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A Novel Form of Stereo Vision in the Praying Mantis

Graphical Abstract



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In Brief

Primate stereopsis effectively crosscorrelates the luminance patterns between the two eyes. Nityananda et al. show that mantis stereopsis, by contrast, is unaffected by disrupting the interocular correlation of luminance. Instead, it relies on detecting luminance change at positions corresponding to appropriate disparities.

Highlights

- Mantis stereopsis detects depth in random-dot images lacking interocular correlation
- It does not rely on matching first-order local motion direction across both eyes
- It compares temporal change in both eyes, making it sensitive to second-order motion
- This is a fundamentally different stereo mechanism from that found in primates



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A Novel Form of Stereo Vision in the Praying Mantis

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SUMMARY

Stereopsis is the ability to estimate distance based on the different views seen in the two eyes [1-5]. It is an important model perceptual system in neuroscience and a major area of machine vision. Mammalian, avian, and almost all machine stereo algorithms look for similarities between the luminance-defined images in the two eyes, using a series of computations to produce a map showing how depth varies across the scene [3, 4, 6–14]. Stereopsis has also evolved in at least one invertebrate, the praying mantis [15-17]. Mantis stereopsis is presumed to be simpler than vertebrates' [15, 18], but little is currently known about the underlying computations. Here, we show that mantis stereopsis uses a fundamentally different computational algorithm from vertebrate stereopsis-rather than comparing luminance in the two eyes' images directly, mantis stereopsis looks for regions of the images where luminance is changing. Thus, while there is no evidence that mantis stereopsis works at all with static images, it successfully reveals the distance to a moving target even in complex visual scenes with targets that are perfectly camouflaged against the background in terms of texture. Strikingly, these insects outperform human observers at judging stereoscopic distance when the pattern of luminance in the two eyes does not match. Insect stereopsis has thus evolved to be computationally efficient while being robust to poor image resolution and to discrepancies in the pattern of luminance between the two eyes.

RESULTS AND DISCUSSION

Vertebrate stereopsis computes something closely related to the cross-correlation between the luminance images captured by left and right eyes [1-10, 12, 14]. The key insights into vertebrate stereopsis were provided by complex stimuli consisting of random-dot patterns, which can be made correlated, anti-correlated, or uncorrelated across both eyes [3, 4, 6-9, 19-22]. It is profoundly disrupted by such manipulations of interocular correlation as predicted for a system that effectively cross-correlates the left and right eye's images. To investigate if similar mechanisms underlie mantis vision, we used our 3D insect cinema [17, 23] to show mantises similar random-dot stimuli comprising a moving target camouflaged against a textured background. We manipulated the interocular correlation of these stimuli in a series of experiments, asking if mantis stereo also cross-correlates luminance patterns received by the two eyes or if insects have evolved a distinct solution.

We first presented mantises with a static random-dot pattern on a monitor at a distance of 10 cm. The pattern consisted of dark and bright dots, correlated between the two eyes, on a gray background (Figure 1A). A patch of dots (the "target") moved over the pattern, spiraling in from the periphery to the center (Figure 1B). In any one monocular frame, the target was indistinguishable from the background pattern (Figure 1A, Movie S1). However, its motion rendered it visible over time. The target was additionally given a binocular disparity (Figures 1A and 1C). In the "crossed" condition, the target disparity was chosen to simulate a target 2.5 cm from the mantis [17] (7.5 cm in front of the monitor), while the background dots had the same magnitude of screen parallax but with left and right swapped. In the "uncrossed" condition, the disparities of target and background dots were swapped. The target parallax was wider than the mantis interocular separation, so in the uncrossed condition, the simulated distance to the target was undefined. In the "zero" condition, all dots had zero screen parallax, with both target and background in the screen plane. We ran two versions of this and all other experiments using two different dot sizes. These were chosen so that the smaller dots subtended an angle similar to the typical acceptance angle of individual ommatidia in mantis eyes [24], while the larger dots subtended an angle 2.4 times greater (see STAR Methods for details). Regardless of dot size, mantises made significantly more strikes when the disparity cues indicated a target 7.5 cm in front of the screen (i.e., in the mantises' catch range) than for the reverse parallax where the distance was undefined (Figure 2A, upper row; Table 1). This shows that mantis stereopsis can discriminate depth in targets that are perfectly camouflaged apart from their motion. Their accuracy was comparable to human performance on the same task adapted for human vision (Figure 2A, lower row; Table S1).

In this stimulus, two cues potentially convey information about target distance. First, there is the disparity between individual dots in both eyes. Following Lee [25], we refer to this as "static disparity," as it is present in individual (static) frames. Humans and other vertebrates [3, 4, 8, 9, 14] use this cue to

distance

= 10 cm



Figure 1. Stimulus Geometry

(A) The stimuli consisted of random dark and bright dots against a gray background. Targets were indistinguishable from the background in any one monocular frame. The stimuli shown here are for the correlated small dots condition.

(B) Depiction of the spiral trajectory followed by targets in all experiments. Red dots depict the center of the target on consecutive frames (0.0167 s apart) from its appearance at the periphery to the final presentation in the center of the screen.

(C) The target stimulus was presented in three disparity conditions, illustrated here as a full disc against a plain background (screen shown faceon). Mantises viewed stimuli on a screen 10 cm away. The colored filters on the mantis's eves ensured separate presentation of stimuli to each eye. In the uncrossed disparity condition, each eye viewed an ipsilateral stimulus with a parallax equal to that in the crossed disparity condition. Since the lines of sight did not converge in front of the screen, the distance from the screen was undefined. In the zero disparity condition, both eyes viewed a stimulus on the screen. In the crossed disparity condition, each eye viewed a stimulus on the contralateral side, resulting in a virtual target where the lines of sight crossed at a simulated distance of 2.5 cm in front of the mantis (7.5 cm in front of the screen). Note that the actual experiments consisted of more complex stimuli and background as shown in (A).

These results show that mantis stereopsis exploits kinetic disparity, i.e., the disparity between moving regions of the image, not the disparity of the luminance image. Since natural scenes often contain several moving objects, mantises still face the stereo correspondence problem, i.e., identifying which moving object in

break camouflage and perceive the target even in single binocular frames. Second, there is "kinetic disparity" [25, 26], the difference in the positions of the moving patch in the two eyes. The position of the moving patch is visible monocularly independent of the particular dot pattern, so kinetic disparity is in principle completely independent of static disparity. We ran further experiments to see how mantis stereopsis depends on these two cues.

We disrupted static disparity by making the stimuli anti-correlated [21] (matching dots were black in one eye and white in the other instead of black in both or white in both; Movie S2) and removed it by using uncorrelated stimuli (dot patterns generated independently in each eye; Movie S3). For both manipulations and both dot sizes, mantises performed similarly as for the original, correlated stimuli (Figures 2B, 2C, upper row; Table 1). In contrast, human stereopsis was severely disrupted by both manipulations (Figures 2B, 2C, lower row; Table S1). These results confirm that human stereopsis depends largely on the correlation of local contrast in both eyes, with only a weak ability to use kinetic disparity. However, they show that mantis stereopsis is fundamentally different.

the left eye corresponds to which moving object in the right. An obvious strategy is to look for objects moving in the same direction, as an object moving upward in the left eye cannot be the same thing as an object moving downward in the right eye. Human stereopsis uses local object motion in the two eyes as a matching constraint when extracting luminance-defined disparity [27].

screen

= 7.5 cm

virtual target

To ask if mantis stereopsis also exploits this, we designed a new stimulus. The target spiraled in as before, but now, the "target" was a notional circular region. As this region moved over the background pattern of dots, the dots within the region began moving with constant speed. If they moved out of the target region, they were replaced on the opposite side. Once the target moved away, they stopped moving (Movie S4). This decouples the first-order local motion of the dots from the second-order target motion around the screen. The stimuli were binocularly uncorrelated, so there was no static disparity, but there was kinetic disparity defined by the location of the local motion. As before, targets were presented with either crossed or uncrossed disparities, but there were now also four motion-direction conditions. In the two opposite-direction



Figure 2. Stereoscopic Depth Perception and Luminance Correlation

(A–C) The target consisted of a spiraling patch of dots with luminance patterns between both eyes being (A) correlated, (B) anticorrelated, or (C) uncorrelated. The background consisted of dots with the same correlation condition and in A) and B) with the same magnitude parallax as the target but of reversed sign. Top row: Strike probability (\pm 95% binomial score confidence interval) across all mantises in the three disparity conditions corresponding to different simulated distances of the target from the screen (See Figure 1). Lighter lines represent data from individuals, with symbols overlapping for some subjects. Data in (A) and (B) from ten replicates for each of n = 20 individuals for the large dots and ten replicates for each of n = 17 individuals for the samall dots; data in (C) from ten replicates for each of n = 7 individuals. Bottom row: probability (\pm 95% binomial score confidence interval) of human participants perceiving the target as in front of the screen for different simulated distances of 0 cm from the screen. Lighter lines represent data from individuals, with symbols overlapping for some subjects. Human observers in (B) and (C) show idiosyncratic strategies [22] (e.g., responding mostly "near" or mostly "far" for all stimuli equally; responding "far" for stimuli close to the screen plane and "near" for stimuli far from the screen plane), but critically, no human observer modulated their responses depending on the sign of the disparity. Data in (A), (B), and (C) are from fifteen replicates for each of n = 10 individuals. Negative numbers indicate simulated distances behind the screen plane and "near" for stimuli far from the screen plane, but critically, no human observer modulated their responses depending on the sign of the disparity. Data in (A), (B), and (C) are from fifteen replicates for each of n = 10 individuals. Negative numbers indicate simulated distances behind the screen plane. The panels with dots above are cartoon illustrations and not examples of the actual stimuli. Asteri

See also Movie S1, Movie S2, Movie S3, and Tables 1 and S1.

conditions, target dots streamed upward in one eye and downward in the other. In the two same-direction conditions, dots within the target areas streamed in the same direction (upward or downward) in both eyes. As expected given the lack of static disparity, human performance with these stimuli was poor (Figure S1; Table S1). In contrast, mantises successfully discriminated depth in all conditions (Figure 3A; Table 1). Remarkably, there was no significant difference between the same-direction and opposite-direction conditions. Mantis stereopsis thus does not exploit local motion direction to aid stereo correspondence.

In a final experiment, we tested whether first-order motion is required at all with another stimulus. In this stimulus, black dots became white and vice versa when the target region passed over them, reverting to their original luminance when it moved away (Movie S5). Thus, in this condition, no dots moved, and the crossed or uncrossed disparities were only conveyed by the position of the luminance flip in each eye. Mantises responded to this stimulus and, once more, struck significantly more often to targets in the crossed condition compared to the uncrossed condition (Figure 2B; Table 1). Human performance on the same task was again poor (Figure S2; Table S1). This experiment shows that no coherent first-order motion is necessary for mantis stereopsis. It instead relies on temporal change at positions that convey appropriate disparities.

In summary, mantis stereopsis does not rely on matching static luminance or motion direction cues of moving targets in the two eyes. We have shown that kinetic disparity is a sufficient cue for mantis stereopsis, and its performance is unchanged by the presence or absence of static disparity. Mantises also strike only at moving prey, which necessarily

Table 1. Summary of Statistics for Mantis Experiments				
Experiment		Likelihood Ratio	Degrees of freedom	P Value
Correlated				
	Disparity	450.335	2	<0.001
	Dot Size	1.169	1	0.28
	Disparity × Dot Size	1.431	2	0.489
Anticorrelated				
	Disparity	348.945	2	<.001
	Dot Size	0.913	1	0.339
	Disparity × Dot Size	7.599	2	0.022
Uncorrelated				
	Disparity	112.198	2	<0.001
	Dot Size	0.964	1	0.326
	Disparity × Dot Size	2.309	2	0.315
Matched Motion				
	Motion Condition	0.994	3	0.803
	Disparity	90.209	1	<0.001
	Dot Size	19.998	1	<0.001
	Motion × Disparity	1.924	3	0.588
	Motion × Dot Size	2.394	3	0.495
	Disparity × Dot Size	10.898	1	0.001
	Motion × Disparity × Dot Size	3.71	3	0.294
Luminance Flip				
	Disparity	35.703	1	<0.001
	Dot Size	8.126	1	0.004
	Disparity × Dot Size	0.023	1	0.881
See also Table S1.				

contain kinetic disparity; there is no evidence that mantises can discriminate stereoscopic depth in stationary targets. The simplest model that explains our results is a stereo system built on temporal change at positions corresponding to specific kinetic disparities. Such a system would be blind to disparity in static images and thus could not use stereopsis to break camouflage in stationary scenes. The computation involved is purely a detection of temporal change at appropriate positions. This sensitivity to temporal change makes mantis stereopsis sensitive to second-order motion even when no directional first-order motion is present. Insect visual sensitivity to second-order motion has only been shown previously in flies [28-30]. The temporal filters that comprise the first stage of insect elementary motion detectors [31] would be ideal candidates for the neural basis on which mantis stereopsis is built.

We conclude that stereopsis in mantises is based on kinetic disparity, unlike in any other animal studied. Before the discovery of insect stereopsis, David Lee hypothesized that organisms whose "visual system were attuned to pick up primarily the kinetic structure of the optic array" might be able to use kinetic, but not static, disparity [25]. The praying mantis seems to be a good example of such an organism. Mantis stereopsis is computationally simple enough to implement in a brain of one million neurons, and—remarkably—successfully detects stereoscopic distance in images where human stereopsis fails.

This demonstrates that distinct evolutionary pressures can result in completely different algorithms for binocular stereopsis.

STAR*METHODS

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SUPPLEMENTAL INFORMATION

Supplemental Information includes two figures, one table, and five movies and can be found with this article online at https://doi.org/10.1016/j.cub.2018.01.012.



Simulated distance in front of screen (cm)

Figure 3. Stereoscopic Depth Perception of Targets Defined by Internal Vertical Motion or Temporal Luminance Change

(A) The target consisted of a spiraling region in each eye with a background of dark and bright dots uncorrelated across the two eyes. The position of the region differed between the two eyes (kinetic disparity). Dots within the target regions streamed in either the same vertical direction (Up-Up or Down-Down) or different directions (Up-Down or Down-Up) in both eyes. Down-Down and Up-Up: data from ten replicates for each of n = 6 individuals; Down-Up and Up-Down: data from five replicates for each of n = 6 individuals.

(B) The target consisted of a spiraling region in each eye with a background of dots uncorrelated across the two eyes. Dots in the target regions flipped their luminance from dark to bright and vice versa. The position of the region differed between the two eyes (kinetic disparity). Data from ten replicates for each of n = 7 individual mantises. Strike probability (±95% binomial score confidence interval) across all mantises in the two disparity conditions corresponding to different simulated distances of the target from the screen. Other details as in Figure 2. Central thin lines separate near from far disparities. The panels with dots above are cartoon illustrations and not examples of the actual stimuli. (* indicates a significant main effect of disparity, GLM, p < 0.001). See also Figure S1, Figure S2, Movie S4, Movie S5, Tables 1 and S1.

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AUTHOR CONTRIBUTIONS

V.N. and J.C.A.R. designed the experiments. V.N. carried out all mantis experiments, analyzed the results, carried out statistical analysis, and prepared all figures. G.T. and S.H. coded the stimuli. D.U. and A.S. ran the human experiments, and V.N., D.U., and A.S. analyzed the results from the human experiments. V.N. and J.C.A.R. wrote the manuscript.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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STAR***METHODS**

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER		
Deposited Data				
Raw and analyzed data	This paper	doi.org/10.6084/m9.figshare.5331697		
Experimental Models: Organisms/Strains				
Sphodromantis lineola	Bugz UK, Metamorphosis UK	N/A		

CONTACT FOR REAGENTS AND RESOURCE SHARING

Further information and requests for resources and reagents should be directed to and will be fulfilled by the Lead Contact, Vivek Nityananda (vivek.nityananda@ncl.ac.uk).

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Ethics

All human experiments were carried out as approved by Newcastle Ethics Board approval no. 01267. Informed consent was obtained from all participants.

Mantis Experiments

All experimental individuals were healthy adult female mantises of the species *Sphodromantis lineola*. The mantises were housed individually in semi-transparent cages (dimensions: 7 cm X 7 cm X 9 cm) in a temperature controlled room that was maintained at 25°C. They were fed one adult cricket three times a week and the cages were misted with water. On experiment days, they were not fed any crickets, to maintain motivation. For all experiments, we used a within-subject experimental design and therefore within an experiment, all individuals experienced all treatments. Individuals were used in multiple experiments and so had previous experience of 3D visual experiments as described in this paper.

Human Experiments

All experiments were carried out on adult subjects. The details of subjects for each experiment are as follows: Correlation experiments: ten individuals (8 female and 2 male). Matched Motion experiments: ten individuals (7 female and 3 male). Luminance Flip experiments: ten individuals (8 female and 2 male). All observers were naive to the purpose of the experiment. Informed consent was obtained from all participants, and the procedures of the experiment were in compliance with the Declaration of Helsinki. Ethical approval was obtained by the Faculty of Medical Sciences Ethics Committee at Newcastle University. All observers were tested for stereo vision and none were found to be stereo blind. For all experiments, we used a within-subject experimental design and therefore within an experiment, all individuals experienced all treatments. Since there were only a limited number of male and female individuals for all experiments, we were unable to perform an analysis of the influence of sex on our results.

METHOD DETAILS

Mantis Experiments

In all experiments, individual mantises were fitted with blue and green colored filters to enable the display of 3D stimuli to them. These were tear-drop shaped glasses cut out of filters which had been distributed with a preprint of a previously published paper [32] and had a maximum length of 7 cm. In order to fit the glasses on, the mantises were temporarily immobilized by placing their cages in a freezer (Argos Value Range DD1-05 Tabletop Freezer) for 5-8 min. The mantises were subsequently held down with Plasticine and the glasses were fitted with beeswax and rosin onto the front of the mantis. Once the glasses were fixed, the mantise was released and placed back in its cage. The mantises were allowed to recover overnight and experiments were conducted after this.

All stimuli were displayed on a DELL U2413 LED monitor (1920 × 1200 pixels; 51.8 × 32.4 cm; 60 Hz refresh rate). All stimuli were custom written in MATLAB (Mathworks) with the Psychophysics Toolbox [33]. The mantis was placed on a stand 10 cm away from the screen. All mantises were tested for motivation with a 3D stimulus before and after experiments. This stimulus consisted of a disc swirling in from the periphery to the center of the screen in front of the mantis. The stimulus had crossed disparity across the two eyes and simulated a target of 1 cm diameter, 2.5 cm in front of the mantis. This stimulus has previously been shown to be attractive to mantises and elicit strikes [17]. Experiments were only carried out if the mantis struck at this stimulus twice in a row and the data were used if the mantis did the same after the experiment. Across all experimental conditions five out of 131 experimental runs were

excluded because mantises did not strike after the trials were conducted. All our stimuli used this size and motion of target, and a "trial" is defined as one presentation of this spiral motion (Figure 1B). In all experiments, we left a 60 s pause between trials to avoid habituation to the stimuli. One experimental run consisted of a set of trials presented one after the other in the same session. Depending on the experiment, mantises were presented 20-36 trials per experimental run.

In all experiments, we used a background stimulus consisting of a cyan background covered in dots (Figure 1A). Since the mantis was viewing the background through the green and blue glasses, the cyan background was visible in both eyes and was adjusted to have equal luminance in both eyes, taking account of the mantis spectral sensitivity function [17]. Furthermore, 50% of the dots in each channel (blue or green) had the minimum luminance of zero and the other 50% had the maximum luminance (see [17] for details of the max/min luminance in each channel). This would correspond to 'black' and 'white' dots against a 'gray' background in the appropriate channel. For one set of experiments, we used small dots with a diameter of 25 pixels (corresponding to 1.8° based on the average angle subtended by a pixel across different screen locations, and to 3.9° when directly in front of the mantis; see [34] for a discussion of this difference) and a density of 55 dots in every 100 by 100 pixel square. For the other set of experiments, the background dots consisted of large dots with a diameter of 60 pixels (corresponding to $4.4^{\circ} / 9.4^{\circ}$) and a density of 3 dots in every 100 by 100 pixel square. All experiments were conducted at an ambient temperature of $20-25^{\circ}$ C.

Correlation Experiments

In these experiments, the background consisted of a stationary random dot pattern. The target was a patch of the same pattern, moving coherently over the background (occluding it where it passed). In the correlated condition, the target and background had disparities of opposite sign, so that the target appeared in the crossed condition as a disk moving over a patterned surface, and in the uncrossed condition as a circular hole cut in the surface. During experiments, interleaved trials were run with the disparity of the target patch being crossed, zero or uncrossed in different trials. The disparity in the crossed condition was chosen so as to simulate a target 2.5 cm from the mantis (i.e., 7.5 cm from the screen), which is an attractive distance for the mantis to strike at a target [23]. In the uncrossed condition, the value of the screen parallax was the same as in the crossed condition but the positions of the target in the two eyes were reversed. In the zero disparity condition, both eyes saw the patch at the same location (i.e., on the screen, 10 cm away from the mantis). The target patch in all conditions spiraled in over five seconds from the periphery of the screen to stop in front of the mantis where it moved with small jerky motions for another two seconds. Further details of the target motion are available in previously published studies [17, 23].

We tested mantises (n = 20 for the large dots; n = 17 for the small dots) with these stimuli in two separate experiments. In the first experiment, two correlation conditions were interleaved. In the first condition, both background and target dots were correlated, i.e., white dots in one eye corresponded to white dots in a matching position in the other eye and black dots corresponded to black dots. In the second condition, the dots were anti-correlated, i.e., white dots in one eye corresponded to black dots in a matching position in the other and vice versa. In each experimental run, five trials were run for each of the three disparities in each of these two conditions for a total of 30 trials. This experimental run was carried out twice on each animal, making for a total of ten replicate trials for every combination of disparity and correlation condition and thus a total of 60 trials per mantis. Trials with different combinations of disparity and correlation-type were randomly interleaved through the experiments. A new background was rendered after every trial.

In the second experiment, both background and target dots were uncorrelated, i.e., the position and luminance of dots in one eye did not correspond to any matching position or luminance in the other eye. The disparity in these stimuli was defined purely by the position of the moving target. Mantises (n = 7) were presented with ten replicate trials for each disparity in this experiment, with each experiment thus having thirty trials. A new background was rendered after every trial.

Matched Motion Experiments

To ask whether mantis stereo relied on matching motion direction in both eyes, we defined targets with motion in either the same or different directions in each eye. To avoid depth cues associated with interocular velocity differences, we used vertical motion to define our target regions. The background consisted of uncorrelated small or large dots as described above. A focal target region was defined in each eye with the distance between the centers of these regions equal to the disparity defined screen parallax as in the experiment above. Within these regions, dots continuously moved with either upward or downward motion with a speed of 120 pixels per second. The moving dots vanished when they reached the edge of the region and new dots continuously replaced them from the opposite edge. These motion-defined regions spiraled into the center with the motion as defined in the previous experiments. In four separate conditions, the dots moved upward in both eyes (Up-Up), downward in both eyes (Down-Down), upward in on eye and downward in the other (Up-Down) or the reverse (Down-Up). Each of these conditions were presented with the position of the regions in the eyes being crossed or uncrossed. An experimental run consisted of six replicates each for each of the two disparity conditions for the Up-Up and Down-Down conditions and three replicates each for each of the two disparity conditions for the Up-Down and Down-Up conditions. The lower number of replicates in the latter case reflected our assumption that, while the direction of motion might be important (i.e., Up-Up might be different from Down-Down), eye of presentation would not matter in the mismatched motion condition (i.e., Up-Down would elicit the same response as Down-Up). Each of six mantises were presented with two such experimental runs with all conditions interleaved resulting in a total of 72 trials per mantis. The Up-Up and Down-Down conditions had 12 replicates of each disparity condition and the Up-Down and Down-Up conditions had 6 replicates each for each disparity condition.

Luminance Flip Experiments

To test whether coherent first-order motion was necessary for mantis stereopsis, we designed an experiment which would present the mantis with a moving target region but no moving dots. Since pilot experiments indicated that mantises do not respond at all to dynamic random dot stimuli that remove all monocular cues to target location, we designed another stimulus that removed first-order motion. The background dots in this stimulus were uncorrelated dark and bright dots and the experiment was run with both small and large dots in separate conditions. The target was defined by a focal region in each eye. The distance between the two focal target regions was defined by the disparity defined screen parallax as in the previous experiments. These regions spiraled in with the same motion as the targets in all other experiments. When the region passed over the background dots, these dots changed their luminance polarity, i.e., black dots turned white and white dots turned black. When the region moved on, they reverted to their original polarities. This 'luminance-flipping' was designed to activate the initial stages of the insect motion detectors, while not providing any coherent directional motion. This stimulus was presented in separate trials with the positions in each eye being crossed or uncrossed. In interleaved trials, ten replicates of each of the two disparities were presented to seven mantises making a total of twenty trials per experimental run.

Human Experiments

For all experiments, observers viewed the stimuli on a 3D LG TV. The dimensions of the monitor was 1920 × 1080 pixels, and the refresh rate was 60 Hz. Stereoscopic presentation was ensured through circularly polarized 3D glasses. Observers were seated 70 cm away from the display; at this distance, a single pixel subtended 0.045°. The small dot sizes in the human experiments were changed in proportion to the difference in contrast sensitivity: the mantis CSF peaks at around 0.05 cycles/degree [35], whereas the human CSF peaks at around 3 cycles/degree [36]. This would correspond to a decrease in the angular size of the dots by a factor of 1/60 for the human experiments. In the mantis experiment the small dots had a radius of 1.8° and the large dots had a radius of 4.4°. This would then correspond to stimuli with dots of radius of 0.03° and 0.07° for the human experiments. However, we increased the size of the small dots to 0.045° and the large dots to 1.35° in the human experiments, since this allowed us to improve coverage of the stimulus parameter space. For small dots, the number of dots in the display always corresponded to 10,000, and for large dots it was always 500. For all experiments, we used disparities of -2.65°, -0.28°, -0.18°, -0.09°, 0.09°, 0.17°, 0.25°, and 1.31°. These disparity values were chosen since they correspond to positions in depth which are equidistant from the screen plane: assuming an interocular distance of 6.3 cm, the disparities correspond to virtual distances from the observers of 46.2, 66.4, 67.6, 68.8, 71.2, 72.4, 73.6, and 93.9 cm, respectively. These distances thus covered a range of smaller distances from the screen comparable to those faced by the mantises and two extreme distances from the screen that would be more obvious. The task for the human observers was to respond via a keypress whether the stimulus was "near" or "far" relative to the screen. As the stimulus was presented on a 3D display with horizontal interlacing, gamma correction was performed by equalizing the luminances of the gray background and the anticorrelated dots. For anticorrelated dots at zero disparity, these are simply black and white pixels that are interlaced, whose mean luminance should be equal to the background. The mean luminance was 161 cd/m² for the white dots, and 0.06 cd/m² for the black dots. All other aspects of the human experiments were as in the corresponding mantis experiments.

Correlation Experiments

Ten individuals (8 female and 2 male) were each tested in five sessions. Each session consisted of three repeats each of three correlation conditions and eight disparity conditions. Each individual thus had 72 trials per session and total of 15 replicates for each combination of conditions across all the five sessions. All the conditions were randomly interleaved. The disparity conditions were as described above. The correlation conditions consisted of one condition where the dots were correlated between the two eyes, one where they were anti-correlated and one where they were uncorrelated. The stimuli were otherwise like those described for the mantis experiments.

Matched Motion Experiments

Ten individuals (7 female and 3 male) were each tested in five sessions. Each session consisted of two repeats each of two correlation conditions and eight disparity conditions. Each of these conditions also had two repeats of the Up-Up and Down-Down motion conditions and one each of the Up-Down and Down-Up motion conditions. Each individual thus had 192 trials per session. Across the five sessions each individual had a total of 10 replicates (5 sessions X 2 repeats per session) for each of the Down-Down and Up-Up conditions within each correlation and disparity condition. Each individual also had 5 replicates (5 sessions X 1 repeats per session) for each of the Down-Up and Up-Down conditions within each correlation and disparity conditions within each correlation. All the conditions were randomly interleaved. The disparity conditions were as described for the previous experiment. The correlation conditions consisted of one condition were the dots were correlated between the two eyes and one where they were uncorrelated. The stimuli were otherwise like those described for the mantis experiments.

Luminance Flip Experiments

Ten individuals (8 female and 2 male) were each tested in five sessions. Each session consisted of three repeats each of two correlation conditions and eight disparity conditions. Each individual thus had 48 trials per session and total of 15 replicates (5 sessions X 3 repeats per session) for each combination of conditions across all the five sessions. All the conditions were randomly interleaved. The disparity conditions were as described above. The correlation conditions consisted of one condition where the dots were correlated between the two eyes and one where they were uncorrelated. The stimuli were otherwise like those described for the mantis experiments.

QUANTIFICATION AND STATISTICAL ANALYSIS

Mantis Experiments

Mantises in all experiments were recorded with a Kinobo USB B3 HD Webcam (Point Set Digital Ltd, Edinburgh, Scotland) placed directly beneath the mantis. The position of the camera ensured that the stimuli were not visible in the movies. The movies were therefore subsequently coded blind to the stimulus and the number of strikes made to each stimulus was measured. These were later matched to the parameters for each stimulus presentation, which were recorded separately by the computer during stimulus presentation.

As noted above, experiments were only carried out if the mantis struck at the disc stimulus twice in a row and the data were used if the mantis did the same after the experiment. Across all experimental conditions, five out of 131 experimental runs were excluded because mantises did not strike after the trials were conducted.

For all experiments, we based our calculations of adequate power and the related minimum sample size on previous experiments [17]. Based on these previous results, we obtained an expected effect size (Cohen's D) of 3.6. Such a high effect size implies that for a power of 0.8 in each experiment we would need a smaller minimum sample size of 5 animals and all experiments used a sample greater than this. For all experiments, we used a within-subject experimental design and there was therefore no need for randomization between treatments. Generalized linear models were run for all experiments with animal identity, dot size, and disparity as main factors and the occurrence of a strike as a dependent variable. There was thus no assumption of normality of the data or homogeneity of variances. As the occurrence of a strike is a binary variable ('yes' or 'no'), we used a binomial logistic link function for our model. In the matched motion experiment, the motion condition (Up-Up, Down-Down, Up-Down or Down-Up) was also used as a main factor. The model looked for main effects of and interaction effects between these factors at a significance level of $\alpha = 0.05$. All data were analyzed using IBM SPSS Statistics software version 23 (IBM Corporation). The statistical parameters and results are presented in Table 1.

Human Experiments

As in the mantis experiments, we ran generalized linear models with main and interaction effects of disparity sign (near versus far) and dot size for all experiments at a significance level of $\alpha = 0.05$. For the matched motion experiments we also had motion condition (e.g., Up-Up, Up-Down) as a factor. The dependent variable here was the judgement that the target was near. Since the dependent variable was based on a binary decision (near or far), we used a binary logistic link function in our model. All data were analyzed using IBM SPSS Statistics software version 23 (IBM Corporation). The statistical parameters and results are presented in Table S1.

DATA AND SOFTWARE AVAILABILITY

The data files for the mantises detail the occurrence and number of strikes in response to different disparity, correlation, and motion conditions in each of the experiments detailed above: doi.org/10.6084/m9.figshare.5331697

The data files for the human participants detail their judgement of whether a 3D target was near or far in response to different disparity, correlation, and motion conditions in each of the experiments detailed above.: doi.org/10.6084/m9.figshare.5331697