Cue Disparity and Visual Selective Attention in Praying Mantises

Théo Robert[1*], Tan Yi Ting[1], Dune Ganot[1], Yi Jie Loh[1], Vivek Nityananda[1]

Affiliation

[1]Biosciences Institute, Henry Wellcome Building, Newcastle University, Framlington Place, Newcastle upon Tyne, UK, NE2 4HH

*Correspondence: Theo.Robert@newcastle.ac.uk

Summary

Research on insect selective attention has typically investigated it using stimuli in a single plane. The importance of cues to depth, such as stereoscopic disparity, is less well understood. Recent findings on the neurobiology of mantis stereopsis demonstrated centrifugal neuronal connections from the central brain to peripheral optic areas, suggesting the possibility of attentional modulation. To test this, we investigated whether the disparity of a prior cue influences mantis tracking of 3D targets. We fitted mantises with 3D glasses and presented them with a cue, followed by two 3D stimuli – a high contrast target and a distractor with different contrasts. The cue appeared either on the side of the target or the distractor. We varied the disparity of the cue and measured the influence of the cue on the probability of head saccades to the target. Our results show that, compared to the uncued condition, cues with a crossed or an uncrossed disparity reduced head saccades to a single target when presented on the opposite side of the screen. These effects were not seen for cues with zero disparity. The effects of cues of different disparities did not themselves differ significantly, but crossed and uncrossed disparity cues had a stronger effect than zero disparity cues. Our results show that mantis selective attention is influenced by the presence and position of prior cues with a potential influence of cue disparity. This adds further evidence for the complexity of attention-like processes in insects.

Keywords

Selective attention, Praying mantis, Stereoscopic vision, Cuing, Insect Vision

Introduction

Attention is an essential process by which animals filter out multiple stimuli to focus on the ones of interest [1]. Spatial attention, the allocation of attention to particular regions in space, has been a particularly well studied aspect of attention and the visual properties that guide it are well established, especially in human and non-human primates [2–5]. Yet other animals, including insects, would also benefit from attentional processes – think of a bee choosing one of several flowers in a meadow or a mantis choosing between prey. Studies focusing on attention in insects often do so under the

framework of selective attention – the ability to choose one amongst several targets (for reviews, see [6,7]).

Studies of visual selective attention in insects typically investigate spatial attention within a single plane and have not investigated the influence of depth-related cues [8–10]. In particular, the interaction between insect attention and stereoscopic disparity remains largely unknown. Disparity is the difference in the retinal position of an object on the two eyes. Since this difference is greater for nearer objects and lower for objects that are further away, disparity provides information about the depth of an object independent of other visual characteristics, including angular size and motion. The ability to use disparity to calculate depth is called stereopsis, which is present in several animals [11], including one group of insects, the praying mantids.

Stereopsis has been demonstrated behaviourally in mantises by measuring their probability to strike at and capture prey presented with different disparities [12]. Mantises preferentially strike at prey with disparities corresponding to nearer distances - in a range typically 2.5 to 5 cm away [12–15]. Early studies used prisms to manipulate the disparity of prey [12]. More recently, this was done using an insect 3D cinema, which involves affixing colour filters on each eye of the mantis, enabling the presentation of different stimuli to each eye on a computer monitor [16]. This method has allowed researchers to investigate the mechanisms underlying stereopsis and its role in detecting and capturing prey. Behavioural studies have, for example, shown that mantis stereopsis differs from primate and bird stereopsis by relying on temporal change in visual stimuli rather than static luminance matches in each eye [15]. Neurophysiological studies have also discovered neurons tuned to specific disparities that function similarly to disparity-sensitive cortical cells in vertebrates [17,18]. Importantly, some of these neurons provide feedback connections from the central brain to the visual lobe [17], suggesting the possibility that they might guide attention in 3D space. We therefore set out to test this possibility in a series of behavioural experiments.

We used an insect 3D cinema to present mantises with cues that varied in disparity, duration and lateral location, followed by a choice between a high contrast target and a distractor at different contrasts. Our results showed that a prior cue influences selective attention in mantises. Selective attention was influenced mostly by the contrast of the distractor, the position of the cue and to a lesser extent, by the disparity of the cue.

Materials and Methods

Experimental Model

The mantises in our experiment were all adult female *Sphodromantis lineola*, bred in a dedicated insect housing facility or bought as 4th instar nymphs from Bugz UK. They were raised in the insect

facility and kept in individual plastic containers (dimensions 19.8 by 12.5 by 15.5 cm) at a constant temperature of 25°C. When individuals did not participate in experiments, they were fed 3 times a week with an adult cricket. During experiments, mantises were fed only once a week to increase their motivation to react to stimuli.

Method Details

Experimental Setup

Each mantis was fitted with 3D anaglyph glasses consisting of one red and one purple tear drop shaped transparent light filter (LEE® colour filters, 135 Deep Golden Amber and 797 Purple respectively) fixed in front of the eyes of the mantises using a mixture of wax and rosin (for more details, see [19]). For each mantis, the side of the red and the purple filters was determined randomly. An attachment was also fixed with rosin and wax to the pronotum of the mantises to allow us to later attach them to the experimental stand. Mantises were allowed to recover for a day after this procedure.

On experimental days, mantises were placed hanging upside down with their feet holding a platform, and fixed to the experimental stand using the attachment on their pronotum. This maintained the mantises at a fixed position of 10 cm in front of the centre of a computer screen while allowing them to freely move their head and front limbs. Experimental stimuli were displayed on the monitor (DELL U2413f LED monitor, 1920x1200 pixels resolution, 60 Hz refresh rate, 51.8 by 32.5 cm). A webcam (Kinobo USB B3 HD Webcam) placed under the screen recorded the responses of the mantises.

Experimental stimuli and design

All stimuli were generated using custom-written code with Psychtoolbox [20–22] (version 3.0.15) in Matlab (The Mathworks Inc.,version 2012b). Stimuli were presented in 3D by presenting each eye with stimuli in different colour channels in combination with the anaglyph filters (Fig. 1B). In order to balance the input of each channel through the filters, the RGB gains were adjusted to be (0 1 0) in the green channel and (0 0 0.13) in the blue channel (for more details, see [19]). Stimuli in all experiments were presented against a background that consisted of 50% of the maximum output of each colour taking into account these adjustments. It was thus a mixture of blue and green that would be perceived as equally ‘grey’ for each eye.

During experiments, mantises were first presented with a centring stimulus consisting of a spiralling black disc (RGB values (0 0 0)) that swirled in from the periphery to the centre of the screen (Fig. 1A). After a pause of 10 seconds, mantises in conditions with a cue were presented with a cue on either the left or the right side of the screen 2.8 cm from the centre line and at height of 24.3 cm form the

bottom of the screen. The cue was a disc (1 cm radius) consisting of a group of black and white dots (each of radius 20 px or around 0.54 cm). This disc was stationary but in other respects was identical to that used in previous experiments [23] to elicit prey capture responses when moving.

Immediately after the cue disappeared, two stimuli – a target and a distractor- were presented on the screen. These consisted of two black rectangles (3.5 cm tall by 0.7 cm wide, subtending a horizontal angle of 4°) displayed 7 cm from the vertical centreline of the screen, on opposite sides, and with a binocular disparity simulating a distance of 2.5 cm from the mantis. Both rectangles appeared with their bottom edge a quarter of the screen length from the bottom of the screen (approximately 8.1 cm). They then moved synchronously upward on parallel trajectories with a speed of 324 px/s (9.72 cm/s) until they reached the top of the screen. The target always had a contrast of 1 against the background (target RGB luminance: 0 0 0) while the distractor was presented in different trials with one of five contrasts: 0 (invisible), 0.25, 0.49, 0.75 and 1 (contrast equal to the target). Contrasts, here, are given as Michelson contrast and computed as per the equation:

$$Cm = \frac{Lt - Lb}{Lt + Lb}$$

where Lt is the luminance of the target and Lb is the luminance of the background.

The presentation sides of the cue and target, and the distractor contrast were randomly assigned on a given trial and counterbalanced across trials. One experimental run consisted of two repeats of every combination of the two cue presentation sides, the two target presentation sides and the five distractor contrast values making for a total of 40 trials. A gap of 60 s was given between each trial to prevent habituation to the stimuli.

We ran two experiments investigating cuing on selective attention and a control experiment designed to check whether the monocular location of the cue was responsible for the effects measured with crossed and uncrossed disparity cues.

Experiment 1: Cue Duration 4 s

In this experiment, the cue was presented for a duration of 4 seconds (N=14 mantises) before the targets appeared. The duration of the cue was similar to that previously used to study insect attention [9].

To investigate the role of cue disparity in selective attention we had three disparity conditions (Fig. 1B) presented in separate experimental runs: a Crossed Disparity condition, an Uncrossed Disparity condition and a Zero Disparity condition. We also had an Uncued condition where no cue was presented.

In the Crossed Disparity condition, the cue disparity simulated a cue 2.5 cm from the mantis, i.e. at the same depth as the subsequent 3D stimuli. In the Uncrossed Disparity condition, the cue had the reverse disparity as in the Crossed Disparity condition, i.e. the same absolute parallax but with the stimulus positions in each eye swapped. This therefore simulated an 'impossible' stimulus without any clear depth and served as a control condition. In the Zero Disparity condition the cue was displayed without any disparity between the two eyes and was therefore a 2D cue on the screen, at a depth of 10 cm from the mantis.

These conditions were presented in a random order in a blocked design and the entire set of conditions were presented twice to 13 mantises and once to one mantis that died before the end of the experiment. Except for this last mantis, across all experimental runs, we had eight trials per mantis for every combination of cue condition and distractor contrast value in which the cue was on the same side as the target. We also had eight trials per mantis for every combination of cue condition and distractor contrast value in which the cue was on the side of the distractor.

Experiment 2: Cue Duration 100 ms

In addition to the spatial position and simulated depth of a cue, its duration could also have an impact on its ability to capture the animal's attention. To look at the effect of cue duration we therefore repeated Experiment 1 with a cue duration of 100 ms. We ran this experiment with 16 mantises.

Experiment 3: Cue Offset Experiment

In the Crossed and Uncrossed Disparity conditions of the previous experiments, the monocular position of the cue in each eye differed compared to the Zero Disparity condition. We therefore ran an experiment to test whether any difference in response between conditions was due to disparity or monocular position. Here we presented each of 11 mantises with a cue of 4 s duration in only the Zero Disparity condition, but displaced 1.05 cm either toward the left or the right of its original position (Fig. 1C). The resultant positions of the cue corresponded to the monocular positions of the cue in the Crossed Disparity and Uncrossed Disparity condition. This manipulation offset the cue either toward the centre of the screen (hereafter "centred") or toward the outside of the screen (hereafter "excentred"). All other details of the cue and target presentation were as for the Zero Disparity condition in Experiment 1.

In all experiments, the motivation of the mantis was first tested by presenting a 3D black disc simulated to be at a distance of 2.5 cm from the animal. This disc resembled the centring stimulus (but with crossed disparity) and spiralled in from the periphery to the centre of the screen. The experiment

started only after the mantis attempted to strike at the target for two consecutive presentations of this stimulus. The same stimulus was also run at the end of the experimental run and the mantises' responses or lack of response to two consecutive presentations of the stimulus was noted. The mantis was deemed unmotivated for the experimental run if it did not track any of the stimuli in the run and also did not respond to the motivational stimulus at the end. In these cases that run was discarded. When possible, the same run was presented again to the mantis either on the same or a different day. In all 8 out of 286 experimental runs were discarded.

Quantification And Statistical Analysis

Mantis responses on every trial were recorded blind to the stimuli presented. Cue presentations were indicated on the screen by a small black disc at the bottom of the screen that was visible in the recordings but hidden from the mantis by a card barrier.

Video recordings of every trial were visually examined and the presence or absence and the direction of mantises' head saccade was recorded. After the video analysis, responses were matched with the location of the target and distractor. Trials in which mantis's first saccade was performed toward the target were recorded as 1 and trials in which the first saccade was toward the distractor or in which mantises did not make saccades were recorded as 0. Therefore, the probability of first saccade towards the target (hereafter target saccade probability) can be written as follows:

$$\text{P(target saccade)} = \frac{N(Tfc)}{N(Tfc)+N(Tvc)+N(Tns)}$$

With N(Tfc) the number of trials with a first saccade towards the target, N(Tvc) the number of trials with a saccade towards the distractor and N(Tns) the number of trials without any saccade.

If the mantis performed a saccade toward the cue, before the stimuli appeared, the trial was excluded from further analysis. In total 2.4% of trials (229 out of 9400) were excluded from analysis due to saccades to the cue. Statistical analyses were conducted in R 4.0.4. by fitting generalised linear mixed effect models using the lme4 package [24]. All models included the mantises' ID as a random effect. We used target saccade probability as the dependent variable, coding trials with a first saccade toward the target as 1 and trials with a first saccade toward the opposite side or no saccade as 0. These models were fit using a binomial family and a logit link function.

For the analysis of results we combined data from Experiments 1 and 2 in a model. The independent variables in the model were the contrast of the distractor, the cue duration, and cuing condition. Since we had two possible locations of the cue (target cued or distractor cued) for each of the three cuing disparity conditions and an additional category of uncued trials, there were a total of seven different

cuing condition levels included in the last variable. Additionally, we also considered the interaction between the three independent variables in our analysis.

To determine the significance of an effect and select the most appropriate model, we compared the goodness of fit of models of increasing levels of complexity (Table S1A). The goodness of fit comparisons were conducted using the Likelihood Ratio tests from the anova() function in R. We first compared models with only one of the three main effects (distractor contrast, cue duration and cuing condition) to a null model. We next examined whether the contrast had a similar effect with short and long cues by comparing a model including the main effects of distractor contrast and cue duration and their interaction (contrast*duration) with a model including only the two main effects (contrast + duration). We followed the same procedure to examine whether the effect of distractor contrast was different depending on the cuing condition (contrast * cuing condition compared to contrast + cuing condition). Finally, we analysed whether this last interaction was different depending on the duration of the cue. To do so, we analysed the significance of the three way interaction by comparing the full model (contrast*cuing condition*duration) to a model including the main effects and interactions between only distractor contrast and cuing condition.

Finally, we also used the Uncued condition trials from Experiments 1 and 2 to analyse the effect of distractor contrast on the overall mantis saccade probability to either stimulus. We used a model fitted with a binomial family and a logit link function on the data from each experiment. The effect of the contrast was assessed by comparing a model with only distractor contrast as an independent variable to the corresponding null model.

To analyse the results from Experiment 3, the model selection process was similar to the previous one. First, we compared three models with each of the main effects of distractor contrast, cue position (target side or distractor side) and the offset type (centred or excentred) to a null model. Then, we compared a model with the main effects of distractor contrast and cue position with a model that also included their interaction. Finally, we compared this last model to a full model including the offset side.

Results

Model selection

Compared to a null model, a model including only distractor contrast had a significantly better fit for target saccade probability (Table S1, χ^2=697.570, df=1, p<0.001). A model including only the cuing condition, however, was not significantly better than a null model (χ^2=6.705, df=6, p=0.340). A model including the main effects of distractor contrast and cuing condition and their interaction was

significantly better than a model with contrast alone (χ^2=29.287, df=12, p=0.004). Adding duration as a predictor in this last model did not lead to a significantly better model (χ^2=23.205, df=14, p=0.057). Our best model therefore showed that there was a significant interactive effect of both contrast and cuing condition on saccade probability but not of duration.

Higher contrast distractors reduce target saccade probability

The probability that the first saccade was to the target decreased significantly as distractor contrast increased (Fig. 2A and B, Table S2, Estimate ± standard error=-2.894±0.205, Z=-14.096, p<0.001). This effect can be explained by the fact that, across conditions, as the distractor became more discernible from the background, the probability that mantises saccaded to it increased and therefore the probability that they saccaded toward the target decreased.

The effect was further explained by a second phenomenon: the overall likelihood that the mantises performed any saccade also decreased as the target and distractor had more equal contrasts (Fig 4, Table S6 and S7 ; Comparison to null model: χ^2=99.532, df=1, p<0.001 ; Effect of the distractor contrast: Estimate ± standard error=-1.544±0.159, Z=-9.690, p<0.001), indicating that the mantises were less likely to make any choice at all when the two targets were more equal in contrast.

The effect of cue position and disparity on target saccade probability

When the cue was presented on the side of the target, it did not significantly affect target saccade probability compared to the Uncued condition (Fig. 2A, Table S2, Crossed vs Uncued condition: Estimate ± standard error=-0.268±0.157, Z=-1.710, p=0.087 ; Uncrossed vs Uncued condition: Estimate ± standard error=-0.189±0.156, Z=-1.213, p=0.225 ; Zero Disparity vs Uncued condition: Estimate ± standard error=-0.189±0.156, Z=-1.211, p=0.226). In these cases, there was also no significant interactive effect between distractor contrast and the cue type on target saccade probability compared to the Uncued condition (Crossed vs Uncued condition: Estimate ± standard error=-0.006±0.315, Z=-0.018, p=0.985 ; Uncrossed vs Uncued condition: Estimate ± standard error=0.359±0.300, Z=1.197, p=0.231 ; Zero Disparity vs Uncued condition: Estimate ± standard error=0.334±0.302, Z=1.106, p=0.269).

However, when presented on the opposite side to the target, cues had different effects for different distractor contrasts. When the distractor contrast was zero, only the target was visible. In this case, compared to the Uncued condition, the Crossed and Uncrossed disparity cues reduced the target saccade probability (Fig 2B, Table S2, Crossed vs Uncued condition: Estimate ± standard error=-0.434±0.157, Z=-2.765, p=0.007 ; Uncrossed vs Uncued condition: Estimate ± standard error=-0.441±0.156, Z=-2.830, p=0.005). This was not true of the Zero Disparity condition (Zero Disparity

vs Uncued condition: Estimate ± standard error=-0.195±0.156, Z=-1.251, p=0.211) where a 2D cue was presented, 10 cm away from the mantis. The effect sizes for crossed and uncrossed disparity cues were correspondingly larger than for zero disparity cues. This suggests that in this situation, cues with disparity attracted the mantises' attention, making them less likely to look towards a target subsequently presented on the other side of the screen. Importantly, the cues themselves did not result in saccades and so this result is not explained by an initial change in head direction before the target saccade.

When both target and distractor were present, the effect of a crossed disparity or uncrossed disparity cue and distractor contrast interacted to significantly affect target saccade probability compared to the Uncued condition. The decrease in target saccade probability with increasing distractor contrast was significantly attenuated when the cue was on the side of the distractor (Table S2, Crossed vs Uncued condition: Estimate ± standard error=0.887±0.295, Z=3.011, p=0.003 ; Uncrossed vs Uncued condition: Estimate ± standard error=1.112±0.288, Z=3.857, p<0.001). As the contrast of the distractor increased, the crossed and uncrossed disparity cues thus appeared to progressively have a reduced effect and the target saccade probability became comparable to that in the Uncued condition (Fig. 2B). This significant interactive effect between cue and contrast was, however not seen for a 2D Zero Disparity cue (Zero disparity vs Uncued condition: Estimate ± standard error=0.389±0.300, Z=1.300, p=0.194).

Despite the different effect of cues with different disparities compared to the Uncued condition, we did not find many differences when comparing the effects of these cues with each other. When presented on the side of the distractor, the main effect of a zero disparity cue was not significantly different to that of both crossed and uncrossed disparity cues (Table S3, Crossed disparity vs Zero Disparity condition: Estimate ± standard error=-0.239±0.182, Z=-1.318, p=0.188 ; Uncrossed disparity vs Zero Disparity condition: Estimate ± standard error=-0.247±0.181, Z=-1.366, p=0.172). The interaction with contrast also did not significantly differ for zero disparity and crossed disparity cues (Estimate ± standard error=0.498±0.339, Z=1.467, p=0.142). However, the effect of this interaction with contrast did significantly differ between the zero disparity and uncrossed disparity conditions (Estimate ± standard error=0.722±0.334, Z=2.165, p=0.030). Taken together, these results show that disparity only seems to influence target saccade probability in a limited case.

Monocular cue position of a zero disparity cue does not affect target saccade probability

The monocular positions of stimuli differ for zero disparity cues and the crossed and uncrossed disparity cues (Fig. 1B). We therefore ran an additional experiment to verify whether any differences between cuing conditions observed with the crossed and uncrossed disparity cues was due to the disparity or the monocular position of the cue. We presented a zero disparity cue offset at either of the

monocular positions of the cues with disparity used above. Similar to the results above, target saccade probability significantly decreased with increase of in distractor contrast (Fig. 3; Tables S4 and S5 ; χ^2=52.920, df=1, p<0.001; Effect of distractor contrast: Estimate ± standard error=-1.273±0.179, Z=-7.126, p<0.001). However, the position of the monocular cue did not significantly decrease target saccade probability (χ^2=1.795, df=1, p=0.180). There was also no significant effect of the direction of the cue offset (χ^2=0.210, df=1, p=0.647). The offset did not have a significant interaction with distractor contrast (χ^2=0.859, df=2, p=0.651). Finally, the three way interaction between distractor contrast, cue position and offset direction was also not significant (χ^2=5.819, df=6, p=0.444). Overall, these results confirm that the monocular position of a zero disparity cue does not have an effect on target saccade probability.

Discussion

Our results showed that prior cuing influences selective attention in mantises. Mantis selective attention was influenced mostly by the contrast of the distractor and cue position and to a lesser extent, by the disparity of the cue.

The influence of contrast was as expected. As the two stimuli grew more equal in contrast, the probability of saccading to the target decreased. This is partly explained by an increase in attraction to the distractor when it was more visible. The simultaneous presence of two 3D stimuli (the target and distractor) also appeared to reduce the overall response of mantises to the stimuli. Mantises therefore found it more difficult to selectively attend to either of two when they were identical in all respects. Mantis saccade rates have previously been shown to be reduced when more than one target or distractor was shown simultaneously in a trial [25], which resembles our results. Other work [26] presenting mantises with identical 2D stimuli found that their first saccades were not made clearly towards one or the other target but were more evenly distributed including towards the centre between the stimuli. It is not clear there whether the total proportion of trials with saccades also declined in these trials with two identical stimuli compared to trials with a single target as we observed in our experiment. In dragonflies, which are also predatory insects, an interneuron ensures that one of two paired targets can be selected [8,27]. Flies have also been shown to choose between two stimuli as long as they are far enough apart. With stimuli that are closer together they choose the midpoint of two stimuli [28–30], which has also been seen in mantises [26].

This surprising inability of mantises to choose between two identical stimuli resembles the philosophical paradox of Buridan's Ass (Jean Buridan, c. 1340 as cited in [31]). In the paradox, a donkey equally hungry and thirsty placed at the exact midway between a stack of hay and a source of water finds itself incapable of choosing where to go first and dies of thirst and hunger. Our paradigm appeared to create a situation for the mantises where they failed to choose either of the two identical

prey-like stimuli. This might be related to the mechanisms underlying saccades. Previous research has shown that different neural units may be responsible for triggering saccades towards different areas of mantises' visual field [25]. When several units are activated at the same time, they would compete to initiate a saccade and this competition would increase the chances of saccade initiation failure. How might a mantis catch prey given this apparent limitation to their selective attention? The presence of two identical equidistant prey would likely be extremely rare in their natural environment. Natural differences in distance or prey traits could resolve the problem for the mantis. The selective attention mechanism of the mantis would thus appear to depend on the natural variation in the environment to enable prey selection. This points towards the importance of considering the role of ecology when studying the cognitive abilities of animals.

We find also find an interaction effect between distractor contrast and cuing condition for cues of crossed and uncrossed disparity. In primates, cue position changes attentional performance based on contrast [32,33]. We also do find a contrast-based change in saccade probability that varies depending on cue position. However, the presence of two stimuli means that our results are not directly comparable and we see a change in the effect of the cuing condition for different contrast conditions – as indicated by the interaction effect. Importantly, cues had an effect only when present on the side opposite the target, when they reduce saccades to the target. This supports our hypothesis that target saccades would be higher when the cue was on the target side. However, we do not see an increase of target saccades when the cue is on the same side as the target, which is often seen in similar experiments with primates [32,33].

Most studies of spatial attention in humans and non-human primates have, investigated attention using cues and stimuli in a single plane. Fewer studies have investigated how attention is allocated in three-dimensional space. Studies that have researched this have found that attention can be guided by cues to depth, especially stereoscopic cues [34–40]. Cue disparity also had some influence on mantis selective attention in our experiments. A crossed disparity cue simulated to be near the mantis decreased target saccades if presented on the side opposite to the target. This suggests that it had a distracting effect that took attention away from the target. Importantly, a similar effect on selective attention was also induced by uncrossed disparity cues but not zero disparity (2D) cues. The effects of the crossed and uncrossed disparity cues were largely similar to those of zero disparity cues, except for one effect of the uncrossed disparity cue. Crossed and uncrossed disparity cues also had larger effects than the zero disparity cue. Taken together, these results suggest that disparity could have a small role in mantis attention.

The crossed disparity cues simulated a cue nearer to the mantis while zero disparity cues simulated a farther cue. The fact that the near cues had a larger effect compared to the farther cues suggest that mantis attention could be influenced more by nearer objects compared to farther ones. This would be

similar to some results found in humans [41–43]. It would also seem to fit in with results showing that mantises prefer to strike at stimuli placed 2.5 cm from them and that their probability of striking is dramatically reduced for stimuli further than 5.63 cm [14]. However, cues with uncrossed disparity had a similar effect to crossed disparity cues. Since both crossed and uncrossed disparity cues had the same absolute parallax but with monocular positions swapped, this suggests that mantises might use the absolute parallax independent of monocular position as a cue to attend to targets. This would mean that stereoscopic disparity itself does not have a consistent effect on mantis attention. Previous work nonetheless suggests that mantis saccades are sensitive to depth [26]. One possibility is that it is the presence of two stimuli at the correct distance in each eye or the width that they cover in combination that matters. Given that uncrossed stimuli would not exist in nature, this could also be a rapid way to respond to nearby targets (with crossed disparity) without actually computing stereoscopic disparity.

The similarity in response to cues of crossed and uncrossed disparities is different from previous results about prey capture behaviour. There, mantises were seen to be more likely to strike at crossed disparity targets and not to uncrossed or zero disparity targets [15,16]. The difference in results suggest two points. First, mantises could attend to targets based on the parallax between monocular positions rather than target disparity. Secondly, the decision to capture prey is governed by a separate, possibly later module which does differentiate between crossed and uncrossed disparities. Previous work [19] also has shown that prey detection and prey capture are governed by separate mechanisms and our results add further support for these mechanisms.

Our results can be understood in light of the neural mechanisms underlying stereopsis in mantises. Neurons tuned to specific crossed disparity signals have been recently found in the optic lobes of praying mantises [17,18]. These are binocular neurons that connect to the optic lobes of both eyes and then feed into more central regions of the brain. More relevant to our experiments are neurons that relay information from the central complex to the optic lobe. These neurons have been suggested to serve an attentional function and could be involved in the responses we see to cues. Notably, these centrifugal neurons included neurons that responded to both stimuli simulating nearby targets (TMEcen-neurons) and stimuli with diverging lines of sight (TAcen-neurons) as would occur for our cues with crossed and uncrossed disparity respectively. The neurons that responded to diverging lines of sight responded more strongly to bright stimuli, but given that our cue had both white and black dots, they still could have been stimulated in our study. Our results thus add support to the idea that these neurons could be involved in attentional processing. They further suggest that some of these neurons should potentially govern attention based on the parallax between monocular positions, or the presence of any stimulus, rather than only crossed disparities. Other neurons or a subset of these neurons would presumably then respond only to the crossed disparities and send commands to the motor circuits to enable prey capture.

The involvement of central brain structures in mantis attentional processes is also consistent with the few previous studies on insect attention. Most of these studies have shown that some of the neurons involved are present early on in the nervous system, close to the peripheral sensory neurons [8,10,27,44–49]. However, several different brain areas, including more central areas such as the mushroom bodies [50,51] and the central complex [52] have also been implicated in insect selective attention.

Overall, our results demonstrate that prior cuing and, to a lesser extent, cue disparity can affect mantis selective attention and that these effects are compatible with the known visual neurophysiology of the praying mantis. They thus further our understanding of the sophistication of attention-like abilities in insects.

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Author Contributions

VN and TR designed and ran the experiments, decided on the statistical analysis, prepared the figures and wrote the paper. TR ran the statistical analyses and curated the data. TYT, DG and YL ran the experiments. VN acquired the funding, provided the material support and supervised the project.

Declaration Of Interests

The authors declare no competing interests.

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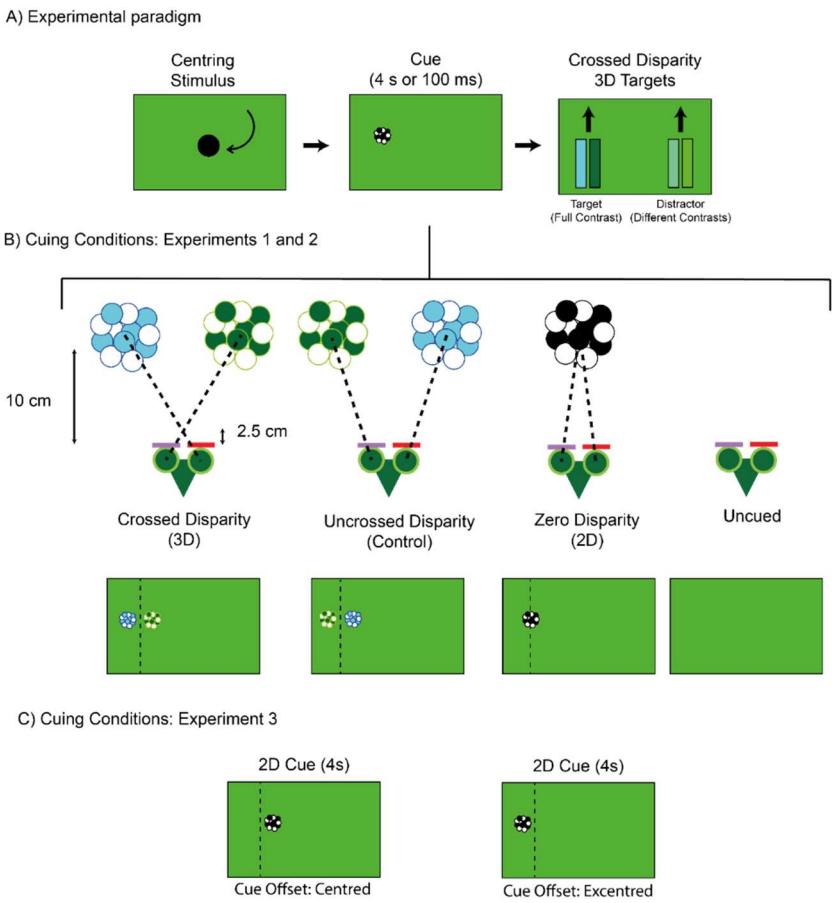

Figure 1: Experimental paradigm. (A) Schematic representation of the experimental design. We first displayed a centring stimulus spiralling towards the centre of the screen. A cue was then presented on the left or the right side of the screen with one of the four disparity conditions, either for 4 s (Experiment 1) or 100 ms (Experiment 2). After the cue disappeared, two crossed disparity rectangular stimuli were displayed, sliding upward. The target was always displayed with a contrast of 1 (full contrast) while the distractor had one of five contrasts: 0 (invisible), 0.25, 0.49, 0.75 and 1 (equal to the target). The positions of the cue, the target and distractor were counterbalanced. (B) Schematic representation of mantises wearing 3D glasses and facing the four cuing conditions in Experiments 1 and 2. The Crossed Disparity condition simulated a cue 2.5 cm from the mantis. The Uncrossed Disparity condition had a cue with the same absolute parallax but with the positions in the right and left eye swapped. The Zero Disparity condition presented the cue on the screen 10 cm from the mantis. No cue was presented in the Uncued condition. Note that the cues are presented in front of the mantis here but were to the side in the experiments as schematically depicted below. (C) Schematic representation of the cuing conditions in Experiment 3. The cue was a 4 s, zero disparity (2D) cue. This was offset either towards the centre of the screen (centred) or the edge (excentred) to match the monocular positions of the crossed and uncrossed disparity cues in the other experiments. The dotted lines are provided for comparison with the stimuli above and were not present during any of the experiments. All cues are here shown to the left of the screen but were displayed on either side on different trials.

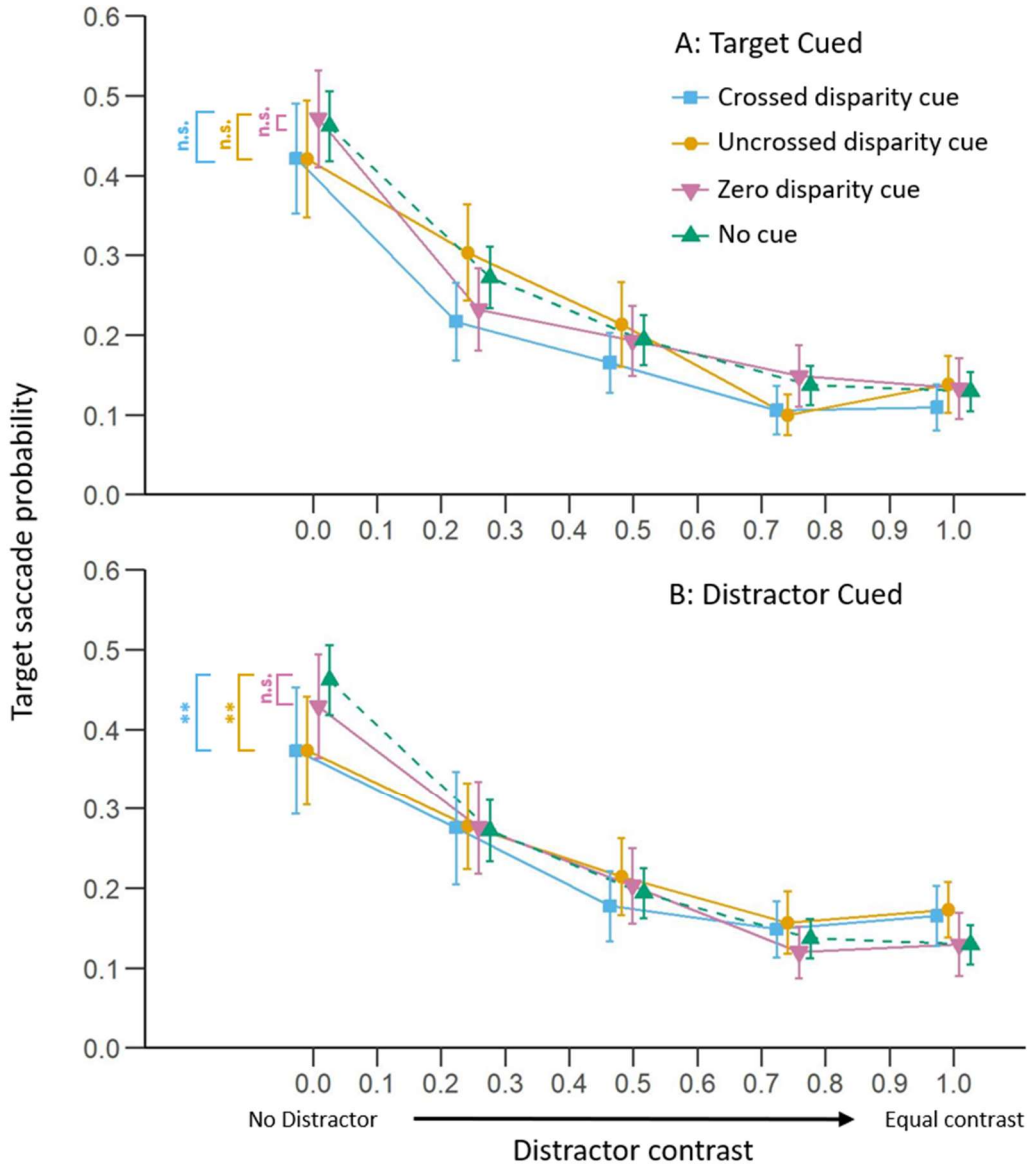

Figure 2: The influence of cue position and disparity on target saccade probability. Mean (± S.E.) proportion of trials with a first saccade towards the target as a function of the Michelson contrast of the distractor. The target always had contrast of 1. The cue was presented either on the side of the target (A) or on the side of the distractor (B). Blue curves represent trials with crossed disparity cues, yellow curves are for trials with uncrossed disparity cues while pink cues are for trial conducted with zero disparity cues. Green curves represent uncued trials and are the same across the two panels. The comparisons to the left are all with respect to the Uncued condition. When comparing between the disparity conditions, only the Uncrossed and Zero Disparity conditions in B were significantly different (see text for further details). Results combine data from both 4 s (Experiment 1) and 100 ms (Experiment 2) cues. ** denotes a p-value < 0.01, n.s. denotes no significant differences.

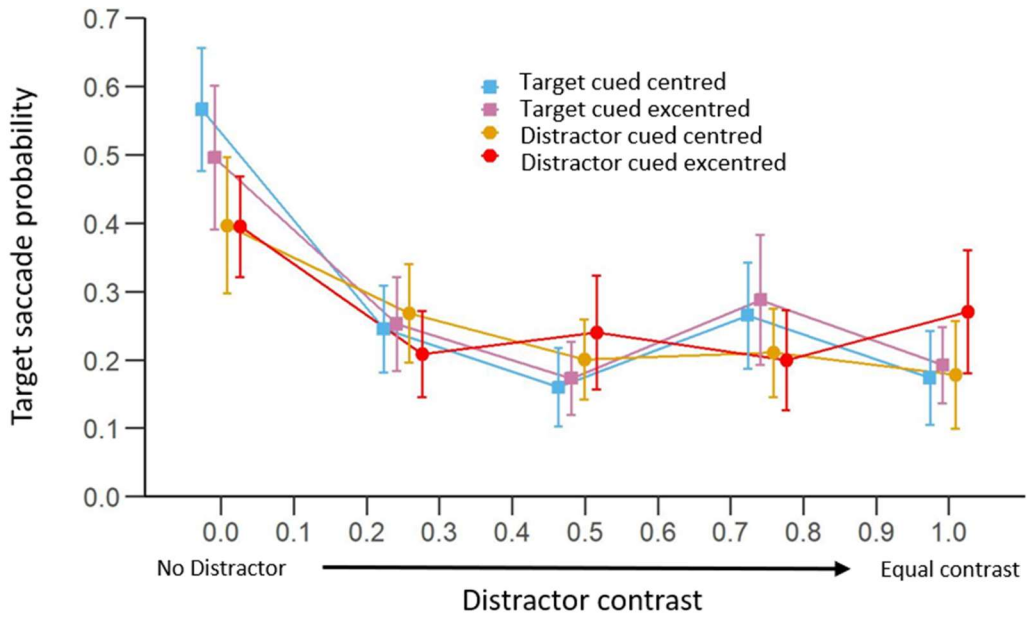

Figure 3: Monocular cue position of a zero disparity cue does not affect target saccade probability. Mean (± S.E.) proportion of trials with a first saccade towards the high contrast target as a function of distractor contrast (Experiment 3). The cue had a duration of 4 s and was either shifted towards the centre of the screen (centred) or towards the outside (excentred) of the screen to match the monocular positions of the cue in the Crossed Disparity condition. Blue and purple curves show results for trials with the cue on the side of the high contrast target and shifted toward the centre and towards the outside of the screen respectively. The yellow and red curves represent the trials with the cue on the opposite side and shifted towards the centre and towards the outside of the screen respectively.

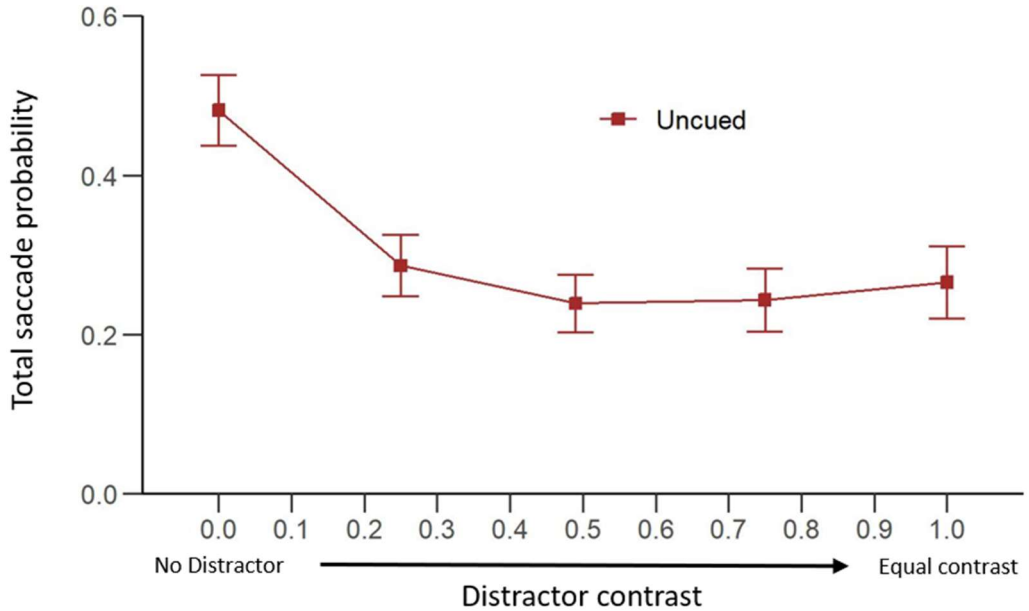

Figure 4: Distractor contrast affects overall saccade probability. Mean (± S.E.) of the individual proportion of Uncued trials with at least one saccade towards either the target or the distractor as function of distractor contrast.