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VISUAL PERCEPTION OF A MOTION AFTEREFFECT IN DOMESTIC CHICKENS (GALLUS GALLUS):

A BEHAVIOURAL ANALYTIC APPROACH

A thesis

submitted in partial fulfilment

of the requirements for the degree

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ABSTRACT

The motion aftereffect (MAE) is an illusory motion in the opposite direction after the sudden halt of a prolonged moving visual stimulus. The human experience of the motion aftereffect has been extensively researched utilising many different experimental approaches. The ability of the avian species to perceive this motion illusion has not been so well researched and such a phenomenon has never been investigated in domestic chickens. The aim of the experiment reported in this thesis was to test whether domestic chickens can perceive a motion aftereffect. Xiao and Gunturkun (2008) carried out a study to investigate whether pigeons could perceive the motion aftereffect. After initially failing to obtain evidence for the effect they modified their procedure and found results that were better but still not strongly suggestive of a robust motion aftereffect. Their methodology was further refined for this thesis to see if evidence for the motion aftereffect could be found in chickens. The chickens received initial discrimination training to differentiate between static, upward and downward moving grating patterns. Once they reached the criterion for this task reliably, each subject underwent test trials where they were exposed to a static pattern after prolonged presentation of a moving grating stimulus. Results from the choice behaviour of the chickens indicated they did not experience a motion aftereffect. This thesis and the previous study would suggest there is not a reliable motion aftereffect for birds. Whether this reflects limitations of the research design or the nature of the avian visual system is still to be determined.

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TABLE OF CONTENTS

Abstract ii

Acknowledgements iii

List of Figures vi

List of Tables vii

General Introduction 1

The Motion Aftereffect in the Human Visual System 2

Psychophysical Methods Used to Study the Motion Aftereffect 3

Visual Illusions in the Avian Species 7

Motion Aftereffect in the Avian Species 12

Experiment Introduction 15

Thesis Research Question: Do Chickens Perceive the MAE? 15

Experiment 20

Method 20

Subjects 20

Apparatus 21

Visual Stimuli 24

Training Procedure 27

Experiment Procedure 32

Results 33

Training Results 33

Test Trials Results 37

Discussion 44

Conclusion 51

References 53

LIST OF FIGURES

Figure 1. An illustration of a standard and reversed Müller-Lyer figure 8

Figure 2. Hypothetical graphs of results 19

Figure 3. Operant chamber response panel and food magazine..... 22

Figure 4. Operant chamber of our experiment 23

Figure 5. An illustration of the static grating pattern as a visual stimuli 25

Figure 6. An illustration of the moving visual stimuli 25

Figure 7. An illustration of the position and colours of response buttons/keys 26

Figure 8. The experimental setup of a training trial in our experiment. 30

Figure 9. The experimental setup of an illusion test trial in our experiment. 31

Figure 10. Percentage corrects per subject during training condition 4..... 35

Figure 11. A subject of our experiment undertaking training..... 36

Figure 12. Results of illusion test trials of all subjects per movement type 38

Figure 13. Percent response ratios for subjects 7.3, 7.4 & 7.5..... 41

Figure 14. Comparison of our results to the Xiao and Gunturkun (2008) study. . 42

LIST OF TABLES

Table 1. The presented training procedure in the experiment..... 28

GENERAL INTRODUCTION

The motion aftereffect (MAE) phenomenon is an illusion of visual motion where after a prolonged gaze at a stimulus moving in a certain direction, a stationery object seems to move in the opposite direction of the former moving stimulus (Mather, Pavan, Campana, & Casco, 2008). There are two forms of MAE, the static and dynamic MAE. The static MAE or SMAE involves a static test pattern commonly viewed from natural surroundings such as the classic waterfall example where after watching the waterfall for a length of time, subsequently observing a stationery object such as a rock makes it appear to move in the opposite direction to the waterfall (Mather et al., 2008). The dynamic MAE or DMAE involves dynamic test patterns, categorised into two forms - counter-phase flicker (Ashida & Osaka, 1995) or a dynamic visual noise pattern (van der Smagt, Verstraten, & van de Grind, 1999) which comprises of a condensed field of randomly moving dots.

The most widely accepted explanation for the MAE is neural adaptation (Anstis, Verstraten, & Mather, 1998). Neural adaptation theorises that cortical direction-selective neurons tuned to a particular direction of movement reduces responsiveness after prolonged exposure to viewing that particular movement (Barlow & Hill, 1963), therefore when a stationery stimulus is subsequently viewed (in the case of MAE), those neurons would produce less firing than normal and its competing comparison neurons would produce more firing hence apparent movement in the opposite direction would be seen. Sutherland first proposed this theory and wrote:

"…the direction in which something is seen to move might depend on the ratios of firing in cells sensitive to movement in different directions, and after prolonged movement in one direction a stationery image would produce less firing in the cells which had just been stimulated than normally, hence movement in the opposite direction would be seen to occur" (Sutherland, 1961, p. 227).

With the enormous amount of research into the MAE phenomenon since Sutherland's theory of neural adaptation for the MAE, new evidence suggests that the MAE cannot be explained simply by neural adaptation. It has been shown that different aftereffects have different underlying motion-processing mechanisms and different cortical areas that are stimulated, which cannot be simply explained by neural adaptation. New theories such as coding optimization, error correction, and shifting the frame of reference are being put forth to explain the function of the MAE and continue to be explored (Anstis et al., 1998).

The Motion Aftereffect in the Human Visual System

Evidence from research has revealed that there are different visual mechanisms at work when perceiving the two different forms of MAE - the SMAE and DMAE. Experiments on the SMAE have shown that it is only induced by first-order motion (Anstis & Mackay, 1980; Derrington & Badcock, 1985; Mather et al., 2008), displays a storage effect (Thompson & Wright, 1994; van de Grind, van der Smagt, & Verstraten, 2004), is temporal-frequency tuned (Kristjánsson, 2001; Pantle, 1974), and displays partial inter-ocular transfer (Moulden, 1980). In contrast, the DMAE is induced by first- and second-order motion (McCarthy, 1993; van der Smagt, Verstraten, Vaessen, van Londen, & van de Grind, 1999), does not display a storage effect (Verstraten, Fredericksen, Van Wezel, Lankheet,

& Van De Grind, 1996), is speed tuned (Ashida & Osaka, 1995), and exhibits complete inter-ocular transfer (Nishida, Ashida, & Sato, 1994). These findings indicate that the SMAE reflects neural adaptation on lower level, first-order motion-sensitive neurons identified in the primary visual cortex (V1 and V2), whereas the DMAE reflects adaptation in higher level second-order motion-sensitive neurons in the Middle Temporal (MT/V5) or Medial Superior Temporal (MST) areas. In conclusion, the visual neural mechanism that is elicited during a MAE experience largely depend upon the adapting and test stimuli involved, and how these stimuli are manipulated (Mather et al., 2008). How these findings have been discovered is detailed in the following section which reviews the experimental methods that are utilised to approach the study of the MAE.

Psychophysical Methods Used to Study the Motion Aftereffect

Single cell recordings of animals were the first method for studying the MAE in a laboratory setting. In 1963, Barlow and Hill (1963) studied the retinal ganglion cells of rabbits which are direction-selective and which only respond when an object is moving in a preferred direction of motion in the visual field. The responsiveness of single units of the retinal ganglion cells were recorded using electrodes that were placed into the retina of a rabbit's eyes. A large black disc with an irregular pattern of pieces of white paper attached to its surface was rotated in the preferred direction of the cells in the rabbit's visual field continuously for one minute, and the number of impulses that occurred per second was recorded. Barlow and Hill (1963) found the activity of the cells after long exposure of a moving stimulus dropped below baseline level when the motion stopped and gradually recovered to baseline levels after 30s. These findings provided evidence that supports the theory of neural adaptation, described above.

Studies of single-cell recordings of adaptation-induced changes have since broadened to other animals such as cats (Giaschi, Douglas, Marlin, & Cynader, 1993; Hammond, Mouat, & Smith, 1988; Marlin, Hasan, & Cynader, 1988; Vautin & Berkley, 1977) and macaque monkeys (Chander & Chichilnisky, 2001; Petersen, Baker, & Allman, 1985). While early studies into adaptation-induced changes have focused mainly on the early visual system, more recent studies have begun examining higher-level cortical cells that may play a role in the visual motion processing pathway during adaptation of the MAE. Instead of measuring the ganglion cells in the retina, Kohn and Movshon (2003; 2004) recorded the adaptation-induced changes in the response of direction-selective cells in the cortical MT area of macaque. The MT cortical area has been widely accepted to be responsible for visual motion perception of the human brain, and so Kohn and Movshon wanted to investigate whether the adaptation/aftereffect occurs at the level of MT cells, or are based on responses originating from V1 cells (primary cortex). Their findings indicate that adaptation is fed forward from V1 but state that there is still a possibility that adaptation may occur in MT neurons themselves. Overall, using the single-cell recording technique to investigate the MAE has provided strong evidence for the adaptation theory of the MAE and has shown that adaptation occurs from the primary visual cortex but also possibly at several other visual cortical sites.

The well-known experimental technique of functional magnetic resonance imaging (fMRI) or human neuroimaging is another method that has been used to investigate the MAE. Human participants in an fMRI study viewed visual stimuli that were back-projected onto a screen by a liquid-crystal projector and viewed binocularly through a mirror above the head coil while they lay inside a fMRI

scanner (Ashida, Lingnau, Wall, & Smith, 2007). The changes in the blood oxygen level dependent (BOLD) response was recorded before, during, and after repeated similar stimuli were presented. The inference is that if a reduction in the BOLD response occurred during the repeated presentation of similar stimuli (fMRI adaptation), this would reflect changes in the responsiveness of cortical cells that is consistent with neural adaptation of the MAE (Fang, Murray, Kersten, & He, 2005). This technique can also display the location of where the MAE occurs in the cortex.

Results from numerous fMRI studies of the MAE indicate that several brain areas are activated during the experience of MAEs (Ashida et al., 2007; He, Cohen, & Hu, 1998; Seiffert, Somers, Dale, & Tootell, 2003; Smith, Greenlee, Singh, Kraemer, & Hennig, 1998; Taylor et al., 2000). Previously, area MT has been the primary area where the MAE was thought to occur (Tootell et al., 1995). However, recent studies have since found evidence that shows visual areas V1, V2, V3, VP, V3A, and V4 are also activated during the MAE phenomenon (Nishida, Sasaki, Murakami, Watanabe, & Tootell, 2003; Seiffert et al., 2003). For instance, Taylor et al. (2000) investigated which brain areas were in activation during the perception of SMAE. Subjects were adapted for 21s to drifting bars or to reversing bars (the control condition) then immediately presented with 21 seconds of stationary bars. In the course of perceiving the SMAE, the fMRI images revealed significant activation of the MT area, along with a network of posterior and anterior cortical sites. Taylor et al. (2000) argue that the joint activity of the two different neural networks (posterior and anterior network) may be involved in the perception of the MAE.

Human transcranial magnetic stimulation (TMS) has also been utilised to study where the MAE phenomenon originates in the brain. TMS studies of the MAE have primarily focused on the application of repetitive transcranial magnetic stimulation (rTMS) to area MT/V5, which is widely believed to be where the MAE occurs (Stewart, Battelli, Walsh, & Cowey, 1999). Théoret, Kobayashi, Ganis, Di Capua, and Pascual-Leone (2002) investigated whether the MAE occurred in the MT/V5 cortical area by applying rTMS to the MT/V5 area of the brain of human subjects. In this study, the participants were seated in front of a computer screen which displayed a radial grating moving anti-clockwise for 30s (adaptation stimulus). They were then immediately shown a static pattern and were asked to report when the perception of MAE ended by pressing a key. During an rTMS test trial, the participants were delivered a 5s train of 20 magnetic impulses to the MT/V5 area while perceiving the MAE. A control condition consisting of trials that recorded the duration of the MAE without rTMS was followed by the rTMS trials to determine whether there was a significant difference between the duration of the MAE with or without rTMS. Théoret et al. (2002) found that rTMS significantly reduced the duration of the MAE, providing further evidence that implicates area MT/V5 in the MAE. There are a number of other transcranial stimulation studies that similarly demonstrate a definite involvement of the area MT in the MAE (Antal et al., 2004; Murd, Einberg, & Bachmann, 2012), but new research using TMS applied to the V2/V3 cortical areas (Campana, Maniglia, & Pavan, 2013) have also produced the same reduction of the MAE with results similar to Théoret et al. (2002) in area MT. This new finding paves the way to explore other cortical areas that may play a

role in the MAE and demonstrates how TMS can be a useful tool for identifying the location of the MAE phenomenon.

Lastly, the MAE phenomenon has been studied using human electrophysiology. Both Visual Evoked Potentials (VEPs) and magnetoencephalography (MEG) have been used. While experiencing the MAE, electrical activity is recorded and compared to the electrical activity while not experiencing the MAE. Results from these studies have shown that a significant increase in activity of the occipital region (the area where MT is located) and the right posterior temporal region occurs while perceiving the MAE, providing even more evidence to support that the human version of the MAE occurs in the MT area (Kobayashi, Yoshino, Ogasawara, & Nomura, 2002; Tikhonov, Händel, Haarmeier, Lutzenberger, & Thier, 2007). Overall, there are many different experimental techniques used to examine the MAE and they all strongly implicate area MT as being involved during the MAE. However there is evidence that other cortical areas may be involved as well but these need to be further researched.

Visual Illusions in the Avian Species

In recent years, there has been an expansion of research into the perception of visual illusions in non-human species as a result of well-established studies into visual illusions in humans. Many studies have discovered that the avian species experience similar illusions as humans, allowing us to gain more knowledge about the capabilities of the avian visual system and compare them to the human visual system. The Müller-Lyer illusion is one of a number of geometric illusions explored in animals. The standard version consists of two parallel lines, one of which ends in inward pointing arrows, the other which ends with outward

pointing arrows. When observing the two lines, the one with the inward pointing arrows appears to be significantly longer than the other. The reversed version of a Müller-Lyer illusion consists of the arrowheads detached from each end of a single line and the direction of the illusion has shown to be reversed; that is, the line with outward-pointing brackets appears to be longer than that of the inward-pointing brackets (see Figure 1). Studies have found that the standard version of the Müller-Lyer illusion is experienced by many of the avian species: pigeons (Nakamura, Fujita, Ushitani, & Miyata, 2006; Nakamura, Watanabe, & Fujita, 2009a, 2009b), ring doves (Warden & Baar, 1929), domestic chickens (Winslow, 1933), grey parrots (Pepperberg, Vicinay, & Cavanagh, 2008), and budgerigars (Watanabe, Nishimoto, Fujita, & Ishida, 2014). According to results in the study by Nakamura et al. (2006), pigeons can perceive the standard Müller-Lyer illusion but not the reversed Müller-Lyer illusion which suggests the avian visual system is similar to the humans visual system but also has differences when it comes to some visual illusions.

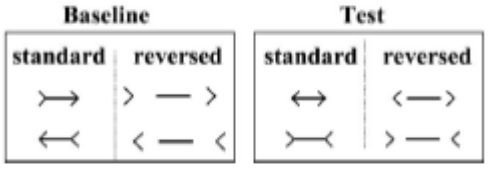

Figure 1. An illustration of a standard and reversed Müller-Lyer figure as depicted in the Nakamura et al. (2006) study. Baseline stimuli were target lines with two brackets in the same orientation (i.e. <-< or >->). Test stimuli of a standard Müller-Lyer figure shows the bottom line appears longer where as a reversed Müller-Lyer figure shows the top line appears longer.

A study conducted by Clara, Regolin, Zanforlin, and Vallortigara (2006) used filial imprinting to determine whether domestic chicks experienced stereokinetic illusions (depth-from-motion illusions). Newly hatched domestic

chicks were exposed to 2-D stereokinetic cone or 2-D stereokinetic cylinder for four hours then given free-choice to approach either a 3-D cone or 3-D cylinder. The results showed that the domestic chicks chose the 3-D stimuli that resembled the stimuli it was exposed to during imprinting indicating that domestic chicks can perceive stereokinetic illusions (Clara et al., 2006).

In the case of pigeons, two studies have addressed the Ponzo illusion. The Ponzo illusion is a geometric-optical illusion where two identical parallel lines are placed across a pair of converging lines similar to railway tracks. The parallel line closer to the top of the converging lines looks longer than the lower parallel line farther from the top. Fujita, Blough, and Blough (1991) and Fujita, Blough, and Blough (1993) demonstrated that pigeons could also perceive the Ponzo illusion by training the pigeons to discriminate between long and short lines without convergent lines, then presented identical parallel lines with varying degrees of converging lines. The results showed the pigeons pecked the "longer" key indicative of being sensitive to the Ponzo illusion.

Amodal completion is the visual ability to complete partially occluded objects and physiological investigations suggest it occurs in the early stages of visual processing (Corballis, Fendrich, Shapley, & Gazzaniga, 1999; Giersch, Humphreys, Boucart, & Kovács, 2000; Murray, Kersten, Olshausen, Schrater, & Woods, 2002). Several studies provide evidence strongly suggesting that domestic chicks have the same ability with respect to amodal completion as humans (Lea, Slater, & Ryan, 1996; Rugani, Regolin, & Vallortigara, 2008). These studies often use the filial imprinting experimental design to test for amodal completion in domestic chicks. In 1995, Regolin and Vallortigara (1995) housed individual newborn chicks with a red cardboard triangle, to which they rapidly imprinted. On

the third day of life, the chicks were presented with pairs of objects composed of either isolated fragments or occluded parts of the imprinting stimulus. Chicks consistently chose to associate with complete or with partly occluded versions of the imprinting object rather than with separate fragments of it. These results indicate that newborn chicks can experience amodal completion. Most prior research conducted on amodal completion in pigeons has failed to show that they can perceive this phenomenon. However, Nagasaka (2008) have recently provided some new evidence to suggest pigeons may perceive amodal completion when the experimental stimuli is moving, instead of the static stimuli used in previous studies which failed to show amodal completion. It is interesting to note that even though pigeons and chickens both belong to the avian species they appear to have differences in their responses to certain visual stimuli.

Rosa Salva, Rugani, Cavazzana, Regolin, and Vallortigara (2013) investigated whether four-day-old domestic chicks could perceive the Ebbinghaus illusion. Nakamura, Watanabe, and Fujita (2008) had previously found that pigeons failed to perceive this illusion. In the Ebbinghaus illusion, a central circle surrounded by small circles appears bigger than an identical central circle that is surrounded by large circles. The study used an observational-learning paradigm to test their theory. At the beginning of the experiment, half the chicks could only find food by a big circle and the other half by a small circle for two days to establish an association between foods with a particular sized circle. On the fourth day, the chicks were placed within an arena with two screens displaying the Ebbinghaus illusory stimuli. Which screen the chicks approached in search for food was recorded as their preference. Results showed the chicks reinforced on a bigger circle preferred the illusory stimuli with smaller outer circles (as the central

circle appears perceptually bigger) and chicks reinforced on a smaller circle preferred the illusory stimuli with bigger outer circles (as the central circle appears perceptually smaller). Both experimental groups demonstrated that domestic chicks could perceive the Ebbinhaus illusion in a similar fashion to humans. Rosa Salva et al. (2013) suggest that chicks may have the same neural substrate that enables visual global perception or visual grouping mechanisms as humans.

Recent evidence also indicates that the avian species can perceive the Zöller illusion, in which parallel lines look non-parallel due to series of short crosshatches superimposed on the lines. Watanabe, Nakamura, and Fujita (2011) trained six pigeons to peck at the narrower or wider of the two gaps at the end of a pair of non-parallel target lines. After adapting the subjects to target lines with randomly oriented crosshatches (which result in no illusion), they tested the pigeons' responses on randomly inserted probe trials, in which crosshatches that should induce the standard Zöllner-like illusion for humans replaced the random-oriented ones. The results suggested that pigeons do perceive an illusion from Zöllner figures, but in the direction opposite to that of humans. Later in 2013, Watanabe, Nakamura, and Fujita utilised the same experimental procedure but tested bantams as subjects and found that bantams, like pigeons, perceived the same reversed Zöller illusion (Watanabe, Nakamura, & Fujita, 2013).

From the research into the perception of illusions by avian species, it has been demonstrated that birds can perceive many illusions similar to the human species but the visual neural pathway thought to produce these illusions are still unclear. In humans, neuroimaging of the brain while undergoing illusionary experience has been used to map the locus of activity associated with illusions,

but the avian species studies have primarily used behavioural paradigms and filial imprinting paradigms to investigate whether avian species experience visual illusions. Researchers have hypothesised that the illusions occurs in the midbrain of the avian brain (Rosa Salva et al., 2013) or in the motion-sensitive neurons in the optic tectum of birds (Clara et al., 2006) – depending on the type of illusion. More research needs to be completed to further understand the physiological activity underlying the illusionary experiences of the avian species.

Motion Aftereffect in the Avian Species

At present, a study by Xiao and Gunturkun (2008) is the only experiment involving avian species known to have demonstrated the possibility that pigeons can perceive the motion aftereffect. Xiao and Gunturkun (2008) used a behavioural paradigm and examined the choice behaviour of pigeons by training them first to discriminate grating patterns either moving upward, downward or static (still). The pigeons peck different coloured keys associated with a particular grating pattern (moving up, down or static). They were then exposed to a moving grating pattern for a length of time before switching to a static pattern. If pigeons pecked a moving grating pattern in the opposite direction of the moving pattern it was exposed to prior to the static pattern, then that strongly suggested that the pigeon perceived a motion after effect.

Xiao and Gunturkun (2008) conducted two successive experiments in their study where their first experiment produced average response ratios for three possible outcomes of 31.9% illusion, 44.8% no illusion, and 23.3% static. That is, the pigeons perceived the MAE 31.9% of the test trials. They believed the causation for their weak results were due to two reasons; (1) the brief exposure to

the static pattern (1s) at the end of the adaptation phase, and (2) the lack of instructing the pigeons to respond to the static pattern at the end of the adaptation phase. They suggested therefore that the pigeons responded equally to the adapting visual stimulus and the illusion-eliciting stimulus.

To rectify these problem, Xiao and Gunturkun (2008) conducted a second experiment which increased the length of static pattern display to 3s, and developed a method that specifically trained the pigeons to make their choices according to the last perceived movement on the central display key. This additional training method consisted of displaying two different visual stimuli that were successively shown on the central key. The pigeons had to respond to the second displayed stimulus to gain access food. If the subjects pecked an incorrect key, all lights were switched off for 10s with no food delivery. The pigeons needed an average of two months to learn this task and the training paid off as the MAE tests results showed the pigeons' average response ratios for the three choices of grating pattern were 60.4% for illusion, 32.8% for no illusion, and 6.8% for static. Xiao and Gunturkun (2008) produced greater illusion result in their second experiment than their first experiment, and thus they concluded that it is highly likely that pigeons can see the MAE.

After their reports indicating the possibility that pigeons can perceive the MAE, Xiao and Gunturkun (2008) proposed that the neural mechanism underlying the MAE for pigeons originates from the avian nucleus lentiformis mesencecephali (nLM) of the pretectum which may be homogolous to the nucleus of the optic tract of mammals. This proposition was devised from the data collected by Niu, Xiao, Liu, Wu, and Wang (2006) who recorded the activity of the nLM - the motion-sensitive pretectal neurons in pigeons, and looked for post-

responses to cessation of prolonged stimulus motion. Pigeons were placed under anaesthesia while confined in a stereotaxic apparatus where they were presented with the visual moving stimuli of a grating pattern generated by a computer screen for a series of durations (3-180s). Results of the Niu et al. (2006) study showed evoked excitatory responses in the preferred direction and inhibitory after-responses to cessation of prolonged motion. According to Niu et al. (2006), this is an indication that pigeons can perceive the MAE and suggests that visual illusions in birds occur at the earliest stage of central information processing and implying that the visual forebrain in birds or cortex in mammals may not be a prerequisite for processing visual motion illusions.

To date, research into the motion aftereffect of avian species consists of only two studies (Niu et al., 2006; Xiao & Gunturkun, 2008), utilising two quite different experimental techniques. Further evaluation of this illusory phenomenon in avian species is needed to establish concrete evidence that the avian species can perceive this illusion homologous to human species. Our current experiment seeks to replicate the fundamental behaviour paradigm procedure and results conducted by Xiao and Gunturkun (2008) but using domestic chickens instead of pigeons as well as utilising new technology such as touch screens to generate the moving grating patterns and pecking side buttons. Other changes were also made to overcome limitations that we believe existed in the Xiao and Gunturkun (2008) experiment. These modifications will be detailed in the following experiment section of the study and an analysis of these modifications will be examined in the discussion section of this thesis.

EXPERIMENT INTRODUCTION

Thesis Research Question: Do Chickens Perceive the MAE?

The objective of our current experiment is to test whether domestic chickens can perceive a MAE using a modification of the procedure used in the second experiment by Xiao and Gunturkun (2008).

Subjects: For our current experiment we chose to use domestic chickens as subjects instead of pigeons.

Apparatus: Technology has advanced rapidly since Xiao and Gunturkun (2008) conducted their study. While the use of mechanical keys in an animal experiment chamber is still commonly used, for greater flexibility we utilised a touch screen monitor, to project our visual stimuli and record peck locations. This is unlike Xiao and Gunturkun (2008) who used a relatively small (5cm x 5 cm) display for stimuli and mechanical keys around the stimuli for recording responses. This allows the touch screen to record the pecks made onto the visual stimuli and pecks made elsewhere on the touch screen.

Method: The basic procedure with studying the MAE in birds is to show them a moving stimulus (the adapting or inducing stimulus) for a reasonable period of time and then to present them with a static pattern (illusion eliciting stimulus) and to test if they see the static pattern. One obstacle that posed a challenge in the study by Xiao and Gunturkun (2008) was the difficult task of training the pigeons to report on what they perceived during the presentation of the static pattern – the illusion-eliciting stimulus, not the adapting visual stimulus. The data from their first experiment found the pigeons' choice responses of perceiving "illusion" and "no illusion" (reporting the adapting stimulus) was the

same. Xiao proposed two reasons for this occurrence; they were either seeing only a weak movement illusion or that the pigeons were not specifically trained to make their choices according to the illusion-eliciting stimulus (the static pattern) at the end of the adaptation phase. To counteract this perceived problem, Xiao built-in an additional step into the training stage of their second experiment where the pigeons were instructed to make their choices according to the last perceived movement on display.

This difference in the procedure produced a major change where the average "illusion" choice significantly increased from 31.9% in the first experiment to 60.4% in the second experiment. However, in our current experiment we are proposing an entirely new technique to eliminate this problem by introducing a colour change to the background of the central key when the illusion-eliciting stimulus is displayed (background cue). This modification was implemented instead of training the hens to respond to the last visual stimulus displayed on the central key because it took Xiao and Gunturkun (2008) two months to train the pigeons to successfully master the task and we endeavoured to eliminate this particular process, in an attempt to speed up the training procedure (potentially a saving of two months). The importance of the background colour change from black to grey is that it acts as a signal for the subjects to respond according to the visual stimulus shown on the grey background as opposed to the former adapting visual stimulus on the black background. This step was placed at the onset of training where the background turned grey during the response phase. Then later in the illusion test trials, the background turns grey at onset of the illusion-eliciting phase and remains grey in the response phase.

Another modification we made in our current experiment that differed from the original procedure of Xiao and Gunturkun (2008) was to omit the requirement of making 30 pecks onto the central key during the 30 seconds of the adaptation phase in order to activate the response keys in a trial. Xiao and Gunturkun (2008) put this technique in place to guarantee the pigeon's retina had sufficient exposure time to the adapting stimulus in order to produce a MAE. Prior experience with chickens suggested that this training criterion would take a very long time to achieve. Instead we decided to rely on the bird's normal tendency to peck moving stimuli, on the assumption that this would be sufficient to induce the illusion. For that reason, we attempted to speed up training by simply monitoring the pecking performance of our chickens throughout the adaptation phase of each trial during the training sessions and required that they pecked the adapting stimulus twice at the end of a 3s display, before response keys could be activated.

The final modification we implemented to improve upon the method in the Xiao and Gunturkun (2008) study was to systematically simplify the discrimination task training into further smaller steps to acquire faster learning of the correspondence between the visual stimuli and the colour/location of the three response keys. When the chickens were presented with the conditional discrimination training, they were firstly given independent training sessions of each particular visual stimulus, paired firstly with its corresponding key, followed by pairing with an alternative response key, and finally all three response keys. Once the chickens mastered the task of associating one particular visual stimuli with its corresponding response key, they moved onto the next visual stimulus until all three were individually trained, then sessions of randomised trials of all three visual stimuli were finally introduced (refer to Table 1). In comparison, Xiao

and Gunturkun (2008) did not individually train each visual stimulus before randomising trials of the three visual stimuli, which took the pigeons at least two weeks to successfully master. With our modification we sought to reduce the length of time the chickens took to learn the discrimination in the training phase of our current experiment.

With the modifications we made to the original procedure of Xiao and Gunturkun (2008), the possible outcomes of our current experiment is illustrated in the form of hypothetical graphs (Figure 2) to demonstrate hypothetical results that indicate chickens can perceive the motion aftereffect illusion (graph A), or that chickens cannot perceive the MAE (graph B). Graph A of Figure 2 displays the two types of illusion test trials (downward or upward) and the control trial (static) which we will implement in our current experiment. If chickens can perceive the MAE, then in a downward trial there should be a high level of responding to the upward response key, where as in an upward trial there should mainly be a high level of responding to the downward response key because the illusory motion perceived should be in the opposite direction of the former moving adapting stimulus. In a static trial it is expected that the chickens will choose the static response key because all they can perceive throughout the trial is a still image. If the chickens do not perceive an MAE, then results would be expected to show responding to all choice keys with no significant difference between them, as illustrated in graph B of Figure 2.

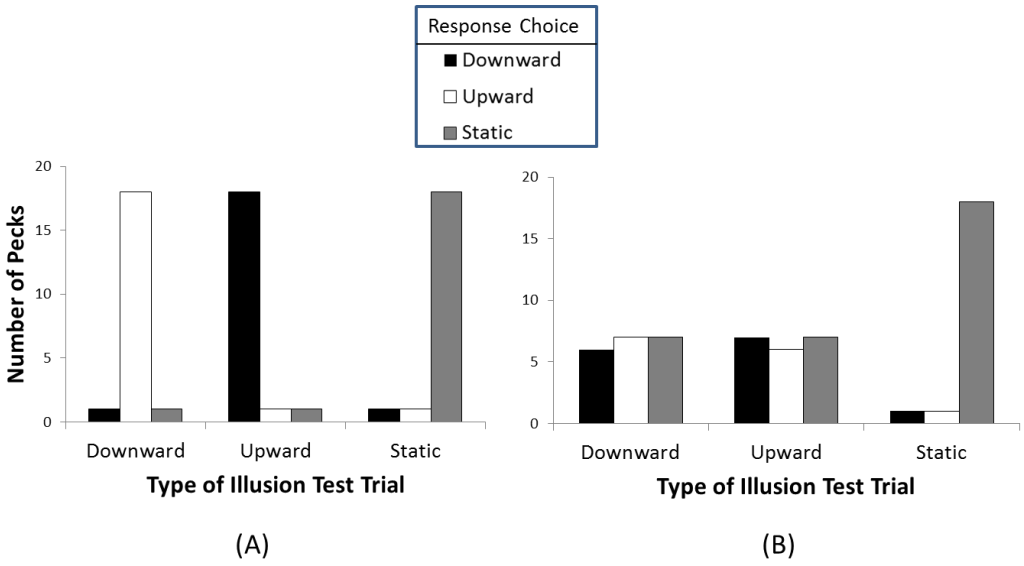

Figure 2. Hypothetical graphs of results where (A) represents illusion perceived and (B) indicates no illusion perceived.

EXPERIMENT

METHOD

Subjects

Subjects were six domestic chickens (three hens and three roosters) (*Gallus gallus domesticus*) numbered 7.1-7.6. All chickens had previous training in pecking a mechanical key to gain wheat from a magazine and participated in no experiments prior to this experiment.

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 always available in their cage 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 were conducted in an operant chamber constructed of plywood board measuring 61cm x 46cm x 56cm. A central magazine delivered 2 seconds access to wheat through an aperture measuring 90mm x 125mm, situated 10cm from the floor of the chamber. A white LED inside the magazine aperture was lit for the duration of wheat access (refer to Figure 3 & Figure 4).

A Dell screen (300mm x 220mm, model number E176FPb) was installed above the magazine aperture. Pecks to the screen were recorded as x, y co-ordinates. A Dell computer (Optiplex model GX260) running a custom-made application controlled the experimental programme. Data recording was event-driven, and session data were also recorded manually.

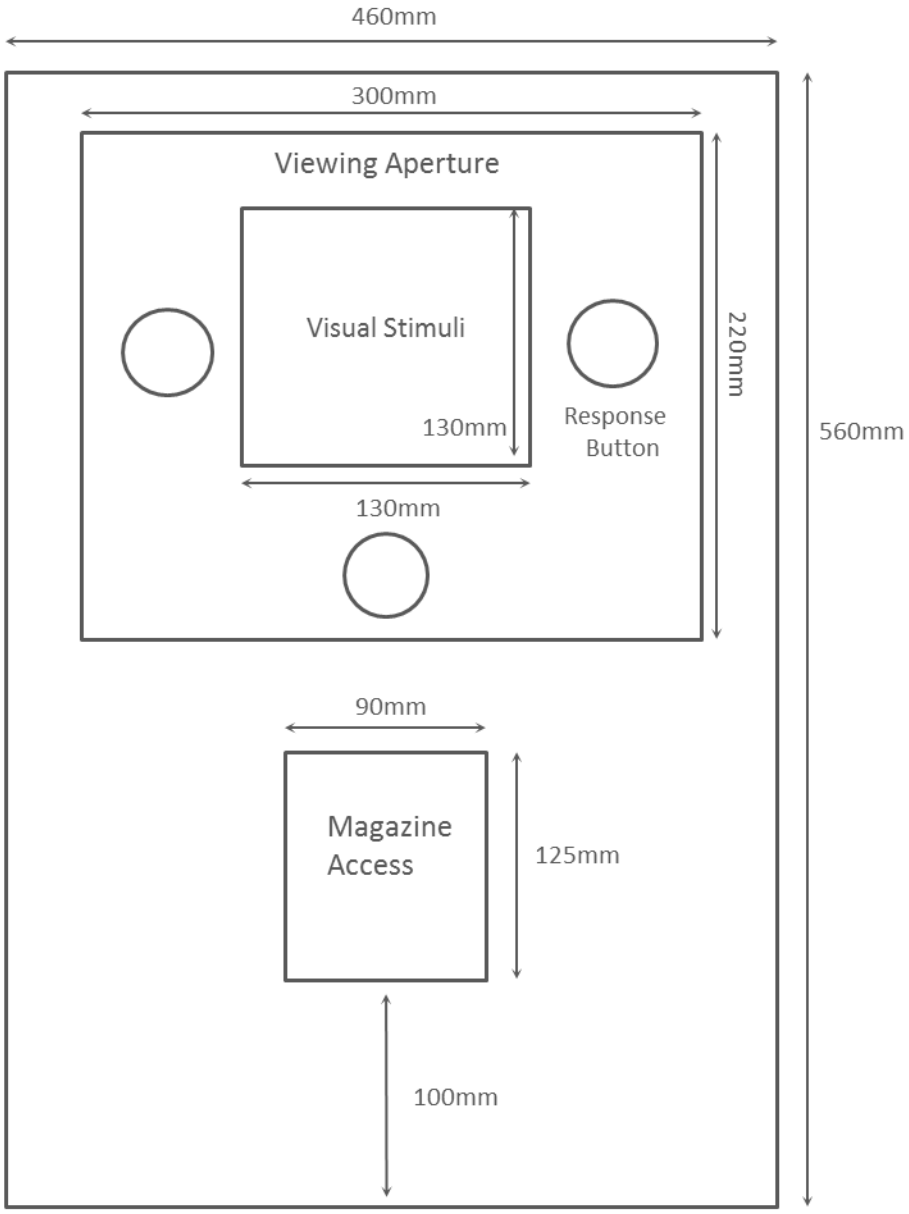

Figure 3. Operant chamber response panel and food magazine.

Figure 4. Operant chamber of our experiment installed with a touch screen monitor which displays visual stimuli on a black background in adaptation phase and grey background in response phase.

Visual Stimuli

The visual stimuli consisted of sinewave grating patterns presented in a square (13cm x 13cm) aperture (see Figure 4 & 3). At a nominal distance of 10 cm from the screen, the stimuli subtended an angle of 66 degrees x 66 degrees. At this distance the spatial frequency of the gratings was 0.12 cycles/deg and a speed of the two moving gratings was 8 deg/s. It had two moving directions: downward or upward and stationery grating pattern was used as a control condition and to generate the illusion at the end of an illusion test trial. The on screen response buttons consisted of coloured patches with an intensity profile based on a 2-D Gaussian profile with a standard deviation = 40 pixels (see Figure 7). For the response phase of a trial, the background for the patches was a neutral grey (image intensity value = 127) which corresponded to a luminance level of 14.5 cd/m^2 (measured using a Minolta-CS100 photometer). The three different colours for the buttons (red, green & yellow) were made by adding or subtracting a value of 128 to/from the appropriate RGB components of the image. For the adaptation phase, the background intensity was 0 (black) (see Figure 6) and a value of 255 was added/subtracted from the relevant RGB values for the buttons.

Figure 5. An illustration of the static grating pattern as a visual stimuli (not in real proportion to the actual experiment).

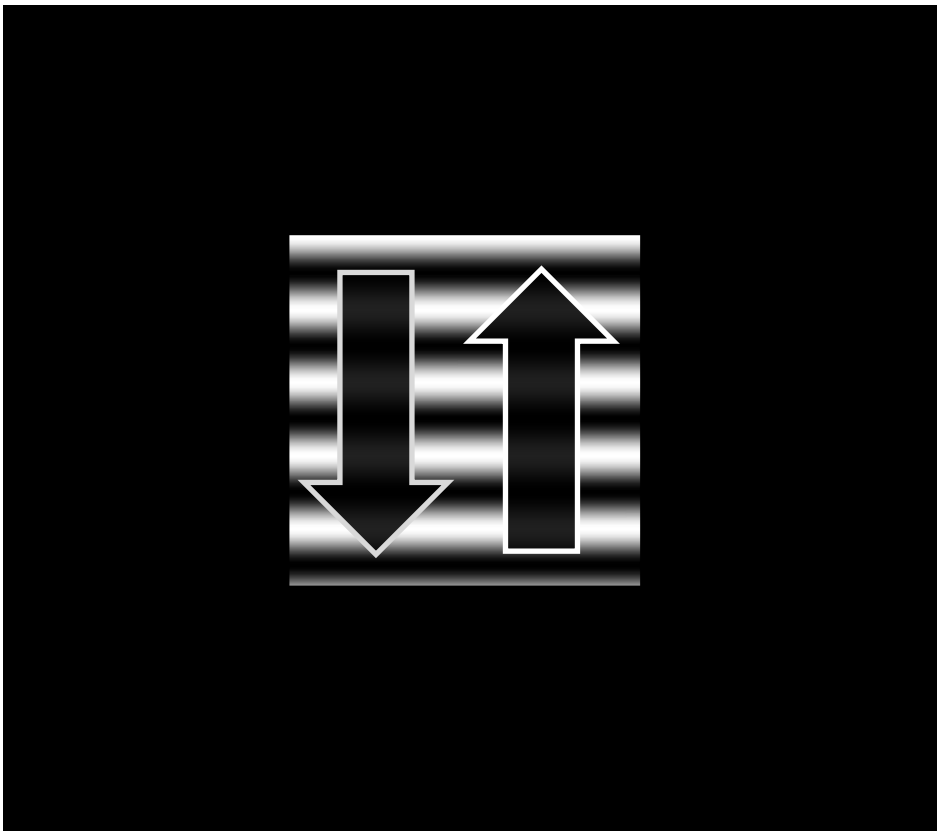

Figure 6. An illustration of the moving visual stimuli either in downwards direction or upwards direction as indicated by the arrows (not in real proportion to that of the actual experiment).

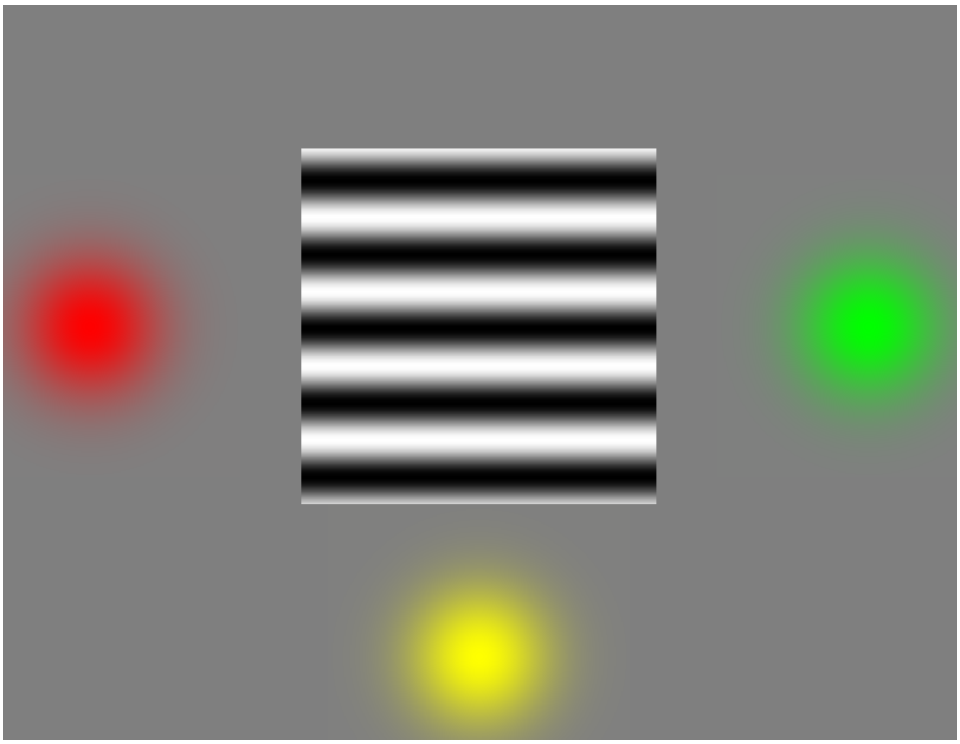

Figure 7. An illustration of the position and colours of response buttons/keys (red, yellow, green) in the shape of Gaussian blobs that surround the display stimuli (not in real proportion of the actual experiment).

Training Procedure

The chickens were first placed into the operant chamber and trained to peck at a grating pattern visual stimulus displayed on the centre of the touch screen using hand-shaping procedure of successive approximation (Foster, Miller & Fleming, 1978). The chickens typically took one 20 minute session to reliably peck the centre of the grating pattern and obtain food from the magazine.

The second step of training required learning to associate individually the three different visual stimuli with its corresponding coloured key: the downward moving grating pattern corresponding to the red key; upward moving grating pattern corresponding to the green key; and the static grating pattern corresponding to the yellow key. Each subject was given one training session a day that consisted of trials with only one particular visual stimulus. A trial began with the visual stimulus displayed in the centre of the screen with a black background for 5s. In the response phase, the background turns grey and the subjects had to peck the visual stimulus once to activate a lit response key. The importance of the grey background is that it acts as a signal for the subjects to respond to the stimulus shown on the grey background as opposed to the former stimulus on the black background. This is designed so that later in the illusion test trials, subjects are trained to report what they perceive during illusion-eliciting phase (grey background), not the adaptation phase (black background). Subjects needed to peck the lit key once within 30s to gain access to the food magazine for 2s. The grating pattern shown was left on during the response phase. 5s inter-trial interval (ITI) then begins with the screen completely black. If subjects did not peck the correct key within 30s, 10s of time-out without lights began, followed by

5s ITI. When the subjects responded correctly 80% of the last 20 trials, they moved onto the next visual stimuli with its corresponding coloured response key. Once all three visual stimuli lead to correct responses on 80% of occasions, the next training phase began. The order of training each grating pattern with its corresponding response key was presented the same for each bird and the schedule of this procedure is presented in Table 1.

The third step of training consisted of a session with randomised trials of all three visual stimuli (downward, upward, or static), where one peck on the visual stimulus activated all three response keys and one peck on the correct key that corresponded to the visual stimulus shown was reinforced by access to the food magazine for 2s. An incorrect peck of a response key led to 10s time out, followed by 5s ITI. Table 1 displays the whole procedure of steps two and three of training and Figure 8 illustrates the sequence of events in a training trial described above.

Once the chickens reached 80% correct for three consecutive days, the adaptation phase of the trials were increased from 5s to 10s, 20s, and lastly to 30s. In this final step in training, the chickens needed to remain above the 80% correct threshold for two consecutive sessions before increasing the time length of the adaptation phase. A timer was set for the 30s adaptation phase where the first peck made onto the visual grating pattern began the adaptation phase. This insured that the chicken was looking at the grating pattern from the onset of the 30s adaptation phase. During the entire training procedure, a session ended when either 40 reinforcements had been given or when the total session time reached to 40 minutes.

Table 1.

The Presented Training Procedure in the Experiment

TRAINING CONDITION	TASK
1	*Learn red key corresponds to DOWNWARD grating pattern* 1. Red key alone. 2. Pair red key with yellow key 3. Pair red key with green key 4. Pair red key with alternating yellow/green key 5. Pair red key with yellow and green key
2	*Learn green key corresponds to UPWARD grating pattern* 1. Green key alone 2. Pair green key with red key 3. Pair green key with yellow key 4. Pair green key with alternating red/yellow key 5. Pair green key with red and yellow key
3	*Learn yellow key corresponds to STATIC grating pattern* 1. Yellow key alone 2. Pair yellow key with red key 3. Pair yellow key with green key 4. Pair yellow key with alternating red/green key 5. Pair yellow key with red and green key
4	*Randomised trials of the 3 grating patterns* 1. Randomly display 1 of 3 grating patterns and all 3 response keys light up, correct peck is reinforced.

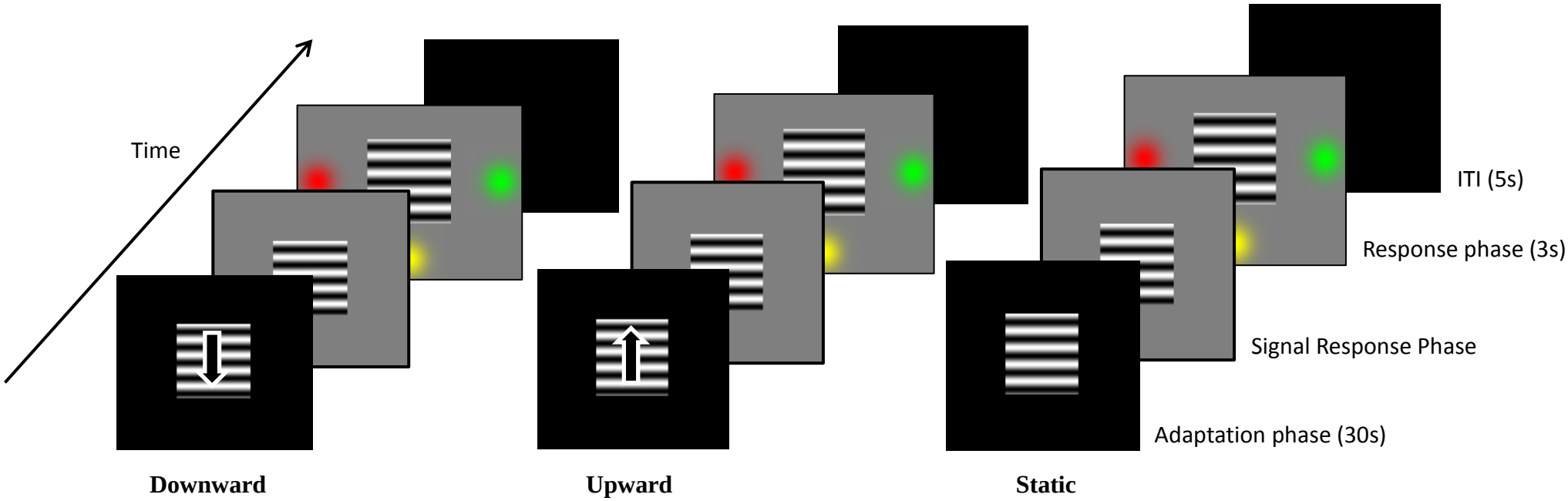

Figure 8. The experimental setup of a training trial in our experiment. Beginning with a 30s display of a grating pattern either moving downwards, upwards or static is followed by a change in the background colour to grey to signal response phase. 2 pecks onto the grating pattern is then needed to activate the three side keys. A peck on a side key will generate reward or punishment then followed by 5s Inter-Trial Interval.

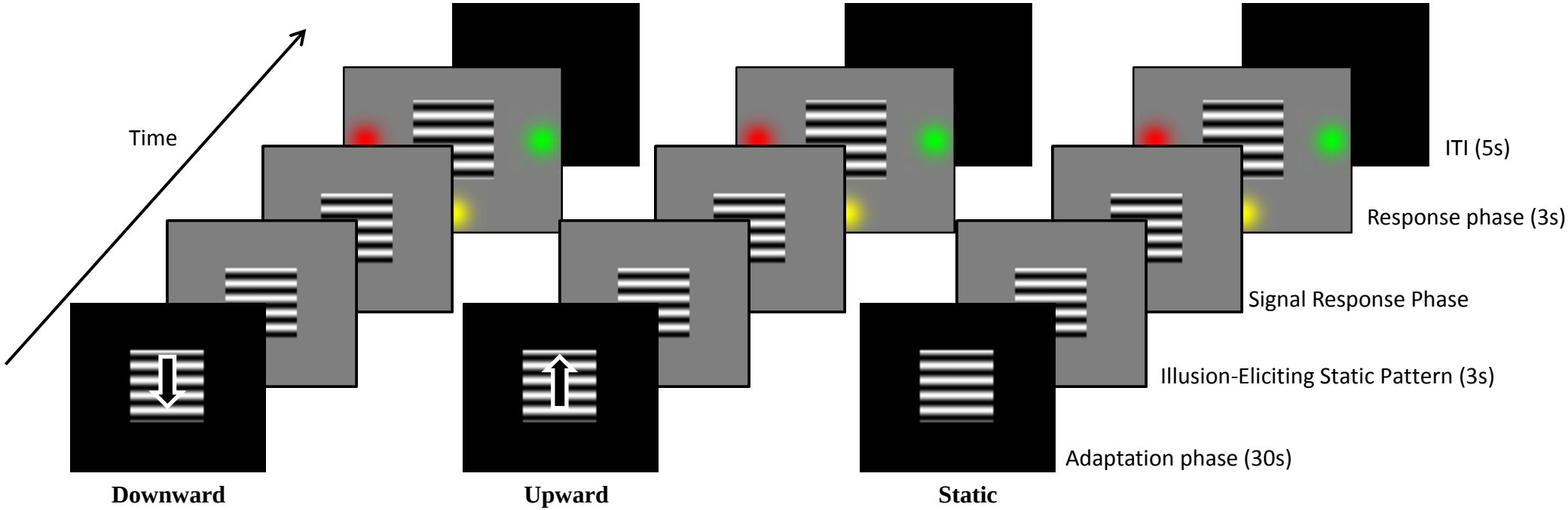

Figure 9. The experimental setup of an illusion test trial in our experiment. A test trial is the same as a training trial except for the insertion of a 3s illusion-inducing static pattern after the adaptation phase.

Experiment Procedure

Test sessions were run using the same subjects and apparatus. In the test sessions, the birds were presented with the same randomised trials of the three different visual stimuli with feedback as in the last training phase (condition 4) of the training procedure. The only difference was that illusion test trials were placed randomly in 1 out of every 10 block of trials without feedback. Illusion test trials start with the same 30s adaptation phase as in the normal trials but at the end of the 30s adaptation phase, an illusion-eliciting phase is added where a 3s static grating pattern (illusion-inducing static pattern) is shown with the background switched to grey – to test for the MAE illusion. After the 3s illusion-inducing static pattern, the chickens needed to peck the static grating twice to generate the three response keys and then the peck of a response key was recorded without feedback in terms of reward or punishment, followed by 5s ITI (refer to Figure 9). Illusion test trials were only effective and counted as part of the results if a choice of a key was made; if the chickens did not peck within the 3s response phase, the trial was omitted from the data. Twenty effective probe trials were collected for each grating pattern, and in total 60 effective probe trials were accumulated.

RESULTS

Training Results

To test for the motion aftereffect illusion in chickens, the subjects first needed to be trained to differentiate between an upward-moving, downward-moving and static (still) grating pattern (see Figure 11). All subjects in the experiment were successfully trained to distinguish between the three different types of grating patterns where the criterion threshold was 80% correct in a session, for two consecutive sessions. The animals required 73 to 88 sessions to reach criterion for the final training condition (Condition 4) of discriminating between different movement grating patterns (M= 82.33, SD= 5.01, n = 6).

Figure 10 shows the percent correct of each subject per session during the final training condition where, on each trial, they were initially presented with 5s of the grating pattern during the adaptation phase. Once criterion was reached, they moved gradually to new conditions that included an increase in the length of the adaptation phase until a 30s adaptation phase produced performance above the criterion threshold. If the criterion was reached for this final 30s condition they progressed onto the test phase. The dotted line in Figure 8 refers to the 80% correct threshold needed to advance to the next training condition. The subjects all started with low accuracy on performing the task during the 5s adaptation phase, but once they eventually reached 80% criterion, they continued to maintain close to or above 80% correct in the subsequent adaptation phase trials. This indicates that the chickens were able to perform the basic task of differentiating between the two directions of movement and the static grating.

Subject 7.3 showed a low level of responding to the green key during upward moving trials in the 20s adaptation phase thus had two training sessions of trials which only consisted of upward trials (Condition 2 of training) to increase responding on the green key as marked as “C2” in Figure 10. After subject 7.3 reached 100% correct in two consecutive session of condition 2 training, it continued back on condition 4 training and gradually met criterion to progress onto testing.

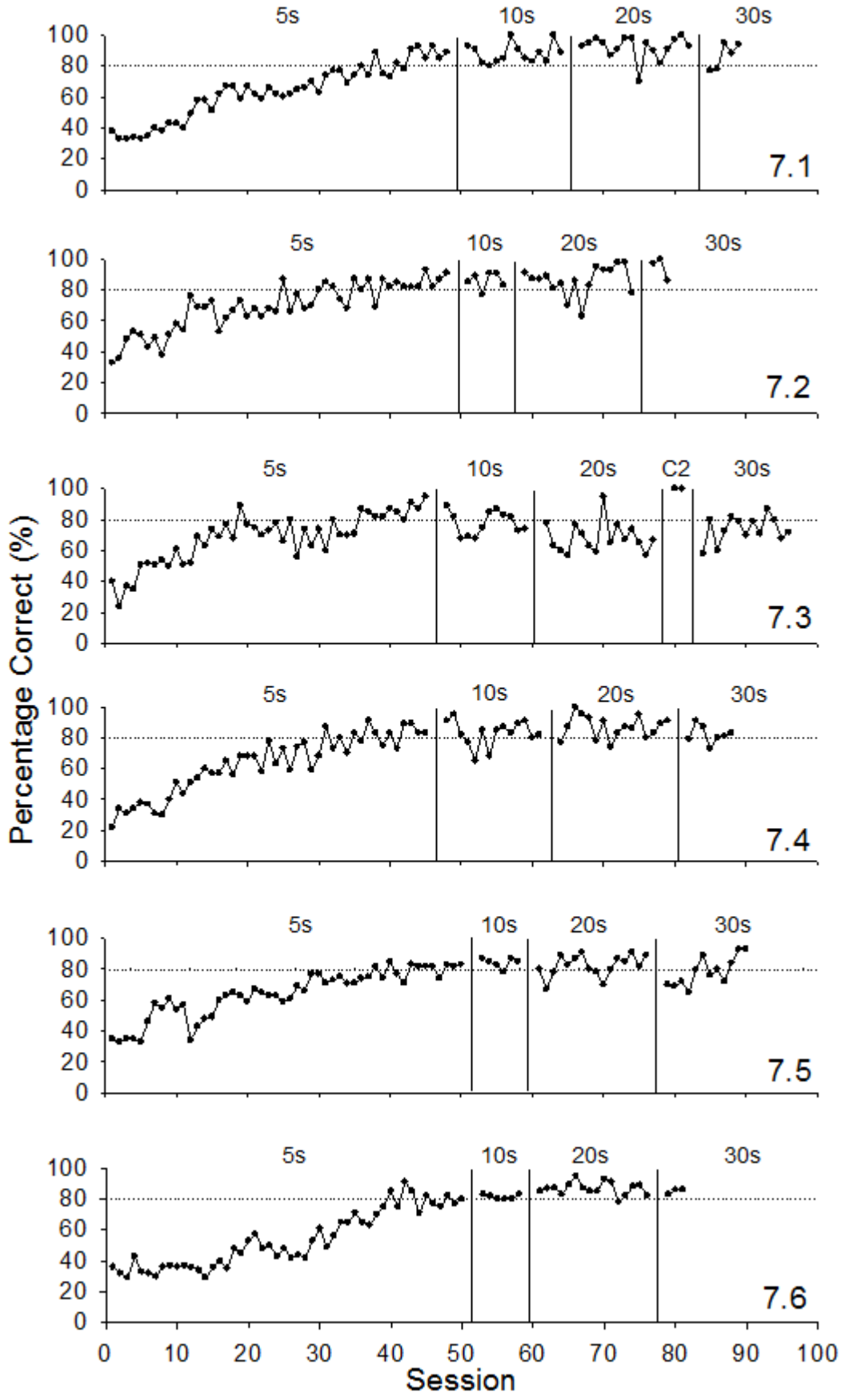

Figure 10. Percentage corrects per subject during training condition 4 over sessions.

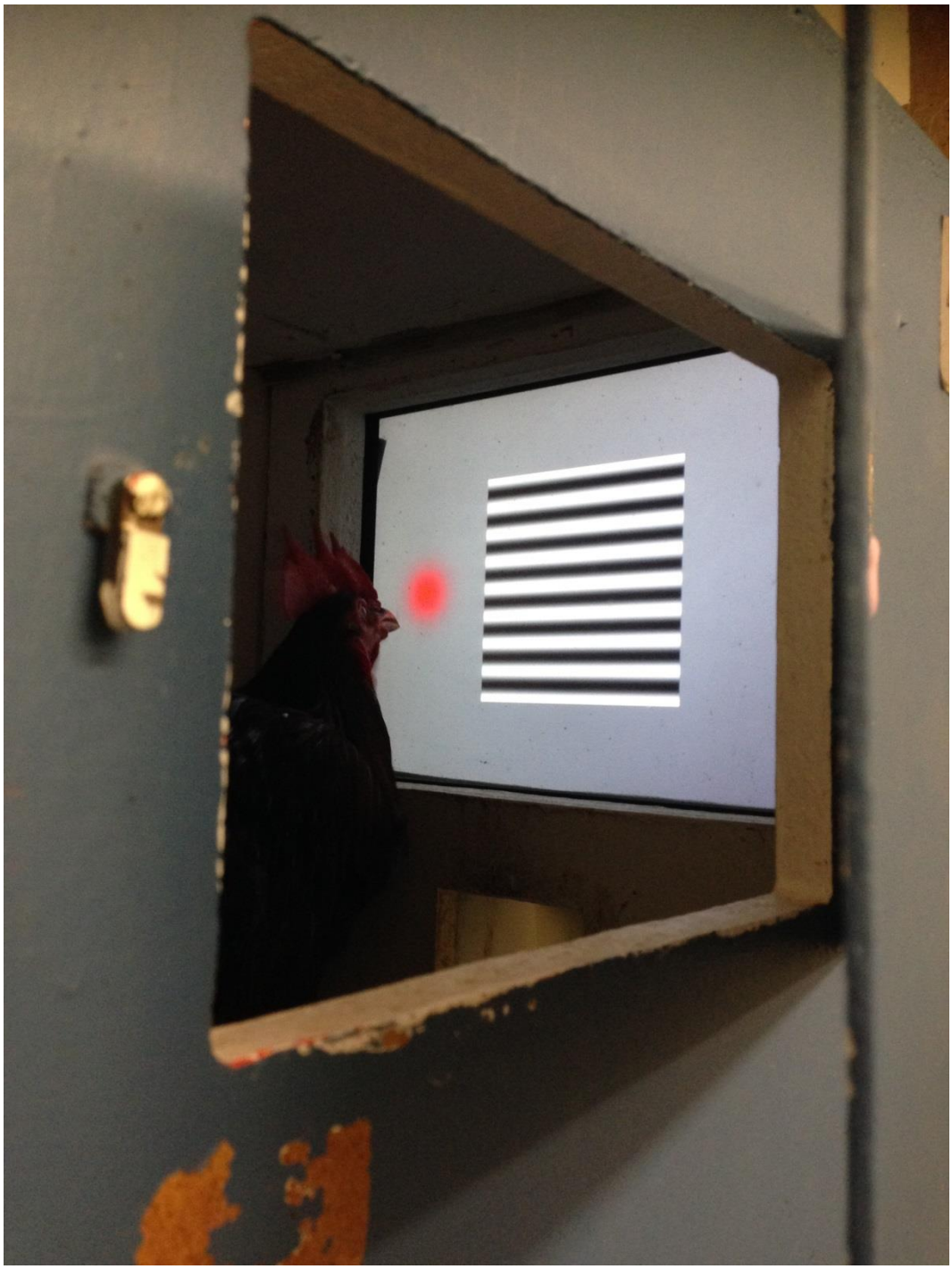

Figure 11. A subject of our experiment undertaking training for the discrimination task prior to illusion testing.

Test Trials Results

The chickens were given illusion test trials to test for the MAE that began by showing the same 30s adaptation phase as in the normal training trials but at the end of the 30s adaptation phase, they were presented a 3s static grating pattern (test grating). After the 3s static pattern is presented, the chickens needed to peck the static grating twice to generate the three response keys to light up and the peck of a response key chosen was then recorded. Subjects 7.3, 7.4, and 7.5 successfully completed 60 effective illusion test trials, 20 test trials for each grating pattern and the average number of sessions to collect the test trials was 14.33 sessions (S.D= 1.155, n = 3). Subjects 7.2 and 7.6 did not reach the criteria of 60 effective illusion test trials due to illness and subject 7.1 experienced technical issues during its test sessions therefore their test data were omitted from statistical analysis. However, the collected illusion test trial data from these animals are displayed in Figure 12 to give an overall view of group performance in the illusion test trials.

Figure 12 & 13 plots the trial type along the X axis with the number of peck responses on the Y axis for each type of response (see figure legend). As shown in Figure 2 a MAE is represented by an opposite key being selected to the trial type e.g. a downward moving grating trial should result in more pecks to the upward key. For upward and downward trial types, there should be very little pecks to the static key.

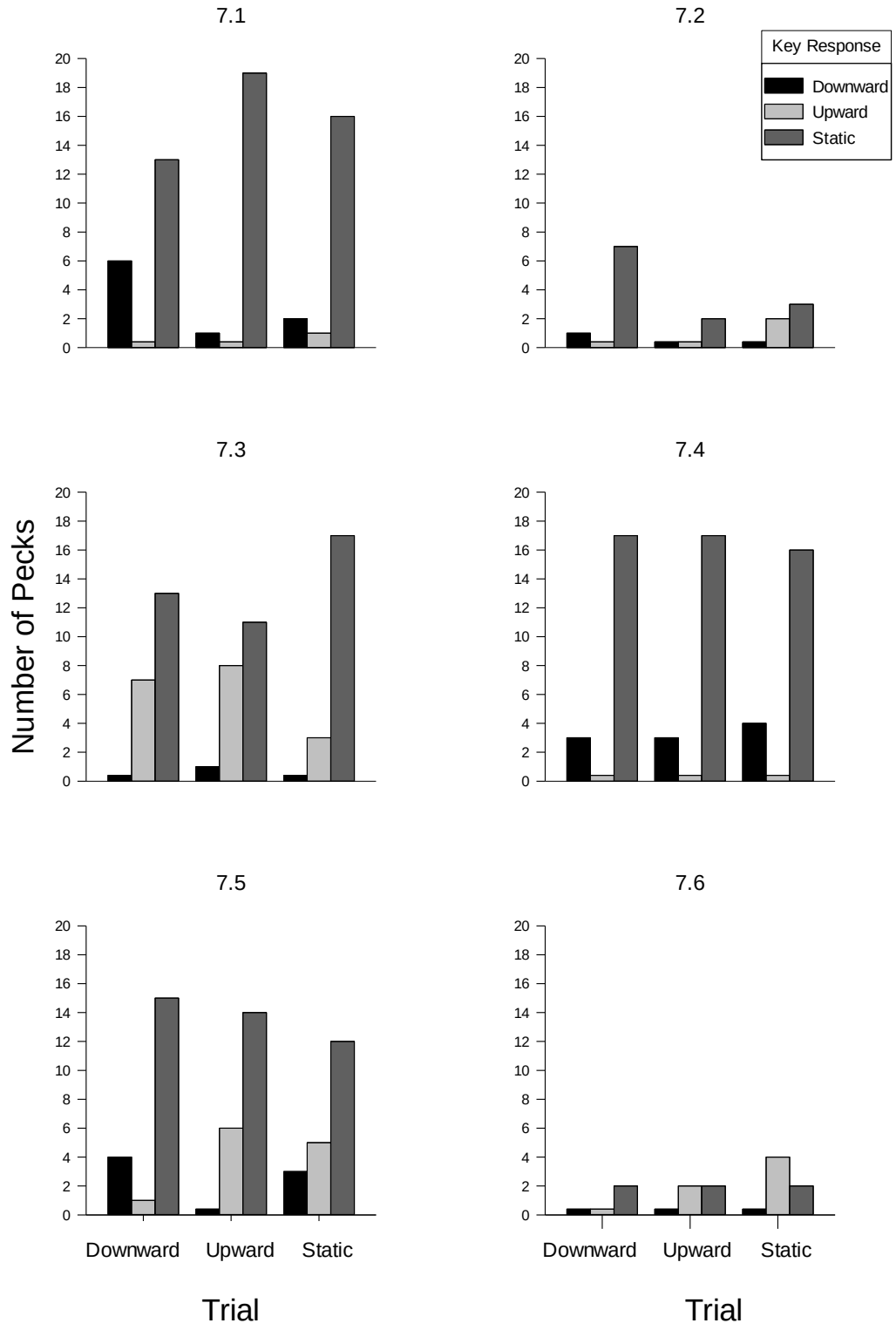

Figure 12. Results of illusion test trials of all subjects per movement type (downward, upward, static) illusion test trial.0 values were set to 0.4 on the graphs to show location of the bars.

A one-way analysis of variance was conducted to evaluate the null hypothesis that in a downward illusion test trial, there is no difference in the level of response pecks for each response key. The independent variable was the choice of response keys, "Downward", "Upward", or "Static". The ANOVA was significant ($F(2,8) = 20.69$, $p=.002$, $n= 3$) thus there is significant evidence to reject the null hypothesis and conclude there is significant difference between the level of response pecks of the response keys. Post hoc comparisons to evaluate pairwise differences between the group means revealed that there was a significant difference between the pairwise means level of response pecks of "Static" and "Downward" keys, and a significant difference between the pairwise mean of number of response pecks of "Static" and "Upward" keys. There were no significant differences between the pairwise means of "Downward" and "Upward" keys. Thus we can conclude that the level of pecking of "Static" choice of response key was significantly higher than the pecking of the other two keys.

A one-way analysis of variance was conducted to evaluate the null hypothesis that in an upward illusion test trial, there is no difference in the level of response pecks for each response key. The independent variable was once again the choice of response keys ("Downward", "Upward", or "Static"). The ANOVA was significant ($F(2,8) = 13.535$, $p=.006$, $n= 3$) thus there is significant evidence to reject the null hypothesis and conclude there is significant difference between the level of response pecks of the response keys. Post hoc comparisons to evaluate pairwise differences between the group means revealed that there was a significant difference between the pairwise means level of response pecks of the "Static" and "Upward" keys, and a significant difference between the pairwise mean of number of response pecks of "Static" and "Downward" keys. There were

no significant differences between the pairwise means of "Downward" and "Upward" keys. Thus we can conclude that the level of pecking of "Static" choice of key after viewing the inducing stimulus was significantly higher than the pecking of the other two keys that indicated upwards or downwards motion.

A one-way analysis of variance was conducted to evaluate the null hypothesis that in a static illusion test trial, there is no difference in the level of response pecks for each key. The independent variable was the choice of response keys ("Downward", "Upward", or "Static"). The ANOVA was significant ($F(2,8) = 26.547$, $p=.001$, $n= 3$) thus there is significant evidence to reject the null hypothesis and conclude there is significant difference between the level of response pecks of the response keys. Post hoc comparisons to evaluate pairwise differences between the group means revealed that there was a significant difference between the pairwise means level of response pecks of "Static" and "Downward" keys, and a significant difference between the pairwise mean of number of response pecks of "Static" and "Upward" keys. There were no significant differences between the pairwise means of "Downward" and "Upward" keys. Thus we can conclude that the level of pecking of "Static" choice of key was significantly higher than the pecking of the other two keys.

These results indicate that in all three contingencies of illusion test trials, the animals opted significantly more for the static pattern, suggesting they did not perceive a motion aftereffect (see Figure 13). The result of choosing significantly more of the static pattern key compared to the other keys in the static illusions test trials was expected because throughout the entire trial, only a static pattern was visible the trials (static test trials acted as a control group in this experiment). However, for the “Upward” and “Downward” test trials, the hens reported

perceiving the static grating significantly more than the moving gratings. This indicates they were reporting the illusion-eliciting static pattern that was shown during illusion-eliciting phase as static – in its true static state, and did not perceived the MAE.

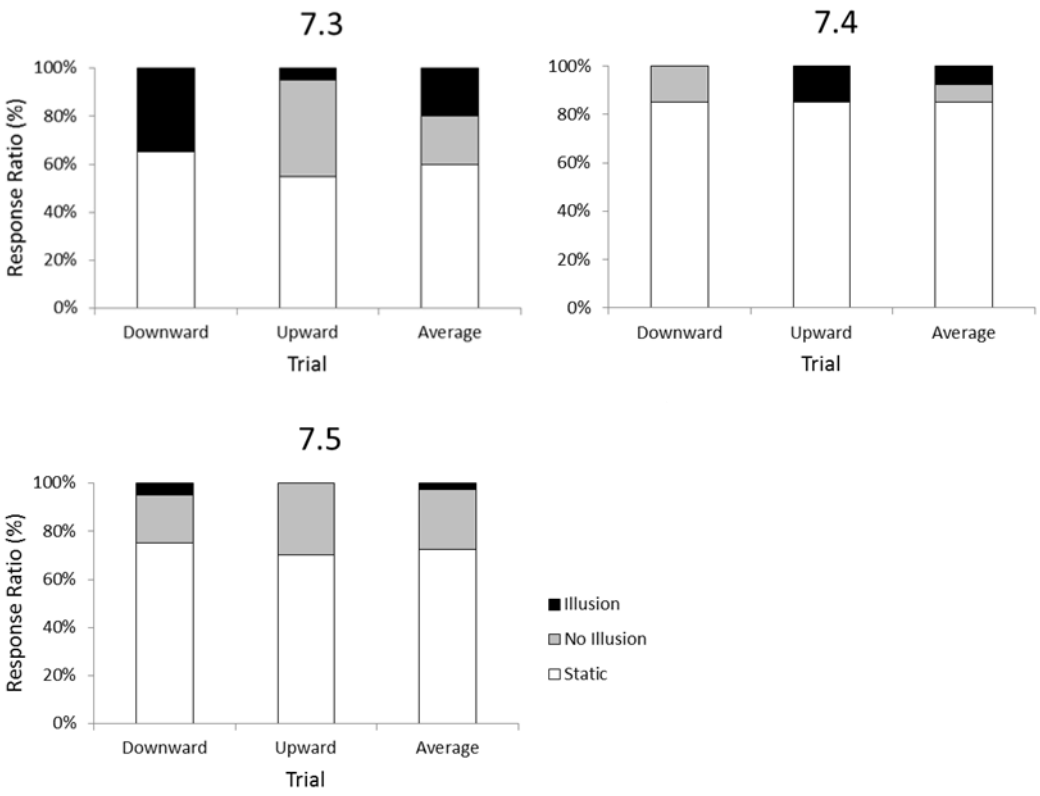

Figure 13. Percent response ratios for subjects 7.3, 7.4 & 7.5 of three possible choices from the illusion test trials: reporting illusion, no illusion or static during test trials.

The results of the illusion test trials were also calculated into percent response ratios to make a direct comparison to Xiao and Gunturkun (2008) results of studying pigeon MAE: (a) separately for downward and upward illusion test trials of each subject; and (b) averaged response ratios of the downward and upward illusion test trials for each subject. These percent response ratios are graphed in Figure 13. Figure 13 clearly shows that for all subjects, the proportion of

perceiving “static” is significantly more than that of perceiving “illusion” or “no illusion” for both movements of illusion test trials. This is also true when averaging the response ratios of the two types of illusion test trials for each subject - the “static” outcome occurred significantly more than “illusion” or “no illusion”.

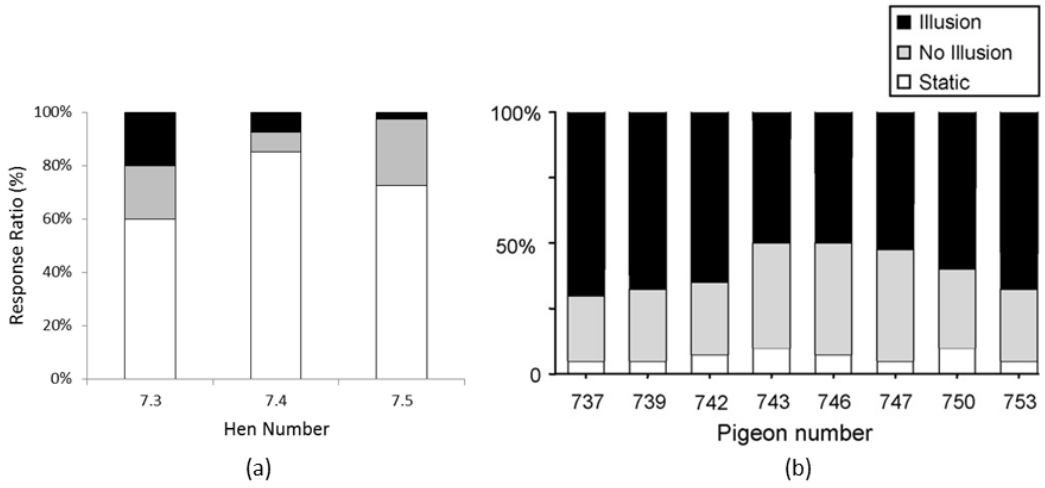

Figure 14. Comparison of our results to the Xiao and Gunturkun (2008) study. Graph (a) shows the percent response ratios of test trials for our experiment where there is significantly more response choices made to the static key. In comparison, graph (b) shows the percent response ratios of test trials of experiment two of the Xiao and Gunturkun (2008) experiment where there is significantly more responses to the illusion key.

Furthermore, a bar graph was generated to combine the results of the averaged response ratios of subjects 7.3, 7.4, and 7.5 of our experiment (graph A) onto one graph as shown in Figure 14. This plotting convention is following Xiao and Gunturkun (2008) and their data is shown in graph B of Figure 14, next to our experiment data to make direct comparison of the two studies. It is clear that our experiment data show that the subjects indicated they perceived “static” (as indicated in white colour in the bars of the graphs) more than “illusion” or “no illusion”, in contrast to the Xiao and Gunturkun (2008) study, where subjects

perceived more “illusion” than “no illusion” or “static”. Our experiment did not produce the same or similar results as the Xiao and Gunturkun (2008) study.

DISCUSSION

Our experiment results indicated that chickens could not perceive the MAE. Thus, the findings do not constitute a replication of the results of Xiao and Gunturkun (2008). Upon closer examination, the changes we made to the original training procedure of Xiao and Gunturkun (2008) may have been responsible for the different results obtained. Possible reasons for the discrepancy will now be discussed.

The chickens reported perceiving a static pattern more than the adapting stimulus movement or the MAE movement during the test trials of our experiment. This suggests they responded correctly to what was displayed on the grey background, not the adapting stimulus. Two possible factors that may have contributed to choosing the static response key: associative learning and insufficient exposure time to the adapting stimulus. The background cue we implemented to signal the chickens to respond according to the visual stimulus projected on the grey background was not only learned by the chickens as the visual stimulus to respond to, but also signalled to the chickens the response phase of a trial. In other words, it is possible the chickens learned to only pay attention on a trial when the background turned grey, as the preceding 30 seconds of black background was irrelevant to obtaining reinforcement on all trials. After obtaining our results, we attached a Go-Pro camera onto the window of the operant chamber and made video recordings of the subjects undergoing the illusion test trials in the operant chamber. We found some chickens made the required pecks to initiate a trial, then made no pecks during the 30 seconds of adaptation phase, then waited until the grey background lit up and proceeded to vigorously peck the displayed stimulus to fulfil the next required peck onto the touch screen to activate the

response keys (thus advancing into the response phase and ultimately food reinforcement). Other behaviours exhibited in the video footage during adaptation phase were pecking outside of the displayed grating, crowing, scratching the box with their feet, walking around the box, pecking the GoPro and looking down and up. The Go-Pro video footage highlighted that some chickens did not continuously peck the adapting visual stimulus as we expected and were displaying other behaviours that were incompatible with attending to the adapting stimulus as expected. The chickens appear to have learnt that the response phase was 30s after the initial peck or that the signal to respond was when they needed to focus, hence they used the least amount of effort to progress to the response phase and obtain food.

Therefore they may not have been experiencing the MAE because they had not been exposed to the adapting stimuli for a sufficiently long time. However further analysis from the Go-Pro video footage also showed subject 7.2, 7.4 and 7.5 did continuously peck throughout the 30 seconds adaptation phase but still failed to generate a MAE result. The standard adaptation duration used in studies to generate a human MAE is 30 seconds (Anstis et al., 1998) which Xiao and Gunturkun (2008) and our current experiment employed because we have no other basis to derive a crucial adaptation duration for the avian species. There are several studies that has shown human visual aftereffects can results from very short adapting exposures of 200 ms or less (Harris & Calvert, 1989; Raymond & Isaak, 1998; Wolfe, 1984) which brings forth the argument that suggests the chickens may have had sufficient exposure time to the adapting stimulus but simply did not possess the neural substrate to produce an MAE. Given no research has been conducted into the adaptation length as a function of chickens

experiencing the MAE, there is an open question which is yet to be answered and needs to be addressed and researched.

In hindsight, one of the limitations of our experiment was the failure to train the chickens to reliably peck at the adapting stimulus evenly throughout the entire adaptation phase thus eliminating the issue of interrupted viewing of the adaptation visual stimulus. Completely omitting the step of peck requirement as devised by Xiao and Gunturkun (2008) was also a mistake in retrospect. It was a weakness of our study to only monitor the number of pecks during the adaptation phase of the training sessions. Failure to continue monitoring pecks during the test phase of our experiment meant that we were unable to detect the drop in pecking behaviour during the adaptation phase of test sessions, which resulted in a confounding variable of the uncertainty of exposure time to the adapting stimulus. For future experiments we recommend regular monitoring of pecks throughout training and testing sessions and generating a histogram of the pecks as they occur during the 30s adaptation phase. We also suggest a new form of peck requirement to ensure the subjects are exposed to the adapting stimulus for the entire duration of the adaptation phase.

Our modified procedure of the Xiao and Gunturkun (2008) experiment consisted of three changes. We have already discussed the implications of introducing the background cue and that omitting the peck requirement might have possibly been a problem because some birds only pecked when the background changed to grey in the test sessions due to the lack of peck requirement and a lack of monitoring of the pecks made in adaptation phase. The final modification we implemented in our experiment was to further simplify the steps in training the birds to match different moving grating patterns to their

corresponding response keys in order to speed up training. The acquisition speed of the discrimination task in our experiment was an average of 82.33 sessions whereas for Xiao and Gunturkun (2008) it was an average of 71.25 sessions. Therefore we were unsuccessful in our attempt to speed up training of the discrimination task. Still we were able to speed up the entire training process by introducing the background cue that eradicated two months of training the birds to peck according to the last displayed visual stimuli in the Xiao and Gunturkun (2008) experiment. We suggest that for future research attempts designed to replicate this experiment, the background cue remains in the procedure because it did train the chickens to respond to the static grating pattern (the MAE eliciting stimulus) as intended. However in order to induce an MAE from the static grating pattern, there needs to be a method in place to make sure the birds are constantly looking at the adapting stimulus (the MAE inducing pattern) in order to elicit a MAE from the static grating pattern.

One of the aims of our experiment was to investigate for commonalities or differences between chickens and pigeons. From our training data collection, chickens successfully mastered the task of associating upward, downward and static grating pattern to its corresponding response keys and learnt this discrimination task at similar speed as found in pigeons (Xiao & Gunturkun, 2008). The implication of these results strongly suggests that chickens possess the same visual capability to discriminate between different directions of movement as pigeons.

However, we did not obtain a perceived MAE positive result from our experiment which possibly indicates that chickens cannot perceive the MAE and these results are opposite to the pigeon results of Xiao and Gunturkun (2008). As

there were limitations in our experiment (see above) which makes us unable to determine that the chickens were unquestionably exposed sufficiently long enough to induce a MAE. We suggest that for future experiments, there needs to be a technique devised to maintain fixation of the bird's retina for the 30s adaptation phase to exclude the possibility that the bird's retina was not being exposed to the adapting stimulus for a sufficient amount of time.

An additional aim of our experiment was to study the effects of using the touch screen as the main apparatus for displaying and recording pecks. The pecking data we collected support our decision to use the touch screen monitor to display the visual stimuli and record pecking behaviour because the touch screen efficiently detected superstitious behaviours of the chickens. For instance, early in training, some chickens would use a swiping motion to peck the moving display and the touch screen to gain access to the food magazine, instead of a frontal peck. This was detected by the touch screen because the point of first contact with the touch screen and the last point of contact were both recorded by the infra-red sensors. As a result of gaining this knowledge, we were able to step in and shaped the pecking behaviour to the frontal peck we desired for the task and eliminated unwanted behaviour from the subjects. Therefore the touch screen is an effective tool to recording pecking behaviour as it has the capability to assist in the elimination of unwanted behaviours that may otherwise go unnoticed in an operant chamber box.

Overall, the intentions of our modifications of Xiao's procedure was to primarily investigate whether chickens can perceive the MAE and speed up the training procedure before testing for a MAE. We succeeded in meeting our aim of speeding up the training procedure but our findings leads us to believe that these

modifications might possibly be the causation of the birds responding significantly more to the static pattern. This ultimately means the chicken's choice responses were not an accurate measurement or true account of their perceived experience when viewing a static pattern after a prolonged exposure to a moving stimulus.

When examining the bar graph results of the Xiao and Gunturkun (2008) study and comparing their results to the results from this study (shown in Figure 14), we not only found that the level of responding to the "illusion" key was different, but also found that the level of responses to the two alternative responses to choosing the "illusion" option were different. From the bar graphs displaying the average response ratios of the results of each subject (shown in Figure 14) we noticed that for the Xiao and Gunturkun (2008) study, the level of responding to "no illusion" was higher than the "static", whereas we obtained more responding to the "static" (refer to Figure 14) than the "no illusion" keys. The definition of "no illusion" was described in the Xiao and Gunturkun (2008) as a response to perceiving the adapting stimulus (illusion inducing pattern), and the "static" was a response to perceiving the static pattern (illusion eliciting pattern). The fact that the chickens in our study were responding more to the "static" key suggests that they were responding to the most recently displayed stimulus (the static grating image) which is what we had trained them to report on, but the data from the pigeons in the Xiao and Gunturkun (2008) study tends to indicate that they were responding more to the adapting stimulus present before the static stimulus appeared. This shows that even after Xiao and Gunturkun (2008) had attempted to train their birds to respond to the second image displayed during the adaptation phase of training in their second experiment, the birds still failed to reliably make a response according to the second image displayed (i.e., the static pattern in the test trials). We obtained more responses to the static pattern than the

adapting stimulus which suggests that the background cue we introduced was a better technique for concentrating the signal response phase on the static grating than that used by Xiao and Gunturkun (2008) to train their pigeons to respond to the second image displayed during the adaptation phase.

In summary, two modifications we implemented in our experiment were ineffective in strengthening the original procedure of Xiao and Gunturkun (2008) but the introduction of the background cue was a huge improvement upon the original procedure. We successfully reduced the training length of the procedure to progress faster into the testing phase and we believe this to be a valuable improvement upon the original procedure. Lastly, we advocate for the use of touch screen displays for presenting the visual stimuli and response keys in this type of experiment.

CONCLUSION

The present study explored the possibility of domestic chickens perceiving an MAE. To our knowledge, the current experiment represents the first behavioural study of the motion aftereffect in domestic chickens. Our experiment indicated that domestic chickens cannot perceive an MAE. We uncovered a number of methodology issues that need to be addressed when looking for evidence of a motion aftereffect in birds. The amount of time that they are exposed to the inducing stimulus can be highly variable and needs to be monitored.

Although we failed to obtain evidence for the existence of an MAE in chickens, the thesis study clearly demonstrated that chickens have the capabilities to accurately discriminate between differing directions of motion. Their performance on the directional motion-detection task was similar to that of pigeons which may underline a commonality of the visual system of the two species. The directional discrimination data provided support for the feasibility of future experiments designed to examine other aspects of motion processing in chickens.

Additionally, we were able to improve upon the original procedure of the Xiao and Gunturkun (2008) study by effectively introducing the background cue we designed and instigated to signal a phase change to the chickens. By providing this signalling procedure we have introduced a behavioural operant experimental design for other researchers to utilise in current through to future relevant applications in both human and animal operant behavioural experiments.

In conclusion, while there are many studies analysing the human motion processing system with extensive research specifically focused on illusory

perceptions such as the MAE, relatively little is known about similar phenomena in the avian motion system. The experiments reported in this thesis show that the MAE is not a robust effect across all birds; it seems to be only modestly evident in pigeons and completely absent in chickens. The measurement of the effect is difficult with non-verbal species such as birds and procedures need to be in place to monitor factors such as the adapting stimulus exposure time.

REFERENCES

Anstis, S., Verstraten, F. A. J., & Mather, G. (1998). The motion aftereffect review. *Trends in Cognitive Sciences, 2*(3), 111-117.

Anstis, S. I., & Mackay, D. (1980). The perception of apparent movement [and discussion]. *Philosophical Transactions of the Royal Society of London B: Biological Sciences, 290*(1038), 153-168.

Antal, A., Varga, E. T., Nitsche, M. A., Chadaide, Z., Paulus, W., Kovács, G., & Vidnyánszky, Z. (2004). Direct current stimulation over MT+/V5 modulates motion aftereffect in humans. *Neuroreport, 15*(16), 2491-2494.

Ashida, H., Lingnau, A., Wall, M. B., & Smith, A. T. (2007). FMRI adaptation reveals separate mechanisms for first-order and second-order motion. *Journal of neurophysiology, 97*(2), 1319-1325.

Ashida, H., & Osaka, N. (1995). Motion aftereffect with flickering test stimuli depends on adapting velocity. *Vision Research, 35*(13), 1825-1833.

Barlow, H. B., & Hill, R. M. (1963). Evidence for a physiological explanation of the waterfall phenomenon and figural after-effects. *Nature, 200*, 1345-1347.

Campana, G., Maniglia, M., & Pavan, A. (2013). Common (and multiple) neural substrates for static and dynamic motion after-effects: A rTMS investigation. *Cortex: A Journal Devoted to the Study of the Nervous System and Behavior, 49*(9), 2590-2594.

Chander, D., & Chichilnisky, E. (2001). Adaptation to temporal contrast in primate and salamander retina. *The Journal of Neuroscience, 21*(24), 9904-9916.

Clara, E., Regolin, L., Zanforlin, M., & Vallortigara, G. (2006). Domestic chicks perceive stereokinetic illusions. *Perception, 35*, 983-992.

Corballis, P. M., Fendrich, R., Shapley, R. M., & Gazzaniga, M. S. (1999). Illusory contour perception and amodal boundary completion: evidence of a dissociation following callosotomy. *Journal of Cognitive Neuroscience, 11*(4), 459-466.

Derrington, A. M., & Badcock, D. R. (1985). Separate detectors for simple and complex grating patterns? *Vision research, 25*(12), 1869-1878.

Fang, F., Murray, S. O., Kersten, D., & He, S. (2005). Orientation-tuned fMRI adaptation in human visual cortex. *Journal of Neurophysiology, 94*(6), 4188-4195.

Fujita, K., Blough, D. S., & Blough, P. M. (1991). Pigeons see the Ponzo illusion. *Animal Learning & Behavior, 19*(3), 283-293.

Fujita, K., Blough, D. S., & Blough, P. M. (1993). Effects of the inclination of context lines on perception of the Ponzo illusion by pigeons. *Animal Learning & Behavior, 21*(1), 29-34.

Giaschi, D., Douglas, R., Marlin, S., & Cynader, M. (1993). The time course of direction-selective adaptation in simple and complex cells in cat striate cortex. *Journal of Neurophysiology, 70*(5), 2024-2034.

Giersch, A., Humphreys, G. W., Boucart, M., & Kovács, I. (2000). The computation of occluded contours in visual agnosia: Evidence for early computation prior to shape binding and figure-ground coding. *Cognitive Neuropsychology, 17*(8), 731-759.

Hammond, P., Mouat, G., & Smith, A. (1988). Neural correlates of motion after-effects in cat striate cortical neurones: monocular adaptation. *Experimental Brain Research, 72*(1), 1-20.

Harris, J., & Calvert, J. (1989). Contrast, spatial frequency and test duration effects on the tilt aftereffect: implications for underlying mechanisms. *Vision research, 29*(1), 129-135.

He, S., Cohen, E. R., & Hu, X. (1998). Close correlation between activity in brain area MT/V5 and the perception of a visual motion aftereffect. *Current Biology, 8*(22), 1215-1218.

Kobayashi, Y., Yoshino, A., Ogasawara, T., & Nomura, S. (2002). Topography of evoked potentials associated with illusory motion perception as a motion aftereffect. *Cognitive Brain Research, 13*(1), 75-84.

Kohn, A., & Movshon, J. A. (2003). Neuronal adaptation to visual motion in area mt of the macaque. *Neuron, 39*(4), 681-691.

Kristjánsson, Á. (2001). Increased sensitivity to speed changes during adaptation to first-order, but not to second-order motion. *Vision Research, 41*(14), 1825-1832.

Lea, S. E. G., Slater, A. M., & Ryan, C. M. E. (1996). Perception of object unity in chicks: A comparison with the human infant. *Infant Behavior and Development, 19*(4), 501-504.

Marlin, S. G., Hasan, S. J., & Cynader, M. (1988). Direction-selective adaptation in simple and complex cells in cat striate cortex. *Journal of Neurophysiology, 59*(4), 1314-1330.

Mather, G., Pavan, A., Campana, G., & Casco, C. (2008). The motion aftereffect reloaded. *Trends in Cognitive Sciences, 12*(12), 481-487.

McCarthy, J. E. (1993). Directional adaptation effects with contrast modulated stimuli. *Vision Research, 33*(18), 2653-2662.

Moulden, B. (1980). After-effects and the integration of patterns of neural activity within a channel. *Philosophical Transactions of the Royal Society of London B: Biological Sciences, 290*(1038), 39-55.

Movshon, J. A., & Kohn, A. (2004). Adaptation changes the direction tuning of macaque MT neurons. *Nature Neuroscience, 7*(7), 764-772.

Murd, C., Einberg, A., & Bachmann, T. (2012). Repetitive TMS over V5/MT shortens the duration of spatially localized motion aftereffect: The effects of pulse intensity and stimulation hemisphere. *Vision Research, 68*, 59-64.

Murray, S. O., Kersten, D., Olshausen, B. A., Schrater, P., & Woods, D. L. (2002). Shape perception reduces activity in human primary visual cortex. *Proceedings of the National Academy of Sciences, 99*(23), 15164-15169.

Nagasaka, Y., & Wasserman, E. A. (2008). Amodal completion of moving objects by pigeons. *Perception, 37*, 557-570.

Nakamura, N., Fujita, K., Ushitani, T., & Miyata, H. (2006). Perception of the standard and the reversed Müller-Lyer figures in pigeons and humans. *Journal of Comparative Psychology, 120*(3), 252-261.

Nakamura, N., Watanabe, S., & Fujita, K. (2008). Pigeons perceive the Ebbinghaus-Titchener circles as an assimilation illusion. *Journal of Experimental Psychology: Animal Behavior Processes, 34*(3), 375-387.

Nakamura, N., Watanabe, S., & Fujita, K. (2009a). Further analysis of perception of reversed Müller-Lyer figures for pigeons (Columba livia). *Perceptual and Motor Skills, 108*(1), 239-250.

Nakamura, N., Watanabe, S., & Fujita, K. (2009b). Further analysis of perception of the standard Müller-Lyer figures in pigeons and humans: Effects of length of brackets. *Journal of Comparative Psychology, 123*(3), 287-294.

Nishida, S. y., Ashida, H., & Sato, T. (1994). Complete interocular transfer of motion aftereffect with flickering test. *Vision Research, 34*(20), 2707-2716.

Nishida, S. Y., Sasaki, Y., Murakami, I., Watanabe, T., & Tootell, R. B. (2003). Neuroimaging of direction-selective mechanisms for second-order motion. *Journal of Neurophysiology, 90*(5), 3242-3254.

Niu, Y. Q., Xiao, Q., Liu, R. F., Wu, L. Q., & Wang, S. R. (2006). Response characteristics of the pigeon's pretectal neurons to illusory contours and motion. *The Journal of Physiology, 577*(3), 805-813.

Pantle, A. (1974). Motion aftereffect magnitude as a measure of the spatio-temporal response properties of direction-sensitive analyzers. *Vision Research, 14*(11), 1229-1236.

Pepperberg, I. M., Vicinay, J., & Cavanagh, P. (2008). Processing of the Müller-Lyer illusion by a grey parrot (psittacus erithacus). *Perception, 37*(5), 765-781.

Petersen, S. E., Baker, J. F., & Allman, J. M. (1985). Direction-specific adaptation in area MT of the owl monkey. *Brain research, 346*(1), 146-150.

Raymond, J. E., & Isaak, M. (1998). Successive episodes produce direction contrast effects in motion perception. *Vision research, 38*(4), 579-589.

Regolin, L., & Vallortigara, G. (1995). Perception of partly occluded objects by young chicks. *Perception & Psychophysics, 57*(7), 971-976.

Rosa Salva, O., Rugani, R., Cavazzana, A., Regolin, L., & Vallortigara, G. (2013). Perception of the Ebbinghaus illusion in four-day-old domestic chicks (Gallus gallus). *Animal Cognition, 16*(6), 895-906.

Rugani, R., Regolin, L., & Vallortigara, G. (2008). Discrimination of small numerosities in young chicks. *Journal of experimental psychology: Animal behavior processes, 34*(3), 388.

Seiffert, A. E., Somers, D. C., Dale, A. M., & Tootell, R. B. (2003). Functional MRI studies of human visual motion perception: texture, luminance, attention and after-effects. *Cerebral Cortex, 13*(4), 340-349.

Smith, A. T., Greenlee, M. W., Singh, K. D., Kraemer, F. M., & Hennig, J. (1998). The processing of first-and second-order motion in human visual cortex assessed by functional magnetic resonance imaging (fMRI). *The Journal of Neuroscience, 18*(10), 3816-3830.

Stewart, L., Battelli, L., Walsh, V., & Cowey, A. (1999). Motion perception and perceptual learning studied by magnetic stimulation. *Electroencephalography and clinical neurophysiology. Supplement, 51*, 334.

Sutherland, N. S. (1961). Figural aftereffects and apparent size. *Quarterly Journal of Experimental Psychology, 13*, 222-228.

Taylor, J. G., Schmitz, N., Ziemons, K., Grosse-Ruyken, M. L., Gruber, O., Mueller-Gaertner, H. W., & Shah, N. J. (2000). The network of brain areas involved in the motion aftereffect. *Neuroimage, 11*(4), 257-270.

Théoret, H., Kobayashi, M., Ganis, G., Di Capua, P., & Pascual-Leone, A. (2002). Repetitive transcranial magnetic stimulation of human area MT/V5

disrupts perception and storage of the motion aftereffect. *Neuropsychologia, 40*(13), 2280-2287.

Thompson, P., & Wright, J. (1994). The role of intervening patterns in the storage of the movement aftereffect. *Perception, 23*(10), 1233-1240.

Tikhonov, A., Händel, B., Haarmeier, T., Lutzenberger, W., & Thier, P. (2007). Gamma oscillations underlying the visual motion aftereffect. *Neuroimage, 38*(4), 708-719.

Tootell, R. B., Reppas, J. B., Dale, A. M., Look, R. B., Sereno, M. I., Malach, R., . . . Rosen, B. R. (1995). Visual motion aftereffect in human cortical area MT revealed by functional magnetic resonance imaging. *Nature, 375*(6527), 139-141.

van de Grind, W. A., van der Smagt, M. J., & Verstraten, F. A. J. (2004). Storage for free: A surprising property of a simple gain-control model of motion aftereffects. *Vision Research, 44*(19), 2269-2284.

van der Smagt, M. J., Verstraten, F. A. J., Vaessen, E. B. P., van Londen, T., & van de Grind, W. A. (1999). Motion aftereffect of combined first-order and second-order motion. *Perception, 28*(11), 1397-1411.

van der Smagt, M. J., Verstraten, F. A. J., & van de Grind, W. A. (1999). A new transparent motion aftereffect. *Nature Neuroscience, 2*, 595–596.

Vautin, R. G., & Berkley, M. A. (1977). Responses of single cells in cat visual cortex to prolonged stimulus movement: Neural correlates of visual aftereffects. *Journal of Neurophysiology, 40*(5), 1051-1065.

Verstraten, F. A. J., Fredericksen, R. E., Van Wezel, R. J. A., Lankheet, M. J. M., & Van De Grind, W. A. (1996). Recovery from adaptation for dynamic and static motion aftereffects: Evidence for two mechanisms. *Vision Research, 36*(3), 421-424.

Warden, C. J., & Baar, J. (1929). The Müller-Lyer illusion in the ring dove, Turtur risorius. *Journal of Comparative Psychology, 9*(4), 275-292.

Watanabe, S., Nakamura, N., & Fujita, K. (2011). Pigeons perceive a reversed Zöllner illusion. *Cognition, 119*(1), 137-141.

Watanabe, S., Nakamura, N., & Fujita, K. (2013). Bantams (Gallus gallus domesticus) also perceive a reversed Zöllner illusion. *Animal Cognition, 16*(1), 109-115.

Watanabe, S., Nishimoto, Y., Fujita, K., & Ishida, M. (2014). Budgerigars (Melopsittacus undulatus) perceive a Müller-Lyer illusion. *The Japanese Journal of Psychonomic Science, 33*(1), 117-118.

Winslow, C. N. (1933). Visual illusions in the chick. *Archives of Psychology, 153*, 80.

Wolfe, J. M. (1984). Short test flashes produce large tilt aftereffects. *Vision research, 24*(12), 1959-1964.

Xiao, Q., & Gunturkun, O. (2008). Do pigeons perceive the motion aftereffect? A behavioral study. *Behavioural Brain Research, 187*(2), 327-333.