

Response of the Praying Mantis, *Sphodromantis Viridis*, to Target Change in Size and to Target Visual Occlusion

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Abstract Mantises (Mantodea, Mantidae) visually detect insect prey and capture it by a ballistic strike of their specialized forelegs. We tested predatory responses of female mantis, *Sphodromantis viridis*, to computer generated visual stimuli, to determine the effects of (i) target size and velocity (ii) discrete changes in target size and (iii) visual occlusion. Maximal predatory responses were elicited by stimuli that (i) subtended $\sim 20^\circ$ – 23° horizontally and $\sim 16^\circ$ – 19° vertically, at the eye, and moved across the screen at angular velocities of $\sim 46^\circ$ – $119^\circ/\text{s}$, (ii) increased in size in a stepwise manner, with step duration ≥ 0.8 s, while stimuli decreasing in size elicited only peering movements, (iii) Stimuli disappearing gradually behind a virtual occlusion elicited one or more head saccades but not actual interception.

Keywords Praying mantis · *Sphodromantis viridis* · vision · stepwise target size change · visual occlusion · predatory strikes

Introduction

Praying mantises (Mantodea; Arthropoda) capture insect prey by rapid, ballistic predatory strikes with their enlarged, specialized forelegs (Prete and Mahaffey 1993). Prey detection and the determination of its distance, size and motion profile (direction, velocity) that precede predatory strikes, are visual (Rossel 1980, 1983; Yamawaki

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2000b) and, prior to strikes, mantises visually track the prey using head and body movements. Mantises estimate prey distance using binocular stereopsis (Rossel 1983). Estimation of distance to non-prey targets, such as surfaces to land upon, is obtained from motion parallax using peering, i.e. side to side head motion (Poteser and Kral 1995; Kral and Poteser 1997; Kral 1998, 2003).

Experiments using mechanically moved or computer-generated visual stimuli have demonstrated that mantises may be employing a computational algorithm to define “prey” (Iwasaki 1990; Yamawaki 2000b). Thus, predatory strikes are preferentially elicited by stimuli fitting a “perceptual envelope” defined by stimulus size, length of leading edge, contrast, location in the visual field, given subtending angles and that move linearly within a given velocity range (Prete and Mahaffey 1993; Prete et al. 2002). Stimulus parameters derived for mantises closely resemble those determining visual prey detection, recognition and capture in the toad, *Bufo bufo* (Ewert 1987). Consequently, a detector system has been proposed (Prete and McLean 1996) whereby mantises have the computational capacity to determine prey velocity and strike preferentially at prey within a given velocity range.

In insects, experiments on target motion have frequently employed targets moving perpendicular to the subject’s body axis and therefore undergoing a relatively small change in apparent size. However, prey and predator moving towards or away from each other will result in, respectively, apparent size increase (looming) or decrease (receding). Distinct responses to looming have been reported both at the behavioral and at the neural levels. For example, a flying locust responds to a visual looming by steering movements and a rapid, stereotyped, wing-beat cessation that leads to a gliding—diving (Santer et al. 2006). At the neural level, neurons have been identified, in the hawkmoth, *Manduca sexta* (Wicklein and Strausfeld 2000) and in the praying mantises (Yamawaki 2000a) that respond selectively to stimulus looming or to receding.

The effects of changes in target apparent size have been mostly tested by moving the target mechanically towards, or away from the subject. In analogue (film) or digital (video/computer) projections, this was achieved by the expansion or reduction of target size. While in mechanically moved targets, changes in apparent size are smooth, in the analogous or digital displays the projections are inevitably a sequence of individual frames displayed at a given rate (mostly 25–30 Hz), tuned to the human visual flicker fusion frequency (e.g., D’Eath 1998). The visual fusion frequency of many insects, however, is considerably higher (Land and Nilsson 2002) and, consequently, a digitally expanding target is most probably perceived by an insect as increasing in size in discrete steps.

While in motion, a prey may undergo partial or complete occlusion by visual obstacles such as leaves or stalks that temporarily obscure it from the predator’s view. This is especially apparent if the prey moves tangential to the predator. To overcome visual prey occlusion and yet capture it at the appropriate moment of reappearance, the predator may need to perform further acts, such as an interception course, with lack of information in parts of the process. The capacity to perform an interception course (Weihs and Webb 1984; Howland 1974) has been demonstrated previously in male hoverflies (*Eristalis sp.* and *Volucella pellucens*; Collett and Land 1978). When hovering in midair male hoverflies respond to a passing female, or to a moving small dark object, by flying an interception course in relation to the direction the female or the

object are moving. Dragonflies (*Odonata*) capture flying insects in the air and their flight is visually directed towards the point of interception. This is achieved by steering to minimize the movement of the prey's image on the retina (Olberg et al. 2007). In the above examples, the targets are in full view throughout, while in praying mantises vegetation may frequently cause a partial or complete obscuring of the target.

The aims of this paper are to determine the effects, on the mantis predatory strikes, of (i) target size and velocity, (ii) changes of target size (looming/receding) and, (iii) target visual occlusion.

Methods

General methods are provided here while specific methods of given experiments are provided in the “Results” section. The subjects ($N=15$) were wild caught, adult female praying mantis, *Sphodromantis viridis* (Forsskål, 1775), 65 ± 1.5 mm (mean \pm S.D.) in body length and 8.5 ± 0.5 mm in head width (at the widest point). Each mantis was housed in a transparent Perspex box ($10\times 15\times 30$ cm) with thin rod perches attached perpendicularly to the walls. Each mantis was fed daily a single cricket (*Gryllus bimaculatus*) and was food deprived for 24 h prior to each experiment. An attempt was made to keep the light/dark regime at 12:12 h. The experiments on stimulus velocity, size and size change (respectively, Experiments 1, 2 and 3) preceded those on stimulus occlusion (Experiment 4) by ca. 12 months. In each experiment, the tested individual, hanging on a rod, was positioned adjacent to the computer screen and with its body axis perpendicular to it so that its head was 25–40 mm from the screen in one set of experiments and ~60–80 mm in a second set of experiments. In experiments 1–3, rectangular paper markers were glued to the dorsum of each individual (Fig. 1) after it had been cooled to 4 °C for several minutes, to enhance tracking precision.

Computer generated visual stimuli (“prey”) were displayed on a computer screen and the response of the tested mantis video filmed (a Sony Handy-Cam Mini DV or a Point Grey Flea digital cameras at 30 frames/s). The screen used was of an IBM laptop

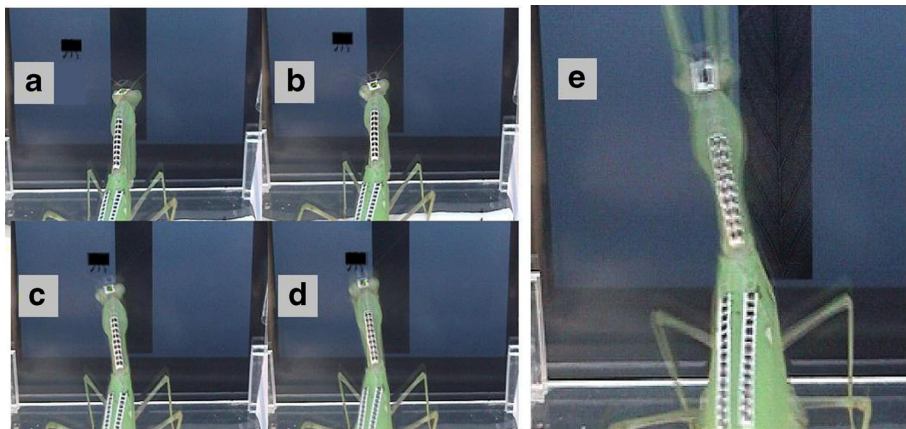


Fig. 1 The tracking (a–d) and striking (e) of a stimulus moving on the TFT screen. e is enlarged to show the strike

(LCD), 800×600 pixels in resolution and single pixel size 0.356×0.356 mm (pixel depth of 24 bits per pixel, refresh rate of 60 Hz, maximal brightness 330 cd/m², effective screen size of 14 in.). For a viewing distance of ~25 mm, each pixel subtended ~0.8° at the mantis' eye. The stimuli used were rectangular in shape, with moving (jittering) appendages, to increase attractiveness. They were presented on a larger, rectangular, background which, at the viewing distance of ~25 mm, subtended 140° at the mantis eye. Stimulus and background brightness were expressed as light intensity values of between 0 and 255 on a linear scale corresponding, respectively, to between 0 and 330 cd/m². The brightness level of the background was 192 (light grey) in one set of experiments and 255 (white) in another, while that of the stimuli was 0 (black). In order to synchronously film the tested mantis and the stimulus, the camera was focused on the plane at which both images were available, with the monitor orthogonal the camera and a mirror reflecting both the stimulus on the screen and the mantis.

The controlled shape parameters of the stimuli were static properties (size, edge orientation, contrast, brightness and texture) and dynamic properties (motion amplitude, motion period, jitter of the legs). We measured (i) head orientation and (ii) latencies to change of head orientation, following the appearance of the stimulus. Testing for the effect of increase in target size (Experiment 3) on the mantis' probability of strike was as follows:

- (a) The initial stimulus was a rectangle $S_0 = H_0 \times V_0$ with $H_0 = 1.8$ mm and $V_0 = 1.4$ mm (i.e., 5×4 pixels) on the screen, subtending ca. 4.5° horizontally and 3.0° vertically at the subject's eye.
- (b) In any given run, the rectangle was made to expand in a stepwise manner, over ten steps of an equal, predetermined duration
- (c) Step durations were between 0.2 s to 2.0 s and the increase phase between steps was instantaneous.
- (d) Each dimension increased linearly so that at time t , the rectangle $S_t = (H_t) \times (V_t)$, with $H_t = H_0 * t$ and $V_t = V_0 * t$.
- (e) Maximal target (rectangle) size attained was ca. 40°×31° (18×14 mm; 50×40 pixels; horizontal x vertical) subtending at the mantis eye.

In runs in which target size decreased, the initial target subtended 40°×31° (18×14 mm; 50×40 pixels) and size decreased in a reverse order to the above described. During any given run, the mantis either struck or did not strike (respectively positive and negative responses) at the stimulus.

To determine the effect of target occlusion on predatory behavior (Experiment 4), the mantises ($N=5$) were presented with a rectangular target, subtending 4.9°×13° (6×16 mm on the screen, at a distance of ~60–80 mm) at the mantis eye, and moving horizontally at an angular velocity of ca.4.5°/s (6.5 mm/s). Target occlusion was achieved by a vertical virtual grey bar, subtending 32° (40 mm) in width, “behind” which the stimulus was made to gradually disappear until completely obscured, without re-appearing. The mantis head and visual stimuli were tracked using a specially developed algorithm. To compute head movements, consecutive frames were sampled at five frame intervals and, for every frame sampled, the position of the center of each eye (the eyes were approximated as circles) and the labrum (covering the mandibles) was marked manually. In the triangle obtained, the head location was defined as the

point of intersection of the line connecting the center of the inter-eye segment and the tip of the labrum. The angular change between consecutive frames was calculated as the change (in degrees) in the angle of the central axis line and the linear/horizontal movement (in pixels/frame) of the length of the section (in pixel units) connecting two consecutive head locations. The position of the camera was such that motion along its optical axis was small, and thus not incorporated into the analysis. In all experiments an attempt was made to keep contrast unchanged.

Results

When a target moved across the computer screen, the head of the mantis was kept stationary at first and, at a given point, moved sharply towards the target, followed by saccadic head movements during tracking and a subsequent strike at the target. Figures 1 and 2 depict the head motion (horizontal velocity) of a mantis, in response to a target moving on the screen at $\sim 62^\circ/\text{s}$ (distance to screen ca. 30 mm). Inter-saccade intervals were of relatively constant durations (0.75–1.0 s).

Target Velocity

The aim of Experiment 1 was to determine the effect of target velocity on strike probability. The target subtended $\sim 11.5^\circ \times 22.5^\circ$ at the mantis eye (linear dimensions: 5 mm \times 10 mm) and was moved horizontally across the screen (L-R runs) at predetermined velocities within the range of $5^\circ/\text{s}$ and $350^\circ/\text{s}$ (linear: ~ 2.0 –170 mm/s). Eight different velocities were tested (ca. 6 tests/individual/velocity).

The results show a quadratic pattern of response, with a clear difference between the probability of strikes to different target velocities (Repeated Measures ANOVA with Hotelling's Trace criteria, $F_{(3,8)}=513203.17$, $p<0.001$). Maximal strike probabilities ($p>0.9$) were observed at velocities of between ca. $96^\circ/\text{s}$ and $197^\circ/\text{s}$ (Fig. 3; linear: ~ 42 –85 mm/s; $N=10$ mantises, 50 runs/individual).

Fig. 2 The horizontal velocity of the mantis head during following and striking (STR) at the target. Horizontal broken line Stimulus motion

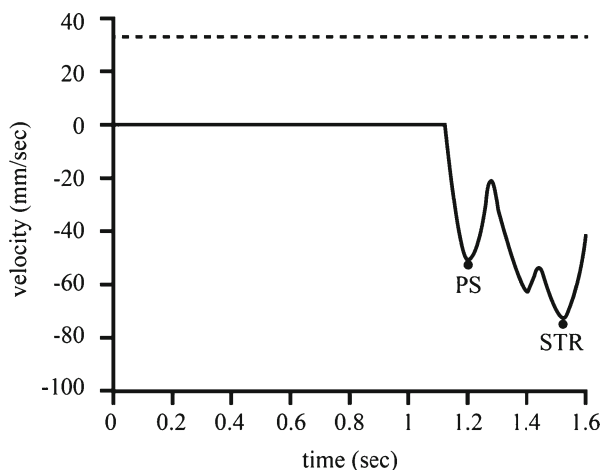
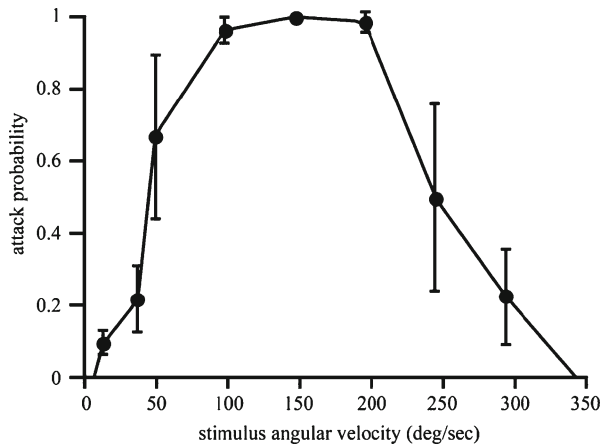


Fig. 3 The probability of strikes as a function of stimulus velocity. Provided are the mean of means \pm SD for 10 mantises, over 8 velocities, for a target subtending ca. $11.5^\circ \times 22.5^\circ$

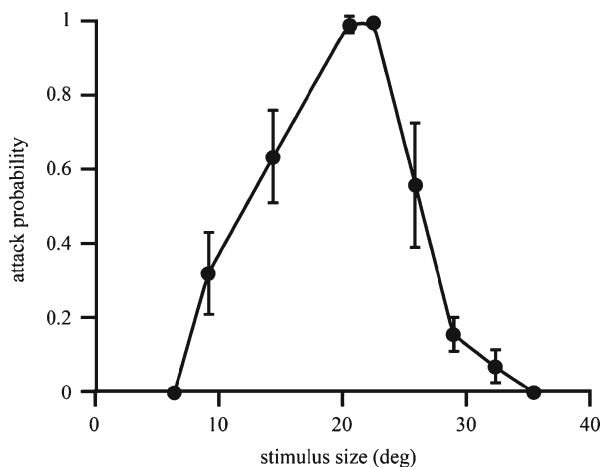


Target Size

The aim of Experiment 2 was to determine the effect of target size on strike probability. All targets were controlled for size so that the length to width ratio was 5:4. The targets were moved horizontally across the screen (L-R runs) at an angular velocity of ca. $68^\circ/\text{s}$ (linear: 30 mm/s, distance to screen ~ 25 mm). Nine different sizes were tested (ca. 5–6 tests/individual/size).

The results show a quadratic pattern of response, with a clear difference between probabilities of strikes to different sized targets (Repeated Measures ANOVA with Hotelling's Trace criteria, $F_{(3,7)}=18172.95$, $p<0.001$). Maximal probability of response ($p>0.9$) was observed for targets subtending $\sim 20^\circ$ – 22° (horizontally) and $\sim 16^\circ$ – 18° (vertically) mantis eye (Fig. 4; $N=10$ mantises, 50 runs/individual).

Fig. 4 The probability of strikes as a function of stimulus size. Provided are the mean of means \pm SD, for 10 mantises over 9 stimulus size groups, for stimulus angular velocity of ca. $69^\circ/\text{s}$



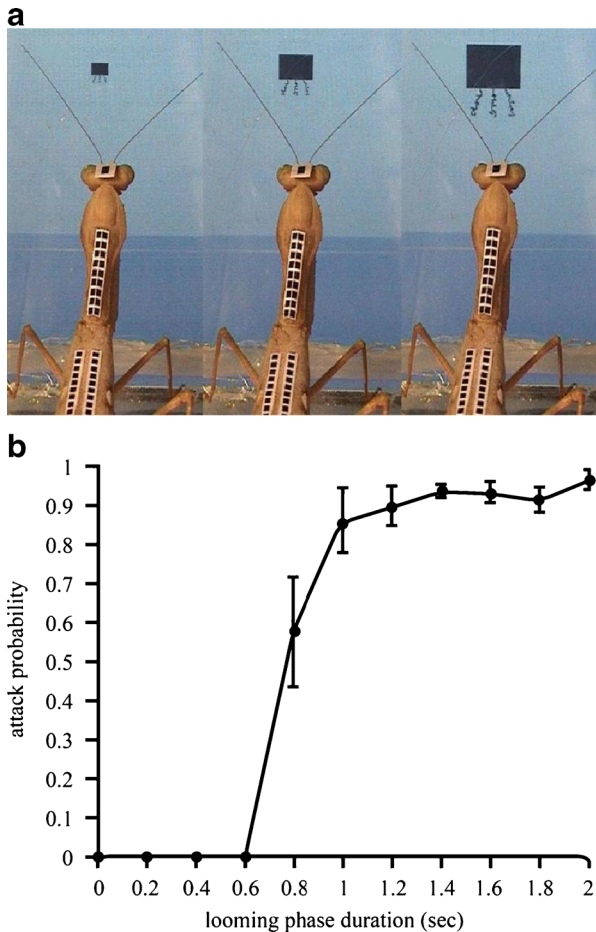
Target Size Change

The aim of Experiment 3 was to determine the effect of looming and receding on strike probability. On each run, target size either increased (Fig. 5a) or decreased in discrete steps of predetermined duration, with the change orthogonal to the mantis’ eye plane. Target sizes ranged between $1^\circ \times 1^\circ$ and $40^\circ \times 31^\circ$. For each step, target position and contrast were unchanged.

Figure 5b depicts the probability of strikes as a function of step duration during looming (a total of 160 runs/mantis, $N=10$ mantises, tested over eight experimental days). For all strikes and for all individuals tested, the response to the increase in size resembled a stepwise, “all or none” phenomenon, with a significant (cubic) increase ($F_{(3,7)}=11790.103, p<0.001$). The threshold of step duration for eliciting predatory strikes was ≥ 0.8 s (Fig. 5b).

In marked contrast, a decrease in target size (160 runs/mantis) elicited only peering motions and no predatory strikes were observed.

Fig. 5 **a** Stimulus looming: The stimulus undergoes a two-fold size increase on the computer screen, at 30 frames (~ 1 s) intervals. **b** The probability of strikes (mean \pm SD) as a function of stimulus looming phase duration



Target Occlusion

The aim of Experiment 4 was to determine the response of the mantises to gradual target occlusion. In the experiment ($N=5$ mantises; a total of 28 runs) the parameters of head motion examined were angular velocity, i.e., the change in gaze direction, and linear velocity, i.e., the change of head location. The mantis head was $\sim 60\text{--}80$ mm from the screen so that the target (16×6 mm) subtended $\sim 13^\circ$ horizontally and $\sim 4.9^\circ$ vertically and was moved at an angular velocity of $\sim 4.5^\circ/\text{s}$ (linear ~ 6.5 mm/s) at the above viewing distance.

Prior to the appearance of the target on the screen, the mantis head was motionless for many seconds. Once detected, the target was immediately tracked with saccadic movements throughout its motion on the screen and during its disappearance phase. Head movements declined following complete occlusion (Fig. 6). In all the runs (28), within the 3 s immediately following the complete target disappearance, the mantises performed one or more head saccades or peering movements (Figs. 7a, b). However, there were no indications of actual tracking and performing an interception course.

Discussion

Invertebrates and vertebrates respond to visual stimuli that may be much simpler than the naturally occurring object. This has led to previous detailed analyses of the relative contribution of stimulus variables such as shape, size and motion in the elicitation and orientation of responses (Ewert 1987; Land 1999). Many examples of visually guided responses pertain to socio-sexual, parental and predatory aspects (Tinbergen 1951; Ewert 1987). Among these, the predatory strikes of praying mantises to mechanical or digital prey models have been extensively studied, showing that the strikes are preferentially elicited by models that fit a certain “perceptual envelope”. This depends on stimulus variables such as overall size, length of leading edge, contrast, location in the visual field and more (Iwasaki 1990; Yamawaki 2000b). Motion variables pertain to the body and its appendages, to orientation (horizontal/vertical; angle of approach) and path pattern (e.g., straight, meandering). Thus, in *Sphodromantis lineola* significantly more strikes were elicited by targets (i) moving within a given velocity range (between

Fig. 6 The number of head saccades before (solid bars) and after (open bars) the target’s complete disappearance (point 0 on the abscissa)

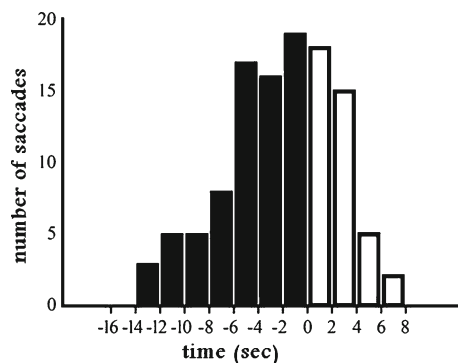
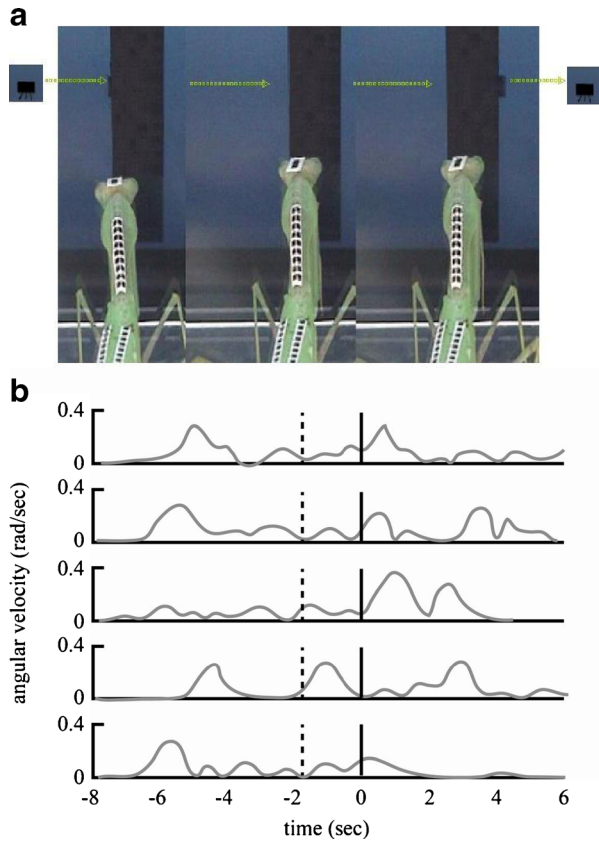


Fig. 7 **a** Consecutive single frames of head motion during the course of target (*solid square* with appendages) visual obstruction. **b** The angular velocity of the head in five sequences, each of an individual mantis, during target visual occlusion. *Hatched vertical line* beginning of occlusion. *Solid vertical line* target fully occluded



ca. $100^\circ/\text{s}$ and ca. $200^\circ/\text{s}$), (ii) of a given edge length (e.g., subtending 12.5° at the eye) and (iii) moving linearly. These behavioral findings were supported by neurophysiological findings of stimulus analysis by the visual system (Prete et al. 1993, 2002; Prete and Mahaffey 1993; Gonka et al. 1999; Prete 1993).

The present study attempted to methodologically modify previous studies on mantises where computer-generated visual stimuli have been used for the determination of stimuli parameters. Comparable with previous studies, praying mantises tested in the present study responded to simple, moving computer images with tracking head motion and mostly with predatory strikes. Stimuli moving perpendicular to the axis of the mantis body, elicited maximal predatory strikes at stimulus velocities of ca. 96° and $197^\circ/\text{s}$ and when the stimulus subtended $\sim 22^\circ\text{H}$ by 18°V of arc. The target velocities here were somewhat higher than those obtained for *Sphodromantis lineola* (Bur.) (Prete et al. 1993) in which maximal strike probability towards a mechanically moved stimulus was at velocities of 35° – $85^\circ/\text{s}$. Also, optimal target size range here, between 20° – 22° (horizontal) and 16° – 18° (vertical) was higher than those obtained previously (Yamawaki 2000b) of prey angles subtending 10° – 11° . The differences in the results, while the body size of the mantises is similar (head width ca. 8.5 mm) supports previous findings that prey size may not be correlated with mantis size (Prete et al. 2011).

An important aspect of target size is that of dynamic changes, i.e. looming or receding, as the distance between viewer and target changes. The neural aspects of responses to looming visual stimuli were reported by Yamawaki and Toh (Yamawaki and Toh 2009a, b), the authors identified a descending neuron sensitive to visual stimuli simulating a looming target. The authors concluded that a looming target causes larger neural responses than a receding target.

Insects and vertebrates respond to visual looming with distinct responses at both the behavioral and the neural levels (Yamamoto et al. 2003 and references therein; Gray et al. 2010). Locusts in flight respond to a visually looming stimulus by closure of their wings and falling down. In mantises, target looming elicits predatory strikes, with maximal strike probability attained when a rectangular, horizontal “prey” is moved towards the mantis at an average velocity of $35^\circ/\text{s}$ (Prete 1992). Prete (loc cit) used square targets with leading horizontal edge size varying smoothly from 1.5 to 30 mm and maximal response was observed with stimuli with leading horizontal edge of between 3 and 6 mm.

In this study, looming elicited predatory strikes while receding elicited only peering movements, but not predatory strikes. Unlike most previous studies, looming here did not involve a change in distance but comprised discrete, not smooth, steps of size increase. These revealed that the duration of steps had a significant effect on the response and that minimal step duration eliciting the response was ca. 0.8 s. In other words, a step-wise increase in target size of step durations shorter than 0.8 s, would not be responded to. These results suggest that for the elicitation of predatory strikes, the target’s image needs to remain unchanged for several hundreds of msec. Obviously, target expansion/contraction involves changes of both area (hence number of ommatidia excited) and of edge length. It remains open if the required trigger is of one or both parameters. Qualitative observations indicate that when phase duration was shorter than 0.8 s, peering movements (c.f., Kral 1998) were apparent. Thus, the mantis may be executing a decision algorithm, including time filtering steps. If the delay is not long enough, the algorithm may reset and start from the beginning. During the reset and restart the mantis performs peering movements.

It should be recalled that stepwise changes are an inherent attribute of digital and analogue presentations and in both film and computer screens, the motion of an object and changes in its dimensions are “chopped” into units displayed most frequently at ca. 40 milliseconds intervals. For the relatively high visual fusion frequency of insects, such displays may well appear as discrete units, unlike the motion of mechanically moved objects.

As noted above, the neural basis of the response to looming in Mantid has been well investigated (Yamawaki and Toh 2003, 2009a, b). In locusts visual neurons have been found that respond selectively to looming and provide the animal with a warning of expected collision. It has been suggested that a peak in the response of the lobular giant movement detector neurons (LGMD), generated 25 ms after a looming object reaches a subtending angle of 17° at the eye, is the trigger for escape behavior. While other reports (e.g., Rind and Santer 2004) state that a peak in LGMD is not required for elicitation of escape behaviors, it is interesting to note that in the present experiment, the predatory strikes were most frequent when a stimulus increasing in size subtended an angle of between 15° – 25° at the eye. During a change in size, a target undergoes changes in area, perimeter length and perimeter or edge motion. In the optic lobes of the

hawkmoth, *Manduca sexta*, neurons that respond selectively to looming and receding stimuli were described, (Wicklein and Strausfeld 2000). While certain neurons respond to non-motion parameters of the image, others respond to moving edges and subsets are excited by image expansion and inhibited by image contraction. These authors propose that cardinal parameters in elicitation of response are changes of perimeter length detected by one class of neurons and expansion or contraction of visual flow fields detected by the 2nd class of neurons.

When a horizontally moving target gradually disappeared behind a virtual occlusion, the mantises mostly continued their tracking head motions for ca. 3 s after the target had been fully out of sight. For a narrow occlusion, this would have resulted in a situation whereby the head was aligned with the point of reappearance behind the occlusion. However this cannot be taken as evidence for the performing of an interception course. The capacity for interception has been demonstrated for several insects and has not yet been demonstrated in mantises. Well studied examples include interception of female flight paths by male hoverflies, (Collett and Land 1975, 1978) and the capture of flying insects by dragonflies (Odonata: Olberg et al. 2000). An obvious difference between the results here and previously reported cases, (e.g., Boeddeker et al. 2003) is that in the above examples the targets remained in full view of the pursuer throughout the approach or chase, while in this study the head motion continues in the absence of the stimulus. If interception were to take place, the point towards which the head needed to be directed had to be calculated in the absence of immediate visual input.

The ability to determine a future location of a disappearing target has been studied in birds (e.g., pigeons, Krachun and Plowright 2007) and mammals (e.g., dogs, Fiset et al. 2000, cats, Fiset and Doré 2006). For example, chicks (*Gallus gallus*) presented with a goal object that was made to disappear between one of two opposite screens, chose the correct screen if the object looked like a social partner (Regolin et al. 1995). While this and other studies indicate that animals can make use of memory in a search algorithm, it needs to be verified in the case of insects. The question of praying mantises' capacity to intercept temporarily invisible targets thus remains open.

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