Evolution in 3D

Lisa Jones

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Faculty of Medical Sciences
Newcastle University
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Abstract

This thesis explores the mechanisms underlying motion vision in the praying mantis (*Sphodromantis lineola*) and how this visual predator perceives camouflaged prey.

By recording the mantis optomotor response to wide-field motion I was able to define the mantis Dmax, the point where a pattern is displaced by such a distance that coherent motion is no longer perceived. This allowed me to investigate the spatial characteristics of the insect wide field motion processing pathway. The insect Dmax was found to be very similar to that observed in humans which suggests similar underlying motion processing mechanisms; whereby low spatial frequency local motion is being pooled over a larger visual area compared to higher spatial frequency motion.

By recording the mantis tracking response to computer generated targets, I was able to investigate whether there are any benefits of background matching when prey are moving and whether pattern influences the predatory response of the mantis towards prey. I found that only prey with large pattern elements benefit from background matching during movement; and above all prey which remain un-patterned but match the mean luminance of the background receive the greatest survival advantage.

Additionally, I examined the effects of background motion on the tracking response of the mantis towards moving prey. By using a computer generated target as prey, I investigated the benefits associated with matching background motion as a protective strategy to reduce the risk of detection by predators. I found the mantis was able to successfully track a moving target in the presence of background motion.

My results suggests that although there are no overall benefits for prey to match background motion, it is costly to move out of phase with the background motion.

Finally, I examined the contrast sensitivity of the mantis wide-field and small target motion detection pathways. Using the mantis tracking response to small targets and the optomotor response to wide-field motion; I measured the distinct temporal and spatial signatures of each pathway. I found the mantis wide-field and small target movement detecting pathways are each tuned to a different set of spatial and temporal frequencies. The wide-field motion detecting pathway has a high sensitivity to a broad range of spatio-temporal frequencies making it sensitive to a broad range of velocities; whereas the small-target motion-detection pathway has a high sensitivity to a narrow set of spatio-temporal combinations with optimal sensitivity to targets with a low spatial frequency.

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Abbreviation

^{o}C	Degrees Celsius
Cd/m^2	Candela per meter square
Cpd	Cycles per degree
CRT	Cathode ray tube
CSTMD1	Centrifugal small target motion detector 1
Dmax	Maximal displacement
EMD	Elementary motion detector
FD	Figure detection cell
FWHM	Full width half maximum
GEE	Generalized estimating equation
Hz	Unit of frequency (1 cycle per second)
J_i	Jump step
LMC	Lamina monopolar cell
LPTC	Lobula plate tangential cell
M_i	Number of responses obtained
N_i	Number of trials carried out
Pix	Pixels
P_m	Probability of the mantis responding
S/F	Spatial frequency
Se	Standard error of the mean
STMD	Small target motion detector
T/F	Temporal frequency
TM	Trans-medulla neurons

Chapter 1: General Introduction

1.1 The Praying Mantis

Praying mantids are a group of predatory insects which are commonly found throughout Asia, Africa and South America. They are members of the Order Mantodea within the class Insecta. Mantodea is a sister group to the order Blattodea (cockroaches and termites), and like the orders Orthoptera (locusts, grasshoppers and crickets) and Phlasmatodea (stick insects), belongs to the insect subdivision Polyneoptera (new wing) (Eggleton *et al.*, 2007). This thesis focussed on one particular species of the praying mantid, *Sphodromantis lineola*, also known as the African lined mantis. The African lined mantis is quite large with females reaching 8cm in length and males around 6 – 7cm. This species of mantis is commonly found in sub-Saharan regions of Africa. Like the majority of mantises, the African lined mantis is an ambush predator which remains stationary whilst waiting for prey to approach, or uses stealthy movements to stalk prey. It is a generalist predator and has been observed in the wild predating on flies, crickets and even larger insects such as locusts (Prete, 1999).

1.2 The Compound Eye

Having a good pair of eyes and a well-developed visual system can give an insect a competitive edge and a survival advantage over those with poor sight. Evolution has created many different types of eye, from insect ocelli, which consist of a single lens and are used to detect rapid changes in horizon position (Land, 2012), to

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many lensed compound eyes which can form complex images of the insect's environment.

1.2.1 Structure

The compound eye is made up of many units called ommatidia. Within each ommatidium, there is a lens which focuses light onto a group of photoreceptors. Typically, a group of eight photoreceptor cells make up a structure called the rhabdom (Hardie, 1986; Nilsson, 1989; Land and Nilsson, 2012). The rhabdom is a long light sensitive structure, which captures light at its tip and guides it down its length. Rhabdoms can be closed (as in ancient orders of insects like the mantids), or open (as in more recent orders such as Diptera) (Hardie, 1986; Nilsson, 1989; Land and Nilsson, 2012). In mantids with a closed rhabdom, each ommatidium has a small 0.5-3° field of view, offset from its neighbours view by an amount equivalent to the inter-ommatidial angle of the eye (Land and Nilsson, 2012). The compound eye works by gathering light viewed by neighbouring ommatidia in a retinotopic projection, which preserves the spatial relationships between neighbouring units and processes this information in the optic lobe and brain. The optic lobe is made up of four different layers: the retina, lamina, medulla, and lobula complex. The structure of each of the first three layers is columnar, preserving the same retinotopic map, whereas in the lobula complex, the retinotopic information is combined in specific ways to generate neurons that respond selectively to particular patterns and directions of motion over wide areas of the eye (Figure1) (Fischbach and Dittrich, 1989; Cuntz *et al.*, 2007; Borst *et al.*, 2010).
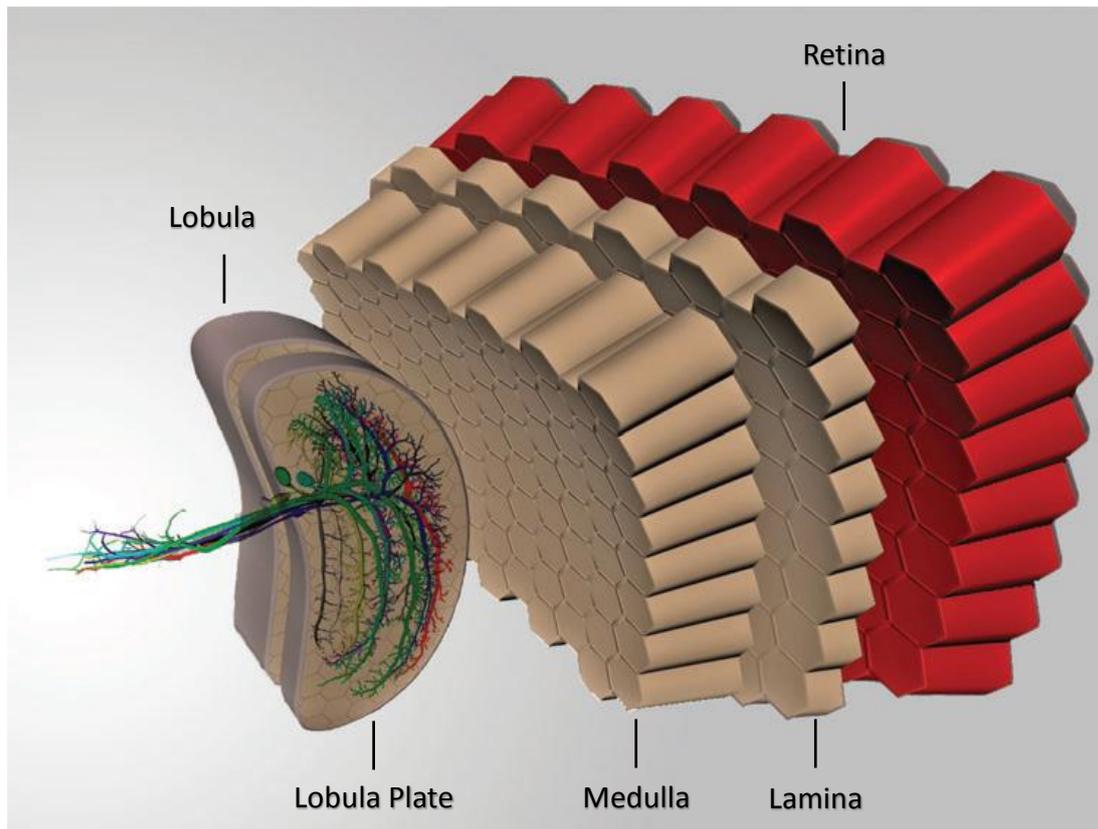
Figure 1. Schematic diagram of the fly optic lobe. The lobula complex in the fly consists of the lobula and the lobula plate. Nine large motion-sensitive neurons sensitive to vertically oriented patterns of motion have been drawn (Cuntz *et al.*, 2007).

1.2.2 Resolution and sensitivity

Despite structural differences, all visual systems are limited by their resolving power and their sensitivity to light. Resolution can be described as the fineness (in angular terms) by which the visual environment is sampled, i.e. how sharp an image can be made. The sensitivity of a visual system is the number of photons a receptor needs to give a criterion response when viewing an image (Land and Nilsson, 2012). In the case of the compound eye, resolution is set by the size of the angle between each ommatidium (the inter-ommatidial angle) and the size of the receptive field of each ommatidium (the acceptance angle). The smaller these two angular parameters the greater the ability of the eye to resolve fine spatial detail and contrast (Götz, 1964;

Rossel, 1979). In a state of light adaption the foveal region of the mantis eye has a mean acceptance angle of 0.74°. The same region of eye when dark adapted at night increases in width to 2°, or dark adapted in dim light 1.1° (Rossel, 1979). This widening of the acceptance angle when moving from a light adapted state to a dark adapted state facilitates photon capture, enabling the eye to capture more light under dark conditions. In contrast the corresponding acceptance angles in the peripheral regions of the eye are 2.4° (light adapted), 3.2° (dark adapted at night) and 6° (dark adapted in dim light) (Rossel, 1979). This means mantids have a greater resolving power under light daytime conditions particularly in foveal region of the eye (Rossel, 1979). In general, insects have poor spatial resolution when compared to humans, however, they have excellent temporal resolution. This makes them specialise in the detection of motion rather than the recognition of fine spatial detail (Franceschini *et al.*, 1989).

1.3 Insect Motion Vision

An animal needs to process many different motion cues in the environment and make appropriate behavioural responses to each type of movement. For example, a small moving object can represent prey or a conspecific, which can trigger a tracking response, whilst a looming object that increases in size and angular speed could indicate an approaching predator, triggering an escape reaction (Beverley and Regan, 1979; Rind and Simmons, 1999; Santer *et al.*, 2006). Motion can also be created by the animal's own movement that causes the whole visual image to move over the retina, often referred to as 'optic flow' (Gibson, 1950). Animals, such as insects, with relatively low spatial resolution have evolved particularly robust neural mechanisms

for motion vision, making motion one of the most important visual cues to these animals (Srinivasan *et al.*, 1999; Borst *et al.*, 2010). Motion vision has been well studied in insects using the optomotor response, which is a turning response triggered by movement of a wide-field image over the retina and used to stabilise the insect relative to its environment (Fermi and Reichardt, 1963; Reichardt and Wenking, 1969; Srinivasan *et al.*, 1999).

1.3.1 Elementary motion detector

Elementary motion detectors (EMD's) sample the brightness of an image at two adjacent points. Using two mirror pathways, one of which is delayed by a filter, the signal is multiplied and then subtracted giving an output which is positive for motion in one direction and negative for motion in the opposite direction. The interaction of the spatially separated pathways means the motion of an object and its direction can be detected when it passes one pathway then the other (Figure 2) (Borst and Egelhaaf, 1989; Douglass and Strausfeld, 1996; Harris *et al.*, 1999; Srinivasan *et al.*, 1999).
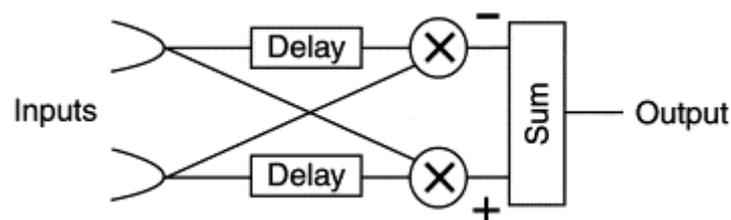
Figure 2. In each elementary motion detector (EMD), the luminance or contrast signal sampled at one input location in the image is correlated with that sampled after a delay at an adjacent input location *(Harris et al., 1999)*.

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1.3.2 Insect motion detecting pathway

Following the Hassenstein and Reichardt elementary motion detection model, scientists have identified cells located in the lobula complex which respond selectively to wide field motion, by either depolarising in response to motion along their preferred direction or hyperpolarising in response to motion in the opposite direction (Hausen, 1984; Joesch *et al.*, 2008; Schnell *et al.*, 2010). These lobula plate tangential cells (LPTCs) are thought to combine information from many local motion detectors, however, the neuronal circuitry underlying these motion detectors has remained unclear until more recently. It is now well established that the primary input to the motion detection system in *Drosophila* is via lamina monopolar cells (LMCs), L1 and L2 (Rister *et al.*, 2007). Like photoreceptors, these cells respond to increases and decreases in light and form the light ON (L1) and light OFF (L2) pathways in the medulla (Figure 3) (Joesch *et al.*, 2010; Strother *et al.*, 2014). Output from these two pathways lead to directionally selective cells T4 (ON pathway) and T5 (OFF pathway), which respond to light (T4) and dark (T5) edges. Both the T4 and T5 cells have 4 subgroups each of which is selective for one of the four cardinal directions (front to back, back to front, upwards and downwards) (Figure 3) (Maisak *et al.*, 2013).
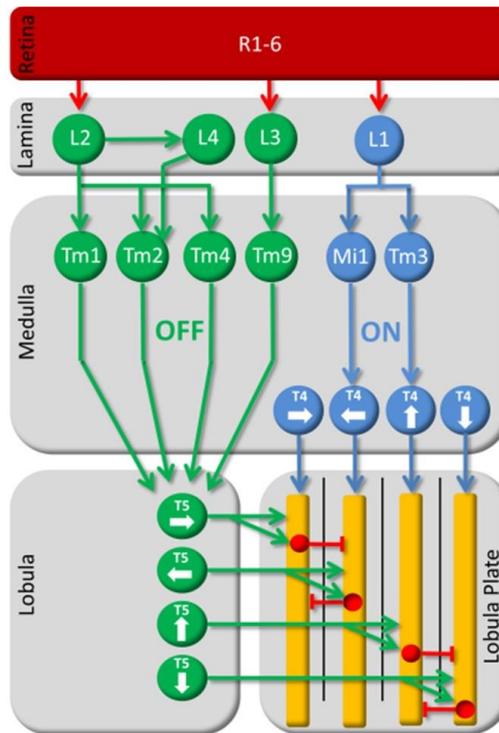
Figure 3. Circuit diagram of the L1 (On, blue) and L2 (OFF, green) pathway leading to directionally selective T4 and T5 cells. Motion information is then spatially integrated into lobular plate tangential cells *(Haag et al., 2016)*.

1.3.3 Direction selectivity

Although great progress has been made in identifying the underlying circuitry involved in directionally selective motion detection, relatively little is known about how direction selectivity is computed and where in the pathway these computations occur. By characterising four trans-medulla neurons (Tm1, Tm2, Tm4 and Tm9; Figure 3) in the OFF pathway, which provide input to the directionally selective T5 neurons (Takemura *et al.*, 2013b; Shinomiya *et al.*, 2014), recent work has brought us closer to identifying the neurons and synapses where the different computational stages of the Hassenstein and Reichardt motion detection model may take place (Serbe *et al.*, 2016; Tuthill and Borghuis, 2016).

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From silencing experiments, it was found that all four Tm neuron types presynaptic to T5 have a cumulative contribution to motion sensitivity and no single Tm neuron type, or pair of Tm neurons, is directly needed for direction selectivity (Serbe *et al.*, 2016). Therefore, motion may be computed in an incremental manner: directional selectivity originating at the level of the T5 dendrites may be sharpened through inhibitory interactions between T5 neurons with opposing preferred directions and pooling of wide-field motion signals in Lobula plate tangential cells (LPTC's) (Serbe *et al.*, 2016; Tuthill and Borghuis, 2016). This also suggests that instead of two temporally distinct input lines as predicted in the Hassenstein and Reichardt motion detection model, the OFF motion pathway in the fly uses at least four. This broadens the detector's performance range and may enhance motion detection across luminance conditions (Serbe *et al.*, 2016; Tuthill and Borghuis, 2016).

1.3.4 EMD tuning

The delay in the elementary motion detector model could be explained by the diverse temporal kinetics which the Tm neurons display: Tm2 and Tm4 were found to be transient (fast adapting), Tm9 is sustained (non-adapting) and Tm1 intermediate (slow adapting). The diversity in the response speed of these neurons to motion stimulus provides a range of temporal filters enabling motion detectors to be tuned to a range of image velocities. These temporal filters make motion detectors sensitive to an image's spatial and temporal properties (O'Carroll *et al.*, 1997).

The neuronal circuitry which has emerged in drosophila provides good support for the Hassenstein and Reichardt elementary motion detection model and

expands our knowledge on how direction selectivity is computed in the motion detection pathway.

1.4 Apparent Motion

Studies investigating the mechanisms underlying motion perception often use computer-generated stimuli creating apparent motion of a small target or a wide field grating (Goodman, 1960; Borst and Bahde, 1988; O'Carroll *et al.*, 1997; Prete *et al.*, 2002; Nordström *et al.*, 2006; Nityananda *et al.*, 2016a). Instead of continuous movement (Figure 4a), apparent motion (Figure 4b) can be described as a series of static images, which are displaced in frequent jump steps stimulating motion detectors. Images which are displaced in small, frequent jump steps are perceived as having a smooth motion whereas images which are displaced by increasing distance are perceived as having a jerky motion.
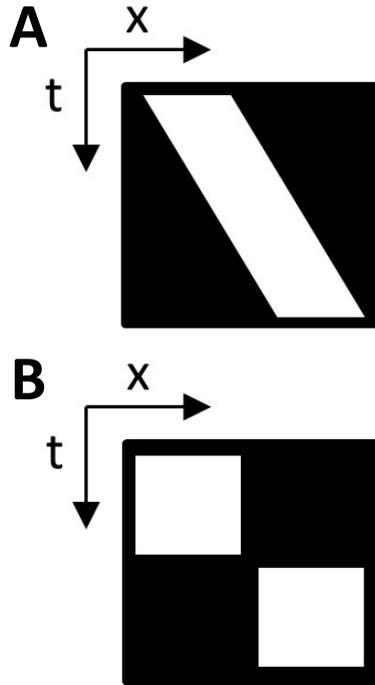
Figure 4 (A) Continuous vs (B) Apparent motion displayed in a x-t plot, where luminance information is shown along a spatial (x) and time (t) axis. At a constant velocity continuous motion produces a smooth luminance profile along the x axis, producing a slanted bar in the x-t plot (A). Apparent motion moving at a the same average velocity is stable in one position for a set time then jumps to a subsequent position (B) *(Haag et al., 2016)*.

Apparent motion has been widely studied in insects to understand how they use visual information to navigate (Cheng *et al.*, 1987), judge distance (Srinivasan *et al.*, 1991) and stabilise their bodies (Land, 1973). For example, the landing response of the house fly is triggered by an expanding image upon the retina (Goodman, 1960; Borst and Bahde, 1988) and the onset of landing is triggered when a combination of spatial frequency and contrast of the pattern reaches a threshold value (Borst and Bahde, 1988).

1.4.1 Dmax

Apparent motion has also been used to understand the visual mechanisms behind human motion detection. Human behavioural studies have shown that by displacing a random chequerboard pattern in increasingly larger jumps, the perception of smooth motion begins to break down, resulting instead in the perception of a jerky movement. Ultimately the perception of coherent motion breaks down when the distance the image is displaced by becomes too large, leaving the participant unable to discriminate which direction the pattern is moving in. The displacement beyond which, coherent motion breaks down has been termed Dmax, or the Braddick limit (Braddick, 1974; Braddick *et al.*, 1980; Morgan, 1992). Dmax has been well studied and characterised in the human visual system however Dmax has yet to be used to study how invertebrates perceive apparent motion.

1.5 Small Target Detection

Detecting prey amongst a cluttered visual environment is a complicated task. Despite possessing a low-resolution compound eye, many insects are able to detect and track small moving objects through complicated environments. When tracking an object, either during flight or by making saccadic head movements, the background image is shifted over the retina creating an optic flow. The insect visual system needs to be able to segregate the movement of the small object (figure or target) from the background motion (ground) (Egelhaaf, 1985; Nordström *et al.*, 2006; Nordström and O'Carroll, 2009; Gonzalez-Bellido *et al.*, 2016). Behavioural studies have shown that flies are able to discriminate objects even when the target matches the texture of the background, as long as there were relative motion cues (Wehrhahn and Reichardt,

1973; Reichardt and Poggio, 1979; Reichardt *et al.*, 1983; Egelhaaf *et al.*, 1988). This led to the suggestion that figure ground discrimination is processed by two functionally different pathways: a wide-field system associated with the optomotor response which responds to optic flow (Hausen, 1982; Reichardt *et al.*, 1983) and a small-field system sensitive to smaller objects (Collett, 1971; Olberg, 1981; Egelhaaf, 1985; Egelhaaf *et al.*, 1988; O'Carroll, 1993; Nordström *et al.*, 2006; Barnett *et al.*, 2007; Duistermars *et al.*, 2007). Recent work suggests these functionally different motion vision pathways may arise in early visual processing, diverging directly down stream of photoreceptors in lamina monopolar cells (Rister *et al.*, 2007; Katsov and Clandinin, 2008).

1.5.1 Small target detecting neurons

Neurons which are selectively sensitive to small features were first described in the optic lobes of hawkmoths and hoverflies (Collett, 1971, 1975). These 'target tracking' neurons responded exclusively to discrete moving features, such as dark and light spots, bars or edges, in a direction-selective manner, and ignored wide field stimuli (Collett 1971). Later, a type of neuron referred to as the 'small target motion detector' (STMD) (O'Carroll, 1993) was characterised in the dragonfly. STMDs were found to be highly selective for targets which occupied <3° of the visual field and were inhibited by wide-field stimuli such as sinusoidal gratings (Nordstrom, 2006; Barnett, 2007; Geurten, 2007).

The mechanisms by which cells obtain their sensitivity for small features is not yet fully understood. Sensitivity to small features could be mediated by a negative-feedback loop from the large-field system, whereby tuning to small features is mediated by inhibition by wide field sensitive neurons (Reichardt, 1983; Egelhaaf,

1985; Warzecha, 1993; Olveczky *et al.*, 2003). This inhibitory feedback means that neurons sensitive to small objects, such as the 'figure detection' (FD) cell found in the blowfly, can only detect the relative motion of objects against a background (Egelhaaf *et al.*, 1988; Olveczky, 2003).

In contrast, STMDs which are sharply tuned to small targets, continue to respond robustly whether the background pattern is moving in the same or the opposite direction (Nordstrom, 2006). This suggests that STMDs do not rely solely on wide field inhibition and use a different mechanism for target tuning. Alternatively, experiments on a type of STMD (CSTMD1) found in the dragonfly, suggest that it is possible that these cells receive lateral inhibition from contralateral counterparts, which sharpens tuning to small moving targets (Geurten, 2007; Bolzon *et al.*, 2009). The CSTMD1 has two dendritic output regions, one of which is localised near input dendrites of its contralateral counterpart. By linking the two visual hemifields the CSTMD1 could allow for direction-selective inhibition between the two hemispheres. This interocular inhibition was found to be much stronger than local inhibition, with almost complete suppression of responses when two targets are viewed by each hemisphere (Bolzon, 2009). This interocular inhibition could possibly allow the dragon-fly to focus on one target in a swarm of prey.

1.6 Camouflage

Natural selection has provided us with some amazing examples of camouflage, which can be seen in a diverse range of animals, from insects which resemble bird droppings (Hebert, 1974) to cephalopods and reptiles which can change colour to match their surroundings (Hanlon and Messenger, 1988; Nery and de Lauro Castrucci,

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1997; Barbosa *et al.*, 2008). Crypsis comprises all traits that reduce an animal's risk of being detected when it potentially could be seen by an observer (Stevens and Merilaita, 2009a; Stevens and Merilaita, 2011). Some of the more well-studied forms of crypsis include background matching and disruptive colouration. Background matching is a form of camouflage employed by prey to reduce the risk of being detected by predators (Endler, 1978; Endler, 1984; Merilaita and Lind, 2005b; Stuart-Fox *et al.*, 2008); by resembling the colour, luminance, or pattern of either one background (specialist) or several backgrounds (compromise) (Merilaita *et al.*, 1999; Merilaita *et al.*, 2001). Disruptive colouration comprises of a set of markings which creates false edges making it difficult for predators to detect a prey's body shape thus enabling them to go undetected (Cuthill *et al.*, 2005; Merilaita and Lind, 2005a; Schaefer and Stobbe, 2006; Stevens and Merilaita, 2009b). By closely matching features found in the background and maintaining a low luminance contrast to the surroundings it becomes difficult for an observer to segregate a stationary object (figure) from the background (ground). This allows prey to blend into the background and remain undetected by visually hunting predators.

1.6.1 Crypsis and motion

One important factor that could enable a visual system to distinguish a figure from the background is movement (Livingstone and Hubel, 1988; Borst and Egelhaaf, 1989; Lamme, 1995; Nordström *et al.*, 2006; Nordström and O'Carroll, 2009). It has often been observed that cryptic animals remain still (Poulton, 1890; Cott, 1940; Heatwole, 1968; Broom and Ruxton, 2005; Eilam, 2005; Zhang and Richardson, 2007), and that crypsis and remaining still are in fact inter-dependent on each other (Ioannou and Krause, 2009; Hall *et al.*, 2013). However, some background matching

prey need to forage and find a mate when visually hunting predators are active (Ie *et al.*, 2000; Honkavaara *et al.*, 2002; Butler, 2005). There have been relatively few controlled experiments into the effectiveness of background matching during prey movement, making it difficult to know whether prey are afforded any benefits from background matching during movement. So far, evidence suggests there are no benefits of background matching in moving prey (Ioannou and Krause, 2009; Hall *et al.*, 2013); although some protective strategies such as 'motion dazzle' can make it difficult for predators to capture prey once detected and rely on the motion of the prey to create a visual illusion (Jackson *et al.*, 1976; Brodie, 1989; Allen *et al.*, 2013; Hämäläinen *et al.*, 2015). These patterns include bars, stripes and zig-zag patterns; which when in motion, are thought to alter the perception of the predator making it difficult for it to judge the speed and direction of prey (Stevens *et al.*, 2008; Scott-Samuel *et al.*, 2011; Stevens *et al.*, 2011; von Helversen *et al.*, 2013; Kelley and Kelley, 2014; Hämäläinen *et al.*, 2015).

1.6.2 Factors affecting crypsis

The effectiveness of background matching can be dependent on many factors, such as background complexity (Merilaita, 2003; Merilaita and Lind, 2005b; Dimitrova and Merilaita, 2011; Dimitrova and Merilaita, 2014), the degree of resemblance to the background (Dimitrova and Merilaita, 2009; Dimitrova and Merilaita, 2011; Dimitrova and Merilaita, 2014) and the visual acuity and sensitivity of the predator (Stevens, 2007; Stevens and Merilaita, 2011). Evidence supporting background matching primary comes from predator–prey experiments measuring the survival rates of cryptic prey (Merilaita et al, 2001, 2003, 2005; Cuthill et al, 2005; Stevens, 2009). Many of these experiments use birds and humans as model predators

(Forsman and Merilaita, 1999; Merilaita *et al.*, 2001; Cuthill *et al.*, 2005; Merilaita and Lind, 2006; Stevens *et al.*, 2008; Hall *et al.*, 2013), which are both groups that have visual systems with high acuity and a high sensitivity to light. This enables them to see objects with a high resolution and the ability to see objects under low lighting conditions. In contrast, there have been few studies investigating the optimisation of background matching as a concealing strategy when viewed by a compound eye, which has relatively low spatial resolution but is finely tuned to detect motion in the environment (Srinivasan *et al.*, 1999; Borst *et al.*, 2010). Therefore, we need studies which investigate whether background matching can offer prey any survival advantages when predated on by an insect predator and whether movement breaks crypsis when perceived by a relatively simple visual system.

1.7 The praying mantis as a visual predator

The praying mantis visual system is thought to be well-developed compared to that of other insects. The mantis has two large compound eyes giving a wide field of view, with just a small blind spot at the back of the neck (Rossel, 1979; Rossel, 1983). The forward-facing nature of the mantids eyes means that they have a binocular overlap of 35° horizontally (e.g. *Tenodera australiae* (Rossel, 1979)). This binocular overlap gives the mantis the advantage of depth perception through binocular vision (Maldonado and Rodriguez, 1972; Rossel, 1983; Nityananda *et al.*, 2016a). The mantis has a specialised foveal region at the front of the eye where interommatidial angles are as small as 0.6°, and an increased ommatidial facet size in comparison with other regions of the eye. This gives the fovea a higher spatial resolution than peripheral regions of the eye (Rossel, 1979; Rossel, 1980). The

periphery of the eye has a reduced spatial resolution but is sensitive to movement. The peripheral eye region detects moving prey, which triggers a saccade, centring the fovea over the target image (Levin and Maldonado, 1970; Rossel, 1979; Rossel, 1980). The image is then held over the fovea by the mantis's smooth or saccadic tracking behaviour. This tracking behaviour precedes the capture of prey and has often been used in behavioural studies as a measure of the mantids interest in prey-like objects (Levin and Maldonado, 1970; Rossel, 1980; Rossel, 1983; Corrette, 1990; Prete, 1993; Prete and Mahaffey, 1993; Prete *et al.*, 2002; Yamawaki, 2003; Yamawaki, 2006).

1.8 Target Identification

The term target is used for small objects that move independently from the background and are pursued for feeding, defensive or mating purposes (Gonzalez-Bellido *et al.*, 2016). Target detection and identification is important for the survival of many insects and is used in tasks such as prey detection (Combes *et al.*, 2013), predator avoidance (Peek and Card, 2016) or finding a mate (Alderman, 2012). To identify a moving object as a target of interest, many predatory insects need to evaluate the object properties and decide whether it is suitable for consumption (Prete and McLean, 1996; Combes *et al.*, 2013; Haselsteiner *et al.*, 2014; Wardill *et al.*, 2015; Gonzalez-Bellido *et al.*, 2016). This evaluation involves determining whether the object is small and near, as opposed to large and far away, since both types of target can subtend the same retinal angle (Figure 5). Distance perception can be estimated through a range of different methods. The praying mantis can use stereopsis to gauge the distance and size of an object (Rossel, 1996; Nityananda *et al.*, 2016a), whilst insects such as locusts can use motion parallax (Schwind, 1989; Sobel,

1990), whereby when the observer moves, an object which is near makes a larger shift across the retina compared with an object which is far away (Kral, 2003).
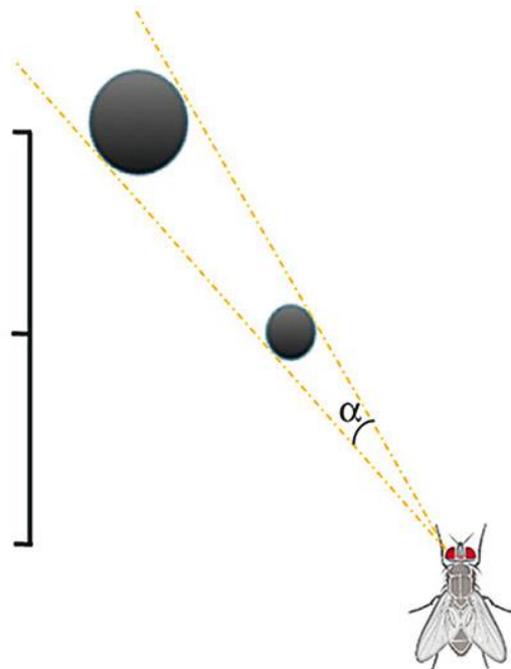
Figure 5. An object that is close and small subtends the same size on the retina (α) as one that is far away and big (Wardill *et al.*, 2015).

1.9 Mantis prey preference

The praying mantis is a generalised opportunistic predator which uses its raptorial forelegs to strike and catch a wide range of insect prey (Corrette, 1990; Prete and Wolfe, 1992; Prete and Mahaffey, 1993). It primarily uses its visual system to detect, identify and track prey before eliciting a predatory strike (Rossel, 1980; Rossel, 1983; Corrette, 1990; Yamawaki, 2000). Interestingly, studies using both mechanical and computer based stimuli have shown the mantis does not identify prey based on a simple template, but uses a computational algorithm to define prey, similar to that seen in the toad (Ewert, 1987; Ewert, 1989; Gonka *et al.*, 2000). The mantis simultaneously assesses a number of visual parameters to identify an object as 'prey'

or 'not prey', including object size, distance, speed, movement pattern and contrast to background (Prete, 1992; Prete, 1993; Prete and Mahaffey, 1993; Prete and McLean, 1996; Yamawaki, 2000; Prete *et al.*, 2002; Yamawaki, 2003; Prete *et al.*, 2012). The mantis is a generalist predator and does not have a sharply tuned prey preference type. *Sphodromantis lineola* has been shown to track black square targets ranging from 10° to 48° and preferentially strikes at 12° x 12° black square targets (Prete, 1993; Prete, 1999; Prete *et al.*, 2002). The distance of a moving target affects the likelihood of the mantis to strike at targets, with the number of strike responses reducing as distance is increased from around 2.5cm (Prete and Mahaffey, 1993; Nityananda *et al.*, 2016a); although distance does not have the same effect upon the tracking behaviour (Prete and Mahaffey, 1993). By moving a target over a horizontally moving patterned background, Prete and Mahaffey (1993) found that background movement reduced the number of strikes the mantis made towards a moving target, however, background movement did not affect the tracking behaviour. These results suggest that the mantis is flexible in which targets it will track, and will readily track targets ranging in size and distance; but shows specificity before attempting to capture prey ensuring the target matches the correct combined target parameters before releasing the strike behaviour (Prete and Mahaffey, 1993; Nityananda *et al.*, 2016a).

1.10 Project outline

In this thesis, I explore mechanisms underlying motion vision in the preying mantid in relation to its predatory behaviour, and how it detects its prey. Firstly, in Chapter 3, I investigate the perception of apparent motion in the mantis. By using

computer generated stimuli, I measure and characterise Dmax in an insect and compare it to that of the human Dmax.

Chapter 4 explores the effects of movement on crypsis through background matching. Prey often need to move when visually hunting predators are active. Although movement is considered to break camouflage, it is not known if there are any benefits associated with background matching when prey are moving.

Chapter 5 explores a related question of whether prey are able to reduce the probability of being detected by predators by matching the motion pattern in their environment. It is thought the swaying behaviour of stick insects is an attempt to mimic background motion, allowing them to blend in to their surroundings; however, there is little evidence to show this type of behaviour carries any survival benefits.

Finally, in Chapter 6, I aim to characterise and compare the distinct temporal and spatial signatures of the praying mantis tracking and optomotor systems. Insect studies have revealed motion detectors tend to be tuned to spatio-temporal combinations which match their behavioural ecology. These studies almost exclusively use drifting wide-field stimuli measuring a response from neurons which monitor optic flow. Few studies have concentrated on small target tracking systems which are interested in detecting and tracking small features such as prey or con-specifics.

Chapter 2: General methods

2.1 Subjects

Mantids used in experiments were acquired from a UK breeder. They were housed individually in plastic boxes (17 cm length, 17 cm width, 19 cm height) with holes in the lid for ventilation. The housing facility was maintained at 25°C with a 12-hour light/dark cycle and the boxes were regularly misted with water to raise the humidity. They were fed one medium-sized field cricket (18 – 25mm) twice per week. The number of individuals used in each experiment can be found within each experimental chapter.

2.2 Experimental set-up

In each experiment mantids were individually positioned in front of a CRT monitor upon which visual stimuli were presented (Figure 6). Subjects were positioned underneath a Perspex perch (5x5cm), which was clamped in front of the CRT screen. We chose to position the mantis upside down hanging from the perch as this is how we observed them hunting prey within their housing facility. We left the mantids unrestrained so as to allow them to behave as naturally as possible.
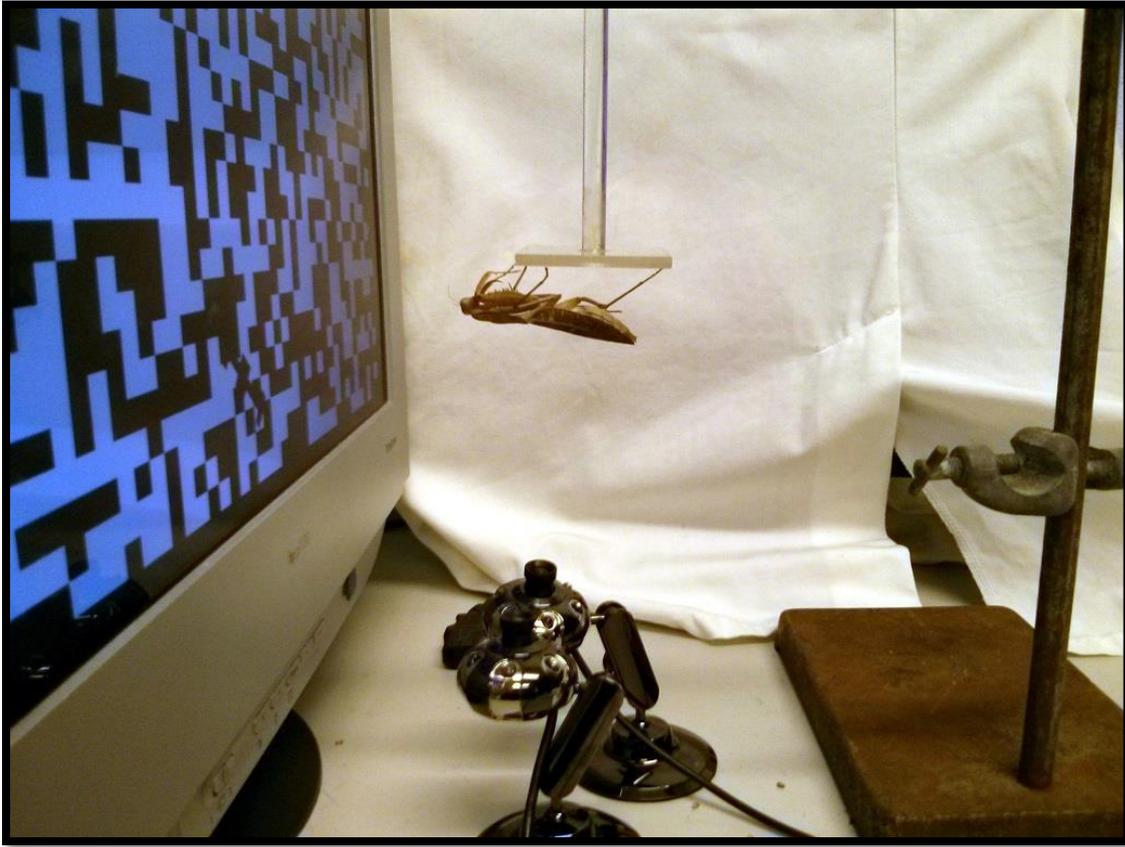
Figure 6. Experimental set up with the mantis viewing the visual stimulus. The web cam is positioned so the observer can record the mantis response blind to the stimulus.

2.2.3 Equipment

In chapter 3 we used a (Hewlett-Packard 21" colour monitor P1130, refresh rate 85Hz) with a resolution of 1600 x 1200 pixels, with a pixel density of 40pixels/cm. In chapters 4, 5 and 6 we used a (Phillips 107B3 colour CRT monitor 33cm x 24.8cm, refresh rate 85Hz) with a resolution of 1280 x 960 pixels, with a pixel density of 38.75pixels/cm. By using electroretinography the maximum resolvable flicker fusion frequency of the mantis (*Tenodera aridifolia sinensis*) was found to be at 50Hz in dark adapted conditions (Prete, 2004). However, the maximum flicker fusion rate of the acute zone remains unknown and is expected to be higher than that of the

rest of the eye. For this reason, we wanted to use a CRT monitor with a high refresh rate to ensure the stimulus appears stable to the mantis observer. Both monitors used throughout the experiments were gamma corrected using a Minolta LS-100 photometer. A wooden box (66L x 53W x 60H cm) was placed around the set-up to prevent disturbance.

A Kinobo USB B3 HD Webcam (Point Set Digital Ltd, Edinburgh, Scotland) was placed directly beneath the mantis to record behaviour. The output of the camera was fed to a DELL Optiplex 9010 computer and to a monitor where an observer could record mantid behaviours in real time. The camera was positioned so that the observer only had a view of the mantis and not of the computer screen to ensure the observer coded the mantis behaviour blind to the stimuli presented. Stimuli were presented in a random order determined by the computer program. Details of the stimulus presented on each trial were recorded by the computer along with the judgments made by the human observer, for later comparison and analysis.

2.2.4 Viewing distance

In chapter 3 the viewing distance of the screen for each mantid was 8cm. The visual angle of the screen subtended 135° horizontally and 122° vertically on the mantids retina with 10 pixels subtending a visual angle of 1.79°. In chapters 4, 5 and 6 the viewing distance of the screen for each mantid was 6cm. The visual angle of the screen subtended 140° horizontally and 128° vertically with 10 pixels subtending a visual angle of 2.4°. We chose these viewing distance so the monitor was out of striking range of the mantis (Rossel, 1983; Nityananda *et al.*, 2016b), preventing them from climbing onto the CRT monitor during the experiment. From pilot trials, we also

found mantids had good a tracking response rate towards small moving targets at this range of distances.

2.3 Experimental procedure

All visual stimuli were created with a custom written script using Matlab (MathWorks) and the Psychophysics Toolbox. Specific details of each visual stimuli can be found in each experimental chapter. Each mantis was shown a series of trials containing the visual stimuli. In between trials, the mantis viewed a static background image of a random chequerboard pattern i.e. a pattern made up of square tiles coloured randomly either black or white with equal probability. Before each presentation of a test stimulus, the mantids head needed to be aligned with the centre of the screen to ensure each test condition passed through the foveal region of the eye. This consisted of a dark circle moving across the background image in a spiral motion from the edge of the screen to the centre. This was to attract the mantids gaze and ensure that its head was finally positioned towards the centre of the screen. Further alignment was made manually by moving the entire background image to the left or the right via the arrow keys, triggering the optomotor response, until the mantis was aligned to the centre of the screen (Nityananda *et al.*, 2015). Once the mantis was aligned, I presented the visual stimuli (detailed in each experimental chapter). Once the test stimuli was presented I recorded the mantids response accordingly for each experiment. Details of behaviours recorded can be found within each experimental chapter. Once the mantids response was recorded, there was an interval of 15 seconds during which the background image was displayed. Then the alignment stimulus was automatically generated to centre the mantids head before the next stimulus was

presented. The stimulus type and behavioural observations for each trial were recorded for later analysis.

2.4 Behaviour

2.4.1 Optomotor response

The optomotor response has been used as a behavioural measure in many studies investigating insect motion vision (Fermi and Reichardt, 1963; Reichardt and Wenking, 1969; Reichardt and Guo, 1986; Duistermars *et al.*, 2007; Trischler *et al.*, 2010; Nityananda *et al.*, 2015). The optomotor response involves a leaning movement of the mantids entire body in the same direction as moving wide field stimuli. It is distinctly different from the saccadic tracking response which is primarily defined by head movements and is seen in response to small moving targets (Prete and Mahaffey, 1993). An example of the mantis optomotor response can be found on the following website (sixth video): http://www.jennyreadresearch.com/2016/mantis-videos/. We used the optomotor response in chapters 3 and 6 to determine whether the mantis could detect movement of a wide field stimuli. Although the optomotor response can be defined by a range of properties, such as the torque response; we only needed to record whether the mantis elicited the optomotor response or not to verify the mantis detected wide field movement. Therefore, we recorded the optomotor response simply as leaned left, leaned right or no response.

2.4.2 Tracking response

The mantis tracking response is defined by the saccadic movement of the mantids head, unlike the optomotor response the body remains stationary. The

mantis moves it head in response to small moving targets in an effort to keep the target image over the foveal region of the eye (Rossel, 1979; Rossel, 1980). We used the tracking response of the mantis in chapters 4, 5 and 6 to measure the mantids predatory response to small moving targets. We recorded each head movement left or right as a single tracking event. An example of the mantis tracking response can be found on the following website (first video):

http://www.jennyreadresearch.com/2016/mantis-videos/

2.4.3 Other behaviours

The mantis peering and strike behaviours were also recorded throughout chapters 4, 5 and 6 towards small moving targets, however these behaviours rarely occurred and therefore were not included in the results sections.

The mantis peering behaviour can be described as a swaying of the mantis prothorax whilst keeping the head looking straight forward and moving linearly. The peering behaviour is used by the mantis to aid in distance estimation of a stationary object (Kral and Devetak, 1999; Kral, 2012).

The mantis strike response is released during prey capture and is displayed when prey like targets come within the prey 'capture range'. It is possible we did not observe this behaviour frequently due to the size of our viewing distance. The optimal prey capture range is approximately 2.5cm, with frequency of strikes reducing as the viewing distance increases (Prete and Mahaffey, 1993; Nityananda *et al.*, 2016a; Nityananda *et al.*, 2016b). An example of the strike behaviour can be found on the following website (second and third video):

http://www.jennyreadresearch.com/2016/mantis-videos/

Chapter 3: Apparent-motion perception by the Praying Mantis (*Sphodromantis lineola*)

3.1 Abstract

Detecting movement using vision is vital to the survival of many animals enabling them to orient, track prey, avoid predators and find a mate. Motion detectors operate in a diverse range of animals from insects to humans. The motion detectors that underlie the optomotor response, a turning response and caused by wide-field motion used to stabilise the insect relative to their environment, respond best to specific patterns and directions of movement. To investigate the properties of motion detectors in a range of visual systems scientists often use the apparent motion of a computer generated wide-field stimulus. Apparent motion can be described as a series of static images which are displaced by a short distance in frequent jump steps; this creates the appearance of smooth motion. By displacing the image in increasingly larger / less frequent jumps, the perception of smooth motion begins to break down, resulting instead in the perception of a jerky movement. Ultimately the perception of coherent motion breaks down when the distance the image is displaced by becomes too large, leaving the participant unable to discriminate which direction the pattern is moving in. The displacement beyond which, coherent motion breaks down has been termed Dmax (Chang and Julesz, 1983). Dmax has been frequently used by vision scientists to investigate the nature of the computations underlying motion detection (Cleary and Braddick, 1990; Glennerster, 1998; Ho and Giaschi, 2009; Wattam-Bell, 2009; Wexler *et al.*, 2013). Dmax was initially thought to represent the limited spatial range of local Reichardt motion detectors. However, it was found by varying the size of the pattern elements that Dmax increases as the pattern element size increases,

whereby a pattern with large elements could make larger jumps before coherent motion breaks down compared to patterns with smaller elements. This, along with other evidence, has led to the theory that there are multiple motion detectors within the visual system which are tuned to different spatial scales, each with a Dmax value dependent on its spatial frequency tuning. I use the praying mantis *Sphodromantis lineola* to measure Dmax in an insect. I wish to determine whether the insect Dmax has a defined spatial limit, independent of the pattern chequer size, or whether, like the human visual system, Dmax is dependent on the pattern spatial frequency. This would allow us to see whether insect motion detectors have a set receptive field or whether like humans there are motion detection mechanisms capable of pooling motion information over a large area depending on the spatial frequency of the pattern. Here we show that as an image is displaced by an increasing distance each frame, the probability of the mantis responding with the optomotor response decreased. By setting Dmax as 50% probability of correct response; I found that the largest jump step a pattern could make before apparent motion began to break down (Dmax) increased as pattern chequer size increased. These findings suggest the insect motion detection system has similar motion processing mechanisms as humans whereby low frequency local motion is being pooled over a larger visual area compared to higher spatial frequency images. These findings are the first time Dmax has been characterised in this way in an insect and highlights similar characteristics to the human Dmax

3.2 Introduction

Motion perception is required to solve many visual tasks such as figure ground segregation when tracking prey and optic flow regulation when maintaining body orientation during self-motion. To do this, animals have motion detectors, which are selective for the direction an object or surround is moving (Hassenstein and Reichardt, 1956; Barlow and Levick, 1965; Reichardt and Poggio, 1976; Van Santen and Sperling, 1985; Reichardt, 1987). In the insect, motion detectors were first studied using the optomotor response, which is a turning response caused by motion of the visual environment and is used by an insect to hold a steady position, or a heading, relative to its visual surroundings (Srinivasan *et al.*, 1999). In the case of the stationary insect, motion of its surroundings to the left causes a turn to the left, with the insect appearing to follow the direction of motion. This occurs because the imposed motion of the surroundings to the left is interpreted by the insect to be due to its own unintended motion to the right, which is then corrected by a corresponding turn to the left. Elementary motion detectors (EMDs) underlie this optomotor response. EMDs sample the luminance of an image at two adjacent points on the retina and correlate the changes at these two points. The signal at the two points is delayed and then multiplied with the un-delayed signal in the adjacent location (Figure 2). The output of one half-correlator is then subtracted from the other to give a directional output which is positive for motion in one direction and negative for motion in the opposite direction (Borst and Egelhaaf, 1989; Egelhaaf *et al.*, 1989; Douglass and Strausfeld, 1996; Harris *et al.*, 1999; Srinivasan *et al.*, 1999).

The range of image velocities to which an elementary motion detector responds is determined by its spatial and temporal input filters. By increasing the spatial separation of the two inputs or decreasing the delay period causes the EMD to

be tuned to higher velocities (O'Carroll *et al.*, 1997). This makes motion processing in EMD's dependent upon a surround's spatial and temporal frequencies (O'Carroll *et al.*, 1997; Borst *et al.*, 2010). Sine wave gratings have often been used to test the properties of different motion detection systems (Campbell and Robson, 1968; Thompson, 1982; O'Carroll *et al.*, 1997). By moving sinusoidal gratings at different speeds, we can study the spatial and temporal filtering mechanisms of movement detectors (Kulikowski and Tolhurst, 1973; Thompson, 1982; O'Carroll *et al.*, 1997).

Following the Hassenstein-Reichardt elementary motion detection model scientists have set out to identify the underlying circuitry involved in motion detection. Although no-one has yet recorded directly from an elementary motion detector, it is now well-established in Drosophila that two neurons, L1 and L2, from two columns of the fly lamina, are responsible for signalling light increments (ON) and light decrements (OFF) at two adjacent points (Joesch *et al.*, 2010; Eichner *et al.*, 2011; Joesch *et al.*, 2013). These neurons provide input for systems designed to detect moving edges. Output from the L1 (Light ON) and L2 (Light OFF) cells eventually lead to the creation of small directionally selective cells in the medulla, T4 and T5 (Figure 3). These cells are tuned to motion traveling in a specific direction within a specific spatiotemporal receptive field (Douglass and Strausfeld, 2003; Takemura *et al.*, 2011; Schnell *et al.*, 2012; Takemura *et al.*, 2013a). This motion information sampled by many small T4 or T5 motion detectors is then pooled in the Lobula Plate by large Tangential Cells (LPTC) (Borst and Egelhaaf, 1989; Franceschini *et al.*, 1989; Borst *et al.*, 2010; Maisak *et al.*, 2013; Borst, 2014; Hidayat *et al.*, 2015). These LPTCs have large receptive fields and are a major component in the optomotor pathway used in body stabilisation (Hausen, 1984; Hausen and Egelhaaf, 1989).

Dmax has been frequently used by vision scientists to investigate the nature of motion detection systems (Braddick, 1974; Braddick *et al.*, 1980; Morgan, 1992). Dmax can be described as the maximal displacement a pattern can make before apparent motion breaks down. Dmax was initially thought to represent the limited spatial range of local Reichardt motion detectors (Braddick, 1974; Braddick *et al.*, 1980). However, it has been found that Dmax increases as the pattern element size increases, i.e. a pattern with large elements can make larger jumps before coherent motion breaks down compared to patterns with smaller elements (Chang and Julesz, 1983; Cleary, 1987; Cleary and Braddick, 1990; Morgan, 1992; Morgan and Fahle, 1992). This has led to the theory that there are multiple motion detectors within the human visual system which are tuned to different spatial scales, each with a Dmax value dependent on its spatial frequency tuning (Cleary and Braddick, 1990; Morgan and Fahle, 1992).

Although Dmax has been widely studied in the human visual system, it has not been studied in insect motion detection systems. In this chapter, I use the praying mantis, *Sphodromantis lineola*, to measure Dmax in an insect. I aim to determine whether the insect Dmax has a defined spatial limit independent of the pattern element size, or as in humans, Dmax is dependent on the pattern spatial frequency. This study investigates whether insect motion detectors have a set receptive field or, like humans, there are motion detection mechanisms capable of pooling motion information over a large area depending on the spatial frequency of the pattern.

3.3 Methods

I used ten adult and four 5th instar female African lined mantids (*Sp*hodromantis lineola). In this chapter, the test stimulus consisted of a random black and white chequerboard pattern i.e. a pattern made up of square tiles coloured randomly either black or white with equal probability, which filled the entire screen. During a trial, the test stimulus was redrawn at regular intervals, each time to the left (or right) of its previous position, so that it appeared to jump across the screen. When the jumps are small enough, this creates the perception of apparent motion and the mantid will respond with the bodily stabilising optomotor response. I manipulated three variables in the test stimuli: the chequer size (size of each tile in the chequerboard, in pixels; Figure 7), the jump step (distance the pattern was displaced at each jump, in pixels) and the direction the pattern moved, left or right (Table 1). Each chequerboard pattern had the same mean luminance (36cd/m2), and patterned backgrounds had equal numbers of white (72cd/m2) and black chequers (0.052cd/m2). The time between jumps was kept proportional to the jump size so as to keep the pattern speed a constant 60 deg/sec in all trials. The experimental procedure used can be found detailed in chapter 2 (section 2.3). After each stimulus was displayed I recorded the mantis optomotor response as one of three responses: lean left, lean right or no response. Each combination shown in table 1 were randomly displayed in blocks of 20 where 10 trials moved left and 10 trials moved right. These blocks were then repeated over several days with each individual mantis. The number of mantises which viewed each tested variable combination is shown in table 1, where each combination was presented a minimum of 20 times.

Decreasing chequer size
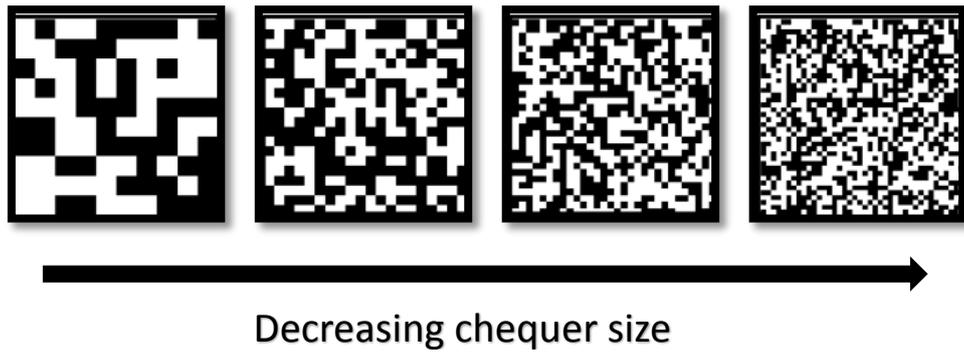
Figure 7. Visual stimuli were chequerboard patterns of different chequer sizes

Table 1 Parameters of the visual stimuli: chequer size and size of the pattern displacement (jump size) in each frame. All the combinations of the pattern chequer size and pattern jump size listed below were presented at random. As the chequer size increased, I increased the jump step in order to find Dmax. All combinations were presented a minimum of 20 times to each mantid.

Chequer size (pixels)	Distance pattern jumped in pixels (*N mantids*)	Direction
1	6 (*13*), 7 (*6*), 8 (*3*), 9 (*6*), 12 (*13*), 15 (*9*), 20 (*9*), 24 (*13*), 27(*12*)	Right/Left
2	6 (*13*), 7 (*3*), 10 (*13*), 12 (*6*), 14 (*6*), 16 (*3*), 18 (*13*), 20 (*6*), 24 (*13*), 28 (*4*), 32 (*12*), 36 (*9*)	Right/Left
4	6 (*13*), 8 (*13*), 14 (*13*), 20 (*13*), 24 (*13*), 28 (*3*), 32 (*11*), 36 (*6*), 40 (*11*)	Right/Left
8	6 (*11*), 8 (*3*), 16 (*11*), 20 (*9*), 24 (*11*), 28 (*9*), 34 (*9*), 36 (*9*), 40 (*13*), 44 (*9*)	Right/Left
16	8 (*13*), 16 (*3*), 32 (*11*), 35 (*9*), 40 (*13*), 50 (*9*), 56 (*3*), 60 (*13*), 70 (*9*), 80 (*3*)	Right/Left
20	10 (*13*), 20 (*11*), 30 (*9*), 40 (*13*), 45 (*9*), 50 (*9*), 60 (*10*), 70 (*3*), 80 (*13*), 100 (*11*)	Right/Left
25	15 (*9*), 25 (*11*), 35 (*9*), 40 (*9*), 50 (*11*), 60 (*9*), 68 (*6*), 70 (*9*), 80, 74 (*2*), 80 (*13*), 100 (*9*), 125 (*3*)	Right/Left
40	20 (*13*), 40 (*13*), 50 (*9*), 58 (*6*), 60 (*9*), 80 (*13*), 100 (*3*), 200 (*3*)	Right/Left

3.4 Data Analysis

The mantids were rarely recorded as leaning in the opposite direction to the direction of stimulus motion (2.2%; in agreement with Nityananda *et al.* (2015)). This indicates when the mantis leaned in the same direction as the stimulus motion, it is attempting to stabilise bodily orientation relative to the stimulus. I used this optomotor stabilisation response as an indicator that the mantis could see the motion of the stimulus. Accordingly, for this experiment, I discarded the small number of trials in which the observer coded the mantis as moving in the opposite direction to the stimulus, and counted a "response" as a movement in the stimulus direction. I then plotted the mean and standard error as the probability of a correct response for each chequer size, as a function of jump step.

In human psychophysics, Dmax is usually measured in a two-alternative forced-choice task where observers report whether a stimulus moved left vs right, or up vs down. When observers cannot perceive motion, they are correct 50% of the time by chance. Dmax is usually defined as the jump step for which observers are halfway between chance and perfect performance, i.e. 75%. In our mantis psychophysics, responses could not be forced. When the mantises could not perceive motion, they did not respond. We therefore define Dmax as the jump step for which mantises responded on half of the trials, i.e. at 50%.

3.4.1 Calculating Dmax

A psychometric function was fitted to the response rate versus step size (per chequer size, figure 8) in order to calculate Dmax, the largest jump step the pattern could make before apparent motion breaks down, and the mantis stopped

responding. To get accurate estimates of Dmax, it is necessary that the difference between the psychometric function values and the data points is minimized. However, one complication is that there are different numbers of trials per condition and this variability must be taken into consideration during the fitting process (i.e. points with more trials have higher certainty and must weigh more in the fitting process). Additionally, even when the number of trials is the same, the uncertainty depends on the response rate (e.g. the confidence interval is larger on an estimated response probability of 0.5, if the mantis responds on 5/10 trials, than on the estimated response probability of 1.0 if the mantis responds on 10/10 trials).

To account for the different certainties of the individual data points we used maximum likelihood estimation to obtain the fits (Figure 8). We assume that the probability of the mantis responding (P_m) has a binomial distribution and then attempt to maximize the likelihood function:

$$\text{likelihood} = \prod_{i=1}^{n} \binom{N_i}{M_i} \times P_m{}^{M_i} \times (1 - P_m)^{N_i - M_i}$$

Where N_i is the number of trials carried out with jump step J_i and M_i is the number of responses obtained. We did this using the Matlab function fminsearch to find the fit parameters σ and D_{max} which minimise the negative log likelihood of the data over all jump steps J_i at a given chequer size:

We then took its logarithm:

$$\log(\text{likelihood}) = \sum_{i=1}^{n} \log\left(\binom{N_i}{M_i}\right) \times M_i \times \log(P_i) + (N_i - M_i) \times \log(1 - P_i)$$

Then maximizing the latter by finding a fit P_m that maximizes the expression:

$$\sum_{i=1}^{n} M_i \times \log(P_i) + (N_i - M_i) \times \log(1 - P_i)$$

After obtaining the Pm fits for each block size, the stepping distance corresponding to 50% probability of motion was calculated and labelled Dmax (Figure 8, dotted line on each plot). Each sigmoid fit is uniquely characterized by its Dmax and an additional parameter (Sensitivity) which determines the curve steepness.

Finally, we used bootstrap resampling to obtain a measure of the certainty of Dmax and Sensitivity values obtained for each block size. We generated 1000 sets containing binomially distributed values for each data point (assuming that probability of motion equals the fitted Pm) and then fed these into the fitting procedure described above to obtain 1000 Dmax and Sensitivity values and calculate their standard deviation per block size.

This process generated the psychometric function parameters that were statistically most likely to yield the response rates that we observed experimentally. Each psychometric function had two parameters: a threshold corresponding to the 50% response rate and a spread parameter that determined the width of the functions' transition period (i.e. the smoothness of the function).
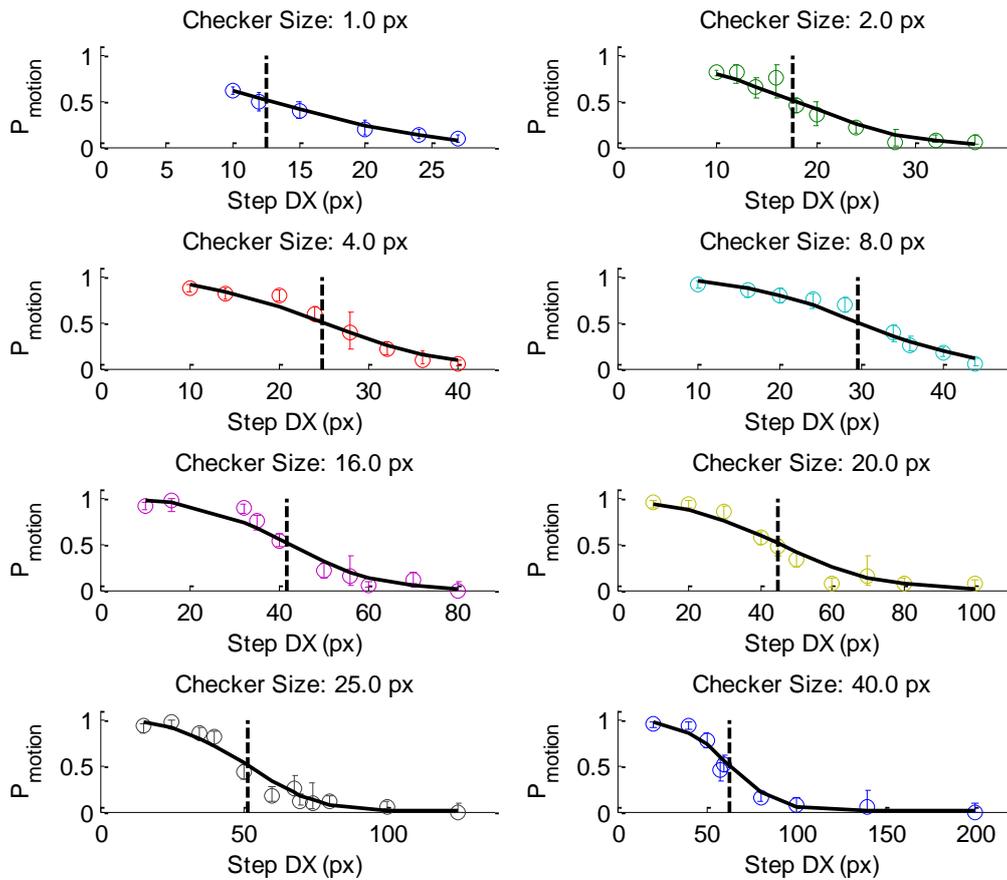
Figure 8: Psychometric function for each pattern block size. We used maximum likelihood estimation to fit the probability of the mantis responding (Pmotion) as a function of pattern jump step (step DX). The pattern jump step corresponding to 50% probability of motion was calculated and labelled Dmax. The vertical dotted line on each plot represents Dmax for each pattern chequer size (pixels). The scale on the x-axis varies according to chequer size plot (*Dmax calculation and psychometric functions carried out and created by Ghaith Tarawheh*).

3.5 Results

For each pattern chequer size, the probability of the mantis responding with an optomotor response decreased as the jump step of the pattern increased (Figure 9). This suggests that when the pattern made a series of small jumps the

mantis perceived the pattern as moving. When the jump steps increased, this perception of apparent motion breaks down, and the mantis is less likely to respond with the optomotor response. I found the probability of the mantis responding with the optomotor response to patterns with small chequers fell below chance (50%) at smaller jump steps compared to patterns with larger chequers (Figure 10).

Using the maximum likelihood fitting to estimate Dmax for each pattern chequer size, we found that as the pattern chequer size increased Dmax also increased (Figure 11). Therefore, patterns with larger elements are able to make larger sucessive jumps before apparent motion begins to break down compared to patterns with smaller elements.

Figure 9. The probability of the mantis making a correct response with increasing pattern jump step. Each graph represents a particular pattern chequer size, where 10 pixels subtended a visual angle of 1.79°. The scale on the x-axis varies according to chequer size. The number of mantids for each data point can be found in Table 1.
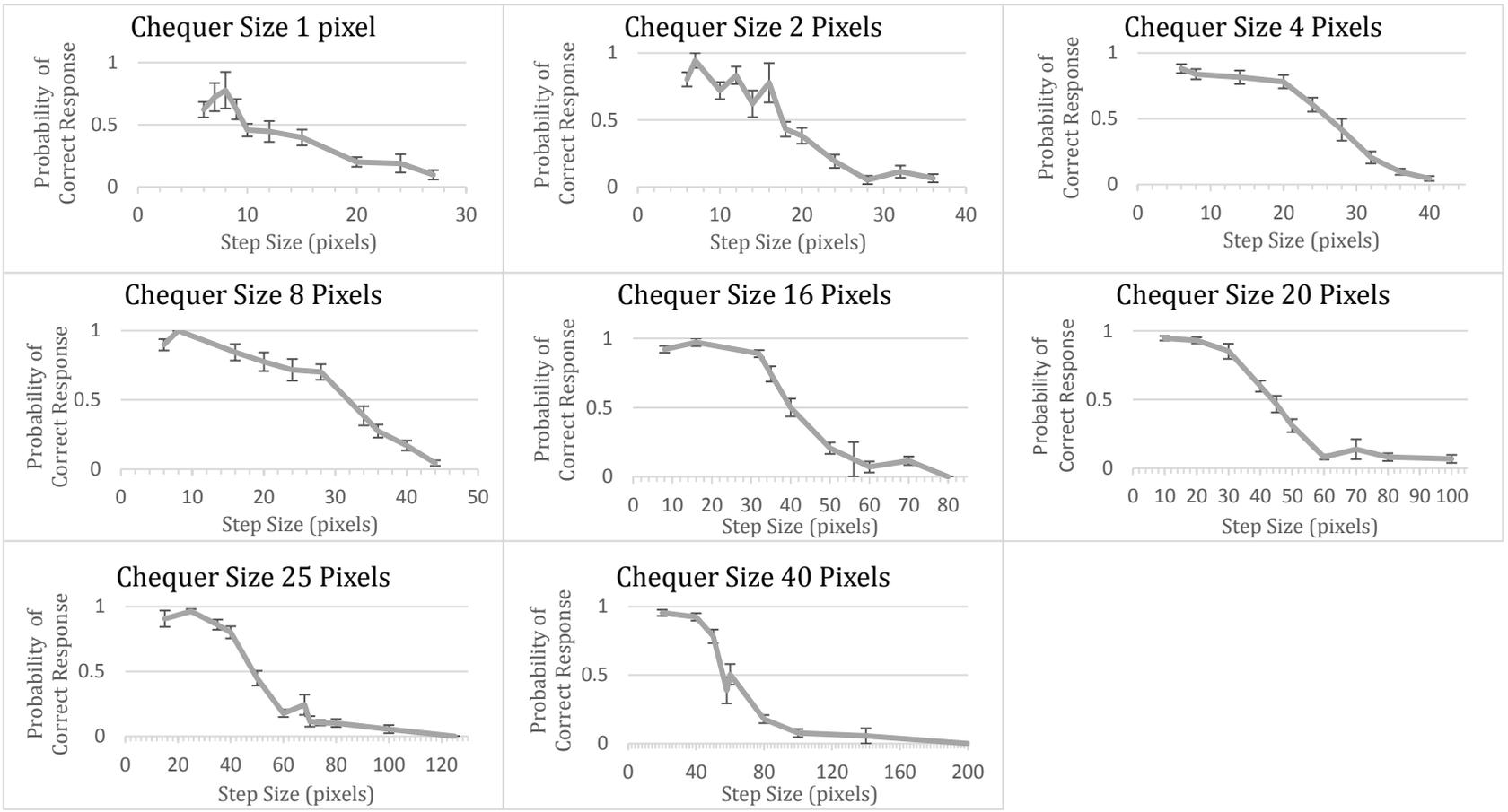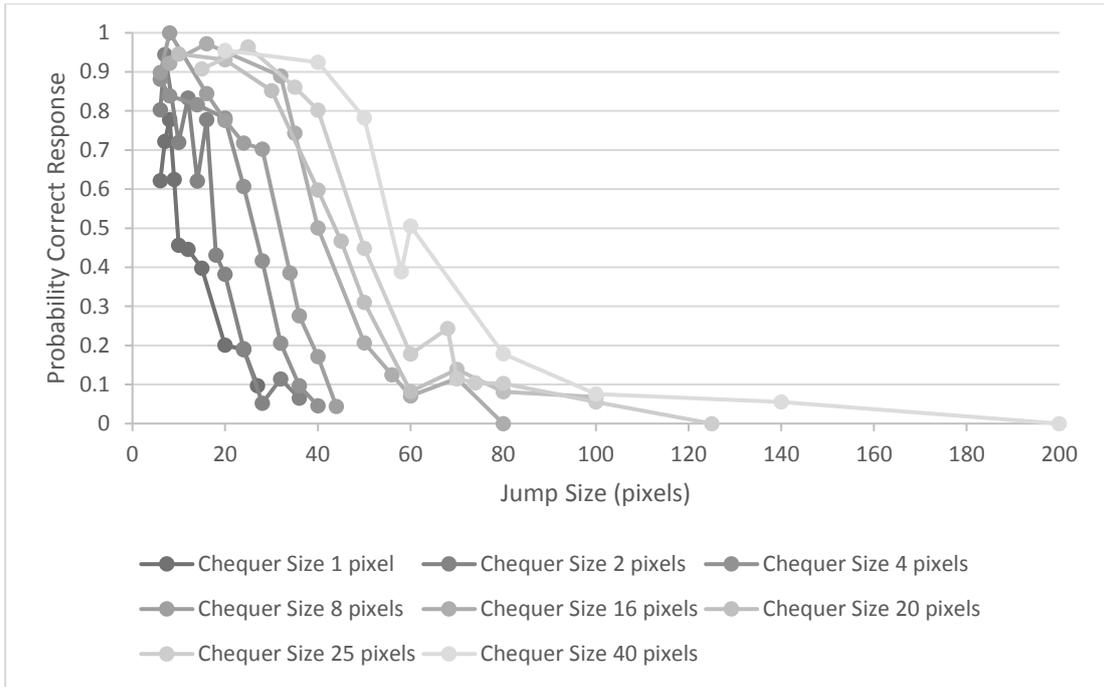
Figure 10. The probability of the mantids making a correct response with increasing pattern jump step for each pattern chequer size, where 10 pixels subtended a visual angle of 1.79°.
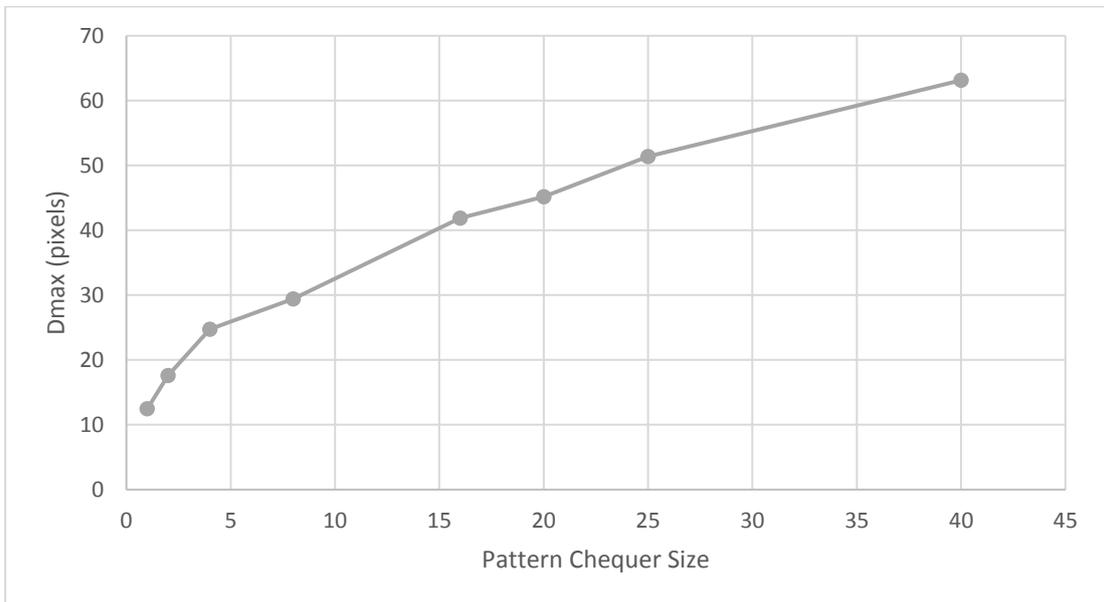
Figure 11. The graph shows Dmax, the largest jumps step the pattern can make before apparent motion breaks down, as a function of pattern chequer size. Using a maximum likelihood fitting we estimated Dmax for each pattern chequer size

3.6 Discussion

My results show that as an image is displaced by an increasing distance each frame, the probability of the mantis responding with the optomotor response decreases. I found that the largest jump step a pattern could make before apparent motion began to break down (Dmax) increased as pattern chequer size increased. This is the first time that Dmax has been characterised in this way in an insect, and highlights similar characteristics to the human Dmax (Cleary and Braddick, 1990; Morgan, 1992).

When the pattern jump step became too large the mantids failed to perceive the pattern as moving coherently in a particular direction and therefore no longer responded with the optomotor response. These results are similar to those found in humans where the perception of apparent motion breaks down as images are displaced by larger distances each frame (Braddick, 1974; Braddick *et al.*, 1980). It was initially thought this Dmax limit represented the spatial limit of elementary motion detectors in the visual system (Braddick, 1974; Braddick *et al.*, 1980). However, like human studies (Chang and Julesz, 1983; Cleary, 1987; Cleary and Braddick, 1990; Morgan, 1992; Morgan and Fahle, 1992) my results show Dmax in the insect does not have a set spatial limit but is dependent on the size of the pattern elements, where Dmax increased with pattern chequer size. If Dmax represented the spatial limit of early motion processing systems, such as the insect elementary motion detectors, Dmax should be independent of pattern spatial frequency. This shows that the mechanisms involved in motion processing may be quite similar in both insects and humans.

Although it is difficult to compare my results directly to those investigating human Dmax, as the human Dmax has been measured in terms of the distance

between like zero crossings (arcmin) and I measured the mantis Dmax in terms of actual pixels; we can clearly see similarities in the characteristics of the human and insect Dmax. Both human and mantis Dmax increases as the size of the pattern elements increases, however the human Dmax stays nearly constant at small pattern chequer sizes and only begins to increase as the pattern chequer size reaches approx. 10 arc min (Figure 12). In comparison, our results show that the insect Dmax increases steadily and does not seem to have this plateau at small pattern element sizes. This may be due to our study not sampling patterns smaller than 1 pixel, however we are limited in how fine we can make our pattern due to the low spatial resolution in insects in comparison to the human visual system.
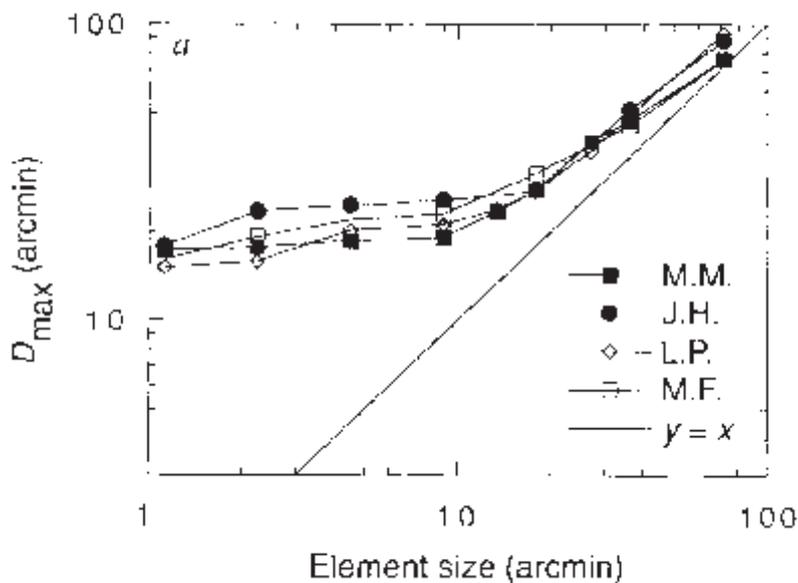
Figure 12. Results of an experiment and model to determine the upper limit for the human Dmax as a function of the size of the elements in random chequerboard patterns. Each set of points represents data from a different observer. Each point is the mean of four readings. Dmax is nearly constant over a range 1-10 arcmin, but arises thereafter. (Morgan, 1992)

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It has been suggested the dependence of Dmax on pattern spatial frequency in humans is reflective of multiple motion processing channels which are tuned to differing spatial frequencies, each with their own Dmax. Channels which are tuned to low spatial frequencies were thought to have larger receptive fields than channels which are sensitive to higher spatial frequencies (Cleary and Braddick, 1990; Morgan, 1992; Morgan and Fahle, 1992). This would allow low frequency patterns to be displaced by larger distances before apparent motion breaks down compared to channels tuned to high frequency patterns. The optic lobes of the insect have a columnar retinotopic structure where by higher order directionally selective neurons in the medulla, lobula and lobula plate collect motion information from multiple columns (Douglass and Strausfeld, 2003; Borst *et al.*, 2010; Joesch *et al.*, 2010; Takemura *et al.*, 2013a). If a similar motion processing mechanism is at play in the insect visual system, it is likely that low frequency local motion is being pooled over a larger visual area compared to higher spatial frequency images. This could explain why low frequency patterns are able to be displaced by a larger jump step and high frequency patterns can only be displaced by a small distance before apparent motion breaks down.

To conclude, I have shown the mantis perceives apparent motion in a similar way to humans, where coherent motion breaks down as the distance a pattern is displaced increases. I have characterised Dmax in an insect model and found like the human Dmax it is dependent on the spatial frequency of the moving pattern.

Chapter 4: Background matching in moving targets

4.1 Abstract

Camouflage is a defensive strategy employed by prey to reduce the risk of being detected by predators. Nearly all research into camouflage strategies, including background matching, have investigated how patterns hide stationary prey, and have predominantly used predator models with high visual acuity, particularly birds and humans. However, many prey need to move when visually hunting predators are active, for example, to forage or find a mate. Although movement is considered to break camouflage, it is not known if there could still be some benefits for moving prey to match the pattern elements in their backgrounds. I investigated this using praying mantids tracking computer-generated targets as prey. The targets were either homogenous black or grey, or were patterned with small, medium and large black and white chequers. The targets moved over a homogenous grey or a black and white chequered background, which had either small, medium or large chequered elements. I found that only prey with large elements in their pattern benefit from matching the background pattern when moving. However, prey that matched the mean luminance of the background and remained unpatterned had a survival advantage over patterned prey, even when the patterned prey benefited from background matching. The mantids were less likely to track prey when they were moving on a heterogeneous patterned background compared to a homogenous grey background. When compared to background matching targets, I found no survival advantage for prey with a compromise pattern moving over similarly patterned backgrounds. Prey pattern size had a strong influence on the probability that a

mantis tracked a target, with mantids being more likely to track a target with large pattern elements compared to small. Although prey with large pattern elements attract a high predatory response from praying mantids, only this prey type was found to benefit from background matching. My results are discussed in relation to camouflage strategies for moving prey and prey preference parameters in the praying mantis.

4.2 Introduction

Predation exerts strong selection pressures on prey, and has led to the evolution of defensive strategies across a wide range of species. These include different forms of camouflage, which allow prey to go undetected either by matching their surroundings (background matching) or by breaking up the bodily outline (disruptive colouration) (Cuthill *et al.*, 2005; Merilaita and Lind, 2005a; Schaefer and Stobbe, 2006; Stevens, 2007). Background matching is a form of camouflage employed by prey to reduce the risk of being detected by predators. By closely matching the background, prey reduce the contrast between their body and the surrounding environment, enabling them to visually 'blend' into the background (Endler, 1978; Endler, 1984). Essentially, the more visually similar to the background the prey colouration and patterning is, the more difficult prey are to detect (Cott, 1940; Edmunds, 1974; Endler, 1978).

The similarity of a prey to its background is often used as a measure of camouflage, for example the peppered moth (*Biston betularia*) against tree bark. However, this assumes that crypsis can be maximised by simply matching a random sample of the background to a high degree. Background complexity and

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heterogeneity can have a large impact on the ability of prey to effectively blend into their surroundings, making it harder for predators to find prey against complex backgrounds (Merilaita, 2003; Merilaita and Lind, 2005b; Dimitrova and Merilaita, 2009; Dimitrova and Merilaita, 2011). Habitats are rarely homogenous and are usually comprised of visually patchy microhabitats, across which prey may need to move in order to search for food, mates and/or shelter. Prey that live in different habitats might adapt to match just one of these microhabitats closely, perhaps the most common background or the one where they spend the majority of their time. However, although this may reduce the risk of being detected in one habitat, it will of course increase the chances of being detected in another (Endler, 1978; Merilaita *et al.*, 1999). Alternatively, prey might be selected to evolve a compromise pattern which minimises predation overall across multiple habitats, rather than minimising it in just one (Merilaita *et al.*, 2001; Dimitrova and Merilaita, 2014).

Camouflage acts to reduce visual cues that allow predators to distinguish an object from its background. One of the basic and fundamental problems that the visual systems of both vertebrates and invertebrates have had to overcome is to segregate an object from its background. From finding a mate to searching for prey, the visual system needs to group the features of an object from other objects and the features of the background. It does this through processing various sources of information from a visual scene such as luminance contrast, objects form, texture, depth and motion information (Livingstone and Hubel, 1988; Borst and Egelhaaf, 1989; Lamme, 1995). By reducing a prey's contrast relative to its background, or by breaking up the bodily outline, camouflage makes it difficult for

a predator to segregate prey from the background (Merilaita and Lind, 2005b; Schaefer and Stobbe, 2006; Stevens, 2007). However, when an object moves, it becomes more apparent through 'figure ground segregation', where the visual system is able to define an object through its motion relative to the background motion (Collett, 1971; Egelhaaf, 1985; Nordström *et al.*, 2006; Geurten *et al.*, 2007).

There are numerous empirical studies measuring the benefits of background matching, which have almost exclusively focused on how patterns enhance the survival of stationary prey (Merilaita *et al.*, 1999; Merilaita *et al.*, 2001; Merilaita, 2003; Cuthill *et al.*, 2006) Some studies have shown bodily markings and even prey movement pattern could give moving prey a survival advantage by reducing capture (Mizutani *et al.*, 2003; Stevens *et al.*, 2008). However, there are few studies that have investigated whether established camouflage strategies, such as background matching, benefit prey when moving. A recent study investigated the effects of motion on a range of camouflage strategies such as background matching and disruptive colouration. Using humans as the predator model, Hall *et al.* (2013) showed that target movement significantly reduced search time in all camouflage strategies compared to stationary targets, effectively breaking camouflage. Prey will often need to move when visually hunting predators are active (Brown, 1992; le *et al.*, 2000; Honkavaara *et al.*, 2002; Brown and Kotler, 2004; Stephens *et al.*, 2007): if camouflage reduces detection only when prey are stationary this will put constraints upon an animal's ability to forage and successfully find a mate.

It is interesting to note that studies of camouflage strategies, whether of stationary or moving prey, have been conducted using vertebrate predator models, particularly birds and humans. These taxa have complex visual systems comprising of a refractive cornea allowing them to focus light upon the retina, an opening pupil which acts to bring an optimal balance between light sensitivity and resolution and a deformable lens allowing them to focus over a range of distances (Land, 2012; Land and Nilsson, 2012). Insect predators, such as praying mantids and dragonflies, have compound eyes, which are very different from the mammalian and avian simple eye. Whilst the compound eye allows a large field of view, the spatial resolution is limited by the width and spatial density of ommatidia, which contain the light sensitive receptors. Although insects have limited spatial acuity, they boast a superior temporal resolution enabling them to see objects moving at high speeds (O'Carroll *et al.*, 1996; Land and Nilsson, 2012; Nityananda *et al.*, 2015). Currently, it is not known how insect predators perceive camouflaged prey, nor whether background matching is an effective strategy against them for moving prey.

In this Chapter, I used praying mantids to investigate the benefits of background matching in moving prey, and test whether background pattern element size affects the ability of predators to detect patterned targets. Praying mantids are opportunistic ambush predators with a well-developed visual system, which they use to locate and capture small prey. They are an ideal model for this study: their visual system is well-studied (Rossel, 1979; Rossel, 1980; Rossel, 1983), they have an array of well-defined predatory behaviours which can be used to measure their responses towards prey (Rossel, 1980; Corrette, 1990; Kral *et al.*,

2000), and they show these behaviours towards computer generated 'prey' presented on computer screens (Prete and Mahaffey, 1993; Prete *et al.*, 2012). Although praying mantids have been used to explore what characteristics of prey (e.g. size, shape, speed) elicit predatory behaviour (Prete and Mahaffey, 1993; Prete and McLean, 1996; Prete *et al.*, 2012) there have been no systematic studies of how camouflage helps moving targets avoid detection from mantids. Mantids rarely respond to stationary prey, which makes it difficult to investigate the benefits of background matching when prey is not moving. However, this makes mantids an ideal model to examine the effects of movement on the detection of background matching prey. This is the first study to use an insect predator to explore the benefits of background matching camouflage patterns in reducing predatory behaviour towards moving prey

4.4 Experiment 1: Investigating the effects of background matching in moving prey.

4.4.1 Introduction

In this first experiment, I investigated whether mantids were less likely to track computer-generated moving prey that had pattern elements that matched the size and contrast of those in their background compared to prey which did not match their background pattern. In addition, I tested if there could be benefits to prey of having compromise camouflage patterns that did not match a specific background pattern but were an intermediate pattern between two backgrounds.

To explore this, I used four different prey types moving across four different backgrounds. I used three high contrast black-and-white 'chequerboard'

patterned prey types, which varied in their pattern chequer size: 5, 10 or 20 pixels. As well as these three different patterned prey types, I also presented black prey (see Figure 13). A variety of praying mantid species have shown strong predatory responses towards black targets which create a high contrast to the background (Prete, 1992; Prete and McLean, 1996). Therefore, black prey were used to ensure that the mantids were responsive even if their predatory behaviour towards patterned prey was low due to the effects of camouflage. These four prey types (black, 5-pixel, 10-pixel and 20-pixel) were presented on four different backgrounds. Three of these matched the black and white chequer patterns of the three prey types (pattern element sizes were 5, 10 or 20 pixels), and the fourth was a uniform grey background with the same mean luminance. Therefore, I was able to compare if background matching was beneficial to each prey type, and also see if tracking prey moving on patterned backgrounds was more challenging for mantids. Based on previous studies (Prete, 1992; Prete and Mahaffey, 1993; Prete and McLean, 1996; Prete *et al.*, 2002), I expected to see a high rate of tracking to the black target compared to patterned targets since it has a greater luminance contrast to all backgrounds. I expected that patterned prey would be more difficult to detect when moving on a heterogeneous complex background compared to a homogenous background (Merilaita, 2003; Stevens *et al.*, 2008).

4.4.2 Methods

The visual stimuli used in this set of experiments consisted of a static background image and a square target (80 pix × 80 pix) subtending $19.3° × 19.3°$ on the mantis retina. The target appeared randomly at the left or right side of the screen, and then travelled across the screen horizontally before returning; this

was repeated for 10 seconds. The target moved with a sinusoidal function with maximum speed of 1166.7pix/sec at the centre of the screen. The target was not visible to the mantis at either edge of the screen when it changed direction.

The procedure followed that in the general methods chapter (section 2.3). After each trial I recorded the mantids behaviour, including: the amount of times the mantis tracked the target (number of head movements the mantis made in either direction), whether or not the mantis showed peering behaviour (defined as leaning from side-to-side), and the number of strikes made at the screen using its forelegs.

The background was either a homogenous grey background or a random black-and-white chequerboard, where each chequer square was generated at 5, 10 or 20 pixels width (Figure 13, E-H). All backgrounds had the same mean luminance ($36cd/m^2$), and patterned backgrounds had equal numbers of white ($72cd/m^2$) and black chequers ($0.052cd/m^2$).

The prey stimulus was either a black homogenous target ($0.052cd/m^2$), or had a chequerboard pattern which matched the mean luminance of the background ($36cd/m^2$). The chequerboard patterns of the prey matched those of the different backgrounds, i.e. they had either a 5, 10 or 20 pixels width (Figure 13, A-D). We know the mantids are able to resolve each target pattern as they responded to patterns as small as 2 pixels in chapter 3 (section 3.5) with the optomotor response.
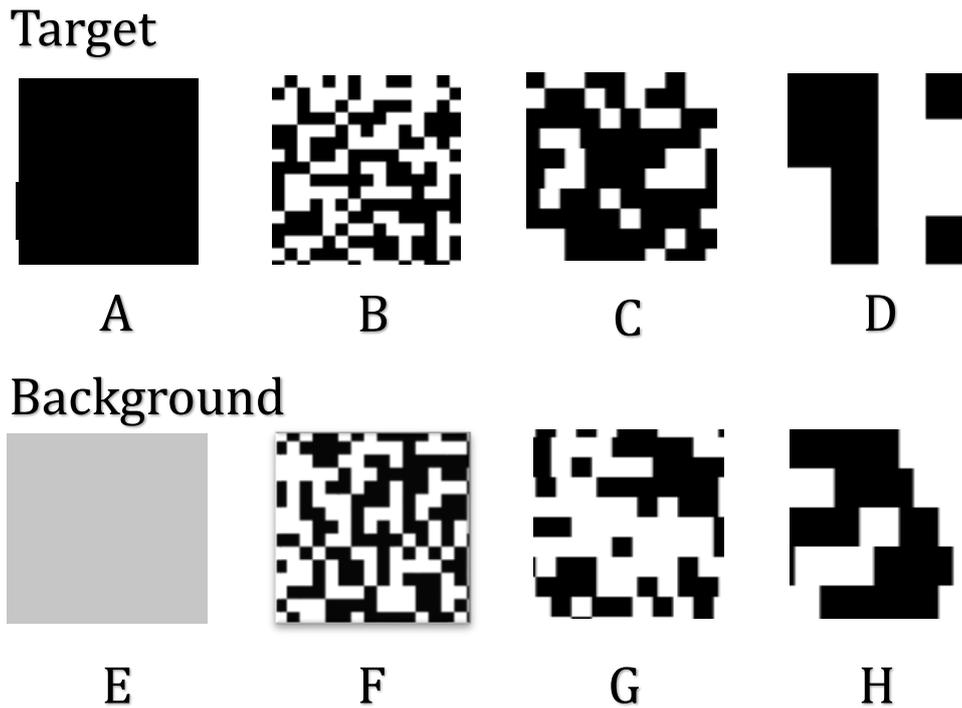
Figure 13. Example of target and background patterns (A) Black Target (B) 5 pixel patterned target (C) 10 pixel patterned target (D) 20 pixel patterned target (E) Homogenous grey background (F) 5 pixel patterned background (G) 10 pixel patterned background (H) 20 pixel patterned background.

All four targets appeared on all four backgrounds (i.e. a 4x4 fully factorial design; Table 2). Within a block of trials, all 16 target and background combinations were presented five times in a random order. Ten mantids completed three blocks of trials, each viewing the 16 conditions a total of 15 times.

Table 2. Test conditions for Experiment 1. Each target appeared on all four backgrounds. The shaded boxes indicate conditions where the prey target matched the pattern of its background.

Background Pattern	Target Pattern (size of chequers)			
Grey	Black	5 pixel	10 pixel	20 pixel
5 pixel chequers	Black	5 pixel	10 pixel	20 pixel
10 pixel chequers	Black	5 pixel	10 pixel	20 pixel
20 pixel chequers	Black	5 pixel	10 pixel	20 pixel

4.4.3 Data Analysis

Statistical analysis was carried out using SPSS V. 22. Data were analysed with a series of generalized estimating equation models (GEE, binary logistic), with target pattern and background pattern as the fixed factors, and mantis as the subject factor. The number of trials where tracking occurred out of the total number of presentations for each condition was used as the dependent variable. I only present analysis of the tracking behaviour as the mantis rarely struck at a target or displayed the peering behaviour.

4.4.4 Results

I found that the probability that the mantids tracked the targets was affected by the target pattern (black, 5 pixel, 10 pixel and 20 pixel) (GEE, χ^2_3= 281.7, P<0.001; Figure 14) and the background pattern (grey, 5 pixel, 10 pixel and 20 pixel) (GEE, χ^2_3= 63.5, P<0.001; Figure 12), and that there was an interaction between target pattern and background pattern (GEE, χ^2_9= 212.8, P<0.001; Figure

14). Mantids where less likely to track targets when they were moving over a patterned background compared to moving over a grey background (Helmert *Post hoc*, $P<0.001$; Figure 14). This indicates that prey might be less likely to be predated upon when moving through a heterogeneous environment. Mantids were more likely to track the black target over patterned targets (Helmert *Post hoc*, $P<0.001$; Figure 14), presumably because of the greater luminance contrast from the background of the black prey compared to the patterned targets. Comparing the patterned targets, mantids were more likely to track 20 pixel patterned target compared to the 5 pixel and 10 pixel patterned target (GEE, pairwise *Post hoc*, $P<0.001$, $P<0.001$; Figure 14). This indicates the mantis predatory response is triggered more by prey that have large contrasting pattern elements.
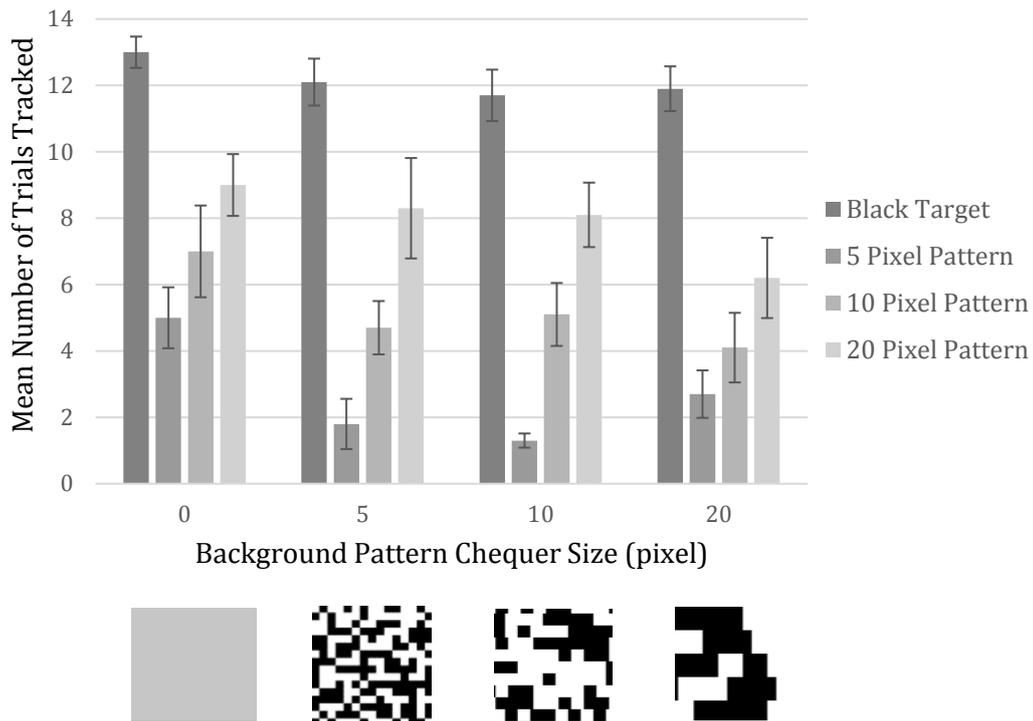
Figure 14. The mean (+/- s.e.) number of trials the mantids responded with the tracking behaviour for each target type moving over each background pattern. Each combination of background and target conditions were displayed 15 times to each mantis, with a sample size of 10 mantids.

To test whether prey benefit from background matching when moving, I compared the number of trials each mantis tracked background matching targets compared to non-background matching targets, using patterned target (5 pixels, 10 pixels and 20 pixels) and patterned background (5 pixels, 10 pixels and 20 pixels) data in a GEE, binary logistic analysis. I found that there was no overall effect of background matching upon the number of trials that the mantids tracked the patterned targets (GEE, χ^2_1= 0.83, P=0.3; Figure 14). There was however an effect of target pattern (GEE, χ^2_2=98.7, P<0.001) and an interaction between

background matching and target pattern (GEE, χ^2_2= 10.52 P=0.005). The data were then split to compare background matching targets to non-background matching targets within each target chequer size. I found that mantids tracked 20 pixel targets less often when they matched their background compared to when moving over a non-matching background (GEE, χ^2_1= 7.63, P=0.006). However, there was no significant difference in the number of trials the mantis tracked either the 5 pixel and 10 pixel patterned target when matching the background pattern as opposed to moving over a non-matching background (5 pixel patterned target: χ^2_1= 0.14, P=0.71; 10 pixel patterned target: χ^2_1= 1.11, P=0.29; Figure 14). Therefore, only the prey with the largest elements appeared to benefit from reduced tracking behaviour when matching their backgrounds.

To test if it could be beneficial for prey to have a compromise pattern in two different habitats compared to a pattern which matches one habitat completely, I selected the data for the 5 pixel, 10 pixel and 20 pixel targets moving over a 5 pixel and 20 pixel background in a GEE, binary logistic model. The number of trials the mantids tracked the 10 pixel target (compromise pattern) was then compared to the number of trials the mantis tracked the 5 pixel and 20 pixel targets pooled across both backgrounds. The 5 and 20 pixel targets matched one of the backgrounds and mismatched the other, whereas the 10 pixel target had a pattern that was intermediate to both backgrounds. I found that there was a significant difference in the number of trials that the mantids tracked the three different targets (GEE, χ^2_2= 78.583, P<0.001; Figure 15) where the mantis tracked the 20 pixel target the most and the 5 pixel target the least (Pairwise, *post hoc*,

P<0.001, Figure 15). However, there was no difference in the number of trials the mantids tracked the compromise 10 pixel target compared to the background matching 5 pixel and 20 pixel targets (Helmerts, *post hoc*, P=0.208; Figure 15). This suggests there are no benefits of having a compromise pattern and that pattern size is the main factor determining the likelihood of the mantis to track a target.
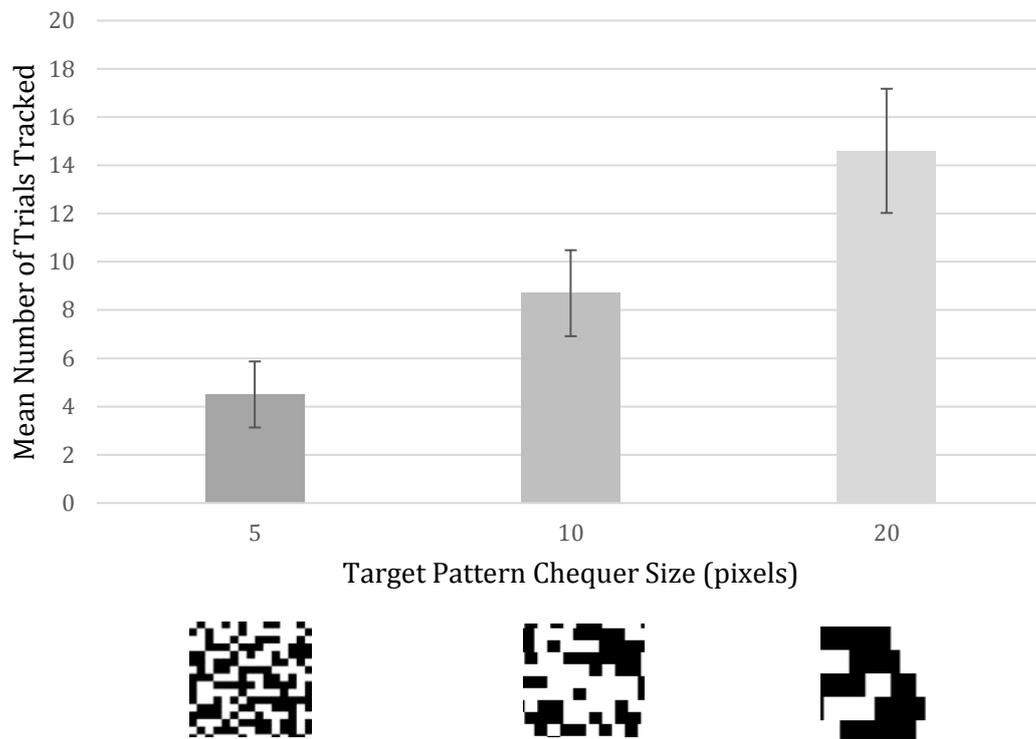
Figure 15. The mean (+/- s.e.) number of trials the mantis tracked each prey type when moving over both the 5 pixel and 20 pixel background (data pooled across both backgrounds). Both the 5 pixel and 20 pixel targets matched one of the backgrounds whereas the 10 pixel target was similar but compromise on both backgrounds. Mantids viewed each target moving over each background 15 times, a total of 30 times for each target.

4.4.5 Discussion

In this experiment, I found that there was only a benefit to background matching to moving prey with large (20 pixel) chequerboard patterns, and not to those prey with smaller elements in their patterns (5 and 10 pixel). All types of prey were less detectable to praying mantids on patterned backgrounds compared to a uniform grey background with the same mean luminance. Mantids displayed a high tracking response to black targets compared to chequerboard targets that matched the background mean luminance. I found no evidence to suggest that an intermediate pattern will benefit prey that inhabit visually different habitats, and that pattern element size is more likely to influence the mantis predatory response.

Whilst these data suggest that prey with larger pattern elements do benefit from background matching whilst moving, to interpret these data in relation to camouflage, it is important to know whether or not these patterns reduce predatory tracking behaviour compared to a uniform grey prey with the same mean luminance. Therefore, I conducted a second experiment to specifically test this, and included a grey target alongside black and patterned prey types.

4.5 Experiment 2: Investigating the effects of background matching in moving prey compared to uniform prey matching the background mean luminance.

4.5.1 Introduction

It is important to know if patterned prey fare better than uniform grey prey in order to better understand the benefits to prey patterning and background matching for the 20 pixel prey. To test this I used four different prey types moving across two different backgrounds. I used two black-and-white patterned prey types, which varied in their pattern element size (5 or 20 pixels), as well as presenting uniform black prey and grey prey (see Figure 16). I selected the 5 pixel and 20 pixel pattern prey types to reduce the number of conditions in the experiment, and explicitly test if chequered prey with low response rates (5 pixel prey) or benefits from background matching (20 pixel prey) would survive better than non-patterned uniform prey. The uniform grey target matched the mean luminance of the background and patterned prey. I also included a black prey to ensure that low tracking rates were not due to inactivity on the part of the mantids.

The four prey types (black, grey, 5 pixel and 20 pixel) were presented on two different backgrounds, which matched the black-and-white chequer patterns of the 5 and 20pixel prey types. Therefore, I was able to compare if background matching was beneficial to each prey type as before, but also test if patterned prey gained a survival advantage when moving over a patterned background compared to un-patterned prey with the same mean luminance. If the 20 pixel prey pattern

affords a camouflage advantage, the grey target moving over a patterned background should be more conspicuous and tracked more often than 20 pixel background matching prey.

4.5.2 Methods

Similar to Experiment 1, the background pattern was a random chequerboard pattern where each chequer square was generated at either 5 pixel or 20 pixel width ($36cd/m^2$); and the target pattern was either a black homogenous target ($0.052cd/m^2$), a grey homogenous target ($36cd/m^2$) or a chequerboard pattern where each chequer was generated at 5 pixel width or 20 pixel width ($36cd/m^2$). All target and background conditions, excluding the black target, were generated with the same mean luminance, and therefore patterned background and targets had equal numbers of white ($72 \ cd/m^2$) and black ($0.052 \ cd/m^2$) chequers (Figure 16).

Target

A   B   C   D

Background

E   F
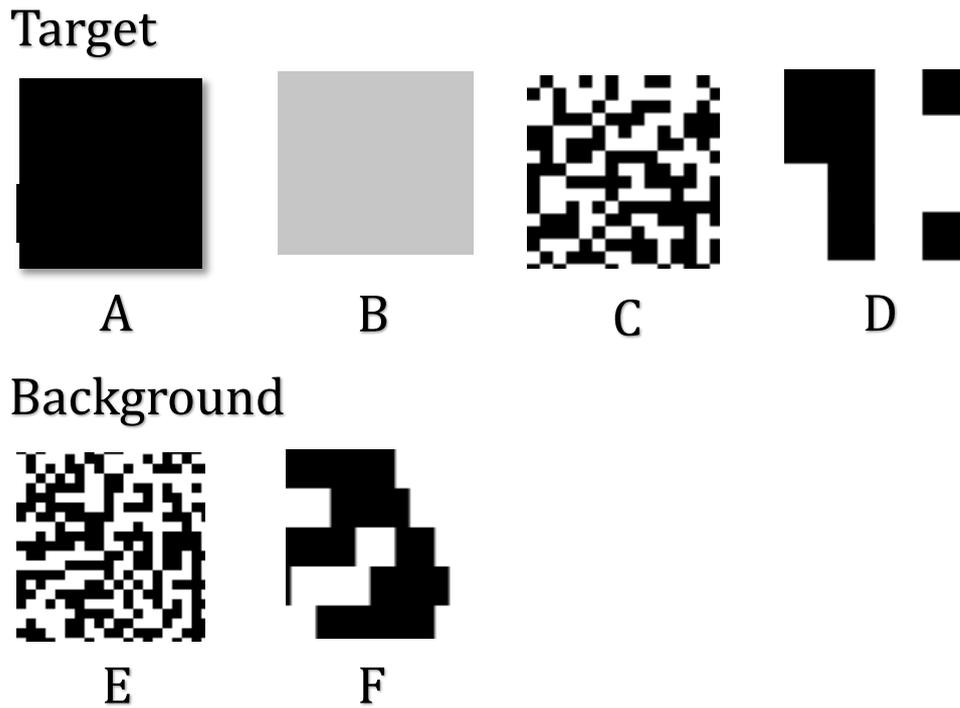
Figure 16 Example of target and background patterns: (A) black target; (B) grey target; (C) 5 pixel target; (D) 20 pixel target; (E) 5 pixel patterned background; (F) 20 pixel patterned background

All targets appeared on both backgrounds (i.e. a 2x4 fully factorial design; Table 3). Each combination of background and target conditions was presented in a random order in a block of trials. Within each block of trials every target and background combination was presented five times. Ten mantids completed three blocks of trials, and viewed each target-background combination a total of 15 times.

Table 3. Table of test parameters for experiment 2. Each target appeared on all four backgrounds. The shaded target and background combinations represent background matching stimuli.

Background Pattern	Target Pattern (size of chequers)			
5 pixels	Black	Grey	5 pixel	20 pixel
20 pixels	Black	Grey	5 pixel	20 pixel

4.5.3 Data Analysis

Statistical analysis was carried out using SPSS V. 22. Data were analysed with a series of generalized estimating equation models (GEE, binary logistic), with target pattern and background pattern as the fixed factors, and mantis as the subject factor. The number of trials where tracking occurred out of the total number of presentations for each condition was used as the dependent variable. I only present analysis of the tracking behaviour as the mantis rarely struck at a target or displayed the peering behaviour.

4.5.4 Results

The likelihood of the mantids to track targets was affected by target pattern (Black, Grey, 5 pixel and 10 pixel) (GEE, χ^2_3= 29.081, P<0.001; Figure 17), but was not effected by background pattern (5 pixel and 10 pixel) (χ^2_1= 0.878, P=0.349; Figure 17). There was an interaction between target pattern and background pattern (χ^2_3= 17.2, P=0.001; Figure 17). Mantids were more likely to track the black target compared to the grey or patterned targets (Helmert *post hoc*, P<0.001; Figure 17). This supports the previous finding that targets that have a large

luminance contrast to the background attract more predatory responses compared to targets that match the mean luminance of the background.
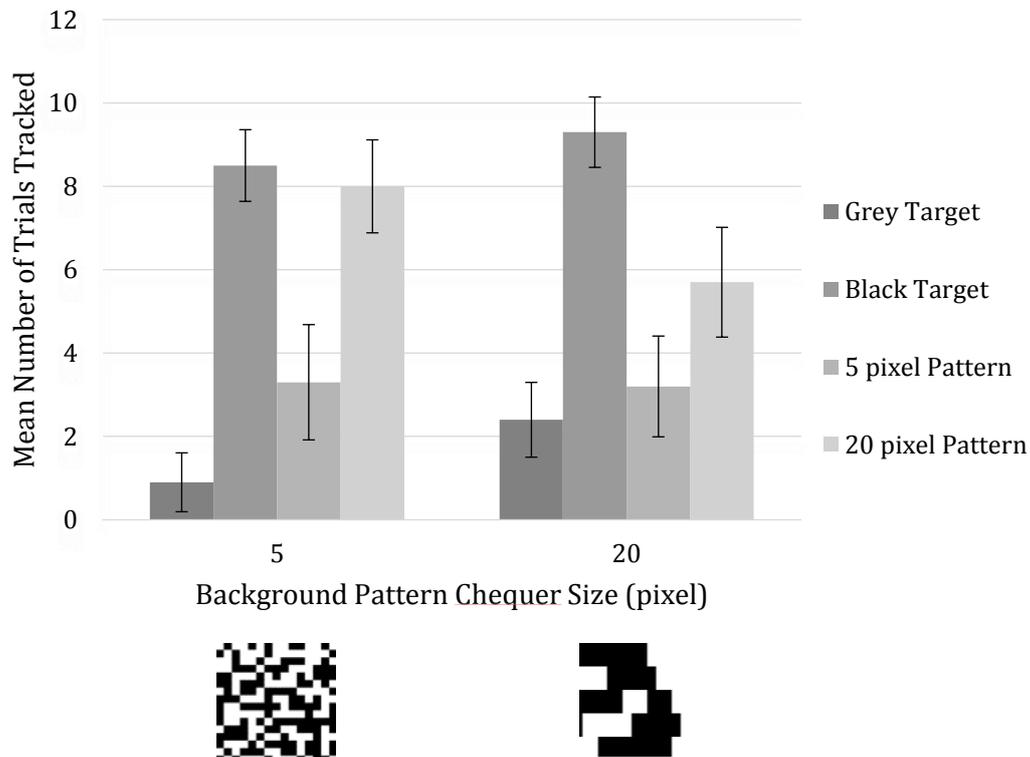
Figure 17. The mean (+/- s.e.) number of trials the mantis responded with the tracking behaviour for each target type moving over each background pattern. Each combination of background and target conditions were displayed to individual mantis 15 times across a total of 10 mantids.

To test whether patterned prey gain a survival advantage over un-patterned grey prey which match the mean luminance of the background, I compared the number of trials that the mantis tracked the grey target to the patterned targets (5 pixel and 20 pixel). I found that there was an effect of target pattern (GEE, $\chi^2_2 = 28.631$, P<0.001; Figure 17), where the mantids tracked the grey

target less than the 5 pixel and 20 pixel patterned targets (GEE, Helmert *post hoc*, P<0.001). Although both the grey and patterned targets both match the mean luminance of the background, the patterned targets contain large, highly contrasting elements, which may attract the mantids' predatory responses.

To test whether prey benefit from matching the background pattern when moving, I used data from both patterned targets over the two patterned backgrounds in a GEE, binary logistic analysis. I compared the number of trials the mantids tracked two patterned targets (5 pixel and 20 pixel) when background matching compared to not matching the background. I found no overall difference in the number of trials the mantids tracked targets which matched the background pattern compared to targets which did not match the background pattern (GEE, χ^2_1= 2.902 P=0.088; Figure 17). I did however find an effect of target pattern (GEE, χ^2_1= 18.7 P<0.001; Figure 17) and a marginal interaction between background matching and target pattern (GEE, χ^2_1= 3.575, P=0.059). The data was then split comparing background matching targets to non-background matching targets within each target chequer size. As in experiment 1, I found benefits of background matching in targets with larger pattern element sizes (20 pixel) compared to small (5 pixel). Where the mantis tracked the background matching 20 pixel patterned target less than the 20 pixel target which did not match the background (GEE, χ^2_1= 6.329 P=0.012; Figure 17). I found no difference in the number of trials the mantids tracked the 5 pixel patterned target when it matched the background compared to when it did not match the background pattern (GEE, χ^2_1= 0.026, P=0.871). This supports my previous finding that only prey with large pattern

elements (20 pixel) benefit from matching the background pattern when moving compared to prey with smaller pattern elements (5 pixel).

To test whether prey which match the background have a survival advantage over prey which remain unpatterned, I compared data from the grey target and the background matching 5 pixel and 20 pixel targets in a GEE, binary logistic analysis, comparing the number of trials the mantids tracked the grey target with the background matching 5 pixel and 20 pixel targets pooled using a Helmerts *post hoc*. I found there was an effect of target pattern upon the mantis tracking response (GEE, χ^2_2= 20.669, P<0.001, Figure 17), where the mantis tracked the grey target less than the background matching 5 pixel and 20 pixel targets (GEE, Helmert *Post* hoc, P<0.001, Figure 17). This indicates that it is more beneficial for prey which match the mean luminance of the background to remain unpatterned compared to matching the background pattern.

4.5.5 Discussion

Consistent with the results of Experiment 1, mantids displayed a high predatory response to black compared to prey that matched the mean luminance of the background (uniform grey and patterned targets). Prey with large pattern elements (20 pixel) were tracked less often when they matched the background pattern whilst prey with smaller elements (5 pixel) were not. However, when compared to the uniform grey targets, background matching 20 pixel prey still had higher tracking rates, suggesting no overall benefit of background matching patterns for moving prey.

4.6 General discussion

This study has shown that only prey with large pattern elements (20 pixel) benefit from background matching when moving. Although it seems that unpatterned grey targets which match the background luminance gain a survival advantage over patterned targets even when the patterned target has a survival benefit from matching the background pattern (20 pixel target). I found that background pattern affects the tracking behavior of the mantis, making it less likely to track targets over heterogeneous background compared to a homogenous grey background. Furthermore, I found that there are no benefits of having a compromise pattern when moving over visually similar backgrounds, when compared to background matching prey. Finally, my study adds to what we know about mantis prey preference (Prete, 1992; Prete and Mahaffey, 1993; Prete and McLean, 1996; Prete *et al.*, 2002; Prete *et al.*, 2012), where mantids seem to be attracted to prey which have a darker contrast than the background (black target) or prey that contain large highly contrasting pattern elements (20 pixel).

Background matching reduces the ability of a predator's visual system to effectively discriminate prey features from the background, and enables prey to blend into the background and go undetected (Cuthill *et al.*, 2005; Merilaita and Lind, 2005b; Merilaita and Stevens, 2011). One of the most important features the visual system uses to enable it to discriminate an object from the background is motion (Collett, 1971; Collett and Land, 1975; Egelhaaf, 1985; Nordström *et al.*, 2006; Geurten *et al.*, 2007). By using targets which matched a random sample of the background, I found that there were no benefits of background matching for moving prey with small pattern elements. However, moving prey with large

pattern elements did benefit from matching the background pattern. This reduction in the mantids tracking response to 20 pixel prey when background matching may be clear due to the high rate at which the mantis tracks this prey over all backgrounds. In comparison, the mantis has a relatively low tracking response to prey with smaller elements (5 pixel target) which may make it difficult for us to see any difference in the number of trials the mantis tracks this prey over the different background types. Surprisingly, prey which match the background luminance and remain unpatterned have a greater survival advantage over background matching prey. I would have expected a grey target moving over a patterned background to be more conspicuous than a background matching target, as it has a clear outline at half luminance between black and white; it may be that a target with a low contrast to the background and without any highly contrasting features does not trigger the mantis predatory response. The mantis shows strong predatory behaviour to moving targets with a high contrast to the background at a wide range of sizes (Prete and McLean, 1996; Prete *et al.*, 2002). Highly contrasting elements within the target pattern may be triggering the mantids' tracking responses. This suggests that any selection pressures produced primarily by mantis predation is likely to select for un-patterned prey which matches the background mean luminance and not for background matching patterned prey.

The mantis showed high predation behavior towards prey which had a large luminance contrast to the background (black target) compared to prey which matched the background mean luminance (grey and patterned targets). This was expected due to neurons found in the insect visual system which are

specifically tuned to identify small moving targets. These small target motion detectors (STMDs) can be size, speed and direction selective and are highly sensitive to small contrasting features (Collett, 1971; O'Carroll, 1993; Nordström *et al.*, 2006). These neurons could also explain why the mantis showed a high predatory response to targets that were patterned with large highly contrasting elements (20 pixel target). It is likely the large pattern elements may have triggered a response from small target detecting neurons. To avoid predation by the mantis prey should ideally evolve to be a low contrast relative to the background or have small elements to their pattern. This will allow them to avoid triggering neurons which have evolved to pick out large highly contrasting features (Collett, 1971; O'Carroll, 1993; Nordström *et al.*, 2006; Geurten *et al.*, 2007).

I found that background pattern affected the likelihood of the mantis to track targets, where the mantis was less likely to track targets when they moved over any of the patterned backgrounds compared to the homogenous grey background. This suggests, when predated on by the mantis, prey gain a survival advantage when traveling through heterogeneous habitats compared to simple homogenous habitats. This agrees with similar findings which suggests complex backgrounds increase the amount of visual information which needs to be processed, therefore, increasing search time and reducing the detection of camouflaged prey (Merilaita, 2003; Merilaita and Lind, 2005a; Dimitrova and Merilaita, 2009; Dimitrova and Merilaita, 2011). This means that background pattern has implications upon the evolution of camouflage strategies over other visually mediated signals such as warning patterns.

Natural scenes are rarely homogenous and are usually comprised of visually differing microhabitats. Prey which move among these patchy environments may be naturally selected to closely match just one of these habitats. This may reduce the risk of being detected in one habitat, however, it may make them more conspicuous in another (Endler, 1978; Merilaita *et al.*, 1999). Alternatively, prey might be selected to evolve a compromise pattern which resembles multiple habitats, therefore reducing detection over many background rather than minimising it in just one (Merilaita *et al.*, 2001; Dimitrova and Merilaita, 2014). I found no benefits to having a compromise pattern when compared to background matching targets; and that prey pattern size was the influencing factor on the likelihood of the mantis to track the background matching and compromise targets. This result may be due to using the 10 pixel target as the 'compromise' pattern. I found that the mantis did not have a great overall preference for this target compared to targets with larger pattern elements (20 pixel). This preference for targets with large elements may have affected the ability to see any benefits to compromise patterns. Further study should include a target with a high mantis preference comparing the survival of the same target when moving over similarly patterned backgrounds 'compromise' compared to a matching background (background matching).

My study sheds light on the benefits of background matching in moving prey and how an insect predator perceives background matching prey. The chequerboard patterns used for the visual stimuli is not a pattern often seen in natural scenes, however, I needed to design a target which would trigger a tracking response from the mantis. I found that targets which contained a random

pattern containing defined edges elicited a strong response over symmetrical patterns and patterns with smoothed edges. This may be due to the high sensitivity of insect elementary motion detectors for contrasting moving edges (Borst and Egelhaaf, 1989; Douglass and Strausfeld, 1996; Srinivasan *et al.*, 1999; Joesch *et al.*, 2010). To trigger a predatory response from the mantis, it was essential to move the target, this restricted us in our ability to compare the benefits of background matching in moving prey to that of stationary prey. It would be interesting to investigate the effects of prey movement pattern on the mantis predatory response towards cryptic prey. Praying mantis often predate small insects such as crickets, and observations in the lab have revealed that crickets often move in a series of quick bouts, remaining stationary between the bouts of movement. Insects may benefit from this type of movement pattern particularly when predated upon by the mantis, since movement seems to be the primary factor in attracting the mantids' attention. If camouflaged prey adopt this type of movement, it will enable them to periodically blend into the background whilst also enabling them to travel between locations.

Chapter 5: Background motion and target tracking in a praying mantis

5.1 Abstract

Camouflage is an adaptation that reduces the chance of prey being detected by visually hunting predators. The most well studied forms of camouflage are morphological adaptations such as background matching, masquerading, and disruptive colouration. Many prey, however, have also adapted their behaviour to maximise the effects of crypsis. It is thought that behaviours such as the swaying behaviour of stick insects is an attempt to mimic background motion, allowing them to blend in to their surroundings. If this type of behaviour is a form of camouflage, then it should reduce the probability of prey being detected, however, there is little evidence to show this type of behaviour carries any survival benefits. I investigated the benefits associated with matching background motion using praying mantids as an insect predator and computer generated black targets as prey. The targets moved over a black-and-white chequered background where the background was either stationary, moving out of phase with the prey or moving in phase with the prey. Using the tracking response of the mantis our study shows that prey movement patterns relative to background motion can have an effect upon prey detection rates. I found that there was no difference in the number of trials that the mantids tracked prey when moving in phase with the background compared to moving over a stationary background. The mantids did, however, track prey more when they were moving out of phase with background motion compared to prey moving in phase with background motion. Our study suggests that although there are no overall benefits for prey to match background motion, it is costly to move out of phase with background motion. This study can add

information to what we know about the benefits of prey matching motion patterns found in their environment.

5.2 Introduction

Camouflage has evolved in a diverse range of species to reduce the chances that prey are detected or recognised by visually hunting predators. The most well-studied forms include: background matching, where prey match the colouration and pattern of their surroundings (Cott, 1940; Endler, 1978; Cuthill *et al.*, 2005); masquerade, where prey reduce identification by mimicking inedible objects within their surroundings (Skelhorn *et al.*, 2010); and disruptive colouration, where a disruptive pattern breaks up the bodily outline (Schaefer and Stobbe, 2006; Stevens and Merilaita, 2009b). It is not just the morphological adaptation that helps prey hide from predators: behaviour can often also play a role. For example, various species of cryptic moth become harder to find after they reposition themselves on their substrate using visual cues (Webster *et al.*, 2009; Kang *et al.*, 2013; Kang *et al.*, 2015).

A common feature associated with crypsis is the need for prey to remain still (Endler, 1978; Merilaita and Lind, 2005b; Ioannou and Krause, 2009; Hall *et al.*, 2013) and consequently, studies have focused predominantly on the survival of stationary prey against a stationary background. Prey, however, need to move when foraging or finding a mate, and environments are rarely static. Environmental motion could add noise to a visual scene, making it more difficult for a predator to detect relevant motion such as moving prey.

Predators need to be able to filter out irrelevant background motion in order to better identify movement patterns associated with prey. Predators often respond preferentially to a particular pattern of movement that indicates prey, and disregard other types of movement as irrelevant background motion (Fleishman, 1986; Peters, 2008; Fleishman and Pallus, 2010). The ability of predators to identify prey through their movement pattern could exert selection pressures on prey to adapt their movements to resemble irrelevant background motion, therefore reducing the risk of detection by predators. This behavioural adaptation can be found throughout a diverse range of species. For example, MacLeay's spectre (*Extatosoma tiaratum)*, a type of stick insect, reacts to environmental cues such as wind with a swaying behavior to match the frequency domain of windblown plants (Bian *et al.*, 2015). The vine snake, *Oxybelis aeneus,* matches movement of surrounding vegetation through visual cues. It is thought these behaviors are intended to imitate background motion allowing prey to blend in with dynamic surroundings (Gans, 1967; Fleishman, 1985; Bian *et al.*, 2015). If the swaying behavior of animals is a form of camouflage, then there should be survival benefits associated with matching the movement patterns in the surrounding environment. There is little evidence to show that the swaying behavior in prey carries any survival benefits.

Many studies investigating the benefits of prey matching background movement patterns have used reptile, human and avian predator models (Fleishman, 1985; Fleishman, 1986; Bian *et al.*, 2015). Few studies have investigated prey concealment using insect models. Insects are highly sensitive to movement and use motion to identify and track prey (Gilbert, 1997; Olberg *et al.*,

2000; Olberg *et al.*, 2007; Wardill *et al.*, 2015). The praying mantis is a good example of an insect predator highly specialised to detect motion (Rossel, 1996; Yamawaki, 2003; Yamawaki and Toh, 2003). The mantis uses motion as a primary characteristic in detecting and identifying prey (Prete and Mahaffey, 1993). It has two largely proportioned eyes relative to the body. A large peripheral area specialised to detect motion and a high acuity fovea which it centres over a moving object of interest (Rossel, 1979; Rossel, 1980). This tracking behaviour makes the mantis an ideal predator model for investigating the effects of motion on prey detection as it is an easily identifiable behaviour (Rossel, 1980; Yamawaki, 2006; Prete *et al.*, 2011).

In this chapter, I will test how background motion affects the detection of prey targets in the praying mantis (*Sphodromantis lineola*). Furthermore, using the mantis as a predator model, I wish to investigate the survival benefits of prey that match the motion of their background. The visual systems of insects are well adapted to sort through visual clutter to locate moving objects such as prey or a possible mate (O'Carroll, 1993; Srinivasan *et al.*, 1999; Nordström *et al.*, 2006). Some mantis species live in dense vegetation where the background is unlikely to be completely stationary (Prete, 1999). Therefore, the mantis visual system must be able to filter irrelevant background motion and distinguish movements of prey like objects. I expect that the mantis will be able to filter out background motion and successfully track a moving prey item. If the mantis was to respond to background motion, it would be continuously tracking irrelevant objects. Furthermore, I expect the mantids to track prey which match the background motion less than prey moving out of phase with background motion or prey

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moving over a stationary background. If the mantis does filter out background motion it is likely prey which match the background motion will be ignored as an irrelevant object.

5.4 Experiment 1: The mantis tracking response to visual stimuli containing background motion

5.4.1 Introduction

A variety of praying mantid species have shown strong predatory responses towards black targets (Prete and McClean 1996), this has also been shown in Chapter 3. Therefore, black prey were used to ensure that the mantids would display a high tracking response, and that differences in the tracking response which may be caused by the experimental conditions would be measurable.

In the first experiment, I investigated if: (1) the tracking response of the mantis occurred when presented with a moving scene, which did not contain a prey target; and, (2) if the praying mantis was able to filter out irrelevant background motion and distinguish a moving target over background motion 'noise'. This will enable us to verify that the mantis recognises the moving target as a prey item and does not track moving background elements when there is no target. I did this by measuring the tracking response of the mantis when presented with a moving background without a moving target to track. I also measured the tracking response of the mantis to a target when it was moving over a static background compared to when it moved over a similar background in motion. I expected to see a lower level of tracking when mantids were presented with a

moving background without a prey like target present compared to conditions containing a moving target. If the mantids were able to filter out irrelevant background motion, I expected a similar level of tracking response when the mantis was presented with a moving target traveling over a moving background and a static background.

5.4.2 Methods

I used a black ($0.052cd/m^2$) computer generated target (80 pixel x 80 pixel) as the prey, which moved centrally along a grey horizontal strip in the centre of the screen (Figure 18). We used a stationary grey strip for the target to move across as prey often move on stationary substrates (e.g. a stick or leaf) with movement in the distant background. The target appeared randomly at the left or right side of the screen, and then travelled back and forth across the screen a total of four times. The target moved with a sinusoidal function, when the position of the target was 0 (the centre of the screen) velocity was maximum (1166.7 pixels/sec) and when the target position reached -1 or 1 (either edge of the screen) velocity was zero. The target was not visible to the mantis at either edge of the screen when it changed direction.

I used three background pattern types to test whether background pattern affected the mantis tracking response to each background movement conditions. The background above and below the central grey strip consisted of a black-and-white chequerboard pattern, where each chequer square had either 5, 10 or 20 pixels' width (Figure 18). All background patterns had the same mean luminance ($36cd/m^2$), and patterned backgrounds had equal numbers of white ($72cd/m^2$) and black chequers ($0.052cd/m^2$). In this experiment, the grey strip ($36cd/m^{2)}$

that the target moved along was 320 pixels in height, where the moving patterned background was 120 pixels above and below the moving target (Figure 18).
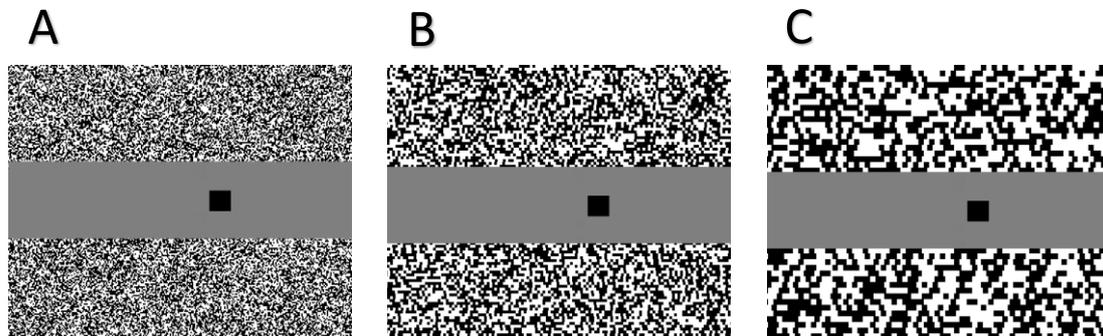
Figure 18. Example of prey moving along the grey strip with either (A) 5 pixel patterned background (B) 10 pixel patterned background (C) 20 pixel patterned background.

To generate a moving background that did not trigger an optomotor response, the background was broken down into alternating rows, 20 pixels in height, which I refer to as 'odd' and 'even' rows. These patterned rows were able to move back and forth horizontally to create background motion. During each prey presentation, the target and odd/even background rows were oscillating horizontally at the same angular velocity but with different phase relationships. Odd and even background rows were always moving with a 180 degree phase difference (i.e. their motion was counter phase) so as to produce no net coherent motion in any direction (Figure 19, A).

I had three conditions: (1) Still with target, where only the target moved across the screen and the background rows remained still; (2) Moving background without target, where background motion was created with odd and even rows without a black target moving along the grey bar (Figure 19, A); (3) Moving

background with target, where a black target was moving across the screen 90°
out of phase with both the odd and even rows (Figure 19, B).

To test whether the background pattern element size affected the mantids'
tracking behaviour, each condition was presented with three different pattern
element sizes: 5 pixel, 10 pixel, and 20 pixel (Table 4). By examining the mantids'
responses to a moving background pattern when no prey target was present, I
could investigate whether or not a moving background pattern would elicit head
movements from the mantids. For example, a large blocky patterned background
(20 pixel) could trigger tracking movements because it contained large elements
in its pattern compared to a fine (5 pixel) pattern. All backgrounds had the same
mean luminance ($36cd/m^2$), and patterned backgrounds had equal numbers of
white and black chequers.
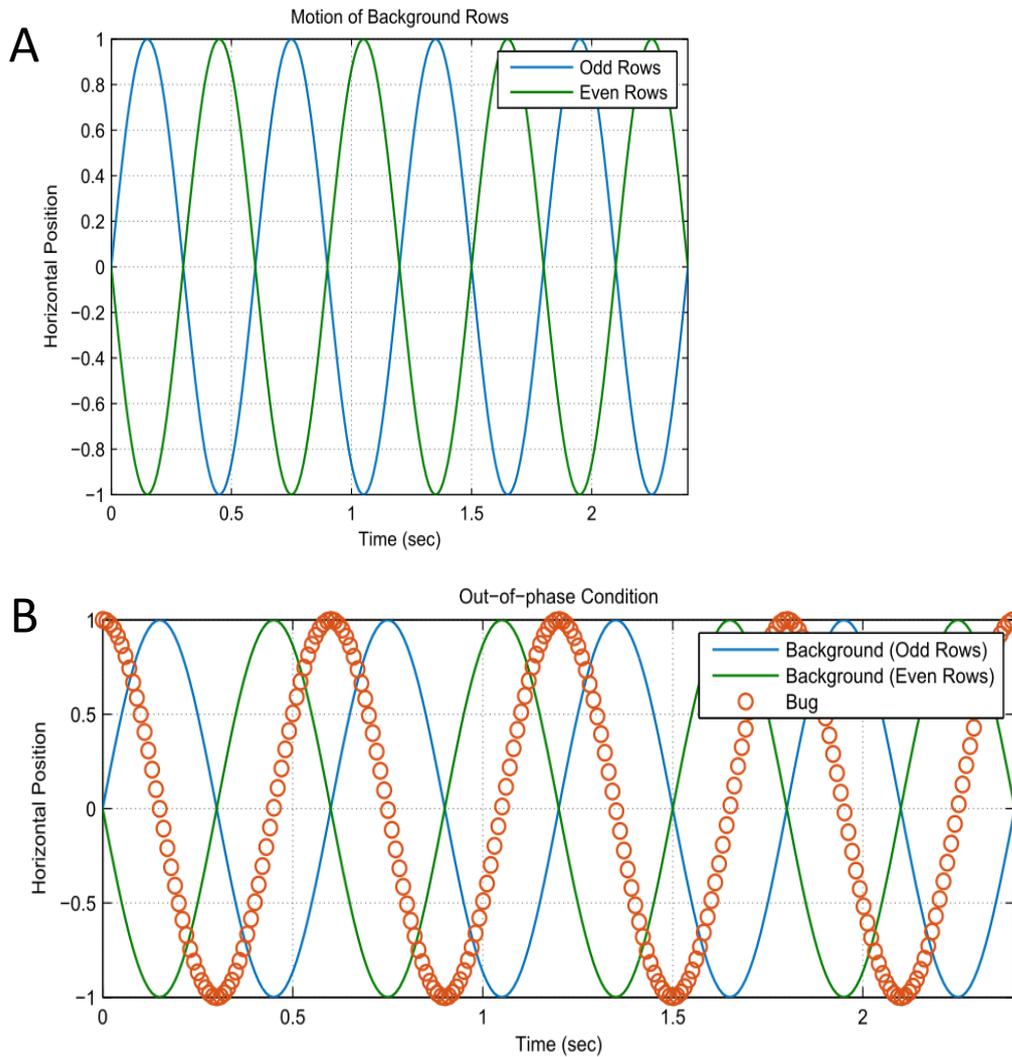
Figure 19 A) Horizontal movement of the patterned odd and even rows which create the background motion B) The horizontal movement of the target relative to the odd and even rows for the out of phase background motion condition.

Table 4 Table of test parameters for Experiment 1.

Visual Condition	Background Pattern		
Still with target	5 pixel	10 pixel	20 pixel
Moving background without target	5 pixel	10 pixel	20 pixel
Moving background with target	5 pixel	10 pixel	20 pixel

The same experimental procedure was followed as that of the previous experiments, detailed in the general methods chapter (see Section 2.3). The test conditions shown in Table 4 were randomly displayed in blocks of 45 trials; within a block of trials all visual stimuli and background pattern combinations were presented five times. Seven mantids completed three blocks of trials, each viewing the 9 conditions a total of 15 times.

5.4.3 Data Analysis

Statistical analysis was carried out using SPSS v22. Data were analysed with a generalized estimating equation (GEE, binary logistic model), with visual condition (Still with target, Background moving without target, and Background moving with target) and background pattern size (5, 10 and 20 pixel) as the independent variables. The number of trials where tracking occurred (out of the total presentations of each condition for each mantis) was used as the dependent variable. Mantis was the subject factor.

5.4.4 Results

The likelihood of a tracking response was affected by the visual condition (GEE, χ^2_2= 53.8, P<0.001), but there was no effect of background pattern (χ^2_2= 1.6, P=0.45), and no interaction (χ^2_4= 4.0, P=0.41; Figure 20). The mantids were less likely to display the tracking response when there was a moving scene without a prey like target compared to a target moving over either a still background (GEE, pairwise *post hoc*, P<0.001) or a moving background (GEE, pairwise *post hoc*, P<0.001). Therefore, whilst the mantids showed tracking behavior in all three conditions, tracking responses were higher when a target was presented. I also found that there was no difference in the number of trials the mantids tracked the

black target when moving over a still background compared to the moving background (GEE, pairwise *post hoc*, P=0.37). This suggests that the mantids may be able to detect prey equally in the absence or presence of background motion.
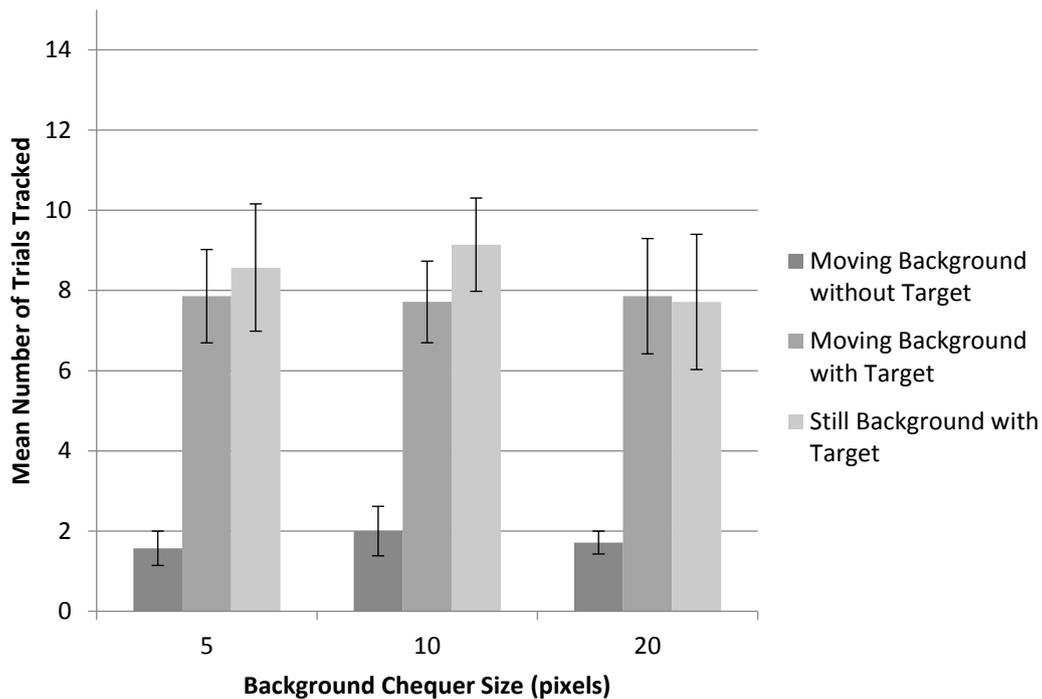
Figure 20: The mean (+/- s.e.) number of times the mantids displayed a tracking response to each condition. Each combination of visual condition and pattern element size were displayed 15 times to each individual mantis, with a sample size of seven mantids.

5.4.5 Discussion

In this experiment, I found that when background motion is displayed without a target, the mantids did make a low level of tracking responses. This could be because the mantis is tracking elements in the moving background. However the mantids made significantly more tracking responses when there was

a target present with either a still or moving background. When there was a target present, mantids tracked on around half of trials, whereas when no target was present, they tracked on only ~13% of trials. This suggests that the mantids identified moving black targets as possible prey items, and were able to successfully track them in the presence of background motion. I found no difference in the amount of trials the mantis tracked the target across a moving or still background suggesting the mantis is able to filter out background motion 'noise'. However it is possible that the mantids may be tracking background motion approximately 10% of the time when the target is moving over a moving background. If this was the case, there may be a suppressive effect of background motion on target tracking, but the noise created by the mantids tracking background motion does not allow us to see that effect.

I found that pattern element size in the background did not affect the overall tracking response of the mantis, either in the presence or absence of prey.

5.5 Experiment 2: The mantis tracking response towards prey that match background movement patterns

5.5.1 Introduction

In the second experiment, I wanted to examine whether it is beneficial for prey to match the phase of background motion. Therefore, I measured the mantids' tracking responses to a target moving in phase with background motion compared to moving out of phase with background motion or moving over a still background. If prey can reduce detection by matching background motion, I

expect the mantis to track the target moving in phase with the background less than the target moving out of phase with the background and the target moving over a still background.

5.5.2 Methods

I used a black ($0.052cd/m^2$) computer generated target (80 pixel x 80 pixel) as the prey, which moved centrally along a grey horizontal strip in the centre of the screen described in section 5.4.2. The target moved at the same speed and in the same manner as the previous experiments (section5.4.2). In this experiment the grey strip which the target moved along was 320 pixels in height, where the moving patterned background was 120 pixels above and below the moving target (Figure 18). This allowed the target to move along a static area but creating motion in the background. I used the same background patterns as in the previous experiment and details of how I created background motion can be found in section 5.4.2.

I used three background movement conditions: Still, where only the target moved across the screen and the background rows remained still; in phase, where the target was moving across the screen in phase with the odd rows and subsequently 180° out of phase with the even rows (Figure 21); out of phase, where the target was moving across the screen 90° out of phase with both the odd and even rows (Figure 21).
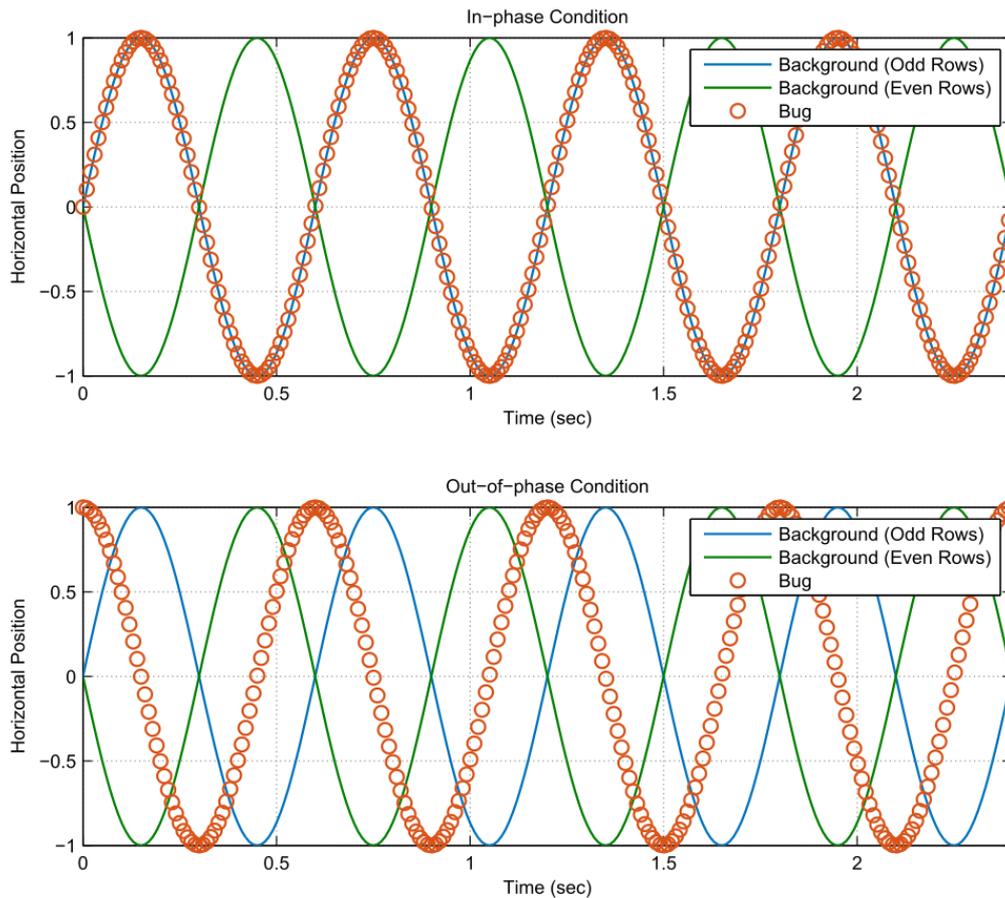
Figure 21: The horizontal movement of the target relative to the odd and even rows for the in phase and out of phase background motion conditions.

To test whether the size of the background pattern elements affected the mantids' abilities to track the target when traveling over a moving background, each background movement condition was presented with three different pattern element sizes; 5 pixel, 10 pixel, 20 pixel (Table 5). All backgrounds had the same mean luminance ($36cd/m^2$), and patterned backgrounds had equal numbers of white and black chequers.

Table 5: Table of test parameters for Experiment 2. The black target appeared with each background movement type combined with each background pattern.

Background Movement Condition	Background Pattern		
Still	5 pixel	10 pixel	20 pixel
Moving in Phase with Target	5 pixel	10 pixel	20 pixel
Moving out of Phase with Target	5 pixel	10 pixel	20 pixel

The same experimental procedure was followed as that of the previous experiment (see Section 2.3). All three background movement types were combined with all three background patterns (i.e. a 3x3 fully factorial design; Table 5). Within a block of trials, all 9 background movement and background pattern combinations were presented five times in a random order. Ten mantids completed three blocks of trials, each viewing the 9 conditions a total of 15 times.

5.5.3 Data Analysis

Statistical analysis was carried out using SPSS v22. Data were analysed with a generalized estimating equation (GEE, binary logistic model), with background movement type (still, in-phase and out-of-phase) and background pattern (5-, 10- and 20-pixel) as the independent variables. The number of trials where tracking occurred (out of the total of 15 presentations for each condition) was used as the dependent variable. Mantis was the repeated factor.

5.5.4 Results

I found that the mantids' tracking behaviour was influenced by the background movement type (GEE, χ^2_2= 20.1, P<0.001; Figure 22), but there was no

main effect of background pattern size (GEE, χ^2_2= 5.4, P=0.067; Figure 22), and no significant interaction between the background pattern size and background movement type (GEE, χ^2_4= 7.9, P=0.092; Figure 22).

The mantids were more likely to track the target when it was traveling out of phase with the moving background compared to in phase (GEE, pairwise, *post hoc,* P=0.003). However, there was no difference in the amount of trials the mantis tracked the target when it moved over a still background compared to moving in phase (GEE, pairwise, *post hoc,* P=0.847) and out of phase (GEE, pairwise, *post hoc,* P=0.132) with the background. This suggests that it is costly for prey to move out of phase with their background motion compared to matching the phase of their background motion, although there were no benefits to moving in phase with background motion compared to moving over a still background.
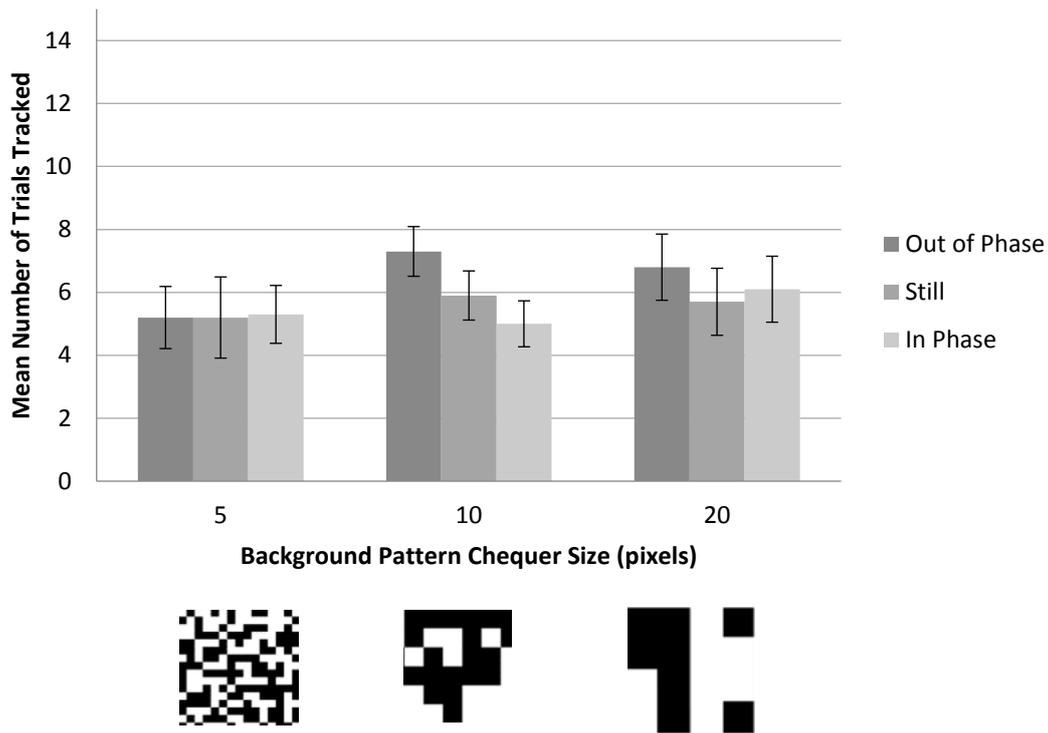
Figure 22. The mean (+/- s.e.) number of times the mantis tracked the black target when traveling over each background movement type with each background pattern type. Each combination of each background movement type and pattern were displayed 15 times to each mantis, with a sample size of 10 mantids.

5.5.5 Discussion

In this experiment, background pattern had no effect on the tracking behaviour of the mantis. I found that there was no difference in the tracking responses of the mantids to a black target traveling over a still background compared to both moving background conditions. However, when background motion was present, I found that the mantids tracked the black target more when it was traveling out-of-phase compared to traveling in-phase with the background motion.

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Since it was perhaps surprising that there were no benefits to moving against a moving background compared to a static one, I decided to repeat the experiment, but this time, use background motion that was directly next to the moving prey target. Therefore, this final experiment investigated if motion proximity was important, and if the ability of the mantis to track prey is impaired when the motion in the background is adjacent to the moving prey.

5.6 Experiment 3: Effect of background motion proximity upon survival of prey which match background motion patterns.

5.6.1 Introduction

In the third experiment, I wanted to examine whether background motion proximity affects whether it is beneficial for prey to match background motion. Therefore, I used the same experimental conditions as the previous experiment, however, I created background motion directly next to the moving target.

5.6.2 Methods

The same visual stimuli and experimental conditions were used as in the previous experiment, details of which can be found in section 5.5.2. The only difference was that the height of the grey strip that the target moved across was 80 pixels in height. This meant that the background motion was directly next to the moving target (Figure 23).
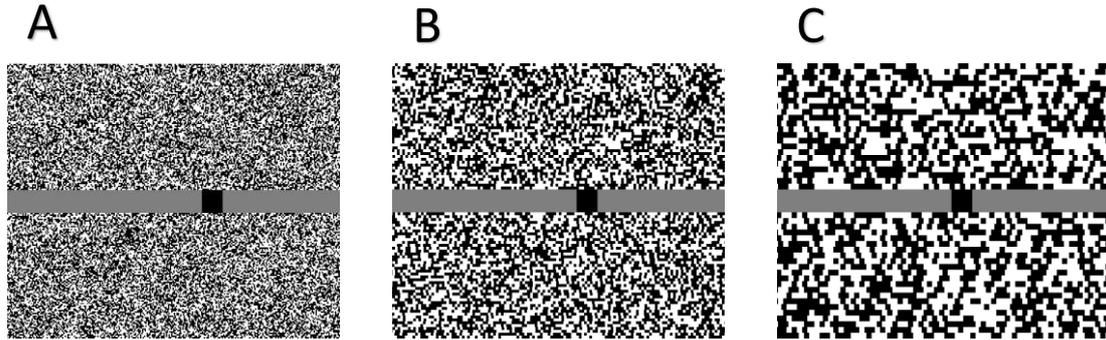
Figure 23. Example of visual stimuli: (A) 5 pixel patterned background; (B) 10 pixel patterned background; (C) 20 pixel patterned background.

The same experimental procedure was followed as that of the previous experiment, details of which can be found in section 2.3. Ten mantids completed three blocks of trials, six of which were used in the previous experiment.

5.6.3 Data Analysis

Statistical analysis was carried out using SPSS v22. Data were analysed with a generalized estimating equation (GEE, binary logistic model), with background movement type (still, in-phase and out-of-phase) and background pattern (5-, 10- and 20-pixel) as the independent variables. The number of trials where tracking occurred (out of the total of 15 presentations for each condition) was used as the dependent variable. Mantis was the repeated factor.

5.6.4 Results

I found that the likelihood of a tracking response was affected by both background movement (GEE, $\chi^2_2 = 26.6$, P<0.001, Figure 24) and background pattern (GEE, $\chi^2_2 = 15.4$, P<0.001, Figure 24). However, there was no significant

interaction between background movement type and background pattern GEE,

$\chi^2_4 = 1.6$, P=8.05, Figure 24).
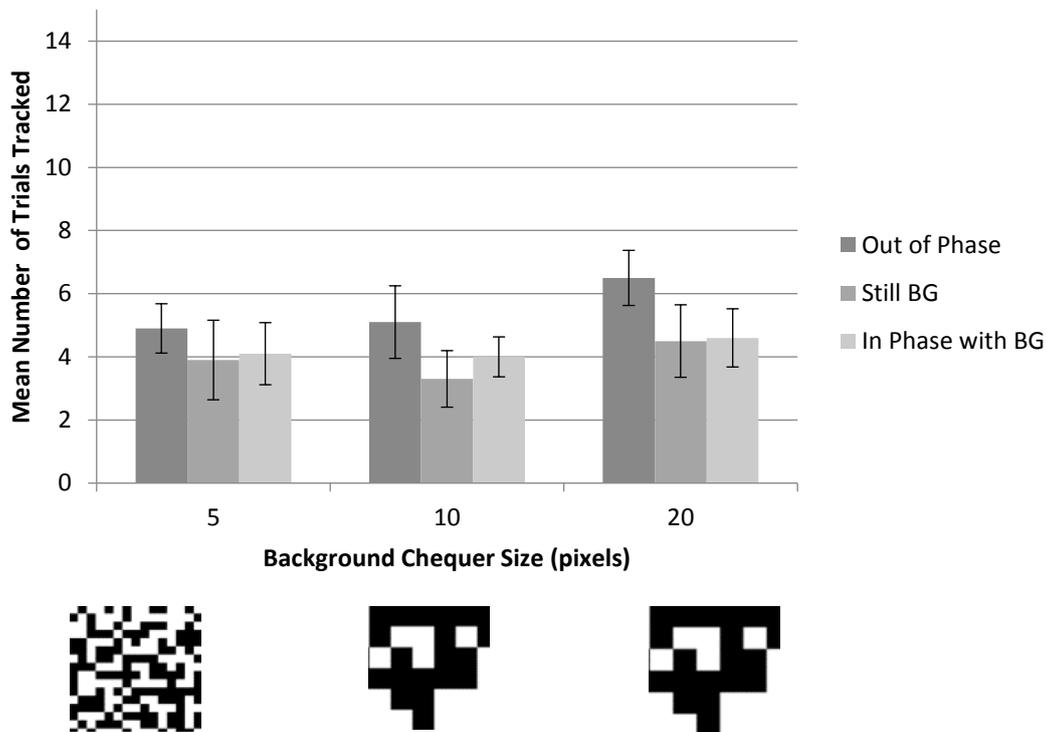
Figure 24. The mean (+/- s.e.) number of times the mantis tracked the black target when traveling alongside each background movement type with each background pattern type. Each combination of each background movement type and pattern were displayed 15 times to each mantis, with a sample size of 10 mantids

I found that the mantids were more likely to track a target moving out of phase with the background compared to in phase (GEE, pairwise, *post hoc*, P=0.001, Figure 24) or moving over a still background (GEE, pairwise, *post hoc*, P=0.001, Figure 24). However, there was no difference in the number of trials the mantis tracked the target moving in phase with the background compared to

moving over a still background (GEE, pairwise, *post hoc*, P=602, Figure 24). This suggests that when background motion is near to prey it is costly to move out of phase with motion in the background compared to matching the background motion or moving in a still environment.

I found that mantids were more likely to track a target moving over a 20 pixel patterned background compared to moving over a 5 pixel pattern (GEE, pairwise, *post hoc*, P=0.001, Figure 24) or a 10 pixel pattern (GEE, pairwise, *post hoc*, P=0.008, Figure 24). This suggests when the background motion is near to the prey, background pattern does have an overall effect, where the mantis is more likely to track prey when traveling over a blocky background (20 pixels) compared to finer patterns (5 pixels, 10 pixels).

5.6.5 Discussion

In this experiment, when background pattern was in close proximity to the target, there was an effect of background pattern upon the mantids' tracking responses, with the mantids more likely to track the black target when traveling over a background with large (20 pixel) pattern elements compared to smaller (5 pixel and 10 pixel) pattern elements. Background motion also had an effect on tracking behaviour, with the out of phase background motion producing more tracking than either of the other two conditions. This suggests that there is a cost to moving out of phase with background motion when the background is adjacent to the prey.

This finding is similar to the previous experiment, when the mantids tracked the black target more when it was traveling out-of-phase with the

background compared to traveling in-phase the background. This suggests that if prey are moving in a dynamic environment, it is likely to be advantageous to move in phase compared to out-of-phase with background motion.

5.7 General Discussion

Taken together, these results show mantids rarely make a tracking response to background motion in the absence of a prey like target. Although there are no overall benefits for prey to match background motion, it seems it is costly to move out of phase with background motion. This has implications for what we know about mantid vision and concealment for moving prey, which I will discuss in turn.

My study shows mantids rarely respond to background motion with the tracking response and can track prey on a moving background. This is in line with studies suggesting the insect visual system contains neurons which are specifically tuned to pick out a small moving targets (Collett, 1971; Warzecha *et al.*, 1993) and are unaffected by wide field background motion (Nordström *et al.*, 2006). Although a behavioural study shows praying mantids are less likely to strike at moving prey when there is background motion (Prete and Mahaffey, 1993), the background motion in that study travelled coherently in one direction, which may have triggered the optomotor system, which in turn may have affected the tracking system (Trischler *et al.*, 2010). Furthermore, background motion did not affect the tracking response of the mantis.

It appears the mantids are able to track targets moving out of phase with the background easier than targets moving in-phase. Results from Experiment 1

suggest that some tracking events towards prey on moving backgrounds might be a response to features in the background. Therefore, I can't be sure that there are no benefits to moving in phase with the background that are masked by tracking responses toward moving background elements. However, I am confident that there is a benefit to prey which move in-phase compared to out-of-phase, as there is no reason why tracking events would differ between the moving background conditions. Therefore, differences in the tracking behaviour between the moving background types will be an effect of prey movement relative to the background motion.

I found no benefits to prey moving in-phase with background motion over moving within a still environment, however prey are more conspicuous when moving out-of-phase with the background. Stick insects remain still and do not display the swaying behaviour if the nearby plant movement is too strong and they can't match the movement of their background (Bian *et al.*, 2015). Visually communicating animals have been known to adapt the speed and frequency of their signal in visually 'noisy' environments, creating a different movement pattern than those found in the background (Fleishman, 1992; Peters, 2008). This suggests that it is costly for prey to move with a different phase than background motion, causing them to become more conspicuous. Therefore, it is more beneficial for prey to remain still if they cannot match background movement patterns.

Chapter 6. Praying mantis contrast sensitivity to wide-field gratings and small moving targets: a contrast frequency comparison of the optomotor and tracking behavioural systems

6.1 Abstract

Contrast sensitivity has long been used as a tool to investigate the spatial and temporal filtering mechanisms of motion detecting pathways in visual systems. Sensitivity to different combinations of spatio-temporal frequencies enables animals to be sensitive to different velocities of motion in their environment. Insect studies have revealed motion detectors tend to be tuned to spatio-temporal combinations which match their behavioural ecology. However these studies almost exclusively use drifting wide-field stimuli and focus on fast flying insects such as flies, bees, locusts or beetles, which use information from neurons monitoring optic flow for tasks such as body stabilisation. Few studies have concentrated on small target tracking systems in predatory insects that sit or stalk their prey. Here, I will characterise and compare the contrast sensitivity of the praying mantis (*Sphodromantis lineola*) tracking and optomotor systems. Using the mantis tracking response to small targets (Gabor filtered windows of sinewave stimuli) and the optomotor response to wide-field motion (drifting sine wave gratings); I measured the distinct temporal and spatial signatures of each pathway and found the mantis wide-field and small target movement detecting pathways are each tuned to a different set of spatial and temporal frequencies. The wide-field motion detecting pathway has a high sensitivity to a broad range of spatio-temporal frequencies making it sensitive to a broad range of velocities; whereas the small-target motion-detection pathway has a high sensitivity to a

narrow set of spatio-temporal combinations with optimal sensitivity to targets with a low spatial frequency moving at 160 degrees per second. This adaptation will enable mantids to track small, fast-moving prey such as flies and crickets. This study outlines the differences in spatial and temporal sensitivity between different movement detection systems in the same species; and adds information to what we know about the contrast sensitivity of visually hunting insects which spend most of their time relatively stationary but hunt fast moving prey.

6.2 Introduction

Visually guided animals need to be able to detect motion to maintain stability, track prey, find a mate or avoid predators. To do this animals have motion-detectors within their visual systems, which are selective to the direction an object is moving. Motion-detectors were first studied in the insect using the optomotor response, which is a turning response caused by wide-field motion and is used to stabilise the insect relative to its surroundings (Fermi and Reichardt, 1963; Reichardt and Wenking, 1969; Srinivasan *et al.*, 1999). These elementary motion detectors' sample the brightness of an image at two adjacent points. Using two mirror pathways, one of which is delayed by a filter, they give an output which is positive for motion in one direction and negative for motion in the opposite direction. The interaction of the spatially separated pathways means the motion of an object and its direction can be detected when it passes one pathway then the other (Borst and Egelhaaf, 1989; Egelhaaf *et al.*, 1989; Douglass and Strausfeld, 1996; Harris *et al.*, 1999; Srinivasan *et al.*, 1999). The same mechanism has been

elaborated and proposed to exist in the human visual system (Van Santen and Sperling, 1984).

One of the most studied characteristics of the motion detection system underlying optomotor responses is its sensitivity to image contrast, defined as the just detectable modulation of the luminance of the image that gives rise to the response, or in the case of a target detector the ability to perceive differences between an object and its background. Sinusoidally modulated gratings (Figure 25) are a good way of studying the sensitivity of a visual system to contrast, as luminance changes regularly in time and in space and the underlying mathematical operations can be inferred, as long as the only involve linear interactions. Human contrast sensitivity can be demonstrated using a stationary sinusoidal grating which varies in spatial frequency and in contrast (Figure 25) (Campbell and Robson, 1968). In this particular stimulus, the spatial frequency gets lower from right to left and the contrast also decreases vertically (with low contrast towards the top of the grating). This means that there is, in humans anyway, a particular spatial frequency at which the sensitivity is particularly good and we can see the pattern down to low pattern contrast, which results in the pattern seeming to extend vertically upwards at this point. The apparent upward extent of each sinusoidal wave (black and white "stripe") indicates the contrast sensitivity for that particular stripe's spatial frequency. In humans the greatest vertical extent or longest stripes are usually seen in the middle of the pattern and at low and high spatial frequencies the pattern contrast sensitivity and hence the vertical stripes' vertical length starts to decline.

Figure 25. Stationary sinusoidal grating decreasing in spatial frequency (towards the right) and decreasing in contrast towards the top. This shows the human contrast sensitivity for different spatial frequencies.

By moving sinusoidal gratings at different speeds we can use contrast sensitivity as a tool to study not only the resolving powers of spatial filtering mechanisms; but also the temporal filtering mechanisms of movement detectors (Kulikowski and Tolhurst, 1973; Thompson, 1982; O'Carroll *et al.*, 1997). Contrast sensitivity is limited by the ability of the eye to capture light and is often used to measure the trade-off between optical sensitivity and visual acuity (Campbell and Robson, 1968; Dvorak *et al.*, 1980).

There are a wide range of studies investigating the insect contrast sensitivity to moving stimuli, however most studies focus on flying insects such as flies, beetles and bees (Reichardt and Wenking, 1969; Dvorak *et al.*, 1980; O'Carroll *et al.*, 1996; O'Carroll *et al.*, 1997). Most insect studies involve taking electrophysiological recordings from wide-field motion detecting neurons in response to wide-field moving gratings (Dvorak *et al.*, 1980; O'Carroll *et al.*, 1996;

Straw *et al.*, 2006; Straw *et al.*, 2008) however, there have been studies which have used behaviour such as the optomotor response (Reichardt and Wenking, 1969; Pick and Buchner, 1979; Reichardt and Guo, 1986; Nityananda *et al.*, 2015). Both neurophysiological and behaviourioural studies have shown the insect's contrast sensitivity is dependent upon the spatial and temporal frequency of the moving grating, suggesting the insect motion detection system is tuned a combination of spatial and temporal properties of a visual stimulus rather than a unique velocity (Reichardt and Wenking, 1969; Pick and Buchner, 1979; Dvorak *et al.*, 1980; Reichardt and Guo, 1986; Hausen and Egelhaaf, 1989; Straw *et al.*, 2008). Although some flying insects are able to extract speed information from an image independently of spatial structure during navigation (Kirchner and Srinivasan, 1989; Srinivasan *et al.*, 1991; Srinivasan *et al.*, 1996).

Sensitivity to different combinations of spatio-temporal frequencies enables animals to be sensitive to different velocities in their environment. Evidence suggests different species of insect have evolved sensitivity to particular spatial and temporal frequencies which match their behavioural ecology (O'Carroll *et al.*, 1996). Fast moving insects, such as flies and bumblebees, have evolved motion detection systems that are sensitive to spatial and temporal frequency combinations which represent high velocities (O'Carroll *et al.*, 1996). In contrast, insects such as hoverflies, which are stationary when hovering but also make quick flights, have a sensitivity to both high and low velocities (O'Carroll *et al.*, 1996; O'Carroll *et al.*, 1997). However, little is known about the contrast sensitivity of relatively sedentary insects such as the praying mantis.

A recent study using the optomotor response to examine the mantis contrast sensitivity has shown that this insect predator is tuned to spatial and temporal frequencies which represent a wide range of speeds, from 20 to 500 degrees per second (Nityananda *et al.*, 2015). This fits with the mantids lifestyle, as they are an ambush predator that remain stationary for long periods of time but prey on fast moving insects such as flies (Nityananda *et al.*, 2015). From an ecological viewpoint, tuning to such high and low speeds could serve the mantis well in both tracking fast moving prey and body stabilisation when stationary and in flight (Brackenbury, 1990; Yager and May, 1990; Cumming, 1996). It is likely this study is recording the sensitivity of early visual mechanisms which serve both the prey tracking system and the bodily stabilising optomotor system (Nityananda *et al.*, 2015).

In this chapter, I compared the contrast sensitivity of the tracking system and optomotor system in the praying mantis, *Sphodromantis lineola*. I used the contrast frequency of drifting sine wave gratings and small Gabor filtered windows of sinewave stimuli at 100% contrast to measure the distinct temporal and spatial signatures of each pathway. I expect to find these systems will differ in their sensitivity to spatial and temporal frequencies. I expect the tracking system will be narrowly tuned to spatial and temporal frequencies which correspond to high velocities, which will enable them to track fast moving prey whilst the optomotor system will be tuned to a broad range of spatial and temporal frequencies, to enable bodily stabilisation when the mantis is both stationary and moving. Furthermore, I examined whether or not either of these systems are

tuned to a particular velocity (40 degrees per second or 160 degrees per second), or if they are tuned separately to the spatial and temporal properties of the stimuli.

6.3 Methods

In this chapter I used six female adult mantids, five of which had been used in experiments in Chapter 4 and one new naive individual. The same experimental procedure was used as in previous chapters, details of which can be found in the general methods chapter (section 2.3). To investigate the processes shaping motion detection in the tracking system of mantids, I used a Gabor patch as the small moving target. A Gabor patch is comprised of a sinusoidal grating within a Gaussian envelope (Figure 26). The spatial frequency of the sinusoidal grating and the temporal frequency at which the target is moved can be varied to allow us to investigate which spatio-temporal frequencies the tracking system is tuned to and whether this tuning is dependent or independent of speed.
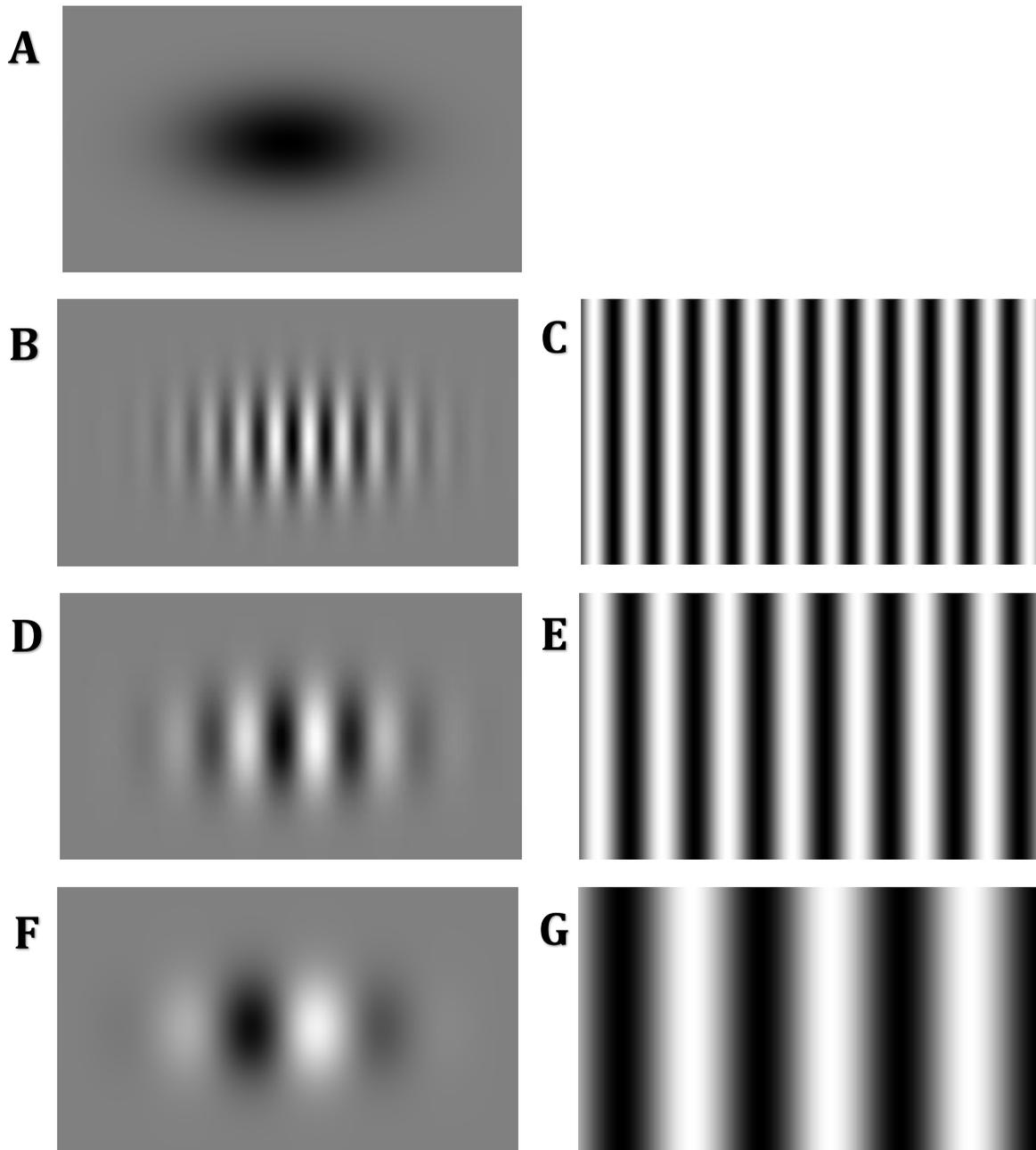
Figure 26. Examples of Gabor patch and wide-field sinusoidal gratings (A) Black Gabor patch (control) (B) Gabor patch 0.2cpd (C) Grating 0.2cpd (D) Gabor patch 0.1cpd (E) Grating 0.1cpd (F) Gabor patch 0.05cpd (G) Grating 0.05cpd

To ensure that I was recording tracking responses to the sinusoidal grating within the Gaussian envelope and not the target's leading edge, the edges of the targets were smoothed (Figure 26). The size of the targets were measured as full

width half maximum (FWHM), which is the distance between 50% transparency points within the targets smoothed edge. Targets were 23° (FWHM) in width and 11.65° (FWHM) in height. Targets appeared randomly at either the left or right side of the screen and travelled across the screen a total of four times. All targets were the same mean luminance and moved over a homogenous grey background.

In previous chapters, I found a moving black target produced the optimum tracking response from the mantids. Therefore, in this experiment, I used a black target as the control to ensure that the mantids were responsive. I used two black control targets, which moved at two different speeds (40 degrees per second and 160 degrees per second). This was to identify whether the mantis had a preference for target speed and allowed me to determine an optimal tracking response to targets moving at these particular speeds.

To test the preferred spatial and temporal frequencies of motion detecting processes within the tracking system, I varied the spatial frequency of the sine grating within the Gabor patch and the temporal frequencies at which the target moved. The spatial and temporal frequencies used were (s/f 0.05 0.1 0.2 cycles/deg) and (t/f 2, 4, 8, 16, 32 cycles/sec Hz, Table 6). These spatial and temporal frequencies were paired to create nine spatio-temporal conditions (Table 6). To reduce the number of experimental conditions needed I chose to test each spatio-temporal condition at 100% contrast. This allowed me enough time to collect a good sample size for the nine chosen experimental conditions. To allow me to investigate whether motion detection in the tracking system is tuned to velocity $\left(\frac{Temporal\ Frequency}{Spatial\ Frequency}\right)$ or is separately tuned to spatial and temporal frequencies, three spatio-temporal conditions matched the speed of a black target

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moving at 40 degrees per second (green, table 6) and three matched the a control target moving at a speed of 160 degrees per second (red in table 6).

Table 6. The spatial and temporal frequency combinations of the sinusoidal Gabor patch and the wide-field sinusoidal grating. Green highlighted conditions matched the speed $\left(\frac{T/F}{S/F}\right)$ of the black control target traveling at 40 degrees per second and red highlighted conditions matched the speed of the black control traveling at 160 degrees per second.

Spatial Frequency (cycle per degree)	Temporal Frequency (cycle per second)			
0.05	2	8	32	
0.1	4	8	16	32
0.2	8	32		

To test which spatio-temporal frequencies the optomotor system is tuned to, I created wide-field motion using a sinusoidal grating which filled the entire screen. I used the same spatial and temporal frequency conditions as those used to create the Gabor patch (Table 6), to enable me to compare the spatio-temporal tuning of the optomotor system to that of the tracking system. Each presentation of the sinusoidal grating moved either left or right for a total of 5 seconds.

Each mantis was given a series of 20 trials containing the Gabor patch and wide-field sinusoidal grating randomly interleaved. Each combination of spatial and temporal frequency was displayed two times within a block of trials, once traveling left and once traveling right. I recorded the mantids behaviour as tracked (left or right) or optomotor response (left or right).

6.3.5 Data Analysis

Statistical analysis was carried out using SPSS v22. Data were analysed with a generalized estimating equation (GEE, binary logistic model), with velocity (40 degrees per second and 160 degrees per second) and spatial frequency (0.05 cycles per degree, 0.1 cycles per degree and 0.2 cycles per degree) as the independent variables. The number of trials where the mantis responded with the optomotor response to the drifting grating, or with the tracking response to the Gabor patch (out of the total presentations of each condition for each mantis) was used as the dependent variable. Mantis was the subject factor.

6.4 Results

The tuning for wide-field motion was broad but shows an optimum for low spatial frequencies of 0.05 cycles per degree moving at temporal frequencies around 2Hz (cycles per second), a contrast speed of 40 (degrees per second) (Figure 27, A). But mantises did still respond albeit less often to higher spatial frequencies of 0.2 cycles per degree moving at speeds of 32.5 Hz a velocity of 160 degrees per second (Figure 2, A).

A Mean N trials responded to, with a wide-field grating
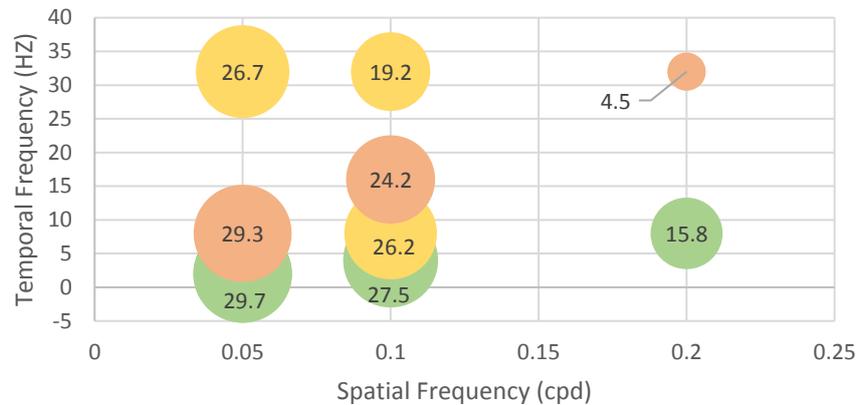
B Mean N trials responded to with a Gabor patch
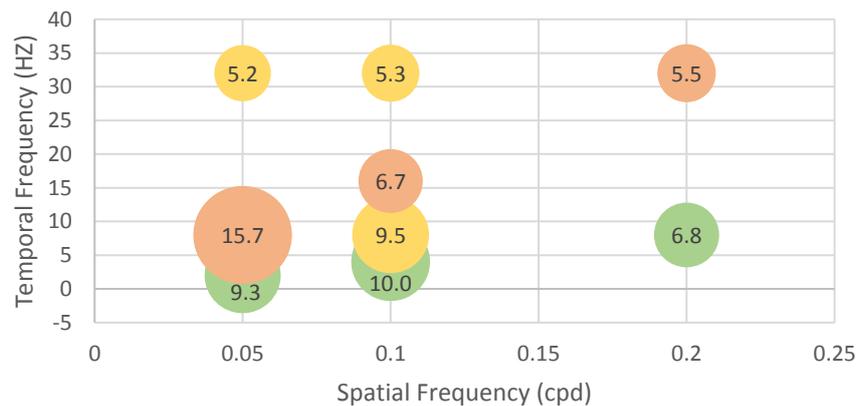
Figure 27. The circle size in both graphs is proportional to the mean number of correct trials (A) The mean number of trials the mantis responded to a moving wide-field sine grating with the optomotor response. Each spatio-temporal condition was displayed to 6 mantises, each mantis viewing each condition a total of 30 times (B) The mean number of trials the mantis responded to the Gabor patch with the tracking response. Each spatio-temporal condition was displayed to 6 mantises, each mantis viewing each condition a total of 30 times. Green highlighted conditions travelled at a speed of 40 degrees per second and red highlighted conditions travelled at a speed of 160 degrees per second. Yellow conditions did not match the speed of a black control and travelled at varied speeds.

The tuning for small target motion detection also shows an optimum for low spatial frequencies of 0.05cpd (cycles per degree) but moving at a temporal frequency of 8Hz, a velocity of 160 degrees per second (Figure 2, B). The sensitivity of the tracking system seems to decline more rapidly away from this optimum when compared to the optomotor system. This decline occurred as spatial and temporal frequencies increase to 0.1 cycles per degree moving at 16Hz and as they decrease to 0.05 cycles per degree moving at 2Hz. This suggests that the small target motion detection system is more specific in its sensitivity to spatio-temporal combinations; with a high sensitivity to a narrow range of spatio-temporal frequencies (Figure 2, B) compared to the wide-field system which has a high sensitivity to a wider range of spatio-temporal frequencies (Figure 27, A).

The probability of the mantids to track the small target was affected by whether it was made up of a solid black Gabor patch or a sinusoidal Gabor patch (GEE, χ^2_3= 22.006, P< 0.001; Figure 28), where the mantis was more likely to track the black control Gabor patch over the sinusoidal Gabor patches (Difference, *post hoc*, P= 0.003). When comparing the number of trials the mantids tracked the black control target results show there is an effect of speed (GEE, χ^2_1= 6.268, P =0.012; Figure 28), where the mantids were more likely to track the black target traveling at 40 degrees per second compared to 160 degrees per second (pairwise, *post hoc*, P= 0.008).
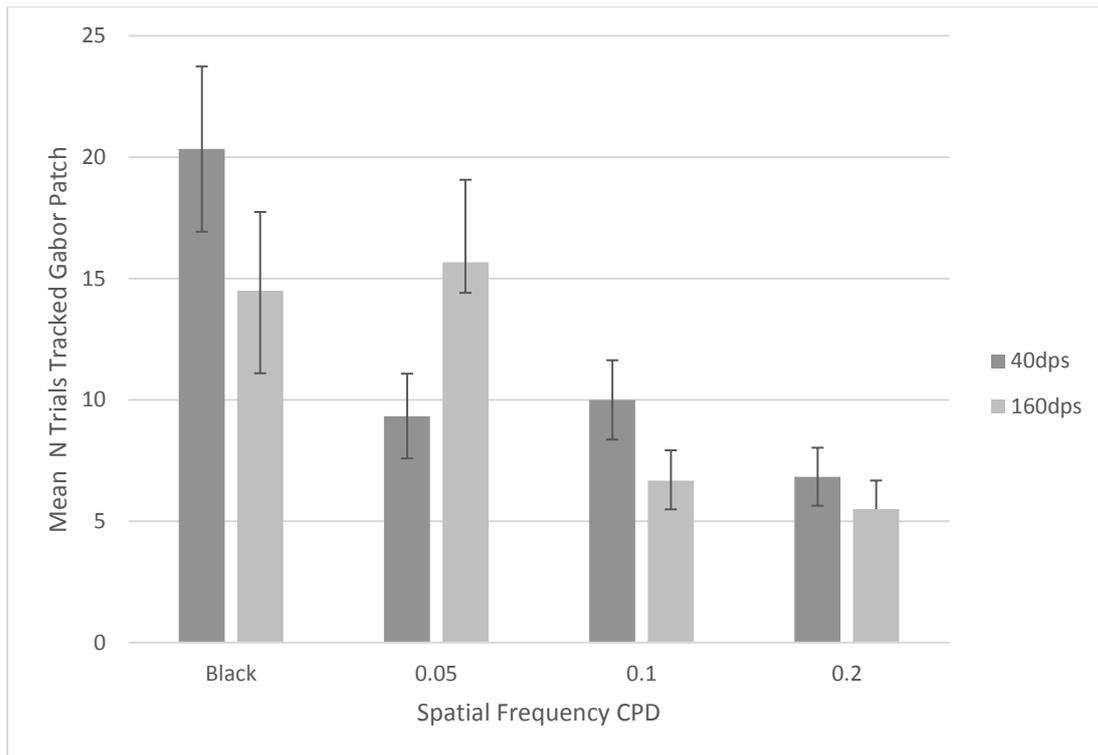
Figure 28. The mean (+/- s.e.) number of trials the mantis tracked the black and sinusoidal Gabor patch at 40 degrees per second and 160 degrees per second over spatial frequencies 0.05 cpd, 0.1cpd and 0.2 cpd. Each condition was displayed to 6 mantises, each mantis viewing each condition a total of 30 times.

To investigate whether the mantis tracking system is tuned to the speed of a target or separately to spatial and temporal features of the stimuli, I compared data from trials containing a sinusoidal Gabor patch only. The probability of the mantis to track the Gabor patch was not affected by the target velocity (40 degrees per second and 160 degrees per second) (GEE, χ^2_1= 0.107, P =0.744; Figure 28) but was affected by its spatial frequency (0.05cpd, 0.1cpd, 0.2cpd) (GEE, χ^2_2= 13.587, P =0.001; Figure 26). This indicates that the likelihood of the mantis to track a Gabor patch was not dependent on its speed but on the spatial frequency of its pattern.

To examine whether the effect of spatial frequency was similar within each velocity (40 degrees per second or 160 degrees per second), the data was split to compare the number of trials the mantis tracked the Gabor patch at each spatial frequency (0.05cpd, 0.1cpd, 0.2cpd) within each velocity type (40 degrees per second, 160 degrees per second). I found that the probability of the mantis to track the Gabor patch was affected by spatial frequency for targets moving at 40 degrees per second (GEE, χ^2_2= 47,679, P <0.001; Figure 28) and 160 degrees per second (GEE, χ^2_2= 17,408, P <0.001; Figure 28). Where the mantids were more likely to track a Gabor patch with a low spatial frequency (0.05cpd) compared to a high spatial frequencies (0.2cpd) within both velocity types, that is both 40 degrees per second (Pairwise, *post* hoc P= 0.052) and 160 degrees per second (Pairwise, *post* hoc, P< 0.001). This suggests that the mantids tracking system is not tuned to a velocity of 40 degrees per second or 160 degrees per second but to targets with low spatial frequencies.

The overall probability of the mantis to respond with the optomotor response was affected by both the velocity (GEE, χ^2_1= 80.473, P< 0.001; Figure 29) and spatial frequency (GEE, χ^2_2= 162.495, P< 0.001; Figure 29) of the drifting sinusoidal grating. The mantis was more likely to display the optomotor response to gratings moving at 40 degrees per second (Pairwise *post hoc*, P< 0.001) and to gratings with lower spatial frequencies (0.05cpd) compared to high spatial frequencies (0.2cpd) (Pairwise, *post hoc*, P< 0.001).
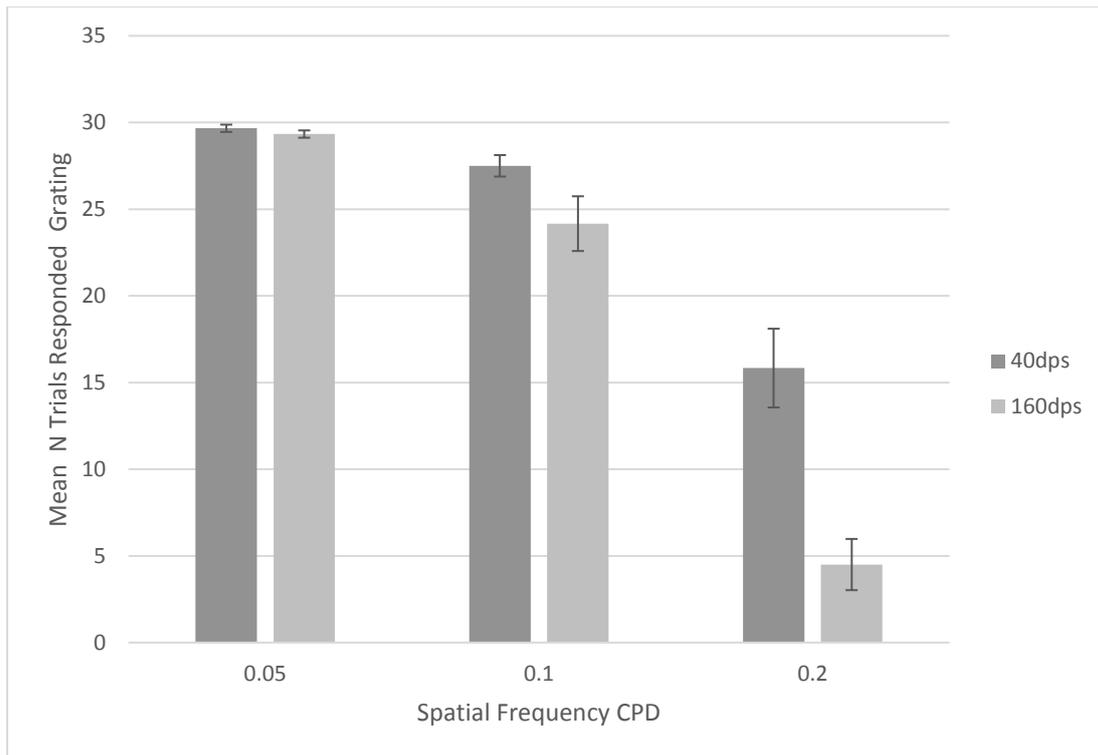
Figure 29. The mean (+/- s.e.) number of trials the mantis responded with the optomotor response to the drifting wide-field grating moving at 40 degrees per second and 160 degrees per second over spatial frequencies 0.05 cpd, 0.1cpd and 0.2 cpd. Each condition was displayed to 6 mantises, each mantis viewing each condition a total of 30 times.

To test whether the mantis optomotor system is tuned to a particular velocity (40 degrees per second or 160 degrees per second), the data were then split to compare the number of trials the mantis displayed the optomotor response to gratings of each spatial frequency (0.05cpd, 0.1cpd, 0.2cpd) within each velocity type (40degrees per second, 160 degrees per second). Results show that the mantis optomotor response was affected by the spatial frequency of the grating at both speeds: 40 degrees per second (GEE, χ^2_2= 80.885, P< 0.001; Figure 29) and 160 degrees per second (GEE, χ^2_2= 742.439, P< 0.001; Figure 29). The mantids

were more likely to display the optomotor response when shown a drifting grating with a low spatial frequency (0.05cpd) compared to a high spatial frequency (0.2cpd) at both velocities, that is both 40 degrees per second (Pairwise, *post* hoc P< 0.001; Figure 29) and 160 degrees per second (Pairwise, *post* hoc P< 0.001; Figure 29). This suggests that the mantis optomotor system is not tuned to a specific speed of either 40 degrees per second or 160 degrees per second, but to the spatial frequency of the drifting grating.

To test whether the tracking system is triggered as easily by the Gabor patch as the optomotor response is by the wide-field drifting grating, I compared the number of trials the mantis responded to the Gabor patch and the wide-field gratings. Overall, the mantis was more likely to display the optomotor response to wide-field stimuli compared to displaying the tracking response to the Gabor patch (GEE, χ^2_1= 142.977, P< 0.001; Figure 30). This suggests the optomotor system is more easily triggered by drifting gratings than the tracking system is by the small moving Gabor patches.

A Spatial Frequency 0.05 (cpd)

B Spatial Frequency 0.1 (cpd)

C Spatial Frequency 0.2 (cpd)
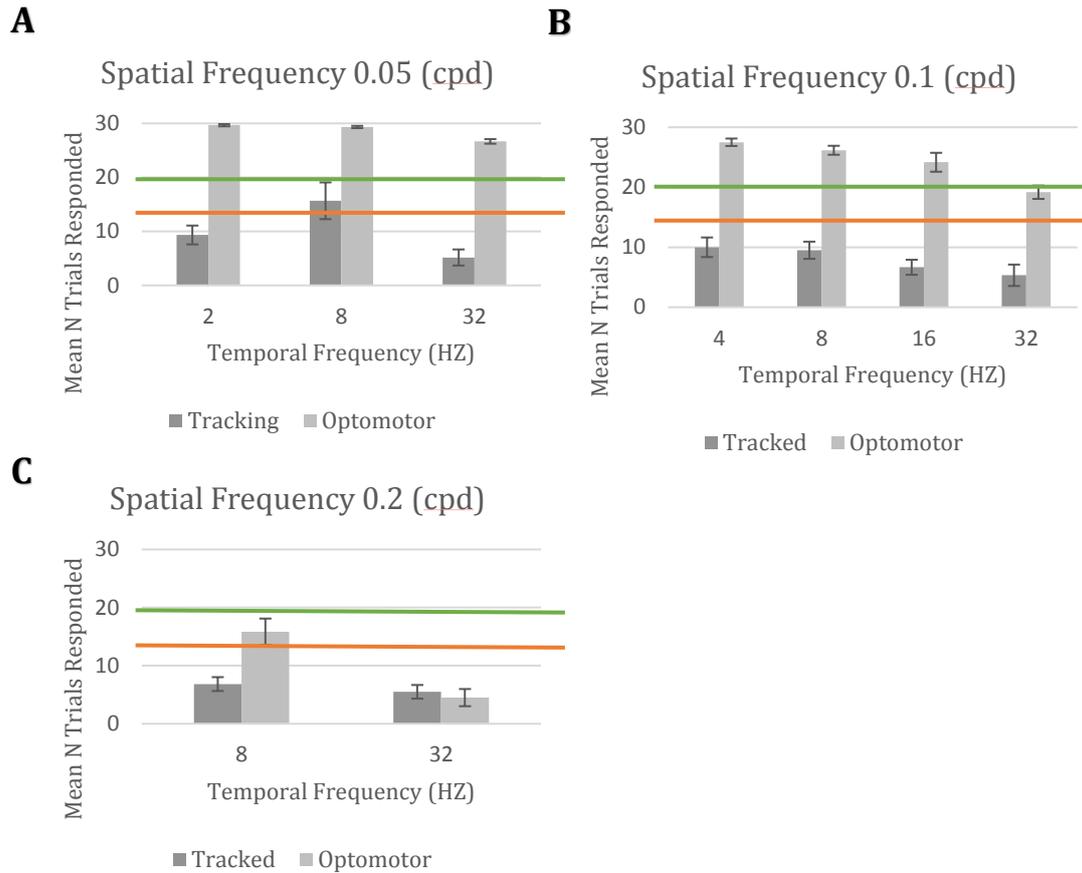
Figure 30: The mean number of trials the mantis responded to the wide-field grating or the Gabor patch with a (A) 0.05cpd (B) 0.1cpd (C) 0.2cpd spatial frequency moving at varying temporal frequencies. Each spatio-temporal condition was displayed as a wide-field grating or a Gabor patch to six mantids a total of 30 times. The mean number of trials the mantis tracked the black control target is represented with the green line (40 degrees per second) and the red line (160 degrees per second).

6.5 Discussion

My results show that the mantis wide-field and small target movement detecting pathways are each tuned differently to a set of spatial and temporal frequencies. The wide-field motion detecting pathway seems to have a high

sensitivity to a broad range of spatio-temporal frequencies whereas the small target motion detection pathway has a high sensitivity to a narrow set of spatio-temporal combinations. Both motion detection pathways seem to be tuned separately to spatial and temporal features of a visual stimulus rather than tuned to a specific speed.

Whilst many studies have used drifting sinusoidal gratings to sample information from neurons within the wide-field motion pathway, which monitor optic flow for tasks such as body stabilisation (Dvorak *et al.*, 1980; Reichardt and Guo, 1986; O'Carroll *et al.*, 1996; Straw *et al.*, 2006; Nityananda *et al.*, 2015). Relatively few studies have investigated the contrast sensitivity of neurons involved in detecting and tracking small moving targets, the so-called small moving target detectors (O'Carroll and Wiederman, 2014). These neurons exclusively respond to small moving visual features of limited extent and are used in tasks such as tracking prey and con-specifics (Collett, 1971; Collett and Land, 1975; Olberg, 1981; Egelhaaf, 1985; O'Carroll, 1993; Nordström *et al.*, 2006; Barnett *et al.*, 2007; Duistermars *et al.*, 2007; O'Carroll and Wiederman, 2014). My results show that the optomotor system and tracking system are different in their sensitivity to spatial and temporal frequencies. The tracking system seems to be most sensitive to a narrow range of spatial -temporal frequency combinations with optimum response around (0.05cpd – 8Hz). Mantids often predate upon small fast moving prey such as flies and crickets. The narrow tuning of the tracking system to targets with spatial frequencies of (0.05cpd) moving at around 160 degrees per second would enable mantids to be highly sensitive to small fast moving objects which may represent prey. This selectivity will enable them to

filter out insignificant features which may be too small to represent prey. This is consistent with our findings in previous experiments, where the mantis had a high optomotor response to smooth moving drifting patterns with a wide range of spatial properties (2 pixel to 40 pixel patterns, chapter 3). In comparison, when tracking small moving targets the mantis was more selective in which targets it tracked, depending on the size of the elements within the targets pattern. This selectivity in the tracking system may be due to suppressive lateral interactions within neurons sensitive to small moving targets (SMTD's), similar to those found in mammalian hypercomplex cells (Hubel and Wiesel, 1959; Hubel and Wiesel, 1968; Henry *et al.*, 1974; Nordström and O'Carroll, 2009). In comparison, the optomotor system is highly sensitive to a wide range of spatio-temporal frequencies with optomotor response dropping only in the very high spatial frequencies (0.2cpd) and high temporal frequencies (32Hz). This makes the optomotor system sensitive to a broad range of velocities, enabling the mantis to monitor optic flow with a range of contrast frequencies.

In both systems, the mantis visual system does not seem to be tuned to a particular speed but is instead tuned separately to a stimulus spatial and temporal features. The mantis responds more to stimuli with low spatial frequencies compared to high spatial frequencies, independent of the stimulus speed. If the mantis was tuned to velocity we would expect to see a similar response rate to stimuli with the same speed, over different spatial frequencies. This is consistent with studies that show the insect visual system relies heavily on the spatial and temporal properties of an image rather on an image's velocity (Reichardt and Wenking, 1969; Pick and Buchner, 1979; Dvorak *et al.*, 1980; Reichardt and Guo,

1986; Hausen and Egelhaaf, 1989; Straw *et al.*, 2008; Yamawaki and Toh, 2009; Nityananda *et al.*, 2015).

The mantis seems to respond more readily to wide-field stimuli with the optomotor response, compared to tracking the Gabor patch. This maybe because motion detection of wide-field stimuli uses spatial integration of many EMD's which sample local motion at different parts of the wide-field moving pattern (Dvorak *et al.*, 1980), therefore creating a large motion signal. Visual pathways which process small visual features are not able to integrate motion at many points in the image and are limited to sharing motion information only with adjacent receptors (O'Carroll and Wiederman, 2014) giving a weak motion signal. The tracking response is also heavily dependent upon a target meeting specific prey-like characteristics and on the internal state of the mantis motivating predatory behaviour (Prete and Mahaffey, 1993). The optomotor system need only have wide-field motion to trigger the mantis to stabilise its body relative to the environment (Liske, 1999; Nityananda *et al.*, 2015).

Chapter 7: General Discussion

In this thesis, I have characterised the insect Dmax and highlighted the similarities between insect and human perception of apparent motion. I have shown, when predated on by the praying mantis, background matching in moving prey is only beneficial to prey with large pattern elements. However, un-patterned grey targets which match the background luminance gain a greater survival advantage over patterned targets, even when the patterned target receives benefits from matching the background pattern. I have added to what is already known about praying mantis prey preference characteristics and the effects background pattern can have on the ability of the mantis to track prey. I have demonstrated that background motion does not inhibit the ability of the mantis to track a moving target and that there are little benefit for prey which match the phase of the background motion. Although, it is more costly for prey to move out of phase with background motion compared to moving in phase or over a still background. Finally, I have shown the mantis wide-field and small target motion detecting pathways are not tuned to specific velocities but are separately tuned to a set of spatial and temporal frequencies. The mantis wide-field motion detecting pathway is tuned to a broad range of spatio-temporal frequencies whereas the small target motion detecting pathways is tuned to a narrow range of spatio-temporal frequencies.

7.1 Apparent-motion perception by the Praying Mantis (*Sphodromantis lineola*)

In humans, it has been shown that the perception of apparent motion breaks down as images are displaced by larger distances each frame (Braddick,

1974, 1980). It was initially thought that this Dmax limit represented the spatial limit of elementary motion detectors in the visual system (Braddick, 1974; Braddick *et al.*, 1980). However, further work revealed Dmax does not have a set spatial limit but is dependent on the size of the pattern elements, where Dmax increased with pattern element size (Chang and Julesz, 1983; Cleary, 1987; Cleary and Braddick, 1990; Morgan, 1992; Morgan and Fahle, 1992). This lead researchers to believe that there are multiple motion detector 'channels' within the human visual system which are tuned to different spatial scales (Campbell and Robson, 1968; Graham and Nachmias, 1971), each with a Dmax value dependent on its spatial frequency tuning.

I have shown that the insect Dmax does not have a set spatial limit but like the human Dmax it is dependent upon the spatial frequency of an image. Images with low spatial frequencies are able to be displaced by larger distances before apparent motion begins to break down compared to high spatial frequencies. This suggests that the vertebrate and invertebrate visual systems have similar underlying motion processing mechanisms; whereby by low frequency local motion is being pooled over a larger visual area compared to higher spatial frequency images.

Currently, the insect model of motion detection involves the linear pooling of motion detectors across the eye which represent a single channel system. It is well established that the pooling of retinotopic elementary motion detectors takes place in the lobula complex of the insect optic lobe. However, it is still unclear whether this motion information is processed by one broadly tuned neural

'channel' or several independent channels more narrowly tuned to different spatial frequencies.

Following the results of this chapter, there has been further work investigating whether insects process motion information with multiple independent channels, differing in spatial frequency tuning, or whether they use a single channel system. Using a psychophysical masking paradigm similar to those in human studies (Stromeyer Iii and Julesz, 1972; Anderson and Burr, 1989; Solomon, 2000; Serrano-Pedraza *et al.*, 2013) and subsequent modelling of experimental data; Tarawneh *et al.* (2016) (in preparation) found that a single channel model could not explain the behavioural data and that it is likely insects possess at least two classes of motion detectors which differ in spatial frequency tuning.

The existence of multiple motion detector 'channels' with differing spatial tuning could go far to explain how some flying insects can estimate image velocity even though EMDs are not speed tuned (Kirchner and Srinivasan, 1989; Srinivasan *et al.*, 1996; Srinivasan *et al.*, 1999). For example, bees have been shown to integrate velocity over time to estimate travelled distances when flying through tunnels independent of the spatial features of the tunnel lining (Srinivasan *et al.*, 1996). It has been suggested that the this speed tuned behaviour in bees is not mediated by motion detection mechanisms which underlie the optomotor response but a different mechanism (Srinivasan *et al.*, 1993). However, an alternative explanation could be that bees have different spatially-tuned detector classes whose outputs are pooled to obtain a speed-tuned response (Horridge, 2009).

7.2 Background Matching in Moving Targets

Movement is one visual cue that enables predators to distinguish prey from the background (Livingstone and Hubel, 1988; Borst and Egelhaaf, 1989; Lamme, 1995; Nordström *et al.*, 2006; Nordström and O'Carroll, 2009). Although there are a number of studies investigating the survival benefits of background matching in stationary prey (Merilaita *et al.*, 1999; Merilaita *et al.*, 2001; Merilaita, 2003; Cuthill *et al.*, 2005), there have been relatively few studies investigating whether background matching offer prey any benefits whilst moving. The few studies which have investigated the effects of movement on the detection and capture of prey have used humans as a predator model (Stevens *et al.*, 2008; Hall *et al.*, 2013). In this study, I investigated whether there were any survival benefits associated with background matching when prey are moving.

Interestingly, I found that grey targets which matched the background mean luminance had a greater survival advantage over patterned prey, even when the patterned prey benefited from background matching. This may be due to the mantids' preference for small moving dark spots (Prete and McLean, 1996; Prete *et al.*, 2012). The dark elements in the 20 pixel patterned prey may be attracting the mantids' attention, triggering the tracking response; whereas a grey target with no pattern features may not meet the criteria of 'prey' vs 'non prey' allowing low contrast homogenous prey to avoid attracting the mantids' interest. This could also explain the mantids' preferences for prey patterned with large dark elements, over prey patterned with small dark elements. The low spatial resolution of the mantis may allow for large dark elements within a prey's pattern to be easily resolved making them more attractive than prey with small elements which may appear blurred to the insect compound eye. This suggests that

selection pressures produced by mantis predation are likely to select for prey which maintain a low contrast to the background and have small pattern features compared to prey with large highly contrasting features. However, prey that do contain large highly contrasting features may gain a survival advantage if they limit their movement to habitats which match their pattern.

Studies using stationary prey have shown background pattern has an effect upon the detection of prey. When background matching prey remain stationary the predator must actively search for discontinuities in the pattern or changes in contrast; therefore by increasing the pattern complexity, the amount of visual information the predator must process also increases (Dimitrova and Merilaita, 2009; Dimitrova and Merilaita, 2011; Dimitrova and Merilaita, 2014). In this study prey moved which made them stand out from the background through figure ground segregation. It is interesting to observe that even when a target is made conspicuous through motion, background pattern still effects the likelihood of prey being tracked by a predator. When the mantis moves it's head to track prey it creates optic flow as the background image shifts over the retina. It is possible tracking a target over a heterogeneous background will create a large amount of motion information which may make it difficult for the mantis to track a target over a complex background, therefore the mantis may prefer to track prey over a homogenous background which does not create optic flow. It would be interesting to observe the natural habitat the African lined mantis selects to ambush prey and whether they choose to hunt in relatively simple habitats with little background clutter.

Studies using stationary targets have shown that prey which move between different habitats might benefit from having a compromise pattern compared to matching one background completely (Merilaita et al. 2001; Merilaita and Dimitrova 2014). My study has shown that any cryptic benefits a compromise pattern may afford prey over differing habitats is eliminated when prey move. This means although compromise patterns offer prey which travel between visually differing habitats a survival advantage; they must ensure they remain stationary when predators are active and move between these habitats when they are less likely to be observed.

In this study, I used quite unnatural visual stimuli, which are not commonly found in nature. When designing the computer generated prey stimuli I needed to design a target that would attract the mantis attention and elicit a high predatory response. To do this our stimuli needed to contain lots of hard edges and highly contrasting pattern elements (Prete and Mahaffey, 1993; Prete and McLean, 1996; Yamawaki, 2003; Prete *et al.*, 2012). I chose to use computer generated images because I would have more control over the target movement, size and pattern enabling me to reduce any confounding factors and more precisely compare my independent variables. In the natural environment, however, prey will not be square with chequerboard patterns.

I could have conducted these experiments using live insects, such as crickets, which are often a similar colour and contrast to their background. For example bush crickets of the genus *Platycleis* are often a dull brown/green colour matching plant stems and leaves in their environment. They can also be found in the same regions as the African lined mantis, making it possible they are one of its

natural prey. Whilst these insects may offer results with a more ecological perspective, it would be difficult to control their presentation in the same way.

7.3 Background Motion and Target Tracking in the Praying Mantis

I found that there were no survival benefits associated with prey which match the phase of background motion; however, my results show that it is clearly more costly to move out of phase with background motion. This means that it is more beneficial for prey to remain still if they are at risk of moving out of phase with motion in their environment.

Studies have shown MacLeay's spectre (*Extatosoma tiaratum*) remain still when movement from nearby vegetation is too strong (Bian *et al.*, 2015). This maybe because they are unable to match the phase and frequency of the motion in their environment. It is possible that they remain still to avoid making themselves conspicuous by moving against background motion when they are unable to match it.

This study used computer generated stimuli to generate a prey-like target and background motion; this meant the stimuli were very 2-dimensional. Moving features at different distances from the mantis has been shown to affect mantids' predatory responses (Rossel, 1983; Prete and Mahaffey, 1993; Nityananda *et al.*, 2016a). In a natural setting, prey will be moving in a 3-dimensional environment, with movement at varying depths relative to the observer. Additionally, background motion within a natural environment would not only differ in phase of motion but also in frequency, with some parts of the background moving at a higher rate than others. This will make it very difficult for prey to match

background motion. Therefore, as my results suggest it may be beneficial for prey to remain still when faced with complex background motion.

7.4 Praying mantis contrast sensitivity to wide-field gratings and small moving targets: a contrast frequency comparison of the optomotor and tracking behavioural systems

Contrast sensitivity is often used as a tool to study the resolving powers of spatial and temporal filtering mechanisms of movement detectors in the visual system (Kulikowski and Tolhurst, 1973; Thompson, 1982; O'Carroll *et al.*, 1997). Most studies have focused on measuring the contrast sensitivity of wide field motion detection system, which is used by animals to monitor optic flow (Dvorak *et al.*, 1980; O'Carroll *et al.*, 1996; Straw *et al.*, 2008; Nityananda *et al.*, 2015). Studies investigating the contrast sensitivity of insect wide field motion detectors have shown insects with differing behavioural ecology have evolved a sensitivity to differing spatial and temporal frequencies. Fast moving insects such as flies and bumblebees have evolved a sensitivity to spatio-temporal frequency combinations which represent fast velocities; whereas insects such as the hoverfly who spend time both stationary when hovering and moving fast during flight have evolved a sensitivity to both low and high velocities (O'Carroll *et al.*, 1997; Nityananda *et al.*, 2015). Whilst these studies have been important in characterising the optical sensitivity and acuity in a range of insects there is relatively little known about the contrast sensitivity of movement detection systems involved in detecting and tracking small targets (O'Carroll and Wiederman, 2014).

My results show that the wide-field (optomotor system) and small target (tracking system) motion detection systems are different in their sensitivity to spatial and temporal frequencies. The tracking system seems to be highly sensitive to a narrow range of spatial -temporal frequency combinations with optimum response around (0.05cpd – 8Hz). It is likely the mantis tracking system has evolved a narrow tuning to targets with low spatial frequencies (0.05cpd) moving at around 160 degrees per second, to enable them to track fast moving prey such as flies and crickets and ignore objects outside of this spatio-temporal envelope, which may represent non-prey items such as moving vegetation or objects too small to represent prey. This narrow tuning could be due to suppressive lateral interactions where tuning to small targets is generated by the presence of an inhibitory zone surrounding an excitatory centre. This is referred to as end-stopping and is seen within the mammalian hypercomplex cell (Hubel and Wiesel, 1959; Hubel and Wiesel, 1962; Henry *et al.*, 1974; Bishop *et al.*, 1980) and in ganglion cells in the vertebrate retina. In the vertebrate retina, we see lateral inhibition of surrounding photo receptors by horizontal cells (Baylor *et al.*, 1971; O'Bryan, 1973; Verweij *et al.*, 2003). This creates a central surround receptive field, whereby light falling on the centre excites the ganglion cell and light falling on the surrounding regions inhibits the cell (Hartline *et al.*, 1956; Hartline and Ratliff, 1957). This negative feedback allows for edge detection and spatial discrimination in early visual processing. In the mammalian hypercomplex cell end-stopping selects for an object of a particular size and speed, where the outer boundaries of an elongated bar triggers inhibitory interactions as the edges move over the inhibitory end zones. A target of optimal size will produce little

suppression; as the outer edges are too close together to trigger suppression from the outer inhibitory zone as it moves over the central excitatory zone of the receptive field, figure 31 (Orban *et al.*, 1979; Bishop *et al.*, 1980; Orban, 2008; Nordström and O'Carroll, 2009). Although hypercomplex cells are found in the mammalian visual cortex, insect small moving target detectors (STMD's) have been found to share similar end stopping properties, such as inhibition from elongated moving bars whilst maintaining a baseline response to wide- field motion (O'Carroll, 1993; Nordström *et al.*, 2006; Nordström and O'Carroll, 2009).

Figure 31: Example of a hypercomplex cell in the cat visual cortex shows selectivity for small moving targets by having an excitatory centre with inhibitory zones either side (Bishop *et al.*, 1980; Nordström and O'Carroll, 2009)

In comparison, the optomotor system is highly sensitive to a wide range of spatio-temporal frequencies with optomotor response dropping only in the very high spatial frequencies (0.2cpd) and high temporal frequencies (32Hz). This makes the optomotor system sensitive to a broad range of velocities, enabling the mantis to monitor optic flow with a range of speeds.

In both systems, mantis response is independent of velocity but is instead dependent on the stimulus spatial and temporal frequencies. For

example the mantis has a higher response to stimuli moving at 160 degrees per second with a low spatial frequency of 0.05 cycles per degree compared to targets moving at 160 degrees per second with a high spatial frequency of 0.2 cycles per degree. This suggests that both the tracking and optomotor system are not tuned to a specific speed, but independently to spatial and temporal features of the visual stimuli. If the mantis was tuned to speed we would expect to see a similar response rate to stimuli with the same contrast frequency (degrees per second), over different spatial frequencies (cycles per degree). This is consistent with studies that show the insect visual system relies heavily on the spatial and temporal properties of an image rather on an image's velocity (Reichardt and Wenking, 1969; Pick and Buchner, 1979; Dvorak *et al.*, 1980; Reichardt and Guo, 1986; Hausen and Egelhaaf, 1989; Straw *et al.*, 2008; Nityananda *et al.*, 2015).

In conclusion, my thesis has uncovered details of mantis motion perception and how this influences predatory choices, shedding light on the strategies most beneficial to prey.

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