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VISUAL DEPTH PERCEPTION VIA MOTION
PARALLAX BY CHICKENS (*GALLUS GALLUS*) IN AN
OPERANT CHAMBER

A thesis submitted in in fulfilment for the

Degree of Masters in Applied Psychology

At The University of Waikato



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ABSTRACT

There are multiple cues animals use to infer depth from the two-dimensional information that passes across the retina. Differential motion of objects across the retina, or motion parallax, has been extensively studied in humans and primates, but little information is available on avian species. This set of experiments utilised an operant chamber and computer-generated stimuli to investigate the parallax discrimination abilities of domestic chickens (*Gallus gallus*). The birds were able to discriminate between a single stationary and a single moving object, but performance dropped to chance, and biased responding developed when parallax stimuli were introduced. A second operant chamber that forced the animals to view stimuli from a distance also resulted in chance performance. Birds may require motion across both eyes to discriminate depth when displayed on a screen.

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Ehara taku toa, he takitahi, he toa takitini

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GENERAL INTRODUCTION

Seeing depth

In animals with single lens eyes, a two dimensional (2-D) image is projected onto the retina. This thesis examines how birds are able to extract 3-D information about the environment from these 2-D images. There are several cues in stationary 2D images that can be used to recover depth (Goldstein, 2002). Larger objects are seen to be closer than smaller objects. A flying aeroplane, while actually very large, is seen as far away due to its small size on the retina. If an object is partially covered by another object, the occluded object is seen as further away. Humans are very good at segmenting figures from background using this cue (Baker & Braddick, 1982; Regan, 1986).

Texture, shading and luminance can give additional depth clues (Hendrix & Barfeld, 1995; Surdick, Davis, King & Hodges, 1997). Objects that are shaded give the impression of depth. Objects with a fine grained texture are seen as closer than objects with a coarse grain. O'Brien and Johnston (2000) found that texture was just as, or more, effective in estimating slant than moving depth cues.

The above sources of depth information are referred to as 'static' or 'pictorial' cues (Goldstein, 2002). From these cues, animals are able to move through, and interact with, a 3D world. When a 2-D image contains motion, additional cues combine to create the perception of depth. Investigations into rotating objects have shown that rotating shapes are seen to have a 3D structure, rigidity and coherence that is not apparent when the image is still; this is referred to as "structure from motion" (Gibson, Olum & Rosenblatt, 1955) or the "kinetic depth effect" (Wallach & O'Connell, 1953).

The problem of how depth is extracted from image motion has a long history. For example, Helmholtz wrote that:

"In walking along, the objects that are at rest by the wayside ... appear to glide past us in our field of view More distant objects do the same way, only more slowly..." (Helmholtz, 1925, p 295).

Motion parallax is the sense of depth created when close objects move across the retina to a greater degree than further away objects. This phenomenon can be viewed monocularly, so is ideal for comparative studies in different species.

Motion parallax can be active; when an organism moves through an environment of stationary objects. Motion parallax also occurs passively, such as when travelling in a vehicle while the limbs themselves are stationary.

When we view moving images on a screen we are extracting 3-D depth information from a 2-D source; the image projected onto the retina is 2-dimensional to begin with. However we can still extract 3-D information from this 2-D source if motion parallax is present. Motion parallax occurs when several 2D stimuli move at different speeds across a screen. Several stationary dots will be seen as a flat plane, but as soon as they begin to move at different speeds, a strong depth percept is created in humans. The stimuli moving slowly are perceived to be further away than faster moving stimuli. This effect can be very strong; when playing video games, players will often move their bodies as if they were actually interacting with the world represented on the screen.

In animals with forward-facing eyes such as humans and owls, each eye receives the image from a slightly different angle. The resulting stereopsis (or stereoscopic

vision) was originally thought to be the primary depth cue in humans (Goldstein, 2000). But this does not explain how species with more lateral eyes successfully interact with their environments. More recent studies have shown that stationary cues, stereopsis, and moving cues have an additive relationship in the perception of depth (Bootsma & Craig, 2002; Van den Berg & Brenner, 1994; Schiller, 2011; Saarela & Landy, 2012). Skill in using binocular depth cues is not indicative of skill in using monocular depth cues, either in the real world or computer simulations (Westerman & Cribbin, 1998).

Anatomy and physiology of depth extraction in the avian visual system

As mentioned above, animals with forward facing eyes have a slightly different angle of view from each eye. The exact position of the eyes determines the size of the binocular field. Predatory birds like owls and raptors have a relatively large binocular field and high visual acuity, and this is reflected in the larger size of the visual Wulst in the brain (Wylie, Gutierrez-Ibanez, Pakan & Iwaniuk, 2009). However most birds have eyes situated more laterally on the skull, affording a very limited binocular field, and even this can be eliminated by head and eye movements (Kral 1998). These species still avoid collisions and perform other precise, visually guided behaviours. Pigeon pecking behaviour is no less accurate when one eye is occluded (Martin & Katzir, 1999).

The fovea is the area in the eye responsible for focused vision. Birds, unlike mammals, have two fovea in each eye, one directed laterally and one frontally. Stereopsis usually requires alignment of each eye's fovea on the object of interest, so that disparity can give 3D cues (Frost 2010). It is likely that the laterally

oriented fovea is used to discern distant moving objects, and the visual system switches to the frontal fovea when the object comes closer (Maldonado, Maturana, & Varela, 1988).

Pigeons possess neurons that respond specifically to motion parallax. Xiao and Frost (2013) displayed random dots in two planes to create parallax stimuli, and measured the response of neurons in the pretectal area of the brain. They found that neurons were at first facilitated but later suppressed by increasing the speed of the second plane. Most tectal cells have an inhibitory surround, so that they respond best to a spot moving through the excitatory centre, as the background moves in the opposite direction (Wylie et al., 2009). Such an arrangement could help with depth extraction (Nakayama & Loomis, 1974).

The principal optic nucleus of the thalamus and the wulst are similar to the lateral geniculate nucleus (LGN) and primary visual cortex (V1) in mammals. The AOS and pretectum are important for analysing “optic flow” (global patterns of motion on the retina generated by observer movement) and for generating compensatory eye movements that stabilise the image in the retina (Wylie et al., 2009). This is referred to as the “optokinetic response” (Atkinson, 1984). All animals stabilise their world by moving in a manner that keeps the whole visual field stable on the retina. Some insects use side-to-side pendulum movements of the head to determine relative and absolute distances. If an object is moved in the opposite direction to head motion, retinal image motion increases, making the object appear nearer. If the object is moved in the same direction as head movements, retinal image motion decreases and the object appears to be further away than it

actually is (Kraal, 1998). Some bird species bob their heads when walking; this is thought to aid in monocular depth realisation in lieu of stereopsis (Nekker, 2007).

Psychophysical methods used to study depth perception

Fechner, Wundt and von Helmholtz (Goldstein, 2000) pioneered the measurement of the mind and sensations, and several methods have since been developed to measure the relationship between stimuli, sensation and perception. In psychophysical experiments with humans, participants are verbally instructed to attend to a specific stimulus feature. They can then give unambiguous verbal feedback concerning what they perceive. In a foundational study on motion parallax, Rogers and Graham's (1979) participants were asked to describe the shape of a virtual surface on a computer screen. The participants had to report on the number of repetitions of the sinewave corrugations and the apparent depth of the corrugations. They were able to perceive the correct 3-D shape of the surfaces from the 2-D screen motion.

Human psychophysical experiments rely on participant's history of verbal behaviour to ensure that instructions are understood and the desired response is elicited. With animals we must create an analogy of this in the operant chamber. Animals cannot directly tell us about how they see their world, but they can be taught to give unambiguous answers to question put to them. Psychophysical experiments must be carefully designed so that the "answers" subjects give are related to the questions researchers are asking. When investigating size discrimination in birds Appelle (1972) became suspicious after his pigeons were able to discriminate between a 59mm diameter circle and a 60mm circle. Upon

examining the equipment, the bulb used to illuminate the comparison stimuli was found to have a slight fault, resulting in a faint line through the circle. The birds were attending to this stimulus feature instead of size.

Animals must then be trained to make a response, using operant methods, in lieu of verbal instruction and feedback. Responses are discreet and of short duration, such as pecking in pigeons and bar pressing in rats. Either a go/no go or a forced choice procedure is usually used. In go/no go studies, a stimulus is presented and then the animal either responds if the stimulus is perceived, or makes no response if not. In forced-choice psychophysical experiments a stimuli is presented then two or more keys are shown. The animal must choose one or the other, and correct responses are reinforced. In studies utilising two or more response keys, the positions are randomly alternated to account for any spatial preference or “handedness”. Nagasako and Wasserman (2008) found that their birds had learnt to peck on the left key instead of attending to the stimulus. When key position was randomised discrimination performance dropped drastically. The keys must also be sufficiently different. Animals respond faster if response levers are different in both colour and shape (Weitz, 1974).

Animals must be motivated to work, by being kept slightly deprived of a resource that is then provided in the operant chamber, food and water being most common. Animals that are too deprived generally perform poorly on discrimination tasks (MacKintosh 1994). An animal that is not motivated to work for the resource being provided may still work for other stimuli that acquire reinforcing properties by virtue of being paired with a reinforcer. Echevarria, Brewer, Burk, Brown, Manuzon & Robinson (2005) gave rats’ access to water before a discrimination task with water as the reinforcer. Predictably, the animals made many more errors

of omission. However they still completed 20-30 trials, indicating that secondary reinforcers may have been partially maintaining performance.

“Noise” or “distractors” is the inclusion of stimuli elements that make discrimination more difficult. Bischoff, Reid, Wylie and Spetch (1999) tested humans and pigeon's ability to detect motion in random dot displays. The dots were either random (0% of dots moving in the same direction) or moving coherently (10% to 100% of dots moving in the same direction). Pigeons performed much worse than humans, especially at low coherency i.e. high noise. Whether noise affects performance depends on both the type of task and type of noise. Simpler tasks are less affected by noise than more complex ones (Maes & de Groot, 2003).

Generalisation to novel stimuli is strong evidence that the animals have learnt the task experimenters set out to teach. If an animal is able to correctly discriminate stimuli never encountered before we can be more confident they have been discriminating based on the correct stimulus dimensions. Animals can be trained to classify visual stimuli into what humans would call nouns. For example, Cerella (1979) trained pigeons to respond to oak-shaped leaves, but not to other leaf shapes that were significantly different from oak. Experimental work on “verb” formation is less extensive. In a study by Asen & Cook (2012) pigeons were shown videos of various animal species walking and running in a characteristic, species specific manner. The birds were able to discriminate between walking and running videos, even if film sequences were sped up, slowed down or viewed from different angles. Animals with previous experience in similar tasks perform subsequent tasks faster (Goto & Lea 1993).

Perception and attention are not one and the same. When asked to count the number of ball passes in a filmed section of a basketball game, few people could recall seeing a man in a gorilla suit walk across the court (Simons & Chabris, 2011). The image of the gorilla passed over the retina, but attention was focused on the counting task. In human psychophysical experiments, participants are often asked to press the space bar or any key to begin the experiment proper, thus ensuring the stimuli are attended to. Animal psychophysical experimental design must ensure that subjects are attending to the stimuli before they make their responses. This “bottom up” attention is a process driven by salient external stimuli, such as the presence of conspecifics or threats. Human psychophysical experiment may require “top down” attention instead, that is, attention motivated by prior knowledge or goals (Katsuki & Constantinidis, 2013). Experimental work with animals necessarily requires the former. Skinner (1953) defined attention not as a class of behaviour, but the measurable relationship between a class of discriminative stimuli, and the operant responses that have previously been associated with consequences in presence of that class.

Depth from moving images

Several stratagems have been developed to investigate visual depth from motion. Point light research is useful in demonstrating how organisms group moving features into significant arrangements. When stationary, the lights are meaningless, but as soon as the lights move, people are able to recognise the lights as being attached to a living, moving organism. Very few points are needed for this, and Jordan, Fallah and Stoner (2006) found that humans could even

recognise gender and mood. This has also been shown in monkeys (Jastaroff, Popivanov, Vogels, Vanduffel & Orban, 2012; Tomonaga, 2001). Point light motion research with birds is less robust; Dittrich, Lea, Barrett and Gurr, (1998) found limited discrimination of point light displays by pigeons, and did not transfer to fully detailed displays. Rats were also unable to generalise to other species (Mackinnon, Troje & Dringenberg, 2010).

In humans, global patterns of image motion, or optic flow, takes precedence over individual points (Van den Berg et al., 1992). Many studies on 2D presentation of motion to avian species have focused on “coherent” motion. Goto, Lea and Dittrich (2002) exposed pigeons to stimuli of dots acting like “sheep” (random motion) or “wolves” (moving towards randomly moving dots). Discrimination of these two categories of motion was limited, and dropped to chance when more “wolves” were added. Cook and Roberts (2007) showed pigeons semi-realistic sequences of flying “through” or “around” a 3D ring. The birds were able to learn this discrimination, but when the video sequence frames were scrambled, the bird's performance dropped.

Structure from motion (sfm) has been extensively studied in animals. A 2D shape will give a strong impression of 3D depth when it is rotated around an axis. Sfm research avoids the confounding of spatial change with temporal change inherent in other motion stimuli. Rotating shapes occupy the same position on the screen throughout the presentation; there is no percept that the object moves from Point A to Point B. Humans report that the perceived direction of rotation can spontaneously reverse, depending on speed (Van den Berg et al. 1992). Birds may have difficulty using additional depth cues to recognise complex shapes;

Friedman, Vuong and Spetch (2009) found that discrimination of human faces by humans was not improved by rotating the images in depth, compared to stationary images. Several studies have shown that depth from sfm and depth from active, static or passive motion parallax are processed similarly (Braunstein & Tittle, 1993; Caudek & Proffitt, 1993). Others however, support a superior effect for observer-induced parallax (Ono & Steinbach, 1990), i.e., the observer needs to be moving to experience depth from parallax.

Heading estimation in humans from optic flow

Optic flow fields have been extensively studied in humans. Random dot displays are generally used, though textured grounds can be just as effective (Wilkie & Kountouriotis, 2013). Both types of display allow perceived direction, coherency, luminance (Wilkie & Kountouriotis, 2013), velocity (Kerzel, 2000) and a host of other stimulus features to be easily manipulated and compared. Cutting and Vishton (1995) found that differential motion, spatial pooling and size-weighted spatial pooling all contributed to the determination of heading, though the displacement of the largest object in the display provided the best predictor of direction. Eye and head movements are easily manipulated and measured in human experiments; judgements of the direction of movement are more accurate with actual eye movements as opposed to those simulated on a screen (Royden, Crowlee & Banks, 1994). Humans tend to use a combination of cues to perceive heading direction, relying on information from composite tau (the changing pattern of size and distance) both when the observer is moving and when the object is moving (Bootsma et al., 2012). This strategy makes perception more resistant to noise (Van den Berg et al., 1994). By integrating motion over large

areas of the visual field it is possible to obtain robust estimates of heading direction (Perrone, 1992).

Depth perception arising from lateral translation of the observer

Motion parallax research with humans typically utilises random-dot patterns moving in two or three planes. The perception of motion tends to break down with more than three planes (Langer, Rekhi, Pereira & Bhatia, 2005; Sauer, Braunstein, Andersen & Bian, 2001). Using translating planes of random-dot patterns allows for other monocular depth cues to be eliminated (Blakemore & Julesz, 1971); cues such as position (Nakayama and Tyler, 1981), and head and eye movements (Nawrot & Joyce, 2006) can be controlled. Schiller Slocum, Jao and Weiner (2011) used random-dot displays to vary the binocular disparity, shading and/or motion parallax of a display with monkeys and humans. They found that depth perception was best for both species when all three cues were combined. With motion parallax cues alone, the display must be sufficiently complex for the perception of depth (Eriksson, 1973). Cao and Schiller (2003) tested rhesus' monkeys on the detection and discrimination of depth using a square consisting of disparate dots (stereopsis) or dots at different velocities (parallax). Detection of depth for both types of stimuli were similar, but discrimination was more effective and quicker when stereopsis was used. This and other work (Graham & Rogers, 1979) suggests that for primates at least, motion parallax contributes the most to depth perception when depth amplitude is close to the limit of the observer's ability to distinguish between two or more planes.

While there are numerous neuropsychophysical studies using random-dot patterns and gratings to study motion parallax in avian species motion parallax (i.e. Xiao

& Frost 2013; Wylie et al., 2009; Nakayama & Loomis, 1974), there are few behavioural studies that do the same (Van der Wilgen, Frost & Wagner, 2002). Parallax displays are a good option for studying depth extraction in birds. They contain global patterns of image motion consistent with what would be perceived from a lateral eyed species but are not as complex as the optic flow fields that simulate forward movement through an environment. These latter stimuli contain a wide range of depths and image velocities and so it is difficult to know what aspect is controlling the behaviour.

Internal and external validity of stimuli

A critique of behavioural laboratory research is that experiments are so artificial that few extrapolations can be made to real-world behaviour. Swaddle (2001) tested wild starlings for symmetry discrimination using random dots. He blamed the limited ecological validity of white dots presented on a screen for the limited success of the results. Impoverished stimuli may account for the failure of owls to discriminate between figure-only and figure-ground stimuli (Van der Willigen et al., 2002).

On the other hand, natural and naturalistic stimuli has many limitations for perceptual research; all variables cannot be controlled, and it can be unclear which aspects of the stimuli animals are responding to. Dittrich and Lea (1993) used videos of real pigeons making various movements, and trained birds to respond either when motion was present or motion was absent. But it is unclear whether the birds were discriminating based on “movement” or a host of other possible cues.

Thesis research question; can chickens recover 3D information from motion in an operant chamber?

Despite many years of research into the problem of how 3-D depth is recovered from 2-D image motion (see above) we still do not have a good idea of how it exactly works or happens. Most studies have concentrated on human or non-human primate depth estimation with some limited work with birds and insects. The set of experiments in this thesis was designed to explore the lateral motion visual depth processing ability of chickens in an operant chamber. This should provide insights into depth perception in general and to provide more information about how birds extract 3-D information.

Previous research on lateral motion has utilised simple motion patterns such as sinewave gratings (Van der Willigen et al., 2003) or natural stimuli such as video footage of conspecifics (Dittrich & Lea, 1993) to investigate this problem.

Research using semi-naturalistic stimuli (such as animated animals; Ansen & Cook, 2012) has the advantage of controlling multiple cues while retaining ecological validity, however there still remains multiple sources of depth cues.

While some studies have looked at the contribution of binocular disparity, motion parallax or both, few have looked specifically at parallax stimuli. Furthermore, past experiments on avian depth perception have tended to examine quite complex stimuli (e.g. Cook, 2000) without first examining basic 2-D motion processing which is a necessary precursor to depth extraction. Most studies have also been carried out on pigeons; far less is known about depth perception in other birds such as chickens. We do not know if chickens can be tested for their motion detection abilities in the same way as pigeons and if such studies can be carried

out in an operant chamber designed for chickens. Our laboratory has used chickens in operant chambers for many years (i.e. Foster et al., 1995) and it would open up the possibility of many more studies on avian vision if it could be demonstrated that chickens readily interpret motion on a 2-D computer display as having 3-D structure and the same relevance as objects in their natural 3-D environments.

Behavioural and neurophysical studies have indicated discrimination performance is superior for vertical or horizontal movement as opposed to oblique motion (Appelle, 1972). The neurons that respond to parallax stimuli in primates (van Wezel & Britten, 2002) and pigeons (Xiao & Frost, 2013) have preferred directions. Are these basic motion processing neurons the same in chickens? If so, we expect the chickens to respond to simple moving stimuli and be able to discriminate different kinds of movement. Patterns of leftward or rightward moving motion with different speeds are perceived by us as having depth. Do chickens see these patterns in the same way as humans? To address these and other questions, this study used simple geometric shapes moving horizontally across the screen. High contrast, white squares on a black background were used in all experiments. This configuration removed, as much as possible, extraneous sources of depth cues including occlusion, shading and position.

In this set of experiments it was decided to incrementally test chicken's motion detection abilities rather than immediately testing with a complex 3D depth extraction task. Resolving depth from a moving 2-D parallax display requires the ability to detect small differences in speed across a large area of the display. If the animals fail to register 3-D depth in a full screen parallax display we do not know if this is because they cannot perceive the depth, that they cannot discriminate

differences in speed or that they could not even see the moving objects in the display. Given that 'basic' motion detection abilities in chickens viewing 2-D screens are largely unknown, the experiments in the thesis were designed to start with simple motion tasks and to progressively move towards more complex 3-D depth estimation.

EXPERIMENT ONE

INTRODUCTION

Discrimination tasks with humans rely on participant's history of verbal behaviour to operate equipment and understand instructions. In studies with animals, each step must be trained before progressing to the next. Young, Beckman and Wasserman's (2006) birds failed to discriminate between animations where one object "caused" another to move, and an animation where the objects did not interact. They speculated that they should have first been trained to simply catch a moving target. With this in mind, the first set of stimuli was designed to test whether the birds could perform the task when the stimuli were as easily discriminable as possible. Although we know from their behaviour that chickens can obviously perceive motion, we first need to know if they can be trained to discriminate a moving object from a static object using our particular screen and chamber set up. The moving stimulus consisted of lateral motion in one direction only, and the stationary stimulus was situated at the midway point of the moving stimulus' path. We wanted to know if the chickens could reliably discriminate between static and moving squares. Pigeons and other avian species have neurons that respond specifically to motion; this and the body of behavioural research where birds are able to discriminate a range of moving and stationary stimuli, in various experiments, indicates that the animals in this experiment should be able to perform the task successfully.

METHOD

Subjects

Subjects were six mixed-breed domestic roosters (*Gallus gallus domesticus*) numbered 3.1-3.6, of various ages at the start of the experiment. All animals had previously been trained to peck a mechanical key for wheat in other, non-psychophysical, experiments.

Each bird was housed individually in a wire cage measuring 51cm x 45cm x 44cm, in a ventilated room with up to 35 other chickens. Lights were on a 12:12 hour light: dark cycle. Water was available ad lib and grit provided once a week. Animals were weighed daily and maintained at 85%, +/- 5% of their free-feeding body weight through supplementary post-experimental feeding of commercial chicken feed.

All procedures complied with the University of Waikato's Animal Ethics Committee requirements.

Apparatus

Experiments took place in an operant chamber constructed of 20-mm thick particle board measuring 580mm x 430mm x 530mm. A central magazine delivered 2 seconds access to wheat through an aperture measuring 95mm x 125mm, situated 100mm from the floor of the chamber. A white LED inside the magazine aperture was lit for the duration of wheat access. An infra-red device recorded whenever the subject's head broke a beam to gain access.

A Dell screen measuring 1200 x 1000 pixels (300mm x 220mm, model number E176FPb) was installed above the magazine aperture. Pecks to the screen were recorded as x, y co-ordinates. Response keys consisted of two circles positioned at $(x, y) = (125, 825)$ pixels (left key) or $(1075, 825)$ pixels (right key). Each key could be either red or green. Stimuli were created using 3DMax (Autodesk 2013) in .avi format, and designed to run at 60Hz.

A Dell computer (Optiplex model GX260) running a custom-made application controlled the experimental program. Data recording was event-driven, and session data was also recorded manually.

Training

Each animal was weighed before being placed in the chamber. As animals had been used in previous experiments, magazine and key pecking training were conducted in the same session. All birds were reliably pecking the blank screen and eating from the magazine within one 30-minute session

Three animals (3.1, 3.2 and 3.3) were reinforced for choosing green after a stationary stimulus and for choosing red after a moving stimulus. The remaining three animals (3.4, 3.5 and 3.6) were reinforced for pecking red after a stationary stimulus and for pecking green after a moving stimulus. On training days one, three and five the stationary stimulus only was presented. On training days two, four and six the moving stimulus only was presented.

A peck to the blank screen was required to begin each trial. After stimulus presentation two keylights of the same colour (either red or green) then appeared at 125, 825 pixels (left key) or 1075, 825 pixels (right key). The animal was required to peck either key to obtain a reinforcer. This continued until 30 reinforcers had been obtained.

Procedure

Sessions took place in the same operant chamber as training sessions, using wheat as a reinforcer. Each trial began with a blank screen that required a peck to begin stimulus presentation. Animals 3.1, 3.2 and 3.3 were reinforced for pecking the green key after the moving stimulus and the red key after the stationary stimulus. Animals 3.4, 3.5 and 3.6 were reinforced for pecking the red key after the moving stimulus and the green key after the moving stimulus.

The stationary stimulus consisted of a solid white square on a black background with sides 40 pixels long (See Fig. 1.1 a). This box appeared in the centre ($X=600$, $Y=500$ pixels) of the screen for a duration of 3 seconds. The moving stimulus was a white box of the same size on a black background. Initial stimulus position the centre of the square at 60, 500 pixels, travelling to 1140, 500 pixels over 3 seconds, equivalent to a screen velocity of 10cm/sec (fig 1.1 b).

After stimulus presentation the keylights were presented and stayed on until a response was made. Keylights were the same size, shape and position as training sessions. The position of the green and red key was semi-randomised so that no more than three consecutive trials had the key on the same side, and that an equal number of left and right presentations occurred in each session.

Correct pecks resulted in 2 seconds access to grain. Incorrect pecks resulted in a time-out of three seconds of black screen. Sessions continued until 30 reinforcers had been received or 40 minutes had elapsed, whichever came first. Two consecutive sessions of at least 80% correct were required for animals to move on to the next experiment.

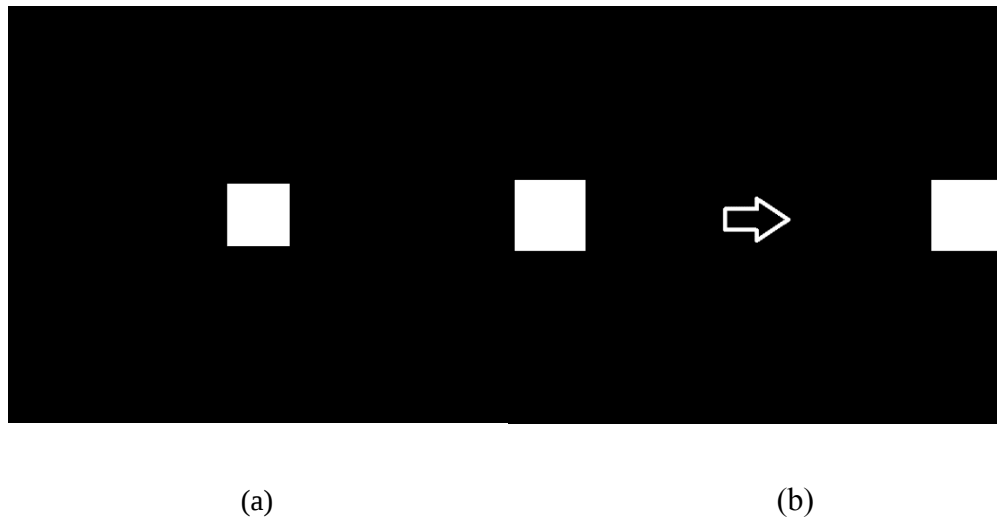


Fig.1.1. (a) stationary stimuli used in experiment one (b) moving stimuli used in experiment one, arrow indicates direction of movement

RESULTS

All animals reached the 80% correct, two consecutive sessions threshold in 8 to 17 sessions ($M=11$ $SD=3.35$) as shown in figure 1.1. Figure 1.2 shows the mean percentage of correct choices per session for all birds. Mean percentage correct was above chance for all sessions, as indicated by the dashed line. Discrimination performance steadily increased over time until performance reached criterion. Figure 1.3 shows the percentage of correct choices per session for each bird. Individual bird's performance also steadily increased over time. After the first five sessions, performance was always above chance.

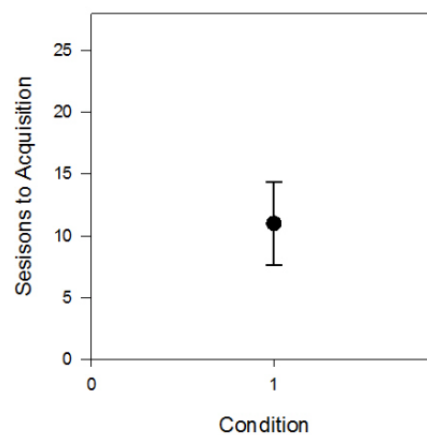


Fig. 1.2. Mean sessions to discrimination threshold. The error bars indicate one standard deviation.

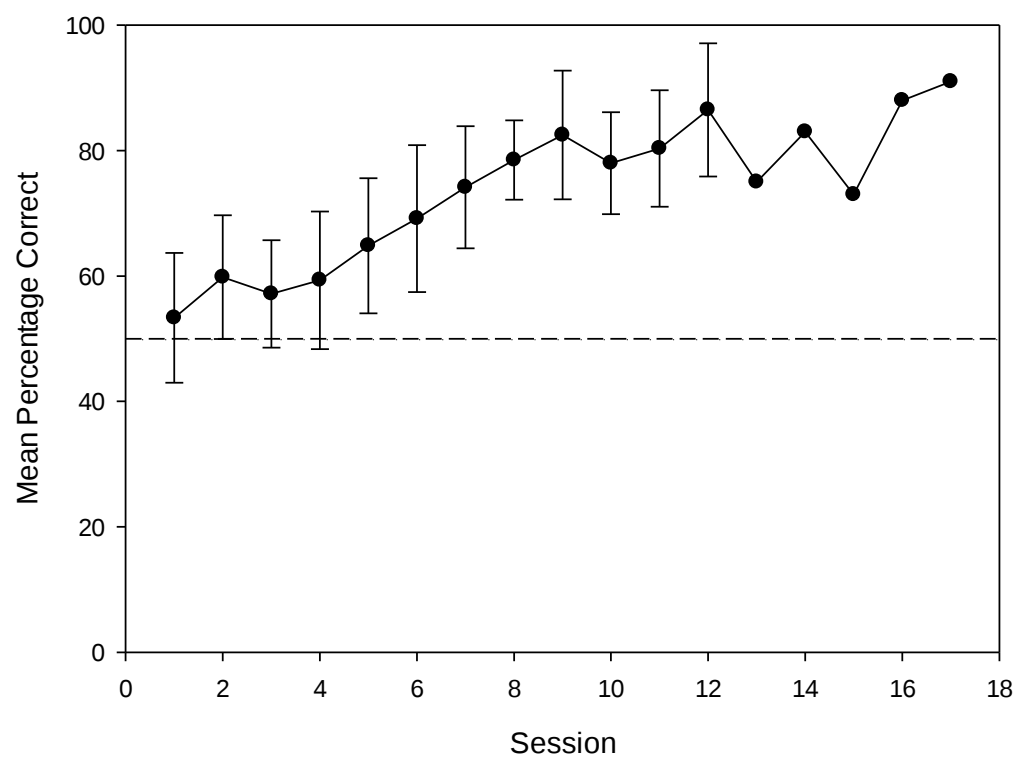


Fig. 1.3. Mean percentage correct for all animals per session. Error bars indicate one standard deviation.

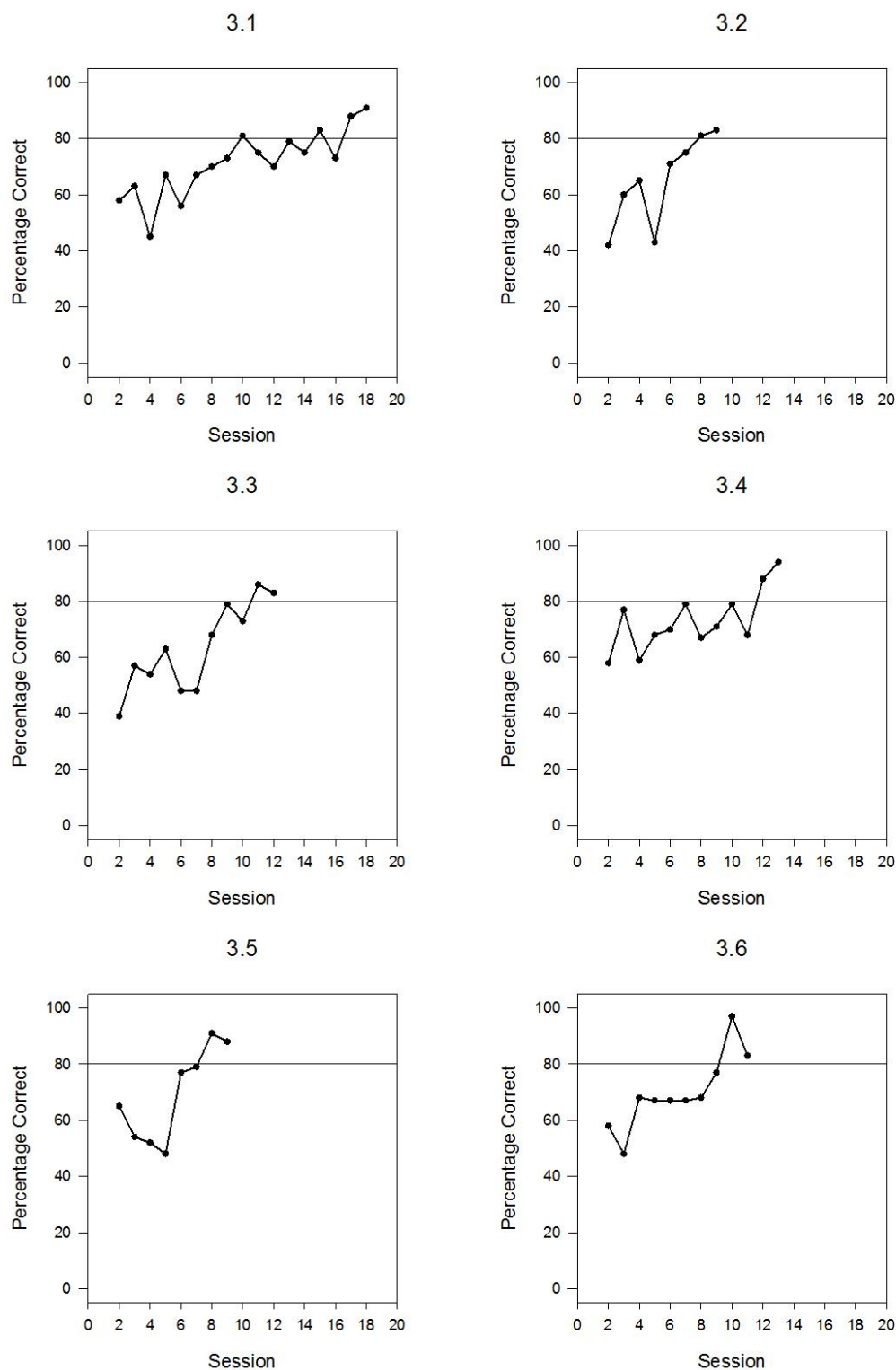


Fig. 1.4. Percentage of correct choices over sessions per animal

DISCUSSION

After five sessions, at most, discrimination accuracy was always above chance.

All birds were able to make a correct choice on 80% or more of trials by 17 sessions, indicating that the birds were capable of performing this basic task.

Studying lateral motion perception requires stimuli that have different spatial and temporal properties. Images must be designed in such a way that only the variable of interest can be used to discriminate between them. Dittrich and Lea (1993) used videos and still frames of conspecifics in an aviary in a moving versus stationary discrimination task. Birds trained to peck in the absence of motion failed to learn the discrimination. It is probable that the birds in the Dittrich and Lea study were responding to background cues in both the moving and stationary trials, instead of motion per se.

Gratings and random-dot kinematograms have the advantage of removing all other depth cues, but have limited ecological validity (Swaddle & Pruett-Jones, 2001). The stimuli used in this experiment lie somewhere between these two extremes. The birds were able to distinguish the two stimuli, which had been designed to eliminate extraneous cues as much as possible. While size, colour and duration are simple to control for, lateral motion necessarily confounds time and space. That is, a change in time requires a change in the physical location of the object. The animals may have been discriminating on this aspect of the stimuli, rather than motion or the lack thereof.

EXPERIMENT TWO

INTRODUCTION

Most research investigating depth perception from motion have utilized “pure” motion such as rotation (e.g. Cook, Beale & Koban, 2011), or natural stimuli such as point light displays (e.g. Brown, Caplan, Rodgers & Vallortigara, 2010). Both of these methods have the advantage of being pure motion, without the confounding effects of stimuli beginning at one point and ending at another. This study is investigating translatory motion of objects, and as such spatial and temporal attributes cannot be completely separated. Previous research has indicated that edge effects, where objects appear and disappear at the edges of the screen are a powerful motion cue (Cook 2000, Cook, Goto & Brooks, 2005). The initial and final position of objects is another strong cue that animals tend to use to make discrimination choices, instead of motion as the researchers intended (Young et al., 2006). Of the two, edge effects were considered to be less desirable in this set of experiments. The second experiment was designed to control for the difference in initial position of the stationary stimulus. If the chickens were discriminating the stimuli in the first experiment solely on the basis of where the stimulus squares were located on the screen (and not the motion) then they should have problems with this new experiment.

METHOD

Subjects, training procedure, apparatus and experimental procedure were the same as the previous experiment. The moving stimulus was also the same used in experiment one. The stationary stimulus was positioned in the same place as the moving stimuli's initial position (20x500 pixels), for a duration of 3 seconds.

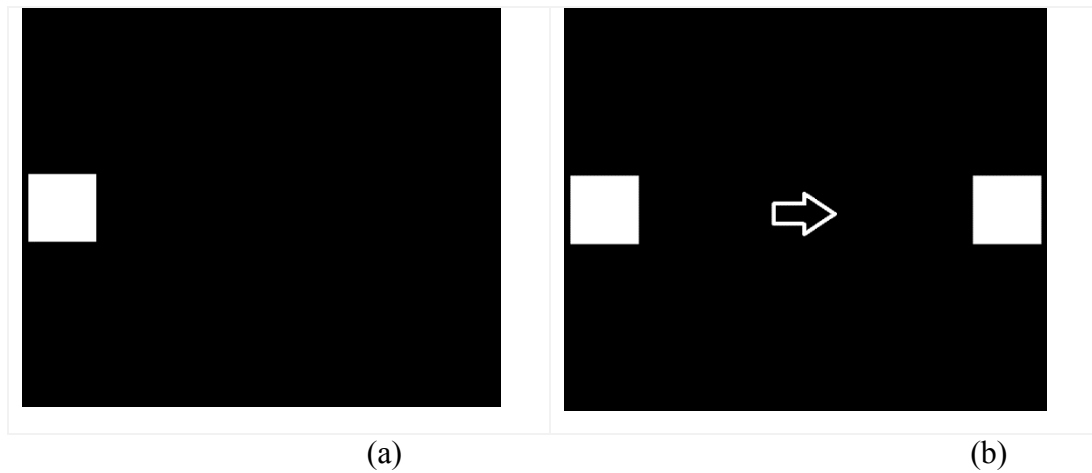


Fig. 2.1. (a) stationary stimuli used in experiment one (b) moving stimuli used in experiment one. Arrow indicates direction of movement.

RESULTS

All animals reached 80% or more correct between 3 and 16 sessions; discounting additional training for subjects 3.4 and 3.5, who were demonstrating an above-chance tendency to make an incorrect response to stationary stimulus (see appendices). Fig. 2.1 shows sessions to acquisition in experiment one (grey circle) compared to session to acquisition in experiment two (black circle). A paired-samples t-test indicated that acquisition times in experiment two ($M=8.5$ $SD=4.60$) was not significantly different from acquisition times in experiment one ($M=11$ $SD=3.35$), $t(5)=-.937$, $p=.392$.

Figure 2.2 shows the mean percentage correct per session for all birds. Performance was initially higher than in experiment one and reached threshold level earlier. Mean discrimination accuracy was always well above chance (dashed line). Figure 6 shows bird's individual performance in experiment one (grey circles) compared to percentage correct per session for experiment two (black circles). All animal's initial performance was higher than in experiment one, and in the case of 3.1 and 3.2 especially, quickly reached the required accuracy.

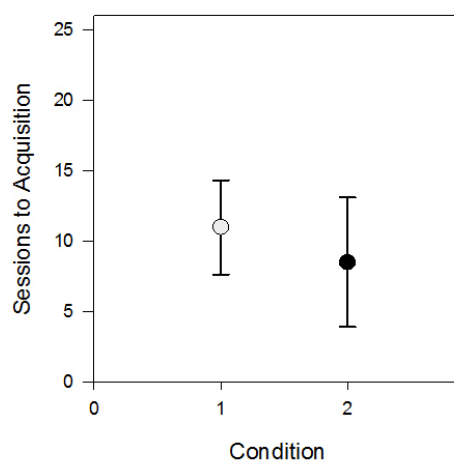


Fig. 2.2. Mean sessions to discrimination threshold for experiment one (grey circle) and experiment two (black circle)

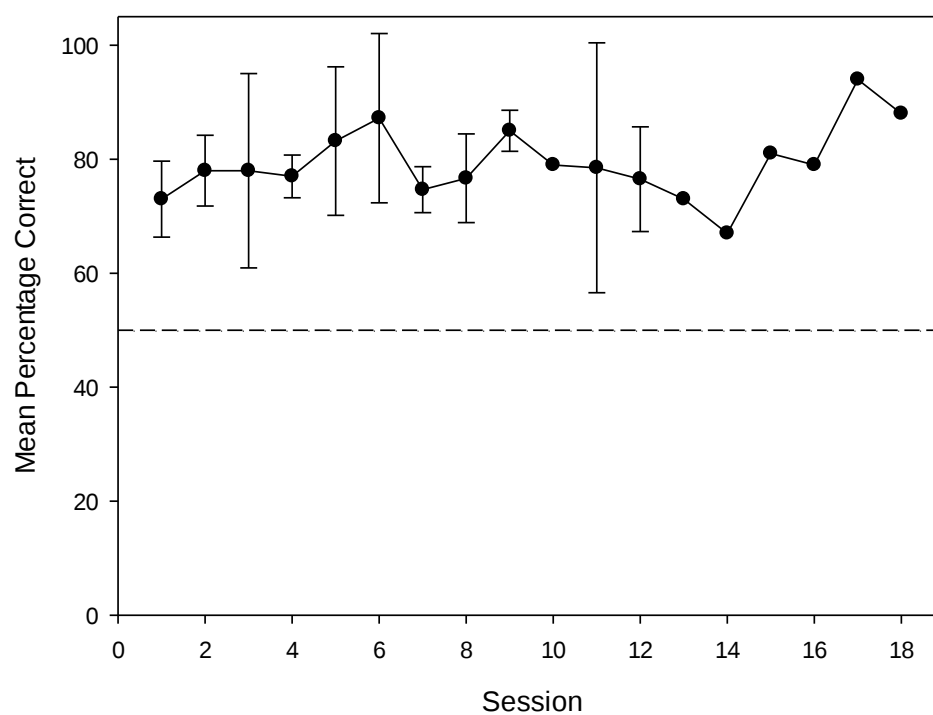


Fig. 2.3. Mean percentage correct for all birds per session. Error bars indicate one standard deviation

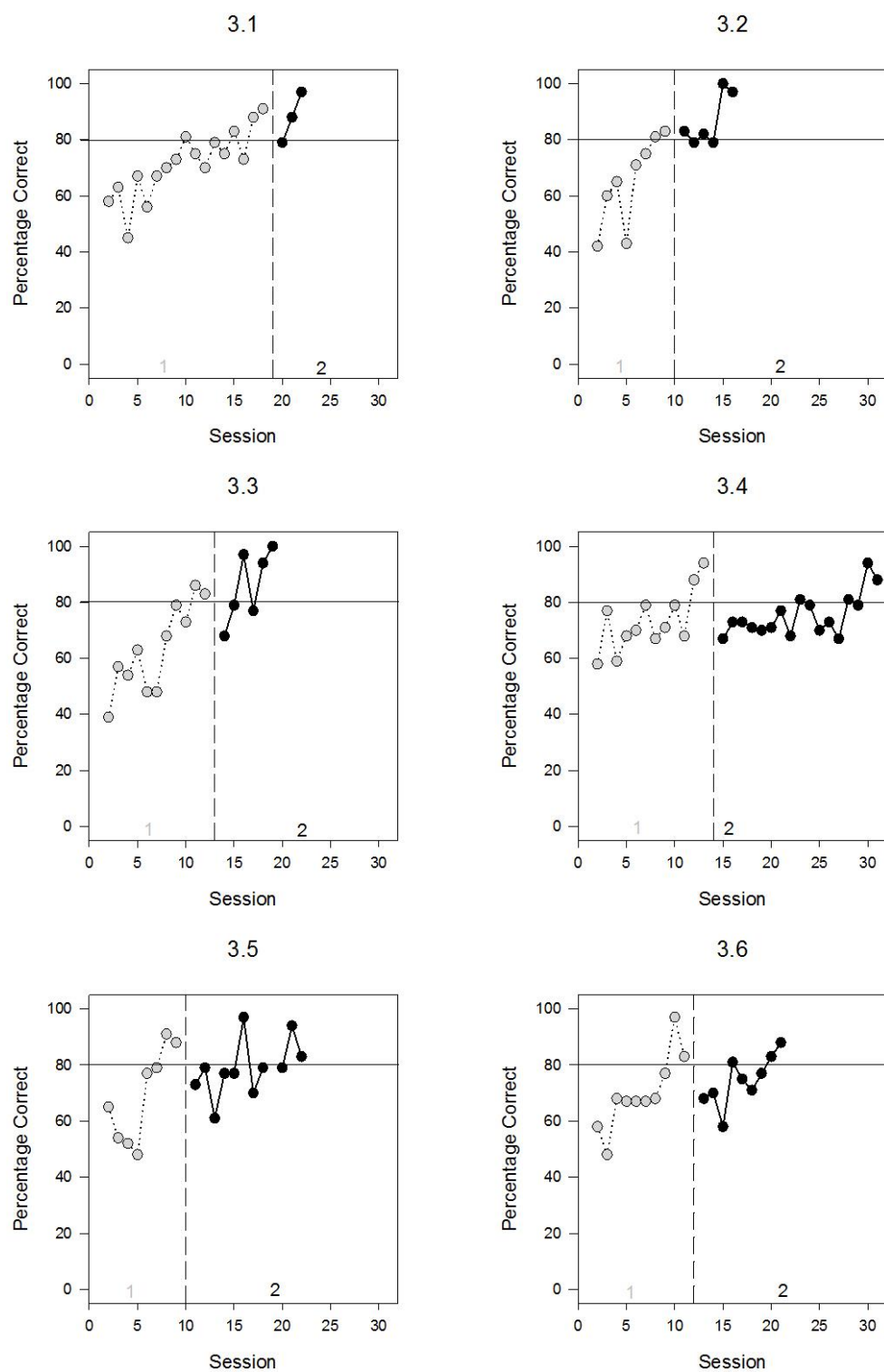


Fig. 2.4. Percentage correct over sessions per bird for experiment one (grey circles) and experiment two (black circles)

DISCUSSION

All birds learned to discriminate the new stimuli successfully. Prior experience should make acquisition of similar tasks faster (Goto & Lea, 2003), but in this experiment there was no significant difference in acquisition time between the two experiments. However, birds 3.1, 3.2 and 3.3 did show a marked improvement between the first and second set of stimuli.

After 8 sessions, four of the six animals had reached threshold performance, so extra training was initiated for the remaining two birds. That two of six animals had difficulty discriminating the novel stationary stimulus is indicative that they may not have been choosing on the basis of “moving” vs. “still” in the previous experiment. The percentage of incorrect responses made by animals 3.4 and 3.5 after stationary stimuli was well above chance. This implies that these animals may have been discriminating based on a spurious stimulus dimension. Without verbal behaviour, animals participating in discrimination tasks must be given their instructions via contingencies placed on reinforcement. Animals attending to spurious stimulus elements in discrimination tasks is well documented (e.g. Nagasakao & Wasserman, 2008). In some species such as mice (Mitchell, Griffin & Timney, 1977). Superstitious behaviour emerges when the difference between stimuli drops below threshold detection. In other species like rats and humans responding becomes random or ceases altogether.

As the two stimuli were identical in all respects except initial and final position, it is possible that the birds were using this aspect of the stimuli, instead of the motion properties, to make their choices. The next set of stimuli was designed to remove, as much as possible, position as a discriminatory cue.

EXPERIMENT THREE

INTRODUCTION

The results of experiment two indicated that at least two animals may not have been discriminating based on the “moving” versus “still” properties of the stimuli. That two birds had a more than chance probability of responding incorrectly to the new stationary stimulus indicated that they may have been using a similar strategy to the Young et al. (2006) birds; attending to position instead of movement. One of the differences in these categories is that stationary stimuli occupy one position on the screen throughout the duration of exposure, whereas moving stimuli begin and end stimulus presentation at opposite ends of the screen. Experiment two controlled for initial position. Experiment three was designed to control for, as much as possible, the fact that moving stimuli occupy multiple spatial positions during presentation, i.e., we are attempting to render the starting and end positions irrelevant for the discrimination task.

METHOD

The stimuli types included in experiment three were extended from two to thirty five. To control for the moving stimulus appearing at all points of the path during stimulus presentation, stationary stimuli were arranged so that initial position could be located at 20, 500; 300, 500; 600, 500; 900, 500, or 1180, 500 pixels (refer to Fig.3.1 a, b, c, d and e). Moving stimuli could have an initial position of 20, 500; 300, 500, or 600, 500 pixels, and travel a distance of either 600, 900 or 1200 pixels (refer to Fig 3.2 a, b, c, d, e and f). Velocity was kept the same as previous experiments (10cm/sec). As such, the stimulus duration could be either 1.03, 1.65, 2.06, 2.48, or 3 seconds. This created 25 different stationary stimuli (five possible positions and five possible durations) and 10 different moving stimuli. Presentation of either category of stimuli was semi random, and instances of each category were presented randomly until the entire range had been presented.

The training procedure was adjusted so that after stimulus presentation only a single keylight was illuminated. Keylight position varied semi-randomly for an equal number of left and right presentations, with no more than three presentations in the same location. Subjects, apparatus and experimental procedure were otherwise the same as experiment one. The aim was to see if it was possible to train the chickens to discriminate static from moving objects when the starting and endpoints of the moving objects no longer provide a reliable source of information.

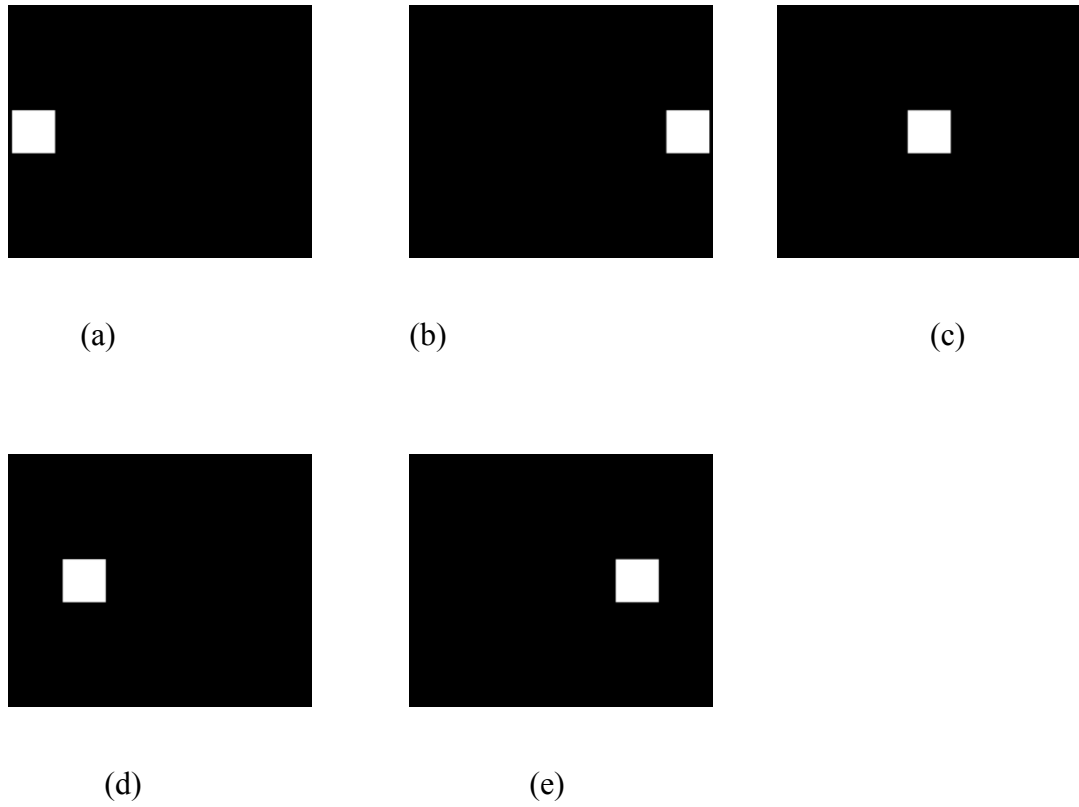


Fig 3.1. Stationary stimuli used in experiment three. The pixel locations of the centre of the square (x, y) at the start and end of the trial were: a): 20,500, (b): 1180,500, (c): 600,500, (d): 300,500 and (e): 900,500 pixels

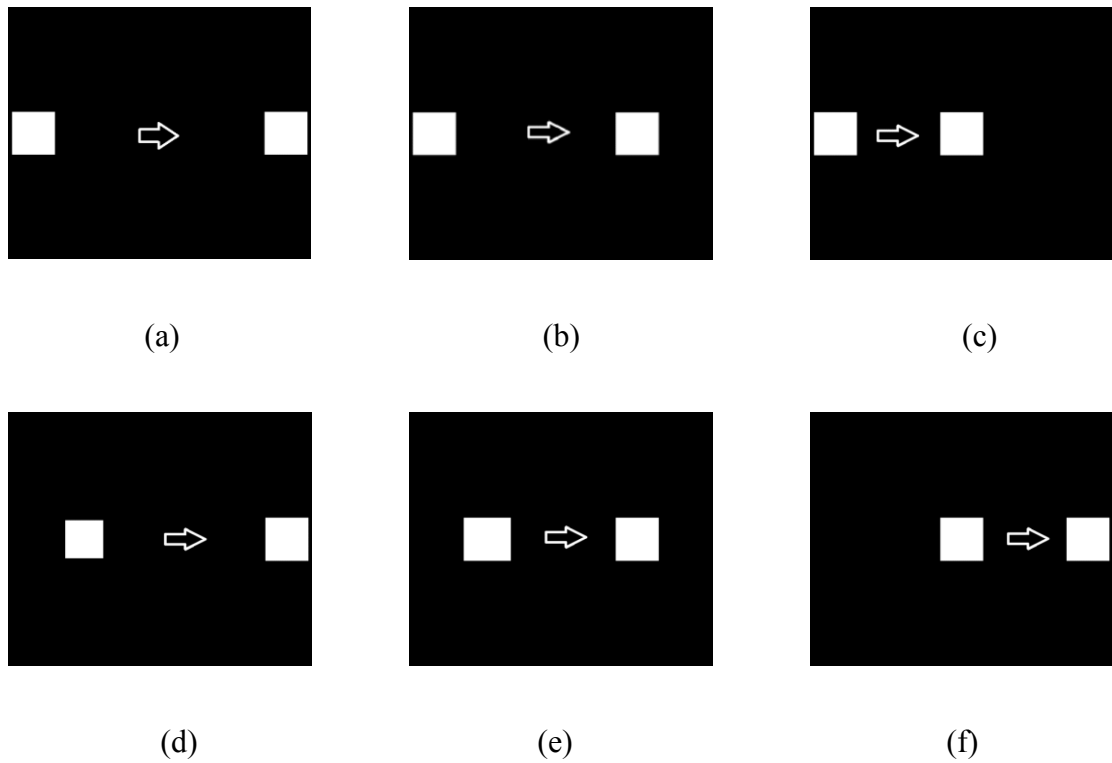


Fig 3.2. Stationary stimuli used in experiment three. The pixel locations of the centre of the square (x, y) at the start and end of the trial were: (a): 20, 500 to 1180, 500 (b) 20:500 to 900:500 (c) 20:500 to 600:500 (d) 300:500 to 1180:500 (e) 300:500 to 900:500 (f) 600:500 to 1180:500.

RESULTS

Excluding animal 3.1, subjects reached threshold criteria in 6 to 20 days ($M=13.8$, $SD=6.10$). Animal 3.1 required extensive retraining to reach threshold performance (see appendices). As shown in figure (3.3), acquisition times for experiment three (black circle) were slightly longer than for experiments one and two (grey circles). Figure 3.4 shows the mean performance per session for all animals excluding 3.1. Accuracy was always above chance (dotted line) and generally very close to, or above the accuracy requirement of 80%. There was less tendency for accuracy to increase over time than in previous experiments. Figure 3.5 describes individual bird's performances in experiments one and two (grey circles, separated by dashed lines) and three (black circles). Performance was less likely to increase over time, or to do so slowly and variably.

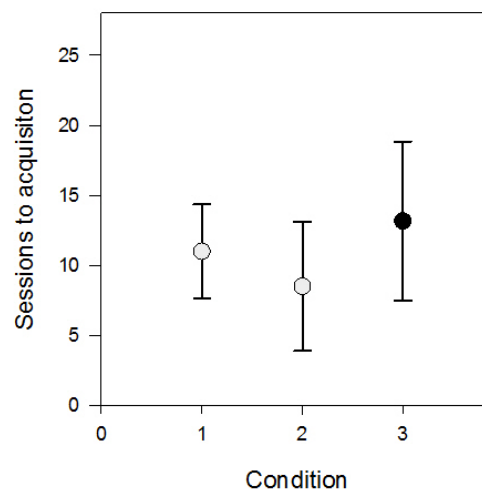


Fig. 3.3. Sessions to acquisition experiments one (grey circle), two (grey circle) and three (black circle). Errors bars indicate one standard deviation.

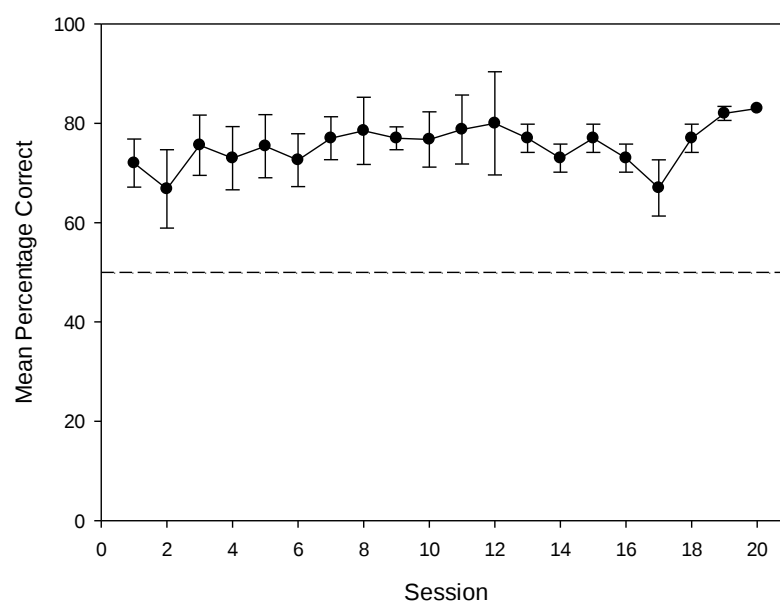


Fig. 3.4. Mean percentage of correct choices for all birds per session. Error bars indicate one standard deviation.

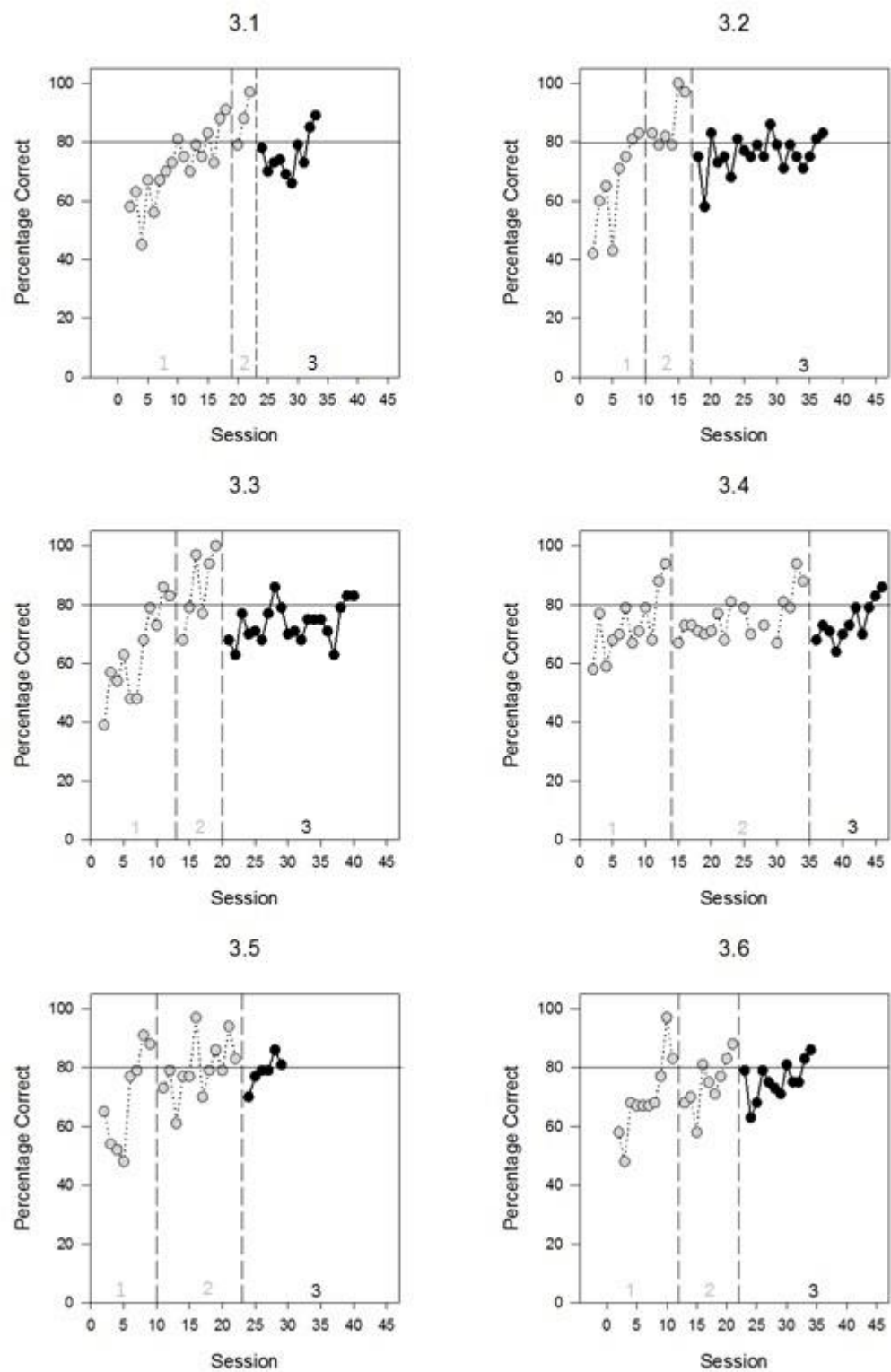


Fig. 3.5. Percentage of correct choices per animal per session for experiment one (grey circles) experiment two (grey circles) and experiment three (black circles).

DISCUSSION

This set of stimuli was a more complete control for initial and final position of stimuli than the previous experiments. Performance did not drop to chance levels with the introduction of the novel stimuli, showing that the new experiment was not treated as a completely new task. Results agree with Spetch, Friedman and Vuong (2006) whose pigeons responded to variously-shaped rigid objects using motion alone.

Animal 3.1 required extensive re-training for performance to reach the threshold criteria. Hodos, Smith and Bonbright (1976) found when discriminating moving versus still images, all subjects required extensive training on both types of stimuli and tended to stabilise quickly. They also found that further training did not improve results. A contingency that prohibited pecks to the screen during stimulus presentation was required for animal 3.1 to achieve threshold performance. Once this contingency was introduced performance quickly reached 80% or more correct. That all other birds were consistently 60% or more correct from the first session indicates that animal 3.1 was not under stimulus control.

Difference in position over time is one of two key aspects of motion parallax. Objects change position on the retina as the observer moves through space, or the camera moves through a scene. All birds' behaviour in this experiment was not confounded by the different starting and end positions of the moving stimuli in order to discriminate moving from static correctly. The other necessary experiment for motion parallax perception is that objects move at different velocities, which the next set of experimental stimuli was designed to address. The previous experiments have shown that it is possible to train the birds to

discriminate moving from non-moving targets. Can they now be made to respond to the speed of the moving targets? Experiment four investigates this.

EXPERIMENT FOUR

INTRODUCTION

The perception of motion parallax requires discrimination of two or more velocities. In the real world, the perception of depth is derived from multiple cues in the environment. When walking through a scene, objects close to the observer move more slowly across the retina than objects located further away. The perception of depth from motion parallax on a 2D screen requires that differential (or relative) motion of objects exists across the screen. When using 2D screens to investigate this, several issues arise. In the real world, depth cues are often intermingled, and it is a combination of them that allows the organism to interact with its environment. Studying motion parallax and velocity in the laboratory allows these cues to be teased apart and their effects studied separately or in various combinations. Experiment four was designed as a simple velocity discrimination using stimuli travelling horizontally, at two different speeds. Stimulus type and duration was kept the same as previous experiments.

METHOD

All aspects of the experiment were the same as previous experiments, except for the stimuli used. A “fast” and a “slow” stimulus replaced the “moving” and “stationary” videos. The “slow” stimulus moved across the screen at 10 cm/sec and had a duration of 3 seconds; the “fast” stimulus moved at 20 cm/sec and had a duration of 1.5 seconds. Both squares moved across the screen from an initial position of 20x600 pixels to a final position of 1180x600 pixels. Animals 3.1, 3.2 and 3.3 were reinforced for pecking red after slow stimuli and green after fast stimuli. Animals 3.4, 3.5 and 3.6 were reinforced for pecking green after slow stimuli and red after fast stimuli.

RESULTS

Five of six animals reached the discrimination threshold within 12-27 sessions ($M = 19.2$, $SD = 6.22$). Animal 3.5 did not reach target performance within 28 sessions. The percentage of correct choices was much more variable than in previous experiments, and increased over time to a lesser extent. Visual observation of the operant chamber revealed an unexpected behaviour and showed that all animals pecked the square during stimulus presentation, and tracked it across the screen. Still frames from footage of a single stimulus presentation (Fig 4.4) clearly shows the birds tracking the square with their heads.

This observation is quantified by graphing the x position of screen pecks over stimulus presentations during the last session in figure 13. The lateral (x) position of pecks, especially for the slow stimuli presentation, closely follows the stimulus pathway. There are far less pecks directed at “fast” stimuli; but this is probably due to the square moving too quickly to be pecked during presentation. Animal 3.1 was working under a contingency that prohibited pecking during stimulus presentation so pecks could not be graphed.

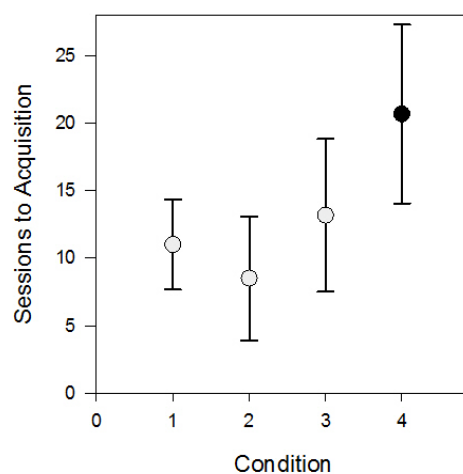


Fig. 4.1. Sessions to acquisition experiments one two, three (grey circles) and four (black circle).

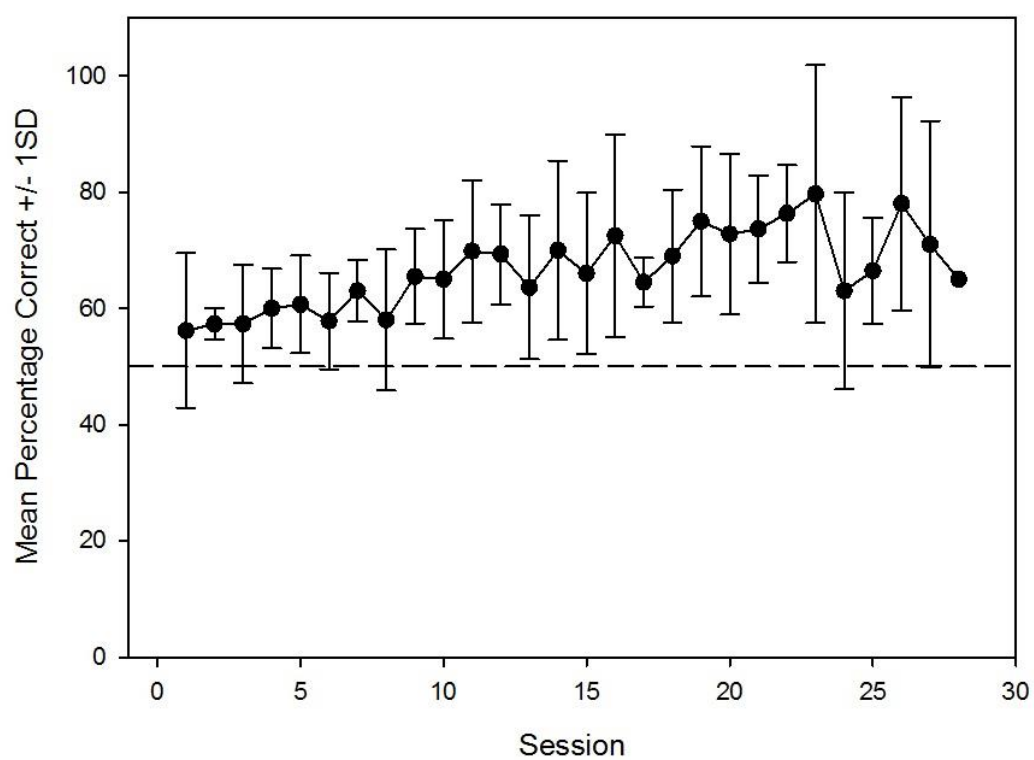


Fig. 4.2. Mean percentage correct for all birds per session. Error bars indicate one standard deviation. Dotted line indicates chance accuracy.

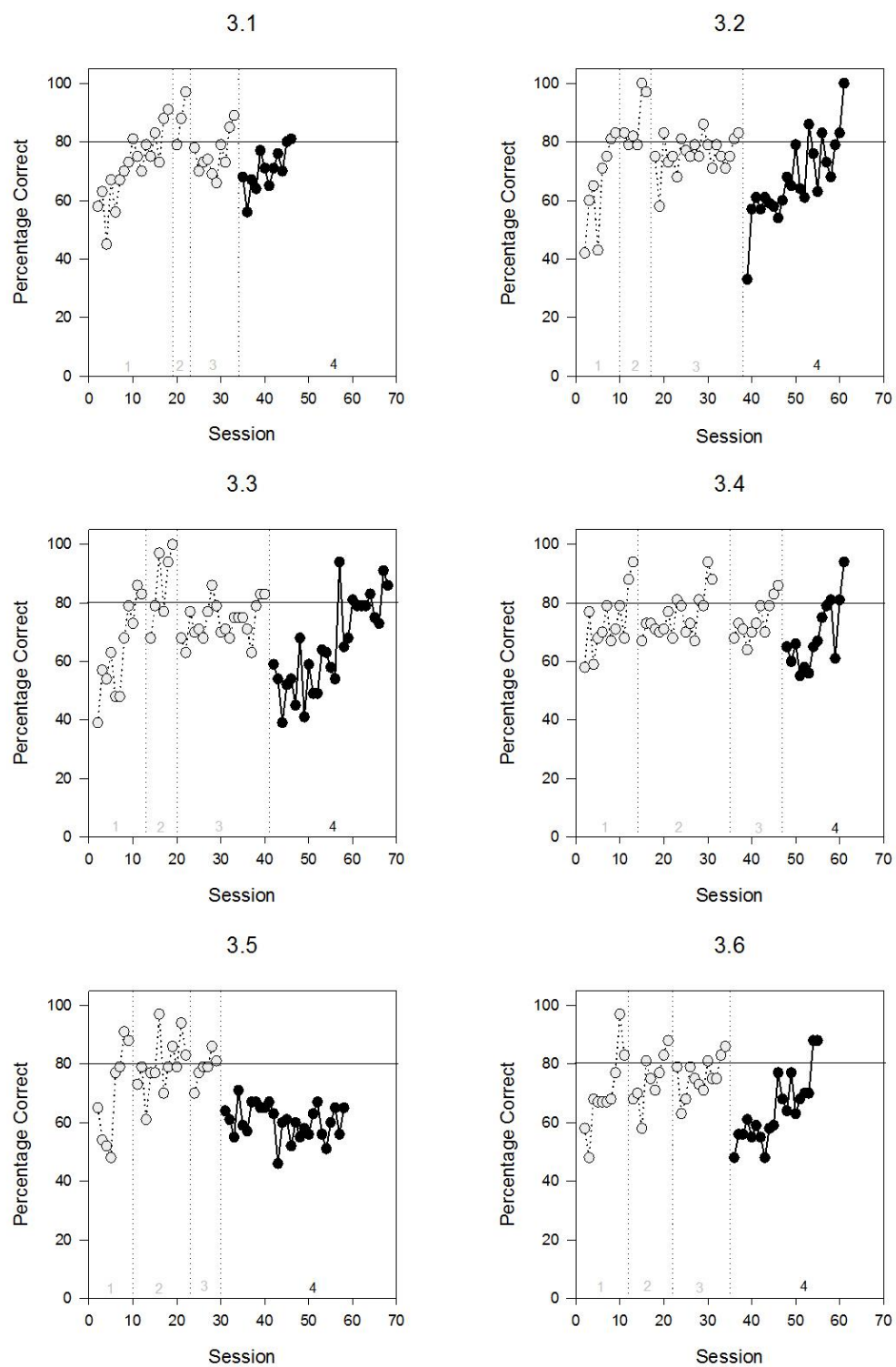


Fig. 4.3. Percentage correct over sessions per bird for experiments one, two and three (grey circles) and experiment four (black circles).

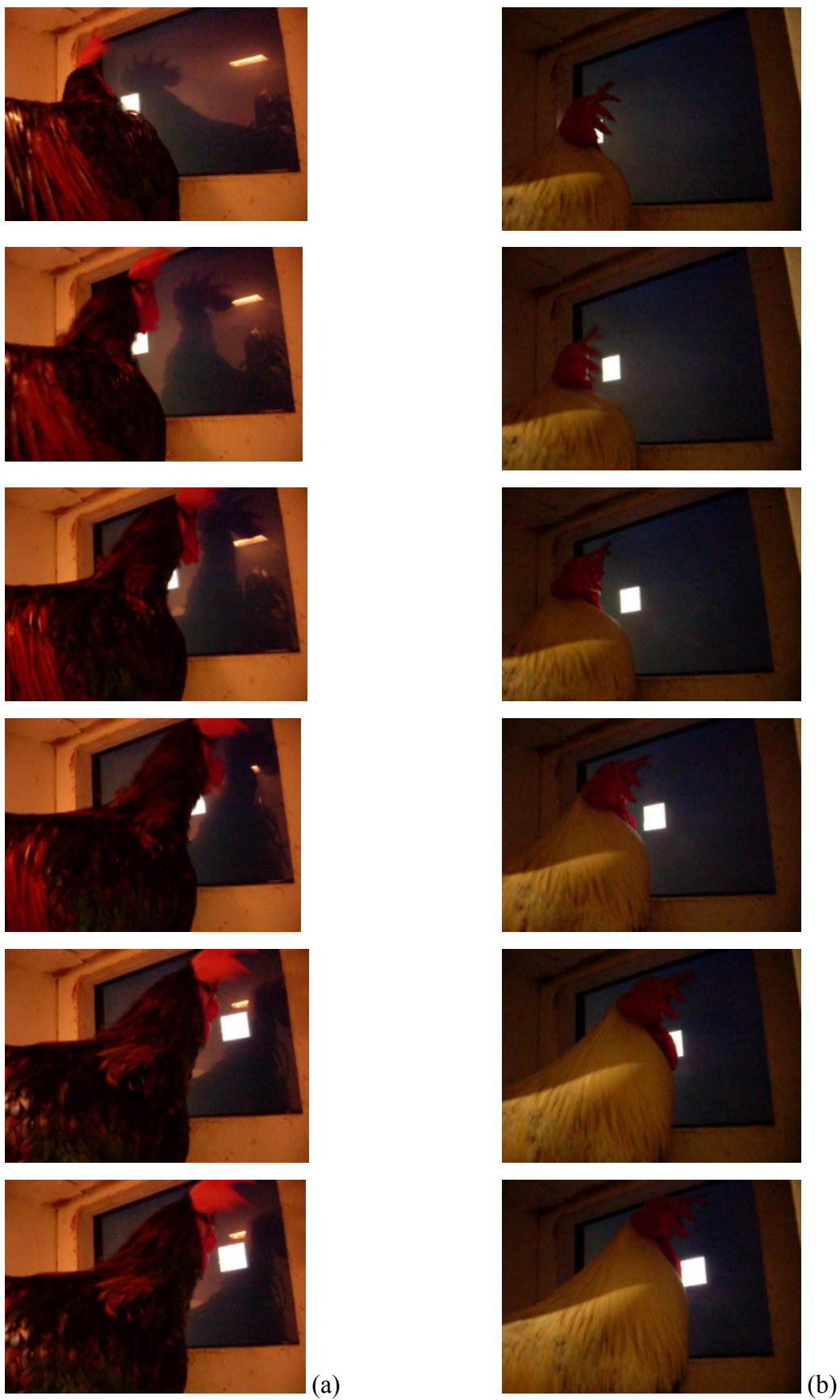


Fig. 4.4. Behavior during stimulus presentation. (a) animal 3.2 (b) animal 3.4.

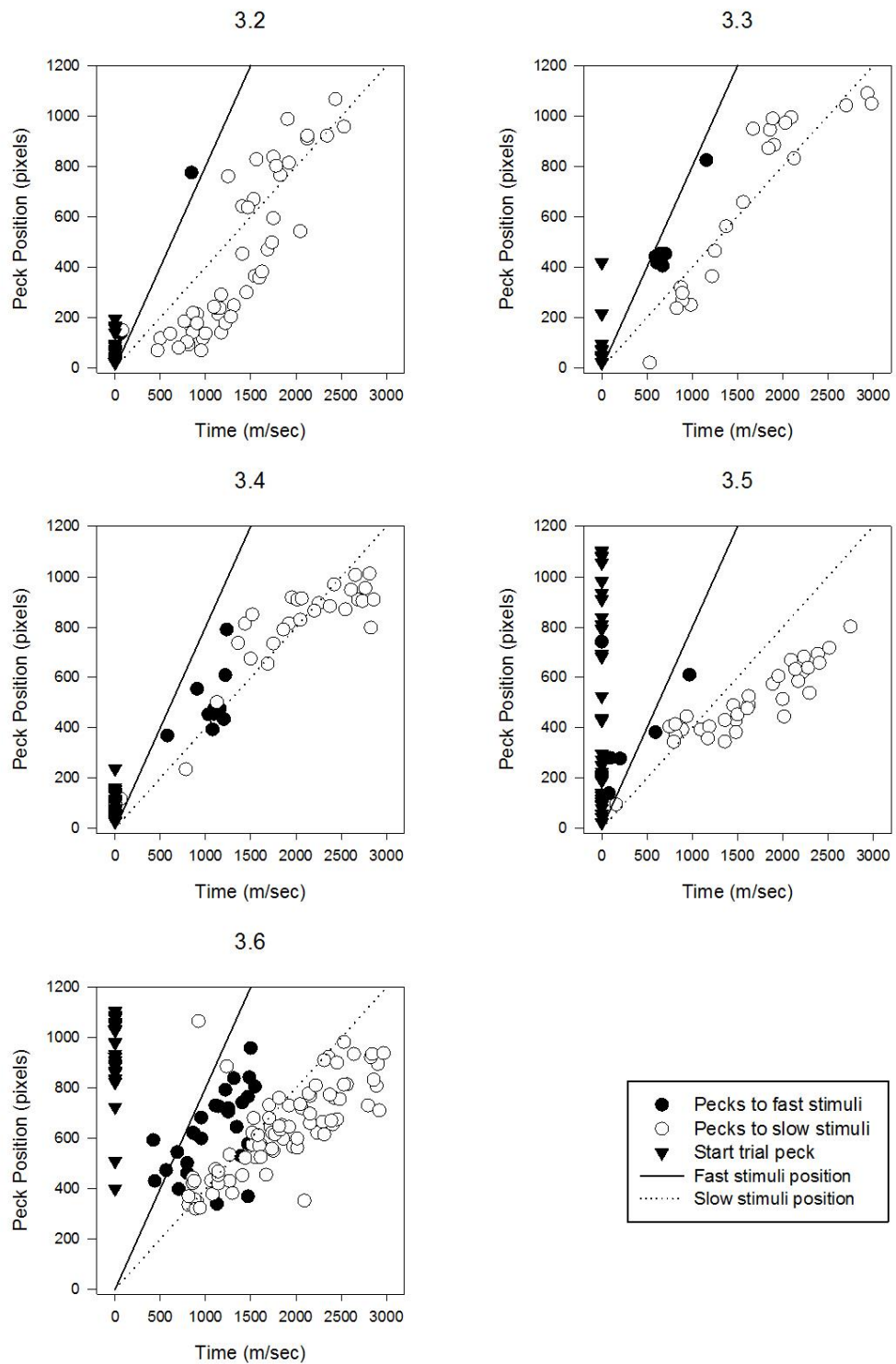


Fig 4.5. Peck position over stimulus presentation. Solid and dotted lines indicate stimulus object path. Y axis indicates horizontal peck position.

DISCUSSION

Performance in this task was initially near chance, indicating that to the animals this was essentially a new task. With the exception of animal 3.5 who never achieved threshold performance, all animals were eventually able to make the correct choice on 80% or more of trials. This is similar to Cook et al. (2011) who found that pigeons were able to categorise an object as rotating quickly or slowly. Studying depth perception by using rotation allows for duration effects to be discounted; cyclical fast and slow stimuli can be presented for the same amount of time because there is no obvious start or end to the stimulus. This is not possible with planar directional motion without introducing edge effects (Ushitani, Fujita & Sato 2004; Cook et al. 2005). A fast directional stimulus would have to disappear and reappear on the screen, or change direction, for duration to be the same as a slow directional stimulus. Neither of these alternatives were practicable in this case, and duration was accepted as a confounding variable.

It became apparent in this experiment that all birds were attempting to “catch” the stimuli by pecking. Graphs of the x position of pecks during stimulus presentation over time clearly show that all birds are tracking the stimuli across the screen. Piscaretta (1982) trained pigeons to “catch” a moving dot by pecking on or near it. The birds generally adopted a lagging technique, pecking just behind to cursor. The birds in this study used a similar strategy; peck position was usually slightly to the left of the rightwards moving stimulus. This unintentional effect was clearer than in an experiment by Wilkie (1986), where birds were required to track a light across keys. That the animals were tracking one object across the screen suggests that they were not attending to the entire stimulus array. The next experiment required that a larger stimulus pattern be presented to the birds in order to test

their ability to detect motion parallax. The tracking behaviour noticed in experiment four needs to be taken into consideration when the results of experiment five are analysed.

EXPERIMENT FIVE

INTRODUCTION

Motion parallax is the perception of depth derived from the differential speed of objects moving across the retina. When using dot displays, the amount of information it contains must be sufficient for this differential velocity to be detected. In the real world when an observer moves through a rigid environment the retinal image contains many different moving objects with multiple velocities. The image motion is also distributed over large parts of the visual field. The motion is 'global' rather than 'local'. Depth from parallax requires information to be integrated over large parts of the visual field. Experiment four showed that the chickens could discriminate the speed of a single moving square. Experiment five was designed to test whether the birds could discriminate between multiple objects moving at the same velocity (flat) and multiple objects moving at two velocities. The latter stimulus contains parallax information and appears to humans as two rigid planes separated in depth.

METHOD

Five birds (3.2, 3.3, 3.4, 3.5 and 3.6) were subjects in this experiment. Apparatus and training procedure were the same as in previous experiments. A contingency that prevented two consecutive reinforcers for responding on the same side was introduced on the 26th session. The second correct response on either key would result in the magazine light being illuminated only. On the 33rd session, experimental procedure was adjusted so that pecks to the screen during stimulus presentation led to a three second white screen. The black, “start trial” screen then occurred, and the next stimuli on the list would be presented.

Stimuli in this experiment consisted of a “flat” video and a “parallax” video, created using 3DMax (Autodesk 2013) and rendered at 60Hz in .avi format. Both films consisted of approximately 30 squares with sides 20 pixels long, i.e. half the size of the single squares used in previous experiments. These squares were arranged randomly across the screen in such a way as to avoid occlusion and edge effects as much as possible. In the “flat” video, all squares moved from left to right with a velocity of 15cm/sec. In the “parallax” video, 50% of the squares moved at 10cm/sec, and 50% of the objects moved with a velocity of 20cm/sec. Therefore the average velocity over the screen was the same as in the flat stimulus case. There were no size cues to depth in these stimuli. Depth has to be derived from the motion alone.

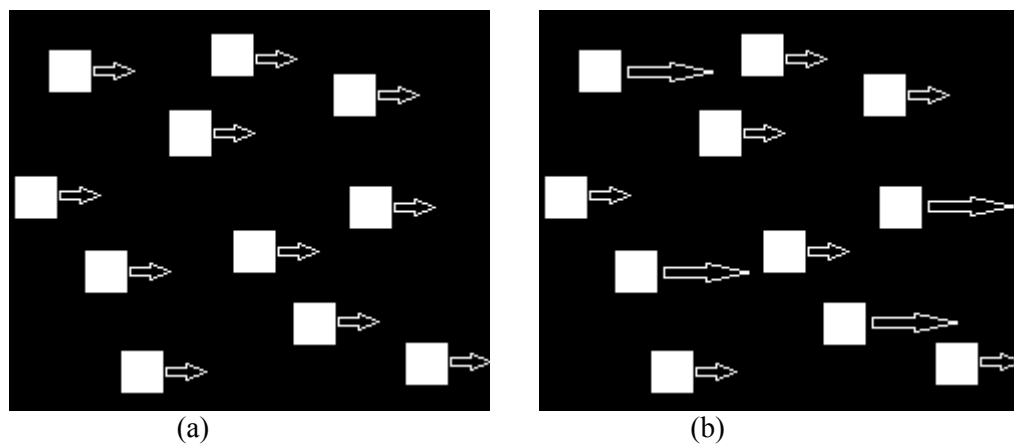


Fig. 5.1. Stimuli used in experiment five. Short arrows indicate squares moving at 10cm/sec. Long arrows indicate squares moving at 20cm/sec. (a) Flat stimuli (b) parallax stimuli.

RESULTS

After hundreds of trials (22-38 sessions) none of the animals reached threshold performance, instead consistently performing around chance. Adjusting the contingencies of reinforcement on day 26, so that two consecutive reinforcers could not be delivered on the same side, had no effect on discrimination accuracy. Neither did the addition of a contingency on day 35, prohibiting pecking during stimulus presentation. Figure 5.1 shows the mean performance over time of all five birds. Performance was initially highly variable, but generally around chance. The side reinforcement contingency (dashed line “a”) and the no pecking during stimulus presentation (dashed line “b”) had the effect of behaviour being less variably closer to chance. Analysis of peck patterns revealed that all subjects except 3.5 were exhibiting a moderate (animals 3.3 and 3.4) to severe (animals 3.2 and 3.6) side bias. Figure (5.3) displays this as the percentage of incorrect responses made to the left key in the last five sessions before side reinforcement and delay contingencies were instituted. Fig (5.4) shows the percentage of errors made to the left key after a side reinforcement contingency was but in place. This reduced side bias, but did not improve accuracy.

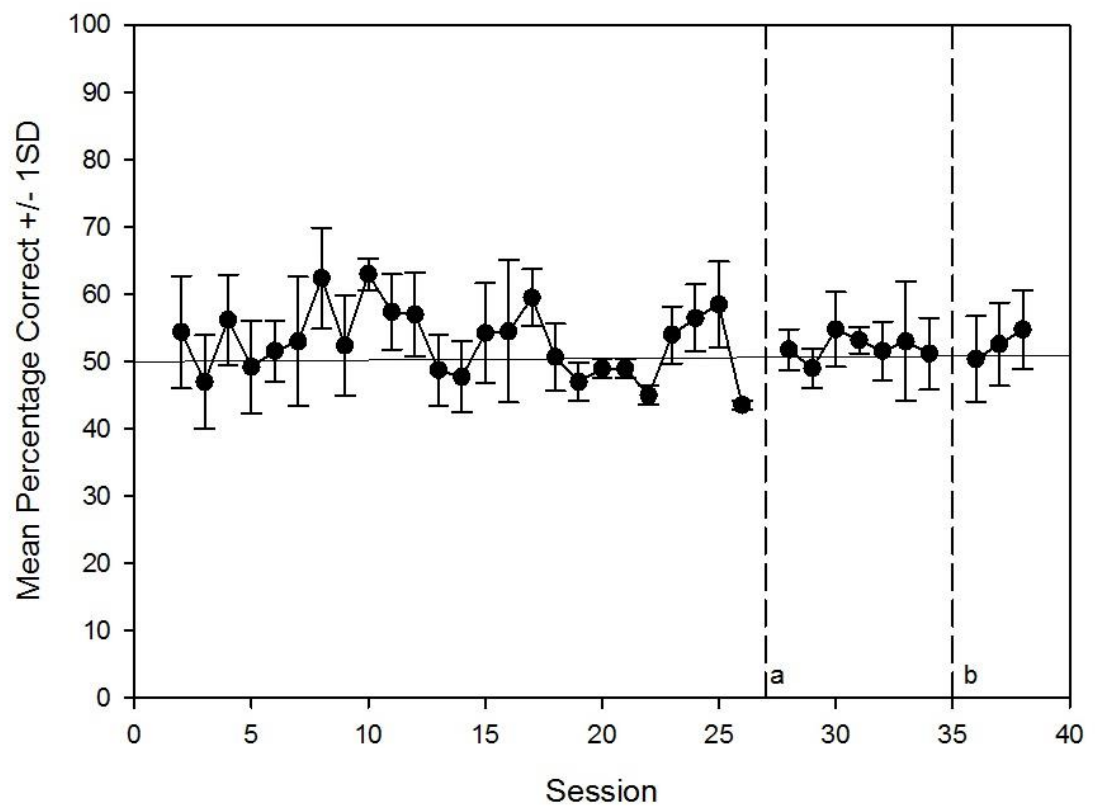


Fig. 5.2. Mean percentage of correct choices for all birds per session. Error bars indicate one standard deviation. Line (a) indicates introduction of side reinforcement contingency. Line (b) indicates introduction of peck prohibition during stimulus presentation.

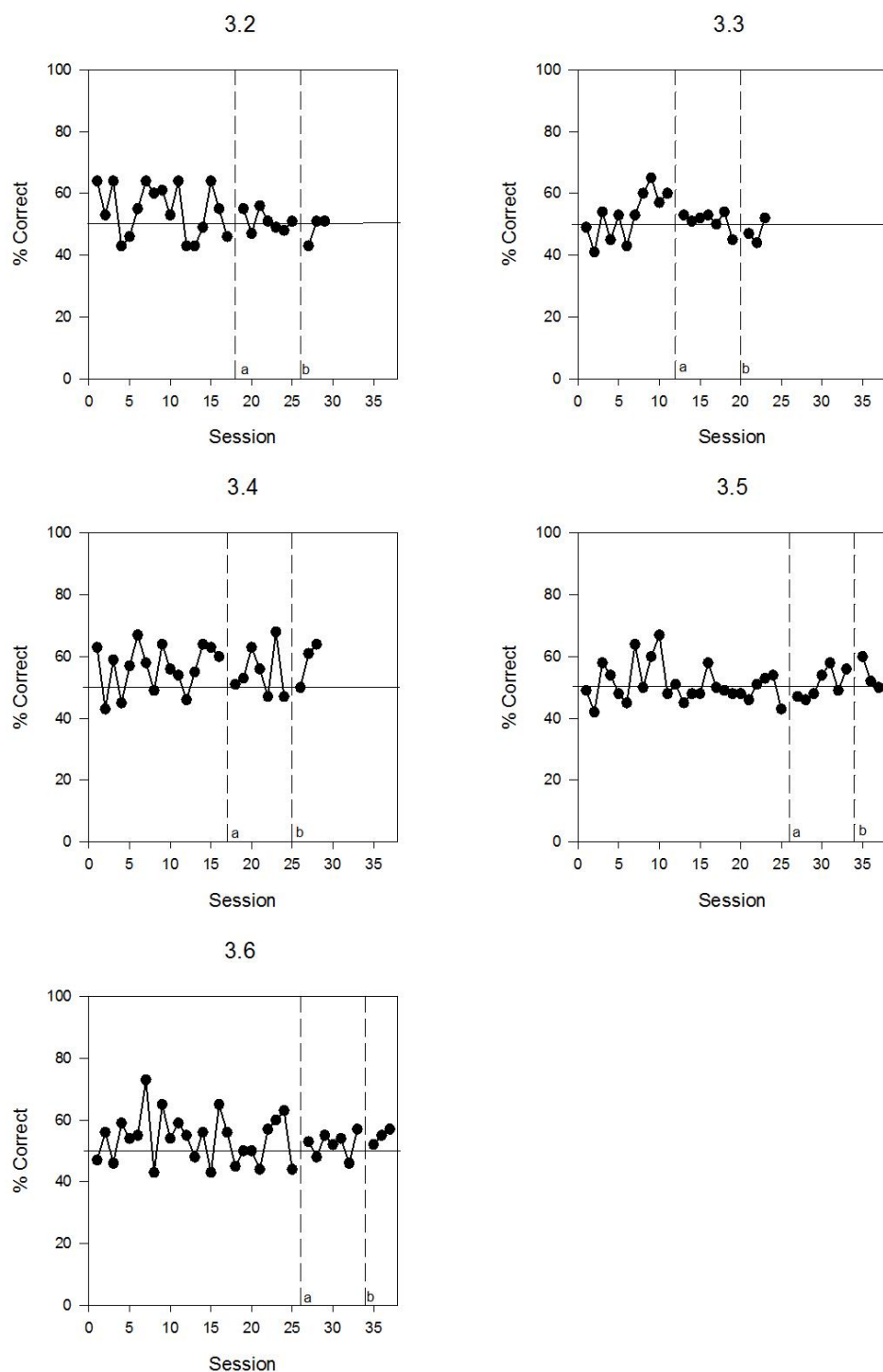


Fig 5.3. Percentage correct over sessions for each bird. Line (a) indicates introduction of side reinforcement contingency. Line (b) indicates introduction of peck prohibition during stimulus presentation.

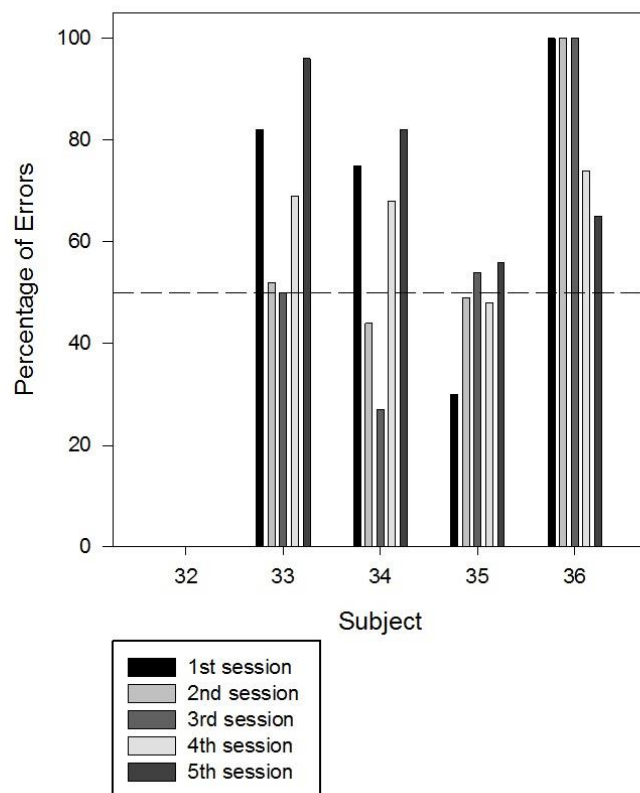


Fig 5.4. Percentage of errors made to the left key per animal during final five sessions prior to side reinforcement contingency

DISCUSSION

Birds are neurologically capable of seeing parallax (Xiao et al. 2006, Frost 2010); motion in depth (looming) is detected by specialised cells in the dorsal-posterior region of the rotundus in the avian brain. (Wylie et al. 2009). One of the possible reasons the birds in experiment five failed to generalize to the more complex stimuli may be that the difference between a single object and multiple objects is too great. An intermediate experiment that required the birds to discriminate multiple objects moving in a single plane from multiple stationary objects may have been more successful.

The side reinforcement contingency actually reduced discrimination performance to chance. So it became obvious that the birds were not discriminating on depth, i.e. the differential speeds of the objects. It had been observed in experiment four that all birds were closely following the stimuli across the screen and emitting multiple pecks as they did so. Adding a whiteout if the screen was pecked during stimulus presentation had no effect on performance; one bird pecked along the very edge of the screen. All other birds continued to follow the stimulus with their heads extremely close to the screen.

Pigeons did not show any discrimination when presented with various Glass patterns (random dot pairs placed so that a global pattern can be seen), suggesting that pigeons process patterns at the local level (Kelly, Bischof, Wong-Wylie & Spetch 2001). Global processing is also necessary for motion parallax processing. Birds are capable of using the global cues present in moving arrays to make

discrimination choices (Nagasako & Wasserman 2008), so it is possible that the birds in this experiment were simply too close to the screen to process the entire object array and respond accordingly. It is probable that it is the lateral, monocular field of view that birds use to discern moving objects on a global scale (Bloch, Rey & Martinoya 1981; Maldonado et al. 1988). That they were able to learn single-object discriminations lends credence to this.

Human parallax studies often utilize moving headrests and eye-movement tracking technology to control for viewing distance (i.e. Nawrot & Joyce 2006). Some work with animals and visual depth perception controlled for head position using manual or chemical restraints such as anesthesia (i.e. Bermejo, Houben & Zeigler 1994). Head fixed pigeons (Remy & Emmerton 1991) were able to transfer discriminations learned using the lateral field to the frontal field, but not vice versa. The authors give a functional account for this; in the natural world, objects will first be viewed laterally, then approached and viewed frontally.

Global motion is thought of as occurring after initial motion detection, or as the perception of the second-order temporal characteristics of the stimulus (Julesz 1971). “Global, as opposed to local, motion, is the perceived direction of a dynamic input when that direction is the result of a combination of many individual motion signals within that stimulus” (Cropper p126 2001) Global motion is what humans see when the display is sufficiently complex (Erikson 1973). Local motion perception is thought to be an “early, fast, pre-attentive” event (Ansis 2012), while the grouping of local movements into a global array is a

slower process, possibly modulated by attentional variables. That the birds were effectively not pausing before responding on the keylights may be indicative that they were responding based on local motion only.

GENERAL DISCUSSION

A very rich schedule like the CRF used in experiments 1-5 can sometimes reduce discrimination accuracy because the animals will eventually receive all of their reinforcements. In this case, “guessing” is an effective strategy. Some species, such as mice, will begin responding on one key only after several consecutive errors, or cease responding altogether (Mitchell 1977). The first four experiments, utilizing only a single object with a continuous reinforcement schedule, were learnt, but performance broke down when multiple objects were introduced (a change from ‘local’ to ‘global’ information). A leaner schedule or an error-correction procedure (McGaughy & Sarter 1998) may have improved performance in the last experiment. Partial reinforcement schedules tend to result in behaviour that is more fully controlled by the contingencies than a continuous reinforcement schedule (Hulse 1962). The simple side reinforcement contingency implemented in experiment five only moved the bird’s behaviour from responding on one side only, to alternating sides regularly. To be effective, this kind of contingency must be unpredictable.

Animals performing operant discrimination tasks are notorious for attending to irrelevant stimulus aspects (Young et al. 2006; Nagasako & Wasserman 2008; Goto et al. 2002). The birds may have been attending to a feature of the single-object stimuli that was not present in the multiple-object displays used in experiment five. The issue is determining whether the task is too difficult, or whether poor performance is the result of experimental artifice. An effective stimulus allows for systematic manipulation whilst remaining behaviourally

relevant (Zanker 2001).

The change from local to global motion in experiment five may have been too extreme, considering the bird's history; prior experience can skew performance on what should be simple tasks. Pigeon's discrimination of a moving object failed when the direction of motion was reversed, possibly due to the birds previously always approaching the response key from the right only (Goto & Lea 2003). The stimuli used in these experiments also only travelled in one direction; incorporating right-left as well as left-right motion may have prevented the side bias seen in experiment five.

The apparatus must also be consistent with what we are attempting to measure. The operant chamber used in this set of experiment allowed the animals to stand extremely close to the screen while stimuli were being presented. This is not the most accurate analogue of how display screens are usually viewed by humans, and would have prevented the animals from viewing the entirety of the display.

EXPERIMENT SIX

INTRODUCTION

Gallus are able to perceive depth; this much is obvious from their complex behavioural repertoire, as well as the extensive neuro-psychophysical evidence. The failure of the animals in the previous set of experiments to discriminate flat stimuli from stimuli with depth must then be due to procedural and/or apparatus inadequacies.

A modified chamber was designed to better emulate how visual information is received by chickens in the real world. There is evidence that poor performance in depth perception research can be due to the equipment used; women tend to perform more poorly than men on navigation tasks in simulated 3D environments (Postma, Jager, Kessels, Koppeschaar & van Honk, 2004). Tan, Czerwinski and Robertson (2006) used displays much larger than the standard, and found no difference in performance between genders. They attribute this to the better optical flow cues that a larger display provides. In humans, composite information is more useful for estimating depth than individual components (Bootsma & Craig 2002). In the previous chamber the subjects were able to peck the screen; no contingencies were in place that required them to view the display in its entirety. Peripheral vision i.e., seeing the entirety of the visual field, is important for accurately representing spatial structures in order to navigate (Turano, Yu, Hao & Hicks, 2005). Avian species have two fovea; research shows that the lateral fovea is used for depth perception and navigation, while the central fovea is utilised for accurate close-range viewing (Wylie et al., 2009). Research with humans can

control for the effect of head and eye movements using adjustable apparatus or by measuring retinal movement (e.g., Nawrot & Joyce, 2006).

Generally, animals with previous experience in similar tasks perform subsequent tasks faster (Goto & Lea, 1993). The single-object nature of the stimuli used in experiments 1-5 may have allowed the animals to discriminate solely on local cues, and when these were no longer applicable in experiment five, performance broke down instead of adjusting to the new contingencies. New, psychophysically naïve animals were therefore used in experiment six.

This experiment tested to see if the birds could discriminate stimuli that depicted a single flat surface in motion versus two surfaces separated in depth while located at a viewing position that was on average 30cm back from the screen. A barrier with an aperture in it was used to keep the birds away from the screen surface. To a human observer, the multiple moving square stimuli visible through the aperture appear either as a single surface or two surfaces separated in depth. Are the birds able to distinguish these two cases as well?

METHOD

Subjects

Subjects were 6 brown shaver hens of various ages. All had been used in previous, non-psychophysical, experiments. Each bird was housed individually in a wire cage measuring 51cm x 45cm x 44cm, in a ventilated room with up to 35 other chickens. Lights were on a 12:12 hour light: dark cycle. Water was available ad lib and grit provided once a week. Animals were weighed daily and maintained at 85%, +/- 5% of their free-feeding body weight through supplementary post-experimental feeding of commercial chicken feed. All procedures complied with the University of Waikato's Animal Ethics Committee requirements.

Apparatus

The operant chamber measured 600mm long, 450mm wide and 530mm tall, constructed of 4mm particleboard. An aperture measuring 33mm by 400 mm by 280 mm, continuous with the upper edge of one wall, allowed visual access to a second chamber, measuring 300mm by 400mm by 280mm. A screen (Dell Model E176FPb) occupied the entire far wall of this second chamber, and displayed the stimuli.

Another aperture located at the bottom edge of the response panel measuring 85 mm by 120 mm allowed access to a magazine that delivered 2 seconds of access to wheat as a reinforcer. Two response keys 30mm in diameter were situated either side of the viewing aperture, 95 mm from the top edge of the wall and 60mm from the outer edge. Both keys could be lit by either a green or red LED, with a brightness of 300 micro-candelas. Each key was surrounded by a metal plate 70mm wide x 140 mm high (refer Fig. 6.1)

The birds were required to break two intersecting beams to begin stimulus presentation. The lateral beam was located 50mm from the bottom edge of the viewing aperture. The vertical beam was located 13mm from the top and bottom of the viewing aperture (refer to Fig. 6.2). From this position the chickens were able to view the entire screen, but were prevented from moving closer than 30cm.

A white LED in the centre of the viewing chamber roof indicated when the next trial was ready to begin and the beams were able to be broken. Stimuli were the same as used in experiment five, with the addition that both “flat” and “parallax” stimuli moved from right to left as well as left to right, creating four separate videos. Stimuli were created using 3DMax (Autodesk 2013) and rendered at 60fps

in .avi format. Both films consisted of approximately 30 squares with sides 20 pixels long, i.e. half the size of the single squares used in previous experiments. These squares were arranged randomly across the screen in such a way as to avoid occlusion and edge effects as much as possible (see Fig. 5.1). In the “flat” video, all squares with a velocity of 15cm/sec. In the “parallax” video, 50% of the squares moved at 10cm/sec and 50% of the objects with a velocity of 20cm/sec. There were no size cues to depth in these stimuli. Depth has to be derived from the motion alone.

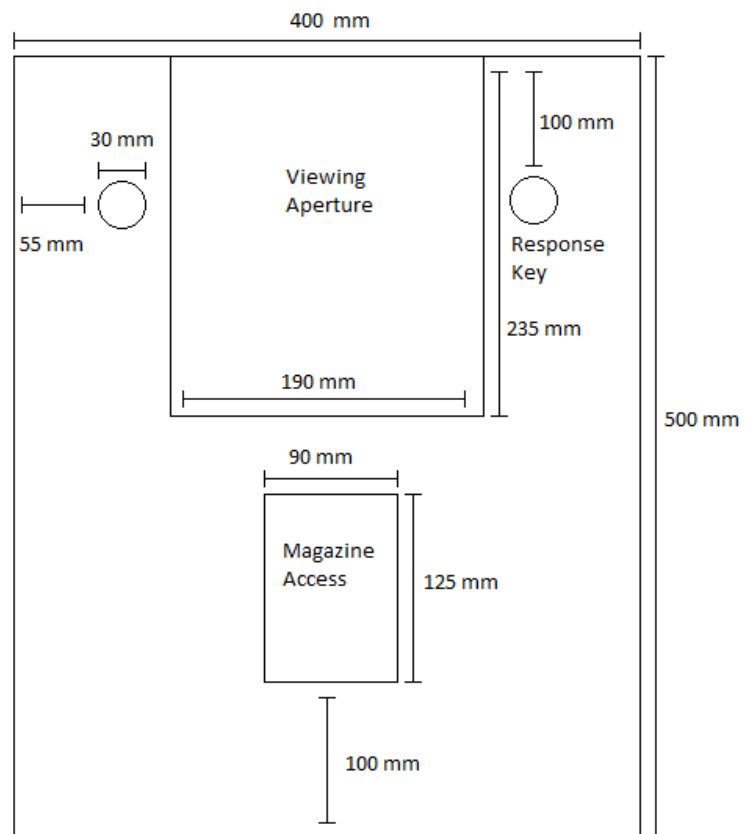


Fig. 6.1. Operant chamber response panel

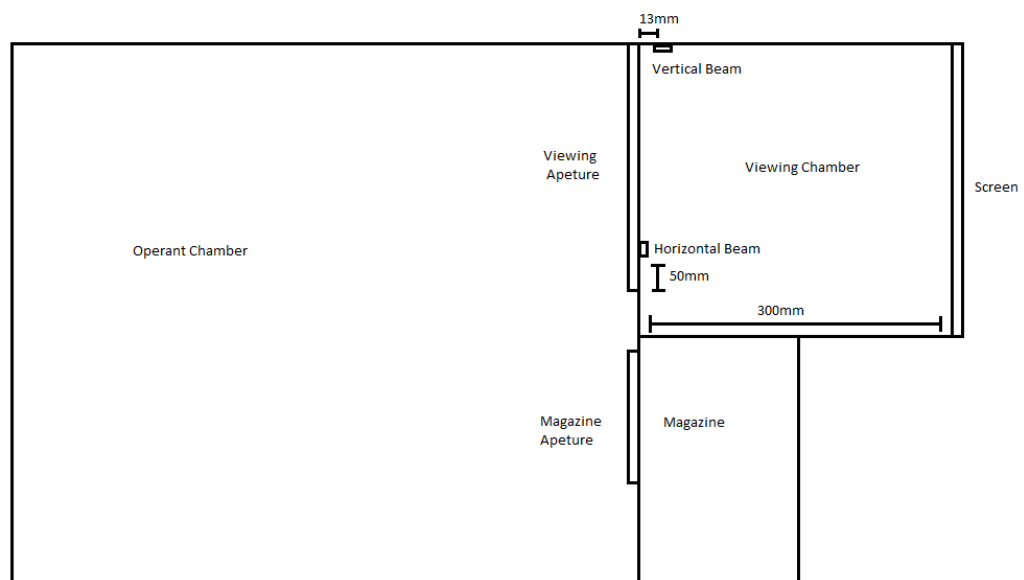


Fig. 6.2. Side view of operant chamber

Training

All birds were hand-shaped to break the beams in the viewing chamber by inserting their heads. Once this behavior was occurring reliably, the operant chamber was closed and training proper began. Training consisted of 6 sessions in total. Each trial was signaled by the white house light, and once both the lateral and horizontal beams were broken, stimulus presentation began. On training days one, three and five, flat stimuli only were displayed, followed by a single key being illuminated (red for animals 4.1, 4.2 and 4.3, and green for animals 4.4, 4.5 and 4.6). On training days 2, four and six, only parallax stimuli were displayed, followed by a single key being illuminated (green for animals 4.1, 4.2 and 4.3, and red for animals 4.4, 4.5 and 4.6). Every response resulted in 2 seconds access to wheat. The position of the keylight was controlled by a semi-random side reinforcement contingency, so that the lighted key appeared no more than twice on the same side. This was in order to avoid side-biased responding that appeared in previous experiments.

Procedure

The beginning of each trial was indicated by the white house light; this remained lit until both beams had been broken. Stimulus presentation consisted of three seconds, varying semi-randomly between flat and parallax stimuli. Reinforcers were on a VR2 schedule; reinforcers were delivered, on average, for every second correct response, but varied semi-randomly from one to three responses. Keylight position was varied semi-randomly, so that no more than three correct keys occurred consecutively on the same side.

For animals 4.1, 4.2 and 4.3, a peck to the green key after parallax stimuli and the red key after flat stimuli was reinforced, and for animals 4.4, 4.5 and 4.6 responding to the red key after parallax stimuli and to the green key after flat stimuli was reinforced, via 2 seconds access to wheat. Incorrect responses resulted in a 3 second time out, before the next trial began. A two-second inter-trial-interval was also in effect.

Sessions continued until 40 reinforcers had been received or 2400 seconds had elapsed, whichever occurred first.

RESULTS

All animals consistently performed near chance. After 14 sessions this showed no signs of improving. Fig 6.3 shows the mean percentage correct obtained for each session. All were extremely close to chance (dotted line), with very little variation. Individual bird's performance is displayed in Fig 6.4. Discrimination accuracy was extremely close to chance (dotted line) for all animals. Fig 6.5 displays the percentage of responses directed at the red key over the last five sessions for each bird. Animals 43 and 45 showed an extreme bias towards pecking red, with the remaining animals exhibiting non-biased performance.

None of the animals received the full amount of reinforcers available before sessions timed out at 2400 seconds. The number of reinforcers received in each session was between 14 and 39 (median 33) over the last five sessions.

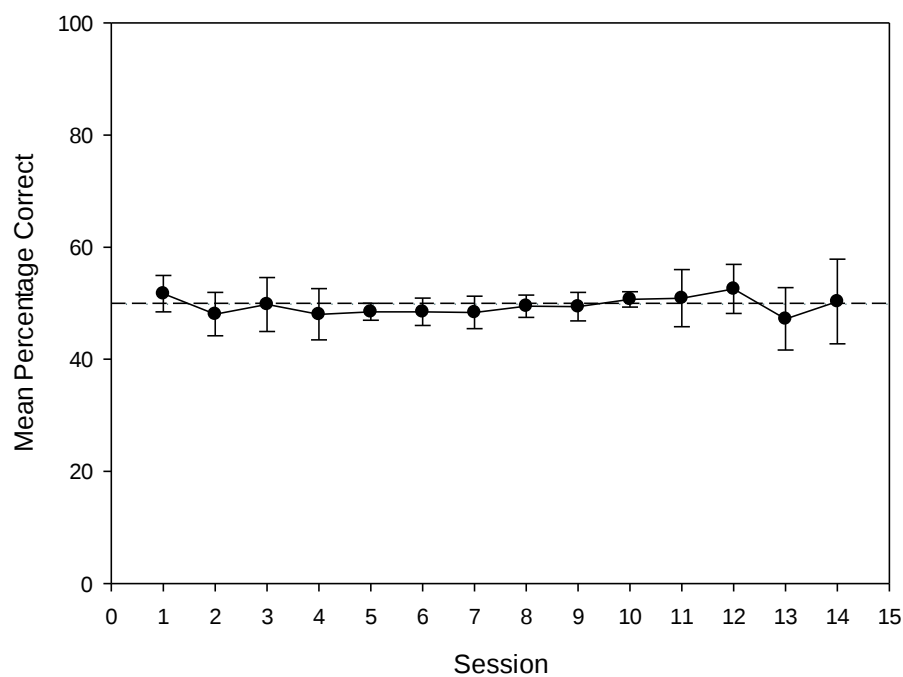


Fig 6.3. Mean percentage correct for all animals per session. The error bars indicate one standard deviation. Dotted line indicates chance performance.

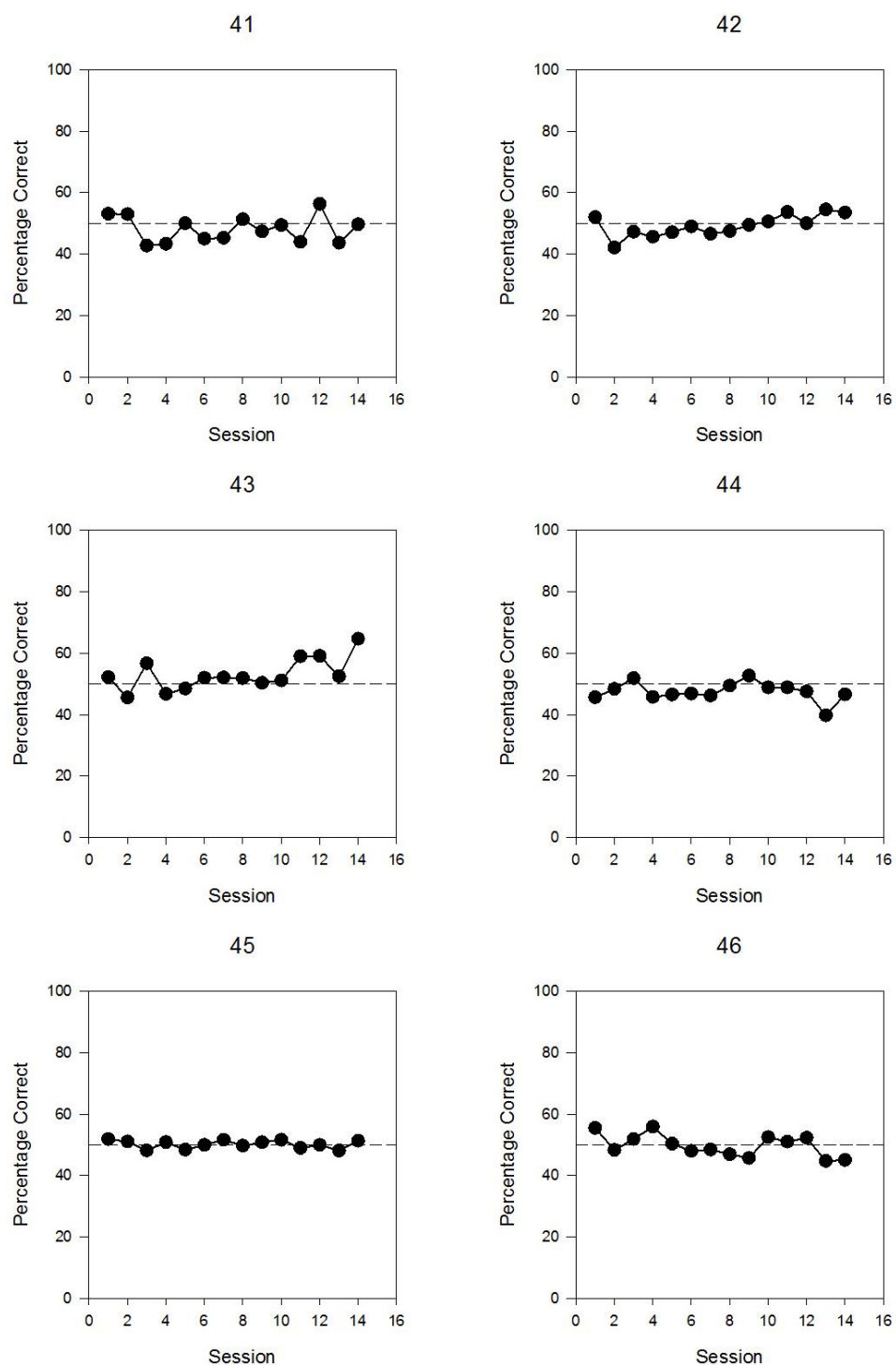


Fig 6.4. Percentage correct per animal over session. Dotted line indicates chance performance

DISCUSSION

There was no evidence that the animals were able to discriminate between the two different ‘depth’ stimuli. Experiment six attempted to reduce side biased responding by implementing a more unpredictable, leaner schedule. Two of the animals developed a colour bias instead, and the remaining four animals responded randomly. That the schedule of reinforcement was too rich could have been the case in previous experiments, but with this group of animals it was not so. That the birds were consistently receiving fewer than the full number of reinforcers available indicates this. An inter-trial interval generally improves performance in discrimination tasks (D'Amato, 1973). A 20-sec ITI was more effective than a 1-sec ITI for pigeons in a matching task. (Roberts 1980). It had no effect in this particular experiment however.

Although there was a requirement for the birds to break the beams inside the viewing chamber, this does not guarantee that they will then attend to the stimulus. Attention to the stimulus can be improved through increasing the response requirement (for a review see Honig and Urcuioli 1981). One alternative could have been to require that the birds remain with their heads breaking the beams for the entirety of stimulus presentation. Conversely, the discrimination choice may be made almost instantaneously by the subject, and information available later in the trial can be ignored, limiting improvement in accuracy (Kiani, Hanks & Shadlen 2008). Requiring the animal to wait until presentation has concluded before making keylights available introduced a delayed-matching-to-sample (DMTS) component to the experiment that was unintended. Pigeon's

ability to discriminate accurately decreases as a function of the length of delay in DMTS experiments (Grant 1975).

EXPERIMENT SEVEN

INTRODUCTION

Experiment six was implemented in order to determine if changes to the experimental paradigm would lift discrimination above chance. In experiment one, the keylights were not operational until the stimuli had finished being displayed. This had the effect of unintentionally creating a delayed-matching-to-sample (DMTS) task. The birds were required to wait until the end of stimulus presentation, look at the keylights and then choose their response. Stimulus presentation was only 3 seconds, but research has shown that longer delays result in decreased accuracy (Roberts & Kraemer 1982; Grant 1975).

Viewing the stimuli for the entire duration may not be necessary. The presentation duration of a stimulus is less important than the time the subject spends attending to that stimulus (Foster et al. 1995). Rats require only 1-2 sniffs of an odorant in order to discriminate accurately (Schwarz et al., 2010). However, longer sampling times are associated with greater accuracy, especially for more complex stimuli (Guttenberger & Wasserman, 1985; Shimp & Moffitt, 1977).

A large proportion of psychophysical experimentation employs a “go left or go right” paradigm as opposed to “choose the correct colour” that has been used in this set of experiments (i.e. Nagasako & Wasserman 2008; Bischof et al. 1999). This is advantageous because the animal is not required to decide which alternative to choose by looking, but can respond as soon as they have made their discrimination choice.

METHOD

Subjects and apparatus were the same as those in the previous experiment. Once the beams inside the viewing chamber had been broken, the stimuli were displayed and the keylights were activated simultaneously. All other aspects of the experimental procedure were as in the previous experiment.

Both keylights were lit white. For animals 41, 42 and 43, pecks to the left key after flat stimuli and the right key after parallax stimuli were reinforced. For animals 44, 45 and 46, pecks to the right key after flat stimuli and to the left key after parallax stimuli were reinforced. All other aspects of the experiment were the same as in experiment one.

Training

Two sessions were conducted with both stimuli types, but only the correct keylight lit. These continued until 40 reinforcers or 2400 seconds had elapsed, whichever came first. On the third day, sessions proper began.

RESULTS

Performance began at or around 50% for all animal, and after (15) days there was no increase in accuracy. No biases were in evidence, with all animals responding incorrectly to 50% of each type of stimuli, and equally on each key.

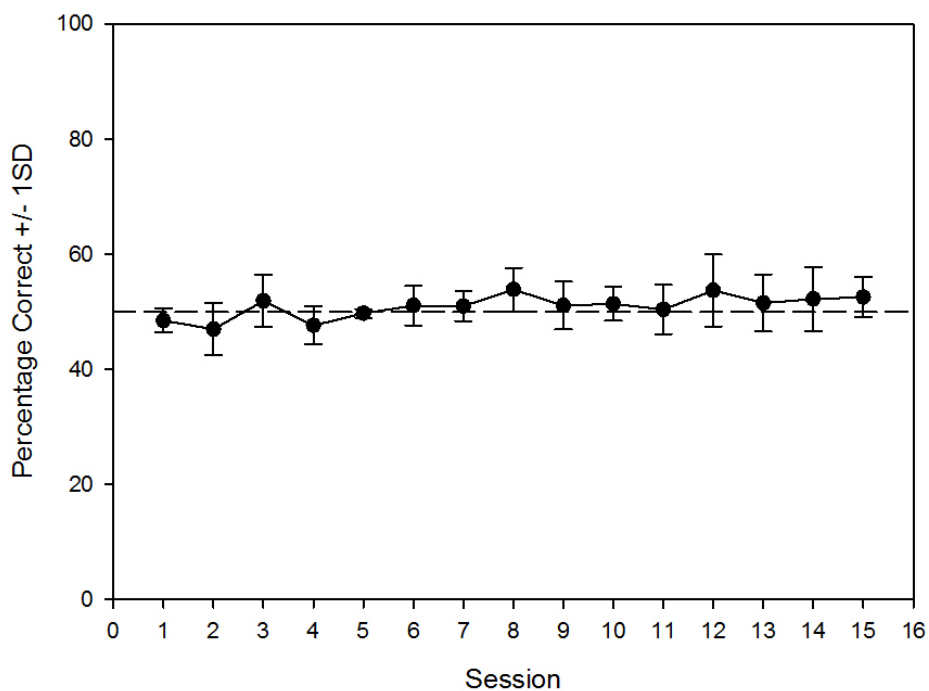


Fig 7.1. Mean percentage correct over session for all animals. Error bars indicate one standard deviation

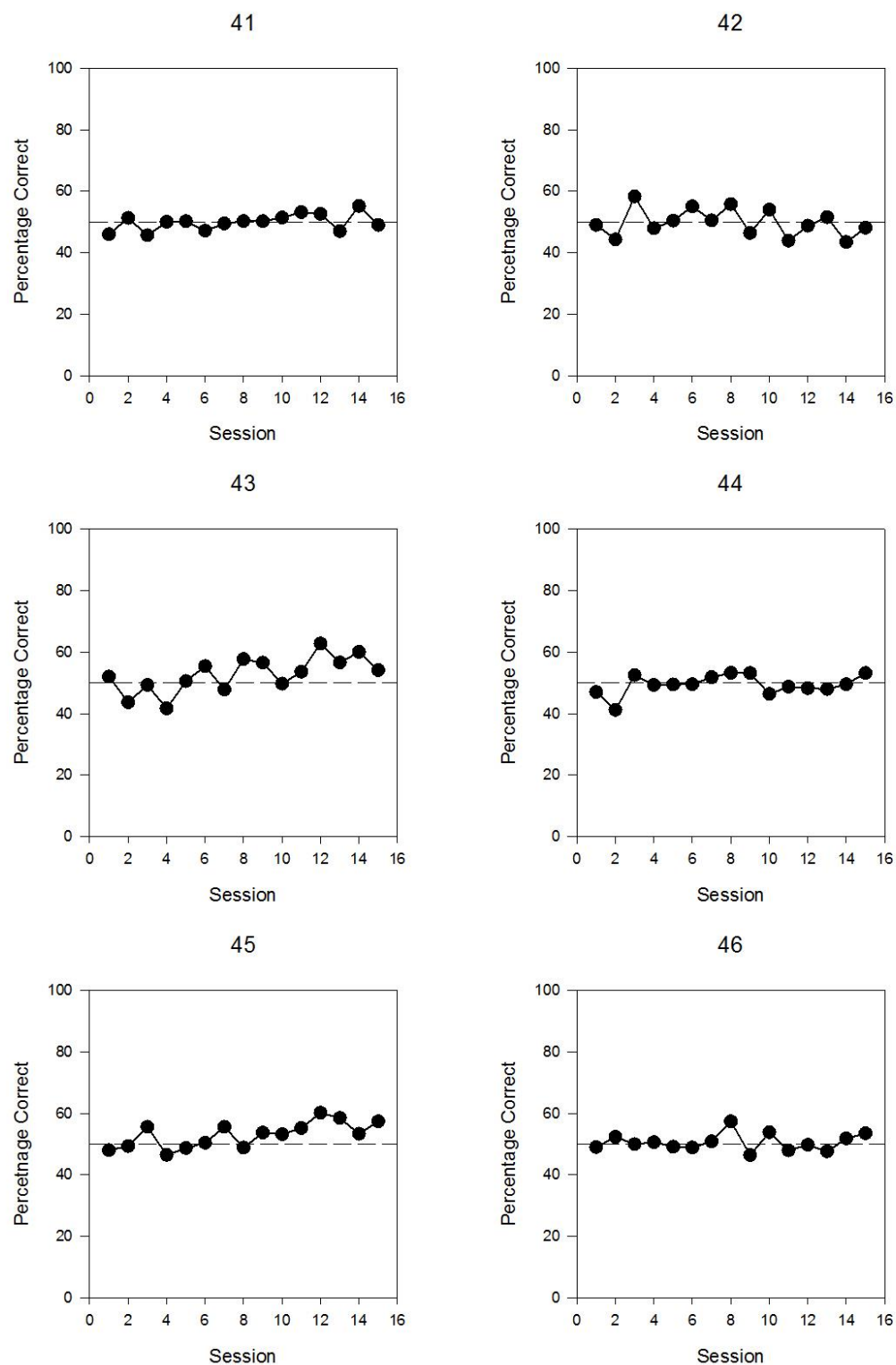


Fig 7.2. Percentage correct over sessions per animal. Dotted line indicates chance performance

DISCUSSION

Changing the experimental paradigm from a colour choice to side choice had no effect on performance, with accuracy consistently around chance levels. There is some evidence that ending the decision process while the display is still visible limits the possible improvement that could have come with more extensive stimulus exposure (Burr & Santoro, 2001).

For simple discriminations, subjects may not need to view a stimulus for the entire duration. The discrimination task then becomes a memory task, as the keylights are not available immediately. That allowing the keylights to be immediately available did not lift performance above chance indicates that this is not the case for this experiment. For humans at least, parallax information is processed over a larger temporal window compared to other visual cues such as colour (Caudek & Proffitt, 1993). Chickens may also require a comparatively long time for differential motion to register in their visual systems or they simply may not have the ability to extract depth from the type of parallax stimuli used in experiment seven.

GENERAL DISCUSSION

A series of experiments were carried out to see if chickens were able to detect and respond appropriately to stimuli depicting 3-dimensional scenes while viewing 2-D displays containing motion parallax. In order for animals to complete a discrimination task, they first require the perceptual and neural systems to classify stimulus features. They must then have the ability to link those features with a response, and to associate that response with its consequences (Phillmore, 2008). Chickens possess these systems, and were able to respond accurately the single-object stimuli. When multiple objects moving in on and two planes were introduced, bias developed and performance dropped to chance levels. The conclusion from this would have to be that the birds in our experiments were not able to extract depth from parallax under the experiments tested. There are several reasons why this may have been the case, as discussed below.

Optical Factors

Detecting visual motion involves first analysing 2-D velocity, and using that information to recover 3-D structure (Gibson et al., 1955; Sereno, 1992). The principal optic nucleus and wulst in the avian brain are homologs of the lateral geniculate nucleus and primary visual cortex in mammals. The AOS and pretectum are important for analysing optic flow and generating the optokinetic response. Motion in depth is detected by specialised cells in the dorsal-posterior region of the rotundus (Wylie et al., 2009; Frost, 2010).

Chickens, and most other bird species, have eyes located laterally on their heads. In pigeons, a species with a similar morphology, there is a frontal system for binocular information approximately 25° below the horizon and extending about 10° to each side of the axis of the beak (Martinoya & Bloch, 1981). The rest of the visual field is the lateral system which operates monocularly (Roberts & Kraemer, 1982). Pigeon's pecking behaviour is just as accurate with one eye occluded, and in any case, eye movements can terminate binocularity. Martin (1999) suggests that each eye provides a separate field, increasing accuracy through superfluity of information. Multiple depth cues from monocular vision may be particularly important to controlling bird's motor responses (Davies & Green, 1994). That chickens possess these neurological structures, and the anatomy of their eyes, indicates that they are capable of processing and acting upon parallax information.

The first four experiments utilised single object stimuli. Detecting movement in those experiments required the processing of local motion only. Global motion on the other hand, as used in experiments five, six and seven, "is the perceived direction of a dynamic input when that direction is the result of a combination of many individual motion signals within that stimulus" (Cropper, 2001, p126).

There is some evidence that unlike humans, birds process patterns at a local level (Kelly, 2001) and require motion across both eyes to register depth (Bagavatula, Claudianos, Ibbotson & Srinivasan, 2011). Combining these signals into a global motion percept may be reliant on the properties of the stimulus, as opposed to the motion-detection abilities of the organism being studied (Zanker, 2001). Stimuli which are more easily manipulated along the continuum of "flat" to "depth"

would have allowed us to more systematically investigate the parallax processing abilities of the animals.

Ecological Validity

A common argument against the stimuli used in laboratories is that they are not realistic approximations of the world animals interact with (Cook, 2000). Bird's visual environment does not consist of random-dot patterns, or white squares on a black background as used in this set of experiments. Learning to respond to this kind of stimuli may be a problem of learning to extract the information necessary to make a successful choice (Willigen, Frost & Wagner, 2003). Some of the more impressive abilities of animals were not discovered until more realistic displays were used in research (Cook, 2000). It may be that multiple white squares moving on a black background was simply too different from the parallax information chickens would normally receive in their environment. Displays incorporating more information than those used in these experiments, but still simple enough to allow systematic manipulation may be more successful.

An animal may not physically be able to discriminate between two sets of stimuli, or the differences may have no behavioural relevance. Technically, the operant response is unrelated to the stimulus being investigated (Skinner, 1953) but pigeons will work better for food when discriminating visual stimuli, and tones for avoiding shock (Foree & Lolordo, 1973). The operant response is also morphologically different depending on the type of reinforcer used; pecks directed at keylights when working for food are shorter and possess a larger beak

amplitude than pecks to keylights when water is the reinforcer (Ploog & Zeigler, 1997). Different species may be “pre-wired” to respond to some stimulus dimensions but not others (Gilbert & Sutherland, 1969). Preferred stimuli are learnt faster than non-preferred stimuli (Devore & Linster, 2013), and low levels of environmental enrichment for experimental animals has been linked to “pessimistic” judgements of difficult-to-discriminate stimuli (Matheson, Asher & Bateson, 2008).

The Vestibular System

The vestibular system integrates sensory and motor information to maintain an animal's balance and control its eye movements. Performing a unilateral vestibular ganglionectomy on chickens' results in difficulties with balance and posture, some of whom do not recover (Shao et al., 2009). Birds are well-known for their ability to keep their heads still while their body is moved, and most birds will bob their heads back and forth as they walk, with one head bob synchronised with one step (Dawkins, 2002). Bobbing can be produced through optic flow alone, and is not present on animals walking on a treadmill (Friedman, 1975). This motion probably stabilises the image on the retina and helps to determine self-motion from motion of objects (Frost, 1978; Troje & Frost, 2000). Shape discrimination during various parts of the head bobbing cycle was slower and less accurate when stimuli were displayed in the lateral, as opposed to the frontal, view (Ortega, Stoppa, Güntürkün & Troje, 2009).

The birds in this set of experiments may have had difficulty seeing the depth in

the final experiments due to this lack of input from their vestibular systems.

There is some evidence that, in humans, depth perception from self-produced parallax is more effective (Ono & Steinbach, 1990; Graham & Rogers, 1979) than passively viewed parallax, as was used in this study. The viewing aperture in experiments six and seven two was relatively small (90mm by 125mm). However, there was sufficient space for the birds to move their head and necks. A different setup utilising optic flow via movement through the environment may be more successful with this particular chamber and screen combination.

Operant Chamber Behaviour

One problem with studying vision in operant chambers with freely moving animals is we cannot precisely control viewing distance, and data may therefore be skewed. This became apparent in experiment four where it was discovered that the birds were pecking at the moving square as it moved. This meant that their view of the square was from a very close viewpoint compared to that expected when the experiment was designed. Many studies with humans and primates utilise head fixing to control for this (Kinai et al., 2008; Nawrot & Joyce, 2006). However, animals require a long time to become habituated to such forms of restrictive apparatus. Restricted movement may also affect the perception, e.g., Owls are unable to discriminate texture if they are prevented from making peering movements (Van der Willigen et al., 2002). The use of eye tracking is another method employed by human and primate researchers to control for the effects of freely moving animals (i.e. Nawrot & Joyce 2006; Kinai et al., 2008). This method is not feasible with many avian species as they possess two fovea in each eye

(Cook, 2000). Additionally, bird's saccades are sometimes asymmetrical or occur in one eye only (Bloch, Rivaud & Martinoya, 1984).

In the first four experiments, all animals stood extremely close to the screen and pecked the white square, in the case of moving stimuli tracking it across the screen. This is not an accurate homolog of how screens are normally used by humans, nor would it be possible for the birds to see the entire array in experiment five. The construction of a new chamber with a viewing aperture and the screen situated 300mm back from the wall was an attempt to create more realistic viewing experiments. It may be that the chamber dimensions were not ideal for parallax viewing; the screen distance may have been beyond the focussing distance of the birds for the viewing strategy they adopted while located near the aperture (Martin, 1999).

Another common experimental apparatus to research avian vision is to display various patterns on the interior walls of narrow tunnels. The flight pattern of budgerigars in such a tunnel (Bhagavatula et al., 2011) varied significantly depending on the pattern presented. When one side was horizontally striped and one side vertically, the birds flew much closer to the horizontal wall. When one wall was vertically striped on one blank, they occasionally collided with the latter. The image motion in both cases was much stronger for the wall carrying horizontal stripes, and so the differential motion across each eye caused the difference in flight. Even when not airborne, birds may use this system to navigate through the world. This suggests that presenting the chickens with stimuli located

on two screens on either side of the head may better tap into their navigation and depth extraction abilities.

A peck to the blank screen was required in experiments one to four in order to begin each trial. Without this, there was no way to ensure the birds were focused on the screen as each trial began. Breaking the infrared beams inside the viewing aperture replaced the initial screen peck as the observing response in experiments six and seven. Both of these responses are analogous to pressing a key in human psychophysical experiments when the participant is ready to begin. The difference is that humans have an extensive history of understanding and acting on instructions; we have only the contingencies in the operant chamber to ensure animals are actually attending to the stimuli.

Training

Research with humans relies on their extensive history of reinforcement with their verbal community. Without this prior history, instructions could not be understood nor results reported. Animals require carefully designed experiments to ensure they are responding as required. Prior training generally results in better performance on later discrimination tasks (Goto & Lea 2003, Wilkinson & Kirkpatrick, 2009). Pre-exposure to the stimuli without any consequences attached can also improve learning speed; Gibson and Walk (1956) placed circles and triangles on the home cage walls of their rats; these animals were able to discriminate between the shapes more rapidly than animals who had not been pre-exposed.

Animals of all species are notorious for attending to irrelevant aspects of the stimuli (Goto & Lea, 2003; Nagasakoa & Wasserman, 2008). This was the case with animal 34 in experiment two; it required extensive retraining to achieve the same level of accuracy that the other birds achieved within 16 sessions or less. The only difference between stimuli in experiment one and experiment two was the position of the stationary stimuli; the subject was attending to position rather than the stationary property of the square. This was also the case for animal 31 in experiment three, who also required extensive training to reach the 80% or more correct threshold.

Introducing multiple objects in experiment five may have been too great a step from the single-object displays used in the previous four experiments. An animal's history of reinforcement can interfere with discrimination performance if the task is too novel. When the original cohort of birds developed a rightwards bias, Wilkinson and Kirkpartick (2009) tested the same stimuli with experimentally naïve birds. These animals did not display the same bias, though their performance was less accurate, and much slower. That four of the five birds used in the first four experiments developed extreme side biases, as well as their previous history in responding to single object displays, was the rationale behind using new animals in the second set of experiments.

Methodology

In experiments six and seven, the methodology was altered to include a 2-second variable-interval contingency. It was possible that the birds in the first four

experiments were making a speed-accuracy trade-off when the stimuli became much more complex. Animals are not perfect detecting organisms; from an evolutionary standpoint, less optimal performance is desirable if the rewards for increased accuracy are minimal (Abraham et al., 2004; Uchida and Mainen, 2003). It is possible that the birds made the effort for simple stimuli (experiments one to four), but when the display became more complex, resorted to a side bias (experiment five) or a guessing (experiment six) strategy, because they should still receive their full allotment of reinforcers eventually. That the birds in experiment six never received the full amount of reinforcers available precludes this.

Open economies like those used in these experiments, provide additional food in the home cage to maintain optimum body weight (85%, $\pm 5\%$ at this laboratory). It could be argued that the animals in experiments five and six were not as accurate as they could be, because they would get their full quota of food regardless of their behaviour. While it is desirable to have the entire quota delivered within the operant chamber (Schwartz (2010) recommends an additional training session rather than giving water for free), 85% of free feeding bodyweight is sufficient motivation to work for food, especially on the leaner schedules in experiments five, six and seven.

The three second black out in place for experiments one to four was probably not sufficiently punishing to control behaviour. Longer ITI's result in greater accuracy in a range of learning tasks (Holland, 1999). A long ITI can also discourage superstitious behaviour such as licking in rats (Schwartz et al., 2010). An ITI as part of the experimental methodology from the beginning, as opposed to only a

time out or reinforce delivery, may have prevented the necessity of retraining animals in experiments two and three.

Observers do not necessarily use all of the information available in a trial to make a decision, information may instead be of decreasing usefulness as the trial progresses (Luna, Hernandez, Brody & Romo, 2005; Kiani et al., 2008). Forcing the birds in this set of experiments to delay making their response until the stimulus has ceased to be displayed may have contributed to the side bias and guessing responses seen in the later experiments. The unintentional delay-matching-to-sample task was corrected in experiment seven with no effect. This indicates that the potential delay between the animal making their choice and making their response had not affected their accuracy. It is possible that, like humans, motion information is processed over a certain length of time (Caudek, & Proffitt, 1993).

While many psychophysical studies employ a go/ no go paradigm to test abilities (i.e. Goto et al. 2002), it is difficult to determine if a “no go” response is a response or merely an omission (Murphy, Nordquist & van der Staay, 2013). This set of experiments used a two alternative forced-choice methodology because it allows more complete analysis of responses to both types of stimuli being presented, as the animal must make an active response to choice stimuli types (Kay, Beshel & Martin, 2006).

In the first five experiments, the stimuli moved in one direction only; from left to right. This was to render the discrimination task as simple as possible to perform,

but had the unintentional effect of encouraging side bias to develop when the stimuli became more complex. Stimuli should have moved in both directions from experiment one. Adding a contingency in experiment five that two consecutive reinforcers could not be received on the same side reduced responding to chance levels. In experiment six, 2 of the six animals developed a colour bias instead. Biased responding often occurs when the discrimination is too difficult; mice will quickly begin responding on one key only after several errors (Schwarz et al., 2010). There are algorithms that automatically change the probability of stimuli if response biases begin to develop (Knutsen, Pietr & Ahissar, 2006), but this can interfere with stimulus control by altering the cues within response and reinforcement history (Schwarz et al., 2010).

Future Directions

Future research should utilize a wider range of stimuli early in testing to avoid the biased responding that occurred in this set of experiments. The training and experimental procedure must also be complex and lean enough to avoid predictability or non-attentive responding.

Other vision research has utilized more naturalistic or interactive apparatus such as the flying tunnels in Bhagavatula et al. (2011). Allowing the birds to use both of their eyes to view stimuli, or to engage their vestibular system with experimental procedures that require movement through the environment, could yield more satisfying evidence of these animal's depth perception abilities.

CONCLUSION

In conclusion, chickens are able to make discriminations between a single moving and stationary object, and to discriminate between two different speeds. When multiple object stimuli were introduced however, performance broke down. The multiple object stimuli require the detection of speed differences over large parts of the bird's visual field for depth to be extracted correctly. The animals never managed to make this transition from 'local' to 'global' processing. Side biased responding also developed at this stage. When the ability to do this was removed, performance dropped to chance. A new chamber was constructed that prevented the animals standing too close, naïve animals were used, a longer ITI was introduced and stimuli that moved in both directions were added. The response paradigm was also adjusted, from "choose red or green" to "choose left or right". Although there were several other cues that could have been used to make their choices, none of these changes resulted in above chance performance. The stimuli used contained obvious depth to human eyes, but requiring the birds to view the screen in the same way may not activate the necessary systems. Birds may need speed differences across both eyes in order to make a choice regarding depth. More research is necessary to determine what, if any, aspects of the training process, operant chamber or stimuli could be altered to lift accuracy above chance.

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APPENDICES

Experiment Two

After 8 sessions subject 3.4 was exhibiting a consistent bias towards responding incorrectly after stationary stimulus. Two sessions of stationary stimulus retraining (dotted line (a) in fig 8.1) did not lift performance above 80%. A further 3 days of training (dotted line (b) in Fig 8.1) also failed to increase discrimination above 80%. Six days of training (dotted line (c) in Fig 8.1), alternating stimuli type between sessions, were required before accuracy increased sufficiently for the bird to move to the next experiment .

Subject 3.5 also demonstrated a consistent bias towards responding incorrectly to the stationary stimulus after 8 sessions. Two sessions of stationary stimulus training were implemented (dotted line (d) in fig 8.2), and accuracy increased to above threshold, although the bias continued to be in evidence.

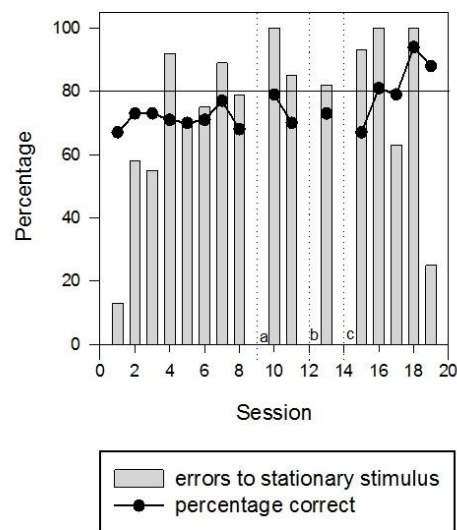


Fig 8.1. Animal 3.4 experiment two errors to stationary key over overall percentage correct. (a) indicates two days stationary stimulus retraining. (b) indicates three sessions of retraining. (c) indicates six session of retraining.

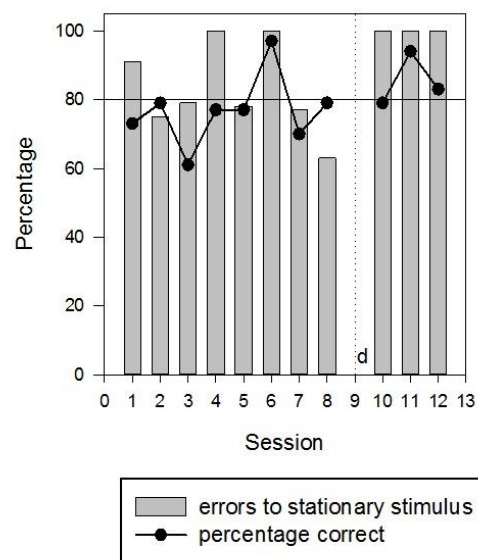


Fig 8.2. Animal 3.5 experiment two errors to stationary stimulus over overall percentage (d) indicates two days of stationary stimulus training.

Experiment Three

Animal 3.1 required extensive retraining to reach threshold performance in experiment three. After 27 sessions performance remained highly variable and below performance threshold. 6 days retraining (solid line (a) in Fig 8.3), repeating experiment one for five sessions (solid line (b) in Fig 8.3) and a further 6 sessions of training (solid line (c) in Fig 8.3) had no effect on accuracy. A side reinforcement contingency implemented (solid line (d) in Fig 8.3) where no two reinforcers were available consecutively for responding on the same key. This also had no effect on discrimination performance after eight sessions, so a delay contingency was implemented (solid line (e) in Fig 8.3), where pecking the screen was prohibited during stimulus presentation. It required a further 12 sessions for performance to attain the level of accuracy required to move to the next experiment.

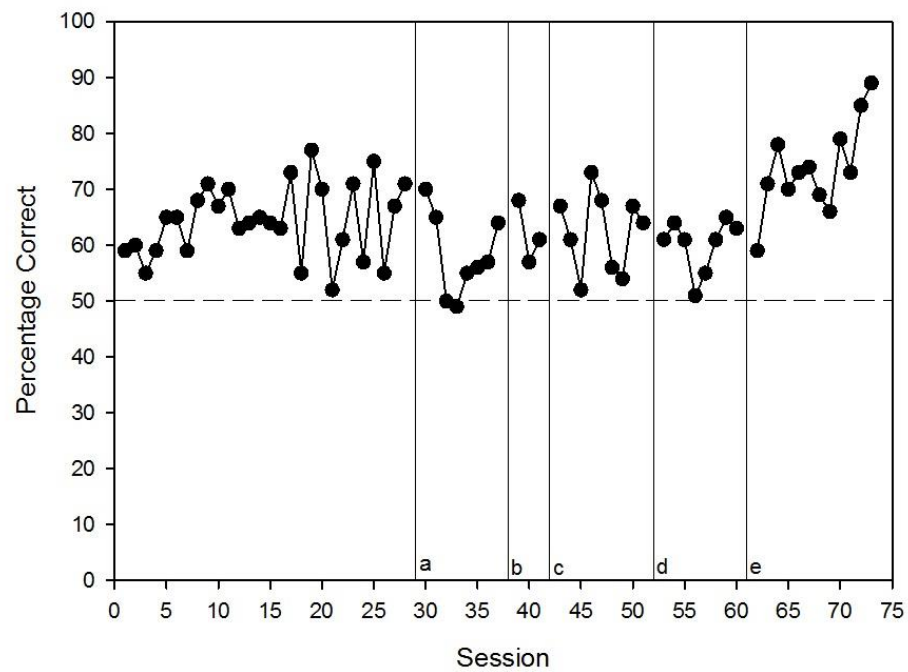


Fig 8.3. Animal 3.1 experiment three, percentage correct over session. (a) indicates 6 sessions retraining. (b) indicates animal repeated experiment one for five sessions. (c) indicates six retraining sessions. (d) indicates implementation of side reinforcement contingency. (e) indicates implementation of prohibiting pecking during stimulus presentation

