

RESEARCH ARTICLE

Visual stimulus characteristics that elicit tracking and striking in the praying mantises *Parasphendale affinis*, *Popa spurca* and *Sphodromantis lineola*

Frederick R. Prete*, Robert Theis, Salina Dominguez and Wil Bogue

Northeastern Illinois University, Department of Biology, 5500 North St Louis Avenue, Chicago, IL 60625, USA

*Author for correspondence (fprete@neiu.edu)

SUMMARY

We tested three species of praying mantis, *Parasphendale affinis*, *Popa spurca* and *Sphodromantis lineola*, with computer-generated stimuli that differed in size, contrast, configuration and movement pattern to determine the effects of these parameters on visual tracking and striking behavior. Overall, black disks moving erratically against a white background were strong releasers of both behaviors. When stimulus presentation order was randomized by size, *P. affinis* and *P. spurca* struck at progressively higher rates as the stimuli enlarged up to 44 deg; *S. lineola* struck most at intermediate sized (10–20 deg) disks. When disks were size-ordered from small to large, *P. affinis* and *S. lineola* struck at the smaller disks at higher rates; however, when the order was reversed, the early appearance of large disks suppressed subsequent responses to the smaller disks. Stimulus order did not differentially affect the responses of *P. spurca*. All species responded at higher rates to black disks moving against a white background versus the reverse. However, only *P. spurca* and *S. lineola* responded at higher rates to relatively darker grey disks, only *P. affinis* responded to mottled grey disks moving against an identically patterned background, and only *P. spurca* struck more frequently in response to rectangular stimuli oriented parallel (versus orthogonal) to their direction of movement. In conjunction with data on other species, these results support the hypothesis that praying mantises recognize prey based on assessment of several category-specific, spatiotemporal features, e.g. size, contrast, speed, movement pattern and leading edge length.

Key words: prey identification, object recognition, vision, praying mantis, Mantodea.

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INTRODUCTION

Sighted animals face a number of vision-based challenges, one of the most difficult of which is object recognition (e.g. Pinto et al., 2008). Although there is some ambiguity in the use of the term, herein, ‘object recognition’ implies that two computational problems have been solved: object segmentation (a discrete object has been seen as separated from the background against which it appears), and object identification (the object has been classified as an exemplar of a specific category, e.g. as ‘prey’ versus ‘non-prey’) (De Winter and Wagemans, 2004; DiCarlo and Cox, 2007).

Object recognition is difficult for two reasons. First, the retinal image cast by any particular object will vary based on the distance and perspective from which it is viewed, its illumination, and the degree to which it may be occluded (Pinto et al., 2008). Second, the constituent members of a particular category may vary considerably in appearance. Hence, for visually guided, opportunistic predators such as praying mantises, object recognition within the context of predation (i.e. prey recognition) will be particularly difficult given the variety of potential prey items on which they feed, the unpredictably with which any particular prey item may appear, and the potential complexity of the background against which a prey item may be viewed (e.g. Dale, 2005; Fagan and Hurd, 1994; Hurd et al., 1994; Hurd, 1999; Kral, 2012; Moran and Hurd, 1994; Nickle and Harper, 1981; Prete and Wolfe, 1992; Ridpath, 1977).

Behavioral and electrophysiological data collected on several mantis species suggest that prey recognition is implicit; that is, it is based on assessing several category-specific, spatiotemporal

features of a stimulus rather than on an explicit, matching-to-template strategy (e.g. Prete et al., 2011; Prete et al., 2013; see also Ewert, 2004). These shared features include object size, object-to-background contrast, speed, movement pattern and leading edge length (Gonka et al., 1999; Prete, 1999a; Prete et al., 2011; Prete et al., 2012; Prete et al., 2013; see also Rossel, 1980; Rossel et al., 1992; Poteser et al., 1998; Yamawaki, 2000; Yamawaki, 2006).

The purpose of the present study was to test the consistency of previously collected data on mantis prey recognition within a phylogenetic context. We tested three species, *Parasphendale affinis* Giglio-Tos 1915, *Popa spurca* Stål 1856 and *Sphodromantis lineola* Burmeister 1838, that nest within phylogenetically separate lineages that include several previously tested taxa. Each species occurs within one of the larger subclades that contain previously tested species (based on Svenson and Whiting, 2009) (G. J. Svenson and F. Wieland, personal communication). We hypothesized that these three species would be most similar to their respective nearest relatives, but also that they would share the fundamental behavioral response characteristics displayed by the other species that have been tested.

MATERIALS AND METHODS

Mantises

We selected two species for which no behavioral data have been previously reported, *Parasphendale affinis* (Fig. 1E) and *Popa spurca* (Fig. 1F), and a species on which some behavioral data have been published, *Sphodromantis lineola* (e.g. Kral and Prete, 2004).

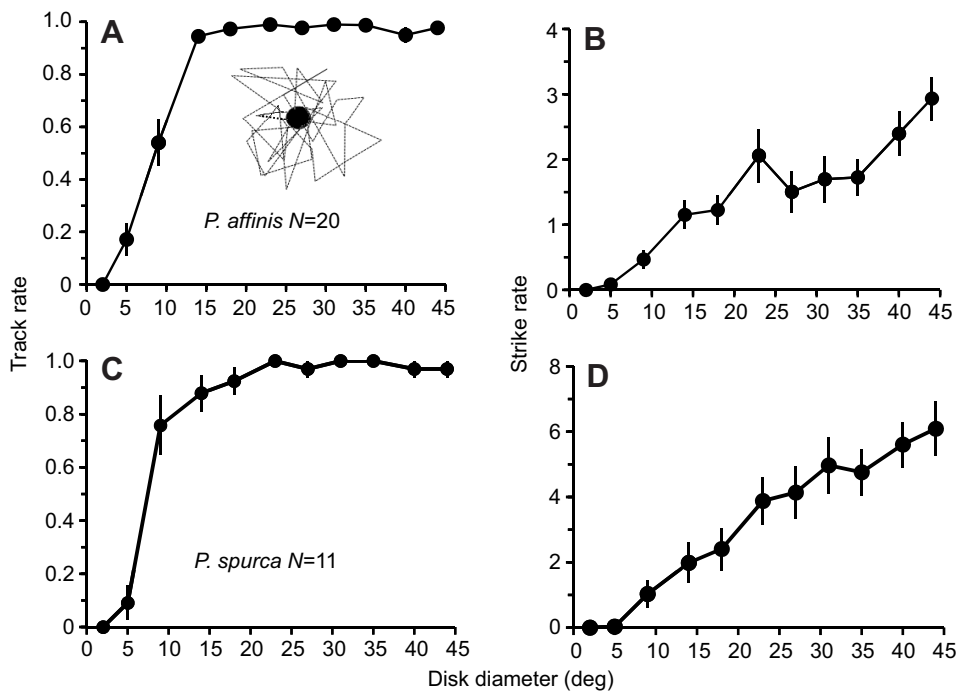
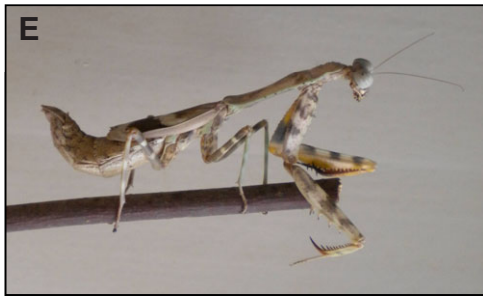


Fig. 1. Track and strike rate by *Parasphendale affinis* and *Popa spurca* (A,B and C,D, respectively) to erratically moving, computer-generated black disks moving against a white background. Stimuli were randomized by size and moved along the path depicted in the inset (A). For both species, track rate elevated quickly and was consistently high in response to disks ≥ 14 deg in visual diameter. Strike rate increased progressively as disks enlarged. (E) Female *P. affinis*. Photo taken by and used with the kind permission of Linda van Zomeren (www.keepinginsects.com). (F) Female *P. spurca* photographed in Madagascar in 2008 by Gavin Svenson (<http://mantodearesearch.com>) and used with his kind permission.



Popa spurca is a relatively slender, savanna-dwelling, ‘twig’ mimic found in the southwest and central eastern parts of Africa (Schwarz, 2004) (F. Wieland, personal communication). *Parasphendale affinis* is distributed in Ethiopia, Kenya and Somalia, and is often found perched in bushes. *Sphodromantis lineola* is a large brown or green mantis widely distributed in Africa south of the Sahara and in southern Spain (F. Wieland, personal communication).

In all cases, young adult females were selected from non-inbred laboratory-reared cohorts. Mantises were housed in individual containers held within a larger enclosure maintained on a 12 h:12 h light:dark cycle at 30°C in the light and 25°C in the dark [for culturing methods, see Prete (Prete, 1999b)].

All experimental animals were treated appropriately, and we operated in accordance with all applicable ethical and animal care guidelines.

Experimental set-up

All mantises were tested according to protocols previously described in detail (e.g. Kral and Prete, 2004; Prete et al., 2013). Each mantis was anesthetized briefly with CO₂, after which its wings and foreleg tarsi were removed (to prevent the mantis from pulling on the computer screen), and a small wood tether was affixed to the dorsal pterothorax with sticky wax; each was allowed more than 24 h to recover prior to testing.

As in previous studies, during tests, mantises were held by their tethers in a white, 11 cm high semi-cylindrical arena facing a Dell

flat-screen computer monitor (Round Rock, TX, USA) from a distance of 25 mm in an otherwise dimly lit room (62 lx; monitor: 1024×768 pixels, pixel size=0.75×0.75 deg of visual angle at 25 mm). Each mantis was allowed at least 5 min to adapt to the arena before the first trial, and inter-trial intervals varied from 30 s to 2 min.

While suspended, mantises reflexively held a hollow Styrofoam or plastic foam ball (which weighed less than the mantis) with their mesothoracic and metathoracic legs. Tethering did not restrict any of the mantis’ movements, or affect life expectancy (Prete, 1999b). The numbers of mantises used (*N*) in each experiment are indicated in the Results and corresponding figures. In those cases where data points are the means of different numbers of mantises, the range is indicated. Individuals within experiments were tested in random order, on random days (median number of trials per stimulus per mantis=4). During experimental periods, mantises were fed two live crickets per week, which kept them healthy and responsive.

Stimuli and behaviors

We tested mantises with circular (disks) or rectangular computer-generated stimuli that were black moving against a white background or the reverse (Michelson contrast ratios=±0.97), homogeneous grey disks moving against a series of progressively darker grey backgrounds (Michelson contrast ratios=-0.7 to +0.8), or mottled grey disks moving against an identically patterned background. Disks moved around the visual field center in an irregular, ‘erratic’

path (inset, Fig. 1A) at 143 deg s^{-1} . These stimuli are used to assess responsiveness to rapidly moving objects such as those that might appear unpredictably within the natural environment. Rectangular stimuli included squares and elongated rectangles for which one edge length remained fixed at 14 deg and the other was extended either parallel or orthogonal to its direction of movement. Unless noted otherwise, rectangular stimuli moved horizontally across the computer screen, through the visual field center at 180 deg s^{-1} . These stimuli are used to assess responsiveness to luminance edge length and stimulus orientation. Unless indicated otherwise, stimuli appeared in random or counter-balanced order.

Two behaviors were scored: visual tracking (turning the head and/or prothorax so as to follow the moving stimulus), and striking with the forelegs. Approaching behavior (i.e. attempting to walk toward the stimulus) rarely occurred in these species and was not analyzed (Prete et al., 2011). As in previous studies, tracking was considered a binomial event (i.e. the mantis either tracked during a trial or it did not; maximum events=one per trial). However, multiple strikes could occur on a given trial. Individual response rates were calculated as the number of behaviors divided by the number of trials per stimulus for each mantis (e.g. if a mantis struck at a stimulus five times in a total of four trials, the response rate=1.25).

Overall response rates were calculated as means of individual response rates ($\pm 1 \text{ s.e.m.}$). During experiments in which mantises viewed a series of progressively larger disks (from sub- to supra-threshold sizes), overall response rates transitioned from low to high levels as is typical in psychophysical experiments. Such response patterns approximate a sigmoid curve for which an estimated threshold (T) is defined as the (interpolated) stimulus size to which a subject's response rate is (or would be) 0.50, and we have used that convention here (e.g. Geisheider 1997).

Body measurements were collected from ethanol-preserved specimens according to operational definitions provided elsewhere (Prete et al., 2002; Kaltenpoth, 2005).

Statistics

The Friedman test (Fr) for non-parametric repeated measures data was used to assess overall behavioral responses (e.g. Friedman, 1937). *Post hoc* and other two sample comparisons were carried out with

the Wilcoxon paired-sample test (converted to z -scores). *Post hoc* tests were applied conservatively and only to answer specific experimental questions; multiple comparisons were Bonferroni corrected ($\alpha=0.05$; individual probabilities are reported in the text). Body measurements were analyzed by standard statistical tests. When used, parametric tests were performed only after the data were checked for normality. Statistics were calculated in Microsoft Excel with the appropriate added modules (www.advancedanalyticsllc.com), or in Data Desk (www.datadesk.com).

RESULTS

Body size

Body measurements for *P. affinis* and *P. spurca* are listed in Table 1; comparable data for *S. lineola* have been reported previously (Prete et al., 2002). *Sphodromantis lineola* ($N=49$) had larger head widths and lengths ($2.97 \leq t \leq 22.55$, $P < 0.0046$), and longer forelegs than either *P. affinis* or *P. spurca* ($t \geq 22.21$, $P < 0.0001$). However, their prothorax was no longer than that of the other species, and their average overall body length was only slightly (3.33 mm) longer than that of *P. affinis* ($t \geq 13.83$, $P = 0.0001$). In all measures except overall body length, *P. affinis* were larger than *P. spurca*.

Both foreleg and prothorax length were strongly correlated with head width in *P. affinis* ($r \geq 0.828$, $F_{1,18} \geq 41.4$, $P < 0.0001$). This was also the case for *P. spurca*, although the correlations were less robust ($r \geq 0.594$, $F_{1,18} \geq 9.26$, $P < 0.0073$). Further, within both species, foreleg length and prothorax length were better predictors of head width than was overall body length ($r = 0.463$ and 0.207 , respectively) (see also Prete et al., 2012). Similar relationships have been reported for *S. lineola* (Prete et al., 2002).

There were no systematic relationships between body measurements and the sizes of the stimuli that elicited striking behavior in any of the three species (see also Prete et al., 2011; Prete et al., 2013). For instance, despite having significantly longer forelegs, both *P. affinis* and *S. lineola* were more responsive to smaller stimuli than was *P. spurca* (e.g. Fig. 2).

Erratically moving disks

Parasphendale affinis ($N=20$) and *P. spurca* ($N=11$) responded similarly to the erratically moving disks when presentations were

Table 1. Measures of mantis (*Parasphendale affinis* and *Popa spurca*) body parts ranked by mean values (mm)

Species	N	Mean \pm s.d.	Min.	Max.	Species comparison
Head width					
<i>P. affinis</i>	21	9.35 \pm 0.48	8.4	10.6	$t=13.15$
<i>P. spurca</i>	20	7.78 \pm 0.23	7.2	8.2	$P \leq 0.00001$
Head length					
<i>P. affinis</i>	22	6.71 \pm 0.38	6	7.7	$t=2.25$
<i>P. spurca</i>	20	6.49 \pm 0.21	6.1	6.8	$P \leq 0.034$
Prothorax length					
<i>P. affinis</i>	22	20.66 \pm 0.97	18.9	23.1	$t=4.19$
<i>P. spurca</i>	19	19.53 \pm 0.71	18.8	21.4	$P \leq 0.0002$
Body length					
<i>P. spurca</i>	18	66.8 \pm 3.9	58.9	72.2	$t=3.17$
<i>P. affinis</i>	22	63.4 \pm 2.88	57.7	68.2	$P \leq 0.003$
Coxa					
<i>P. affinis</i>	21	13.08 \pm 0.82	11.9	14.8	$t=3.43$
<i>P. spurca</i>	20	12.39 \pm 0.37	11.9	13.3	$P \leq 0.015$
Femur					
<i>P. affinis</i>	21	16.33 \pm 0.85	14.7	18.4	$t=8.38$
<i>P. spurca</i>	20	14.47 \pm 0.52	13.6	15.8	$P \leq 0.0001$
Tibia					
<i>P. affinis</i>	21	10.9 \pm 0.61	9.8	12	$t=5.36$
<i>P. spurca</i>	20	10.09 \pm 0.31	9.45	10.7	$P \leq 0.0001$

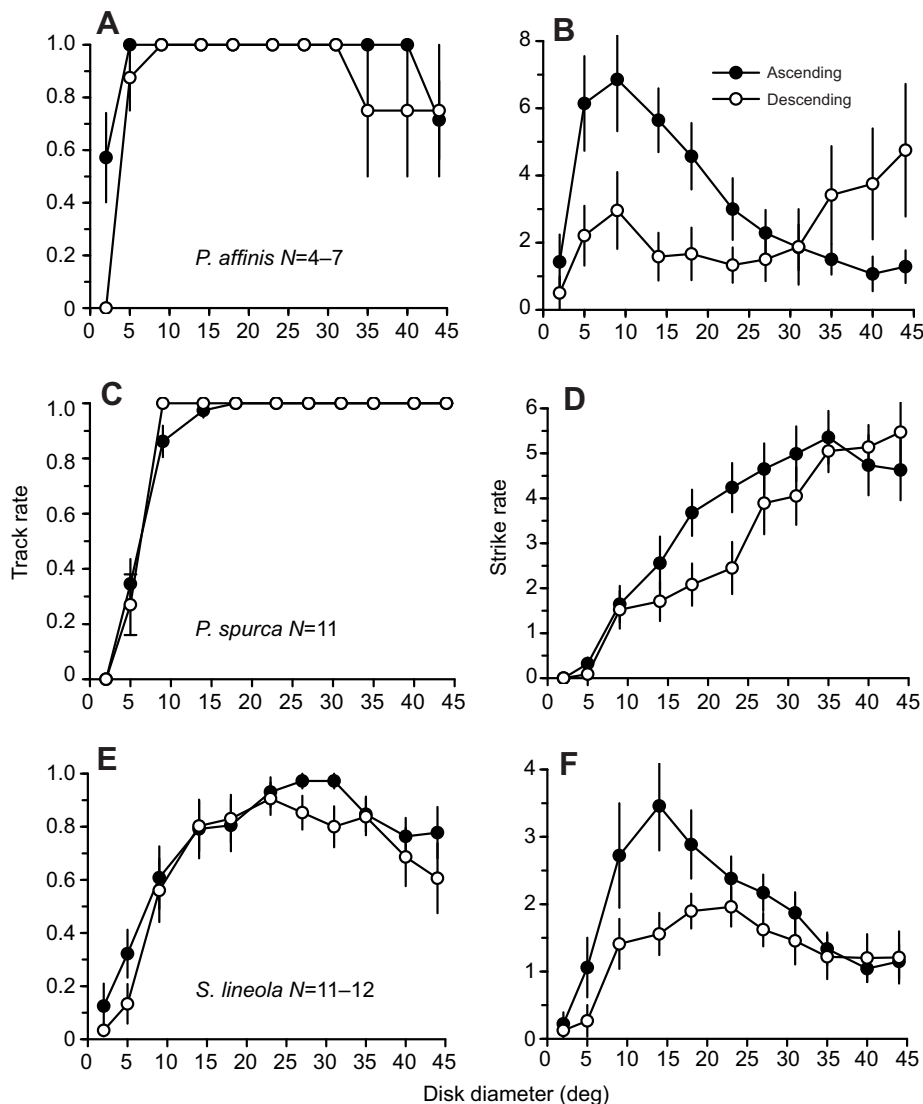


Fig. 2. Track and strike rate by *P. affinis* (A,B), *P. spurca* (C,D) and *Sphodromantis lineola* (E,F) to erratically moving, computer-generated black disks moving against a white background. Stimuli were presented in order from small to large (ascending series) or the reverse (descending series). The overall patterns of tracking did not differ between series, and were similar to those in experiments in which the stimuli were randomized by size. Presentation order affected the strike rate of *P. affinis* and *S. lineola* (B and F, respectively) but not *P. spurca* (D). In the former two cases, peak strike rates in the ascending series were elicited by stimuli smaller than when the stimuli were randomized by size. Presentation of the largest stimuli first in the descending series depressed strike rate in response to the smaller stimuli. In general, response thresholds were lower in the ascending series than they were when the stimuli were presented randomly.

randomized by size, and the overall effects of increasing disk size were significant for tracking and striking in both species ($Fr \geq 86.24$, $P \leq 0.00001$; Fig. 1A–D). Disks with a visual diameter as small as 5 deg elicited low levels of tracking in both species. Then, as disk size enlarged to 9 deg, track rate increased significantly (≥ 2.75 , $P \leq 0.006$), and remained high in response to the larger disks ($T = 8.6$ and 7.4 deg, respectively). In contrast, strike rate rose gradually and progressively as disk size increased from 9 to 44 deg with an initial significant rate change between the 5 and 14 deg disks for *P. affinis* (≥ 1.98 , $P \leq 0.048$; $T = 6.9$ deg), and between the 5 and 23 deg disks for *P. spurca* (≥ 2.92 , $P \leq 0.0033$; $T = 9.2$ deg). In this experimental paradigm, *S. lineola* has been shown to strike most in response to intermediate sized disks (10–20 deg), and at lower rates in response to both smaller and larger disks (Prete and Mahaffey, 1993; Kral and Prete, 2004).

To assess whether stimulus order affects response rates, we tested *P. affinis* ($N = 4-7$), *P. spurca* ($N = 11$) and *S. lineola* ($N = 11-12$) with erratically moving disks ordered by size from smallest to largest (ascending series) or the reverse (descending series); the series were randomized across test days.

Again, the effects of disk size on track rate were significant for all three species ($Fr \geq 23.21$, $P \leq 0.003$), and the overall response patterns were similar to those in the previous random order

experiment with just one exception (Fig. 2A,C,E). In this experiment, *P. affinis* tracked the smallest (2 deg) disk above threshold level (0.57 ± 0.17 , mean \pm s.e.m.) in the ascending series, and the 4 deg disk at a rate of 0.88 ± 0.13 in the descending series. These were smaller disk sizes than in the random order experiment, and smaller than those for *P. spurca* (6.3 and 6.2 deg, respectively) and *S. lineola* in this experiment (7.5 and 8.4 deg, respectively).

The pattern of striking behavior elicited by the ascending and descending stimulus series differed for *P. affinis* and *S. lineola*, but not for *P. spurca* (Fig. 2B,D,F). In the latter case, disk size affected strike rate in both series ($Fr \geq 78.46$, $P \leq 0.00001$), but the overall response patterns did not differ between series, or from that in seen the random order experiment. However, in this experiment, stimulus size thresholds were smaller (cf. Fig. 2D, Fig. 1D; $T = 5.5$ and 6.1 deg, respectively).

Increasing (but not decreasing) stimulus size had a significant effect on the strike rates of *P. affinis* ($Fr \geq 46.24$, $P \leq 0.00001$; Fig. 2B). In the ascending series, this species struck at a rate of 1.43 ± 0.81 in response to the smallest (2 deg) disk, and displayed a maximum strike rate of 6.86 ± 1.54 in response to the 9 deg disk ($T < 2$ deg). Thereafter, strike rate declined as disks enlarged. In the descending series, the overall strike rate to the smaller (2–27 deg) disks was significantly lower than in the ascending series (≥ 2.15 , $P \leq 0.0156$).

Disk size had a significant effect on the strike rate of *S. lineola* in both the ascending and descending series ($F_{r \geq 48.1}, P < 0.00001$; Fig. 2F). In the former, the stimulus size threshold was just 3 deg, and the peak strike rate (3.46 ± 0.66) was elicited by the 14 deg disk, with significantly lower rates elicited by both smaller and larger stimuli ($2 \text{ deg} < 14 \text{ deg} > 35 \text{ deg}, z \geq 1.96, P \leq 0.05$). This is the same overall pattern emitted by *S. lineola* in response to erratically moving disks presented in random size order (e.g. Kral and Prete, 2004). In the descending series, there were no between-stimulus differences when disks were 9 deg or larger and, again, the rates in response to the smaller (2–27 deg) disks were significantly lower than they were in the ascending series ($z \geq 2.15, P = 0.0316; T = 5.8 \text{ deg}$).

Stimulus–background contrast

Results of the contrast experiments are shown in Fig. 3. Overall, the track and strike rates of *P. affinis* ($N = 10$) did not differ in response to the relatively darker versus brighter grey disks, and their track rate did not differ in response to the black disk moving against the white background versus the reverse. However, their strike rate to the black disk on the white background was significantly higher than to the reverse ($z \geq 2.66, P = 0.0076$). *Parasphendale affinis* also

responded to the mottled grey (18 and 35 deg) disks moving against a similarly patterned background with the highest rate to the larger disk ($z \geq 2.26, P \leq 0.024$; Fig. 3A,B).

The response patterns of *P. spurca* ($N = 12$) and *S. lineola* ($N = 3$) differed from those of *P. affinis*. *Popa spurca* both tracked and struck at higher rates in response to the relatively darker versus brighter grey disks ($z \geq 4.82, P = 0.001$), and to the black disk on the white background versus the reverse ($z \geq 2.955, P \leq 0.0031$). However, their response rates to the mottled grey disks were not statistically different from zero (Fig. 3C,D). *Sphodromantis lineola* responded similarly (Fig. 3E,F). Overall, their response rates were higher to the relatively darker versus brighter grey disks, and to the black disk moving against the white background versus the reverse ($z \geq 2.06, P \leq 0.039$). This species did not respond to the mottled grey disks.

Stimulus orientation: parallel versus orthogonal

When presented with rectangular stimuli moving horizontally with their long axis oriented parallel or orthogonal to the direction of movement, neither *P. affinis* ($N = 10$) nor *S. lineola* ($N = 4$) discriminated between orientations in either tracking or striking

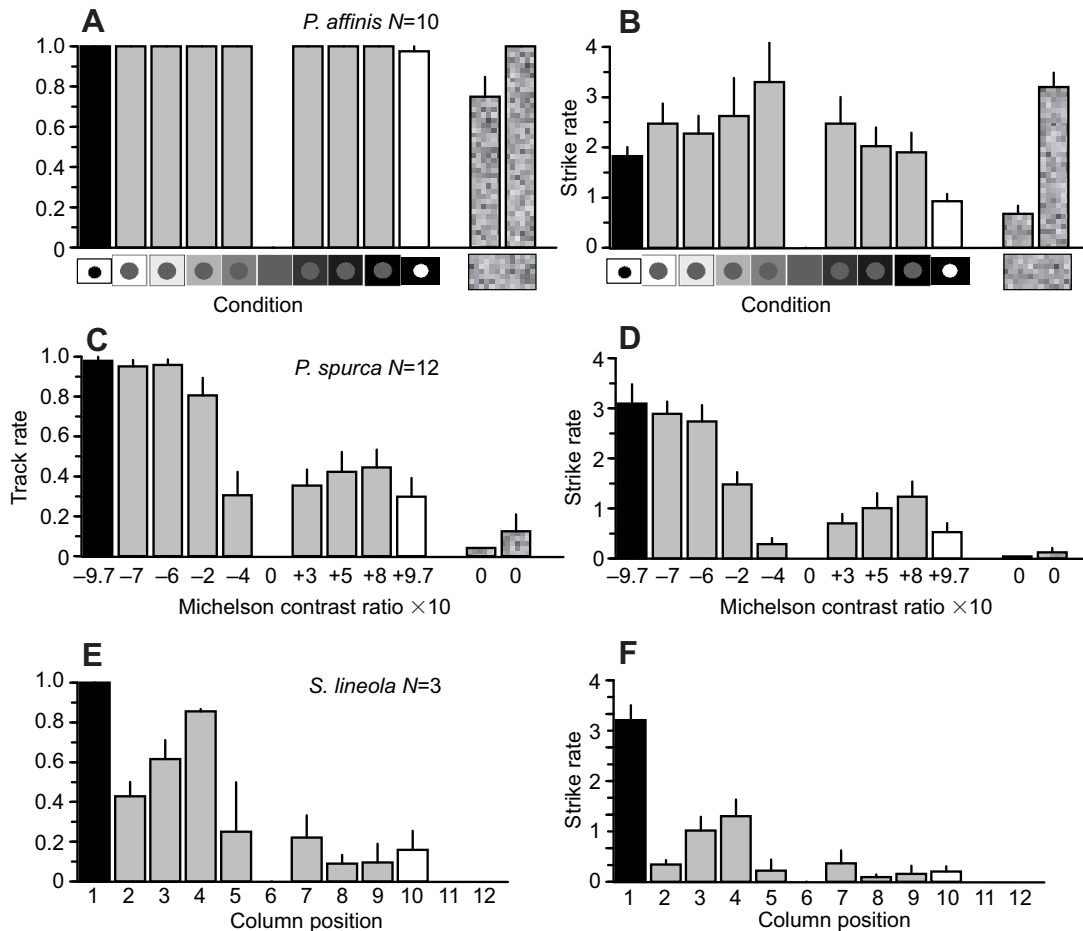


Fig. 3. Track and strike rate by *P. affinis* (A,B), *P. spurca* (C,D) and *S. lineola* (E,F) to erratically moving, computer-generated 18 deg disks that were black moving against a white background or the reverse (column positions 1 and 10, respectively), grey moving against progressively darker grey backgrounds (column positions 2–9), or mottled grey disks (18 and 35 deg) moving against an identically patterned background (column positions 11 and 12, respectively). *Parasphendale affinis* consistently tracked all stimuli irrespective of contrast ratio (abscissae in C,D). However, *P. spurca* and *S. lineola* tracked the relatively darker disks (columns 1–5) at higher rates than the relatively brighter disks (columns 7–10). All three species struck at higher rates in response to the black disk moving against a white background versus the reverse (columns 1 versus 10). However, only *P. spurca* and *S. lineola* struck at higher rates in response to the relatively darker versus brighter grey disks (columns 2–5 versus 7–9). Only *P. affinis* responded above threshold levels to the mottled grey disks (A,B).

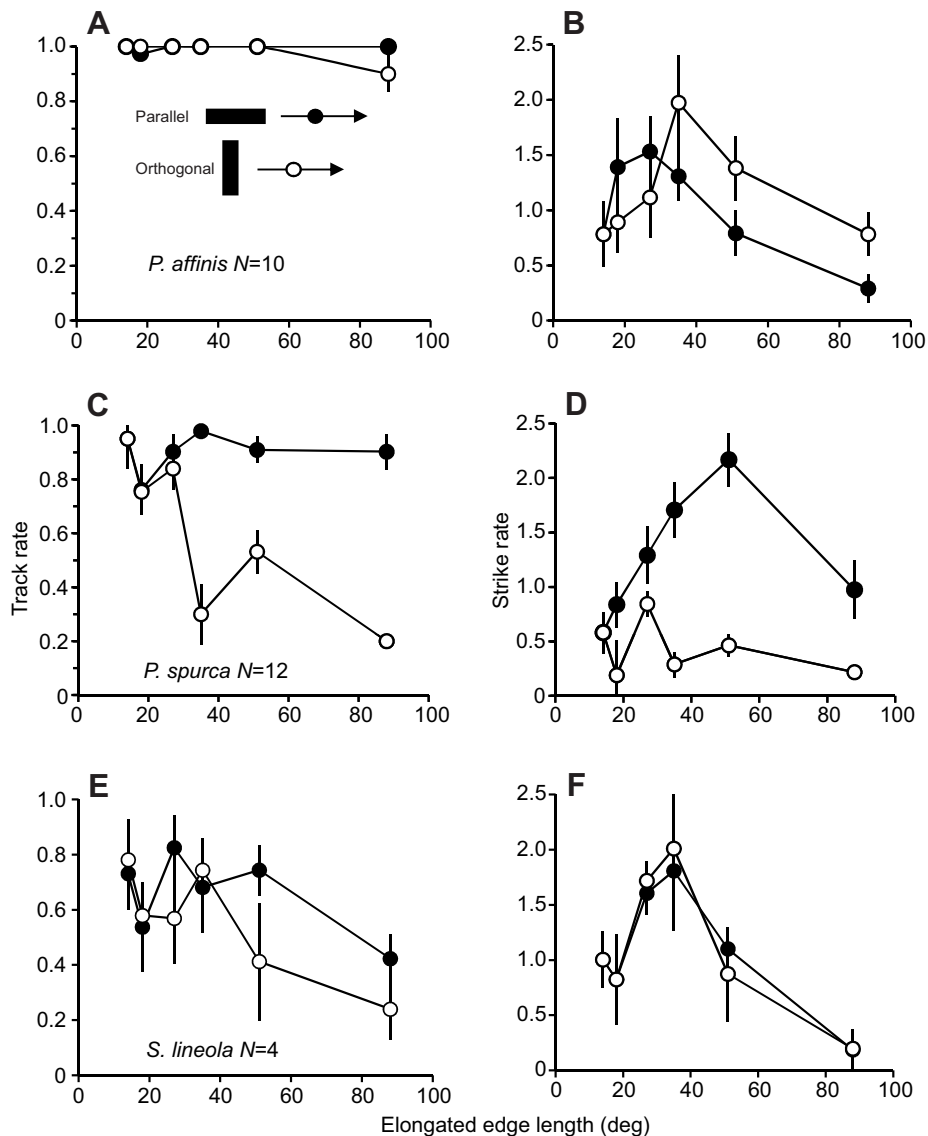


Fig. 4. Track and strike rate by *P. affinis* (A,B), *P. spurca* (C,D) and *S. lineola* (E,F) in response to horizontally moving rectangular stimuli for which one edge was fixed at 14 deg and the other was extended either parallel or orthogonal to its direction of movement. Only *P. spurca* distinguished between stimulus orientations in either tracking or striking when the elongated edge length was ≥ 35 deg.

(Fig. 4A,B,E,F). However, increasing stimulus size (irrespective of orientation) affected the strike rates of both species ($24.86 \geq Fr \geq 11.48$, $0.00015 \leq P \leq 0.042$). In both cases, strike rates were highest in response to stimuli that were 14 deg \times 27–35 deg, and lower in response to both larger and smaller stimuli.

In contrast, *P. spurca* displayed a robust preference for parallel stimuli in both tracking and striking when the stimulus lengths were ≥ 35 deg (Fig. 4C,D). In the former case, all parallel stimuli were tracked at consistently high rates irrespective of size. However, lengthening the stimuli in the orthogonal direction significantly depressed track rate ($Fr \geq 59.66$, $P \leq 0.0001$). There was an analogous effect on strike rate. Stimuli in the parallel orientation elicited progressively higher strike rates up to a length of 35 deg; thereafter, strike rate declined ($Fr \geq 28.46$, $P \leq 0.00003$). Stimuli in the orthogonal orientation elicited only low levels of striking irrespective of length.

Moving versus stationary stimuli

Fig. 5 depicts the response rates of *P. affinis* and *P. spurca* ($N=8$ each) to black square stimuli (2–44 deg edge lengths) that moved linearly from 148 deg right of center to visual field center and then stopped (speed = 74 deg s^{-1}). Overall, the track rates mirrored those seen in previous experiments. For both *P. affinis* and *P. spurca*,

rates increased rapidly as stimulus edge lengths enlarged beyond 2 deg ($Fr \geq 44.96$, $P \leq 0.0001$), with an initial significant change between the 2 \times 2 and 9 \times 9 deg squares ($z \geq 2.58$, $P \leq 0.0097$; $T=4.3$ and 3.8 deg, respectively).

Stimulus size significantly affected the strike rate of *P. affinis* both during stimulus movement and up to 30 s after the stimuli stopped ($Fr \leq 36.78$, $P \leq 0.00007$; Fig. 5B). However, during stimulus movement, strike rates were highest in response to the larger stimuli; after the stimuli stopped, strike rates were highest in response to the smaller stimuli ($z \geq 2.93$, $P \leq 0.0034$). *Popa spurca* responded only at very low strike rates (≤ 0.31) in this experiment, and *S. lineola* ($N=5$) did not respond at all (data not shown).

DISCUSSION

A phylogenetically organized comparison of the behavioral responses of 11 species of praying mantis to the types of visual stimuli used in the present study is shown in Fig. 6. Although the data set is substantial, it is still quite small given the overall diversity of the Mantodea (Svenson and Whiting, 2009). Further, because mantises are difficult to rear and are short-lived as adults, no single species has been tested exhaustively. These caveats notwithstanding, some fundamental behavioral similarities between the species are

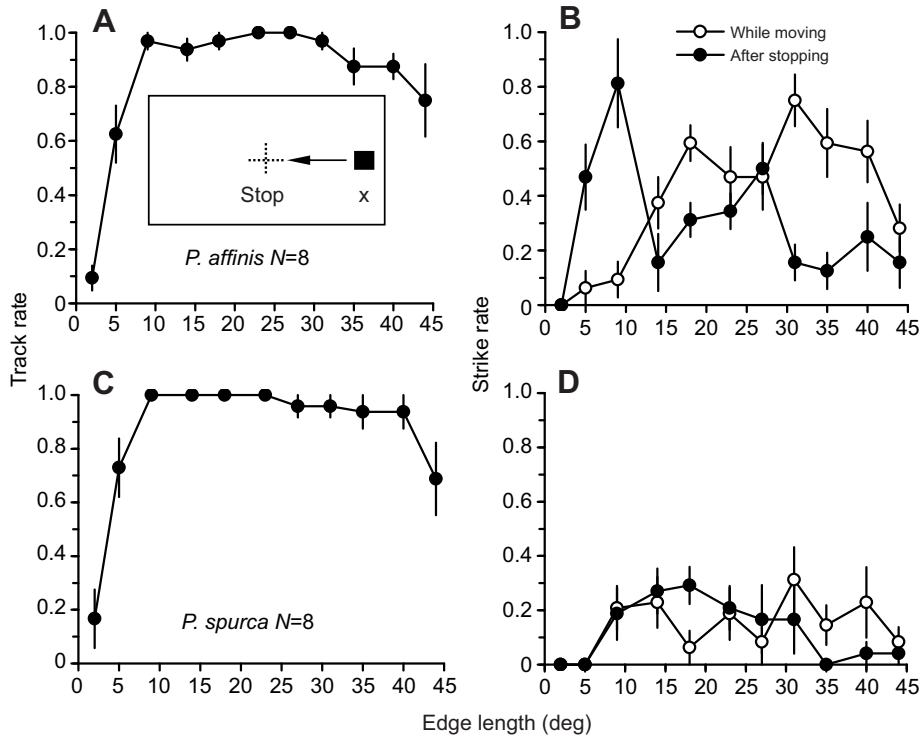


Fig. 5. Track and strike rate by *P. affinis* (A,B) and *P. spurca* (C,D) in response to square stimuli (2–44 deg edge lengths) that moved linearly from 148 deg right of center to visual field center and then stopped (inset). The patterns of tracking did not differ from those seen in other experiments. However, *P. affinis* struck at higher rates in response to the larger (18–40 deg) stimuli when they were moving and the smaller stimuli (5–9 deg) after they stopped. *Papa spurca* struck at very low rates (≤ 0.31) in response to these stimuli, and *S. lineola* ($N=5$) did not respond at all (data not shown).

evident. Unfortunately, because so little is known about mantis ecology outside of a few temperate zone species (Hurd, 1999), it is impossible to make strong claims about the relationships between species differences in behavior and the particulars of their ecological niches (but see Kral, 2012; Prete et al., 2012). Nevertheless, because the Mantodea are all visually guided predators that feed primarily on arthropods, similarities in the ways in which potential prey items are recognized would be expected.

The recognition of an object as potential prey (i.e. ‘prey recognition’) implies that the object is seen as separated from the background against which it appears, and that it has been identified as an exemplar of the category ‘prey’ (e.g. Braddick, 1993). Visual tracking alone indicates only that the former has occurred. Approaching or striking at the stimulus indicates that it has been identified as prey (e.g. Rossel, 1991). To be clear, ‘prey recognition’ refers only to the probability that a stimulus elicits certain behaviors (i.e. activates motor pattern generators) that can lead to prey capture. No other assumptions are made as to the perceptual or motivational state(s) of the mantis. That is, this transduction of sensory input into motor output does not necessarily include any particular object being represented explicitly. Hence, approaching or striking may be elicited by stimuli that do not appear prey-like from a human perspective [e.g. a snake, a bird or a same-sized conspecific (Prete, 1995; Prete and Wolfe, 1992)].

Stimulus contrast

In general, stimuli that are darker than the background against which they move are strong releasers of tracking, approaching and/or striking in all 11 of the species tested. With the exception of *P. affinis*, all species tracked black stimuli moving against a white background at higher rates than the reverse, and four out of the seven more frequently tracked relatively darker grey stimuli moving against grey backgrounds (data not shown). Likewise, black stimuli moving against a white background consistently elicited higher rates of striking than the reverse condition, and three out of four species

tested struck at higher rates in response to relatively darker grey stimuli (Fig. 6, columns I and II, respectively). The finding that higher strike rates are elicited by relatively darker stimuli is consistent with electrophysiological data recorded from the so-called descending contralateral movement detector (DCMD) interneurons in *S. lineola*. These interneurons respond most frequently to the same stimuli that elicit strikes in intact mantises, including stimuli that are relatively darker *versus* brighter than the background against which they move (Berger, 1985; Gonka et al., 1999; see also Popkiewicz and Prete, 2013).

The predilection to recognize relatively darker visual stimuli as potential prey makes sense in that moving objects in the environment will generally appear as luminance decrements in the visual field (i.e. darker than the average background luminance). Interestingly, in the reverse condition – small bright objects on a darker background – the objects are recognized as droplets of water by at least two species of mantis (Prete et al., 1992). The preference for relatively darker prey-like stimuli may also explain the higher rates of striking elicited by red (*versus* blue or green) visual stimuli in *Hierodula membranacea* and *Euchomenella macrops* (Prete et al., 2012; Prete et al., 2013). All else being equal, mantis electroretinograms elicited by red light are lower in amplitude than those elicited by blue or green light, suggesting that red stimuli may appear darker than do blue or green (Popkiewicz and Prete, 2013; Sontag, 1971).

Image movement

Assessing object movement is a difficult information-processing task in that it requires two sometimes conflicting computations. One computation is the perceptual binding of luminance changes across adjacent visual sampling units caused by the internal pattern (i.e. reflective) irregularities within a moving object such as those seen in the mottled grey stimuli used here. The second computation is recognizing that equally proximate local velocity differences represent the object’s edges [i.e. the boundary between the object and the background (e.g. Braddick, 1993)].

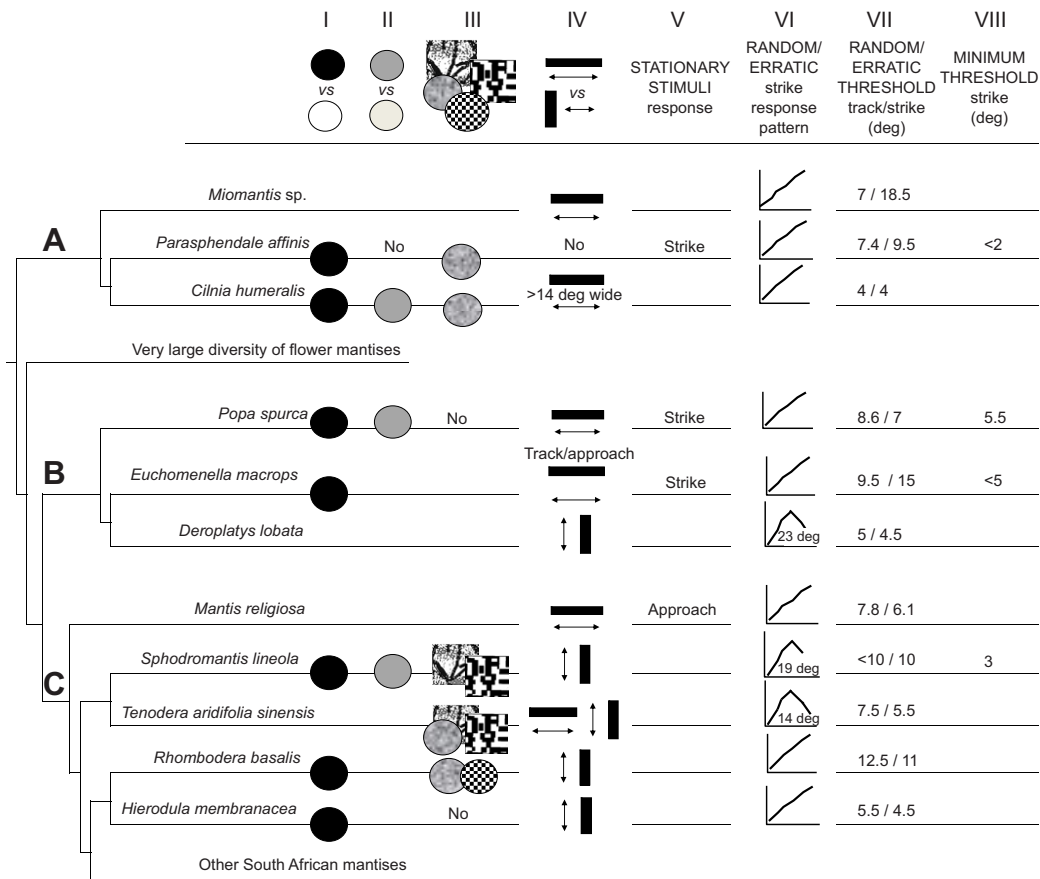


Fig. 6. A phylogenetically organized comparison of the behavioral responses of 11 species of praying mantis tested with the visual stimuli used in the present study. Each of the three species tested in this study is a member of one of the three larger subclades denoted A, B or C (at the left of the diagram). Not all species have been tested under all conditions (blank spaces); 'No' indicates that the species was tested but did not respond as follows. Column I: A black disk indicates higher strike rates elicited by black stimuli moving against a white background versus the reverse. II: A grey disk indicates higher strike rates elicited by darker (versus brighter) grey stimuli moving against a grey background. III: Symbols depict patterned stimuli that elicited tracking and striking when moving against matching backgrounds. IV: Symbols indicate higher rates of striking or other indicated behaviors elicited by elongated stimuli moving parallel versus orthogonal to their direction (as indicated by arrows). V: Behaviors elicited by stationary stimuli after they have stopped moving. VI: Symbols indicate the strike response pattern elicited by erratically moving disks when stimulus presentation order was randomized by size. Mantises either responded at progressively higher rates as stimuli enlarged, or struck most at an intermediate sized stimulus (as indicated). VII, VIII: The smallest stimulus size thresholds for striking in the experimental protocols described in the text. Thresholds are smaller after stimuli have stopped moving (*P. affinis* and *Euchomenella macrops*), and when they are not preceded by larger stimuli (*P. affinis*, *P. spurca* and *S. lineola*). Neither stimulus size thresholds nor sizes that elicited the highest response rates were related to species size. Phylogenetic tree courtesy of G. Svenson.

The finding that several species of mantis will track patterned stimuli moving against similarly patterned backgrounds suggests that they perceive the synchronous movement of local luminance decrements as an intact object (e.g. Barlow, 1981; Julesz, 1971; Kral and Prete, 2004). However, there appears to be species differences in the intra-stimulus contrast ratios necessary for these types of stimuli to elicit either tracking or striking. For instance, *P. affinis* responded to the mottled grey stimulus used here but *P. spurca* and *S. lineola* did not. However, in previous studies *S. lineola* has both tracked and struck at synchronously moving arrays of subthreshold black dots or rectangles moving against similarly patterned black and white backgrounds (Prete and Mahaffey, 1993; Prete and McLean, 1996) (Fig. 6, column III).

Some early literature suggested that a stimulus itself had to be moving in order to elicit prey-catching behavior from a mantis. However, it is not the stimulus but rather the retinal image of the stimulus that needs to move, and the latter can be caused by movement of either the stimulus or the mantis. For instance, *Mantis religiosa*, *E. macrops*, *P. affinis* and *P. spurca* will approach and/or

strike at stationary stimuli after the stimuli have stopped (Prete et al., 2011; Prete et al., 2012; Prete et al., 2013) (Fig. 6, column V). However, the behaviors are generally preceded by head movements (e.g. side-to-side peering), which serves to sweep the object's image back and forth across the retinae (Kral, 2012).

In the field, striking at a stationary object is probably less likely than it is in experiments in which stimuli appear against a homogeneous background. The reason is that in the field, peering will create simultaneous small-field (object) and large-field (background) movement. The latter has been shown to suppress both striking behavior in intact mantises and spike rate frequency in DCMD interneurons (e.g. Prete and Mahaffey, 1993; Gonka et al., 1999). This interaction between large-field and small-field movement is also evident in the switch from smooth to saccadic tracking when a small-field stimulus moves against a heterogeneous versus a homogeneous background (Rossel, 1980). Saccadic tracking stabilizes the heterogeneous background image (between the saccades), which prevents large-field movement from inhibiting striking. However, in a different context (e.g. when navigating within

the environment), mantises can use information extracted from the relationship between small-field and large-field movement to accurately gauge the relative position of objects in three-dimensional space (Walcher and Kral, 1994; Kral, 2012).

Stimulus orientation

In all but one of the species tested, stimuli elongated parallel to their direction of movement elicited higher rates of tracking and approaching or striking than stimuli oriented orthogonally. However, in several cases the preference was influenced by or interacted with stimulus size (*Cilnia humeralis* and *Deroplatys lobata*), contrast (*Rhombodera basalis*), direction [e.g. dorsal to ventral *versus* horizontal in *S. lineola* (Kral and Prete, 2004)] or predatory strategy (*E. macrops*). The only absolute exception was *P. affinis*, which has not distinguished between stimulus orientations in any of the experimental protocols used to date (Fig. 6, column IV).

The preference for stimuli oriented parallel to their direction of movement may be a product of the fact that mantises apparently attend preferentially to the leading edge of a moving stimulus (Kral and Prete, 2004), as do anuran predators (Ewert, 2004). A stimulus moving orthogonal to its direction of movement leads with its longest edge, which would make it less likely to elicit predatory behavior if the leading edge is sufficiently large. In addition, behavioral studies on several species of mantis including *M. religiosa*, *Tenodera aridifolia sinensis* and *Polyspilota* sp. have demonstrated that they use elongated vertical luminance edges as cues related to habitat construction, and the estimation of the relative distances to potential perch sites rather than as cues for prey recognition (reviewed by Kral, 2012). In these instances, mantises tend to prefer long, vertical, high-contrast boundaries such as those created by stalks and branches (Hyden and Kral, 2005). These boundaries will create extended luminance edges that move orthogonal (rather than parallel) to their direction when they sway back and forth in the breeze, or when the mantis peers at them.

Stimulus speed and movement pattern

We used erratically moving stimuli randomized by size to assess the responses that would be elicited by the stochastic appearance of rapidly moving objects in the natural environment. Overall, these experiments have yielded several interesting findings. The first is that each species displays one of two overall patterns of striking when presented with these stimuli. Some species, such as *T. a. sinensis*, *S. lineola* and *D. lobata*, strike most frequently at stimuli within a restricted size range, and less frequently at both smaller and larger stimuli. Others, including *P. affinis* and *P. spurca*, strike at progressively higher rates as stimulus size increases even up to improbably large dimensions (Fig. 6, column VI). However, if stimuli move linearly rather than erratically, some species will display smaller stimulus size preferences. For instance, when presented with linearly moving stimuli that come to a complete stop, *E. macrops* and *P. affinis* strike most frequently at stimuli several times smaller than those that elicit the highest strike rates when moving erratically (Fig. 6, columns VII, VIII). We believe that there are two reasons for this. First, the sudden appearance of any object in the visual field can elicit a brief burst of spikes (an onset response) in the DCMD interneurons, the occurrence of which is correlated with striking behavior (Gonka et al., 1999). This is not to say that DCMD activity *per se* is sufficient to cause a strike, but rather that the initial, sudden appearance of an object can elicit neural activity that may, directly or indirectly, initiate a strike (see also Cleal and Prete, 1996). Second, as we have argued elsewhere, local luminance flicker caused by the leading and trailing edges of a very large

stimulus moving erratically in conjunction with the associated visual tracking movements that it elicits can create luminance flicker similar to that caused by a fast-moving smaller object (Prete et al., 2013). The latter is one of the reasons we posit that mantises are periodically documented catching anomalously large prey (reviewed by Prete and Wolfe, 1992).

In all five species so tested, stimulus speed and size interact. In general, increasing the speed of an erratically moving stimulus depresses the probability that it will elicit both approaching behavior (irrespective of its size) and striking behavior (if the stimulus is small). However, increasing stimulus speed tends to increase strike rate in response to large stimuli up to some maximum speed (e.g. Prete and Mahaffey, 1993; Prete et al., 1993; Prete et al., 2011). These behavioral data are consistent with the effects of stimulus speed on the spike rates of DCMD interneurons in *S. lineola* (Gonka et al., 1999; see also Yamawaki and Toh, 2009).

Prior experience

The probability that a particular behavior will occur in response to a visual stimulus can be affected by a prior stimulus in a variety of animals from arthropods (e.g. Cross and Jackson, 2009) to primates (e.g. Buckner et al., 1998). In mantises, this effect can be particularly robust if the first stimulus is very large, in which case it can depress responses to prey-like stimuli even after 5 days of food deprivation (e.g. Prete et al., 1993). In the experiments reported here, viewing the largest stimuli first in a series ordered from largest to smallest significantly depressed the strike rates to the smaller stimuli in *S. lineola* and *P. affinis*, but not in *P. spurca*.

The neurophysiological mechanisms underlying the effects of prior experience have not been explored in mantises. However, we do know that the probability that *S. lineola* will ‘freeze’ (remain motionless and unresponsive) increases and the probability that they will track a stimulus decreases over repeated presentations of the same stimulus even after 8–9 days of food deprivation (Prete et al., 1993). The depressing effects of a previously seen stimulus may reflect the putative hierarchical organization of mantis behavior in which the defensive strategy (freezing) supersedes predatory behaviors under certain conditions (Edmunds and Brunner, 1999; Liske, 1999).

At the neural network level, we know that DCMD activity in *S. lineola* is inhibited by simultaneous large-field movement (Gonka et al., 1999) but we do not know whether this suppression lasts beyond the stimulus presentation. However, in other orthopteroids such as the locust, threatening visual stimuli (e.g. those that elicit defensive kicking) and environmental stressors (e.g. high temperatures) can suppress the activity of small-field-movement-sensitive visual interneurons such as the DCMD (Money et al., 2006; Heitler, 1983), and DCMD responsiveness can be modulated by more centrally located protocerebral interneurons (Bacon et al., 1995; Gray, 2005).

Implicit representation of prey

It is generally understood that appearance-based object recognition is a particularly difficult task because of both the inherent variability of object images and the potentially obscuring effects of the background. In the case of mantis prey recognition, this problem is compounded by the fact that the insects must recognize not one, but any number of different looking, sometimes previously unseen, objects as potential prey. Hence, not only must the object be segmented from a potentially complex array of background clutter, it must also be identified as an exemplar of the category ‘prey’.

Given the size of the mantis’ brain, the resolution of its visual system, and the potential uniqueness of any particular prey item, it

is improbable (if not impossible) that the mantis stores prey images explicitly as unique neural representations. A plausible alternative strategy is that its central nervous system represents 'prey' implicitly in terms of the spatiotemporal features shared by members of the category including object size, object-to-background contrast, speed, movement pattern and leading edge length. The strength of this strategy lies in the algorithms (or decision rules) in terms of which an object is identified rather than the specific, underlying neural architecture [i.e. the 'software' versus the 'hardware', respectively (Ewert, 2004)]. This is evidenced by the similarities in the prey-recognition algorithms used by animals with very different brains, for instance, amphibians (Ingle, 1983; Roth, 1987; Ewert, 2004), the amphibious fish *Periophthalmus koehleuteri* (Ewert, 2004), cuttlefish (Darmaillacq et al., 2004) and mantises (Kral and Prete, 2004). Even more interesting is the fact that creatures much smaller than mantises, for instance, the jumping spider *Evarcha culicivora*, can combine different subsets of category-specific stimulus elements into a coherent perception of a potential prey item (Nelson and Jackson, 2012; see also Harland and Jackson, 2000). Hence, the strategy of representing prey implicitly seems to be widespread.

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AUTHOR CONTRIBUTIONS

All authors participated in designing the experiments, and in data collection, representation and interpretation. Statistical analyses and manuscript preparation were done by F.R.P. and R.T.

COMPETING INTERESTS

No competing interests declared.

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