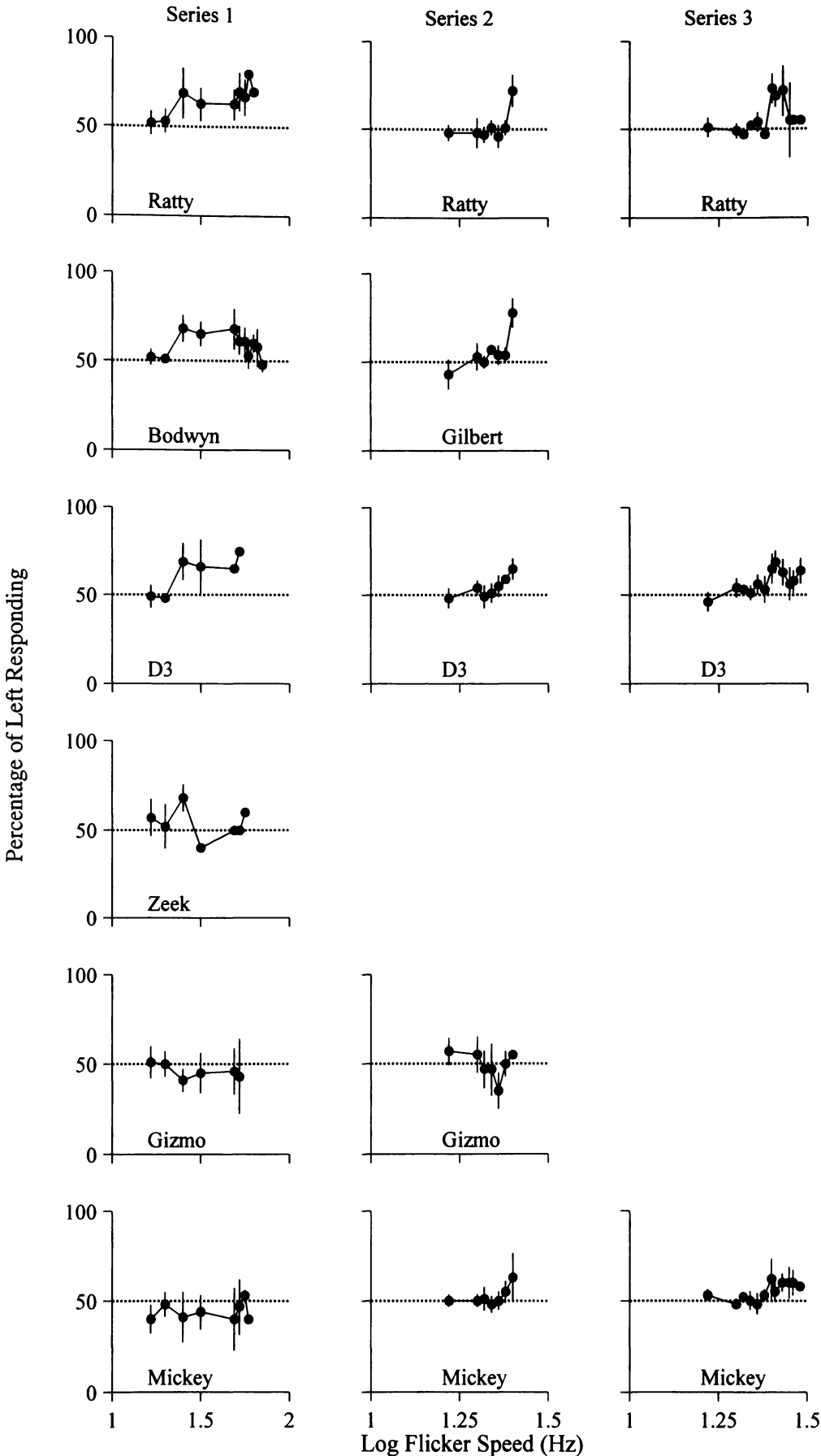


Figure 6.5. Percentage of responding to the left lever averaged over threshold sessions presented as a function of the log of the flicker speed for all three series.

50 %. From the graphs it appears that response bias was not stable across flicker speeds, with a bias towards the left at the faster flicker speeds for most possums.

Discussion

The aim of this experiment was to determine if changing the method of presenting stimuli (i.e., from successively to simultaneously) would alter subsequent CFF estimations. Data from the three threshold conditions presented here indicate that, for the majority of possums, the change to a simultaneous task had little effect on the CFF thresholds or on the shape of the function obtained. That is, the abrupt change in performance seen in Experiment 5 between 24.00 and 25.00 Hz was also present in these results, indicating that the method of stimulus presentation is unlikely to be contributing to the phenomenon. The 4 possums who had extensive experience with the previous, successive task (Experiments 1 to 5), had difficulty learning the current task as is shown by the long period of training required. Due to order effects (i.e., this was the second task trained for all four experienced possums) it is difficult to determine whether this simultaneous task was 'harder' for these subjects or not. The 3 naïve possums (Gilbert, Gizmo and Mickey) learnt the simultaneous discrimination relatively quickly and reached a 90 % criterion easily (despite difficulties encountered with maintaining responding). Thus, it seems likely that the difficulties encountered with the experienced possums learning the current discrimination may be solely due to learning a second discrimination task. The effect of extensive training on an organism's ability to learn a subsequent task has been termed over-learning.

A search of the over-learning literature suggested that extensive practice with one task should not detrimentally affect the learning of a second task (or a reversal of the original task), and in most cases appears to facilitate the learning (e.g., Driskell, Willis & Copper, 1993; Ishida & Papini, 1997; Nakagawa, 2000). While species differences in the ability to learn successive visually-based discrimination tasks have been found, Rachlin (1976) suggests that some of these differences may depend on the modality tested. He suggests that animals which have difficulty learning a subsequent visually-based task (or simply the reversal of the original task) may prove capable if the tasks were based on another modality (e.g., auditory). The difficulties seen in the current experiment in teaching these experienced possums a new visually-based task are similar to the problems encountered by Kirkby and Williams (1979) when attempting to train possums repeated reversals of a visual discrimination and it is not clear why this should be so. It would be interesting to see if such problems occur when teaching possums an auditory discrimination.

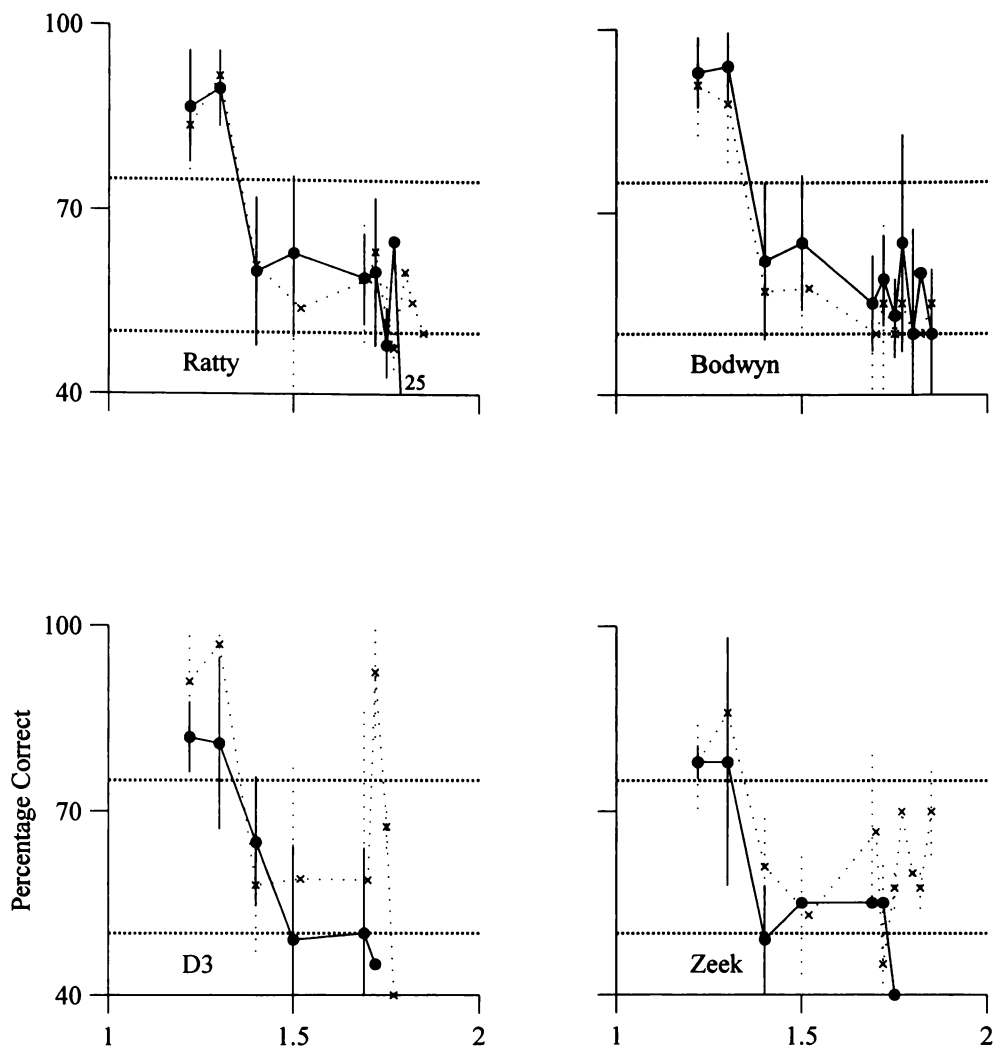
As the current experiment had two correct responses (left or right depending on which side was flickering), a 75 % threshold calculated from overall accuracy is appropriate and has been recommended for two stimulus simultaneous discriminations (e.g., Hesse,

1986, Madigan & Williams, 1987; Treutwein, 1995). Using a 75 % criterion, the threshold interpolated from the average data paths of the first condition was 22.35 Hz ($s_x = 0.99$), identical to that derived from Experiment 4 where the same range of flicker speeds were presented successively. Figure 6.6 presents the average data from the final condition in Experiment 4 (represented by crosses) with the average data from the first condition in the current experiment (represented by filled circles) for comparison. As Max and Silver died before participating in the current experiment, comparisons between these two conditions are only possible with 4 possums. The similarities in the functions from Experiment 4 and the current experiment are clear, illustrating the lack of any systematic difference between the threshold functions obtained from successive and simultaneous conditional discrimination tasks. Interestingly, the need to reduce the performance criterion for some of the possums, due to difficulties learning the required task, does not seem to have had any effect on the subsequent threshold functions or threshold estimates.

The second condition presented the same range of flicker speeds as Experiment 5 and an average 75 % threshold value of 24.41 Hz ($s_x = 0.73$) was interpolated from the individual average data paths. This threshold value is again very similar to that found with the same stimuli presented successively (Experiment 5, 75 % threshold estimated to be 24.5 Hz). Presented at the bottom of Figure 6.6 is a comparison of Ratty and D3's (being the only two possums who completed both threshold conditions) averaged data from both the second condition (represented by filled circles) and from Experiment 5 (represented by crosses). Both possums' current (Condition 2) data paths are similar to those seen in Experiment 5. That is, accuracy remained high over all flicker speeds until 25 Hz when accuracy dropped below 75 %. However, the average data in Condition 2 (same flicker speeds as Experiment 5 with simultaneous presentation) tends to be higher at all of the flicker speeds than those from Experiment 5. This increase in accuracy is interesting in light of the need to reduce the criterion performance required for threshold sessions to begin for both Ratty and D3. This again suggests that the change to a 85 % criterion (down from 90 %) had no detrimental effect on subsequent behaviour during threshold estimations.

Threshold estimates (based on 75 % correct) from the third condition resulted in identical estimates for Ratty and Mickey (24.55 and 24.81 Hz respectively) to those found in Condition 2. However, as noted earlier, D3's data path did not fall uniformly and a threshold of 25.11 Hz was derived from the first time her data path fell below 75 %. This pattern of higher percentage correct at the faster flicker speeds than seen in either of the previous conditions may suggest that D3 had learnt to discriminate between the stimuli based on another cue (other than luminance as this was equalised throughout the current experiment) during Conditions 2 and 3. Alternatively, the increase in percentage correct could be due to some form of practice effect.

Experiment 6 Series 1 (●) compared with Experiment 4 Equal-luminance (x)



Experiment 6 Series 2 (●) compared with Experiment 5 20-25 Hz (x)

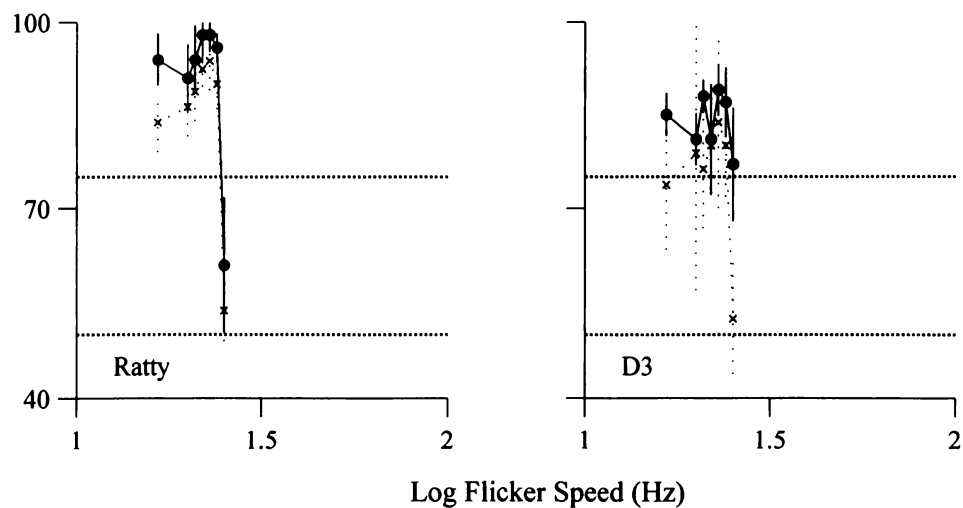


Figure 6.6. Comparisons of average data paths from Series 1 & 2 of the current experiment with the Equal-luminance condition of Experiment 4 (first four graphs) and Experiment 5 respectively.

Presented in Table 6.5 are stimulus threshold estimates (using 75 % overall correct) from Experiments 4 and 5 and the first and second conditions from the current experiment for the 4 possums who completed these experiments. While a range of threshold criteria have been used when analysing data from conditional discrimination experiments, the most common values used are 50 or 75 % overall correct. With simultaneous or forced-choice experiments, 75 % correct has been termed the ‘standard’ threshold value as this value is said to give rise to an estimate of sensory ability which is halfway between chance and perfect responding (e.g., Madigan & Williams, 1987; Treutwein, 1995). As can be seen in Table 6.5, even with the apparent bias towards the left lever at the higher flicker speeds seen in the current experiment, the threshold estimates found here are very similar to those calculated earlier (using 75 % correct as threshold criterion). If the CFF estimates from the previous, successive, experiments had been derived using 50 % correct, as suggested by the same authors who assert that 75 % correct is the appropriate threshold criterion for simultaneous experiments (e.g., Madigan & Williams, 1987; Treutwein, 1995), then a marked difference between estimates would be apparent. With the current data, 75 % correct in the simultaneous experiments equates to the same level of discriminability as 75 % correct in the successive experiments, calling into question the need for different criteria depending on the method of stimulus presentation. It must be noted here that using 50 % correct as criteria for both types of experiments would also result in a high degree of agreement between CFF estimates, as can be seen in Table 6.5, although CFF estimates are more variable across individuals at 50 %.

In conclusion, whether the stimuli were presented successively or simultaneously did not alter the shape of the threshold functions. The current, simultaneous presentation method resulted in similar data paths and threshold estimates to the previous successive method. This would suggest that either the sudden drop seen here is inherent to CFF determinations or that the drop is a product of some unique feature of the possums’ visual system. As discussed previously, it does not seem likely that this pattern of responding is common to CFF experiments with other species. Investigating possums’ discriminative ability with another modality may serve to determine if this pattern is common to possums responding on discriminative tasks, or a function of CFF investigations with possums.

Table 6.5

Comparison of CFF estimates from successive (Experiments 4 and 5) and simultaneous (current experiment) flicker experiments using both 50 and 75 % correct as threshold criterion.

	20.00-71.00 Hz				20.00-25.00 Hz			
	Experiment 4		Condition 1		Experiment 5		Condition 2	
	75 %	50 %	75 %	50 %	75 %	50 %	75 %	50 %
Ratty	22.74	26.77	22.50	26.67	24.41	25.10	24.60	25.31
Bodwyn	22.10	26.13	22.97	26.88	24.55	25.15	-	-
D3	22.82	26.03	21.88	29.69	24.18	25.09	25.20	27.70
Zeek	22.20	27.20	20.52	24.83	24.41	25.00	-	-
Average	22.47	26.53	21.97	27.02	24.39	25.09	24.90	26.51
St Dev.	0.37	0.55	1.06	2.01	0.15	0.06	0.42	1.69

Experiment 7[†]

According to Gates and Aitkin (1982), the importance of auditory information to brushtail possums is reflected in their ‘prominent’ ears and abundant vocalisations. Winter (1976, cited Gates & Aitkin, 1982) recorded at least 24 separate calls made by possums which he believed were used for communicating with conspecifics. These calls ranged in frequency from 500 Hz to at least 12 kHz and it is reasonable to assume that the auditory abilities of possums will relate to this vocalisation range. While there are no published behavioural determinations of possums’ auditory abilities, Aitkin et al. (1979) measured the microphonic potential of possums’ cochlea and found that the cochlea was most sensitive to frequencies between 700 Hz and 1 kHz and capable of responding to frequencies up to 30 kHz. Gates and Aitkin (1982), while mapping the auditory cortex of the possum, found that the cortex was sensitive to a range of frequencies from 330 Hz to 39 kHz.

While cochlea and cortex potentials are useful in determining the physical potential of the auditory system, they cannot determine what the animal will actually be able to detect. What is required for this is a behavioural determination of auditory thresholds. Several authors have pointed out the need for such investigations with brushtail possums (e.g., Aitkin, 1995; Gates & Aitkin, 1982).

Auditory thresholds have been measured in a wide variety of species using a range of behavioural techniques including; Conditioned Suppression (e.g., Heffner & Heffner, 1985b (Cat); Ravizza, Heffner & Masterton, 1969 (Opossum)), Go/ No Go procedures (e.g., Awbrey et al., 1988 (Beluga); Barton et al., 1984 (Quail)) and Two-Stimuli Discrimination techniques (e.g., Gerstein et al., 1999 (Manatee); Temple, Foster & O’Donnell, 1984 (Hen)). Regardless of method used, the majority of audiograms are determined by presenting an organism with a single tone, training some discriminative behaviour in the presence and absence of the tone, and then manipulating intensity (dB) until accuracy (or occurrence) of behaviour falls to some pre-determined criterion. This procedure is then repeated for a number of different tones. For example, Kelly et al., (1986) trained two water-deprived ferrets to respond differentially in the presence and absence of a training ‘noise’ (540 ms of noise at 85 dB) in order to receive water. The ferrets were trained to initiate a trial by touching a central water spout. If a noise was played, they were then required to touch the right water spout, and if a no-noise trial occurred, they were required to touch the left spout. Once the animals were responding reliably above 90 % correct, threshold sessions began. A pure tone (at 85 dB) replaced the ‘noise’ stimulus during threshold sessions. Kelly et al.

[†]This experiment has been published as Signal, T., Foster, T. M., Temple, W. (2001). Determination of auditory thresholds in the brushtail possum. *Physiology & Behavior*, 23, 195-200.

used a 'block trial' descending method of limits (similar to that used in Experiments 1 to 5), with intensity decreasing by 10 dB over successive blocks of 50 trials. If percentage correct was below 90 % at the end of a block of 50 trials a further 50 trials at the same intensity occurred before any further decrement in intensity. Thus once percentage correct fell below 90 % all tones were presented for 100 trials. This procedure was repeated with tones ranging from 62 Hz to 32 kHz. Kelly et al. used the intensity level where overall accuracy was at 60 % correct as their measure of threshold. Threshold intensity of each tone was then presented as an audiogram and compared to audiograms derived for other species.

While Kelly et al. (1986) present audiograms of four other species (dog, cat, racoon and least weasel) only the cat and least weasel studies are referenced. Both of these audiograms were determined by Heffner and Heffner (1985b, 1985c) using a conditioned suppression paradigm where threshold was taken to be the stimulus intensity that resulted in a 0.25 suppression ratio. Kelly et al. (1986) make no mention of any manipulations done to the data from Heffner and Heffner's experiments in order to make sensible comparisons between the experiments (given the divergent threshold criteria and experimental methods) but conclude that the audiogram presented for the ferret is similar to those of the other species presented, particularly that of the dog. As discussed earlier, the extent to which thresholds determined by conditioned suppression methods will differ from thresholds determined in other manners is unknown (Blough & Blough, 1977). Thus the level of diversity in the analysis of discriminative performance needs to be considered when making comparisons between experiments and species.

The aim of the following experiment was to train possums to perform an auditory discrimination and to determine stimulus threshold for an 880 Hz tone. While many auditory threshold determinations have been conducted using conditioned suppression techniques, the current study used essentially the same method as used in the successive flicker experiments (Experiments 1 to 5), that is, a two-stimulus conditional-discrimination. This was to allow comparisons between patterns of responding across two modalities in the possum.

Although data obtained under this method should not be compared directly with auditory thresholds determined with conditioned suppression techniques, a number of other auditory threshold determinations have used a conditional discrimination (e.g., Kelly et al., 1986; Temple et al., 1984) or Go/No go method (e.g., Szymanski, Bain, Kiehl, Pennington, Wong, & Henry, 1999), particularly with larger animals and aquatic species. Interestingly, while Heffner and colleagues use conditioned suppression methods extensively, with larger animals they use conditional discrimination techniques (e.g., Heffner & Heffner, 1980 (Elephant); Heffner & Heffner, 1983a (Horse)). This would seem to suggest that

conditioned suppression techniques are not the method of choice when testing larger, difficult to restrain, nonhuman animals.

One concern with auditory experiments necessitated a change to the procedure used in the flicker experiments. As tone intensity varies depending on the animal's position in relation to the source of the tone, it is important that the animal is positioned in approximately the same place when a tone is played (Blough and Blough, 1977). To facilitate this, auditory experiments normally use an 'observing' or orientating response (e.g., Heffner & Heffner, 1980; Kelly et al., 1986). For example, Kelly et al. (1986) required their subjects to make an initial response on a central spout to start every trial, which meant that they were in the same position at the beginning of every trial. Without such an initial orientating response, variations in accuracy could be due to the animal's varying position rather than to changes in the intensity of the tone (Blough & Blough, 1977). Thus, in the following experiment, a central lever was added to the response panel and the possums were required to press this lever to initiate a trial.

The initial training stimulus was an 880 Hz tone (at 80 dB), chosen as it fell within the most sensitive range of the possums' cochlear as identified by Aitkin et al. (1979). Each possum was tested individually, however due to background noise levels in the testing environment, one possums' auditory ability was re-tested in a sound attenuated chamber.

Method

Subjects

Six intact, experimentally naïve, adult brushtail possums served as subjects. The 3 females (Mica, Buggy, and Kiri) and 3 males (Gypsy, Ebony and Murphy) were captured as pouch young with their mothers. As outlined in Experiment 1, all possums were moved into individual cages with ad lib access to water and fed pellets, dock and apples daily once they reached sexual maturity or 2 kg (whichever came first). These individual cages were attached to each other along one side of a room with the room containing a total of 12 possums. All experimental sessions occurred within this room (with the exception of the sessions held in the sound-attenuated chamber). The experiment began approximately one year from weaning. The possum room was maintained on a 12 hr:12 hr reversed light/dark cycle and temperature was kept stable with the use of heaters and air conditioning. Food was restricted to a level where each possum would respond when provided with food as a consequence, but that did not result in weight loss (as measured by regular weighing).

Apparatus

As for the earlier flicker experiments, an individual response panel was permanently attached to each possums' home cage. Initially the panel contained a central amber light (small 'grain' 24-W bulb with plastic amber cover) and there was a hole in the panel,

directly below the light, through which a removable lever could be inserted. There was a central hole towards the bottom of the panel, which allowed access to the food hopper.

In subsequent conditions, there were three amber lights in the panel and directly below these were three round holes through which levers could be inserted. Figure 7.1 shows the dimensions of the final response panel. The levers were removed after each session so that they could not be damaged. Mounted centrally, 5 cm above each panel, was a Digitor A9772 three-way speaker. The speaker was capable of broadcasting a range of frequencies (100 Hz to 16 kHz). A Med Associates, ANL-926 Programmable Audio Generator, was used to produce the tones required. The programmable ANL-926 could produce tones ranging from 10 Hz to 35 kHz at intensities ranging from 20 to 100 dB. Whenever an effective response was made on a lever a brief, 0.05 s, feedback beep sounded from a separate speaker attached to the back of the panel. A mix of steam-flaked barley and carob chips (at a 15:1 ratio (by volume), chips ranged from 2 to 5 mm in length) was accessible through the large central hole when the food hopper was raised for 2 s. While the food hopper was operating, the amber lights were dark and no responses on the levers were registered. A computer controlled all of the experimental events and recorded data using the MED/PC system. Response-by-response data were collected along with the total number of correct and incorrect responses made (for both tone-on and tone-off trials) and the number of reinforcers gained on each trial type.

Procedure

Each session began with insertion of the response levers. To minimise background noise, the room extractor fan was initially turned off. However, due to heat problems in subsequent sessions the fan was only turned off during threshold testing. With the fan off, other possums' movements (reaching 20 to 30 dB) caused the only noise in the cage room. Daily sessions started approximately two hours into the dark phase of the light/dark cycle. All other details of the room were identical to those in the flicker experiments.

Lever-press training. This part of the training was identical to that used in Experiment 1. Once the possums were obtaining more than 80 reinforcers on a VI 15-s schedule within a 40-min session, experimental sessions were started for each possum successively so that only one apparatus was active at any given time. Sessions were terminated after either 40-min had elapsed or 100 reinforcers had been obtained. They also terminated if a period of 5 min with no lever pressing occurred.

The experimenter examined session-by-session plots of the number of reinforcers obtained within a session under the VI 15-s schedule after each session. Once these were judged visually stable (i.e., not trending) by at least two other members of the lab, the next stage of training began.

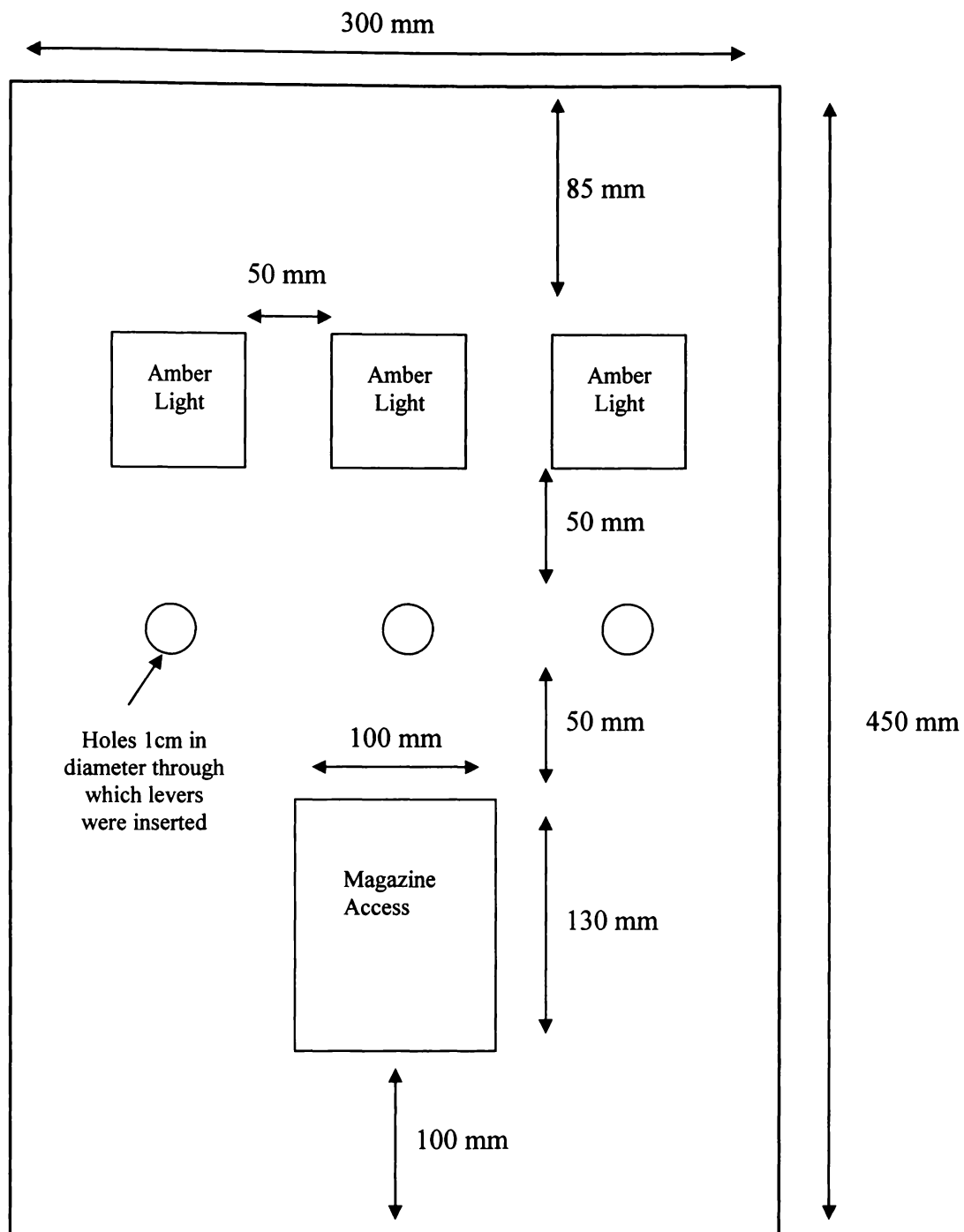


Figure 7.1 Dimensions of final possums response panel for the tone-on vs. tone-off discrimination task.

Side-lever training. At this point two side levers and lights were placed in each panel (one either side of the central light or lever as in Figure 7.1). For two sessions after the insertion of these levers each possum was required to press the central lever (with only the central light lit) to begin a trial. Then, either one of the side lights (pseudo-randomly arranged using a version of the Gellerman (1933) series) would be lit and pressing the lever below this light was reinforced with 2-s access to the food hopper followed by a 3-s ITI. Incorrect responses resulted in 2-s blackout followed by the 3-s ITI. No tones were presented during these two sessions.

Discrimination training. A trial-by-trial procedure (as in the flicker experiments) in which tone-on (880 Hz at 80 dB) and tone-off trials alternated pseudo-randomly according to a version of the Gellerman (1933) series was used to train the required discrimination. This ensured that there would be no more than three consecutive tone-on or tone-off trials, and that the number of each type of trial would be approximately equal within a session. When the central light was lit a press on the central lever initiated a trial. On tone-on trials, responses on the right lever were defined as correct, while on tone-off trials responses on the left lever were defined as correct. The light above the lever associated with a correct response for the current trial was lit. A trial continued until there was a response on a side lever or 60 s had elapsed since the central lever response. If the latter occurred, an aborted trial was recorded and a 2-s blackout followed. On tone-on trials, the tone remained playing until the possum responded on either lever or 60 s had elapsed without a response. A 3-s ITI followed every completed (or aborted) trial. All correct responses resulted in 2-s access to the food hopper and a brief beep. Incorrect responses were followed 2 s of blackout prior to the 3-s ITI. Once each possum completed at least four sessions with accuracy at or above 90 % correct, both side lights were lit following the central lever press. Once each possum was performing accurately (above 90 % correct) at this stage (i.e., with both side light lit), the number of reinforcers gained for each trial type was controlled as for the flicker experiments, and a further RI 12.5-s schedule was also in effect. After five consecutive sessions at, or above 90 % correct, threshold trials began.

Threshold trials. Before each threshold session, the intensity (dBA) of the tone was checked using a Testo™ dB meter and adjusted to 80 dBA if needed. Each threshold session began with 20 mixed tone-on (880 Hz at 80 dBA) and tone-off trials. The sound intensity (on tone-on trials) was then decreased by 8 dB with blocks of 20 mixed tone-on and tone-off trials at each dB. The tone was kept at 880 Hz. If the percentage of correct responses at the completion of a set of 20 trials was 50 or larger, the tone was again reduced by 8 dB and another 20 trials conducted.

When the percentage of responses correct fell to below 50 for a set of 20 trials, or the tone was at 0 dB, the series was stopped and a further 20 trials at 80 dB (training

intensity) followed before the session was terminated. Correct responses continued to be reinforced on an intermittent basis at all intensity levels, a beep always sounded after a correct response and an extra 2 s of blackout followed all incorrect responses. Threshold sessions continued until 10 sessions had been successfully completed, that is, percentage correct over the final block of trials was 80 or greater.

Each threshold-trial session was followed by a session where the tone-on trials were at 80 dB. If a possum's percent correct for this session was 90 or greater the next session would be a threshold-trial session. If percent correct responding fell below this criterion level, non-threshold sessions would continue for this animal until percent correct responding was again greater than or equal to 90.

Sound-attenuated chamber. One possum (Kiri) repeated the threshold determination in a sound-attenuated chamber, with the response panel being removed from her home cage and re-attached to a cage inside a separate chamber. Training and threshold sessions within this chamber were identical to those in Kiri's home cage and occurred after she had successfully completed 10 threshold sessions in her home cage and reached criterion level of performance in the sound-attenuated chamber. Kiri completed five threshold sessions in the sound-attenuated chamber.

Results

Figure 7.2 shows the percentage of correct responses during training as a function of session number. The two sessions of side-lever training are shown in Section A. With the exception of Bugsy, all 6 possums immediately performed this initial task at a high level of accuracy. Once tone-on trials were added (Section B), either behaviour remained at a high level of accuracy or accuracy increased quickly. Section C presents data from sessions where both sidelights were lit and intermittent reinforcement was in effect. At the start, all 6 subjects performed at chance levels (approximately 50 %). For 5 of the 6 possums, percentage correct increased over subsequent sessions. Mica's accuracy, however, remained around 50-60 %. Extending the reinforcement schedule (RI 10 s, Section D, and RI 12.5 s, Section E) had little effect on percentage correct for 5 of the 6 possums, however, percentage correct slowly increased for Mica. Murphy and Kiri both reached criterion level of performance after approximately 30 sessions with the RI 12.5 s, Ebony took 77 sessions while the remaining possums needed 50-55 sessions to reach criterion.

Figure 7.3 shows the data from the individual threshold sessions for each possum. Each panel presents the data from one possum for a session with the first session at the top and the last session at the bottom of the graph. Percentage correct is plotted as a function of

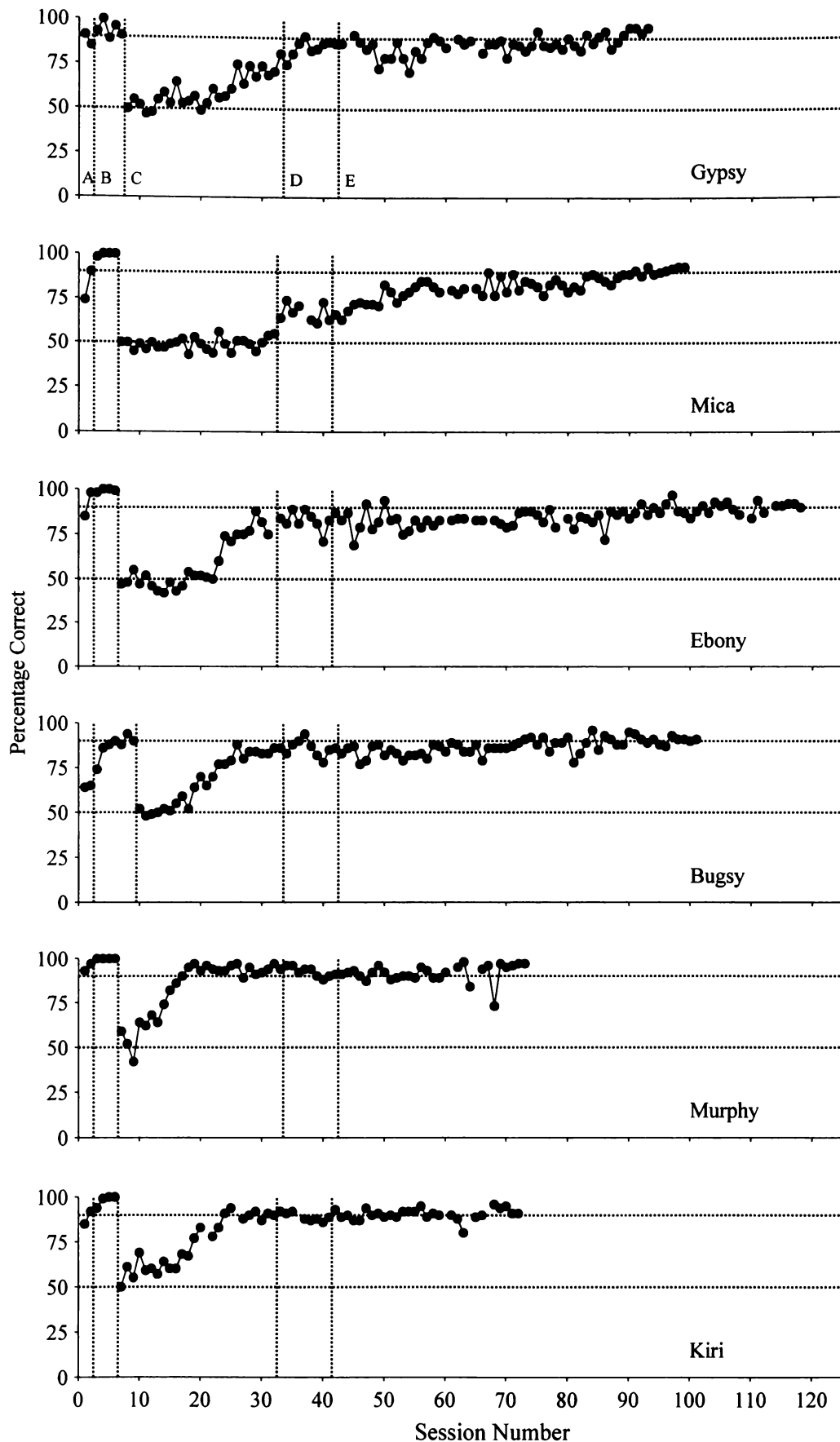


Figure 7.2. Percentage correct gained each session over five training conditions
 A:Lever training, B:Discrimination training, C:Both lights on,
 D & E:Increasing levels of intermittent reinforcement (D:RI10-s,
 E:RI12.5-s).

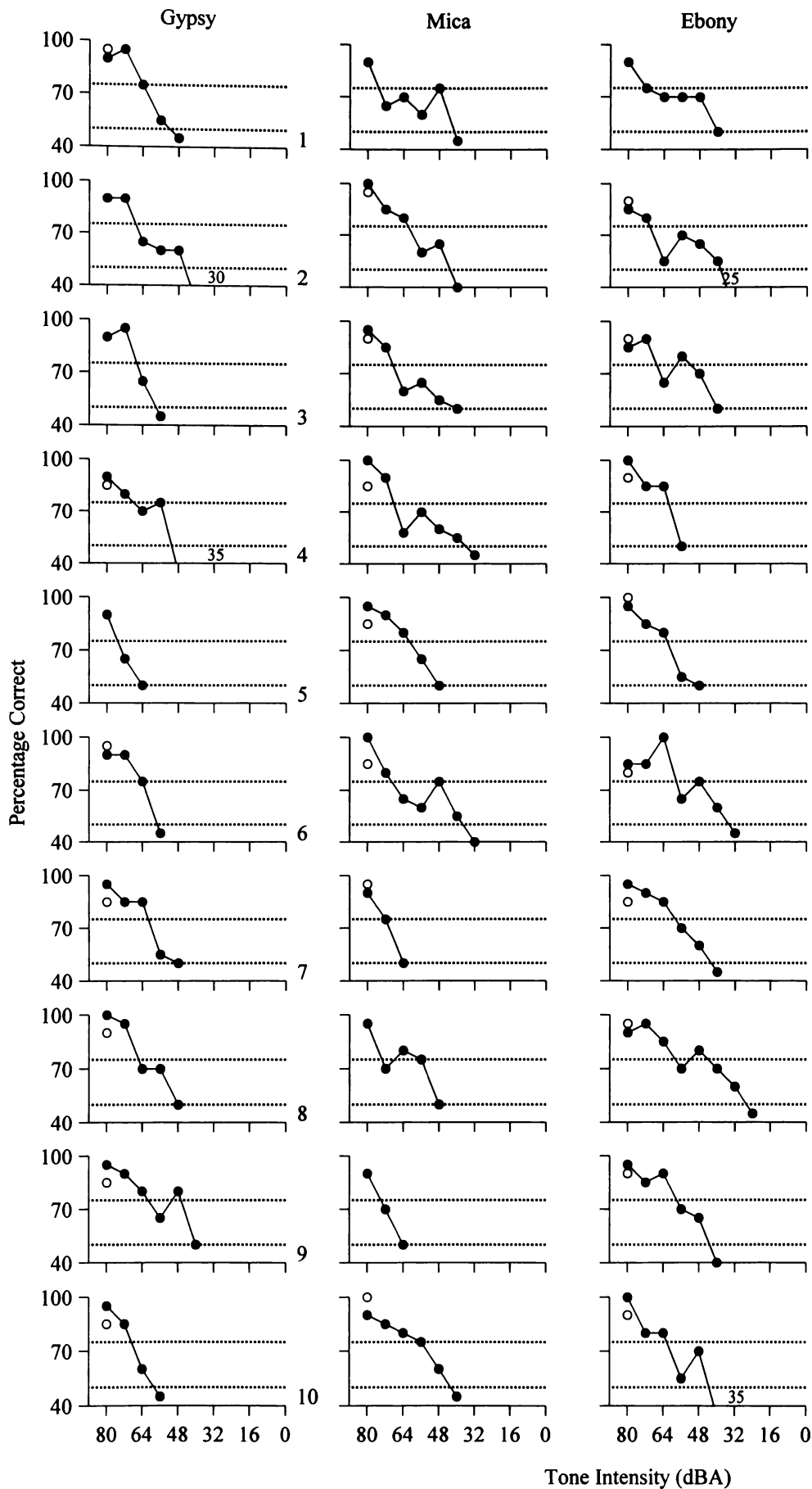


Figure 7.3. Percent correct in each threshold session as a function of tone intensity (dBA).

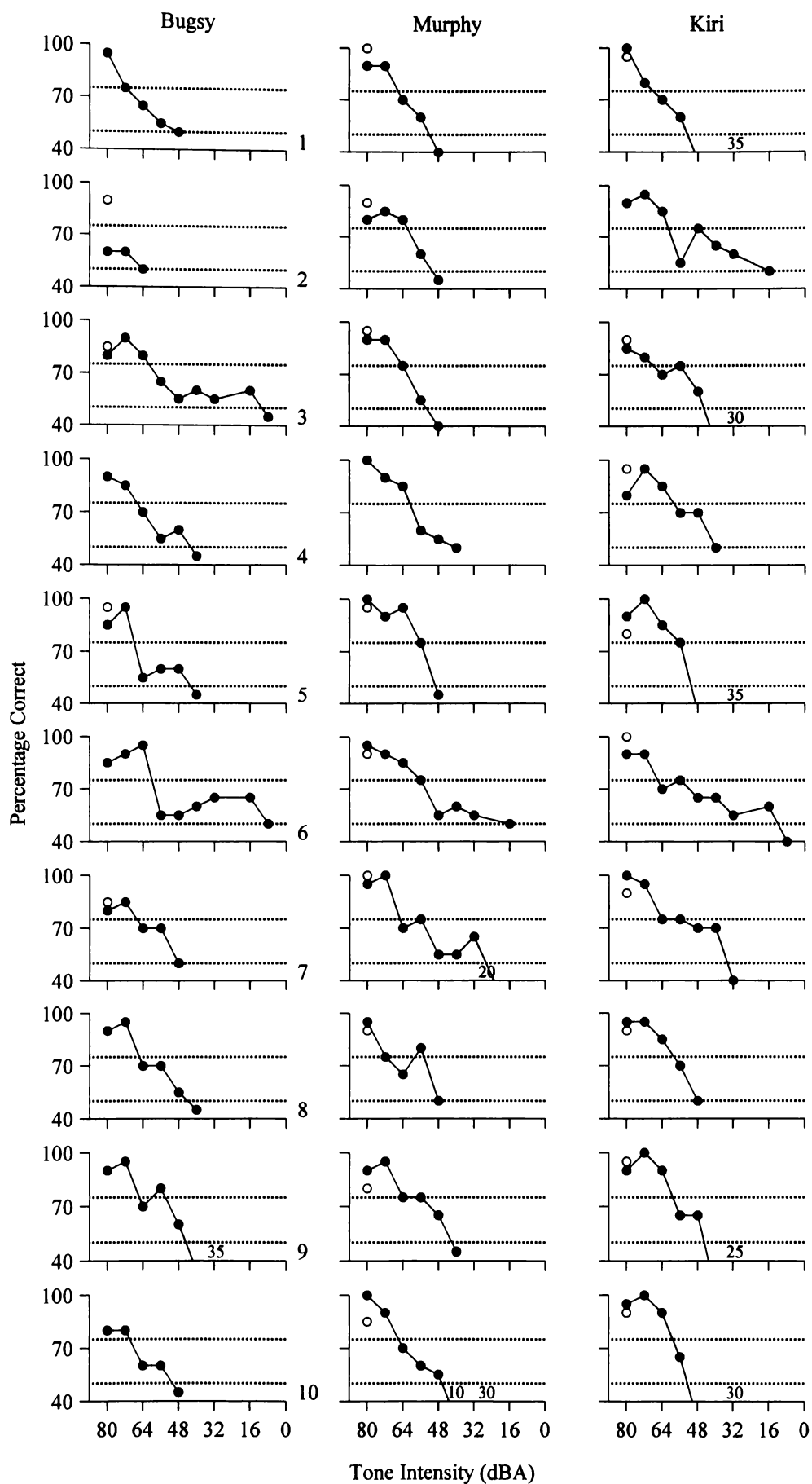


Figure 7.3 cont. Percentage correct in each threshold session as a function of tone intensity (dBA).

the stimulus intensity (dBA) and the horizontal dotted lines are at 50 % and 75 %. The unfilled circle on each graph represents the percentage correct gained on the final block of trials at the training intensity level (80 dBA). In instances where percentage correct over the final block of trials was identical to accuracy over the initial block of trials no unfilled circle can be seen. Where the percentage correct gained fell below 40 % (the lower limit of the y-axis), the percentage correct value for that stimulus is written on the graph. Kiri and Murphy completed 10 threshold sessions. Buggy and Gypsy required one and two extra sessions, respectively, as both ceased responding during earlier sessions. Both Mica and Ebony required two extra threshold sessions as their percentage correct on the final block of trials did not reach criterion (80 %) in two sessions. Analysis of these 'failed' threshold sessions revealed that performance during the rest of the session was essentially identical to those sessions where criterion performance was reached. In all threshold sessions, percentage correct fell below 50 % before all of the programmed intensities had been presented. For all 60 data paths, percentage correct decreased as stimulus intensity (dBA) decreased, although not all data paths show a monotonic decrease. However, there is no apparent change in the pattern of responding across the successive threshold sessions for any of the possums.

The average data from the 10 threshold sessions for each possum, as well as the overall average (across possums) are presented in Figure 7.4. The vertical lines at each data point indicate a range of one standard error either side of the mean, while the unfilled circles indicate the average percentage correct gained during the re-presentation of the training stimulus. As in Figure 7.3, where the percentage correct gained fell below 40 % the percentage correct value for that stimulus is written on the graph. The six data paths are very similar with the data crossing the 75 % line at an average intensity of 64 dBA ($s_x = 3.1$) interpolated from the graphs. There is a gradual decrease in percentage correct across most of the functions, with some fluctuations around 50 % correct at the lower stimulus intensity levels.

Log d (using the Hautus correction) and ROC analysis of the averaged data are presented on the left in Figure 7.5. Log d is plotted as a function of stimulus intensity (dBA) with the log d estimate of performance on the final presentation of the training tone indicated by an unfilled circle, the horizontal lines are at 0.48 and 0 respectively. All six data paths are orderly, decreasing as the sound intensity decreases and all are similar to the average percentage correct analyses. ROC plots are presented on the right of Figure 7.5 with the probability of being correct on a tone-on trial (Hit) plotted as a function of the probability of being incorrect on a tone-off trial (False Alarm) and the data points are joined in the order of presentation. In all six ROC plots, the data points fall to the left of the minor diagonal ranging from the top left corner to below the major diagonal. These points below the major

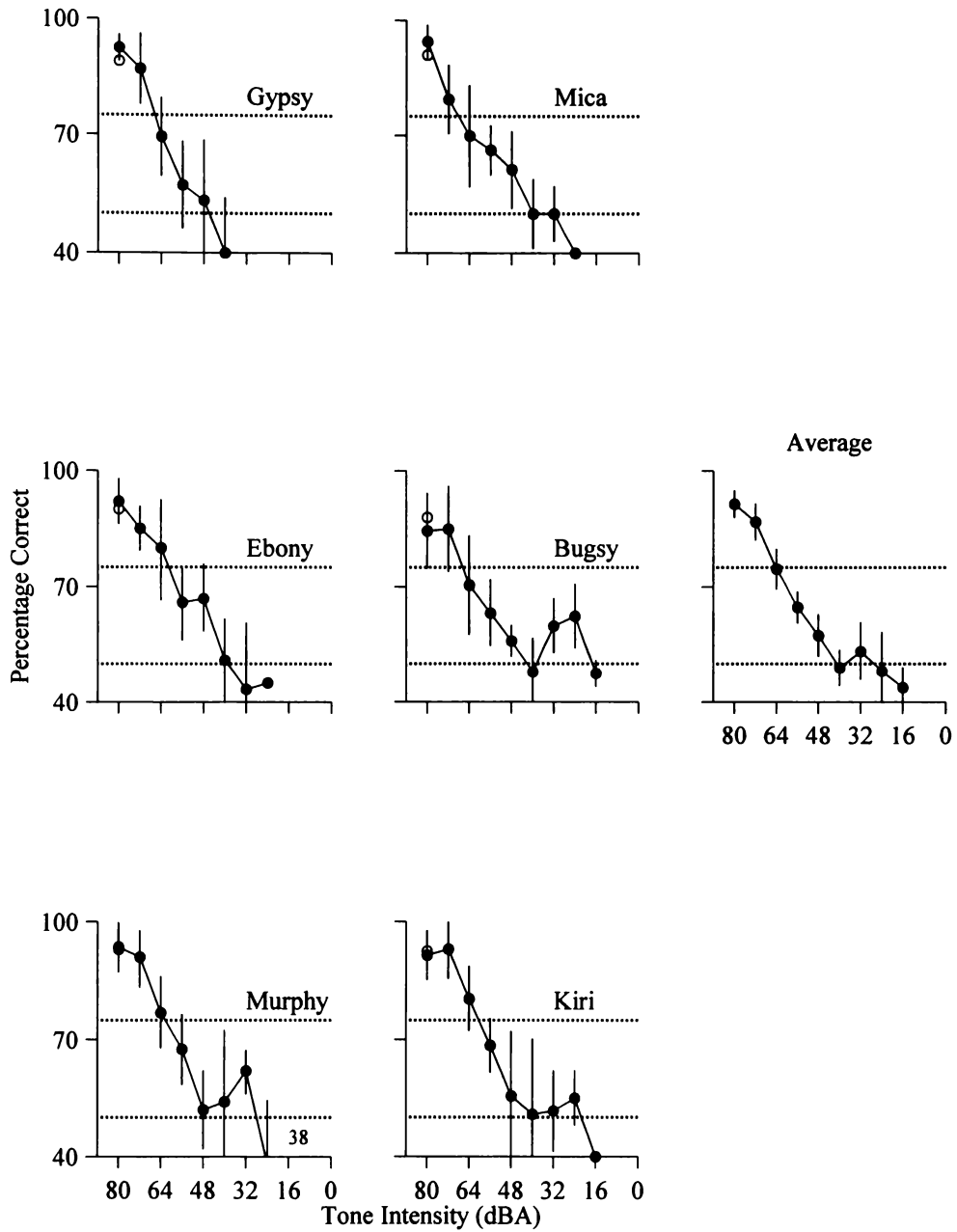


Figure 7.4. Average percentage correct gained over 10 threshold sessions as a function of tone intensity (dBA).

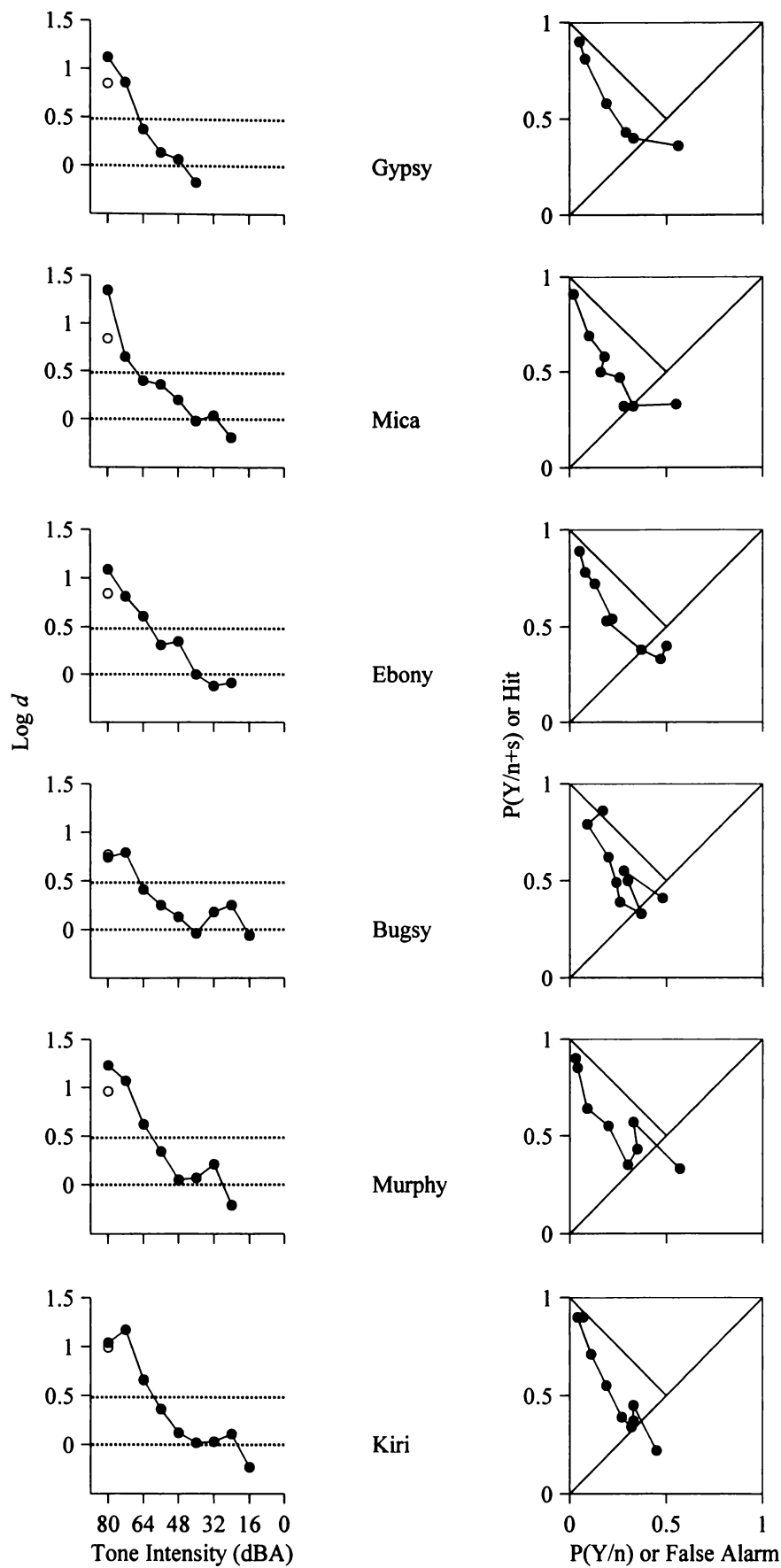


Figure 7.5. Log d and ROC plots of data averaged over 10 threshold sessions.

diagonal indicate worse than chance levels of responding at the lowest intensity (dBA) levels.

Table 7.1 presents the individual threshold estimates using 75 % correct, 50 % correct, a log d of 0.48 (equivalent to 75 % correct) and a log d 0 (equivalent to 50 % correct) as threshold criteria. From this it is apparent that the lowest variability in threshold estimates is derived from using a log d value of 0.48 as threshold and that the resultant estimate of 64.81 dBA is very similar to that interpolated from the figures using 75 % (64.09 dBA) as the threshold criterion.

The average log c values for each possum are presented in Figure 7.6 as functions of stimulus intensity (dBA). For most of the possums, log c is closer to zero at the highest and lowest stimulus intensity levels (dBA) indicating less bias at these points. The remaining data points are all below zero, indicating varying levels of bias towards the left lever (correct lever for tone-off trials). The unfilled circles indicate the log c estimates of bias in the final block of trials at the training intensity (80 dBA). For all six possums, this value is much higher than any of the others and indicates a large bias towards responding on the right lever (correct for tone-on trials).

Sound-attenuated chamber

Data from Kiri's five sessions in the sound-attenuated chamber and the average of these appear in Figure 7.7 as in Figure 7.4. The data paths are very similar across the five sessions with the average data path falling to 75 % at 66 dBA (value interpolated from the figure). The rightmost graph re-presents the average of these sessions with the average data path determined from the threshold data obtained in Kiri's home cage (represented by x) for comparison. As can be seen in this graph, although the two data paths are similar, the data path from the sound-attenuated chamber results in a higher threshold estimate (66 dBA) than found in the home cage (60 dB).

Discussion

One aim of the current experiment was to train possums in a conditional discrimination based on an auditory stimulus. The current data show that the initial discrimination between tone-on (at 80 dB) and tone-off trials was learnt by all 6 possums. Thus, the current method (which was similar to that used in Experiments 1 to 5) proved successful in training the possums on an auditory discrimination. As in Experiment 1, the ease with which this training occurred is in direct contrast with the difficulties reported by other researchers working with possums (e.g., Webster, 1975). Although the scope of the current experiment was limited to training and testing at a single tone (880 Hz), the success of the current experiment suggests that it would be possible using the current methods to determine a full audiogram for the brushtail possum.

Table 7.1
Threshold estimates (dBA) based on different criteria and interpolating directly from the average or log d data paths, as is appropriate.

	75 %	50 %	50 %	Log d of 0.48	Log d of 0
	tone-on trials only				
Gypsy	66.51	46.02	59.65	66.90	45.67
Mica	68.21	40.00	56.00	69.06	40.57
Ebony	61.14	39.00	46.43	62.41	39.79
Bugsy	66.48	42.05	56.4	67.08	41.94
Murphy	62.22	28.00	54.12	62.26	28.00
Kiri	60.00	21.33	53.60	61.16	21.39
Average	64.09	36.07	54.37	64.81	36.23
St. Dev.	3.39	9.39	4.44	3.26	9.40

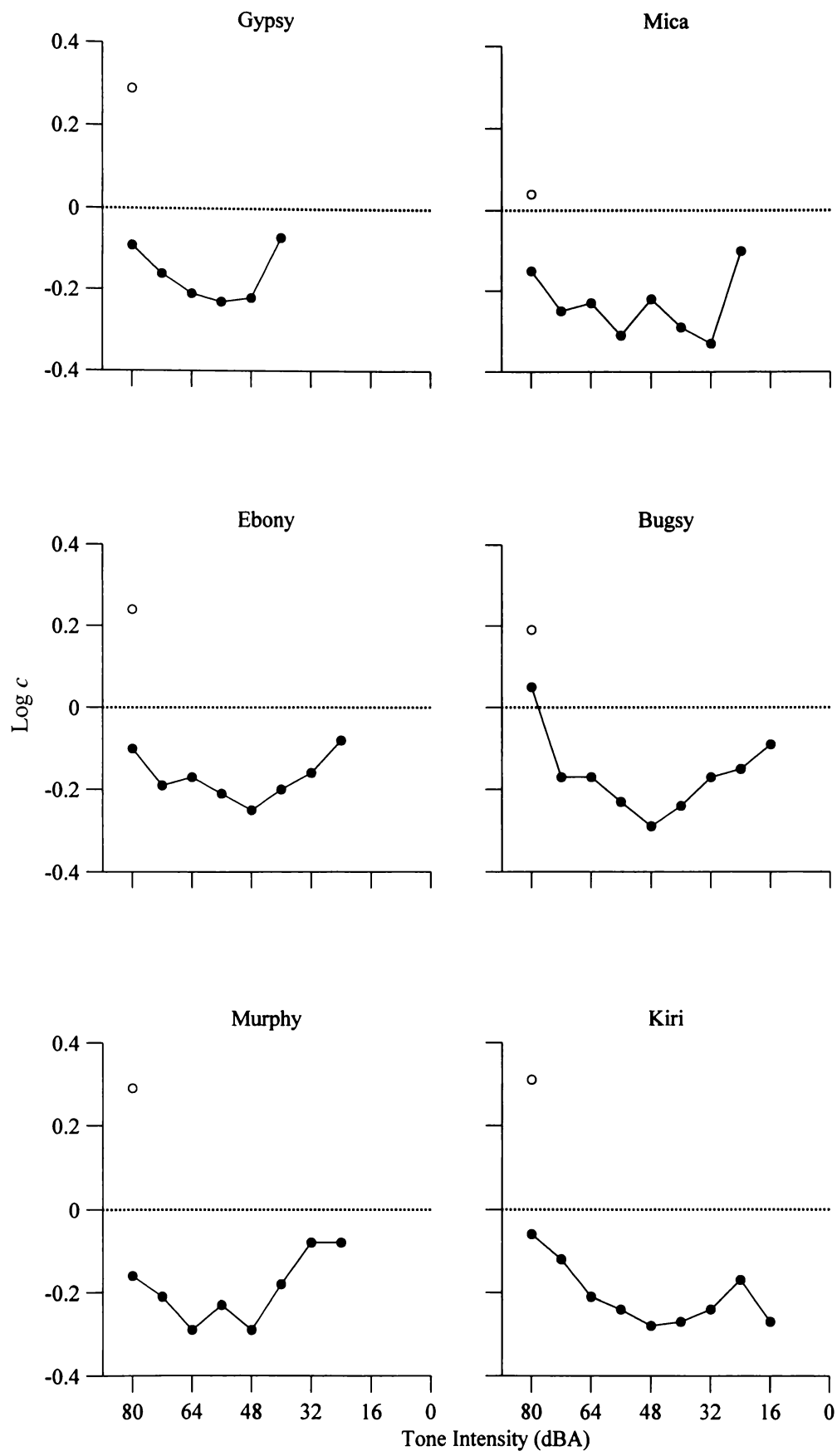


Figure 7.6. Log c analyses (with Hautus correction) of average data from 10 threshold sessions.

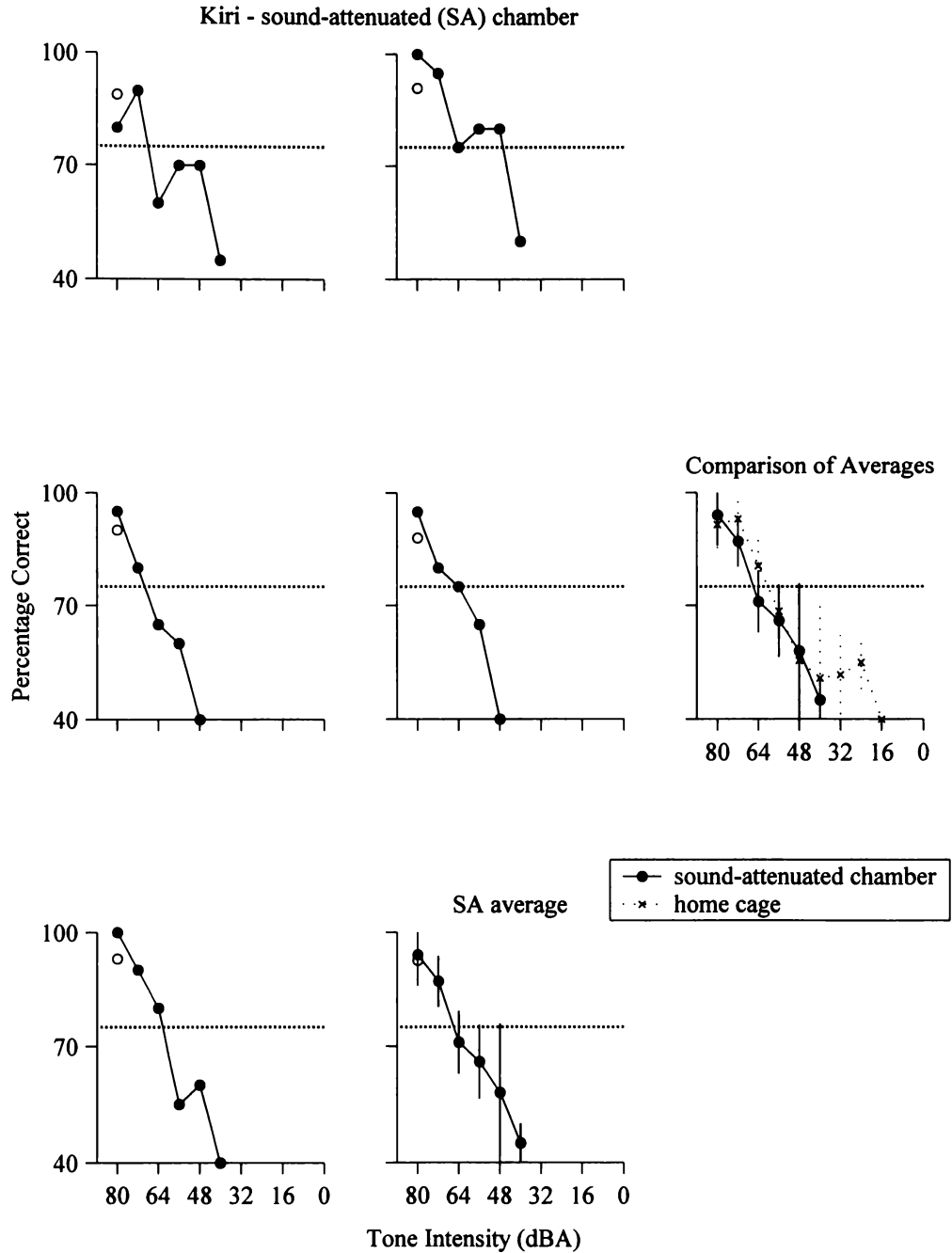


Figure 7.7. Data paths from Kiri's five threshold sessions in the sound-attenuated chamber, averaged and compared to the average function from home threshold sessions.

One concern with the current experiment was the communal nature of the testing environment. As all of the training and subsequent testing sessions were conducted within the communal cage room it is possible that the relatively high threshold estimate for discriminative ability at 880 Hz (average of 64 dBA) reflects an interaction with the level of background noise present in the room. Presenting one possum with threshold sessions within a sound-attenuated chamber tested this possibility. The results of these extra threshold sessions indicate that background noise was unlikely to have adversely affected discriminative performance, thus any further testing of auditory ability could occur solely within the communal environment rather than necessitating isolation in individual chambers.

Another aim of the current experiment was to vary stimulus intensity to determine whether percentage correct changed in a similar way to that found when the flicker rate was varied in the earlier studies. Percentage correct during threshold sessions in this auditory discrimination changed gradually as stimulus intensity reduced, with no sign of rapid change in percentage correct. This is in contrast to the pattern seen in Experiments 4 and 5, suggesting that shape of the data path seen in those experiments may have more to do with possums responding on a CFF discrimination task than possums *per se*. It remains a possibility that the shape of the function found in the flicker experiments is common to visual determination with possums, in order to test this a further visually-based discrimination needs to be tested.

A further difference between the current experiment and the flicker experiments was the presence of bias in the current threshold data. Log *c* analyses (Figure 7.6) indicated the presence of a consistent bias toward the left lever throughout the threshold sessions (for all 6 possums) until the final block of training-intensity trials where it changed to a strong right lever bias. This pattern of biased responding (towards the left lever) is also apparent in the ROC plots (Figure 7.5), a pattern which was not present in the previous flicker experiments. The presence of response bias suggests that the possums are responding differently on the two trial types (i.e., tone-on and tone-off).

DeMello (1989) suggested that performance on the two trial types in a conditional discrimination should be examined separately to determine what pattern of responding underlies the overall percentage correct. She outlined two possible extreme patterns of responding under conditional discriminations with successive presentation of two stimuli as discriminability decreases (with only one stimulus varied). The first pattern was one where accuracy (as measured by percentage correct) remains high on stimulus-absent trials (e.g., tone-off trials) but decreases on stimulus-present trials (e.g., tone-on trials) as the stimulus is decreased along the continuum being investigated. This pattern would result in bias towards the response associated with the stimulus-absent trials. The other extreme pattern of responding was for percentage correct to fall equally on both trial types. In this situation,

there would be little or no response bias and data on ROC plots should fall along the minor diagonal. This would be the pattern of responding predicted under SDT when the subject's decision criterion falls mid-way between the two underlying distributions.

Of the multitude of published, two-stimulus discrimination studies, only three (DeMello et al., 1992; Nuboer et al., 1992 and Terman, 1970) examined accuracy on the two trial types separately. Both DeMello et al. (1992) and Terman (1970) found that percentage correct on stimulus-absent trials was higher than accuracy on stimulus-present trials. In contrast, percentage correct over the two trial types appeared to decrease equally in Nuboer et al.'s (1992) experiment.

Presented in Figure 7.8 are the average percentage correct gained on the two trial types (tone-on and tone-off) separately in the current experiment, as both individual averages and as an overall average from all of the possums' data. This figure indicates that, for all possums, while percentage correct fell on both types of trials as the stimulus decreased in intensity, percentage correct decreased more rapidly on tone-on trials (indicated by filled circles) than on tone-off trials (represented by crosses). This pattern gives a high proportion of left lever responses (correct on tone-off and incorrect tone-on trials) and the bias seen in the log c and the ROC plots.

Thus, the current data are an example of the first pattern suggested by DeMello (1989), although the accuracy differential is not as extreme as it could be. In contrast, as presented in Figure 7.9, when percentage correct is plotted separately for flicker and steady trials in the final successive flicker experiment (Experiment 5) percentage correct decreased equally over both trial types. From this figure, the difference in the underlying pattern of responding between the current experiment and that found in the flicker experiments is readily apparent.

It is unclear what led to these differences in the underlying patterns of responding between the flicker experiments (1 to 5) and the current auditory experiment. It would be possible to argue that the shape of the function seen in the flicker experiments (i.e., the all-or-none function) may have masked any separation in accuracy between the two trial types as responding was either highly accurate or inaccurate with no intermediate values. That is, there may have been an accuracy differential across the trial types in the flicker experiments if intervening stimuli that fell in the descending portion of the function had been present. However as argued earlier, it would be hard to add stimuli between the values presented in the flicker experiment and it seems unlikely that if it were possible that it would change the result. It is clear from the graphs presented in Figure 7.8 that the difference in percentage correct across the two trial types was present for all possums at both the initial stimulus

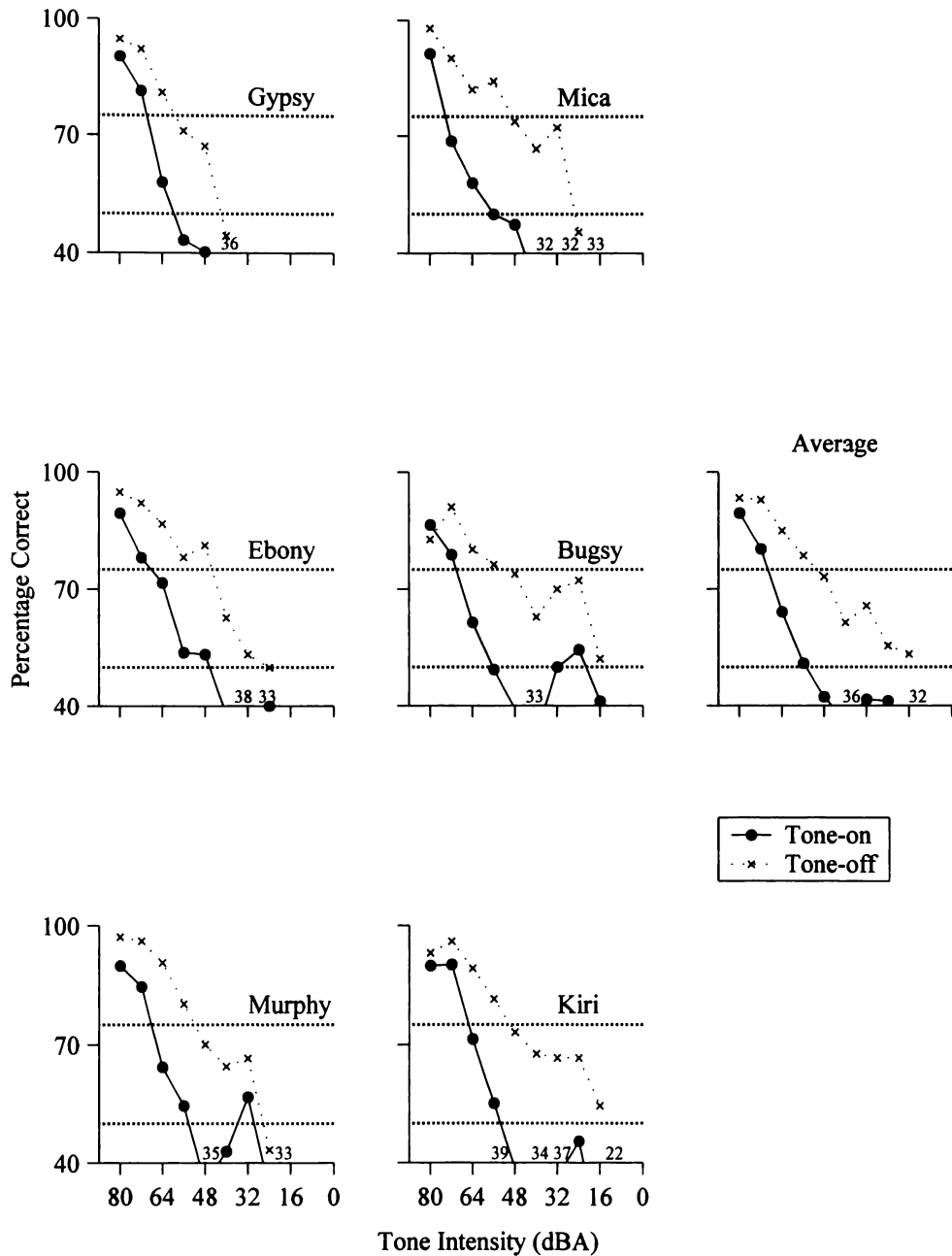


Figure 7.8. Percent correct gained on tone-on and tone-off trials separately presented as individual averages and averaged across possums as a function of tone intensity.

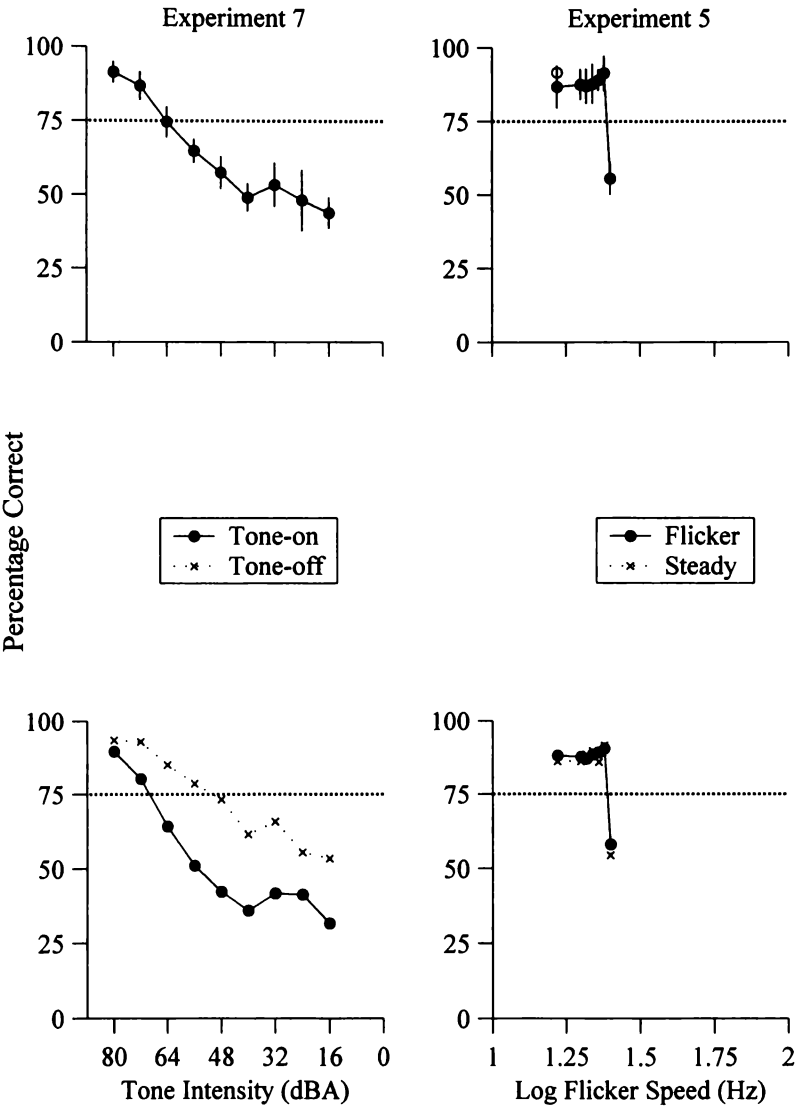


Figure 7.9. Percentage correct presented as an overall average and separated by trial type for Experiments 7 & 5.

(where overall percentage correct was high) and at the final data point (where percentage correct was close to 50 % below threshold) with the auditory stimuli. If only these data points were plotted (i.e., minus the ones for the intervening stimulus values) there would still be a marked difference in percentage correct on the two trial types, that is the data points would still be separated, thus the difference is not due to a lack of intervening steps.

The differences in percentage correct on the two trial types in the current data affects the measures of discriminative ability. For simplicity, consider an experiment in which the stimulus is presented on 50 % of the trials (as in the current experiment). If it were assumed that performance remained correct on the stimulus-absent trials while the stimulus intensity is changed (as in one of DeMello's (1989) suggested patterns of responding), then if the organism were correct on 50 % of the stimulus-present trials (the traditional definition of threshold), then overall percentage correct would be 75 %. However, the situation of estimating threshold is made more complicated if the assumption that behaviour remains accurate on the stimulus-absent is not correct. A value of 75 % overall correct can arise from 50 % correct on stimulus-present trials and 100 % correct on stimulus-absent trials, or 75 % correct on each trial type, or any number of combinations between these limits.

In addition, this overall value will vary if the proportion of stimulus-present trials is not 50 %. To understand this consider 100 trials, 80 of which contain the stimulus and the organism gets 40 (or 50 %) of these correct. If it is 100 % correct on the remaining 20 stimulus-absent trials, it will have been correct on 60 of the 100 or 60 % overall correct. Therefore, the value of overall percentage correct which corresponds to 50 % correct on the stimulus-present trials is not a fixed value and depends, at least, on the proportion of trials which contain the stimulus.

As many experiments have used two stimulus procedures with equal numbers of each trial type, 75% overall accuracy has come to be the standard psychophysical threshold criteria (McKee, Klein & Teller, 1985; Madigan & Williams, 1987; Spong & White, 1971; Treutwein, 1995). However, it is not clear when overall percentage correct is used to determine threshold for experiments using successive presentations of two trial types exactly how this figure has arisen. Two threshold estimates, both based on with 75 % correct overall could have arisen from very different performances. Treutwein (1995), in a review of adaptive psychophysical procedures, presents a hypothetical psychometric function to illustrate the underlying binomial distribution of responses at various levels of percentage correct. While he acknowledges that overall percentage correct depends on the number of trials and the "true" (p. 2505) percentage correct at a given stimulus value he still uses the concept of a pre-selected, fixed threshold criterion based on either overall percentage correct or d' .

While the concept of a fixed sensory threshold is not part of SDT, once d' falls to zero performance has fallen to chance levels, thus when $d' = 0$, overall performance is equal to 50 %. Determining the stimulus value where $d' = 0$ would allow comparisons of discriminative ability to be made across experiments. However, if biased responding occurred (i.e., where accuracy remains high on one trial type while falling on the other) d' would be biased by the relatively higher accuracy on one of the trial types. As d' is calculated by subtracting the z score corresponding to the proportion of False Alarms from the z score corresponding to the proportion of Hits (Stanislaw & Todorov, 1999), response biases would affect this measure of stimulus discriminability just as it does percentage correct measures. To illustrate this, consider a situation where stimulus-present and stimulus-absent trials occur equally. If an organism were 75 % correct on stimulus-absent trials (n) and 75 % correct on stimulus-present trials ($n+s$) (i.e., equally correct on both trial types and 75 % correct overall), the False Alarm rate would be 25 % while the Hit rate would be 75 % and d' would equal 1.34. If, instead, the organism was 100 % correct on stimulus-absent trials (0% False Alarm rate) and only 50 % correct on stimulus-present trials (50% Hit rate), again being 75% correct overall, d' would be incalculable.

As has been shown above for percentage correct and SDT analyses of discriminative performance, behavioural measures (i.e., $\log d$) are also affected by the pattern of responding on the two trial types. As for SDT, there is no concept of a fixed threshold inherent in behavioural theories. The effect of any difference in accuracy between the two trial types on $\log d$ estimates of discriminative ability is complicated. Table 7.2 presents six hypothetical situations with increasing levels of bias towards one response type (using the response matrix presented in Figure 0.2). In this table, S_1 ($n+s$) and S_2 (n) denote the two stimuli and R_1 (correct response on S_1 trials) and R_2 (correct response on S_2 trials) represent the two possible responses. Increasing bias towards making a R_2 response would result in higher levels of accuracy on S_2 trials relative to S_1 trials. The final example in the table is a situation where performance on stimulus-absent (S_2) trials is highly accurate (100 %) while performance on stimulus-present trials (S_1) has fallen to 50 % correct. Overall accuracy in all of these examples is 75 %, with 20 trials of each stimulus. It can be seen from this table that the $\log d$ value increases as the bias towards one alternative increases, until $\log d$ is incalculable in the final example (assuming no use of a Hautus correction). Also presented in this table is the d' estimate for each of the situations. Similarly to $\log d$, d' estimates increase as bias towards one response type increases.

As a side issue, overall percentage correct (and d' and $\log d$) measures will also be affected by the relative occurrence of each trial type. While the relative occurrence of each trial type (or Signal Presentation Probability) was kept equal throughout the current series of experiments, other studies (both CFF and auditory) have used varying numbers of stimulus

Table 7.2
Estimates of discriminative performance over hypothetical situations of changing response bias but equal overall accuracy.

		Stimulus	Response		Overall	Accuracy on	Accuracy on	Log <i>d</i>	<i>d'</i>
		Type	Type		Accuracy	<i>S</i> ₁ trials	<i>S</i> ₂ trials	Estimate	Estimate
			<i>R</i> ₁	<i>R</i> ₂		(<i>R</i> ₁ correct)	(<i>R</i> ₂ correct)		
Equal bias	<i>S</i> _{1 (n+s)}		15	5	75 %	75 %	75 %	0.48	1.34
	<i>S</i> _{2 (n)}		5	15					
Increasing bias towards <i>R</i> ₂ responses	<i>S</i> _{1 (n+s)}		14	6	75 %	70 %	80 %	0.49	1.36
	<i>S</i> _{2 (n)}		4	16					
	<i>S</i> _{1 (n+s)}		13	7	75 %	65 %	85 %	0.51	1.43
	<i>S</i> _{2 (n)}		3	17					
	<i>S</i> _{1 (n+s)}		12	8	75 %	60 %	90 %	0.57	1.53
	<i>S</i> _{2 (n)}		2	18					
	<i>S</i> _{1 (n+s)}		11	9	75 %	55 %	95 %	0.68	1.76
	<i>S</i> _{2 (n)}		1	19					
	<i>S</i> _{1 (n+s)}		10	10	75 %	50 %	100 %	∞	∞
	<i>S</i> _{2 (n)}		0	20					

absent trials, often termed 'catch trials' (e.g., Awbrey et al., 1988; Szymanski et al., 1999), which further complicates comparisons between results from different studies.

Various $\log d$ values have been reported as measures of discriminative ability. For example, DeMello et al. (1992) took as one measure of threshold ability, the stimulus that resulted in a $\log d$ value of 0.48; while Temple et al. (1984) used only the stimulus that resulted in a $\log d$ value of 0 as threshold. In both studies, the authors equated these $\log d$ values to overall percentage correct measures (75 and 50 % respectively). However, whether this was appropriate depends on the pattern of responding across the stimulus-absent and stimulus-present trials. While Temple et al. (1984) do not report the underlying pattern of responding over the two trial types, DeMello et al. (1992) do, and the figures they present show that percentage correct generally decreased more quickly on stimulus-present (in this case grating) trials than on stimulus-absent (grey) trials as stimulus discriminability reduced. The accuracy differential reported by DeMello et al. is not as great or consistent as that seen in the current experiment, but is closer to the current auditory data than the pattern seen in the flicker experiments.

DeMello et al. (1992) suggest that a greater disparity between percentage correct on the two trial types will be found when uncontrolled reinforcement procedures are used. That is, if the relative reinforcement rate is not kept equal across the two trial types one may expect a greater bias, potentially resulting in a pattern of highly accurate responding during stimulus-absent trials and decreasing accuracy on stimulus-present trials (DeMello, 1989). While the current data do show a greater degree of difference in percentage correct over the two trial types than DeMello et al. (1992) report, a controlled reinforcement procedure was in place. This suggests that the reduction in stimulus intensity also affected performance on stimulus-absent (tone-off) trials. Interestingly, once a detectable tone was reinstated at the end of the threshold session, performance on tone-on trials returned to the high level of accuracy seen at the beginning of the session, while performance on tone-off trials increased but not to its previous levels resulting in a change in response bias. It would appear that control by the tone-off stimulus was disrupted by the experience of the quieter tones.

One way of viewing this may be that once the intensity of the tone was decreased to threshold levels, the possums would experience very faint tone-on trials to which they would respond as if it were a tone-off trial. These responses would not result in the reinforcer. As the current experiment utilised a controlled-reinforcement procedure, once a reinforcer had been scheduled for a correct tone-on response, a reinforcer could not be gained for any other type of response until this reinforcer had been delivered. Once the tone intensity was reduced to threshold levels tone-on trials were indistinguishable (by definition) from tone-off trials. Thus, it is possible that the animal may have repeated experiences of non-reinforced tone-off responses (on both true tone-off and faint tone-on trials). This could

result in the possums making a 'tone-on' response in the presence of an apparently 'tone-off' stimulus that may eventually be reinforced, thus reducing control by tone-off stimulus.

This gradual reduction of control (within a session) may not have occurred to the same extent within the flicker threshold sessions due to the 'all-or-none' nature of the discrimination. That is, during the flicker vs. steady threshold sessions the possums would not have had prolonged exposure to near threshold stimuli as the overall functions show highly accurate performance with little or no response bias continuing until percentage correct (on both trial types) drops below threshold (using a 75 % criterion).

If such exposure to near threshold stimuli does interfere with performance on stimulus-absent trials it should be possible to deliberately reduce percentage correct on tone-off trials by increasing exposure to near- or sub-threshold tone-on trials. A further experiment deliberately presented blocks of sub-threshold tone-on trials where reinforcement was only available for correct tone-on responses. The increased experience of sub-threshold tone-on trials should affect performance on subsequent tone-off trials.

In conclusion possums were successfully trained to perform a conditional discrimination between the presence and absence of an 880 Hz tone. From the pattern of responding, it was apparent that the abruptly decreasing function found in the flicker experiments is not a finding common to all threshold determinations in the possum. Interestingly the pattern of responding underlying overall performance in the current experiment was very different from that found in the flicker experiments. While it remains unclear what led to this difference a further, visually-based, threshold determination would assist in resolving whether the lack of parity is due to modality variations.

Experiment 8

The pattern of responding on the two trial types in the previous experiment (Experiment 7) using auditory stimuli was very different from that seen using flickering stimuli. Both patterns were stable across repeated threshold determinations and across individuals.

It was suggested in Experiment 7 that the decrease in percentage correct on stimulus-absent trials (i.e., tone-off trials) may have been due to experience of sub-threshold stimulus-present trials during the threshold determination. Such trials may result in food delivery for apparently incorrect responses.

The aim of the following experiment was to see if experiencing blocks of sub-threshold trials would lead to a deterioration of performance on blocks of true stimulus-absent trials. In this experiment blocks of each type of trial (i.e., stimulus-present and stimulus-absent) were imbedded in a series of ordinary training trials (mixed tone-on and tone-off trials as in Experiment 7) and percentage correct over repeated presentations of these blocks of trials was examined. Throughout the experiment reinforcement continued to be delivered for the defined correct responses as in Experiment 7. In the first condition, a block of 10 tone-off (stimulus-absent) trials was followed by a block of 10 tone-on (stimulus-present) trials with the tone at 40 dB. This intensity was found to be below threshold for all of the possums in Experiment 7 and as such, these sub-threshold tone-on trials should appear to the possums as 'tone-off' trials. Reinforcers were available for correct responses on tone-on trials. Thus for the possum, reinforcers in this situation could be gained for apparently incorrect responses on what might appear to be a tone-off trial (as might have occurred during threshold determinations as tone intensity decreased). The second condition was essentially identical to the first but with the block of 40 dB tone-on trials presented before the 10 tone-off trials. In the third condition, 10 tone-on trials at 0 dB were followed by 10 tone-off trials, with this pattern reversed for the fourth condition. It was expected that this experience of reinforcement for apparently incorrect responses would have an effect on percentage correct on subsequent trials.

Method

Subjects

Three possums from Experiment 7 participated in this experiment, Kiri and Buggy completed all four conditions and Ebony completed the last two conditions. Ebony began responding reliably throughout a session at the time Kiri and Buggy had completed the first two conditions.

Apparatus

The apparatus was the same as in Experiment 7.

Procedure

The basic procedure was identical to that of training sessions in Experiment 7 (i.e., both side-lights lit and intermittent reinforcement) with tone-on trials at 80 dBA. Each possum was required to reach criterion level of performance (i.e., five consecutive sessions above 90 % correct) on these training sessions before beginning the first condition. At least one training session occurred between test sessions to maintain criterion level of performance.

Condition 1 (tone-off first, 40 dB). A test session began with 40 mixed tone-on and tone-off trials with the stimulus intensity on tone-on trials set at 80 dBA. Reinforcers were available for all correct responses during these 40 trials as they were during the training sessions. At the completion of these trials, a block of 10 tone-off trials was presented. Reinforcers during these trials were available on a leaner intermittent schedule (RI 30 s) for correct tone-off responses (i.e., a left-lever press) as a high number of reinforcers could potentially be gained for exclusive responding. Following this, a block of 10 tone-on trials (at 40 dB) were presented, reinforcers during this block of trials were available (RI 30 s) for correct tone-on responses (i.e., a right-lever press). After these two 10 trial blocks, a further 40 mixed standard trials were presented. If the total number of reinforcers gained at this point in the session was fewer than 80, a further series of the 10 tone-off and 10 tone-on trials occurred. This pattern was repeated until more than 80 reinforcers had been delivered (following a block of 40 'normal' trials), or until 60-min had elapsed, whichever came first, at this point the session was terminated. An aborted trial was recorded whenever 60 s had elapsed between a central lever press (which initiated a trial) and a side-lever response. Kiri and Bugsy each completed three sessions in this condition, however Bugsy's second session was not included in any analyses as percentage correct over the mixed tone-on and tone-off trials was consistently below 80 %.

Condition 2 (tone-on first, 40 dB) This condition was identical to the first condition, except that the block of 10 tone-on trials (at 40 dB) occurred before the 10 tone-off trials. Kiri and Bugsy each completed three sessions in this condition.

Condition 3 (tone-on first, 0 dB) This condition was identical to the second condition except that intensity of the block of 10 test tone-on trials was 0 dB. Kiri, Bugsy and Ebony each completed three sessions in this condition.

Condition 4 (tone-off first, 0 dB) This condition was identical to the third condition, except that the block of 10 test tone-off trials occurred before the 10 tone-on trials (at 0 dB). Kiri, Bugsy and Ebony each completed three sessions in this condition.

Results

Figure 8.1 shows the average percentage correct (across all sessions) gained during during normal tone-on (represented by a filled circle), tone-off (represented by a cross), test tone-on (represented by an unfilled circle) and test tone-off (represented by a plus) trials. Data from individual sessions were consistent with the exception of the discarded second session of Buggy's in Condition 1. It is apparent that during Condition 1, experience of test tone-on trials (at 40 dBA) had no effect on percentage correct except during trials with those stimuli (i.e., test tone-on trials).

Both Conditions 2 and 3 presented trials with the tone at 40 and 0 dBA respectively before 10 tone-off trials and in all instances average percentage correct on the test tone-off (represented by a plus) trials was lower than that obtained during the normal tone-off (represented by a cross) and tone-on (represented by a filled circle) trials. Condition 4 replicated the first condition with test tone-on trials (with tone set at 0 dBA) presented after 10 tone-off trials. Kiri's average data show a similar pattern to that seen in the first condition with percentage correct remaining high on all other trials except the test tone-on (unfilled circles) trials. For the other two possums however, percentage correct was lower on the test tone-off trials (plus) than on the normal tone-off (cross) and tone-on (filled circles) trials.

Although it can not be seen in these averaged graphs, percentage correct on normal tone-on (i.e., where tone was set at 80 dBA) trials was consistently high even immediately after blocks of test trials where accuracy had fallen to 50 % or less. Percentage correct gained on normal tone-off (cross) trials was also higher than that gained during the blocks of test tone-off (plus) trials for most sessions.

Discussion

The data from the current experiment show that experience of sub-threshold tone-on trials did affect subsequent performance on tone-off trials to some degree, but only when the tone-off trials occurred in a block immediately following the sub-threshold tone-on trials (Conditions 2 and 3). Any decrement in percentage correct on the test trials (both tone-on and tone-off) did not carry over to the 40 mixed trials that occurred between blocks of test trials with percentage correct on normal tone-on trials (tone at 80 dBA) in particular returning in most cases to 100 % correct. This suggests that any effect of experiencing sub-threshold tone-on trials was transient and easily disrupted as soon as the test stimuli returned to training levels (i.e., intensity of tone-on trials returned to 80 dB).

Thus, while the current data lend some support to the suggestion that the decrement in percentage correct seen in Experiment 7 during the stimulus-absent trials may be due to experience of sub-threshold stimulus-present trials, the effect was not as large (or pervasive)

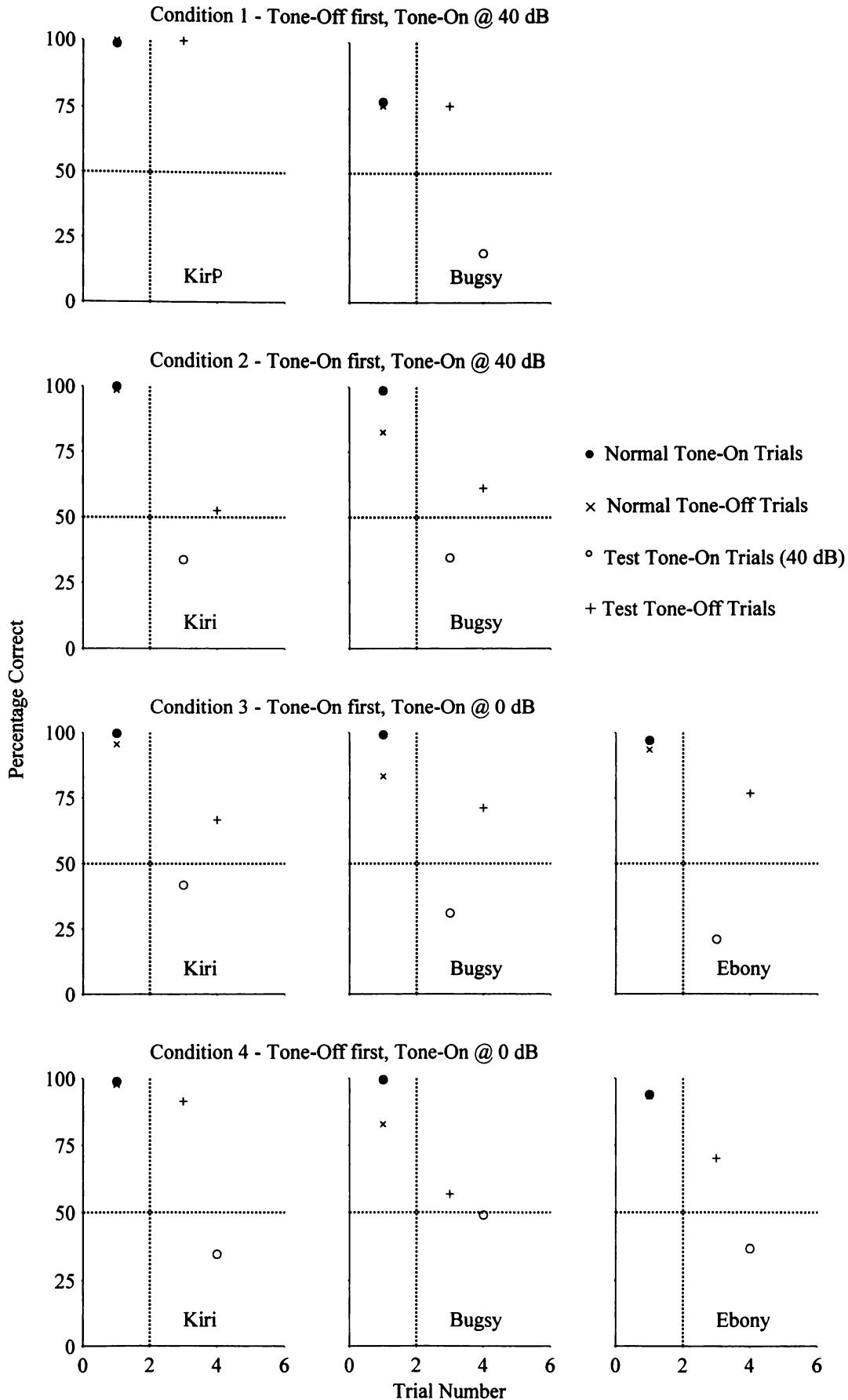


Figure 8.1. Percentage correct gained over normal and test trials averaged across all sessions within each condition.

as anticipated. It was expected that there would be some decrease in percentage correct on both the normal tone-on and tone-off trials following the blocks of test trials. It is possible that a greater effect may occur if the blocks of test trials were larger (e.g., 20 trials rather than 10) however it may prove difficult to maintain responding throughout longer blocks of test trials. This partial effect may however explain why the pattern of differential accuracy over the two trial types was not as extreme as that suggested by DeMello (1989) (i.e., percentage correct remaining high across all levels of stimulus intensity for stimulus-absent trials while decreasing on stimulus-present trials).

It is still unclear, what led to the difference in the underlying pattern of responding across stimulus-absent and stimulus-present trials in the flicker and auditory experiments. One possibility is that the pattern of responding found in the flicker experiments is linked with the all-or-none nature of the threshold function found. Testing another visual discrimination to determine whether this type of function is common to visual threshold determinations with possums will also allow further comparisons between the underlying patterns of responding on another two-stimulus conditional discrimination.

Experiment 9

The successive-presentation flicker discrimination experiments, once luminance was equalised (Experiments 4 and 5), produced relatively all-or-none CFF functions despite contrary findings in the literature for other species (e.g., Loop & Berkley, 1975). Changing to a simultaneous stimulus presentation method with the flickering stimuli (Experiment 6) did not result in a change in the overall shape of the function found. However, when another modality was tested (auditory, Experiment 7) a more gradual psychophysical curve was derived. From these experiments it was concluded that the unusual CFF functions found in Experiments 5 and 6 might be uniquely related to CFF determinations with the possum. It is possible however, that these functions may be the result of the use of visual stimuli with possums.

In the current experiment an alternative, visually-based (bright vs. dim), conditional discrimination was used, and the threshold function was determined using the same methodology as in previous threshold determinations (i.e., block-wise method of limits). However, the current experiment determines a difference threshold (the minimum level of detectable disparity between two stimuli) rather than an absolute threshold (the minimum detectable intensity of a stimulus) as determined in the previous experiments. The current discrimination, (i.e., between a bright and a dim stimulus) was chosen due to the training the possums had already received when learning to make effective lever-presses. That is, during training the possums were taught to respond when the light above the lever was lit, any presses made while the light was not lit were ineffective.

This prior learning may have made it difficult to establish a conditional discrimination between a lit and an unlit stimulus light. There is no reason to assume that there should be any difference in shape between a function derived for a difference threshold and one derived for an absolute threshold (Stebbins, 1970) and as such, the easier bright vs. dim stimulus discrimination was used here. Previous studies presenting results of brightness discriminations (e.g., Boakes, 1969; Macuda & Timney, 1999), suggest that the function derived from this experiment should be one of steadily decreasing accuracy as discriminability is reduced thus resulting in a function similar to that of the auditory experiment (Experiment 7).

A pilot study using the same filament bulbs as in the earlier flicker studies resulted in the successful training of six possums to make the required discrimination between bright ($2.4 \log \text{cd/m}^2$) and dim lights ($x.x \log \text{cd/m}^2$). However, it proved impossible to gain the degree of control required over the luminance of the filament bulbs for threshold testing and they were replaced with Light Emitting Diodes (LEDs). Unfortunately, while it was possible to gain the required level of control over the luminance of the LEDs, they were

substantially dimmer than the filament bulbs, despite being the brightest LEDs available at the time. This meant that the highest possible luminance of the LEDs ($1.0 \log \text{cd/m}^2$) was well below the luminance of the filament bulbs ($2.4 \log \text{cd/m}^2$). Following this change of stimuli, a number of difficulties were encountered in training the possums to the required level of performance with these new stimuli and the following experiment details results from the two possums that reached criterion level of performance (five consecutive sessions above 90 %).

Method

Subjects

Two naïve possums (Nosey and Ernie, both female and approximately five and two years of age respectively) reached criterion level of performance following training and thus received threshold sessions.

Apparatus

As for all of the experiments an individual response panel was permanently attached to each possums' home cage with the same dimensions as described in Experiment 1 except that the two stimulus lights were replaced by a central LED.

In order to produce differing levels of brightness a device was designed by Rob Bakker (Psychology Technician, University of Waikato) similar to that used by Allan and Matthews (1991). Each LED was controlled by a separate device which made the LED flicker at 400 Hz (well above the CFF determined in the earlier experiments) with a square wave pulse. By altering the length of a pulse within one cycle ($1/400^{\text{th}}$ s), 255 discrete brightness levels could be produced, ranging from $1.0 \log \text{cd/m}^2$ to $0.2 \log \text{cd/m}^2$.

Procedure

Each session began with two levers being inserted through the holes in the response panels. Daily sessions started approximately one hour into the dark phase of the light/dark cycle. During the 12-hr dark phase of the cycle no lights were on in the housing room, except during experimental sessions when three red light bulbs (60 W) were on. For the light phase (also 12 hr) three standard 100-W white bulbs were used to illuminate the room. Nosey and Ernie were trained to eat from the magazine and to press levers as outlined in Experiment 1 before beginning discrimination training.

Discrimination training. During this training phase the LED was either at full brightness ($1.0 \log \text{cd/m}^2$) or at the lowest level of brightness possible ($0.2 \log \text{cd/m}^2$). During a bright stimulus trial a response on the right lever was deemed correct, while a response on the left lever was correct during a dim stimulus trial. In both instances, a correct response resulted in 2-s access to the magazine and a beep and a 3-s ITI. For both trial types responding on the incorrect lever resulted in a 2-s blackout period followed by a 3-s ITI.

Bright and dim stimulus trials were pseudo-randomly scheduled using a version of the Gellerman (1933) series as in previous experiments. Reinforcement was delivered for correct responses under a RI 1-s scheduled (controlled for trial type) until accuracy of responding was above 90 % correct. Once Ernie reached this level the RI schedule requirement was gradually increased to RI 12.5 s as in the previous experiments.

Nosey required extra training as she continued to respond at chance levels after 29 sessions. Observations during training sessions revealed that she repeatedly made responses that were not of sufficient force to depress the lever whereupon she would swap and respond on the other lever. Which lever was pressed first did not appear to relate to the stimulus present. Following this observation Nosey was presented with sessions where reinforcement was delivered on a Fixed Ratio (FR) 1 for responses on the left lever only, and during these sessions the stimulus light was lit at $0.2 \log \text{ cd/m}^2$ (dim stimulus, left-lever correct). These sessions stopped once Nosey made 100 correct left-lever responses and no right-lever responses during the session (requiring a total of five sessions). The contingencies were then reversed with the light lit at $1.0 \log \text{ cd/m}^2$ (bright stimulus, right-lever correct) and only effective right-lever presses gaining reinforcement on a FR 1. Again, these sessions stopped once Nosey made 100 correct right-lever responses with no left-lever responses in the session. Nosey was then returned to the normal brightness discrimination training sessions with reinforcement intermittent on a RI 1-s schedule. Nosey remained on RI 1 s for the remainder of the experiment.

Threshold sessions began once a possum achieved the criterion of five consecutive sessions with percentage correct responding at 90 % or better.

Threshold determination. To ensure even, measurable, decreases in luminance, only a small number of stimulus steps were used in the current experiment. Due to this, 40 trials could be presented at each brightness level compared to the 20 trials presented at each stimulus level in the previous experiments. Each threshold-trial session began with a block of 40 trials presenting the training level of brightness disparity. Approximately equal numbers of bright ($1.0 \log \text{ cd/m}^2$) and dim ($0.2 \log \text{ cd/m}^2$) stimulus trials occurred within each block of trials, arranged pseudo-randomly using a version of the Gellerman (1933) series. The intensity of the bright stimulus trials was then decreased along the following series; 0.8, 0.6, 0.4, $0.2 \log \text{ cd/m}^2$ with blocks of 40 trials at each intensity level. As in the earlier successive experiments, if the percentage of correct responses at the completion of a set of 40 trials was 50 % or above, the next intensity level in the series was presented. As soon as the percentage of responses correct fell to below 50 % for a set of 40 trials, or all of the scheduled steps had been presented, the descending series was stopped and there were a further 40 trials at the training intensity level ($1.0 \log \text{ cd/m}^2$). After this, the session was

terminated. Consequences for correct and incorrect responses were identical to those in the training sessions throughout the threshold session.

As in the previous experiments, each threshold session was followed by a training session and further threshold sessions only occurred if percentage correct during the previous training session was 90 % or greater. Five threshold sessions were presented.

Results

Presented in Figure 9.1 are the data from the five threshold sessions as well as the data averaged over these for each possum. Data from successive sessions are presented down the page. Percentage correct is plotted as a function of luminance level, with the horizontal lines indicating 75 and 50 % correct. The percentage correct gained during the final re-presentation of the training brightness is shown by an unfilled circle when it was over 80 % correct and by a plus when it was less than 80 % (these sessions where percentage correct on the final block of trials was below 80 % were not included in any further analyses). In situations where neither a plus or an unfilled circle can be seen, accuracy over the final block of trials was identical to accuracy on the first block of trials. All 10 of the data paths are similar with percentage correct tending to decrease as luminance decreased after an initial increase for five of the 10 graphs. The two bottom graphs in Figure 9.1 present the average of the five threshold sessions for each possum, with the vertical lines at each data point representing one standard error either side of the mean value. These average data paths represent the individual session data well and cross the 75 % line at 0.39 and 0.37 log cd/m² for Nosey and Ernie respectively (values interpolated from the average functions).

The top pair of graphs in Figure 9.2 present the average percentage correct gained on each of the trial types separately as a function of stimulus intensity, where percentage correct fell below 40 % the value of that point is printed on the graph. For Nosey, there is a marked difference between the average percentage correct gained on dim stimulus (represented by crosses) and bright stimulus (represented by filled circles) trials. Dim stimulus trials resulting in consistently higher percentage correct values. The degree of disparity between percentage correct increased as stimulus discriminability decreased. In contrast, Ernie's data show little initial difference in percentage correct over the two trial types however, this disparity increased when stimulus discriminability decreased and with percentage correct on dim stimulus trials (crosses) being higher than that of the associated bright stimulus trials (filled circles).

Log *c* estimates are presented in the second pair of graphs (Figure 9.2), plotted as functions of stimulus intensity. From these graphs it is apparent that there were differing levels of bias across all stimulus intensity levels. For Nosey, response bias towards the left-lever (the correct response on dim stimulus trials) increased as the stimuli got less

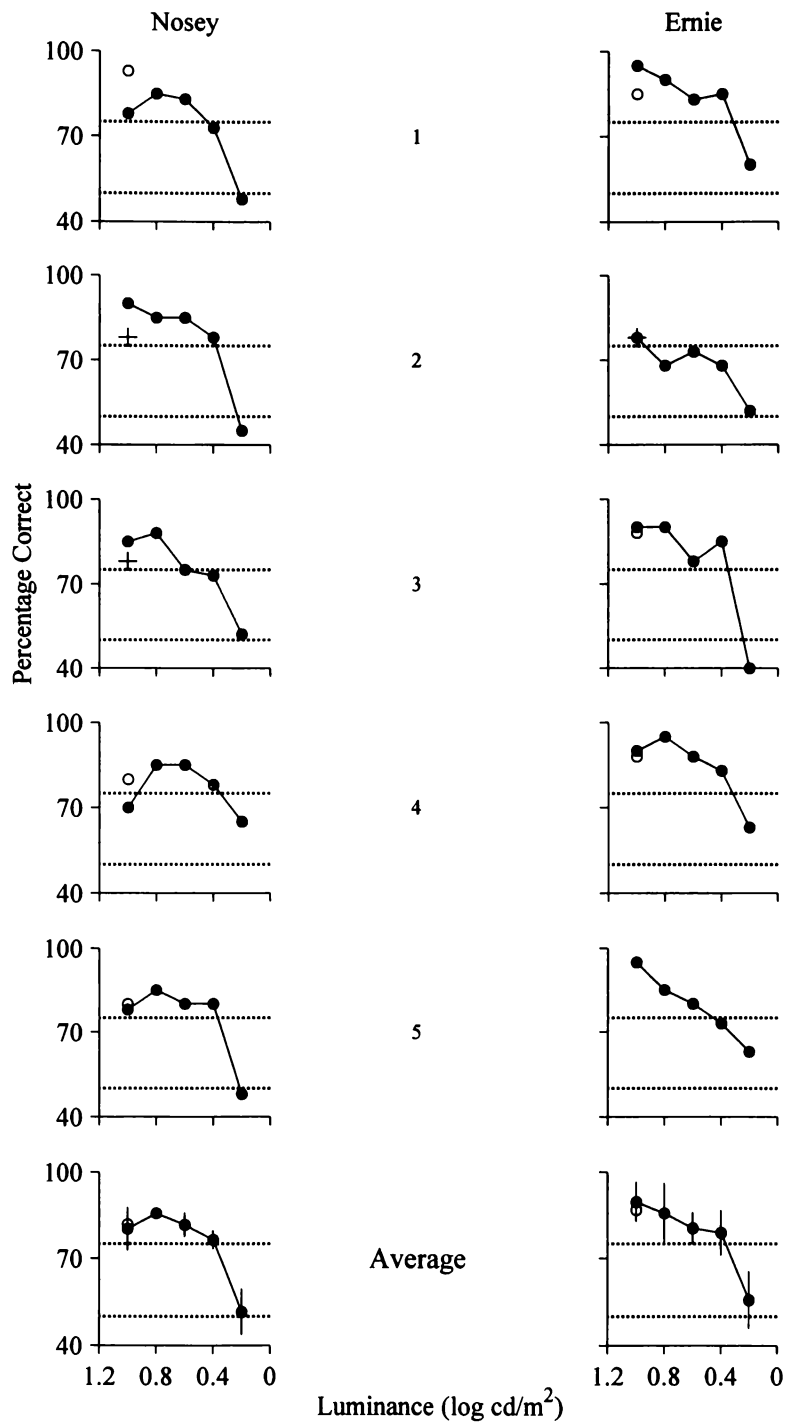


Figure 9.1. Percentage correct gained each threshold session and averaged as a function of stimulus intensity.

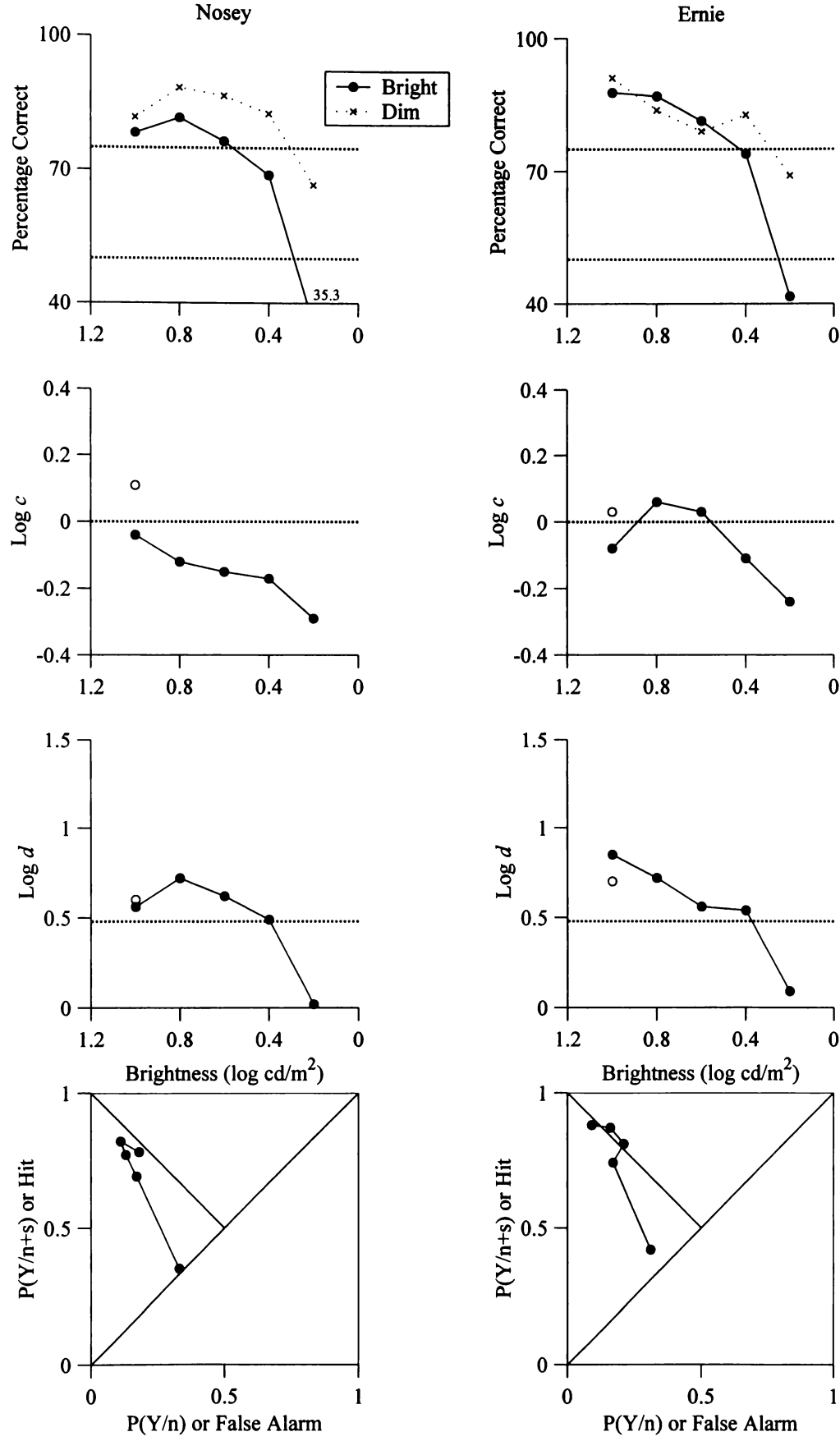


Figure 9.2. Percent correct gained as a function of stimulus intensity across both trial types, Log *c*, Log *d* and ROC plots of the average data.

discriminable. The $\log c$ values determined for Ernie show that a left lever bias developed at the two dimmest stimulus intensity values with little consistent bias at the earlier intensity values. For both possums the bias reverses (towards the right lever) during the re-presentation of the training intensity stimuli.

Log d estimates are presented in the third pair of graphs, again plotted as a function of stimulus intensity. These graphs show a similar pattern to the average percentage correct graphs in Figure 9.1, in that the $\log d$ values generally decrease gradually as stimulus discriminability reduced, and both functions fall below a $\log d$ of 0.48 at approximately the same point with values of 0.396 and 0.373 $\log \text{cd/m}^2$ for Nosey and Ernie respectively (values interpolated from the functions).

The bottom pair of graphs in Figure 9.2 are ROC plots of the average data joined in order of presentation with the points at the top left of the diagram being presented earlier. From these it is apparent that the last two blocks of trials fall the furthest from the minor diagonal, reflecting what was found in the $\log c$ analyses. Interestingly the initial data point (greatest disparity between stimuli) falls some way down the minor diagonal, suggesting that even the training stimuli were not highly discriminable.

Discussion

While the results from the current experiment and the pilot study show that possums can be taught a conditional discrimination between stimuli of differing brightness, the difficulty encountered in training this task with the LED's was not expected. One possible explanation for the training difficulties encountered here with the LEDs was the luminance level of the LEDs. That is, even when the LEDs were at their highest possible luminance level (1.0 $\log \text{cd/m}^2$) they were substantially dimmer than the earlier filament bulbs (2.4 and $x.x \log \text{cd/m}^2$). While the luminance of the LEDs was markedly lower than that of the filament bulbs, the relative disparity between the bright and dim stimulus used in the current experiment was larger than that controlled for in Experiment 4 (average disparity of 0.5 $\log \text{cd/m}^2$) and similar to that between the bright and dim stimulus in the pilot study.

Thus, it would appear that the relatively low luminance of the LEDs contributed to the difficulty in training the current discrimination rather than the level of disparity between the bright and dim stimuli. Log d values found in the current experiment (presented in Figure 9.2) would suggest that even the initial stimuli were not highly discriminable (highest $\log d$ values of 0.72 and 0.85 for Nosey and Ernie respectively). It is possible that if a brighter light source had been used the possums may have learned the task more quickly and to a higher degree of accuracy.

Despite these difficulties, it was possible to produce a difference threshold function for Nosey and Ernie. There was a gradual decrease in percentage correct as the luminance

of the bright stimuli reduced. Thus, although these findings come from only two possums, the current threshold function is similar to the shape of the threshold function derived from Experiment 7 (auditory) than those found with CFF. This would suggest that the abrupt, all-or-none, function found in the flicker experiments is a facet of discriminating flicker frequencies rather than a finding common to all visual stimuli for the possum.

In the current experiment, percentage correct on the stimulus-absent (dim stimulus) trials did (in general) decrease more gradually than that on the associated bright stimulus trials. However the disparity in percentage correct is smaller than that seen in Experiment 7. This may be due to the fact that the stimuli themselves were less discriminable than those in the auditory experiment, e.g., $\log d$ values in the current experiment peak at 0.85, in contrast to $\log d$ values above 1.0 in Experiment 7. Thus, even the initial, most discriminable, stimuli in the current experiment were near-threshold and this may lead to a loss of stimulus control to a greater extent than that seen in Experiment 7. Again, in order to test this, brighter and thus more discriminable, stimuli need to be used.

Notwithstanding the difficulties encountered in the current experiment, it can be concluded that possums can be taught a brightness discrimination. It also suggests that CFF determinations in the possum may somehow be unique in that they result in a very distinct all-or-none pattern of accuracy not found elsewhere in the literature or repeated here with another visually-based determination using the same methodology.

General Discussion

The current series of experiments illustrates that it is possible to train, relatively easily, reliable conditional discriminations in brushtail possums with both visual and auditory stimuli. As this is one of only a few behavioural studies with possums, a number of important husbandry and equipment issues arose during the current series of experiments. Appendix A presents a discussion of these issues with recommendations (in respect to husbandry and equipment) for future research with possums.

The current findings suggest that the psychophysical technique (block-wise method of limits) used throughout this thesis can be used successfully to assess the psychophysical abilities of brushtail possums. The results gained here, were however, in at least some respects, unexpected.

The first unexpected finding was that when using flickering lights as stimuli repeated threshold testing resulted in control of behaviour by the relative luminance of the flickering and steady stimuli rather than by the stimulus dimension intended (i.e., the rate of flicker). None of the published studies of CFF mention any such shift in control, despite some not controlling for relative luminance (e.g., Ploog & Williams, 1995). However, as most published studies of CFF carried out a limited number of threshold determinations at any given luminance, such a shift in stimulus control may not have occurred. In the present studies, the shift in control seems to have started quite early in the experimental series, in that, performance at the faster flicker speeds was better in Experiment 1 than in the final condition of Experiment 4 where luminance was equalised. However, even in Experiment 1 the possums experienced 10 threshold sessions, more than normally presented in most published CFF studies. As previously discussed, this finding highlights the need to make sure that either only the relevant dimension of the stimulus gains control over behaviour. Specifically, any further experiments into CFF must ensure that the luminance of the flickering and steady stimuli are equalised or that relative luminance cues are made irrelevant if meaningful data is to be obtained.

The second unexpected finding was that the CFF functions derived once relative luminance was equalised were unusual, with an abrupt change in percentage correct at 24 Hz. This is less easy to attribute to any procedural effects. As discussed earlier, a search of the CFF literature found that for other species conditioned-suppression techniques found gradual CFF functions with no sign of the all-or-none pattern found here. While there is limited information about how results from conditioned suppression and conditional discrimination experiments compare, both involve a learned behaviour and use some pre-determined degree of change in that behaviour as the stimulus changes to indicate the stimulus value at threshold. As such, there appears to be no reason to assume that the all-or-

none pattern found here would occur with one technique and not the other, although a further experiment using the same stimuli and a conditional discrimination procedure would test this hypothesis. The unusual threshold function found in the current CFF experiments does not appear to be common to CFF determinations with other species. The results of Experiment 9 showed that the all-or-none pattern found is also not common to visual discriminations in possums but seems to be related to the use of flickering stimuli, at least at this luminance. As CFF is affected by the luminance of the flickering stimuli it would be interesting to determine CFF at different luminance levels with possums, to see if the all-or-none shaped function occurred at other luminance levels. A further experiment with another species for which a CFF function is already available (e.g., the cat), but using the current methodology, would also be interesting, in that it would provide a check on whether or not the current procedure somehow contributed to the unusual function although, at this point, this does not seem likely.

Overall the current data suggest that CFF, and hence the ability to detect movement, is somehow different in possums than in other species for which CFF has been studied. As CFF has not been tested with any other marsupial species it would be interesting to see if such a function is common to marsupials. In spite of the difficulties encountered in the series of flicker experiments, the success of the final experiments with luminance equalised, suggests that the current method could now be used to derive a full CFF function for possums across various luminance values.

One issue raised by the present results was the appropriateness of various measures of discriminative ability and the validity of any comparisons made between threshold estimates from differing determination methods or differing stimulus dimensions. The question of how to compare the current results with threshold estimates from other studies that used different techniques (in particular conditioned suppression, as this is another widely used technique) has been discussed previously. However, an experiment directly comparing functions derived from conditioned suppression and conditional discrimination techniques would be very useful and might help determine the relation between results from conditional discrimination and conditioned suppression experiments. Unlike the function derived when flickering stimuli were used, the use of auditory stimuli resulted in data similar to that seen in other species, that is, a gradual decrease in the accuracy of performance as stimulus intensity decreased. As such, it may be appropriate to use the same stimuli as presented in Experiment 7 (auditory) with a conditioned suppression method to derive a threshold function in order to compare the way the suppression ratio changes as stimulus intensity decreases to that obtained under conditional discrimination procedures. However, possums may not prove to be the ideal species to attempt this experiment with. As conditioned-suppression techniques require a stable base-line rate of responding before

beginning testing, it is likely that a very long period of training would be required as large variations in the amount of responding within a session are common with possums.

As discussed in Experiment 7, even when comparing threshold estimates across experiments which both use a conditional discrimination technique there are complications due to the underlying pattern of responding on the two trial types. This is because overall percentage correct can arise from quite different patterns of correct and incorrect responding. Very few two-stimulus conditional-discrimination experiments present the percentage correct on the two trial types separately, however, in the current series of experiments two distinctly different patterns of underlying responding were found. Experiment 8 was conducted to determine if the more difficult discriminations presented within a threshold session might be contributing to this difference. The results were equivocal and although there seemed to be an effect of exposure to difficult or impossible to discriminate stimuli no firm conclusions could be drawn. While it is apparent that experience of sub-threshold stimulus-present trials did have some effect on performance on subsequent trials, to determine the range of this effect requires further investigation.

Overall, the findings from the current series of experiments lead to the suggestion that presentation of data from each of the two trial types separately would be desirable. In a similar fashion to percentage correct based measures, the derived measures of discriminative ability ($\log d$ and d') are also affected by relative performance on the two trial types (as shown in Experiment 7). It seems unlikely that any one universal threshold criterion can be developed. However, if authors give sufficient information (i.e., both overall and separated accuracy functions) others can re-analyse the data presented to suit any threshold criterion chosen.

Despite issues with the appropriateness of various threshold measures the conditional discrimination method used in the auditory experiment proved successful (in that threshold functions were derived and appeared similar to those expected) and it would now be possible to teach possums to discriminate a range of tones and thus derive a full audiogram for possums. A behavioural audiogram would complement existing physiological data and help define the limits and dimensions of possums auditory abilities. Carey, O'Connor, McDonald & Matthews (1997) found that adding an auditory lure to a standard bait station attracted possums to the bait station. Research such as this would be aided by knowledge of the auditory abilities of possums.

In conclusion, the current findings extend experimental methods (see Appendix A) and data analysis techniques to a little researched species and provide the basis for much further research into the psychophysical abilities of the possum and other marsupial species. The current methodologies could be extended to testing of a broader range of

psychophysical abilities such as colour discrimination, taste and olfaction to complement existing physiological data.

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Appendix A

Despite the number of fatalities that occurred during the current series of experiments, possums adapted well to an experimental environment. The majority of deaths that did occur, proved to be due to intestinal problems, highlighting the need to provide captive possums with a diet high in fibre and to reduce fur ingestion (particularly a problem following fights when possums escaped from their cages). Possums also proved to be sensitive to changes in temperature and in a number of cases would not respond during sessions where the room temperature was beyond a 'normal' range. Once this problem was identified, the experimental room was maintained at approximately 20°C and this resulted in most of the possums responding throughout the year.

Possums are not easy to handle, and while safe handling methods have been developed through the course of this thesis (using a tail hold in contrast to Webster's (1975) suggestion of grasping the front paws), possums remain potentially dangerous and in some cases get stressed with handling (as indicated by vocalizations, urination and fur falling out). As such, out-of-cage handling in the current series of experiments was kept to a minimum, with the only intentional removals from the home cage occurring for weighing and occasional vet consultations.

Initially each possum was weighed once a week, however, as their weights did not fluctuate greatly from week to week, weighing moved onto a fortnightly basis. Apart from the essential welfare aspects of keeping a regular record of the possums' weights, weight fluctuations were found to affect possums' responding during experimental sessions, with increases in weight often leading to a decrease in responding. Each possum received a different level of supplemental feeding with some possums requiring much less than others to maintain a stable weight. The only way to determine the appropriate level of supplemental food was through the fortnightly weighing. Due to the need to restrict supplemental food, possums did not begin training until they were fully grown. For the young possums this meant that at least a year would pass before they could begin training. With the possums who were trapped as adults, adjusting to the cage environment in most cases, did not take long (approximately four to six weeks), however, as with the younger possums, experimental sessions could not begin until their weights were stable.

Generally possums proved to be a good laboratory animal although they appear to require more intensive care than some species (e.g., hens) and problems with maintaining behaviour may make them unsuitable for some experimental topics.

Appendix B - Experiment 1 threshold sessions

Possum number, date, number of correct and incorrect flickering trials, number of correct and incorrect steady trials, the number of reinforcements for correct flicker and steady trials, the overall proportion of correct responses in the current block of trials and the current flicker speed.

(0=5.00 Hz, 1= 5.55 Hz, 2=7.14 Hz, 3=10.00 Hz, 4=16.67 Hz, 5=50.00 Hz, 9=5.00 Hz)

subject	date	flicker trials		steady trials		f1st	f1st	%	tag	subject	date	flicker trials		steady trials		f1st	f1st	%	tag
		correct	incorrect	correct	incorrect							correct	incorrect	correct	incorrect				
1	25.06.96	8	0	12	0	8	11	100	0	1	1.08.96	20	0	20	0	20	20	100	3
1	25.06.96	21	0	19	0	21	19	100	1	1	1.08.96	20	0	20	0	20	20	100	4
1	25.06.96	19	0	20	1	18	17	98	2	1	1.08.96	13	7	14	6	7	7	68	5
1	25.06.96	18	2	18	2	7	11	90	3	1	1.08.96	10	0	10	0	6	8	100	9
1	25.06.96	18	0	21	1	18	17	98	4	1	15.08.96	10	0	10	0	8	8	100	0
1	25.06.96	13	2	17	8	10	10	75	5	1	15.08.96	19	0	21	0	19	21	100	1
1	25.06.96	9	1	10	0	5	5	95	9	1	15.08.96	21	0	19	0	21	19	100	2
1	27.06.96	10	0	10	0	6	6	100	0	1	15.08.96	20	0	20	0	20	20	100	3
1	27.06.96	19	1	20	0	15	16	98	1	1	15.08.96	14	6	14	6	9	10	70	4
1	27.06.96	21	0	19	0	21	19	100	2	1	15.08.96	9	6	15	10	7	8	60	5
1	27.06.96	20	0	20	0	20	20	100	3	1	15.08.96	10	0	10	0	6	6	100	9
1	27.06.96	20	0	20	0	20	20	100	4										
1	27.06.96	8	8	13	11	7	8	52	5	2	25.06.96	10	0	10	0	10	9	100	0
1	27.06.96	10	1	9	0	6	7	95	9	2	25.06.96	19	0	21	0	19	21	100	1
1	1.07.96	7	3	9	1	6	3	80	0	2	25.06.96	20	0	20	0	20	20	100	2
1	1.07.96	21	1	18	0	13	15	98	1	2	25.06.96	20	0	20	0	20	20	100	3
1	1.07.96	20	0	20	0	20	20	100	2	2	25.06.96	21	0	19	0	21	19	100	4
1	1.07.96	20	2	18	0	15	13	95	3	2	25.06.96	8	5	16	11	6	9	60	5
1	1.07.96	15	6	15	4	8	12	75	4	2	25.06.96	11	1	8	0	5	3	95	9
1	1.07.96	12	7	12	9	9	6	60	5	2	27.06.96	11	1	8	0	9	7	95	0
1	1.07.96	9	2	9	0	5	8	90	9	2	27.06.96	19	6	14	1	10	10	83	1
1	3.07.96	9	0	10	1	6	8	95	0	2	27.06.96	19	1	20	0	13	15	98	2
1	3.07.96	21	0	19	0	21	19	100	1	2	27.06.96	21	0	19	0	21	19	100	3
1	3.07.96	19	0	21	0	19	21	100	2	2	27.06.96	20	2	18	0	18	17	95	4
1	3.07.96	19	0	21	0	19	21	100	3	2	27.06.96	16	5	15	4	8	11	78	5
1	3.07.96	21	0	19	0	21	19	100	4	2	27.06.96	11	4	5	0	4	2	80	9
1	3.07.96	10	9	10	11	6	6	50	5	2	1.07.96	9	1	10	0	7	7	95	0
1	3.07.96	9	0	11	0	8	8	100	9	2	1.07.96	21	0	19	0	21	19	100	1
1	5.07.96	9	0	9	2	4	7	90	0	2	1.07.96	19	0	21	0	19	21	100	2
1	5.07.96	19	1	19	1	18	16	95	1	2	1.07.96	20	0	20	0	20	20	100	3
1	5.07.96	19	0	21	0	19	21	100	2	2	1.07.96	20	0	20	0	20	20	100	4
1	5.07.96	21	3	16	0	15	14	93	3	2	1.07.96	13	4	15	8	7	8	70	5
1	5.07.96	17	3	17	3	10	9	85	4	2	1.07.96	9	1	10	0	7	6	95	9
1	5.07.96	13	5	15	7	8	9	70	5	2	3.07.96	8	3	9	0	6	9	85	0
1	5.07.96	11	2	7	0	7	4	90	9	2	3.07.96	21	0	19	0	21	19	100	1
1	9.07.96	10	1	8	1	9	5	90	0	2	3.07.96	20	0	20	0	20	20	100	2
1	9.07.96	17	4	17	2	9	12	85	1	2	3.07.96	20	0	20	0	20	20	100	3
1	9.07.96	21	0	19	0	21	19	100	2	2	3.07.96	19	0	21	0	19	21	100	4
1	9.07.96	20	4	16	0	11	13	90	3	2	3.07.96	16	7	12	5	9	6	70	5
1	9.07.96	17	5	15	3	12	11	80	4	2	3.07.96	9	2	9	0	5	7	90	9
1	9.07.96	14	7	14	5	9	8	70	5	2	5.07.96	10	0	10	0	7	8	100	0
1	9.07.96	10	1	9	0	6	8	95	9	2	5.07.96	20	0	20	0	20	20	100	1
1	12.07.96	9	2	8	1	4	5	85	0	2	5.07.96	20	0	20	0	20	20	100	2
1	12.07.96	20	1	19	0	17	17	98	1	2	5.07.96	21	0	19	0	21	19	100	3
1	12.07.96	21	0	19	0	21	19	100	2	2	5.07.96	18	0	21	1	18	18	98	4
1	12.07.96	19	0	21	0	19	21	100	3	2	5.07.96	18	4	16	2	8	10	85	5
1	12.07.96	20	0	20	0	20	20	100	4	2	5.07.96	11	5	4	0	4	2	75	9
1	12.07.96	13	6	14	7	10	7	68	5	2	9.07.96	10	1	9	0	8	7	95	0
1	12.07.96	10	2	8	0	4	7	90	9	2	9.07.96	21	7	12	0	7	8	83	1
1	16.07.96	9	1	9	1	4	5	90	0	2	9.07.96	18	1	21	0	16	17	98	2
1	16.07.96	20	1	19	0	17	19	98	1	2	9.07.96	20	0	20	0	20	20	100	3
1	16.07.96	21	0	19	0	21	19	100	2	2	9.07.96	21	0	19	0	21	19	100	4
1	16.07.96	21	0	19	0	21	19	100	3	2	9.07.96	21	3	16	0	11	13	93	5
1	16.07.96	18	0	22	0	18	22	100	4	2	9.07.96	8	4	8	0	4	3	80	9
1	16.07.96	12	6	14	8	7	7	65	5	2	12.07.96	10	3	7	0	6	5	85	0
1	16.07.96	11	1	8	0	8	6	95	9	2	12.07.96	21	0	19	0	21	19	100	1
1	18.07.96	8	0	12	0	8	10	100	0	2	12.07.96	18	0	22	0	18	22	100	2
1	18.07.96	21	0	19	0	21	19	100	1	2	12.07.96	20	0	20	0	20	20	100	3
1	18.07.96	20	0	20	0	20	20	100	2	2	12.07.96	21	0	19	0	21	19	100	4
1	18.07.96	20	0	20	0	20	20	100	3	2	12.07.96	18	4	15	3	10	11	83	5
1	18.07.96	19	0	21	0	19	21	100	4	2	12.07.96	8	2	10	0	5	5	90	9
1	18.07.96	13	9	10	8	9	7	58	5	2	16.07.96	11	1	8	0	10	6	95	0
1	18.07.96	9	2	9	0	5	7	90	9	2	16.07.96	18	0	22	0	18	22	100	1
1	23.07.96	10	0	10	0	8	8	100	0	2	16.07.96	20	0	20	0	20	20	100	2
1	23.07.96	20	0	20	0	20	20	100	1	2	16.07.96	20	2	17	1	15	13	93	3
1	23.07.96	20	0	20	0	20	20	100	2	2	16.07.96	20	5	14	1	11	10	85	4
1	23.07.96	21	0	19	0	21	19	100	3	2	16.07.96	17	3	19	1	13	14	90	5
1	23.07.96	19	0	21	0	19	21	100	4	2	16.07.96	11	1	8	0	5	7	95	9
1	23.07.96	16	5	15	4	12	10	78	5	2	18.07.96	8	2	8	2	5	4	80	0
1	23.07.96	11	2	7	0	4	6	90	9	2	18.07.96	20	2	17	1	14	13	93	1
1	25.07.96	7	1	11	1	5	9	90	0	2	18.07.96	18	0	22	0	18	22	100	2
1	25.07.96	21	0	19	0	21	19	100	1	2	18.07.96	20	0	20	0	20	20	100	3
1	25.07.96	21	0	19	0	21	19	100	2	2	18.07.96	21	0	19	0	21	19	100	4
1	25.07.96	19	2	19	0	16	16	95											

subject	date	flicker trials		steady trials		f1st	a1st	%	tag	subject	date	flicker trials		steady trials		f1st	a1st	%	tag
		correct	incorrect	correct	incorrect							correct	incorrect	correct	incorrect				
2	1.08.96	18	3	17	2	14	15	88	5	4	3.07.96	19	1	19	1	11	12	95	3
2	1.08.96	9	3	8	0	5	4	85	9	4	3.07.96	16	3	18	3	13	15	85	4
2	6.08.96	8	1	10	1	4	6	90	0	4	3.07.96	12	7	12	9	10	8	60	5
2	6.08.96	20	2	17	1	12	10	93	1	4	3.07.96	8	3	8	1	4	5	80	9
2	6.08.96	19	0	21	0	19	21	100	2	4	5.07.96	8	2	8	2	7	3	80	0
2	6.08.96	20	0	20	0	20	20	100	3	4	5.07.96	21	0	19	0	16	16	100	1
2	6.08.96	20	0	20	0	20	20	100	4	4	5.07.96	18	0	22	0	18	22	100	2
2	6.08.96	20	3	16	1	12	11	90	5	4	5.07.96	18	1	19	2	17	17	93	3
2	6.08.96	8	2	10	0	4	5	90	9	4	5.07.96	19	3	16	2	11	8	88	4
										4	5.07.96	13	4	15	8	9	11	70	5
										4	5.07.96	8	3	9	0	6	5	85	9
3	25.06.96	20	0	20	0	20	20	100	1	4	9.07.96	8	4	8	0	3	5	80	0
3	25.06.96	19	0	21	0	19	21	100	2	4	9.07.96	21	0	19	0	21	19	100	1
3	25.06.96	21	0	19	0	21	19	100	3	4	9.07.96	20	0	20	0	20	20	100	2
3	25.06.96	11	6	14	9	6	8	63	4	4	9.07.96	20	0	20	0	20	20	100	3
3	25.06.96	10	1	9	0	8	6	95	9	4	9.07.96	19	0	21	0	19	21	100	4
3	27.06.96	10	1	9	0	10	9	95	0	4	9.07.96	12	4	15	9	9	7	68	5
3	27.06.96	21	1	18	0	19	17	98	1	4	9.07.96	9	0	11	0	5	7	100	9
3	27.06.96	19	4	17	0	8	11	90	2	4	16.07.96	8	3	9	0	7	5	85	0
3	27.06.96	17	4	17	2	10	8	85	3	4	16.07.96	20	1	18	1	16	16	95	1
3	27.06.96	20	6	13	1	7	9	83	4	4	16.07.96	20	0	20	0	20	20	100	2
3	27.06.96	10	6	13	11	9	6	58	5	4	16.07.96	18	2	18	2	15	13	90	3
3	27.06.96	9	2	9	0	5	5	90	9	4	16.07.96	14	2	19	5	8	12	83	4
3	1.07.96	11	2	7	0	6	5	90	0	4	16.07.96	14	4	15	7	10	7	73	5
3	1.07.96	20	3	17	0	9	11	93	1	4	16.07.96	8	2	9	1	4	7	85	9
3	1.07.96	20	0	20	0	20	19	100	2	4	18.07.96	9	2	8	1	6	7	85	0
3	1.07.96	21	1	18	0	20	18	98	3	4	18.07.96	19	0	21	0	19	21	100	1
3	1.07.96	15	4	17	4	6	8	80	4	4	18.07.96	21	0	19	0	21	19	100	2
3	1.07.96	14	4	16	6	8	7	75	5	4	18.07.96	20	0	20	0	20	20	100	3
3	1.07.96	11	2	7	0	5	5	90	9	4	18.07.96	20	0	20	0	20	20	100	4
3	3.07.96	9	0	11	0	5	6	100	0	4	18.07.96	12	2	19	7	8	8	78	5
3	3.07.96	20	3	16	1	10	9	90	1	4	18.07.96	10	2	8	0	5	7	90	9
3	3.07.96	19	1	20	0	10	13	98	2	4	23.07.96	7	2	9	2	4	6	80	0
3	3.07.96	20	1	19	0	15	13	98	3	4	23.07.96	19	3	16	2	12	10	88	1
3	3.07.96	18	0	20	2	16	14	95	4	4	23.07.96	19	0	21	0	19	21	100	2
3	3.07.96	16	6	13	5	8	8	73	5	4	23.07.96	20	0	20	0	20	20	100	3
3	3.07.96	8	2	10	0	4	6	90	9	4	23.07.96	19	0	20	1	19	19	98	4
3	5.07.96	11	0	9	0	11	8	100	0	4	23.07.96	8	7	12	13	7	4	50	5
3	5.07.96	20	0	20	0	20	20	100	1	4	23.07.96	8	0	12	0	7	12	100	9
3	5.07.96	19	2	19	0	11	11	95	2	4	26.07.96	11	1	8	0	9	6	95	0
3	5.07.96	21	4	15	0	8	10	90	3	4	26.07.96	19	0	21	0	19	21	100	1
3	5.07.96	18	5	15	2	11	11	83	4	4	26.07.96	20	0	20	0	20	20	100	2
3	5.07.96	16	2	18	4	10	8	85	5	4	26.07.96	20	0	20	0	20	20	100	3
3	5.07.96	10	2	8	0	4	6	90	9	4	26.07.96	19	1	18	2	13	13	93	4
3	9.07.96	9	2	9	0	6	9	90	0	4	26.07.96	15	2	19	4	11	11	85	5
3	9.07.96	21	1	18	0	19	18	98	1	4	26.07.96	10	2	8	0	7	8	90	9
3	9.07.96	21	3	16	0	12	11	93	2	4	29.07.96	10	3	7	0	5	3	85	0
3	9.07.96	18	2	20	0	13	15	95	3	4	29.07.96	21	0	19	0	20	18	100	1
3	9.07.96	19	2	18	1	17	17	93	4	4	29.07.96	18	0	22	0	18	22	100	2
3	9.07.96	11	6	13	10	6	5	60	5	4	29.07.96	17	2	18	3	9	8	88	3
3	9.07.96	10	2	8	0	7	4	90	9	4	29.07.96	17	1	18	4	16	15	88	4
3	16.07.96	11	2	7	0	10	6	90	0	4	29.07.96	9	5	14	12	7	6	58	5
3	16.07.96	20	2	18	0	10	12	95	1	4	29.07.96	8	2	10	0	6	9	90	9
3	16.07.96	19	0	21	0	14	15	100	2	4	1.08.96	8	3	8	1	6	4	80	0
3	16.07.96	21	0	19	0	21	19	100	3	4	1.08.96	19	2	17	2	11	12	90	1
3	16.07.96	16	6	14	4	9	11	75	4	4	1.08.96	21	0	19	0	21	19	100	2
3	16.07.96	12	5	15	8	10	8	68	5	4	1.08.96	18	0	22	0	18	22	100	3
3	16.07.96	10	3	6	1	5	4	80	9	4	1.08.96	20	0	20	0	20	20	100	4
3	23.07.96	11	0	9	0	7	7	100	0	4	1.08.96	11	5	14	10	11	7	63	5
3	23.07.96	18	0	22	0	17	19	100	1	4	1.08.96	9	1	9	1	5	6	90	9
3	23.07.96	20	0	20	0	20	20	100	2										
3	23.07.96	21	0	19	0	21	19	100	3	5	25.06.96	20	0	20	0	20	20	100	3
3	23.07.96	19	3	16	2	10	9	88	4	5	25.06.96	16	3	17	4	10	11	83	4
3	23.07.96	13	4	18	5	9	9	78	5	5	25.06.96	11	1	8	0	8	7	95	0
3	23.07.96	11	2	7	0	3	5	90	9	5	25.06.96	19	0	21	0	19	21	100	1
3	25.07.96	10	0	10	0	6	6	100	0	5	25.06.96	21	0	19	0	21	19	100	2
3	25.07.96	20	3	17	0	15	15	93	1	5	25.06.96	3	2	19	16	3	2	55	5
3	25.07.96	21	0	19	0	21	19	100	2	5	27.06.96	10	0	9	1	6	5	95	0
3	25.07.96	21	0	19	0	21	19	100	3	5	27.06.96	18	2	18	2	16	16	90	1
3	25.07.96	17	2	20	1	13	15	93	4	5	27.06.96	20	0	20	0	20	20	100	2
3	25.07.96	17	3	17	3	10	12	85	5	5	27.06.96	19	0	21	0	19	21	100	3
3	25.07.96	11	3	6	0	5	3	85	9	5	27.06.9								

subject	date	flicker trials		steady trials		fitt	wrt	%	tag	subject	date	flicker trials		steady trials		fitt	wrt	%	tag	
		correct	incorrect	correct	incorrect							correct	incorrect							
5	9.07.96	19	0	21	0	19	21	100	2	6	16.07.96	7	4	7	2	4	4	70	0	
5	9.07.96	19	0	21	0	19	21	100	3	6	16.07.96	11	1	8	0	3	6	95	1	
5	9.07.96	18	2	17	3	15	13	88	4	6	16.07.96	20	1	19	0	18	17	98	2	
5	9.07.96	10	1	18	11	7	6	70	5	6	16.07.96	19	0	21	0	19	21	100	3	
5	9.07.96	9	0	11	0	5	5	100	9	6	16.07.96	21	0	19	0	21	19	100	4	
5	12.07.96	11	1	8	0	7	3	95	0	6	16.07.96	17	2	18	3	8	10	88	5	
5	12.07.96	20	0	20	0	19	20	100	1	6	18.07.96	8	2	9	1	6	3	85	0	
5	12.07.96	20	0	20	0	20	20	100	2	6	18.07.96	20	2	17	1	16	16	93	1	
5	12.07.96	19	0	21	0	19	21	100	3	6	18.07.96	20	0	20	0	20	20	100	2	
5	12.07.96	21	0	19	0	21	19	100	4	6	18.07.96	20	0	20	0	20	20	100	3	
5	16.07.96	10	1	9	0	3	5	95	0	6	18.07.96	18	1	20	1	12	14	95	4	
5	16.07.96	19	0	20	1	13	13	98	1	6	22.07.96	8	0	12	0	7	9	100	0	
5	16.07.96	21	0	19	0	21	19	100	2	6	22.07.96	21	0	19	0	21	19	100	1	
5	16.07.96	21	0	19	0	21	19	100	3	6	22.07.96	20	0	20	0	20	20	100	2	
5	16.07.96	18	0	22	0	18	22	100	4	6	22.07.96	20	0	20	0	20	20	100	3	
5	16.07.96	11	5	15	9	7	7	65	5	6	24.07.96	11	1	8	0	6	3	95	0	
5	16.07.96	11	0	9	0	8	6	100	9	6	24.07.96	20	0	20	0	20	20	100	1	
5	18.07.96	10	0	10	0	5	5	100	0	6	24.07.96	20	0	20	0	20	20	100	2	
5	18.07.96	19	1	20	0	15	16	98	1	6	24.07.96	19	0	21	0	19	21	100	3	
5	18.07.96	21	0	19	0	21	19	100	2	6	24.07.96	17	2	17	4	10	10	85	4	
5	18.07.96	20	0	20	0	20	20	100	3	6	26.07.96	9	1	10	0	5	8	95	0	
5	18.07.96	19	0	20	1	16	15	98	4	6	26.07.96	21	0	19	0	21	19	100	1	
5	18.07.96	7	1	20	12	7	10	68	5	6	26.07.96	21	0	19	0	21	19	100	2	
5	18.07.96	10	2	8	0	9	7	90	9	6	26.07.96	18	0	22	0	18	22	100	3	
5	23.07.96	10	1	9	0	8	9	95	0	6	26.07.96	20	0	20	0	20	20	100	4	
5	23.07.96	20	0	20	0	20	20	100	1	6	26.07.96	7	5	14	14	6	5	52	5	
5	23.07.96	20	0	20	0	20	20	100	2	6	26.07.96	9	2	8	1	5	3	85	9	
5	23.07.96	21	0	19	0	21	19	100	3	6	29.07.96	7	3	9	1	5	4	80	0	
5	23.07.96	17	0	21	2	9	12	95	4	6	29.07.96	21	0	19	0	18	17	100	1	
5	23.07.96	9	3	17	11	7	3	65	5	6	29.07.96	20	0	20	0	20	20	100	2	
5	23.07.96	9	2	7	2	3	6	80	9	6	29.07.96	20	0	20	0	20	20	100	3	
5	25.07.96	20	0	20	0	20	20	100	1	6	1.08.96	11	1	8	0	8	8	95	0	
5	25.07.96	20	0	20	0	20	20	100	2	6	1.08.96	20	0	20	0	20	20	100	1	
5	25.07.96	19	0	21	0	19	21	100	3	6	1.08.96	20	0	20	0	20	20	100	2	
5	25.07.96	18	1	18	3	13	13	90	4	6	1.08.96	21	0	19	0	21	19	100	3	
5	25.07.96	9	6	14	11	6	6	58	5	6	1.08.96	19	0	21	0	19	21	100	4	
5	25.07.96	8	2	9	1	5	3	85	9	6	6.08.96	8	1	10	1	5	6	90	0	
5	29.07.96	8	2	9	1	5	6	85	0	6	6.08.96	21	0	19	0	18	16	100	1	
5	1.08.96	9	1	9	1	7	7	90	0	6	6.08.96	21	0	19	0	21	19	100	2	
5	1.08.96	19	0	21	0	17	18	100	1	6	6.08.96	18	0	22	0	18	22	100	3	
5	1.08.96	20	0	20	0	20	20	100	2	6	8.08.96	11	1	8	0	5	6	95	0	
5	1.08.96	13	2	19	6	7	11	80	5	6	8.08.96	19	0	21	0	18	18	100	1	
5	1.08.96	11	1	8	0	7	3	95	9	6	8.08.96	19	0	21	0	19	21	100	2	
5	6.08.96	10	1	8	1	6	4	90	0	6	8.08.96	21	0	19	0	21	19	100	3	
5	6.08.96	20	0	20	0	15	16	100	1	6	8.08.96	21	0	19	0	21	19	100	4	
5	6.08.96	20	0	20	0	20	20	100	2	6	8.08.96	8	8	13	11	5	8	52	5	
5	6.08.96	19	0	21	0	19	21	100	3	6	8.08.96	11	0	9	0	9	6	100	9	
5	8.08.96	9	0	11	0	6	8	100	0	6	13.08.96	11	0	9	0	11	8	100	0	
5	8.08.96	18	0	21	1	14	15	98	3	6	13.08.96	18	0	22	0	18	22	100	1	
5	8.08.96	20	0	20	0	20	20	100	4	6	13.08.96	20	0	20	0	20	20	100	2	
5	8.08.96	13	4	16	7	10	8	73	5	6	13.08.96	20	2	17	1	15	14	93	3	
5	8.08.96	8	4	5	3	5	5	65	9	6	13.08.96	21	0	1	9	12	1	8	100	4
5	13.08.96	19	1	18	2	15	12	93	1	6	13.08.96	6	5	17	12	5	8	58	5	
5	13.08.96	18	0	22	0	18	22	100	2	6	13.08.96	11	1	8	0	7	4	95	9	
5	13.08.96	20	0	20	0	20	20	100	3	6	15.08.96	11	0	9	0	7	8	100	0	
5	13.08.96	21	0	19	0	21	19	100	4	6	15.08.96	20	0	20	0	10	12	100	1	
5	13.08.96	9	5	14	12	6	7	58	5	6	15.08.96	19	0	21	0	18	17	100	2	
5	13.08.96	8	1	11	0	7	8	95	9	6	15.08.96	21	0	19	0	21	19	100	3	
6	25.06.96	10	1	9	0	10	7	95	0	6	15.08.96	20	0	20	0	20	20	100	4	
6	25.06.96	19	0	21	0	19	21	100	1	6	15.08.96	11	3	17	9	5	8	70	5	
6	25.06.96	20	0	20	0	20	20	100	2	6	15.08.96	10	1	9	0	9	6	95	9	
6	25.06.96	20	0	20	0	20	20	100	3	6	21.08.96	10	1	9	0	6	8	95	0	
6	25.06.96	20	0	19	1	16	16	98	4	6	21.08.96	19	1	20	0	17	19	98	1	
6	27.06.96	8	0	11	1	6	3	95	0	6	21.08.96	21	1	18	0	11	11	98	2	
6	27.06.96	21	1	18	0	16	16	98	1	6	21.08.96	20	1	19	0	16	14	98	3	
6	27.06.96	20	0	20	0	20	20	100	2	6	21.08.96	20	0	20	0	20	20	100	4	
6	27.06.96	20	0	20	0	20	20	100	3	6	21.08.96	10	5	16	9	8	8	65	5	
6	27.06.96	19	0	21	0	19	21	100	4	6	21.08.96	10	1	9	0	6	7	95	9	
6	1.07.96	10	0	10	0	9	10	100	0											
6	1.07.96	20	0	20	0	20	20	100	1											
6	1.07.96	21	0	19	0	21	19	100	2											
6	1.07.96																			

Appendix C - Experiment 2 threshold sessions

Possum number, date, number of correct and incorrect flickering trials, number of correct and incorrect steady trials, the number of reinforcements for correct flicker and steady trials, the overall proportion of correct responses in the current block of trials and the current flicker speed.

(0=5.00 Hz, 1= 16.67 Hz, 2=20.00 Hz, 3=25.00 Hz, 4=33.33 Hz, 5=50.00 Hz, 9=5.00 Hz)

flicker trials									steady trials										
subject	date	correct	incorrect	correct	incorrect	fltr	srtr	%	tag	subject	date	correct	incorrect	correct	incorrect	fltr	srtr	%	tag
1	23.08.96	9	2	9	0	8	5	90	0	2	4.09.96	19	3	18	0	9	12	93	2
1	23.08.96	20	1	18	1	16	16	95	1	2	4.09.96	21	0	19	0	21	19	100	3
1	23.08.96	20	0	20	0	20	20	100	2	2	4.09.96	19	2	18	1	15	16	93	4
1	23.08.96	20	3	17	0	15	15	93	3	2	4.09.96	17	7	13	3	9	8	75	5
1	23.08.96	16	3	18	3	10	11	85	4	2	4.09.96	10	2	8	0	5	7	90	9
1	23.08.96	18	3	16	3	14	15	85	5	2	6.09.96	11	2	7	0	6	6	90	0
1	23.08.96	9	3	8	0	8	5	85	9	2	6.09.96	19	5	15	1	10	10	85	1
1	27.08.96	8	0	10	2	7	8	90	0	2	6.09.96	17	3	18	2	13	15	88	2
1	27.08.96	16	5	15	4	12	10	78	1	2	6.09.96	20	1	18	1	20	18	95	3
1	27.08.96	19	3	16	2	13	13	88	2	2	6.09.96	17	5	15	3	10	12	80	4
1	27.08.96	17	4	15	4	12	13	80	3	2	6.09.96	19	2	18	1	15	13	93	5
1	27.08.96	14	5	17	4	11	12	78	4	2	6.09.96	11	0	9	0	11	9	100	9
1	27.08.96	18	4	16	2	14	11	85	5	2	10.09.96	10	1	9	0	7	8	95	0
1	27.08.96	11	0	9	0	6	8	100	9	2	10.09.96	20	0	20	0	20	20	100	1
1	29.08.96	10	1	9	0	4	6	95	0	2	10.09.96	20	0	20	0	20	20	100	2
1	29.08.96	12	10	10	8	7	7	55	1	2	10.09.96	19	3	16	2	16	16	88	3
1	29.08.96	11	0	9	0	7	8	100	9	2	10.09.96	17	7	14	2	11	9	78	4
1	4.09.96	8	3	8	1	6	3	80	0	2	10.09.96	15	11	9	5	5	7	60	5
1	4.09.96	18	1	18	3	12	14	90	1	2	10.09.96	11	1	8	0	7	5	95	9
1	4.09.96	16	4	16	4	8	9	80	2	2	12.09.96	11	0	9	0	8	9	100	0
1	4.09.96	8	8	12	12	7	6	50	3	2	12.09.96	20	0	20	0	20	20	100	1
1	4.09.96	10	1	9	0	7	7	95	9	2	12.09.96	20	0	20	0	20	20	100	2
1	6.09.96	8	4	7	1	6	5	75	0	2	12.09.96	19	4	17	0	15	15	90	3
1	6.09.96	17	5	14	4	9	10	78	1	2	12.09.96	19	5	14	2	9	9	83	4
1	6.09.96	14	6	14	6	8	9	70	2	2	12.09.96	18	4	16	2	10	12	85	5
1	6.09.96	8	10	10	12	5	6	45	3	2	12.09.96	10	3	7	0	9	5	85	9
1	6.09.96	10	2	8	0	8	5	90	9	2	16.09.96	8	4	7	1	5	4	75	0
1	10.09.96	11	0	9	0	11	8	100	0	2	16.09.96	21	0	19	0	21	19	100	1
1	10.09.96	20	0	20	0	20	20	100	1	2	16.09.96	19	0	21	0	19	21	100	2
1	10.09.96	18	4	17	1	12	12	88	2	2	16.09.96	18	7	13	2	11	9	78	3
1	10.09.96	21	3	16	0	12	12	93	3	2	16.09.96	17	4	15	4	10	12	80	4
1	10.09.96	17	4	16	3	10	13	83	4	2	16.09.96	9	3	8	0	5	3	85	9
1	10.09.96	16	9	11	4	10	7	68	5	2	7.10.96	7	2	9	2	2	6	80	0
1	10.09.96	10	1	9	0	5	8	95	9	2	7.10.96	17	2	17	4	11	8	85	1
1	12.09.96	8	1	11	0	7	10	95	0	2	7.10.96	21	0	19	0	18	17	100	2
1	12.09.96	21	0	19	0	21	19	100	1	2	7.10.96	17	0	22	1	17	19	98	3
1	12.09.96	20	0	20	0	20	20	100	2	2	7.10.96	18	2	18	2	10	11	90	4
1	12.09.96	17	6	14	3	9	9	78	3	2	7.10.96	19	1	18	2	16	15	93	5
1	12.09.96	17	4	17	2	12	14	85	4	2	7.10.96	10	0	10	0	10	10	100	9
1	12.09.96	19	7	12	2	11	10	78	5	2	9.10.96	9	2	9	0	7	5	90	0
1	12.09.96	9	3	8	0	4	5	85	9	2	9.10.96	20	1	18	1	16	16	95	1
1	16.09.96	9	2	8	1	7	5	85	0	2	9.10.96	19	0	21	0	19	21	100	2
1	16.09.96	15	5	15	5	9	11	75	1	2	9.10.96	19	3	17	1	14	11	90	3
1	16.09.96	20	0	20	0	20	20	100	2	2	9.10.96	18	4	16	2	10	13	85	4
1	16.09.96	14	7	12	7	7	7	65	3	2	9.10.96	17	6	13	4	11	11	75	5
1	16.09.96	14	7	14	5	10	9	70	4	2	9.10.96	9	2	9	0	5	4	90	9
1	16.09.96	18	4	16	2	11	12	85	5										
1	16.09.96	11	2	7	0	6	5	90	9	3	23.08.96	9	1	9	1	4	6	90	0
1	18.09.96	11	0	9	0	9	9	100	0	3	23.08.96	19	0	21	0	19	21	100	1
1	18.09.96	20	0	20	0	20	20	100	1	3	23.08.96	21	0	19	0	21	19	100	2
1	18.09.96	20	1	19	0	17	19	98	2	3	23.08.96	20	2	18	0	16	16	95	3
1	18.09.96	15	8	13	4	8	7	70	3	3	23.08.96	17	2	18	3	9	8	88	4
1	18.09.96	19	3	16	2	12	13	88	4	3	23.08.96	14	4	17	5	9	9	78	5
1	18.09.96	20	4	16	0	11	11	90	5	3	23.08.96	10	1	9	0	4	7	95	9
1	18.09.96	10	3	7	0	5	5	85	9	3	27.08.96	11	0	9	0	9	6	100	0
1	9.10.96	8	2	9	1	5	3	85	0	3	27.08.96	16	1	20	3	15	14	90	1
1	9.10.96	20	1	18	1	14	15	95	1	3	27.08.96	16	2	19	3	7	12	88	2
1	9.10.96	20	0	20	0	20	20	100	2	3	27.08.96	15	6	13	6	10	6	70	3
1	9.10.96	18	4	16	2	9	10	85	3	3	27.08.96	16	5	14	5	11	13	75	4
1	9.10.96	17	2	19	2	12	13	90	4	3	27.08.96	15	8	13	4	7	8	70	5
1	9.10.96	17	4	15	4	10	8	80	5	3	27.08.96	10	2	7	1	5	5	85	9
1	9.10.96	9	2	9	0	6	8	90	9	3	10.09.96	11	0	9	0	10	8	100	0
										3	10.09.96	20	0	20	0	20	20	100	1
2	23.08.96	10	2	7	1	6	4	85	0	3	10.09.96	18	3	18	1	15	16	90	2
2	23.08.96	20	0	20	0	20	20	100	1	3	10.09.96	18	6	13	3	7	6	78	3
2	23.08.96	20	0	20	0	20	20	100	2	3	10.09.96	16	6	14	4	7	9	75	4
2	23.08.96	19	4	17	0	12	12	90	3	3	10.09.96	15	7	13	5	7	6	70	5
2	23.08.96	18	5	14	3	12	12	80	4	3	10.09.96	10	2	7	1	7	4	85	9
2	23.08.96	16	8	12	4	8	8	70	5	3	4.10.96	8	1	9	2	5	5	85	0
2	23.08.96	10	1	9	0	6	6	95	9	3	4.10.96	12	4	16	8	9	10	70	1
2	27.08.96	11	0	9	0	10	9	100	0	3	4.10.96	21	0	19	0	21	19	100	2
2	27.08.96	20	0	20	0	20	20	100	1	3	4.10.96	10	2	19	9	7	10	73	3
2	27.08.96	20	0	20	0	20	20	100	2	3	4.10.96	15	6	14	5	10	7	73	4
2	27.08.96	19	5	16															

subject	date	flicker trials		steady trials				tag	subject	date	flicker trials		steady trials				tag		
		correct	incorrect	correct	incorrect	flit	arft				correct	incorrect	correct	incorrect	flit	arft			
3	9.10.96	16	4	17	3	12	11	83	4	5	12.09.96	20	0	20	0	20	100	2	
3	9.10.96	20	0	20	0	19	18	100	5	5	12.09.96	12	4	17	7	9	9	73	3
3	9.10.96	11	0	9	0	11	9	100	9	5	12.09.96	13	8	11	8	7	8	60	4
3	11.10.96	9	1	10	0	9	8	95	0	5	12.09.96	8	2	9	1	5	6	85	9
3	11.10.96	21	0	19	0	21	19	100	1	5	16.09.96	10	1	9	0	6	8	95	0
3	11.10.96	19	2	19	0	18	18	95	2	5	16.09.96	19	1	19	1	16	14	95	1
3	11.10.96	17	2	18	3	10	11	88	3	5	16.09.96	20	3	16	1	11	10	90	2
3	11.10.96	19	1	19	1	15	16	95	4	5	16.09.96	8	7	14	11	5	9	55	3
3	11.10.96	15	5	14	6	11	11	73	5	5	16.09.96	9	0	10	1	6	5	95	9
3	11.10.96	9	6	5	0	3	3	70	9	5	9.10.96	11	1	8	0	6	5	95	0
										5	9.10.96	19	1	20	0	16	17	98	1
4	13.09.96	10	2	7	1	8	6	85	0	5	9.10.96	20	0	20	0	20	20	100	2
4	13.09.96	8	7	14	11	4	7	55	1	5	9.10.96	20	0	20	0	20	20	100	3
4	13.09.96	9	1	9	1	9	8	90	2	5	9.10.96	19	3	16	2	17	16	88	4
4	7.10.96	9	0	11	0	7	10	100	0	5	9.10.96	14	6	15	5	8	10	73	6
4	7.10.96	14	5	14	7	10	7	70	1	5	9.10.96	10	0	10	0	9	8	100	9
4	7.10.96	20	0	19	1	16	15	98	2	5	11.10.96	10	0	9	1	5	6	95	0
4	7.10.96	18	0	22	0	18	22	100	3	5	11.10.96	18	1	19	2	13	11	93	1
4	7.10.96	16	3	17	4	14	12	83	4	5	11.10.96	18	2	18	2	12	11	90	2
4	7.10.96	16	3	16	5	10	10	80	5	5	11.10.96	12	4	15	9	7	10	68	3
4	7.10.96	9	2	8	1	6	6	85	9	5	11.10.96	15	6	15	4	10	9	75	4
4	9.10.96	8	1	10	1	4	7	90	0	5	11.10.96	14	8	12	6	7	8	65	5
4	9.10.96	18	3	16	3	12	10	85	1	5	11.10.96	11	1	8	0	8	5	95	9
4	9.10.96	20	1	18	1	14	12	95	2	5	15.10.96	10	1	9	0	6	5	95	0
4	9.10.96	17	1	21	1	16	17	95	3	5	15.10.96	21	0	19	0	20	19	100	1
4	9.10.96	16	1	19	4	9	12	88	4	5	15.10.96	19	0	21	0	19	21	100	2
4	9.10.96	20	1	18	1	18	16	95	5	5	15.10.96	19	0	21	0	19	21	100	3
4	9.10.96	10	0	10	0	10	10	100	9	5	15.10.96	21	0	19	0	21	19	100	4
4	11.10.96	10	0	10	0	8	5	100	0	5	15.10.96	17	2	17	4	11	12	85	5
4	11.10.96	17	1	20	2	14	14	93	1	5	15.10.96	9	2	9	0	8	5	90	9
4	11.10.96	18	1	19	2	10	13	93	2										
4	11.10.96	15	2	18	5	10	10	83	3	6	23.08.96	8	0	12	0	7	11	100	0
4	11.10.96	15	4	15	6	14	11	75	4	6	23.08.96	21	0	19	0	21	19	100	1
4	11.10.96	18	2	19	1	15	15	93	5	6	23.08.96	21	0	19	0	21	19	100	2
4	11.10.96	8	1	8	3	3	5	80	9	6	23.08.96	18	3	18	1	15	14	90	3
4	15.10.96	10	0	10	0	9	10	100	0	6	23.08.96	17	3	18	2	8	12	88	4
4	15.10.96	11	2	19	8	8	8	75	1	6	23.08.96	12	6	13	9	9	7	63	5
4	15.10.96	16	3	16	5	10	10	80	2	6	23.08.96	10	0	10	0	5	6	100	9
4	15.10.96	16	1	18	5	11	10	85	3	6	29.08.96	11	0	9	0	5	4	100	0
4	15.10.96	19	0	21	0	19	20	100	4	6	29.08.96	16	2	18	4	9	11	85	1
4	15.10.96	19	0	21	0	19	21	100	5	6	29.08.96	18	1	19	2	15	13	93	2
4	15.10.96	11	0	9	0	11	9	100	9	6	29.08.96	12	3	18	7	8	8	75	3
4	17.10.96	9	2	8	1	6	7	85	0	6	29.08.96	17	6	13	4	9	11	75	4
4	17.10.96	11	2	19	8	10	9	75	1	6	29.08.96	16	3	17	4	12	12	83	5
4	17.10.96	19	1	18	2	14	15	93	2	6	29.08.96	10	1	9	0	9	7	95	9
4	17.10.96	17	3	17	3	10	13	85	3	6	4.09.96	10	0	9	1	8	7	95	0
4	17.10.96	18	1	19	2	14	11	93	4	6	4.09.96	20	0	20	0	20	20	100	1
4	17.10.96	19	0	21	0	19	21	100	5	6	4.09.96	20	0	20	0	20	20	100	2
4	17.10.96	10	0	10	0	10	10	100	9	6	4.09.96	11	4	17	8	8	9	70	3
4	22.10.96	10	1	9	0	6	5	95	0	6	4.09.96	15	4	15	6	10	12	75	4
4	22.10.96	21	0	19	0	21	19	100	1	6	4.09.96	18	4	16	2	11	10	85	5
4	22.10.96	10	7	15	8	8	12	63	2	6	4.09.96	8	1	10	1	4	6	90	9
4	22.10.96	11	0	9	0	8	6	100	9	6	6.09.96	9	0	10	1	7	5	95	0
4	24.10.96	8	1	10	1	6	5	90	0	6	6.09.96	21	0	19	0	16	16	100	1
4	24.10.96	17	2	17	4	13	11	85	1	6	6.09.96	19	0	21	0	19	21	100	2
4	24.10.96	18	1	19	2	12	12	93	2	6	6.09.96	9	5	16	10	6	6	63	3
4	24.10.96	17	3	17	3	14	13	85	3	6	6.09.96	11	0	9	0	8	8	100	9
4	24.10.96	12	5	16	7	7	10	70	4	6	10.09.96	11	0	9	0	7	8	100	0
4	24.10.96	13	8	11	8	9	6	60	5	6	10.09.96	19	1	20	0	18	18	98	1
4	24.10.96	6	2	9	3	3	6	75	9	6	10.09.96	19	0	21	0	19	21	100	2
4	28.10.96	10	1	9	0	10	9	95	0	6	10.09.96	17	5	14	4	13	11	78	3
4	28.10.96	19	0	21	0	19	21	100	1	6	10.09.96	14	4	15	7	10	9	73	4
4	28.10.96	21	0	19	0	21	19	100	2	6	10.09.96	15	3	18	4	9	12	83	5
4	28.10.96	14	1	19	6	10	12	83	3	6	10.09.96	11	1	8	0	8	4	95	9
4	28.10.96	10	5	15	10	8	5	63	4	6	12.09.96	11	0	9	0	6	5	100	0
4	28.10.96	10	1	8	1	6	6	90	9	6	12.09.96	18	1	19	2	16	16	93	1
										6	12.09.96	20	0	20	0	20	20	100	2
5	30.08.96	10	0	9	1	8	6	95	0	6	12.09.96	19	3	18	0	16	16	93	3
5	30.08.96	20	0	20	0	20	20	100	1	6	12.09.96	18	5	14	3	10	9	80	4
5	30.08.96	20	0	20	0	20	20	100	2	6	12.09.96	13	5	15	7	7	11	70	5
5	30.08.96	6	8	13	13	5	6	48	3	6	12.09.96	10	1	9	0	6	3	95	9
5	30.08.96	10	0	10	0	8	9	100	9	6	16.09.96	8	2	8	2	5	5	80	0
5	4.09.96	10	0	9	1	7	8	95	0	6	16.09.96	14	4	17	5	10	11	78	1
5	4.09.96	20	0	20	0	19	17	100	1	6	16.09.96	21	0	19	0	14	11	100	2
5	4.09.96	19	0	21	0	19	21	100	2	6	16.09.96	19	1	18	2	14	14	93	3
5	4.09.96	12	5	14	9	8	5	65	3	6	16.09.96	16	2	19	3	9	12	88	4
5	4.09.96	10	4	16	10	6	9	65	4	6	16.09.96	16	1	20	3	11	11	90	5
5	4.09.96	12	5	15	8	10	7	68	5	6	16.09.96	11	1	8	0	5	5	95	9
5	4.09.96	11	0	9	0	5	7	100	9	6	4.10.96	9	1	10	0	4	6	95	0
5	6.09.96	11	1	8	0	5	7	95	0	6	4.10.96	19	3	16	2	12	10	88	1
5	6.09.96	16	2	18	4	12	10	85	1	6	4.10.96	20	0	20	0	20	20	100	2
5	6.09.96	18	1	19	2	10	12	93	2	6	4.10.96	14	7	13	6	7	9	68	3
5	6.09.96	11	4																

subject	date	flicker trials		steady trials		sft	erft	%	tag
		correct	incorrect	correct	incorrect				
6	9.10.96	20	0	20	0	20	20	100	2
6	9.10.96	17	3	17	3	15	15	85	3
6	9.10.96	14	5	16	5	8	10	75	4
6	9.10.96	20	1	18	1	18	17	95	5
6	9.10.96	9	2	9	0	6	4	90	9

Appendix D - Experiment 3 threshold sessions (Large stimulus change threshold sessions in bold)

Possum number, date, number of correct and incorrect flickering trials, number of correct and incorrect steady trials, the number of reinforcements for correct flicker and steady trials, the overall percentage of correct responses in the current block of trials and the current flicker speed.

(0=16.67 Hz, 1=20.00 Hz, 2=25.00 Hz, 3=33.33 Hz, 4=50.00 Hz, 5=52.60 Hz, 6=55.60 Hz, 7=58.80 Hz, 8=62.50 Hz, 9=66.67 Hz, 10=71.42 Hz, 13=16.67 Hz)

flicker trials										steady trials										flicker trials										steady trials									
subject	date	correct	incorrect	correct	incorrect	frt	arft	%	tag	subject	date	correct	incorrect	correct	incorrect	frt	arft	%	tag	subject	date	correct	incorrect	correct	incorrect	frt	arft	%	tag										
1	23.11.96	9	5	6	0	3	5	75	0	1	16.12.96	11	0	9	0	11	9	100	8	1	16.12.96	8	3	8	1	6	8	80	9										
1	23.11.96	7	3	8	2	7	4	75	2	1	16.12.96	11	2	7	0	5	5	90	10	1	16.12.96	10	2	8	0	8	4	90	13										
1	23.11.96	11	2	7	0	7	7	90	3	1	16.12.96	10	2	8	0	8	4	90	13	1	18.12.96	8	2	7	3	5	5	75	0										
1	23.11.96	9	2	8	1	5	7	85	4	1	18.12.96	9	4	7	0	5	4	80	2	1	18.12.96	10	3	6	1	6	6	80	4										
1	23.11.96	9	3	8	0	7	5	85	5	1	18.12.96	10	3	6	1	6	6	80	4	1	18.12.96	8	4	6	2	4	5	70	6										
1	23.11.96	10	1	9	0	5	7	95	6	1	18.12.96	9	5	6	0	3	3	75	8	1	18.12.96	10	4	6	0	7	4	80	10										
1	23.11.96	10	2	7	1	7	5	85	7	1	18.12.96	11	2	7	0	5	7	90	13	1	18.12.96	11	2	7	0	5	7	90	13										
1	23.11.96	8	1	10	1	5	7	90	8	1	18.12.96	9	5	6	0	3	3	75	8	1	18.12.96	10	4	6	0	7	4	80	10										
1	23.11.96	11	1	8	0	5	6	95	9	1	18.12.96	11	2	7	0	5	7	90	13	1	18.12.96	11	2	7	0	5	7	90	13										
1	23.11.96	9	2	9	0	8	5	90	10	1	18.12.96	11	2	7	0	5	7	90	13	1	18.12.96	11	2	7	0	5	7	90	13										
1	23.11.96	11	1	8	0	6	6	95	13	1	18.12.96	11	2	7	0	5	7	90	13	1	18.12.96	11	2	7	0	5	7	90	13										
1	27.11.96	8	5	5	2	4	3	65	0	2	10.12.96	10	0	9	1	4	6	95	0	2	10.12.96	10	0	9	1	4	6	95	0										
1	27.11.96	11	0	9	0	11	9	100	2	2	10.12.96	8	2	9	1	5	6	85	1	2	10.12.96	11	1	8	0	10	7	95	2										
1	27.11.96	6	2	10	2	4	6	80	4	2	10.12.96	11	1	8	0	10	7	95	2	2	10.12.96	11	1	8	0	10	7	95	2										
1	27.11.96	7	2	8	3	3	5	75	6	2	10.12.96	8	2	9	1	5	9	85	3	2	10.12.96	11	1	8	0	10	7	95	2										
1	27.11.96	9	3	6	2	6	4	75	8	2	10.12.96	9	4	5	2	7	3	70	4	2	10.12.96	11	1	8	0	10	7	95	2										
1	27.11.96	9	0	11	0	9	11	100	10	2	10.12.96	8	5	5	2	3	3	65	5	2	10.12.96	11	1	8	0	10	7	95	2										
1	27.11.96	11	0	9	0	11	9	100	13	2	10.12.96	9	0	11	0	8	10	100	6	2	10.12.96	11	0	9	0	11	9	100	4										
1	29.11.96	9	2	7	2	5	4	80	0	2	10.12.96	10	0	10	0	10	10	100	7	2	10.12.96	11	0	9	0	11	9	100	8										
1	29.11.96	8	1	11	0	7	10	95	1	2	10.12.96	11	0	9	0	11	9	100	8	2	10.12.96	11	0	9	0	11	9	100	8										
1	29.11.96	6	5	5	4	4	3	55	2	2	10.12.96	7	0	11	2	5	7	90	9	2	10.12.96	11	0	9	0	11	9	100	8										
1	29.11.96	9	2	7	2	6	4	80	3	2	10.12.96	9	2	7	2	4	4	80	10	2	10.12.96	11	0	9	0	11	9	100	8										
1	29.11.96	5	3	8	4	3	4	65	4	2	10.12.96	9	2	9	0	5	5	90	13	2	10.12.96	11	0	9	0	11	9	100	8										
1	29.11.96	6	4	5	5	2	5	55	5	2	12.12.96	9	1	10	0	7	7	95	0	2	12.12.96	10	1	10	0	7	7	95	0										
1	29.11.96	10	1	9	0	9	4	95	6	2	12.12.96	10	0	10	0	10	10	100	2	2	12.12.96	10	0	10	0	10	10	100	2										
1	29.11.96	10	1	9	0	5	7	95	7	2	12.12.96	8	2	7	3	4	5	75	4	2	12.12.96	10	0	10	0	10	10	100	2										
1	29.11.96	9	3	6	2	4	5	75	8	2	12.12.96	5	3	8	4	5	3	65	6	2	12.12.96	10	0	10	0	10	10	100	2										
1	29.11.96	6	2	10	2	6	4	80	9	2	12.12.96	8	1	8	3	6	7	80	8	2	12.12.96	10	0	10	0	10	10	100	2										
1	29.11.96	8	3	7	2	3	6	75	10	2	12.12.96	9	1	10	0	9	9	95	10	2	12.12.96	10	0	10	0	10	10	100	2										
1	29.11.96	11	0	9	0	11	9	100	13	2	12.12.96	11	0	9	0	11	9	100	13	2	12.12.96	11	0	9	0	11	9	100	13										
1	3.12.96	6	6	5	3	3	4	55	0	2	16.12.96	10	1	8	1	7	7	90	0	2	16.12.96	10	1	8	1	7	7	90	0										
1	3.12.96	10	0	10	0	10	10	100	2	2	16.12.96	8	2	8	2	6	7	80	1	2	16.12.96	10	1	9	0	8	5	95	2										
1	3.12.96	9	0	9	2	8	7	90	4	2	16.12.96	10	1	9	0	8	5	95	2	2	16.12.96	10	1	9	0	8	5	95	2										
1	3.12.96	8	3	8	1	5	4	80	6	2	16.12.96	10	1	8	1	6	7	90	3	2	16.12.96	10	1	8	1	6	7	90	3										
1	3.12.96	10	1	8	1	4	6	90	8	2	16.12.96	8	4	7	1	3	4	75	4	2	16.12.96	10	1	9	0	8	5	95	2										
1	3.12.96	9	2	9	0	3	5	90	10	2	16.12.96	8	3	7	2	6	4	75	5	2	16.12.96	10	1	9	0	8	5	95	2										
1	3.12.96	11	2	7	0	9	4	90	13	2	16.12.96	9	2	7	2	5	7	80	6	2	16.12.96	10	1	9	0	8	5	95	2										
1	5.12.96	10	2	8	0	7	4	90	0	2	16.12.96	7	3	9	1	4	5	80	7	2	16.12.96	11	0	9	0	10	9	100	8										
1	5.12.96	9	0	11	0	9	11	100	1	2	16.12.96	11	0	9	0	10	9	100	8	2	16.12.96	11	0	9	0	10	9	100	8										
1	5.12.96	9	2	8	1	8	5	85	2	2	16.12.96	7	4	6	3	4	4	65	9	2	16.12.96	11	0	9	0	10	9	100	8										
1	5.12.96	10	2	7	1	5	6	85	3	2	16.12.96	8	3	7	2	5	5	75	10	2	16.12.96	11	0	9	0	10	9	100	8										
1	5.12.96	9	2	9	0	4	6	90	4	2	16.12.96	11	1	8	0	7	7	95	13	2	16.12.96	11	0	9	0	10	9	100	8										
1	5.12.96	11	1	8	0	8	6	95	5	2	18.12.96	10	2	8	0	8	4	90	0	2	18.12.96	10	2	8	0	8	4	90	0										
1	5.12.96	9	1	10	0	7	10	95	6	2	18.12.96	10	1	9	0	5	7	95	2	2	18.12.96	10	1	9	0	5	7	95	2										
1	5.12.96	11	3	6	0	7	3	85	7	2	18.12.96	11	0	9	0	11	9	100	4	2	18.12.96	11	0	9	0	11	9	100	4										
1	5.12.96	10	2	8	0	3	7	90	8	2	18.12.96	8	0	12	0	8	12	100	6	2	18.12.96	10	0	10	0	10	10	100	6										
1	5.12.96	9	4	7	0	4	4	80	9	2	18.12.96	10	0	10	0	10	10	100	8	2	18.12.96	10	0	10	0	10	10	100	8										
1	5.12.96	10	1	9	0	8	5	95	10	2	18.12.96	11	0	9	0	11	9	100	10	2	18.12.96	11	0	9	0	11	9	100	10										
1	5.12.96	11	1	8	0	4	6	95	13	2	18.12.96	9	1	10	0	9	10	95	13	2	18.12.96	9	1	10	0	9	10	95	13										
1	7.12.96	11	1	8	0	10	8	95	0	2	20.12.96	9	1	9	1	9	8	90	0	2	20.12.96	10	0	10	0	10	10	100	1										
1	7.12.96	10	0	10	0	10	10	100	2	2	20.12.96	10	0	1																									

subject	date	flicker trials		steady trials		frft	arft	%	tag	subject	date	flicker trials		steady trials		frft	arft	%	tag
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2	9.01.97	11	0	9	0	11	9	100	2	3	3.01.97	10	0	10	0	10	10	100	6
2	9.01.97	5	2	9	4	4	5	70	4	3	3.01.97	9	2	7	2	6	6	80	8
2	9.01.97	10	2	7	1	5	5	85	5	3	3.01.97	8	2	10	0	7	6	90	10
2	9.01.97	8	2	8	2	6	6	80	6	3	3.01.97	10	3	6	1	3	4	80	13
2	9.01.97	6	7	4	3	4	4	50	10	3	7.01.97	11	1	8	0	5	6	95	0
2	9.01.97	10	2	8	0	4	5	90	13	3	7.01.97	9	2	8	1	6	4	85	1
2	23.01.97	8	1	11	0	5	6	95	0	3	7.01.97	6	4	7	3	4	6	65	2
2	23.01.97	9	3	6	2	5	3	75	1	3	7.01.97	9	3	7	1	3	5	80	3
2	23.01.97	8	3	7	2	3	6	75	2	3	7.01.97	9	2	7	2	6	3	80	4
2	23.01.97	9	2	8	1	5	5	85	3	3	7.01.97	7	6	5	2	3	3	60	5
2	23.01.97	8	2	7	3	6	4	75	4	3	7.01.97	7	4	5	4	2	4	60	6
2	23.01.97	8	3	8	1	5	5	80	5	3	7.01.97	8	2	9	1	8	8	85	7
2	23.01.97	8	2	8	2	5	7	80	6	3	7.01.97	11	0	9	0	11	9	100	8
2	23.01.97	9	0	9	2	8	5	90	7	3	7.01.97	9	1	9	1	6	8	90	9
2	23.01.97	8	0	12	0	8	12	100	8	3	7.01.97	7	3	8	2	5	3	75	10
2	23.01.97	11	0	9	0	11	9	100	9	3	7.01.97	9	1	9	1	4	5	90	13
2	23.01.97	9	1	9	1	8	8	90	10	3	9.01.97	6	2	10	2	3	6	80	0
2	23.01.97	10	3	7	0	6	4	85	13	3	9.01.97	10	0	10	0	10	10	100	2
2	25.01.97	11	0	9	0	6	8	100	0	3	9.01.97	6	4	5	5	4	3	55	4
2	25.01.97	9	1	10	0	8	5	95	2	3	9.01.97	8	3	8	1	4	4	80	6
2	25.01.97	10	1	8	1	6	6	90	4	3	9.01.97	6	1	8	5	5	3	70	8
2	25.01.97	10	0	10	0	10	10	100	6	3	9.01.97	9	4	6	1	2	4	75	10
2	25.01.97	9	0	11	0	9	11	100	8	3	9.01.97	10	1	9	0	5	7	95	13
2	25.01.97	10	0	10	0	10	10	100	10	3	13.01.97	5	3	6	6	2	4	55	0
2	25.01.97	11	1	8	0	8	7	95	13	3	13.01.97	8	3	8	1	5	4	80	1
2	29.01.97	7	2	9	2	5	8	80	0	3	13.01.97	9	2	7	2	5	4	80	2
2	29.01.97	10	2	7	1	7	3	85	1	3	13.01.97	8	1	9	2	5	4	85	3
2	29.01.97	9	2	8	1	4	6	85	2	3	13.01.97	8	2	8	2	3	5	80	4
2	29.01.97	8	2	9	1	7	7	85	3	3	13.01.97	9	3	6	2	7	4	75	5
2	29.01.97	9	3	7	1	9	7	80	4	3	13.01.97	7	2	10	1	6	9	85	6
2	29.01.97	8	2	7	3	4	6	75	5	3	13.01.97	8	3	7	2	4	4	75	7
2	29.01.97	8	4	7	1	6	5	75	6	3	13.01.97	9	4	5	2	6	3	70	8
2	29.01.97	10	0	9	1	7	8	95	7	3	13.01.97	7	3	8	2	3	7	75	9
2	29.01.97	9	1	10	0	8	8	95	8	3	13.01.97	9	1	8	2	4	5	85	10
2	29.01.97	10	1	8	1	8	8	90	9	3	13.01.97	10	2	8	0	9	4	90	13
2	29.01.97	9	2	8	1	4	6	85	10										
2	29.01.97	8	3	8	1	7	3	80	13	4	25.11.96	5	4	8	3	4	3	65	0
										4	25.11.96	10	1	9	0	7	8	95	1
3	6.12.96	10	2	7	1	5	7	85	0	4	25.11.96	6	2	7	5	4	3	65	2
3	6.12.96	7	1	11	1	4	5	90	1	4	25.11.96	7	1	10	2	5	6	85	3
3	6.12.96	6	2	8	4	4	3	70	2	4	25.11.96	10	0	9	1	7	8	95	4
3	6.12.96	5	2	7	6	4	3	60	3	4	25.11.96	9	0	10	1	9	7	95	5
3	6.12.96	7	1	10	2	4	5	85	4	4	25.11.96	10	0	10	0	10	10	100	6
3	6.12.96	9	0	9	2	5	6	90	5	4	25.11.96	10	0	9	1	9	8	95	7
3	6.12.96	2	5	5	8	2	1	35	6	4	25.11.96	7	0	12	1	4	6	95	8
3	6.12.96	9	1	9	1	9	9	90	13	4	25.11.96	9	1	9	1	5	7	90	9
3	10.12.96	7	1	11	1	6	8	90	0	4	25.11.96	9	0	9	2	7	3	90	10
3	10.12.96	10	0	10	0	10	10	100	2	4	25.11.96	9	0	11	0	8	11	100	13
3	10.12.96	8	2	7	3	4	3	75	4	4	27.11.96	9	0	9	2	6	4	90	0
3	10.12.96	5	3	8	4	3	4	65	6	4	27.11.96	6	1	11	2	5	7	85	2
3	10.12.96	8	1	8	3	7	4	80	8	4	27.11.96	5	0	9	6	5	5	70	4
3	10.12.96	9	0	10	1	6	6	95	10	4	27.11.96	9	0	10	1	6	5	95	6
3	10.12.96	8	2	8	2	3	5	80	13	4	27.11.96	8	1	9	2	5	6	85	8
3	12.12.96	9	2	9	0	5	6	90	0	4	27.11.96	8	1	8	3	7	6	80	10
3	12.12.96	10	1	8	1	7	7	90	1	4	27.11.96	8	1	10	1	5	5	90	13
3	12.12.96	7	1	9	3	7	7	80	2	4	29.11.96	8	2	9	1	4	4	85	0
3	12.12.96	8	3	7	2	7	4	75	3	4	29.11.96	8	0	10	2	6	8	90	1
3	12.12.96	11	1	8	0	5	7	95	4	4	29.11.96	8	1	8	3	6	3	80	2
3	12.12.96	7	3	9	1	3	5	80	5	4	29.11.96	8	0	11	1	8	11	95	3
3	12.12.96	8	3	7	2	8	5	75	6	4	29.11.96	5	3	6	6	4	3	55	4
3	12.12.96	9	1	8	2	5	6	85	7	4	29.11.96	5	2	9	4	4	3	70	5
3	12.12.96	6	3	8	3	2	5	70	8	4	29.11.96	11	0	9	0	8	7	100	6
3	12.12.96	9	1	8	2	8	4	85	11	4	29.11.96	10	0	10	0	10	10	100	7
3	12.12.96	9	3	7	1	4	6	80	12	4	29.11.96	7	2	9	2	5	6	80	8
3	12.12.96	10	0	10	0	6	6	100	13	4	29.11.96	8	2	8	2	4	5	80	9
3	16.12.96	8	1	9	2	7	6	85	0	4	29.11.96	10	1	8	1	8	6	90	10
3	16.12.96	10	0	10	0	10	10	100	2	4	29.11.96	9	1	10	0	6	8	95	13
3	16.12.96	9	1	8	2	7	7	85	4	4	6.12.96	9	0	10	1	5	8	95	0
3	16.12.96	7	4	8	1	6	5	75	6	4	6.12.96	6	2	8	4	3	4	70	2
3	16.12.96	6	4	6	4	1	4	60	8	4	6.12.96	10	1	8	1	8	5	90	4
3	16.12.96	11	0	9	0	10	8	100	10	4	6.12.96	9	0	11	0	9	11	100	6
3	16.12.96	9	0	11	0	9	11	100	13	4	6.12.96	9	0	10	1	8	7	95	8
3	19.12.96	11	0	9	0	5	6	100	0	4	6.12.96	6	2	7	5	4	4	65	10

subject	date	flicker trials		steady trials		frt	arft	%	tag	subject	date	flicker trials		steady trials		frt	arft	%	tag
		correct	incorrect	correct	incorrect							correct	incorrect	correct	incorrect				
4	13.12.96	9	1	10	0	7	8	95	0	5	3.12.96	8	4	6	2	6	4	70	7
4	13.12.96	10	0	10	0	10	10	100	1	5	3.12.96	9	2	7	2	3	5	80	8
4	13.12.96	10	0	9	1	10	9	95	2	5	3.12.96	7	4	7	2	4	4	70	9
4	13.12.96	6	1	10	3	5	4	80	3	5	3.12.96	9	1	8	2	7	6	85	10
4	13.12.96	9	0	9	2	5	7	90	4	5	3.12.96	9	3	8	0	5	6	85	13
4	13.12.96	8	1	10	1	5	5	90	5	5	5.12.96	11	0	9	0	10	8	100	0
4	13.12.96	10	0	9	1	10	8	95	6	5	5.12.96	10	0	10	0	10	10	100	2
4	13.12.96	10	0	10	0	10	10	100	7	5	5.12.96	7	0	11	2	5	6	90	4
4	13.12.96	9	0	11	0	9	11	100	8	5	5.12.96	6	3	7	4	2	5	65	6
4	13.12.96	10	0	10	0	10	10	100	9	5	5.12.96	8	3	6	3	7	3	70	8
4	13.12.96	10	0	9	1	8	7	95	10	5	5.12.96	9	0	11	0	9	11	100	10
4	13.12.96	7	2	9	2	5	4	80	13	5	5.12.96	11	0	9	0	11	9	100	13
4	17.12.96	7	1	10	2	5	6	85	0	5	7.12.96	9	0	11	0	6	10	100	0
4	17.12.96	11	0	9	0	11	9	100	2	5	7.12.96	11	0	9	0	11	9	100	1
4	17.12.96	10	0	10	0	10	10	100	4	5	7.12.96	10	0	10	0	10	10	100	2
4	17.12.96	9	0	11	0	9	11	100	6	5	7.12.96	10	0	10	0	10	10	100	3
4	17.12.96	10	0	10	0	10	10	100	8	5	7.12.96	9	1	8	2	5	6	85	4
4	17.12.96	11	0	9	0	11	9	100	10	5	7.12.96	6	3	9	2	5	3	75	5
4	17.12.96	8	0	11	1	5	7	95	13	5	7.12.96	9	3	7	1	3	6	80	6
4	19.12.96	10	0	9	1	8	8	95	0	5	7.12.96	10	2	7	1	7	6	85	7
4	19.12.96	9	0	11	0	9	11	100	1	5	7.12.96	6	4	7	3	3	3	65	8
4	19.12.96	10	0	9	1	10	7	95	2	5	7.12.96	9	6	3	2	5	2	60	9
4	19.12.96	8	0	11	1	5	7	95	3	5	7.12.96	6	4	6	4	2	5	60	10
4	19.12.96	9	1	8	2	5	5	85	4	5	7.12.96	10	0	10	0	6	6	100	13
4	19.12.96	9	0	10	1	7	7	95	5	5	10.12.96	11	1	8	0	10	7	95	0
4	19.12.96	9	0	11	0	7	8	100	6	5	10.12.96	8	0	12	0	8	12	100	2
4	19.12.96	9	0	10	1	8	5	95	7	5	10.12.96	7	4	6	3	6	3	65	4
4	19.12.96	9	1	8	2	5	6	85	8	5	10.12.96	7	2	7	4	3	5	70	6
4	19.12.96	6	1	10	3	3	6	80	9	5	10.12.96	6	2	9	3	4	5	75	8
4	19.12.96	11	1	8	0	9	6	95	10	5	10.12.96	6	5	4	5	2	2	50	10
4	19.12.96	9	0	11	0	9	11	100	13	5	10.12.96	10	1	9	0	9	5	95	13
4	3.01.97	11	1	8	0	6	6	95	0	6	14.11.96	9	2	7	2	4	4	80	0
4	3.01.97	9	1	10	0	6	8	95	2	6	14.11.96	8	2	9	1	4	4	85	1
4	3.01.97	10	1	8	1	10	8	90	4	6	14.11.96	5	3	7	5	3	4	60	2
4	3.01.97	9	1	9	1	5	5	90	6	6	14.11.96	5	3	7	5	3	4	60	2
4	3.01.97	8	0	10	2	5	6	90	8	6	14.11.96	7	1	8	4	5	3	75	3
4	3.01.97	10	1	8	1	7	6	90	10	6	14.11.96	3	5	7	5	2	2	50	4
4	3.01.97	8	0	12	0	7	9	100	13	6	14.11.96	8	0	9	3	4	6	85	5
5	14.11.96	7	1	9	3	5	6	80	0	6	14.11.96	8	2	8	2	6	5	80	7
5	14.11.96	11	0	9	0	10	6	100	2	6	14.11.96	11	0	9	0	5	7	100	8
5	14.11.96	5	3	8	4	4	5	65	4	6	14.11.96	8	1	10	1	6	4	90	9
5	14.11.96	4	7	3	6	2	3	35	6	6	14.11.96	6	2	8	4	6	5	70	10
5	14.11.96	11	0	9	0	8	6	100	13	6	14.11.96	9	1	8	2	4	6	85	13
5	20.11.96	0	0	11	9	0	1	55	0	6	19.11.96	8	1	9	2	5	3	85	0
5	20.11.96	10	0	9	1	5	7	95	1	6	19.11.96	8	3	7	2	4	4	75	2
5	20.11.96	10	0	10	0	9	7	100	2	6	19.11.96	5	4	5	6	2	4	50	4
5	20.11.96	5	1	9	5	5	3	70	3	6	19.11.96	7	4	7	2	4	4	70	6
5	20.11.96	5	1	8	6	2	4	65	4	6	19.11.96	8	4	6	2	5	3	70	8
5	20.11.96	3	4	8	5	2	3	55	5	6	19.11.96	9	2	7	2	5	4	80	10
5	20.11.96	5	2	8	5	3	5	65	6	6	19.11.96	8	0	12	0	6	10	100	13
5	20.11.96	8	2	7	3	6	3	75	13	6	21.11.96	8	2	7	3	6	4	75	0
5	22.11.96	10	0	9	1	9	7	95	0	6	21.11.96	8	0	12	0	6	10	100	2
5	22.11.96	10	0	10	0	10	10	100	1	6	21.11.96	11	0	9	0	11	9	100	4
5	22.11.96	8	1	9	2	6	5	85	2	6	21.11.96	10	0	10	0	10	10	100	6
5	22.11.96	8	2	7	3	5	6	75	3	6	21.11.96	9	1	9	1	6	7	90	8
5	22.11.96	4	5	7	4	2	4	55	4	6	21.11.96	10	1	8	1	5	5	90	10
5	22.11.96	8	3	7	2	7	4	75	5	6	21.11.96	9	1	10	0	8	5	95	13
5	22.11.96	7	3	6	4	4	6	65	6	6	25.11.96	9	1	9	1	5	4	90	0
5	22.11.96	7	0	11	2	4	6	90	7	6	25.11.96	10	2	7	1	6	4	85	1
5	22.11.96	11	0	9	0	10	7	100	8	6	25.11.96	6	4	8	2	5	6	70	2
5	22.11.96	10	0	10	0	10	10	100	9	6	25.11.96	8	3	7	2	3	5	75	3
5	22.11.96	10	0	10	0	10	10	100	10	6	25.11.96	10	2	7	1	8	5	85	4
5	22.11.96	11	0	9	0	11	9	100	13	6	25.11.96	9	1	10	0	6	9	95	5
5	25.11.96	7	2	9	2	5	5	80	0	6	25.11.96	11	0	9	0	11	9	100	6
5	25.11.96	10	0	9	1	5	7	95	2	6	25.11.96	10	0	10	0	10	10	100	7
5	25.11.96	8	1	9	2	6	4	85	4	6	25.11.96	10	0	10	0	10	10	100	8
5	25.11.96	5	5	5	5	3	2	50	6	6	25.11.96	11	0	9	0	11	9	100	9
5	25.11.96	9	1	8	2	4	6	85	8	6	25.11.96	8	0	12	0	8	12	100	10
5	25.11.96	5	4	8	3	3	4	65	10	6	25.11.96	10	0	10	0	10	10	100	13
5	25.11.96	9	1	9	1	7	5	90	13	6	27.11.96	10	0	10	0	5	5	100	0
5	27.11.96	11	0	9	0	11	8	100	0	6	27.11.96	11	0	9	0	8	6	100	2
5	27.11.96	9	0	11	0	9	11	100	1	6	27.11.96	7	0	11	2	6	8</		

subject	date	flicker trials		steady trials		fitt	wft	%	tag
		correct	incorrect	correct	incorrect				
6	3.12.96	7	1	8	4	5	3	75	10
6	3.12.96	10	1	9	0	5	7	95	13
6	5.12.96	10	0	9	1	5	7	95	0
6	5.12.96	8	1	11	0	7	6	95	1
6	5.12.96	8	0	10	2	5	7	90	2
6	5.12.96	11	0	9	0	11	9	100	3
6	5.12.96	8	1	10	1	8	8	90	4
6	5.12.96	9	2	7	2	5	6	80	5
6	5.12.96	9	2	8	1	6	4	85	6
6	5.12.96	10	0	10	0	5	6	100	7
6	5.12.96	11	0	9	0	11	9	100	8
6	5.12.96	8	0	12	0	8	12	100	9
6	5.12.96	10	1	9	0	9	7	95	10
6	5.12.96	9	0	9	2	4	6	90	13
6	7.12.96	11	0	9	0	11	8	100	0
6	7.12.96	9	0	11	0	9	11	100	0
6	7.12.96	10	1	8	1	6	4	90	2
6	7.12.96	8	1	9	2	5	6	85	4
6	7.12.96	9	1	10	0	5	5	95	6
6	7.12.96	10	3	7	0	6	4	85	8
6	7.12.96	11	0	9	0	5	6	100	13
6	10.12.96	11	0	9	0	6	8	100	0
6	10.12.96	10	0	10	0	9	7	100	1
6	10.12.96	10	0	10	0	10	10	100	2
6	10.12.96	11	0	9	0	11	9	100	3
6	10.12.96	7	0	12	1	7	11	95	4
6	10.12.96	10	0	10	0	7	4	100	5
6	10.12.96	10	1	8	1	4	7	90	6
6	10.12.96	7	2	9	2	5	5	80	7
6	10.12.96	11	0	9	0	10	8	100	8
6	10.12.96	10	0	10	0	10	10	100	9
6	10.12.96	10	0	10	0	10	10	100	10
6	10.12.96	11	0	9	0	11	9	100	13

Appendix E - Experiment 4 threshold sessions

Possum number, date, number of correct and incorrect flickering trials, number of correct and incorrect steady trials, the number of reinforcements for correct flicker and steady trials, the overall proportion of correct responses in the current block of trials and the current flicker speed.

(0=16.67 Hz, 1= 20.00 Hz, 2=25.0 Hz, 3=33.33 Hz, 4=50.00 Hz, 5=52.60 Hz, 6=55.60 Hz, 7=58.80 Hz, 8=62.50 Hz, 9=66.67 Hz, 10=71.42 Hz, 13=16.67 Hz)

Relay

subject	date	flicker trials		steady trials		ftr	str	%	tag	subject	date	flicker trials		steady trials		ftr	str	%	tag
		correct	incorrect	correct	incorrect							correct	incorrect						
1	13.01.97	9	4	6	1	2	4	75	0	5	25.01.97	7	2	9	2	5	8	80	8
1	13.01.97	11	2	7	0	6	4	90	1	5	25.01.97	10	3	6	1	4	5	80	9
1	13.01.97	6	6	5	3	4	4	55	2	5	25.01.97	8	5	6	1	5	2	70	10
1	13.01.97	8	4	5	3	2	3	65	3	5	25.01.97	11	0	9	0	10	9	100	13
1	13.01.97	8	2	8	2	6	6	80	4	5	22.02.97	11	2	7	0	6	4	90	0
1	13.01.97	9	4	6	1	6	3	75	5	5	22.02.97	9	0	11	0	5	7	100	1
1	13.01.97	11	2	7	0	3	6	90	6	5	22.02.97	10	0	9	1	10	7	95	2
1	13.01.97	7	3	9	1	4	5	80	7	5	22.02.97	8	0	11	1	5	7	95	3
1	13.01.97	10	2	8	0	7	5	90	8	5	22.02.97	9	1	8	2	5	5	85	4
1	13.01.97	9	4	5	2	4	4	70	9	5	22.02.97	8	1	9	2	6	6	85	5
1	13.01.97	9	3	8	0	4	5	85	10	5	22.02.97	8	2	9	1	6	7	85	6
1	13.01.97	11	2	7	0	5	5	90	13	5	22.02.97	7	5	5	3	1	2	60	7
1	17.01.97	11	1	8	0	6	6	95	13	5	22.02.97	8	3	6	3	6	3	70	8
1	22.01.97	9	2	8	1	4	6	85	0	5	22.02.97	9	0	11	0	9	11	100	9
1	22.01.97	6	5	5	4	3	3	55	1	5	22.02.97	11	0	9	0	11	9	100	10
1	22.01.97	8	3	6	3	6	4	70	2	5	22.02.97	9	2	9	0	5	9	90	13
1	22.01.97	7	4	7	2	3	5	70	3	5	25.02.97	7	2	9	2	5	6	80	0
1	22.01.97	6	4	6	4	4	2	60	4	5	25.02.97	11	0	9	0	7	5	100	1
1	22.01.97	7	3	6	4	2	5	65	5	5	25.02.97	8	0	11	1	8	10	95	2
1	22.01.97	7	4	8	1	7	4	75	6	5	25.02.97	8	3	6	3	6	3	70	3
1	22.01.97	11	0	9	0	4	7	100	7	5	25.02.97	9	0	10	1	5	7	95	4
1	22.01.97	10	1	9	0	9	8	95	8	5	25.02.97	7	2	9	2	4	5	80	5
1	22.01.97	8	2	8	2	6	5	80	9	5	25.02.97	8	2	8	2	7	4	80	6
1	22.01.97	9	2	7	2	4	5	80	10	5	25.02.97	8	2	7	3	3	6	75	7
1	22.01.97	9	1	10	0	6	5	95	13	5	25.02.97	6	2	9	3	4	6	75	8
1	24.01.97	10	1	9	0	9	9	95	13	5	25.02.97	7	2	7	4	6	3	70	9
1	28.01.97	8	3	7	2	2	6	75	0	5	25.02.97	8	3	8	1	4	3	80	10
1	28.01.97	11	0	9	0	11	9	100	1	5	25.02.97	11	0	9	0	5	5	100	13
1	28.01.97	7	0	11	2	5	7	90	2	5	27.02.97	11	2	7	0	5	5	90	0
1	28.01.97	8	3	6	3	4	4	70	3	5	27.02.97	8	1	11	0	6	8	95	1
1	28.01.97	10	2	8	0	6	4	90	4	5	27.02.97	10	0	10	0	10	10	100	2
1	28.01.97	10	0	10	0	9	9	100	5	5	27.02.97	8	3	6	3	4	3	70	3
1	28.01.97	11	0	9	0	11	9	100	6	5	27.02.97	9	1	10	0	5	5	95	4
1	28.01.97	8	0	12	0	8	12	100	7	5	27.02.97	10	0	9	1	7	8	95	5
1	28.01.97	9	0	10	1	9	7	95	8	5	27.02.97	7	2	8	3	7	6	75	6
1	28.01.97	10	3	6	1	4	5	80	9	5	27.02.97	6	3	7	4	5	3	65	7
1	28.01.97	9	2	9	0	6	6	90	10	5	27.02.97	8	1	8	3	4	4	80	8
1	28.01.97	11	0	9	0	7	8	100	13	5	27.02.97	4	3	9	4	2	4	65	9
1	25.02.97	9	0	11	0	8	11	100	0	5	27.02.97	7	2	8	3	3	5	75	10
1	25.02.97	11	0	9	0	11	9	100	1	5	27.02.97	11	2	7	0	7	3	90	13
1	25.02.97	9	0	10	1	8	9	95	2	6	19.12.96	7	2	9	2	4	3	80	0
1	25.02.97	8	3	7	2	6	3	75	3	6	19.12.96	10	1	9	0	7	5	95	1
1	25.02.97	10	2	7	1	4	7	85	4	6	19.12.96	9	1	8	2	5	7	85	2
1	25.02.97	7	2	10	1	5	6	85	5	6	19.12.96	7	2	9	2	5	6	80	3
1	25.02.97	9	2	8	1	8	5	85	6	6	19.12.96	10	1	8	1	10	7	90	4
1	25.02.97	11	1	8	0	5	6	95	7	6	19.12.96	9	0	11	0	9	11	100	5
1	25.02.97	9	1	10	0	4	5	95	8	6	19.12.96	10	0	11	0	10	9	100	6
1	25.02.97	11	0	9	0	8	7	100	9	6	19.12.96	11	0	9	0	11	9	100	6
1	25.02.97	9	0	10	1	8	9	95	10	6	19.12.96	10	0	10	0	10	10	100	7
1	25.02.97	10	1	9	0	6	4	95	13	6	19.12.96	9	0	11	0	9	11	100	8
1	28.02.97	10	1	9	0	4	6	95	0	6	19.12.96	10	0	10	0	10	10	100	9
1	28.02.97	11	0	9	0	11	9	100	1	6	19.12.96	11	0	9	0	11	9	100	10
1	28.02.97	9	0	11	0	9	11	100	2	6	19.12.96	9	0	11	0	9	11	100	13
1	28.02.97	10	1	9	0	9	9	95	3	6	3.01.97	11	0	9	0	11	8	100	0
1	28.02.97	10	2	7	1	4	5	85	4	6	3.01.97	9	0	11	0	9	11	100	1
1	28.02.97	8	3	9	0	5	4	85	5	6	3.01.97	11	0	9	0	11	9	100	2
1	28.02.97	11	1	8	0	6	7	95	6	6	3.01.97	9	2	9	0	4	6	90	3
1	28.02.97	10	1	9	0	10	9	95	7	6	3.01.97	10	2	7	1	5	4	85	4
1	28.02.97	9	1	9	1	9	8	90	8	6	3.01.97	10	1	9	0	6	6	95	5
1	28.02.97	10	2	7	1	5	6	85	9	6	3.01.97	9	0	11	0	8	9	100	6
1	28.02.97	8	4	7	1	7	4	75	10	6	3.01.97	10	0	10	0	10	10	100	7
1	28.02.97	10	1	9	0	4	6	95	13	6	3.01.97	11	0	9	0	11	9	100	8
										6	3.01.97	5	5	6	4	3	2	55	9
5	23.12.96	9	2	8	1	3	6	85	0	6	3.01.97	9	2	7	2	4	6	80	10
5	23.12.96	11	0	9	0	11	9	100	1	6	3.01.97	9	0	11	0	6	7	100	13
5	23.12.96	6	0	12	2	4	7	90	2	6	9.01.97	6	2	8	4	2	6	70	0
5	23.12.96	7	2	7	4	4	5	70	3	6	9.01.97	7	3	6	4	4	4	65	1
5	23.12.96	9	2	8	1	6	3	85	4	6	9.01.97	9	2	9	0	8	5	90	2
5	23.12.96	7	5	5	3	5	4	60	5	6	9.01.97	8	1	9	2	5	7	85	3
5	23.12.96	7	4	5	4	3	4	60	6	6	9.01.97	11	0	9	0	11	9	100	4
5	23.12.96	7	3	8	2	5	6	75	7	6	9.01.97	8	0	12	0	8	12	100	5
5	23.12.96	9	1	9	1	9	9	90	8	6	9.01.97	11	0	9	0	11	9	100	6
5	23.12.96	8	3	6	3	3	3	70	9	6	9.01.97	10	0	10	0	10	10	100	7
5	23.12.96	5	3	9	3	3	4	70	10	6	9.01.97	8	1	9	2	6	7	85	8
5	23.12.96	10	2	7	1	8	6	85	13	6	9.01.97	10	0	9	1	5	6	95	9
5	25.01.97	9	2	9	0	6	3	90	0	6	9.01.97	8	2	9	1	6	3		

flicker trials										steady trials										flicker trials										steady trials									
subject	date	correct	incorrect	correct	incorrect	flit	arft	%	tag	subject	date	correct	incorrect	correct	incorrect	flit	arft	%	tag	subject	date	correct	incorrect	correct	incorrect	flit	arft	%	tag										
5	31.01.97	7	6	3	4	1	1	50	9	6	11.02.97	6	3	8	3	5	3	70	7	6	11.02.97	7	1	8	4	5	6	75	8										
5	31.01.97	6	1	11	2	5	8	85	10	6	11.02.97	7	1	8	4	5	6	75	8	6	11.02.97	7	1	9	3	5	6	80	9										
5	31.01.97	11	1	8	0	7	6	95	13	6	11.02.97	7	1	9	3	5	6	80	9	5	6.02.97	8	2	9	1	4	6	85	0										
5	6.02.97	8	2	9	1	4	6	85	0	6	11.02.97	9	3	7	1	7	4	80	10	5	6.02.97	11	0	9	0	8	6	100	1										
5	6.02.97	11	0	9	0	8	6	100	1	6	11.02.97	10	0	9	1	5	7	95	13	6	6.02.97	6	2	8	4	4	70	2											
5	6.02.97	6	2	8	4	4	4	70	2	Equal-luminance																													
5	6.02.97	5	4	6	5	2	4	55	3	1	17.09.97	9	3	8	0	5	3	85	0	1	17.09.97	11	1	8	0	2	6	95	1										
5	6.02.97	7	2	7	4	5	3	70	4	1	17.09.97	7	4	6	3	3	0	65	2	1	17.09.97	11	1	8	0	2	6	95	1										
5	6.02.97	6	2	10	2	5	5	80	5	1	17.09.97	7	4	6	3	3	0	65	2	1	17.09.97	4	3	7	6	1	5	55	3										
5	6.02.97	7	4	6	3	3	4	70	7	1	17.09.97	4	3	7	6	1	5	55	3	1	17.09.97	7	4	5	4	4	1	60	4										
5	6.02.97	8	3	6	3	3	4	70	7	1	17.09.97	6	4	8	2	3	3	70	5	1	17.09.97	6	4	8	2	3	3	70	5										
5	6.02.97	5	3	8	4	4	3	65	8	1	17.09.97	7	4	5	4	4	1	60	4	1	17.09.97	5	6	4	5	6	4	50	6										
5	6.02.97	7	3	6	4	6	5	65	9	1	17.09.97	6	4	8	2	3	3	70	5	1	17.09.97	6	4	8	2	3	3	70	5										
5	6.02.97	4	5	5	6	2	4	45	10	1	17.09.97	5	6	4	5	3	1	45	6	1	17.09.97	11	4	5	0	1	4	80	13										
5	6.02.97	10	2	8	0	6	5	90	13	1	17.09.97	11	4	5	0	1	4	80	13	1	19.09.97	8	3	7	2	2	2	75	0										
5	8.02.97	10	0	9	1	8	5	95	0	1	19.09.97	8	3	7	2	2	2	75	0	1	19.09.97	10	1	9	0	3	4	95	1										
5	8.02.97	7	0	12	1	3	6	95	1	1	19.09.97	10	1	9	0	3	4	95	1	1	19.09.97	6	2	7	5	3	1	65	2										
5	8.02.97	7	1	9	3	6	6	80	2	1	19.09.97	6	2	7	5	3	1	65	2	1	19.09.97	5	6	5	4	2	2	50	3										
5	8.02.97	10	2	7	1	6	4	85	3	1	19.09.97	5	6	5	4	2	2	50	3	1	19.09.97	6	4	6	4	2	0	60	4										
5	8.02.97	7	2	9	2	5	7	80	4	1	19.09.97	6	4	6	5	1	2	60	5	1	19.09.97	6	3	6	5	1	2	60	5										
5	8.02.97	9	3	6	2	4	4	75	5	1	19.09.97	6	3	6	5	1	2	60	5	1	19.09.97	4	6	6	4	1	1	50	6										
5	8.02.97	8	2	8	2	6	4	80	6	1	19.09.97	4	6	6	4	1	1	50	6	1	19.09.97	4	3	6	7	2	4	50	7										
5	8.02.97	5	4	6	5	3	2	55	7	1	19.09.97	4	3	6	7	2	4	50	7	1	19.09.97	6	4	6	4	2	1	60	8										
5	8.02.97	7	2	7	4	2	4	70	8	1	19.09.97	6	4	6	4	2	1	60	8	1	19.09.97	4	3	7	6	1	4	55	9										
5	8.02.97	5	1	11	3	4	5	80	9	1	19.09.97	4	3	7	6	1	4	55	9	1	19.09.97	5	4	5	6	4	2	50	10										
5	8.02.97	7	3	7	3	5	4	70	10	1	19.09.97	5	4	5	6	4	2	50	10	1	19.09.97	9	2	9	0	3	2	90	13										
5	8.02.97	11	3	6	0	6	5	85	13	1	19.09.97	9	2	9	0	3	2	90	13	1	24.09.97	10	0	9	1	4	4	95	0										
5	11.02.97	9	0	11	0	8	10	100	0	1	24.09.97	10	0	9	1	4	4	95	0	1	24.09.97	10	3	7	0	5	2	85	1										
5	11.02.97	11	0	9	0	11	9	100	1	1	24.09.97	10	3	7	0	5	2	85	1	1	24.09.97	5	1	9	5	3	6	70	2										
5	11.02.97	6	4	6	4	5	4	60	2	1	24.09.97	5	6	3	6	3	1	40	3	1	24.09.97	5	6	3	6	3	1	40	3										
5	11.02.97	7	3	7	3	3	5	70	3	1	24.09.97	5	6	3	0	3	5	90	13	1	24.09.97	8	2	10	0	3	5	90	13										
5	11.02.97	7	4	5	4	5	3	60	4	1	24.09.97	8	2	10	0	3	5	90	13	1	29.09.97	10	4	6	0	3	3	80	0										
5	11.02.97	5	4	8	3	4	5	65	5	1	29.09.97	10	4	6	0	3	3	80	0	1	29.09.97	11	1	8	0	2	1	95	1										
5	11.02.97	5	5	5	5	2	3	50	6	1	29.09.97	11	1	8	0	2	1	95	1	1	29.09.97	6	7	4	3	3	1	50	2										
5	11.02.97	7	2	7	4	4	5	70	7	1	29.09.97	6	7	4	3	3	1	50	2	1	29.09.97	8	2	7	3	3	2	75	3										
5	11.02.97	6	4	7	3	6	4	65	8	1	29.09.97	8	2	7	3	3	2	75	3	1	29.09.97	5	6	4	5	1	2	45	4										
5	11.02.97	5	4	5	6	3	3	50	9	1	29.09.97	5	6	4	5	1	2	45	4	1	29.09.97	10	3	7	0	0	3	85	13										
5	11.02.97	3	5	5	7	1	3	40	10	1	11.09.97	8	3	9	0	4	2	85	0	1	11.09.97	10	2	8	0	1	4	90	1										
5	11.02.97	9	2	8	1	5	4	85	13	1	11.09.97	10	2	8	0	1	4	90	1	1	11.09.97	5	3	6	6	3	2	55	2										
5	13.02.97	10	0	9	1	5	4	95	0	1	11.09.97	5	3	6	6	3	2	55	2	1	11.09.97	2	3	8	7	2	5	50	3										
5	13.02.97	9	0	10	1	5	7	95	1	1	11.09.97	6	1	8	5	4	2	70	4	1	11.09.97	6	1	8	5	4	2	70	4										
5	13.02.97	7	1	10	2	5	4	85	2	1	11.09.97	5	3	7	5	5	2	60	5	1	11.09.97	5	3	7	5	5	2	60	5										
5	13.02.97	4	5	5	6	3	3	45	3	1	11.09.97	6	1	8	5	4	2	70	4	1	11.09.97	6	4	6	4	1	1	60	6										
5	13.02.97	11	1	8	0	5	6	95	13	1	11.09.97	5	3	7	5	5	2	60	5	1	11.09.97	6	4	6	4	1	1	60	6										
6	31.01.97	11	1	8	0	5	6	95	0	1	11.09.97	3	3	6	8	1	3	45	7	1	11.09.97	8	4	8	0	1	3	80	13										
6	31.01.97	7	2	9	2	5	6	80	1	1	11.09.97	8	4	8	0	1	3	80	13	2	11.09.97	9	2	7	2	1	2	80	0										
6	31.01.97	8	0	9	3	7	4	85	2	2	11.09.97	9	2	7	2	1	2	80	0	2	11.09.97	8	1	9	2	2	4	85	1										
6	31.01.97	5	4	7	4	3	5	60	3	2	11.09.97	8	1	9	2	4	3	0	65	2	2	11.09.97	6	3	7	4	3	0	65	2									
6	31.01.97	7	1	8	4	5	5	75	4	2	11.09.97	6	3	7	4	3	0	65	2	2	11.09.97	4	1	8	7	1	5	60	3										
6	31.01.97	6	2	8	4	6	5	70	5	2	11.09.97	6	3	7	4	3																							

flicker trials											steady trials										
subject	date	correct	incorrect	correct	incorrect	flit	arft	%	tag	subject	date	correct	incorrect	correct	incorrect	flit	arft	%	tag		
2	22.10.97	5	3	7	5	3	2	60	2	4	9.10.97	6	6	5	3	4	1	55	2		
2	22.10.97	4	4	6	6	4	3	50	3	4	9.10.97	6	2	8	4	0	3	70	3		
2	22.10.97	3	3	6	8	3	1	45	4	4	9.10.97	6	3	6	5	3	2	60	4		
2	22.10.97	8	1	11	0	2	6	95	13	4	9.10.97	4	5	7	4	3	2	55	5		
										4	9.10.97	7	2	7	4	4	3	70	6		
3	19.09.97	8	1	8	3	4	5	80	0	4	9.10.97	6	4	6	4	1	2	60	7		
3	19.09.97	9	1	9	1	6	6	90	1	4	9.10.97	6	3	7	4	2	4	65	8		
3	19.09.97	3	5	5	7	3	2	40	2	4	9.10.97	5	3	6	6	3	2	55	9		
3	19.09.97	9	1	8	2	4	5	85	3	4	9.10.97	5	5	6	4	3	3	55	10		
3	19.09.97	9	0	11	0	8	10	100	4	4	9.10.97	9	3	7	1	5	3	80	13		
3	19.09.97	11	0	9	0	11	9	100	5												
3	19.09.97	5	1	9	5	4	4	70	6	5	17.09.97	9	0	10	1	1	3	95	0		
3	19.09.97	4	6	4	6	2	3	40	7	5	17.09.97	10	0	10	0	0	2	100	1		
3	19.09.97	10	1	8	1	8	6	90	13	5	17.09.97	0	3	6	11	0	0	30	2		
3	30.09.97	10	0	10	0	3	2	100	0	5	17.09.97	8	2	10	0	1	1	90	3		
3	30.09.97	11	0	9	0	1	1	100	1	5	17.09.97	9	0	11	0	3	2	100	4		
3	30.09.97	1	1	10	8	0	3	55	2	5	17.09.97	10	0	10	0	1	3	100	5		
3	30.09.97	3	2	7	8	3	1	50	3	5	17.09.97	1	2	7	10	1	0	40	6		
3	30.09.97	4	4	6	6	2	3	50	4	5	17.09.97	8	0	12	0	2	1	100	13		
3	30.09.97	7	0	10	3	1	2	85	5	5	19.09.97	10	1	8	1	0	1	90	0		
3	30.09.97	6	2	7	5	2	1	65	6	5	19.09.97	8	0	12	0	3	2	100	1		
3	30.09.97	2	6	6	6	1	1	40	7	5	19.09.97	1	1	9	9	1	1	50	2		
3	30.09.97	10	0	10	0	6	5	100	13	5	19.09.97	5	2	7	6	4	2	60	3		
3	2.10.97	10	0	9	1	2	2	95	0	5	19.09.97	3	6	5	6	1	1	40	4		
3	2.10.97	7	3	9	1	3	3	80	1	5	19.09.97	11	1	8	0	1	1	95	13		
3	2.10.97	4	3	6	7	4	2	50	2	5	23.09.97	9	0	10	1	1	3	95	0		
3	2.10.97	4	5	5	6	2	3	45	3	5	23.09.97	9	0	10	1	1	0	95	1		
3	2.10.97	6	2	8	4	0	2	70	13	5	23.09.97	2	1	8	9	2	1	50	2		
3	6.10.97	11	1	8	0	4	4	95	0	5	23.09.97	2	3	8	7	1	2	50	3		
3	6.10.97	9	0	11	0	3	3	100	1	5	23.09.97	2	3	7	8	2	2	45	4		
3	6.10.97	4	0	9	7	3	3	65	2	5	23.09.97	11	0	9	0	4	3	100	13		
3	6.10.97	3	1	10	6	3	1	65	3	5	25.09.97	11	0	9	0	3	3	100	0		
3	6.10.97	2	2	7	9	2	1	45	4	5	25.09.97	9	0	11	0	0	1	100	1		
3	6.10.97	10	1	9	0	1	5	95	13	5	25.09.97	0	2	7	11	0	1	35	2		
3	8.10.97	9	1	10	0	6	4	95	0	5	25.09.97	9	0	11	0	1	0	100	13		
3	8.10.97	11	0	9	0	5	5	100	1	5	29.09.97	8	0	12	0	1	3	100	0		
3	8.10.97	3	0	10	7	2	5	65	2	5	29.09.97	11	0	9	0	3	1	100	1		
3	8.10.97	4	3	8	5	4	2	60	3	5	29.09.97	0	0	10	10	0	2	50	2		
3	8.10.97	3	5	5	7	3	2	40	4	5	29.09.97	1	0	10	9	1	0	55	3		
3	8.10.97	11	2	7	0	2	1	90	13	5	29.09.97	0	0	9	11	0	2	45	4		
3	15.10.97	9	0	10	1	4	3	95	0	5	29.09.97	9	0	11	0	2	1	100	13		
3	15.10.97	8	3	6	3	1	3	70	1												
3	15.10.97	3	2	9	6	2	2	60	2	6	10.10.97	10	0	9	1	5	3	95	0		
3	15.10.97	4	4	5	7	2	3	45	3	6	10.10.97	8	1	10	1	3	6	90	1		
3	15.10.97	5	3	7	5	1	2	60	13	6	10.10.97	4	0	9	7	3	3	65	2		
3	23.10.97	8	1	9	2	3	0	85	0	6	10.10.97	3	2	9	6	1	3	60	3		
3	23.10.97	8	0	11	1	2	5	95	1	6	10.10.97	3	1	8	8	2	0	55	4		
3	23.10.97	5	2	8	5	4	2	65	2	6	10.10.97	4	1	9	6	2	2	65	5		
3	23.10.97	3	5	4	8	3	2	35	3	6	10.10.97	1	4	7	8	1	1	40	6		
3	23.10.97	8	1	10	1	3	6	90	13	6	10.10.97	9	1	9	1	5	2	90	13		
										6	22.10.97	8	0	12	0	5	7	100	0		
4	23.09.97	7	2	7	4	2	2	70	0	6	22.10.97	10	0	9	1	3	3	95	1		
4	23.09.97	9	2	8	1	7	4	85	1	6	22.10.97	4	2	8	6	2	1	60	2		
4	23.09.97	4	4	6	6	2	2	50	2	6	22.10.97	2	2	8	8	2	1	50	3		
4	23.09.97	3	3	6	8	1	4	45	3	6	22.10.97	3	1	8	8	3	2	55	4		
4	23.09.97	8	2	10	0	4	4	90	13	6	22.10.97	3	0	11	6	3	6	70	5		
4	25.09.97	9	2	7	2	4	2	80	0	6	22.10.97	4	0	10	6	4	3	70	6		
4	25.09.97	8	2	8	2	3	2	80	1	6	22.10.97	3	2	7	8	2	3	50	7		
4	25.09.97	5	2	8	5	2	1	65	2	6	22.10.97	5	3	9	3	3	2	70	8		
4	25.09.97	3	4	5	8	1	2	40	3	6	22.10.97	4	2	7	7	3	1	55	9		
4	25.09.97	7	2	10	1	5	5	85	13	6	22.10.97	4	0	10	6	3	3	70	10		
4	29.09.97	6	0	11	3	3	5	85	0	6	22.10.97	9	1	9	1	4	6	90	13		
4	29.09.97	7	1	8	4	4	2	75	1	6	28.10.97	8	2	9	1	3	1	85	0		
4	29.09.97	3	1	9	7	1	1	60	2	6	28.10.97	8	2	7	3	2	3	75	1		
4	29.09.97	5	3	7	5	5	2	60	3	6	28.10.97	3	2	9	6	2	4	60	2		
4	29.09.97	5	1	8	6	1	4	65	4	6	28.10.97	4	2	7	7	3	2	55	3		
4	29.09.97	2	3	9	6	2	2	55	5	6	28.10.97	2	3	7	8	1	3	45	4		
4	29.09.97	4	3	7	6	2	3	55	6	6	28.10.97	8	3	8	1	4	1	80	13		
4	29.09.97	5	0	9	6	3	3	70	7	6	4.11.97	8	2	9	1	4	2	85	0		
4	29.09.97	3	2	9	6	3	2	60	8	6	4.11.97	9	1	9	1	3	5	90	1		
4	29.09.97	4	1	8	7	4	2	60	9	6	4.11.97	5	0	9	6	1	1	70	2		
4	29.09.97	6	1	9	4	2	4	75	10	6	4.11.97	3	4	8	5	2	2	55	3		
4	29.09.97	10	1	9	0	4	5	95	13	6	4.11.97	4	2	7	7	3	1	55	4		
4	1.10.97	6	2	8	4	2	6	70	0	6	4.11.97	2	2	8	8	2</					

Appendix F - Experiment 5 threshold sessions

Possum number, date, number of correct and incorrect flickering trials, number of correct and incorrect steady trials, the number of reinforcements for correct flicker and steady trials, the overall proportion of correct responses in the current block of trials and the current flicker speed.

(0=16.67 Hz, 1= 20.00 Hz, 2=21.00 Hz, 3=22.00 Hz, 4=23.00 Hz, 5=24.00 Hz, 6=25.00 Hz, 13=16.67 Hz)

flicker trials										steady trials										flicker trials										steady trials									
subject	date	correct	incorrect	correct	incorrect	f1ft	sft	%	tag	subject	date	correct	incorrect	correct	incorrect	f1ft	sft	%	tag	subject	date	correct	incorrect	correct	incorrect	f1ft	sft	%	tag										
1	16.12.97	8	3	9	0	5	6	85	0	3	17.02.98	0	0	0	0	0	0	80	3	3	17.02.98	0	0	0	0	0	0	100	4										
1	16.12.97	10	2	8	0	1	2	90	1	3	17.02.98	7	2	9	2	3	2	80	5	3	17.02.98	0	0	0	0	0	0	100	4										
1	16.12.97	10	2	7	1	3	2	85	2	3	17.02.98	0	0	0	0	0	0	50	6	3	17.02.98	7	2	9	2	3	0	80	13										
1	16.12.97	9	1	10	0	3	2	95	3	3	17.02.98	0	0	0	0	0	0	0	13	1	16.12.97	11	0	9	0	4	100	4											
1	16.12.97	11	0	9	0	4	4	100	4	3	4.03.98	5	2	8	5	0	1	65	0	1	16.12.97	10	3	7	0	1	2	85	5										
1	16.12.97	2	2	8	8	1	1	50	6	3	4.03.98	7	4	5	4	1	1	60	1	3	4.03.98	7	4	5	7	1	3	45	6										
1	16.12.97	11	1	8	0	3	4	95	13	3	4.03.98	7	4	7	2	0	1	70	2	3	4.03.98	9	2	8	1	3	2	85	3										
1	18.12.97	10	2	8	0	5	3	90	0	3	4.03.98	9	2	8	1	3	2	85	3	3	4.03.98	9	3	6	2	5	3	75	4										
1	18.12.97	10	2	7	1	1	1	85	1	3	4.03.98	9	3	6	2	5	3	75	4	3	4.03.98	7	5	7	1	2	3	70	5										
1	18.12.97	9	2	9	0	2	4	90	2	3	4.03.98	7	5	7	1	2	3	70	5	3	4.03.98	4	4	5	7	1	3	45	6										
1	18.12.97	10	1	9	0	1	1	95	3	3	4.03.98	4	4	5	7	1	3	45	6	3	4.03.98	10	4	6	0	4	3	80	13										
1	18.12.97	11	2	7	0	2	1	90	4	4	16.12.97	9	0	10	1	4	5	95	0	1	18.12.97	5	2	7	6	3	2	60	6										
1	18.12.97	7	1	11	1	2	4	90	5	4	16.12.97	8	1	10	1	4	2	90	1	1	18.12.97	10	0	10	0	4	4	100	2										
1	18.12.97	5	2	7	6	3	2	60	6	4	16.12.97	9	0	10	0	4	4	100	2	1	22.12.97	10	3	6	1	3	2	80	0										
1	18.12.97	10	0	10	0	5	3	100	13	4	16.12.97	10	0	10	0	9	1	2	4	95	3	16.12.97	10	0	9	1	2	4	95	3									
1	22.12.97	10	3	6	1	3	2	80	0	4	16.12.97	10	0	10	0	9	1	2	4	95	3	16.12.97	10	0	9	1	2	4	95	3									
1	22.12.97	10	2	8	0	5	5	90	1	4	16.12.97	10	0	9	1	2	3	80	4	1	22.12.97	9	3	8	0	9	2	8	5	13									
1	22.12.97	9	3	8	0	5	2	85	2	4	16.12.97	7	2	9	2	2	3	80	4	1	22.12.97	10	2	8	0	9	2	8	5	13									
1	22.12.97	10	2	8	0	2	3	90	3	4	16.12.97	9	0	9	2	1	0	90	5	1	22.12.97	11	1	8	0	4	4	95	4										
1	22.12.97	11	1	8	0	4	4	95	4	4	16.12.97	2	4	7	7	0	2	45	6	1	22.12.97	9	1	10	0	9	1	4	95	13									
1	22.12.97	9	1	10	0	1	5	95	5	4	16.12.97	10	0	9	1	4	1	95	13	1	22.12.97	3	2	7	8	2	0	50	6										
1	22.12.97	3	2	7	8	2	0	50	6	4	18.12.97	8	0	12	0	5	3	100	0	1	22.12.97	9	2	9	0	3	3	90	13										
1	22.12.97	9	2	9	0	3	3	90	13	4	18.12.97	9	0	10	1	2	4	95	1	1	29.12.97	8	1	8	3	4	5	80	0										
1	29.12.97	8	1	8	3	4	5	80	0	4	18.12.97	9	1	8	2	3	3	85	2	1	29.12.97	7	2	9	2	3	2	85	3										
1	29.12.97	7	2	9	2	3	2	80	1	4	18.12.97	7	1	10	2	1	3	85	3	1	29.12.97	10	0	9	1	3	2	85	4										
1	29.12.97	10	0	9	1	3	1	95	2	4	18.12.97	8	0	9	3	2	2	85	4	1	29.12.97	9	1	9	1	4	2	90	5										
1	29.12.97	9	1	9	1	1	3	90	3	4	18.12.97	9	1	9	1	4	2	90	5	1	29.12.97	8	0	10	2	4	2	95	6										
1	29.12.97	8	0	10	2	2	4	90	4	4	18.12.97	3	2	8	7	2	1	55	6	1	29.12.97	10	1	8	1	2	2	95	13										
1	29.12.97	10	1	8	1	4	5	90	5	4	18.12.97	10	0	9	1	2	2	95	13	1	29.12.97	1	2	10	7	1	5	85	0										
1	29.12.97	1	2	10	7	1	0	55	6	4	22.12.97	8	0	9	3	1	5	85	0	1	29.12.97	10	0	10	0	3	5	85	1										
1	29.12.97	10	0	10	0	5	3	100	13	4	22.12.97	6	0	11	3	5	3	85	1	1	29.12.97	10	0	10	0	4	2	100	13										
2	16.12.97	9	2	9	0	6	4	90	0	4	22.12.97	11	0	9	0	5	3	100	2	1	22.12.97	8	1	9	2	2	5	85	3										
2	16.12.97	10	1	8	1	4	5	90	1	4	22.12.97	9	0	10	1	3	3	95	4	1	22.12.97	8	0	10	1	3	3	95	4										
2	16.12.97	10	3	7	0	2	2	85	2	4	22.12.97	10	0	9	1	3	2	95	5	1	22.12.97	10	0	9	1	3	2	95	5										
2	16.12.97	10	0	10	0	5	5	100	3	4	22.12.97	1	2	10	7	1	1	55	6	1	22.12.97	10	0	10	0	3	2	100	13										
2	16.12.97	11	1	8	0	2	1	95	4	4	22.12.97	10	0	10	0	7	1	1	55	6	2	16.12.97	8	1	11	0	8	2	3	85	0								
2	16.12.97	8	1	11	0	7	6	95	5	4	29.12.97	9	1	8	2	3	3	85	0	1	29.12.97	6	0	11	3	2	2	85	1										
2	16.12.97	5	6	4	5	0	3	45	6	4	29.12.97	6	0	11	3	2	2	85	1	1	29.12.97	10	1	8	1	3	2	90	2										
2	16.12.97	11	1	8	0	5	5	95	13	4	29.12.97	10	1	8	1	3	3	90	2	1	29.12.97	8	1	10	1	3	3	90	3										
2	18.12.97	10	1	9	0	5	5	95	0	4	29.12.97	8	1	10	1	3	3	90	3	1	29.12.97	9	1	8	2	3	4	85	4										
2	18.12.97	11	2	7	0	5	3	90	1	4	29.12.97	9	1	8	2	3	4	85	4	1	29.12.97	9	0	10	1	2	2	95	5										
2	18.12.97	9	2	9	0	3	5	90	2	4	29.12.97	9	0	10	1	2	2	95	5	1	29.12.97	11	1	8	0	3	3	45	6										
2	18.12.97	11	1	8	0	3	5	95	3	4	29.12.97	2	4	7	7	2	3	45	6	1	29.12.97	10	0	10	0	4	2	100	13										
2	18.12.97	10	2	8	0	5	2	90	4	4	29.12.97	10	0	10	0	4	2	100	13	1	29.12.97	10	1	9	0	6	6	95	5										
2	18.12.97	10	1	9	0	6	6	95	5	5	16.12.97	10	0	9	1	3	2	95	0	1	29.12.97	4	4	5	7	4	3	90	1										
2	18.12.97	4	4	5	7	4	3	45	6	5	16.12.97	8	0	10	2	3	3	90	1	1	29.12.97	8	0	10	2	2	1	90	2										
2	18.12.97	8	2	10	0	3	5	90	13	5	16.12.97	8	0	10	2	2	1	90	2	1	29.12.97	9	1	9	1	4	2	90	3										
2	22.12.97	9	1	9	1	4	4	90	0	5	16.12.97	8	0	10	0	2	2	100	3	1	29.12.97	9	2	8	1	3	2	90	3										
2	22.12.97	9	2	8	1	3	3	85	1	5	16.12.97	11	0	9	0	2	2	100	3	1	29.12.97	11	1	8	0	5	2	95	6										
2	22.12.97	11	1	8	0	5	2	95	2	5	16.12.97	6	1	11	2	2	1	85	4	1	29.12.97	9	2	9	0	4	4	90	3										
2	22.12.97	9	2	9	0	4	4	90	3	5	16.12.97</																												

subject	date	flicker trials		steady trials		fit	err	%	tag
		correct	incorrect	correct	incorrect				
6	17.12.97	9	1	8	2	2	0	85	5
6	17.12.97	5	1	11	3	2	5	80	6
6	17.12.97	9	1	9	1	3	2	90	13
6	19.12.97	9	0	9	2	3	4	90	0
6	19.12.97	8	1	10	1	2	3	90	1
6	19.12.97	8	1	8	3	0	2	80	2
6	19.12.97	7	2	8	3	2	0	75	3
6	19.12.97	9	0	10	1	5	4	95	4
6	19.12.97	11	0	9	0	3	2	100	5
6	19.12.97	3	1	11	5	1	4	70	6
6	19.12.97	10	1	9	0	5	6	95	13
6	20.01.98	10	2	8	0	4	3	90	0
6	20.01.98	8	1	10	1	3	1	90	1
6	20.01.98	8	1	9	2	2	2	85	2
6	20.01.98	9	1	8	2	2	4	85	3
6	20.01.98	7	2	9	2	1	2	80	4
6	20.01.98	11	1	8	0	3	3	95	5
6	20.01.98	3	2	9	6	2	2	60	6
6	20.01.98	10	1	8	1	2	1	90	13
6	22.01.98	8	1	9	2	4	1	85	0
6	22.01.98	10	0	9	1	2	5	95	1
6	22.01.98	7	1	11	1	3	2	90	2
6	22.01.98	8	1	9	2	3	5	85	3
6	22.01.98	11	0	9	0	7	4	100	4
6	22.01.98	8	0	11	1	3	6	95	5
6	22.01.98	3	1	8	8	3	1	55	6
6	22.01.98	9	1	9	1	2	3	90	13

Appendix G - Experiment 6 threshold sessions

Possum number, date, number of correct and incorrect flickering trials, number of correct and incorrect steady trials, the number of reinforcements for correct flicker and steady trials, the overall proportion of correct responses in the current block of trials and the current flicker speed.

Series 1

(0=16.67 Hz, 1= 20.00 Hz, 2=25.00 Hz, 3=33.33 Hz, 4=50.00 Hz, 5=52.60 Hz, 6=55.60 Hz, 7=58.80 Hz, 8=62.50 Hz, 9=66.67 Hz, 10=71.42 Hz, 13=16.67 Hz)

subject	date	left		right		lft	rft	%	tag	subject	date	left		right		lft	rft	%	tag
		correct	incorrect	correct	incorrect							correct	incorrect	correct	incorrect				
1	24.07.98	10	0	8	2	3	3	90	0	2	2.12.98	9	2	2	7	4	2	55	4
1	24.07.98	10	1	7	2	3	3	85	1	2	2.12.98	7	2	4	7	3	2	55	5
1	24.07.98	0	0	0	0	0	0	65	2	2	2.12.98	7	4	2	7	2	2	45	6
1	24.07.98	11	0	5	4	3	3	80	3	2	2.12.98	9	0	10	1	5	6	95	13
1	24.07.98	7	2	4	7	3	4	55	4										
1	24.07.98	10	1	5	4	4	5	75	5	3	22.10.98	7	1	9	3	5	2	80	0
1	24.07.98	7	3	2	8	3	2	45	6	3	22.10.98	10	0	10	0	2	6	100	1
1	24.07.98	8	1	8	3	5	3	80	13	3	22.10.98	10	1	3	6	4	3	65	2
1	28.07.98	9	0	11	0	4	5	100	0	3	22.10.98	7	2	2	9	2	2	45	3
1	28.07.98	9	1	9	1	6	4	90	1	3	22.10.98	9	2	7	2	5	4	80	13
1	28.07.98	7	4	3	6	3	2	50	2	3	12.11.98	9	2	7	2	3	3	80	0
1	28.07.98	4	4	6	6	2	4	50	3	3	12.11.98	8	1	9	2	3	3	85	1
1	28.07.98	6	5	5	4	1	2	55	4	3	12.11.98	11	0	5	4	7	4	80	2
1	28.07.98	9	1	3	7	4	3	60	5	3	12.11.98	9	0	6	5	2	5	75	3
1	28.07.98	6	4	5	5	2	3	55	6	3	12.11.98	6	5	2	7	3	2	40	4
1	28.07.98	10	1	3	6	3	2	65	7	3	12.11.98	9	1	9	1	3	5	90	13
1	28.07.98	4	5	1	10	2	0	25	8	3	17.11.98	7	4	8	1	3	4	75	0
1	28.07.98	9	1	7	3	4	6	80	13	3	17.11.98	8	1	9	2	5	4	85	1
1	6.08.98	9	1	8	2	5	5	85	0	3	17.11.98	10	1	4	5	3	3	70	2
1	6.08.98	10	0	8	2	4	4	90	1	3	17.11.98	4	6	3	7	1	2	35	3
1	6.08.98	10	1	3	6	1	3	65	2	3	17.11.98	10	0	9	1	3	2	95	13
1	6.08.98	6	2	5	7	3	2	55	3	3	26.11.98	9	2	9	0	3	6	90	0
1	6.08.98	7	3	4	6	3	2	55	4	3	26.11.98	6	4	7	3	4	2	65	1
1	6.08.98	9	2	3	6	4	2	60	5	3	26.11.98	6	4	5	5	3	4	55	2
1	6.08.98	6	3	3	8	1	3	45	6	3	26.11.98	4	7	4	5	2	1	40	3
1	6.08.98	11	0	9	0	4	4	100	13	3	26.11.98	6	2	10	2	5	3	80	13
1	3.09.98	7	1	8	4	5	4	75	0	3	1.04.99	9	1	8	2	4	5	85	0
1	3.09.98	10	0	10	0	7	8	100	1	3	1.04.99	7	4	7	2	1	3	70	1
1	3.09.98	8	3	1	8	1	1	45	2	3	1.04.99	6	3	5	6	4	1	55	2
1	3.09.98	8	1	10	1	4	4	90	13	3	1.04.99	8	2	2	8	3	2	50	3
1	7.01.99	7	1	10	2	6	3	85	0	3	1.04.99	8	3	4	5	3	3	60	4
1	7.01.99	8	2	9	1	2	5	85	1	3	1.04.99	6	2	3	9	1	2	45	5
1	7.01.99	8	3	7	2	4	4	75	2	3	1.04.99	9	2	9	0	4	6	90	13
1	7.01.99	7	2	6	5	3	4	65	3										
1	7.01.99	9	2	5	4	5	3	70	4	4	6.08.98	8	3	7	2	5	2	75	0
1	7.01.99	5	5	4	6	2	0	45	5	4	6.08.98	3	5	7	5	1	3	50	1
1	7.01.99	10	0	7	3	5	7	85	13	4	6.08.98	7	3	6	4	4	5	65	2
2	31.07.98	7	1	10	2	3	6	85	0	4	6.08.98	5	6	6	3	1	3	55	3
2	31.07.98	0	0	0	0	0	0	90	1	4	6.08.98	5	4	6	5	4	2	55	4
2	31.07.98	10	0	6	4	5	3	80	2	4	6.08.98	6	5	5	4	5	3	55	5
2	31.07.98	0	0	0	0	0	0	50	3	4	6.08.98	5	5	3	7	2	2	40	6
2	31.07.98	5	6	4	5	1	4	45	4	4	6.08.98	7	3	10	0	3	4	85	13
2	31.07.98	7	2	10	1	4	3	85	13	4	2.12.98	9	0	6	5	5	3	75	0
2	8.09.98	11	0	9	0	7	3	100	0	4	2.12.98	10	0	10	0	5	5	100	1
2	8.09.98	8	0	10	2	2	6	90	1	4	2.12.98	7	4	2	7	0	2	45	2
2	8.09.98	8	2	2	8	3	1	50	2	4	2.12.98	9	0	10	1	6	5	95	13
2	8.09.98	9	2	3	6	2	3	60	3	4	8.12.98	7	2	9	2	4	3	80	0
2	8.09.98	6	3	4	7	3	3	50	4	4	8.12.98	11	0	7	2	3	4	90	1
2	8.09.98	8	3	5	4	5	3	65	5	4	8.12.98	7	3	2	8	4	2	45	2
2	8.09.98	6	4	5	5	3	4	55	6	4	8.12.98	9	1	9	1	5	6	90	13
2	8.09.98	9	1	8	2	4	4	85	7	4	17.12.98	10	1	6	3	4	4	80	0
2	8.09.98	8	3	4	5	3	4	60	8	4	17.12.98	10	0	7	3	4	6	85	1
2	8.09.98	5	3	7	5	3	2	60	9	4	17.12.98	6	3	3	8	2	2	45	2
2	8.09.98	6	4	7	3	5	4	65	10	4	17.12.98	10	0	8	2	7	4	90	13
2	8.09.98	9	2	8	1	2	5	85	13	4	8.01.99	8	1	8	3	3	4	80	0
2	10.09.98	10	1	8	1	3	6	90	0	4	8.01.99	6	5	7	2	3	3	65	1
2	10.09.98	9	1	9	1	4	6	90	1	4	8.01.99	6	3	3	8	2	3	45	2
2	10.09.98	6	3	4	7	4	1	50	2	4	8.01.99	10	1	8	1	5	4	90	13
2	10.09.98	8	2	6	4	4	3	70	3	5	5.11.98	7	1	11	1	4	3	90	0
2	10.09.98	9	2	4	5	3	3	65	4	5	5.11.98	10	0	10	0	6	7	100	1
2	10.09.98	6	3	7	4	2	4	65	5	5	5.11.98	9	2	9	0	3	4	90	2
2	10.09.98	6	5	4	5	2	2	50	6	5	5.11.98	8	1	10	1	5	4	90	3
2	10.09.98	4	5	6	5	2	3	50	7	5	5.11.98	4	7	4	5	4	2	40	4
2	10.09.98	4	7	2	7	3	1	30	8	5	5.11.98	8	2	9	1	3	5	85	13
2	10.09.98	10	0	10	0	5	4	100	13	5	26.11.98	10	0	8	2	4	5	90	0
2	7.10.98	10	0	9	1	5	7	95	0	5	26.11.98	10	1	9	0	9	8	95	1
2	7.10.98	11	0	9	0	7	7	100	1	5	26.11.98	3	5	8	4	2	2	55	2
2	7.10.98	6	2	6	6	4	3	60	2	5	26.11.98	8	2	8	2	3	6	80	3
2	7.10.98	9	1	7	3	3	5	80	3	5	26.11.98	3	8	4	5	3	0	35	4
2	7.10.98	9	2	3	6	2	3	60	4	5	26.11.98	7	2	9	2	3	6	80	13
2	7.10.98	6	3	4	7	3	3	50	5	5	2.12.98	8	1	10	1	4	4	90	0
2	7.10.98	8	3	4	5	3	2	60	6	5	2.12.98	10	1	9	0	7	4	95	1
2	7.10.98	7	3	5	5	3	1	60	7	5	2.12.98	7	3	7	3	3	4	70	2
2	7.10.98	7	3	5	5	3	4	60	8	5	2.12.98	8	1	7	4	5	6	75	3
2	7.10.98	8	3	4	5	4	4	60	9	5	2.12.98	7	3	7	3	4	4	70	4
2	7.10.98	4	4	6	6	3	4	50	10	5	2.12.98	5	6	4	5	4	2	45	5
2	7.10.98	8	2	9	1	4	3	85	13	5	2.12.98	8	1	10	1	5	7	90	13
2	2.12.98	10	1	9	0	5	4	95	0	5	22.12.98	9	1	9	1	4	4	90	0
2	2.12.98	10	0	10	0	6	6	100	1	5	22.12.98	11	0	8	1	2	5	95	1
2	2.12.98	8	1	6	5	5	4	70	2	5	22.12.98	4	4	8	4	3	2	60	2
2	2.12.98	8	2	5	5	2	5	65	3	5	22.12.98	6	5	9	0	4	2	75	3

subject	date	left		right		lft	rrft	%	tag
		correct	incorrect	correct	incorrect				
5	22.12.98	3	7	7	3	3	5	50	4
5	22.12.98	1	9	7	3	1	2	40	5
5	22.12.98	9	2	7	2	4	5	80	13
5	7.01.99	9	2	6	3	4	2	75	0
5	7.01.99	6	3	9	2	2	5	75	1
5	7.01.99	6	5	8	1	4	4	70	2
5	7.01.99	5	5	7	3	5	3	60	3
5	7.01.99	8	2	5	5	5	3	65	4
5	7.01.99	5	6	2	7	1	1	35	5
5	7.01.99	8	0	9	3	4	6	85	13
6	3.11.98	9	0	11	0	7	9	100	0
6	3.11.98	11	0	9	0	5	3	100	1
6	3.11.98	5	5	6	4	3	4	55	2
6	3.11.98	7	2	8	3	4	4	75	3
6	3.11.98	5	5	9	1	3	5	70	4
6	3.11.98	2	9	5	4	1	0	35	5
6	3.11.98	8	1	11	0	5	4	95	13
6	5.11.98	6	3	11	0	5	2	85	0
6	5.11.98	8	3	9	0	2	5	85	1
6	5.11.98	3	6	10	1	3	2	65	2
6	5.11.98	4	7	7	2	3	4	55	3
6	5.11.98	4	6	8	2	3	3	60	4
6	5.11.98	6	3	7	4	5	2	65	5
6	5.11.98	5	5	4	6	1	2	45	6
6	5.11.98	11	0	9	0	4	5	100	13
6	17.11.98	8	2	10	0	3	6	90	0
6	17.11.98	8	3	8	1	4	3	80	1
6	17.11.98	2	6	7	5	2	3	45	2
6	17.11.98	8	2	8	2	5	2	80	13
6	2.12.98	10	1	9	0	5	6	95	0
6	2.12.98	8	0	11	1	5	7	95	1
6	2.12.98	8	2	7	3	4	2	75	2
6	2.12.98	6	5	5	4	3	1	55	3
6	2.12.98	8	1	7	4	4	5	75	4
6	2.12.98	8	3	5	4	4	4	65	5
6	2.12.98	5	5	5	5	1	4	50	6
6	2.12.98	3	7	5	5	3	1	40	7
6	2.12.98	11	0	8	1	7	5	95	13
6	4.12.98	7	1	12	0	2	6	95	0
6	4.12.98	11	0	9	0	5	5	100	1
6	4.12.98	5	5	5	5	3	2	50	2
6	4.12.98	4	6	5	5	3	2	45	3
6	4.12.98	10	1	8	1	4	5	90	13

Series 2

(0=16.67 Hz, 1= 20.00 Hz, 2=21.00 Hz, 3=22.00 Hz, 4=23.00 Hz, 5=24.00 Hz, 6=25.00 Hz, 13=16.67 Hz)

subject	date	left		right		lft	rrft	%	tag	subject	date	left		right		lft	rrft	%	tag
		correct	incorrect	correct	incorrect							correct	incorrect	correct	incorrect				
1	17.03.99	9	2	9	0	5	5	90	0	2	26.03.99	9	0	11	0	3	6	100	2
1	17.03.99	9	1	8	2	6	5	85	1	2	26.03.99	11	0	9	0	7	6	100	3
1	17.03.99	10	0	10	0	5	6	100	2	2	26.03.99	9	1	7	3	3	3	80	4
1	17.03.99	11	0	9	0	5	4	100	3	2	26.03.99	8	1	8	3	4	1	80	5
1	17.03.99	8	0	12	0	5	4	100	4	2	26.03.99	10	0	3	7	2	3	65	6
1	17.03.99	9	1	10	0	2	5	95	5	2	26.03.99	10	1	9	0	4	5	95	13
1	17.03.99	11	0	3	6	4	3	70	6	2	15.04.99	9	1	8	2	6	4	85	0
1	17.03.99	8	1	11	0	4	4	95	13	2	15.04.99	11	0	8	1	4	3	95	1
1	26.03.99	11	0	9	0	5	6	100	0	2	15.04.99	9	0	10	1	4	7	95	2
1	26.03.99	7	1	12	0	6	6	95	1	2	15.04.99	11	0	8	1	9	6	95	3
1	26.03.99	10	1	9	0	7	8	95	2	2	15.04.99	10	0	9	1	4	6	95	4
1	26.03.99	10	0	10	0	5	5	100	3	2	15.04.99	10	0	10	0	6	6	100	5
1	26.03.99	10	0	9	1	8	5	95	4	2	15.04.99	10	1	2	7	3	2	60	6
1	26.03.99	10	1	9	0	2	5	95	5	2	15.04.99	7	1	10	2	4	2	85	13
1	26.03.99	6	3	5	6	3	1	55	6	2	26.04.99	7	3	10	0	3	7	85	0
1	26.03.99	7	3	10	0	4	5	85	13	2	26.04.99	9	2	9	0	3	3	90	1
1	30.03.99	9	1	10	0	7	7	95	0	2	26.04.99	8	1	9	2	4	3	85	2
1	30.03.99	9	1	10	0	6	4	95	1	2	26.04.99	10	1	8	1	6	4	90	3
1	30.03.99	10	1	9	0	6	7	95	2	2	26.04.99	9	1	10	0	4	6	95	4
1	30.03.99	9	0	11	0	4	5	100	3	2	26.04.99	10	0	10	0	5	6	100	5
1	30.03.99	10	0	10	0	7	5	100	4	2	26.04.99	10	1	6	3	6	3	80	6
1	30.03.99	10	1	9	0	5	6	95	5	2	26.04.99	7	1	10	2	3	6	85	13
1	30.03.99	7	1	4	8	1	4	55	6	2	28.04.99	5	6	7	2	3	1	60	0
1	30.03.99	11	0	9	0	7	4	100	13	2	28.04.99	9	0	11	0	2	4	100	1
1	15.04.99	9	2	9	0	6	6	90	0	2	28.04.99	10	1	9	0	7	4	95	2
1	15.04.99	9	0	10	1	6	5	95	1	2	28.04.99	10	0	8	2	3	6	90	3
1	15.04.99	8	3	9	0	3	3	85	2	2	28.04.99	10	0	9	1	5	5	95	4
1	15.04.99	9	1	9	1	6	6	90	3	2	28.04.99	11	0	8	1	9	5	95	5
1	15.04.99	9	1	10	0	6	6	95	4	2	28.04.99	5	3	2	10	1	1	35	6
1	15.04.99	11	0	9	0	5	5	100	5	2	28.04.99	10	0	10	0	3	6	100	13
1	15.04.99	6	2	4	8	3	4	50	6	2	4.05.99	7	1	10	2	3	2	85	0
1	15.04.99	9	1	9	1	6	4	90	13	2	4.05.99	10	0	8	2	2	4	90	1
1	22.04.99	10	1	9	0	6	5	95	0	2	4.05.99	11	0	9	0	6	4	100	2
1	22.04.99	9	1	8	2	5	3	85	1	2	4.05.99	9	0	9	2	4	3	90	3
1	22.04.99	9	1	10	0	5	5	95	2	2	4.05.99	11	0	9	0	4	5	100	4
1	22.04.99	11	0	9	0	6	7	100	3	2	4.05.99	10	0	9	1	6	6	95	5
1	22.04.99	8	0	12	0	5	4	100	4	2	4.05.99	10	0	4	6	4	3	70	6
1	22.04.99	10	0	9	1	4	5	95	5	2	4.05.99	11	0	7	2	4	6	90	13
1	22.04.99	10	1	5	4	3	5	75	6										
1	22.04.99	9	0	9	2	8	5	90	13										
2	26.03.99	9	0	11	0	5	5	100	0	3	16.04.99	9	2	8	1	3	5	85	0
2	26.03.99	11	0	9	0	7	4	100	1	3	16.04.99	7	1	9	3	4	3	80	1
										3	16.04.99	9	2	9	0	6	7	90	2
										3	16.04.99	8	2	7	3	4	2	75	3

Appendix H - Experiment 7 threshold sessions

Possum number, date, number of correct tone-on (right) and tone-off (left) trials, number of incorrect tone-on and tone-off trials, the number of reinforcements for correct tone-on and tone-off trials, the overall proportion of correct responses in the current block of trials and the current tone intensity.

(0=80 dB, 1= 72 dB, 2=64 dB, 3=56 dB, 4=48 dB, 5=40 dB, 6=32 dB, 7=24 dB, 8=16 dB, 9=8 dB, 10=0 dB, 13=80 dB)

subject	date	correct		incorrect		lrrt	rrft	%	tag	subject	date	correct		incorrect		lrrt	rrft	%	tag
		right	left	right	left							right	left						
7	1.08.97	10	8	1	1	5	4	90	0	8	29.08.97	5	7	5	3	1	2	60	4
7	1.08.97	9	10	1	0	3	6	95	1	8	29.08.97	4	7	6	3	4	2	55	5
7	1.08.97	5	10	4	1	3	1	75	2	8	29.08.97	3	6	8	3	1	1	45	6
7	1.08.97	3	8	7	2	2	2	55	3	8	29.08.97	8	9	1	2	4	2	85	13
7	1.08.97	3	6	8	3	3	2	45	4	8	15.09.97	10	9	1	0	3	0	95	0
7	1.08.97	9	10	0	1	5	8	95	13	8	15.09.97	7	11	2	0	1	5	90	1
7	5.08.97	9	9	2	0	4	7	90	0	8	15.09.97	7	9	3	1	4	1	80	2
7	5.08.97	6	12	2	0	3	3	90	1	8	15.09.97	6	7	5	2	3	2	65	3
7	5.08.97	4	9	7	0	3	3	65	2	8	15.09.97	3	7	5	5	2	2	50	4
7	5.08.97	3	9	7	1	2	1	60	3	8	15.09.97	10	7	1	2	3	5	85	13
7	5.08.97	4	8	6	2	3	2	60	4	8	26.09.97	11	9	0	0	7	4	100	0
7	5.08.97	3	3	8	6	3	1	30	5	8	26.09.97	7	9	3	1	3	1	80	1
7	5.08.97	8	10	1	1	5	6	90	13	8	26.09.97	6	7	4	3	1	5	65	2
7	14.08.97	9	9	1	1	6	3	90	0	8	26.09.97	5	7	6	2	4	3	60	3
7	14.08.97	9	10	1	0	5	7	95	1	8	26.09.97	5	10	3	2	5	5	75	4
7	14.08.97	5	8	6	1	2	1	65	2	8	26.09.97	5	8	5	2	4	2	65	5
7	14.08.97	3	6	6	5	2	2	45	3	8	26.09.97	4	7	7	2	3	4	55	6
7	14.08.97	10	8	0	2	4	4	90	13	8	26.09.97	3	5	6	6	0	2	40	7
7	18.08.97	9	9	2	0	4	6	90	0	8	26.09.97	9	8	2	1	4	3	85	13
7	18.08.97	8	8	2	2	2	3	80	1	8	14.10.97	10	8	1	1	2	4	90	0
7	18.08.97	6	8	3	3	3	2	70	2	8	14.10.97	7	8	3	2	4	2	75	1
7	18.08.97	6	9	4	1	2	2	75	3	8	14.10.97	4	6	6	4	2	2	50	2
7	18.08.97	2	5	9	4	1	1	35	4	8	14.10.97	11	8	0	1	5	4	95	13
7	18.08.97	8	9	1	2	5	2	85	13	8	23.10.97	10	9	1	0	5	4	95	0
7	21.08.97	9	9	1	1	4	5	90	0	8	23.10.97	5	9	4	2	1	4	70	1
7	21.08.97	5	8	5	2	3	2	65	1	8	23.10.97	7	9	4	0	4	3	80	2
7	21.08.97	5	5	6	4	5	3	50	2	8	23.10.97	6	9	4	1	4	4	75	3
7	21.08.97	8	10	0	2	3	3	90	13	8	23.10.97	3	7	6	4	2	1	50	4
7	27.08.97	8	10	1	1	5	7	90	0	8	23.10.97	9	10	1	0	5	4	95	13
7	27.08.97	9	9	2	0	5	5	90	1	8	4.11.97	8	10	2	0	3	4	90	0
7	27.08.97	8	7	2	3	6	3	75	2	8	4.11.97	4	10	5	1	3	2	70	1
7	27.08.97	2	7	8	3	1	2	45	3	8	4.11.97	3	7	7	3	3	2	50	2
7	27.08.97	11	8	0	1	2	4	95	13	8	4.11.97	9	9	2	0	4	3	90	13
7	1.09.97	10	9	0	1	3	2	95	0	8	10.11.97	7	11	2	0	2	4	90	0
7	1.09.97	9	8	0	3	2	0	85	1	8	10.11.97	8	9	3	0	4	5	85	1
7	1.09.97	8	9	2	1	3	6	85	2	8	10.11.97	7	9	3	1	3	3	80	2
7	1.09.97	6	5	5	4	3	2	55	3	8	10.11.97	6	9	4	1	3	1	75	3
7	1.09.97	3	7	6	4	2	4	50	4	8	10.11.97	6	6	5	3	4	2	60	4
7	1.09.97	11	6	0	3	5	3	85	13	8	10.11.97	2	7	6	5	2	5	45	5
7	23.09.97	10	10	0	0	4	5	100	0	8	10.11.97	10	10	0	0	4	5	100	13
7	23.09.97	10	9	1	0	4	4	95	1										
7	23.09.97	5	9	3	3	2	3	70	2	9	8.09.97	9	9	2	0	3	4	90	0
7	23.09.97	7	7	3	3	5	3	70	3	9	8.09.97	7	8	3	2	5	3	75	1
7	23.09.97	5	5	6	4	4	3	50	4	9	8.09.97	5	9	5	1	4	3	70	2
7	23.09.97	9	9	0	2	2	5	90	13	9	8.09.97	7	7	4	2	2	3	70	3
7	29.10.97	9	10	1	0	4	2	95	0	9	8.09.97	5	9	3	3	4	3	70	4
7	29.10.97	8	10	2	0	4	5	90	1	9	8.09.97	4	6	6	4	0	3	50	5
7	29.10.97	8	8	3	1	4	5	80	2	9	8.09.97	10	8	1	1	5	4	90	13
7	29.10.97	4	9	5	2	3	3	65	3	9	16.09.97	9	8	1	2	4	5	85	0
7	29.10.97	8	8	2	2	6	4	80	4	9	16.09.97	8	8	3	1	4	3	80	1
7	29.10.97	5	5	6	4	3	3	50	5	9	16.09.97	5	6	4	5	4	2	55	2
7	29.10.97	8	9	0	3	2	4	85	13	9	16.09.97	6	8	4	2	3	3	70	3
7	7.11.97	10	9	1	0	6	4	95	0	9	16.09.97	5	8	6	1	4	5	65	4
7	7.11.97	6	11	2	1	4	6	85	1	9	16.09.97	2	9	6	3	1	3	55	5
7	7.11.97	4	8	6	2	1	3	60	2	9	16.09.97	1	4	10	5	1	2	25	6
7	7.11.97	5	4	6	5	4	2	45	3	9	16.09.97	10	8	0	2	6	3	90	13
7	7.11.97	9	8	0	3	4	2	85	13	9	18.09.97	8	9	2	1	3	2	85	0
										9	18.09.97	10	8	1	1	4	4	90	1
8	20.08.97	7	11	2	0	1	5	90	0	9	18.09.97	4	9	4	3	1	3	65	2
8	20.08.97	5	8	6	1	2	1	65	1	9	18.09.97	7	9	4	0	4	5	80	3
8	20.08.97	5	9	5	1	3	3	70	2	9	18.09.97	7	7	3	3	4	2	70	4
8	20.08.97	4	8	6	2	0	2	60	3	9	18.09.97	5	5	5	5	4	2	50	5
8	20.08.97	7	8	4	1	4	1	75	4	9	18.09.97	10	8	1	1	3	5	90	13
8	20.08.97	1	8	7	4	1	2	45	5	9	24.09.97	11	9	0	0	5	2	100	0
8	20.08.97	9	9	1	1	5	3	90	13	9	24.09.97	8	9	2	1	5	4	85	1
8	22.08.97	11	9	0	0	3	2	100	0	9	24.09.97	7	10	2	1	2	4	85	2
8	22.08.97	8	9	2	1	3	1	85	1	9	24.09.97	3	7	7	3	3	4	50	3
8	22.08.97	7	9	3	1	3	5	80	2	9	24.09.97	11	7	0	2	8	5	90	13
8	22.08.97	5	7	6	2	3	2	60	3	9	2.10.97	11	8	0	1	6	3	95	0
8	22.08.97	4	9	5	2	3	5	65	4	9	2.10.97	7	10	1	2	1	5	85	1
8	22.08.97	2	6	8	4	2	1	40	5	9	2.10.97	8	8	3	1	5	4	80	2
8	22.08.97	11	8	0	1	6	3	95	13	9	2.10.97	5	6	5	4	2	3	55	3
8	26.08.97	11	8	0	1	4	3	95	0	9	2.10.97	3	7	7	3	3	2	50	4
8	26.08.97	7	10	2	1	1	4	85	1	9	2.10.97	11	9	0	0	5	4	100	13
8	26.08.97	6	6	5	3	4	2	60	2	9	7.10.97	9	8	2	1	3	3	85	0
8	26.08.97	4	9	6	1	3	1	65	3	9	7.10.97	7	10	2	1	4	3	85	1
8	26.08.97	3	8	7	2	2	2	55	4	9	7.10.97	11	9	0	0	5	4	100	2
8	26.08.97	4	6	7															

subject	date	correct		incorrect		lft	rrft	%	tag	subject	date	correct		incorrect		lft	rrft	%	tag
		right	left	right	left							right	left	right	left				
9	13.10.97	9	9	2	0	1	2	90	1	10	16.10.97	9	9	2	0	5	6	90	0
9	13.10.97	6	11	2	1	1	2	85	2	10	16.10.97	8	8	2	2	4	2	80	1
9	13.10.97	7	7	4	2	5	4	70	3	10	16.10.97	8	8	2	2	6	5	80	2
9	13.10.97	5	7	5	3	4	1	60	4	10	16.10.97	5	7	6	2	1	3	60	3
9	13.10.97	4	5	6	5	2	4	45	5	10	16.10.97	4	8	4	4	3	2	60	4
9	13.10.97	10	7	1	2	1	3	85	13	10	16.10.97	2	7	8	3	1	3	45	5
9	15.10.97	9	9	2	0	5	4	90	0	10	16.10.97	11	8	0	1	8	6	95	13
9	15.10.97	7	12	1	0	4	2	95	1										
9	15.10.97	7	10	3	0	3	7	85	2	11	3.07.97	10	8	1	1	1	4	90	0
9	15.10.97	7	7	4	2	3	3	70	3	11	3.07.97	6	12	2	0	4	3	90	1
9	15.10.97	5	11	4	0	3	3	80	4	11	3.07.97	5	9	6	0	3	2	70	2
9	15.10.97	6	8	5	1	6	3	70	5	11	3.07.97	2	10	8	0	2	1	60	3
9	15.10.97	5	7	5	3	2	3	60	6	11	3.07.97	0	8	10	2	0	0	40	4
9	15.10.97	4	5	6	5	2	3	45	7	11	3.07.97	11	9	0	0	3	5	100	13
9	15.10.97	10	9	1	0	5	6	95	13	11	8.07.97	7	9	3	1	3	3	80	0
9	22.10.97	9	10	1	0	4	5	95	0	11	8.07.97	8	9	3	0	2	4	85	1
9	22.10.97	8	9	3	0	4	3	85	1	11	8.07.97	5	11	4	0	3	1	80	2
9	22.10.97	8	10	1	1	4	2	90	2	11	8.07.97	4	8	7	1	0	2	60	3
9	22.10.97	6	8	5	1	3	4	70	3	11	8.07.97	0	9	10	1	0	0	45	4
9	22.10.97	5	8	5	2	4	4	65	4	11	8.07.97	10	10	0	0	5	3	100	13
9	22.10.97	3	5	7	5	1	4	40	5	11	10.07.97	7	11	2	0	3	2	90	0
9	22.10.97	11	7	0	2	5	3	90	13	11	10.07.97	9	9	2	0	4	4	90	1
9	20.11.97	9	11	0	0	4	5	100	0	11	10.07.97	5	10	5	0	3	3	75	2
9	20.11.97	7	9	4	0	6	7	80	1	11	10.07.97	4	7	6	3	2	4	55	3
9	20.11.97	7	9	3	1	5	2	80	2	11	10.07.97	2	6	9	3	2	2	40	4
9	20.11.97	4	7	6	3	2	3	55	3	11	10.07.97	8	11	0	1	5	3	95	13
9	20.11.97	6	8	5	1	4	4	70	4	11	14.07.97	11	9	0	0	3	7	100	0
9	20.11.97	2	5	6	7	1	4	35	5	11	14.07.97	9	11	0	0	5	5	100	1
9	20.11.97	10	8	0	2	7	5	90	13	11	14.07.97	9	8	2	1	8	4	85	2
										11	14.07.97	5	7	4	4	1	3	60	3
10	13.08.97	10	9	1	0	6	8	95	0	11	14.07.97	7	7	4	2	2	3	70	4
10	13.08.97	5	10	4	1	4	2	75	1	11	14.07.97	6	10	4	0	3	4	80	5
10	13.08.97	6	7	5	2	2	4	65	2	11	14.07.97	5	8	4	3	4	3	65	6
10	13.08.97	3	8	7	2	3	2	55	3	11	14.07.97	4	5	6	5	3	2	45	7
10	13.08.97	2	8	8	2	2	4	50	4	11	14.07.97	11	7	0	2	4	2	90	13
10	13.08.97	10	8	1	1	2	2	90	13	11	18.07.97	11	9	0	0	4	3	100	0
10	19.08.97	6	6	5	3	4	3	60	0	11	18.07.97	8	10	0	2	6	3	90	1
10	19.08.97	4	8	6	2	3	3	60	1	11	18.07.97	9	10	1	0	2	6	95	2
10	19.08.97	3	7	7	3	3	2	50	2	11	18.07.97	7	8	4	1	4	4	75	3
10	19.08.97	8	9	3	0	5	5	85	13	11	18.07.97	1	8	8	3	1	2	45	4
10	25.08.97	8	8	1	3	3	3	80	0	11	18.07.97	11	9	0	0	4	2	100	13
10	25.08.97	9	9	1	1	5	5	90	1	11	22.07.97	10	9	1	0	6	4	95	0
10	25.08.97	8	8	3	1	5	6	80	2	11	22.07.97	7	11	2	0	4	7	90	1
10	25.08.97	4	9	4	3	3	2	65	3	11	22.07.97	8	9	3	0	4	3	85	2
10	25.08.97	4	7	7	2	3	2	55	4	11	22.07.97	7	8	3	2	4	4	75	3
10	25.08.97	5	7	5	3	3	5	60	5	11	22.07.97	5	6	4	5	5	2	55	4
10	25.08.97	5	6	5	4	3	4	55	6	11	22.07.97	4	8	6	2	2	4	60	5
10	25.08.97	6	6	5	3	4	3	60	7	11	22.07.97	6	5	5	4	4	3	55	6
10	25.08.97	4	5	5	6	3	1	45	8	11	22.07.97	4	6	5	5	2	5	50	7
10	25.08.97	10	7	0	3	4	5	85	13	11	22.07.97	11	7	0	2	3	1	90	13
10	28.08.97	11	7	0	2	4	2	90	0	11	28.07.97	8	11	0	1	4	4	95	0
10	28.08.97	6	11	2	1	3	6	85	1	11	28.07.97	10	10	0	0	2	4	100	1
10	28.08.97	6	8	4	2	5	5	70	2	11	28.07.97	7	7	4	2	3	2	70	2
10	28.08.97	5	6	6	3	2	2	55	3	11	28.07.97	6	9	3	2	2	3	75	3
10	28.08.97	4	8	5	3	2	1	60	4	11	28.07.97	6	5	5	4	4	3	55	4
10	28.08.97	4	5	7	4	4	2	45	5	11	28.07.97	6	5	4	5	2	0	55	5
10	28.08.97	9	7	1	3	3	4	80	13	11	28.07.97	6	7	4	3	4	7	65	6
10	5.09.97	8	9	0	3	3	2	85	0	11	28.07.97	2	2	9	7	1	0	20	7
10	5.09.97	9	10	1	0	3	4	95	1	11	28.07.97	8	8	0	4	3	4	80	13
10	5.09.97	6	5	5	4	3	2	55	2	11	31.07.97	7	12	1	0	4	4	95	0
10	5.09.97	4	8	5	3	4	2	60	3	11	31.07.97	6	9	4	1	1	2	75	1
10	5.09.97	5	7	6	2	2	5	60	4	11	31.07.97	6	7	5	2	3	2	65	2
10	5.09.97	3	6	7	4	3	1	45	5	11	31.07.97	7	9	2	2	5	3	80	3
10	5.09.97	10	8	0	2	4	6	90	13	11	31.07.97	5	5	6	4	1	2	50	4
10	9.09.97	8	9	0	3	5	5	85	0	11	31.07.97	10	7	0	3	5	4	85	13
10	9.09.97	9	9	1	1	8	7	90	1	11	4.08.97	7	11	2	0	4	2	90	0
10	9.09.97	10	9	1	0	5	5	95	2	11	4.08.97	9	10	1	0	4	4	95	1
10	9.09.97	3	8	6	3	1	4	55	3	11	4.08.97	7	8	4	1	2	4	75	2
10	9.09.97	5	6	6	3	4	1	55	4	11	4.08.97	6	9	3	2	3	3	75	3
10	9.09.97	5	7	5	3	3	2	60	5	11	4.08.97	5	8	6	1	5	4	65	4
10	9.09.97	5	8	5	2	4	5	65	6	11	4.08.97	3	6	6	5	3	2	45	5
10	9.09.97	6	7	5	2	3	3	65	7	11	4.08.97	10	8	1	1	3	3	90	13
10	9.09.97	3	7	5	5	1	2	50	8	11	6.08.97	10	10	0	0	5	6	100	0
10</																			

subject	date	correct		incorrect				%	tag
		right	left	right	left	lrft	rrft		
12	4.07.97	8	10	0	2	5	4	90	9
12	9.07.97	8	9	2	1	3	6	85	0
12	9.07.97	8	8	2	2	3	1	80	1
12	9.07.97	7	7	4	2	2	2	70	2
12	9.07.97	5	10	3	2	3	2	75	3
12	9.07.97	4	8	6	2	5	8	60	4
12	9.07.97	2	4	9	5	4	7	30	5
12	9.07.97	9	9	0	2	3	3	90	9
12	11.07.97	6	10	4	0	3	3	80	0
12	11.07.97	9	10	0	1	2	1	95	1
12	11.07.97	8	9	2	1	3	2	85	2
12	11.07.97	6	8	5	1	3	1	70	3
12	11.07.97	4	10	4	2	5	6	70	4
12	11.07.97	3	7	8	2	6	3	50	5
12	11.07.97	10	9	0	1	5	7	95	9
12	15.07.97	8	10	1	1	2	1	90	0
12	15.07.97	11	9	0	0	2	2	100	1
12	15.07.97	8	9	2	1	4	4	85	2
12	15.07.97	6	9	4	1	4	6	75	3
12	15.07.97	3	4	8	5	2	3	35	4
12	15.07.97	8	8	0	4	3	2	80	9
12	17.07.97	8	10	1	1	2	2	90	0
12	17.07.97	8	10	2	0	1	1	90	1
12	17.07.97	7	7	4	2	5	2	70	2
12	17.07.97	5	10	3	2	4	5	75	3
12	17.07.97	5	8	6	1	3	2	65	4
12	17.07.97	4	9	6	1	5	3	65	5
12	17.07.97	4	7	6	3	3	3	55	6
12	17.07.97	6	6	5	3	5	7	60	7
12	17.07.97	2	6	7	5	5	5	40	8
12	17.07.97	10	10	0	0	6	3	100	9
12	21.07.97	11	9	0	0	1	2	100	0
12	21.07.97	7	12	1	0	2	4	95	1
12	21.07.97	6	9	4	1	3	2	75	2
12	21.07.97	7	8	4	1	2	0	75	3
12	21.07.97	5	9	4	2	3	6	70	4
12	21.07.97	6	8	5	1	3	2	70	5
12	21.07.97	3	5	7	5	2	4	40	6
12	21.07.97	10	10	0	0	5	3	100	9
12	23.07.97	10	9	0	1	4	5	95	0
12	23.07.97	10	9	1	0	4	4	95	1
12	23.07.97	7	10	2	1	2	3	85	2
12	23.07.97	5	9	5	1	5	3	70	3
12	23.07.97	4	6	7	3	4	3	50	4
12	23.07.97	8	10	0	2	2	5	90	9
12	25.07.97	10	8	0	2	4	2	90	0
12	25.07.97	11	9	0	0	4	5	100	1
12	25.07.97	7	11	1	1	4	5	90	2
12	25.07.97	6	7	4	3	3	3	65	3
12	25.07.97	5	8	6	1	6	4	65	4
12	25.07.97	2	3	7	8	3	3	25	5
12	25.07.97	11	8	0	1	2	2	95	9
12	29.07.97	10	9	0	1	1	1	95	0
12	29.07.97	11	9	0	0	5	2	100	1
12	29.07.97	7	11	1	1	4	5	90	2
12	29.07.97	5	8	5	2	3	2	65	3
12	29.07.97	3	3	8	6	5	3	30	4
12	29.07.97	9	9	0	2	3	3	90	9

subject	date	tone-on		tone-off		tone-on		tone-off		%
		corr	inc	corr	inc	rft	rft			
9	26.05.99	2	8	0	0	2	0	20		
9	26.05.99	0	0	9	1	0	4	90		
9	26.05.99	20	1	18	1	12	11	1		
9	26.05.99	2	8	0	0	1	0	20		
9	26.05.99	0	0	7	3	0	5	70		
9	26.05.99	20	0	20	0	11	12	100		
9	28.05.99	18	1	15	6	9	8	1		
9	28.05.99	3	7	0	0	2	0	30		
9	28.05.99	0	0	5	5	0	1	50		
9	28.05.99	20	1	16	3	12	9	1		
9	28.05.99	4	6	0	0	1	0	40		
9	28.05.99	0	0	6	4	0	3	60		
9	28.05.99	20	0	18	2	15	15	1		
9	28.05.99	3	7	0	0	3	0	30		
9	28.05.99	0	0	6	4	0	4	60		
9	28.05.99	20	0	16	4	8	8	90		
10	17.03.99	20	0	16	4	10	11	1		
10	17.03.99	4	6	0	0	3	0	40		
10	17.03.99	0	0	5	5	0	0	50		
10	17.03.99	21	0	17	2	9	9	1		
10	17.03.99	5	5	0	0	3	0	50		
10	17.03.99	0	0	6	4	0	4	60		
10	17.03.99	21	0	16	3	8	9	1		
10	17.03.99	0	1	0	0	0	0	0		
10	30.03.99	20	0	16	4	8	8	1		
10	30.03.99	5	5	0	0	4	0	50		
10	30.03.99	0	0	6	4	0	3	60		
10	30.03.99	19	0	18	3	7	8	1		
10	30.03.99	5	5	0	0	3	0	50		
10	30.03.99	0	0	6	4	0	1	60		
10	30.03.99	21	0	16	3	8	6	1		
10	30.03.99	3	7	0	0	1	0	30		
10	30.03.99	0	0	7	3	0	3	70		
10	30.03.99	0	0	0	0	0	0	0		
10	3.05.99	18	1	19	2	10	6	1		
10	3.05.99	4	6	0	0	2	0	40		
10	3.05.99	0	0	5	5	0	2	50		
10	3.05.99	21	0	17	2	9	11	1		
10	3.05.99	3	7	0	0	3	0	30		
10	3.05.99	0	0	8	2	0	3	80		
10	3.05.99	20	0	17	3	10	9	1		
10	3.05.99	2	8	0	0	0	0	20		
10	3.05.99	0	0	7	3	0	2	70		
10	3.05.99	20	0	17	3	11	8	93		
12	16.03.99	19	1	20	0	4	5	1		
12	16.03.99	2	8	0	0	1	0	20		
12	16.03.99	0	0	7	3	0	1	70		
12	16.03.99	19	0	19	2	7	3	1		
12	16.03.99	2	8	0	0	1	0	20		
12	16.03.99	0	0	7	3	0	1	70		
12	16.03.99	21	0	19	0	6	9	1		
12	16.03.99	4	6	0	0	2	0	40		
12	16.03.99	0	0	7	3	0	2	70		
12	16.03.99	20	0	20	0	8	6	1		
12	16.03.99	5	5	0	0	4	0	50		
12	16.03.99	0	0	6	4	0	4	60		
12	16.03.99	20	0	19	1	6	7	1		
12	16.03.99	4	6	0	0	2	0	40		
12	16.03.99	0	0	8	2	0	4	80		
12	16.03.99	19	0	19	2	6	6	95		
12	30.03.99	20	0	19	1	7	7	1		
12	30.03.99	5	5	0	0	1	0	50		
12	30.03.99	0	0	5	5	0	1	50		
12	30.03.99	20	0	19	1	5	4	1		
12	30.03.99	5	5	0	0	3	0	50		
12	30.03.99	0	0	2	8	0	1	20		
12	30.03.99	19	0	19	2	8	9	1		
12	30.03.99	5	5	0	0	1	0	50		
12	30.03.99	0	0	4	6	0	2	40		
12	30.03.99	21	0	19	0	9	6	1		
12	30.03.99	4	6	0	0	2	0	40		
12	30.03.99	0	0	7	3	0	3	70		
12	30.03.99	20	0	20	0	10	11	100		
12	26.04.99	19	0	21	0	7	4	1		
12	26.04.99	4	6	0	0	3	0	40		
12	26.04.99	0	0	7	3	0	2	70		
12	26.04.99	19	0	18	3	4	6	1		
12	26.04.99	5	5	0	0	2	0	50		
12	26.04.99	0	0	7	3	0	2	70		
12	26.04.99	21	0	18	1	7	8	1		
12	26.04.99	4	6	0	0	3	0	40		
12	26.04.99	0	0	5	5	0	1	50		
12	26.04.99	20	1	19	0	5	6	1		
12	26.04.99	5	5	0	0	2	0	50		
12	26.04.99	0	0	10	0	0	3	100		
12	26.04.99	19	0	20	1	5	6	1		
12	26.04.99	4	6	0	0	2	0	40		
12	26.04.99	0	0	9	1	0	2	90		
12	26.04.99	19	0	21	0	10	8	100		

Condition 4

subject	date	tone-on		tone-off		tone-on		tone-off		%
		corr	inc	cor	inc	rft	rft			
9	24.06.99	19	1	19	1	8	7	1		
9	24.06.99	0	0	8	2	0	2	80		
9	24.06.99	4	6	0	0	1	0	40		
9	24.06.99	20	0	19	1	8	10	1		
9	24.06.99	0	0	7	3	0	2	70		
9	24.06.99	3	7	0	0	3	0	30		
9	24.06.99	21	0	18	1	11	9	1		
9	24.06.99	0	0	7	3	0	3	70		
9	24.06.99	4	6	0	0	0	0	40		
9	24.06.99	15	0	16	0	7	8	100		
9	6.07.99	6	14	18	2	6	6	1		
9	6.07.99	0	0	8	2	0	2	80		
9	6.07.99	3	7	0	0	2	0	30		
9	6.07.99	20	0	17	3	9	7	1		
9	6.07.99	0	0	5	5	0	2	50		
9	6.07.99	4	6	0	0	3	0	40		
9	6.07.99	21	0	19	0	10	11	1		
9	6.07.99	0	0	7	3	0	3	70		
9	6.07.99	1	2	0	0	0	0	33		
9	12.07.99	20	0	19	1	5	7	1		
9	12.07.99	0	0	6	4	0	1	60		
9	12.07.99	3	7	0	0	3	0	30		
9	12.07.99	20	0	18	2	8	8	1		
9	12.07.99	0	0	8	2	0	3	80		
9	12.07.99	4	6	0	0	3	0	40		
9	12.07.99	19	0	16	5	8	7	1		
9	12.07.99	0	0	6	4	0	3	60		
9	12.07.99	3	7	0	0	2	0	30		
9	12.07.99	14	1	11	5	6	6	81		
10	17.05.99	21	0	16	3	11	9	1		
10	17.05.99	4	6	0	0	1	0	40		
10	17.05.99	0	0	8	2	0	0	80		
10	17.05.99	20	1	12	7	0	0	1		
10	17.05.99	1	9	0	0	0	0	10		
10	17.05.99	0	0	10	0	0	0	100		
10	17.05.99	18	0	18	4	0	0	1		
10	21.06.99	20	0	14	6	12	10	1		
10	21.06.99	0	0	10	0	0	10	100		
10	21.06.99	5	5	0	0	5	0	50		
10	21.06.99	19	0	15	6	10	9	1		
10	21.06.99	0	0	4	6	0	2	40		
10	21.06.99	5	5	0	0	2	0	50		
10	21.06.99	21	0	15	4	4	6	1		
10	21.06.99	0	0	5	5	0	1	50		
10	21.06.99	5	5	0	0	1	0	50		
10	21.06.99	4	0	3	0	1	3	100		
10	7.07.99	20	0	16	4	11	8	1		
10	7.07.99	0	0	6	4	0	3	60		
10	7.07.99	4	6	0	0	1	0	40		
10	7.07.99	19	0	19	2	8	9	1		
10	7.07.99	0	0	6	4	0	5	60		
10	7.07.99	6	4	0	0	2	0	60		
10	7.07.99	21	0	18	1	11	12	1		
10	7.07.99	0	0	6	4	0	3	60		
10	7.07.99	5	5	0	0	3	0	50		
10	7.07.99	10	0	9	2	6	4	90		
12	3.05.99	19	0	21	0	6	7	1		
12	3.05.99	3	7	0	0	1	0	30		
12	3.05.99	0	0	9	1	0	5	90		
12	3.05.99	21	0	19	0	9	5	1		
12	3.05.99	4	6	0	0	2	0	40		
12	3.05.99	0	0	7	3	0	2	70		
12	3.05.99	20	0	20	0	6	7	1		
12	3.05.99	3	7	0	0	2	0	30		
12	3.05.99	0	0	9	1	0	2	90		
12	3.05.99	20	0	18	2	5	4	1		
12	3.05.99	3	7	0	0	3	0	30		
12	3.05.99	0	0	8	2	0	4	80		
12	3.05.99	19	0	18	3	7	6	93		
12	18.06.99	19	1	20	0	6	8	1		
12	18.06.99	0	0	10	0	0	0	100		
12	18.06.99	2	8	0	0	1	0	20		
12	18.06.99	19	0	21	0	6	6	1		
12	18.06.99	0	0	10	0	0	3	100		
12	18.06.99	3	7	0	0	0	0	30		
12	18.06.99	21	0	19	0	5	3	1		
12	18.06.99	0	0	10	0	0	1	100		
12	18.06.99	4	6	0	0	2	0	40		
12	18.06.99	20	0	20	0	5	8	1		
12	18.06.99	0	0	9	1	0	2	90		
12	18.06.99	4	6	0	0	2	0	40		
12	18.06.99	20	0	19	1	10	6	1		
12	18.06.99	0	0	9	1	0	3	90		
12	18.06.99	4	6	0	0	2	0	40		
12	18.06.99	19	0	21	0	6	9	100		
12	23.06.99	19	0	21	0	3	6	1		
12	23.06.99	0	0	9	1	0	2	90		
12	23.06.99	4	6	0	0	0	0	40		
12	23.06.99	21	0	19	0	6	4	1		
12	23.06.99	0	0	8	2	0	0	80		
12	23.06.99	5	5	0	0	2	0	50		

subject	date	tone-on		tone-off		tone-on		tone-off	
		corr	inc	corr	inc	rft	rft	%	
12	23.06.99	18	2	20	0	5	7	1	
12	23.06.99	0	0	10	0	0	2	100	
12	23.06.99	6	4	0	0	1	0	60	
12	23.06.99	19	1	19	1	6	5	1	
12	23.06.99	0	0	7	3	0	2	70	
12	23.06.99	3	7	0	0	2	0	30	
12	23.06.99	19	0	21	0	6	6	1	
12	23.06.99	0	0	9	1	0	1	90	
12	23.06.99	4	6	0	0	3	0	40	
12	23.06.99	21	0	19	0	5	6	100	

Appendix J - Experiment 9 threshold sessions

Possum number, date, number of correct and incorrect bright trials, number of correct and incorrect dim trials, the number of reinforcements for bright and dim trials, the overall percentage of correct responses in the current block of trials and the current luminance of the bright light (in log cd/m²).

(0=1.0, 1=0.8, 2=0.6, 3=0.4, 4=0.2, 13=1.0)

subject	date	bright		dim		brft	drft	%	tag	subject	date	bright		dim		brft	drft	%	tag
		corr	inc	corr	inc							corr	inc	corr	inc				
1	1.06.01	14	5	17	4	5	7	78	0	4	2.05.01	16	2	20	2	6	8	90	0
1	1.06.01	19	2	15	4	9	6	85	1	4	2.05.01	18	2	18	2	10	9	90	1
1	1.06.01	16	5	17	2	3	7	83	2	4	2.05.01	16	5	15	4	6	8	78	2
1	1.06.01	12	7	17	4	5	5	73	3	4	2.05.01	17	4	17	2	10	6	85	3
1	1.06.01	7	12	12	9	4	3	48	4	4	2.05.01	5	13	11	11	4	6	40	4
1	1.06.01	19	2	18	1	10	8	93	13	4	2.05.01	18	2	17	3	4	6	88	13
1	26.07.01	17	4	19	0	5	4	90	0	4	31.05.01	19	1	19	1	16	14	95	0
1	26.07.01	13	6	21	0	5	6	85	1	4	31.05.01	18	2	18	2	5	8	90	1
1	26.07.01	15	5	19	1	4	5	85	2	4	31.05.01	17	2	16	5	7	4	83	2
1	26.07.01	14	6	17	3	7	5	78	3	4	31.05.01	17	4	17	2	4	6	85	3
1	26.07.01	6	15	12	7	4	5	45	4	4	31.05.01	9	11	15	5	7	8	60	4
1	26.07.01	15	4	17	4	1	3	80	13	4	31.05.01	20	0	14	6	8	5	85	13
1	10.08.01	16	2	18	4	7	3	85	0	4	6.07.01	14	6	17	3	5	7	78	0
1	10.08.01	17	3	18	2	6	8	88	1	4	6.07.01	13	7	14	6	8	7	68	1
1	10.08.01	16	5	14	5	3	5	75	2	4	6.07.01	13	8	16	3	8	9	73	2
1	10.08.01	15	6	14	5	8	4	73	3	4	6.07.01	11	8	16	5	5	5	68	3
1	10.08.01	6	12	15	7	2	6	52	4	4	6.07.01	8	12	13	7	5	4	52	4
1	10.08.01	16	4	15	5	4	4	78	13	4	6.07.01	15	6	16	3	9	8	78	13
1	14.08.01	13	5	15	7	3	6	70	0	4	14.08.01	19	2	17	2	4	6	90	0
1	14.08.01	16	4	18	2	4	1	85	1	4	14.08.01	21	0	17	2	10	6	95	1
1	14.08.01	16	5	18	1	5	7	85	2	4	14.08.01	18	1	17	4	2	5	88	2
1	14.08.01	15	6	16	3	6	5	78	3	4	14.08.01	15	4	18	3	7	6	83	3
1	14.08.01	8	10	18	4	5	7	65	4	4	14.08.01	10	11	15	4	6	4	63	4
1	14.08.01	17	3	14	6	8	6	78	13	4	14.08.01	17	4	18	1	6	7	88	13
1	17.08.01	16	5	15	4	3	4	78	0	4	16.08.01	18	1	20	1	9	9	95	0
1	17.08.01	18	3	16	3	5	8	85	1	4	16.08.01	18	2	16	4	5	3	85	1
1	17.08.01	15	4	17	4	7	3	80	2	4	16.08.01	17	3	15	5	1	3	80	2
1	17.08.01	13	6	19	2	4	6	80	3	4	16.08.01	15	6	14	5	4	5	73	3
1	17.08.01	7	14	12	7	5	7	48	4	4	16.08.01	9	10	16	5	3	3	63	4
1	17.08.01	19	2	13	6	7	4	80	13	4	16.08.01	19	1	19	1	13	11	95	13