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1 Small or far away? Size and distance perception in the praying mantis.

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20 Abstract

21 Stereo vision is an important but costly process seen in several evolutionary distinct lineages  
22 including primates, birds and insects. Many selective advantages could have led to the evolution of  
23 stereo vision, including range finding, camouflage breaking and estimation of object size. In this  
24 paper, we investigate the possibility that stereo vision enables praying mantises to estimate the size  
25 of prey by using a combination of disparity cues and angular size cues. We used a recently developed  
26 insect 3D cinema paradigm to present mantises with virtual prey having differing disparity and  
27 angular size cues. We predicted that if they were able to use these cues to gauge the absolute size of  
28 objects, we should see evidence for size constancy where they would strike preferentially at prey of  
29 a particular physical size, across a range of simulated distances. We found that mantises struck most  
30 often when disparity cues implied a prey distance of 2.5 cm; increasing the implied distance caused a  
31 significant reduction in the number of strikes. We, however, found no evidence for size constancy.  
32 There was a significant interaction effect of the simulated distance and angular size on the number

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3 33 of strikes made by the mantis but this was not in the direction predicted by size constancy. This  
4 34 indicates that mantises do not use their stereo vision to estimate object size. We conclude that other  
5 35 selective advantages, not size constancy, have driven the evolution of stereo vision in the praying  
6 36 mantis.  
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11 38 Keywords: Size constancy, Stereo vision, *Sphodromantis lineola*

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14 39 Introduction

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16 40 Stereo vision is a remarkable computational capability. It uses complex algorithms to take advantage  
17 41 of the disparity between the views of the world seen by each eye [1–4]. This is a costly process with  
18 42 its own dedicated neural matter and computational power [3,4]. It has nonetheless evolved to be a  
19 43 specialized perceptual capacity in humans and in other animals including owls [5], horses [6] and  
20 44 insects [7]. It appears, furthermore, to have evolved independently in at least three evolutionary  
21 45 lineages [7,8] . This suggests that there must be large selective advantages to stereo vision that  
22 46 benefit the animals in which it has evolved.  
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28 47 What possible advantages could stereo vision confer? The binocular disparities detected by a stereo  
29 48 vision system depend on the distance from the eyes to the object. Stereo vision is therefore  
30 49 profoundly related to distance. In primates, this relationship is complicated by our highly mobile  
31 50 eyes, which means there is no fixed mapping from binocular disparity to distance. Probably for this  
32 51 reason, we are better at discriminating the relative depth between adjacent objects rather than the  
33 52 absolute distance to an object [2]. Critically, we can still detect this relative depth boundary even if  
34 53 the object in question would otherwise be perfectly camouflaged against the background. A key  
35 54 advantage of stereo vision may therefore be that it confers the ability to detect camouflaged objects  
36 55 [9]. We know that humans, monkeys and owls can all use their stereo vision in this way [9–11]. This  
37 56 kind of “camouflage breaking” could be an important evolutionary advantage – think of a predator  
38 57 spotting prey against a similar-looking background. A related advantage of binocular, if not strictly  
39 58 stereoscopic, vision may be that it helps animals see more of the background behind an object,  
40 59 enabling a degree of ‘x-ray’ vision [12] This could help an animal spot a predator hidden behind  
41 60 vegetation clutter.  
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52 61 In animals where the eyes are fixed in the head, like insects, or nearly so, like owls, stereo vision may  
53 62 be equally important for judging the absolute distance to an object. This would be useful to an owl  
54 63 trying to catch prey or a praying mantis reaching for a fly at particular depth, and we know that  
55 64 mantises do indeed use absolute disparity information in this way [7,13]. There is further evidence  
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3 65 that mantises might be sensitive to prey at different distances even within their catch range and  
4 66 adjust their strikes accordingly [14]. This is similar to how toads, with very low ocular mobility, adjust  
5 67 their tongue extensions to capture prey based on distance information provided by absolute  
6 68 disparity cues [15]. It has been suggested that stereo vision in mantises is specialized for this range-  
7 69 finding function and thus possibly simpler than primate stereo [16].

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11 70 Information about absolute distance could also be used to calibrate other cues. For example,  
12 71 disparity cues in combination with angular size could allow animals to unambiguously judge the  
13 72 physical (as opposed to apparent) size of objects [17], distinguishing between a small object that is  
14 73 nearby or a large object that is far away. This could be advantageous if, for example, a predator  
15 74 needed to catch prey of a particular size. It could also make all the difference for an organism trying  
16 75 to decide whether an object is a small prey animal (and could be captured) or a large predator (and  
17 76 requires defensive action).

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24 77 It should be noted however, that cues unrelated to disparity could also help an organism judge both  
25 78 absolute and relative depth. These include motion parallax, shading, focus blur and relative object  
26 79 size. Humans make use of these cues [18] and under appropriate circumstances these can be more  
27 80 useful for depth perception than disparity [19]. Other animals also make use of similar cues to tell  
28 81 depth. Mantises, for example, make use of motion parallax to judge the width of gaps they need to  
29 82 jump across [20].

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34 83 There are thus several possible advantages to stereo vision, but which of these advantages leads to  
35 84 the evolution of stereo vision might differ in each animal. Each of the advantages listed above would  
36 85 be important only in the context of the specific ecology of each species. Animals in denser habitats  
37 86 might have a greater need for x-ray vision; predators whose prey has evolved background-matching  
38 87 coloration might have a greater need for camouflage breaking; while predators that specialize on  
39 88 specific prey might need to judge object size and distance more accurately. It is important therefore  
40 89 to explore the advantages to each animal known to have stereo vision in relation to their ecology. In  
41 90 this paper, we investigate whether praying mantises use their stereo vision to help judge prey size as  
42 91 well as distance.

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50 92 Praying mantises are specialized visual predators with a high degree of binocular visual overlap (35°  
51 93 in *Tenodera australiae* [21]). Many species of mantises capture prey by sitting motionless until prey  
52 94 passes by within their catch range [22]. They then reach out with a rapid reaching motion of their  
53 95 forelegs – called a strike –and capture their prey [23]. Stereo vision is thus a big advantage to them  
54 96 and early experiments indicated that they were capable of using binocular cues to judge depth [24].

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3 97 Stereopsis in praying mantises was first demonstrated by placing prisms in front of mantis's eyes and  
4 98 bringing a fly closer to the mantis [7]. Since mantises typically strike only when the approaching prey  
5 99 is perceived to be in the correct catching range (around 2.5-5 cm for several species) [23], the strikes  
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8 100 are a good measure of their judgements of depth. These experiments showed that mantises were  
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10 101 striking based not on absolute distance to the fly but on disparity cues that were manipulated using  
11 102 the prisms. Since these experiments were conducted, however, we know little about the  
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13 103 mechanisms of mantis stereopsis and what advantages it might confer to mantises.

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15 104 One of the barriers to further investigation of mantis stereopsis has been the lack of experimental  
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17 105 paradigms using 3D virtual stimuli that have revolutionised the study of stereo vision in primates.  
18 106 We therefore recently developed an insect cinema where we used anaglyph technology with  
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20 107 mantises wearing blue and green filters on their eyes (Fig 1a) to show mantises virtual 3D stimuli  
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22 108 [13]. Using this set-up we definitively demonstrated stereopsis in mantises and opened up the  
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24 109 possibility of further investigations into mantis stereo vision. In this paper, we use this 3D insect  
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26 110 cinema to explore how mantises use disparity and angular size cues to assess the size of objects and  
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28 111 make their decisions to make predatory strikes. We were especially interested to see if mantises  
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30 112 show size constancy, the phenomenon where an organism combines depth information and image  
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32 113 size to compute an object's physical size [17,25]. If they specialized on a particular size of prey, we  
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34 114 would expect them to be able to respond selectively to combinations of disparity and angular size  
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36 115 cues that corresponded to a specific absolute size of prey (Table 1).

37 116 Size constancy would appear to be important for praying mantises given their behavioural ecology.  
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39 117 Mantises will catch and eat insects such as locusts, but sufficiently large locusts are entirely capable  
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41 118 of eating the mantis instead. Mantises are also predated by larger species such as birds. It might well  
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43 119 be important, therefore, for mantises to avoid striking at prey that was too large.

44 120 An early study comparing deimatic responses (threat displays) of monocular and binocular mantises  
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46 121 showed that monocular mantises responded to similar angular sizes of birds while binocular  
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48 122 mantises responded based on the distance cues to the birds [26]. This suggested that binocular  
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50 123 mantises could perhaps take distance into account when responding to differently sized objects.  
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52 124 Another study specifically investigated size constancy to prey objects using prisms to manipulate the  
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54 125 disparity cues available to the mantis independently of the size of the stimulus presented [14]. This  
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56 126 study found no evidence for size constancy in the mantis; mantises struck at stimuli of a constant  
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58 127 angular size. This is a surprising result given the potential value to the mantis of knowing the true  
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60 128 size of prey. One possibility is that mantises were able to view the prey stimulus at its true distance,  
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without disparity manipulated by the prisms, when it first appeared in the periphery of the display

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3 130 screen. Another possible factor is that prisms move the entire visual scene, not just the target,  
4 131 nearer to the mantis, which might influence its striking behaviour. Our methods would be able to  
5 132 prevent both these problems. Since our 3D glasses are fixed to the head, the mantis fovea would  
6 133 always view the stimuli with the intended disparity cues, and these cues would apply only to the  
7 134 simulated prey item while the rest of the visual scene would present constant, veridical cues. We  
8 135 therefore revisited this important question with our completely different stereoscopic display  
9 136 technology to test whether we could find evidence for size constancy in the praying mantis.

## 137 Methods

### 138 *Experimental subjects*

139 We carried out all experiments on female mantises of the species *Sphodromantis lineola*. We housed  
140 the mantises in individual plastic boxes (7 cm length X 7 cm breadth X 9 cm height) with holes in  
141 their lids to allow for ventilation. The mantises could move freely within the boxes. The boxes were  
142 stored in a housing facility, which we maintained at 25°C. We cleaned the boxes, misted them with  
143 water, and fed each mantis a live cricket twice a week.

### 144 *Stimuli and display*

145 We used a DELL U2413 LED monitor to display the stimuli to the mantis. This monitor has  
146 narrowband spectral output in the blue and green regions of the spectrum and we have previously  
147 shown that it is effective at producing an illusion of 3D to the mantises in conjunction with the  
148 anaglyph glasses we used [13]. The monitor has a resolution of 1920 X 1200 pixels and a 60 Hz  
149 refresh rate and is 51.8 cm wide by 32.4 cm high. All stimuli were custom written in Matlab  
150 (Mathworks) using the Psychophysics Toolbox. All stimulus presentations consisted of a dark swirling  
151 disc against a uniform bright background that spiralled in from the periphery to the centre of the  
152 screen in five seconds (for further details of the stimulus and the display see [13]). The disc had an  
153 angular position  $\theta(t) = 4\pi t$  and a radial position  $r(t) = 10(1 + \cos(\min(t\pi/5, \pi)))$  cm. The disc  
154 thus spiralled in from a distance of 20 cm towards the centre of the screen, with smooth initial  
155 acceleration and final deceleration, over a duration of 5 seconds. At the centre of the screen, the  
156 disc moved with subtle jerky motions for a further two seconds and then vanished. This stimulus  
157 reliably elicits strikes when presented with a diameter of 1 or 2 cm and zero disparity, with the  
158 screen being 2.5 cm from the mantis, i.e. within the catching range.

159 We should note that light from LED monitors is linearly polarised, and several insects are known to  
160 be sensitive to linear polarisation. However, this polarisation would apply equally to all stimuli

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3 161 presented on the screen and would not affect the illusory perception of depth generated by the use  
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5 162 of anaglyph glasses.

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7 163 *Preparation and fixation of the 3D glasses*

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9 164 To be able to present the mantis with different disparity cues, we fitted each mantis with green and  
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11 165 blue glasses (Fig 1a). These glasses were teardrop shaped with a maximum length of around 7 mm  
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13 166 and cut out of filters distributed with a preprint of previously published paper [27]. We have  
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15 167 previously shown that these filters have very low spectral overlap and are effective in conveying an  
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17 168 illusion of 3D to the mantises [13].

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19 169 Before fixing the glasses, we placed the entire cage in which the mantis was housed in a freezer  
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21 170 (Argos Value Range DD1-05 Tabletop Freezer) for 5-7 minutes to immobilize it. We then took the  
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23 171 mantis out and held it down under a microscope using Plasticine® modelling clay (Flair Leisure  
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25 172 Products plc). We fixed the glasses onto the mantis using a mixture of beeswax and rosin, which we  
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27 173 melted and applied using a Denta Star S ST 08 wax melter. The assignment of the blue and green  
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29 174 glasses to the left and right eyes was counterbalanced across all insects used in the study. We also  
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31 175 fixed a small component, designed for electronics, onto the base of the mantis's pronotum. This fit  
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33 176 into a counterpart on the experimental stand and held the mantis in place during experiments while  
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35 177 leaving the movement of the head and forelimbs unrestricted. After fixing the glasses and the  
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37 178 component, we released the mantises and placed them in their cages. We gave them at least 24  
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39 179 hours to recover before we carried out any experiments.

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41 180 *Experimental set-up*

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43 181 We fixed the mantis onto a stand using the component attached to its pronotum. We positioned the  
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45 182 mantis upside down, a position mantises are comfortable with while hunting, and provided them  
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47 183 with a cardboard disc which it held onto for stability (Fig 1b). We placed the stand so that the  
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49 184 distance between the mantis and the screen was 10 cm. The stand was the one used by Rossel [7] in  
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51 185 his earlier experiments investigating stereo vision.

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53 186 *Experimental protocol*

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55 187 We presented the stimuli to each mantis in several runs during which we varied the disparity and  
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57 188 angular size of the disc stimulus (Fig 2). We used disparity to present virtual stimuli at different  
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59 189 simulated distances from the mantis (Fig 2); the physical distance of the stimuli was always the same  
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190 (i.e. the distance of the screen, 10 cm from the mantis). Each combination of simulated distance and  
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192 190 angular size corresponded to a specific simulated object size (Table 1). Each run consisted of 24 trials  
encompassing four different angular sizes of the disc each presented in six different disparity

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3 193 conditions. The trials were presented in random order with a pause of 60 seconds between each  
4 194 trial. The four angular sizes used were 7.49°, 11.25°, 16.87° and 25.31°. Three of the six disparity  
5 195 conditions were “crossed disparity” conditions where we presented the image visible to each eye  
6 196 contralateral to that eye, so that the lines of sight from the two eyes crossed in front of the screen  
7 197 (Fig 2). In these conditions, we presented targets at simulated distances of 2.5 cm, 3.75 cm and 5.63  
8 198 cm from the mantis. All these distances are approximately within the catch range of the mantis [23].  
9 199 Assuming an interocular distance of 0.7 cm, these corresponded to parallaxes (the physical  
10 200 separations between the left and right images on the screen, Fig 2) of 2.1 cm, 1.16 cm and 0.54 cm  
11 201 respectively. The other three conditions were control conditions where we presented stimuli with  
12 202 the same parallax on the screen as the first three but with the left and right images swapped, i.e.,  
13 203 ipsilateral to the eyes that could view them. These conditions presented the mantis with stimuli  
14 204 where the left and right eye images failed to converge. They cannot be interpreted as images of a  
15 205 single object, let alone one within the catch range, and we therefore expected to them be  
16 206 unattractive to the mantis. We tested six mantises with ten experimental runs of 24 trials each and  
17 207 one more mantis with six experimental runs.

#### 28 208 *Data recording and analysis*

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30 209 For every presentation of a stimulus, we recorded the mantis’s response using a Kinobo USB B3 HD  
31 210 Webcam (Point Set 248 Digital Ltd, Edinburgh, Scotland) camera placed underneath the mantis. The  
32 211 camera did not have a view of the monitor and all recordings were thus blind to the stimulus  
33 212 condition. We analysed the recorded videos manually. For each trial, we noted the number of times  
34 213 the mantis made predatory strikes with its forelegs as well as the times it moved its head to track  
35 214 the stimulus (referred to as “strikes” and “tracks” below). The parameters of the stimulus  
36 215 corresponding to each stimulus presentation were saved by the computer and after the videos were  
37 216 analysed we matched the recorded number of strikes with the corresponding stimulus parameters.

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45 218 To see if there were significant main effects of both simulated distance and angular size on the  
46 219 number of strikes made by the mantises, we ran a Generalized Linear Model with the number of  
47 220 strikes for each individual presentation as the dependent variable. Since this involved count data, we  
48 221 assumed a Poisson distribution with a log-linear link function. We used the identity of the animal,  
49 222 the simulated distance and the angular size as factors in the model. We used the model to  
50 223 investigate a main effect of the simulated distance, the angular size and an interaction effect  
51 224 between the simulated distance and angular size. We ran separate models for the crossed and  
52 225 uncrossed disparity presentations. We also ran models for each of these conditions using the

226 absolute size in mm instead of angular size as a factor. Finally, we also ran models with the number  
227 of tracks in individual trials as a dependent variable.

228 To assess if the simulated distance and the angular size had independent effects on the number of  
229 strikes made by the mantis, we ran a chi-squared test. We next assessed if the mantises preferred a  
230 particular simulated distance after accounting for the main effect of angular size. To do this, we  
231 normalized the number of strikes made by each individual for every simulated distance by the  
232 maximum number of strikes made by that individual in response to any angular size for that  
233 distance. We then ran a two-way Friedman's ANOVA to see if there was a significant effect of  
234 simulated distance and angular size on the normalized number of strikes. If there was a preferred  
235 distance regardless of angular size, we should then expect to find a significant effect of the distance  
236 but not the angular size on the normalized number of strikes.

237 To assess evidence for size constancy, we normalized the number of strikes made by each individual  
238 for every angular size by the maximum number of strikes made by that individual in response to any  
239 simulated distance for that angular size. We then ran a two-way Friedman's ANOVA to see if there  
240 was a significant effect of simulated distance and angular size on the normalized number of strikes. If  
241 mantises showed a preferred physical size independent of distance, we should then expect to find a  
242 significant effect of both the distance and the angular size on the normalized number of strikes. A  
243 fixed physical size preference would also further predict that the number of strikes would be greater  
244 for larger angular sizes at closer distances, and for smaller angular sizes at farther distances.

## 245 Results

246 In the crossed disparity trials, screen parallax simulated targets in front of the screen. We found a  
247 significant main effect of both simulated distance (Generalized Linear Model, Likelihood ratio  $\chi^2_2 =$   
248 135.431,  $P < 0.001$ ) and angular size (Generalized Linear Model, Likelihood ratio  $\chi^2_3 = 33.369$ ,  $P <$   
249 0.001) on the number of strikes made during a presentation (Fig 3a). There was also a significant  
250 interaction effect between simulated distance and angular size (Generalized Linear Model,  
251 Likelihood ratio  $\chi^2_4 = 36.768$ ,  $P < 0.001$ ) on the number of strikes made during a presentation (Fig  
252 3a). We also confirmed that simulated distance and angular size did not have independent effects on  
253 the number of strikes made (Chi-squared test,  $\chi^2_6 = 31.323$ ,  $P < 0.001$ ). We found similar results  
254 when we used the simulated absolute size as a predictor of the number of strikes rather than  
255 angular size (Fig 3b).

256 We also saw a significant main effect of the angular size (Generalized Linear Model, Likelihood ratio  
257  $\chi^2_3 = 139.159$ ,  $P < 0.001$ ) and simulated distance (Generalized Linear Model, Likelihood ratio  $\chi^2_2 =$

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3 258 24.304,  $P < 0.001$ ) on the number of tracks made during a presentation. The interaction effect of  
4 259 simulated distance and angular size on the number of tracks made was not significant (Generalized  
5 260 Linear Model, Likelihood ratio  $\chi^2_6 = 7.106$ ,  $P = 0.311$ ). Having shown that both simulated distance  
6 261 and angular size have a significant effect on strike rate, we then asked whether mantises show a  
7 262 consistent preference for a given distance or size.

11 263 *Mantises have a clear distance preference*

14 264 Whether we examine tracks or strikes, the mantises show a clear preference for targets at a  
15 265 simulated distance of 2.5 cm (blue circles in Fig 3), rather than 3.75 cm or 5.63 cm (orange squares,  
16 266 black triangles). We asked if there was a preference for a simulated distance after controlling for the  
17 267 main effect of angular size. We normalized the number of strikes for every simulated distance by the  
18 268 maximum number of strikes for any angular size for that distance. We found a significant effect of  
19 269 simulated distance on the normalized number of strikes (Fig 4a, Friedman's two-way ANOVA  $\chi^2_2 =$   
20 270 13.64,  $P < 0.01$ ) but not of angular size (Fig 4a, Friedman's two-way ANOVA  $\chi^2_3 = 5.39$ ,  $P = 0.145$ ).  
21 271 This indicates that mantises do not prefer all simulated distances equally even after we control for  
22 272 angular size effects through normalization.

29 273 We can be confident that this preference is indeed driven by the distance simulated by the parallax,  
30 274 rather than some other aspect of the stimulus, by comparing results in the uncrossed control  
31 275 condition (Fig 5a and b). As expected, the response rates in the uncrossed disparity condition were  
32 276 much lower than those seen for crossed disparity (Fig 5a and b). In addition, in this condition there  
33 277 was no significant main effect of the simulated distance (Generalized Linear Model, Likelihood ratio  
34 278  $\chi^2_2 = 0.065$ ,  $P = 0.968$ ) on the number of strikes in each presentation. There was also no significant  
35 279 interaction effect between simulated distance and angular size (Generalized Linear Model,  
36 280 Likelihood ratio  $\chi^2_6 = 2.264$ ,  $P = 0.894$ ) on the number of strikes in each presentation. Angular size,  
37 281 however, did have a significant main effect (Generalized Linear Model, Likelihood ratio  $\chi^2_3 = 36.073$ ,  
38 282  $P < 0.001$ ). The results in the uncrossed condition confirm that the effect of parallax in the crossed  
39 283 condition was due to the simulation of near distance, as intended. If, say, the mantis visual system  
40 284 simply summed images from the two eyes and then struck preferentially at the larger combined  
41 285 image associated with larger disparity, then we would have seen the same effect for both crossed  
42 286 and uncrossed conditions.

53 287 Our results therefore show that mantises have a strong preference for prey at a distance of 2.5 cm  
54 288 as compared to prey that is further away, when these distances are indicated solely by binocular  
55 289 disparity. The ordering of the distance preference is not affected by the angular size of the prey,  
56 290 although the strength of the preference may be.

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3 291 *Mantises show no consistent size preference*  
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5 292 We now turn to the critical question of size constancy. In contrast to distance, we found that angular  
6 293 size preferences are not consistent. At the closest simulated distance of 2.5 cm, the mean number of  
7 294 strikes was highest for a prey angular size of 11.25° but for simulated distances of 3.75 or 5.63 cm  
8 295 this shifted to 25.31° (Fig 3a; Table 2). We examined if there was a preference for any angular size  
9 296 after controlling for the main effect of distance by normalizing the number of strikes for every  
10 297 angular size by the maximum number of strikes for any simulated distance for that angular size. We  
11 298 found a significant effect of both simulated distance (Fig 5b, Friedman's two-way ANOVA  $\chi^2_2 =$   
12 299 36.65,  $P < 0.01$ ) and angular size (Fig 4b, Friedman's two-way ANOVA  $\chi^2_3 = 9.67$ ,  $P = 0.02$ ) on the  
13 300 number of normalized strikes. This suggests that even after the main effect of simulated distance is  
14 301 controlled for, we still have an interaction effect between simulated distance and angular size with  
15 302 different preferences for angular size depending on the simulated distance. This interaction is,  
16 303 however, not in the direction that one would expect if the mantises had size constancy. The  
17 304 mantises thus did not prefer any specific object size independent of simulated distance.  
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27 305 Discussion  
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30 306 We used our "insect 3D cinema" to investigate the influence of binocular disparity and angular size  
31 307 cues on mantises' decisions to strike at prey. We know that mantises use both size and distance in  
32 308 deciding whether to strike at potential prey, and we know that they can judge distance from  
33 309 binocular disparity alone. We were interested in whether mantises use the distance information  
34 310 provided by disparity to calibrate angular size in order to perceive the correct physical size of objects  
35 311 over a range of distances. This correct perception is known as size constancy [17,25]. To examine  
36 312 this, we tested whether mantises strike selectively at prey that is both at a particular distance and of  
37 313 a particular physical size. This would require their preference for angular size to depend on the  
38 314 target distance.  
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45 315 We found that disparity had an overall influence on the number of strikes made by the mantises and  
46 316 that angular size did indeed influence the mean number of strikes differently for different  
47 317 disparities. Mantises struck most often for targets whose disparity indicated they were 2.5 cm from  
48 318 the animal, and made fewer strikes for disparities that indicated distances of 3.75 and 5.63 cm,  
49 319 confirming that disparity cues clearly influence their decisions to strike. This confirms Rossel's [14]  
50 320 conclusion that mantises can use binocular disparities to discriminate objects at 3.5, 4.5 and 5.5 cm.  
51 321 This is certainly what we would expect based on the optics. The angle  $\alpha$  subtended by the mantid's  
52 322 eye separation  $l$  at a distance  $D$  is given by  $l = 2D \tan(\alpha/2)$ . For an interocular distance of 0.7 cm, the  
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3 323 difference in  $\alpha$  for a target at 4.5 vs 5.5 cm is  $1.6^\circ$ , much larger than the interommatidial separation  
4 324 at the fovea, around  $0.5^\circ$  [21]. The minimum discriminable distance  $\delta D$  depends on the baseline  
5 325 distance  $D$ :  $\delta D = \delta\alpha (4D^2 + l^2)/4l$ . If we make the conservative assumption that the smallest detectable  
6 326 disparity change  $\delta\alpha$  is the interommatidial separation,  $0.5^\circ$ , we predict that mantises should be able  
7 327 to discriminate distances of 3 mm at 5 cm, or 1 cm at 10 cm, or 5 cm at 20 cm. Distances  $>80$  cm  
8 328 would be indistinguishable from infinity.

9  
10 329 The preference for distance was consistent, independent of object size (Fig 4a). In contrast, mantises  
11 330 displayed no consistent preference either for angular *or* physical size (Fig 4b, Fig 3b). Mantises struck  
12 331 at an angular size of  $11.25^\circ$  for the closest simulated distance and at the highest angular size of  
13 332  $25.31^\circ$  for the higher simulated distances, i.e. the preferred angular size varied with distance.  
14 333 However, the variation was not consistent with a single preferred physical size (Fig 3b). A consistent  
15 334 preference for prey of a particular physical size would predict that mantises should strike at greater  
16 335 angular sizes of prey perceived to be close, and smaller angular sizes of prey perceived to be farther  
17 336 away. Instead, we found that mantises struck at smaller angular sizes for the closest simulated  
18 337 distance, and at the highest angular sizes for the higher simulated distances (Fig 3, Fig 4b).

19  
20 338 A previous study [14] of the influence of distance on size estimation in the praying mantis used  
21 339 prisms and objects presented on a TV screen to address a similar question. This study also showed  
22 340 that mantises do not consistently prefer prey of a given physical size, and argued that the angular  
23 341 size predominantly drives their prey catching behaviour. Our results differ from the results of this  
24 342 study. In our study, mantises do not consistently prefer prey of a given angular size: their preferred  
25 343 angular size reduces for closer prey. The previous study examined angular sizes from  $15^\circ$ - $60^\circ$ ; it did  
26 344 not test mantises at the lower angular sizes we did and it is possible that this is why it did not see the  
27 345 effect we did. It also used a different species of *Sphodromantis* (*S. viridis* rather than *S. lineola*), and  
28 346 we noted some further, potentially important methodological differences in the Introduction. Our  
29 347 results show that in *S. lineola*, disparity-defined distance does alter the preference for angular size.

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31 348 It is possible that mantises do use their stereo vision to deduce true physical size – i.e. that they have  
32 349 size constancy – but that their preference for prey physical size genuinely varies with distance. For  
33 350 example, capturing prey near the limit of their catch range could be more energetically expensive.  
34 351 They might therefore only strike out at prey that is farther away when it also appears to be bigger  
35 352 and therefore worth the energetic cost. Alternatively, the way the mantis' forelegs unfold during the  
36 353 strike might make it more difficult to capture larger prey that is nearby, compared to smaller prey.  
37 354 Rossel [14] found, for example, that at shorter distances the femur impacts on prey from above,  
38 355 while at longer distances it impacts from below.

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3 356 It is also possible that mantis stereopsis, and thus size constancy, works only over a limited range.  
4 357 For example at farther distances, mantises might rely mainly on angular size to judge prey size, while  
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6 358 at nearer distances they use the combination of disparity and angular size. It is interesting to  
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8 359 compare the crossed and uncrossed disparity conditions with this idea in mind. The peak number of  
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10 360 strikes in the uncrossed disparity conditions is the same as that for the farther simulated distances in  
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12 361 the crossed disparity conditions: both occurred at an angular size of 25.31°. This might perhaps  
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14 362 argue that when disparity cues are ambiguous or do not indicate nearby objects, mantises default to  
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16 363 using angular size as the cue on which to base their decisions to strike.

17 364 Size estimation has been studied in other insects [14,28] and there has so far been no clear  
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19 365 indication of size constancy in insects. Some studies have suggested that dragonflies do not use  
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21 366 angular size alone to estimate prey size [28] and our data would also support this idea in mantises,  
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23 367 even though they do not show any evidence for size constancy. In the previous study of size  
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25 368 estimation and its dependency on distance in mantises [14], the author found results similar to ours  
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27 369 showing that distance influenced the probability of striking in mantises. As we found in our study,  
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29 370 he, however, also showed that there is no preference for an absolute (mm) size. It might be possible  
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31 371 that size constancy matters in a different context – one of distinguishing between predators and  
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33 372 prey [26], which involves larger disparities than the ones we have presented in our experiment. It  
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35 373 might also be interesting to examine size constancy in different species of praying mantises. The  
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37 374 species we tested, *Sphodromantis lineola*, appears to be quite generalist in its choice of prey and this  
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39 375 might explain why we fail to see any evidence of size constancy in this species. Other species that  
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41 376 specialize on specific prey might show more evidence for size constancy.

42 377 Our study provides no evidence that mantises can use binocular disparity to compute the absolute  
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44 378 size of prey. Stereo vision nonetheless has major advantages for the mantis. It definitely helps the  
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46 379 mantis judge whether prey is at a depth within capture range or not, as indicated by the clear  
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48 380 preference for near distances simulated only by disparity. While mantises can also use motion  
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50 381 parallax for depth judgements, they appear to use this more for judging the gaps they might need to  
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52 382 jump over [29]. Furthermore, using motion parallax would require them to move. This would give  
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54 383 their position away to prey and would thus work against their predatory strategy. Stereo vision thus  
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56 384 enables them to judge prey distance without moving and to strike only when prey is at the right  
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58 385 depth. Another possible selective advantage is that stereo vision might enable mantises to spot a  
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60 386 camouflaged object, similar to primates and owls. This is an intriguing possibility and has not yet  
387  
388 been tested. Further work thus remains to be done to fully understand the evolution of stereo vision  
in insects and how its mechanisms differ from those in primates and other animals.

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8  
9 392 colour filters.  
10

11 393 Author contributions

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13  
14 394 V.N. and J.R. designed the behavioural experiments. V.N. and G.B. carried out the behavioural  
15 395 experiments. V.N. analysed the behavioural experiments. G.T. programmed the stimuli for all  
16 396 experiments. V.N. and J.R. wrote the paper.  
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20 397 Competing interests

21  
22 398 We have no competing financial interests.  
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25 399 Ethics statement

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27 400 This study conforms to the ethical guidelines of the country and university it was carried out in.  
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30 401 Data accessibility

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32 402 The datasets supporting this article have been uploaded as part of the Supplementary Material.  
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3 476 Tables

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5 477 Table 1.

		Angular Size (°)			
		7.5	11.25	16.88	25.31
Simulated Distance (cm)	2.5	0.33	0.49	<b>0.74</b>	1.11
	3.75	0.49	<b>0.74</b>	1.11	1.68
	5.63	<b>0.74</b>	1.11	1.68	2.53

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17 479 Simulated sizes (cm) for every combination of simulated distances and prey angular sizes presented  
18 480 to the mantises. The entries in red are an example of the expected pattern of conditions at which  
19 481 the mantises would strike maximally if they struck at prey of a specific absolute size, i.e., if they  
20 482 displayed size constancy. In our example, their most preferred absolute size is 0.74 cm.

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29 485 Table 2.

		Angular Size (°)			
		7.5	11.25	16.88	25.31
Simulated Distance (cm)	2.5	0.47	<b>0.72</b>	0.62	0.41
	3.75	0.07	0.17	0.28	<b>0.34</b>
	5.63	0.00	0.00	0.05	<b>0.15</b>

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40 487 Mean number of strikes per trial, for every combination of simulated distance and prey angular size  
41 488 presented to the mantises. The highest mean number for every simulated distance is marked in red.  
42 489 The pattern fails to follow that indicated by size constancy as indicated in Table 1.

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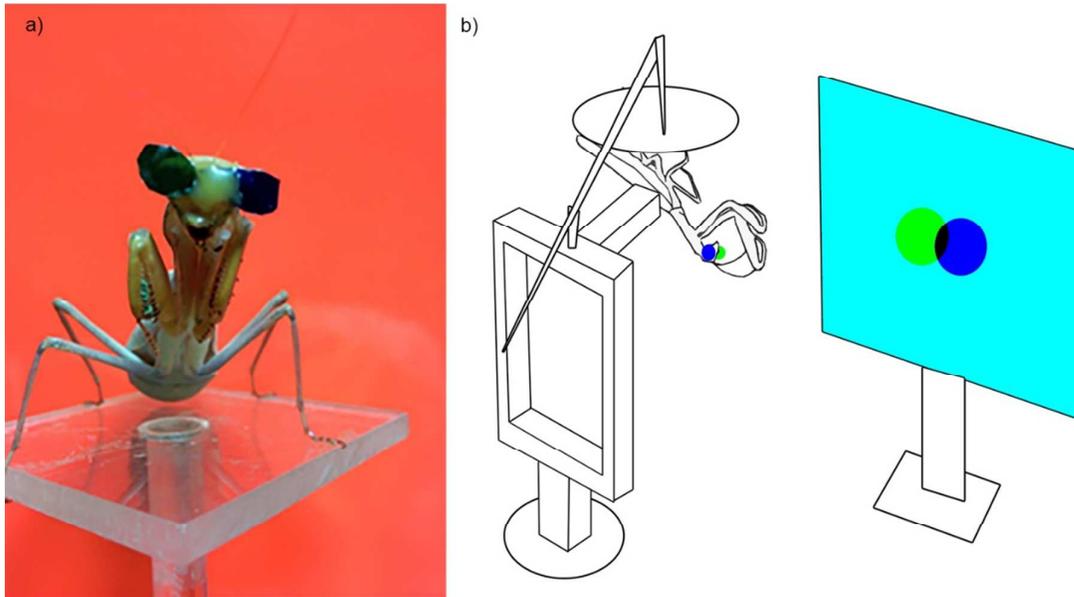
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3 496 Figures

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5 497 Fig 1

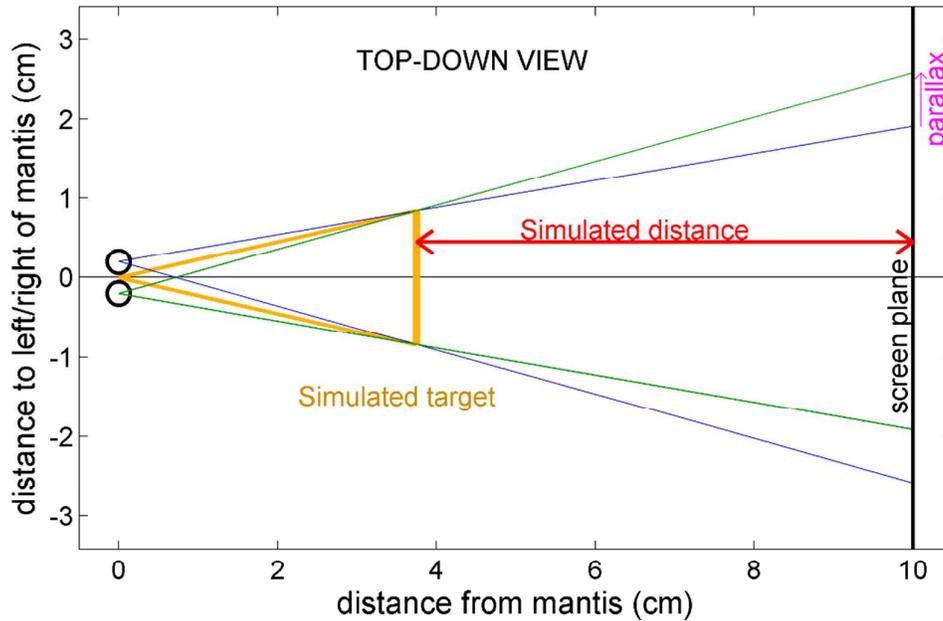


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499 Insect 3D cinema. a) Mantises were fitted with green-blue colour glasses. b) 3D virtual targets were  
500 presented to the mantises in a 3D insect cinema. Fig 1b reproduced with permission from [13].

501

502 Fig 2



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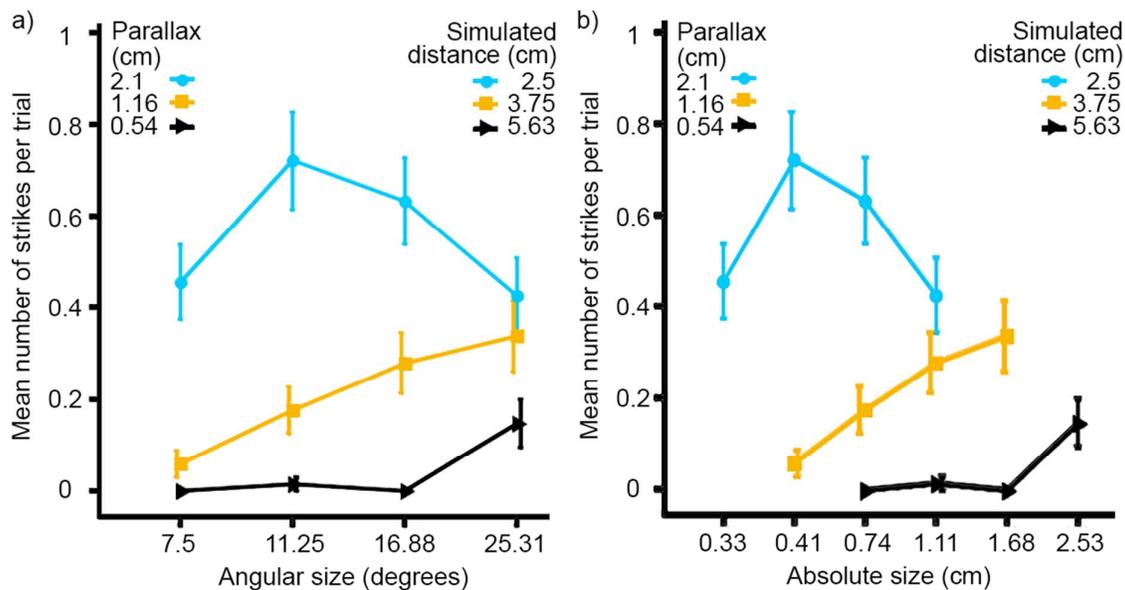
504 Top-down view showing how presenting stimuli with on-screen parallax simulates an object in front  
 505 of the screen. The blue and green dashed lines show how to compute the image position in order to  
 506 simulate a disk at 3.75 cm in front of the mantis. We use the term parallax to refer to the difference  
 507 in on-screen position between left and right images.

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511 Fig 3



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513 Behavioural response of mantises in the crossed disparity condition. Mean number of strikes in  
 514 response to different parallaxes (and the corresponding simulated distances) plotted as a function of  
 515 a) the angular size of the simulated target and b) the absolute size of the simulated object. Error bars  
 516 indicate standard error. Overlapping bars have been staggered so they can be viewed clearly.

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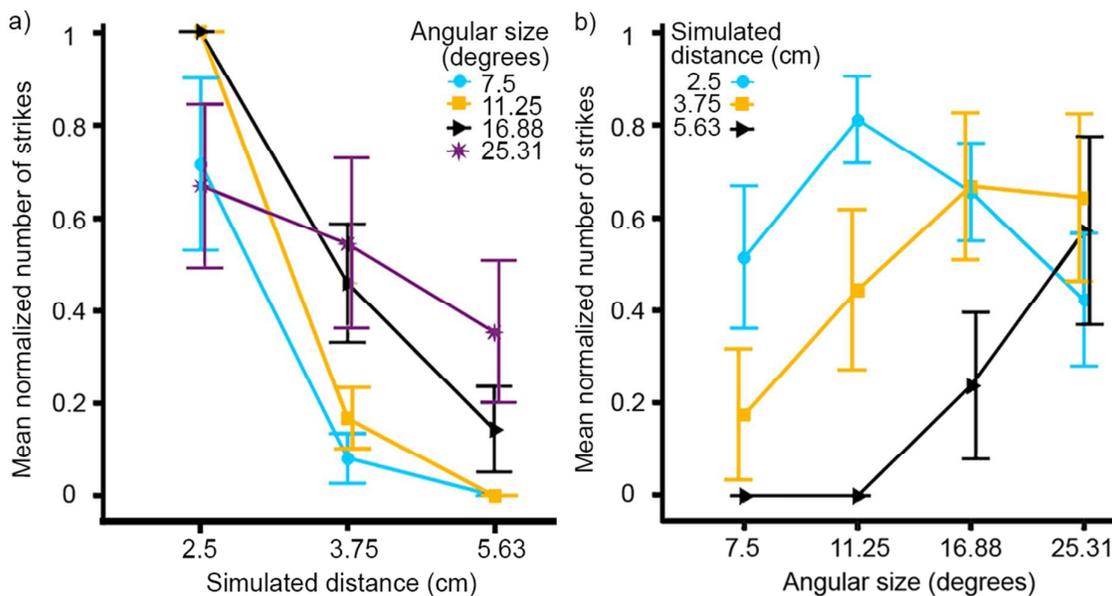
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525 Fig 4

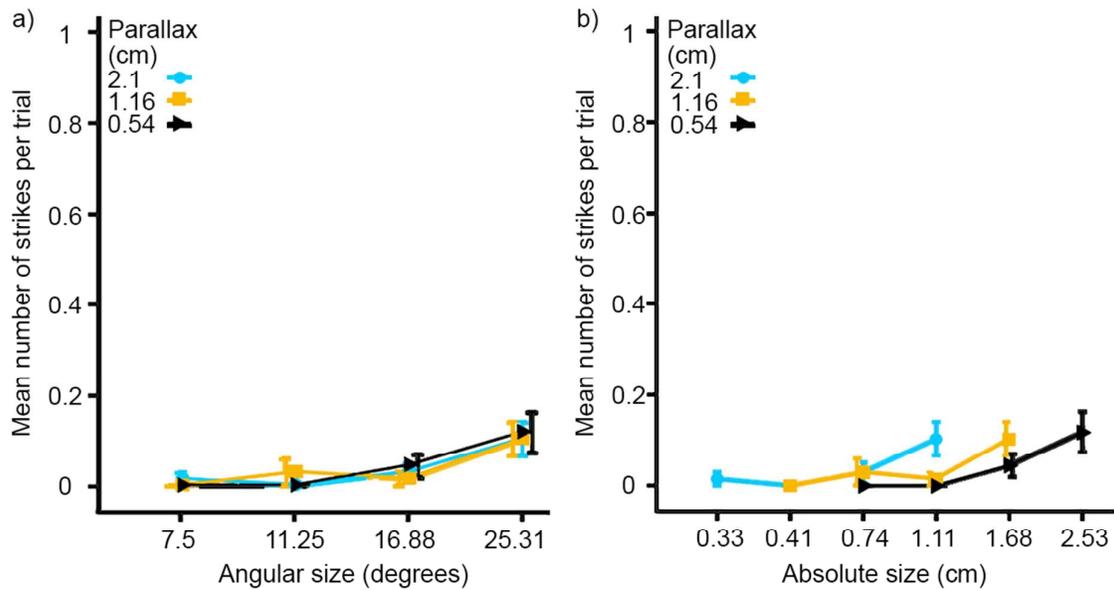


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527 Normalized behavioural responses of the mantises in the crossed disparity condition. Mean  
 528 normalized number of strikes in response to different angular sizes and simulated distances. Strikes  
 529 were normalized by a) the maximum number of strikes to any angular size for a given simulated  
 530 distance and b) the maximum number of strikes to any simulated distance for a given angular size.  
 531 See text for details. Overlapping bars have been staggered so they can be viewed clearly.

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534 Fig 5



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536 Behavioural response of mantises in the uncrossed disparity condition. Mean number of strikes in  
537 response to different parallaxes as a function of a) the angular size of the simulated target and b) the  
538 absolute size of the simulated object. Error bars indicate standard error. Overlapping bars have been  
539 staggered so they can be viewed clearly.

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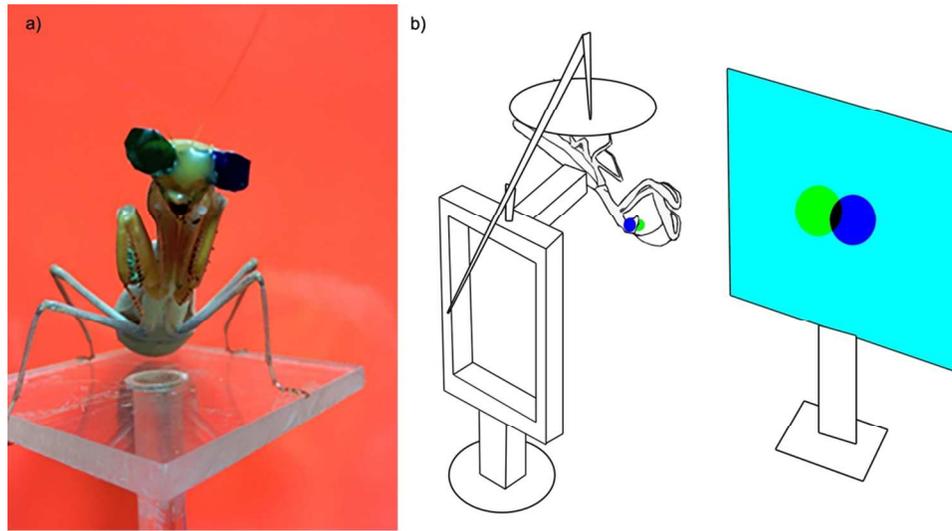


Fig 1. Insect 3D cinema. a) Mantises were fitted with green-blue colour glasses. b) 3D virtual targets were presented to the mantises in a 3D insect cinema. Fig 1b reproduced with permission from [12].  
105x55mm (300 x 300 DPI)

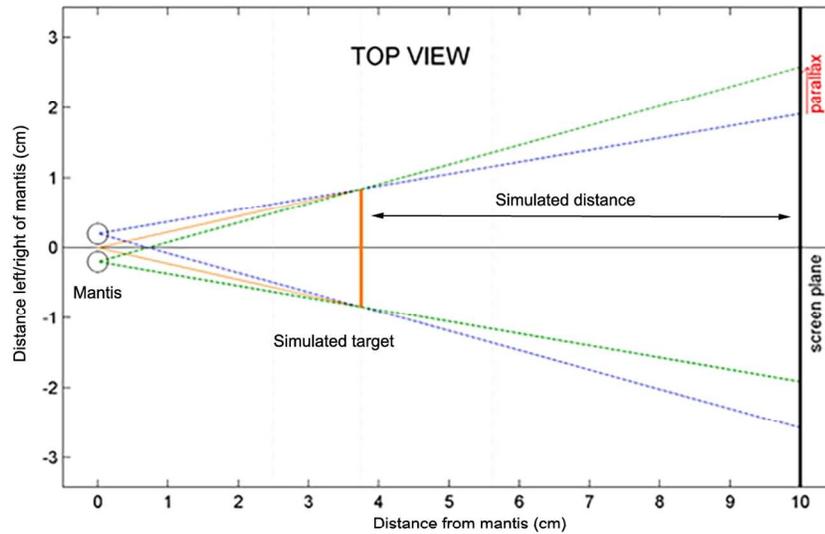


Fig 2. Top-down view showing how presenting stimuli with on-screen parallax simulates an object in front of the screen. The blue and green dashed lines show how to compute the image position in order to simulate a disk at 3.75 cm in front of the mantis. We use the term parallax to refer to the difference in on-screen position between left and right images.  
159x119mm (300 x 300 DPI)

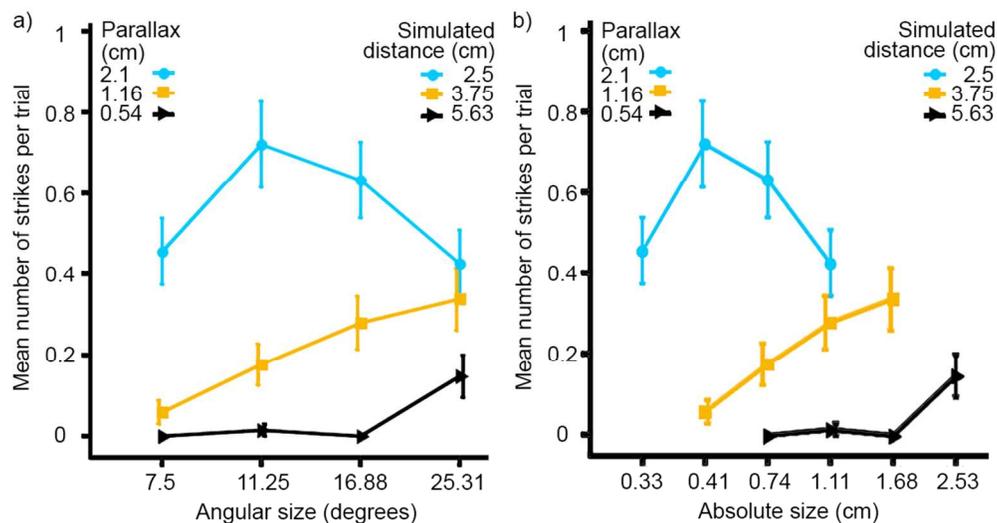


Fig 3. Behavioural response of mantises in the crossed disparity condition. Mean number of strikes in response to different parallaxes (and the corresponding simulated distances) plotted as a function of a) the angular size of the simulated target and b) the absolute size of the simulated object. Error bars indicate standard error. Overlapping bars have been staggered so they can be viewed clearly.  
160x86mm (200 x 200 DPI)

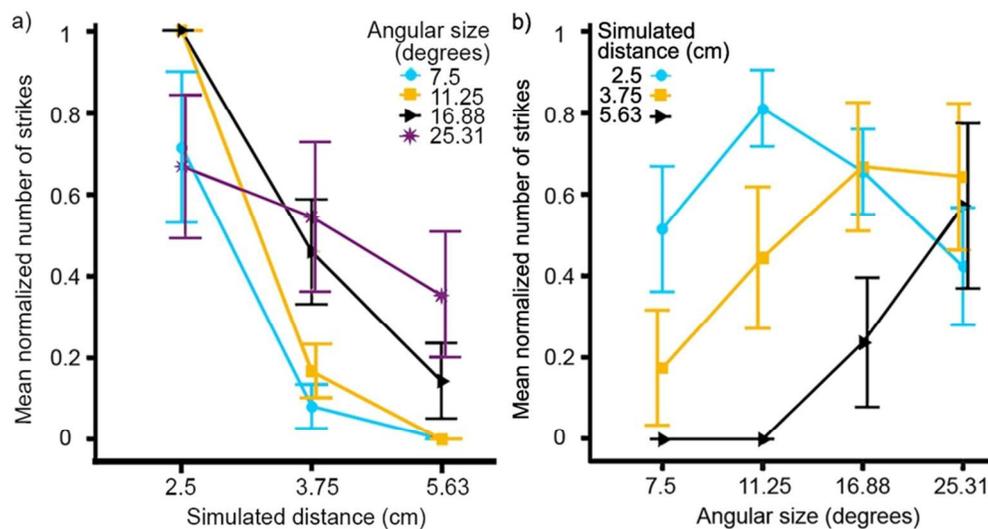


Fig 4. Normalized behavioural responses of the mantises in the crossed disparity condition. Mean normalized number of strikes in response to different angular sizes and simulated distances. Strikes were normalized by a) the maximum number of strikes to any angular size for a given simulated distance and b) the maximum number of strikes to any simulated distance for a given angular size. See text for details. Overlapping bars have been staggered so they can be viewed clearly.  
85x46mm (300 x 300 DPI)

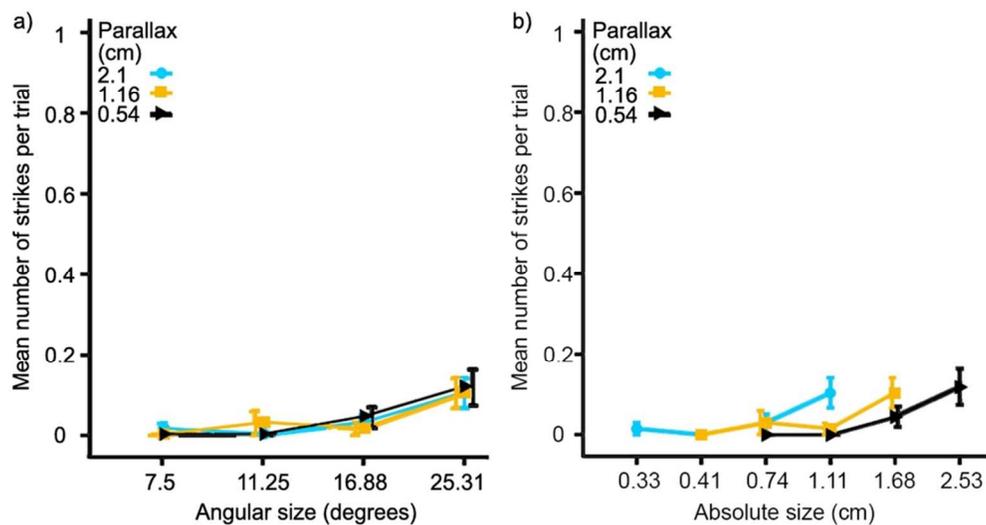


Fig 5. Behavioural response of mantises in the uncrossed disparity condition. Mean number of strikes in response to different parallaxes as a function of a) the angular size of the simulated target and b) the absolute size of the simulated object. Error bars indicate standard error. Overlapping bars have been staggered so they can be viewed clearly.

86x46mm (300 x 300 DPI)