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ARTICLE

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Effects of luminance, size, and angular velocity on the recognition of nonlocomotive prey models by the praying mantis

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Abstract Adult females of the mantis *Tenodera angustipennis* were presented with the "nonlocomotive" prey model, a static rectangle with two lines oscillating regularly at its sides, generated on a computer display. The models were varied in rectangle luminance (black, gray, and light gray), rectangle height (0.72, 3.6, and 18mm), rectangle width (0.72, 3.6, and 18mm), and angular velocity of oscillating lines (65°, 260°, and 1040°/s) to examine their effects on prey recognition. Before striking the model, the mantis sometimes showed peering movements that involved swaying its body from side to side. The black model of medium size (both height and width) elicited higher rates of fixation, peering, and strike responses than the large, small, or gray model. The model of medium angular velocity elicited a higher strike rate than that of large or small angular velocity, but angular velocity had little effect on fixation and peering. We conclude that mantises respond to a rectangle in deciding whether to fixate, and to both rectangle and lines in deciding whether to strike after fixation.

Key words Prey recognition · Peering · Vision · Mantis · Insect

Introduction

Praying mantises feed primarily on adult and larval arthropods (Barrows 1984). Mantises are considered to be an opportunistic predator because their prey selection depends mainly on the relative abundance of prey (Bartley 1983). To recognize various prey animals, mantises appear to use visual motion as a cue. For example, mantises readily strike locomotive prey models, which are blocks moving in a straight line (Iwasaki 1990; Prete 1990). It has been demonstrated that the luminance, size, and velocity of locomotive models affect the response rates of strike by mantises (Prete and McLean 1996; Prete 1990; Prete et al. 1993).

In addition to the locomotive models, the "nonlocomotive" model consisting of a static rectangle and two moving lines more effectively elicits predatory behavior of mantises than the rectangle or lines alone (Yamawaki 1998). In this case, nonlocomotive means that the model position does not change but some of its parts move. Although both rectangle and moving lines of the model are necessary for eliciting strike, what mantises respond to is not clear. For example, there is a possibility that mantises merely respond to the one of moving lines adjacent to the edge (of the rectangle). In other words, the edge may attract the mantis' attention, and moving lines adjacent to the edge may be more noticeable than moving lines alone. One other possibility is that moving lines attract mantis attention and elicit fixation. The static rectangle alone may be sufficient for eliciting strike once mantises fixate it. In addition to these two possibilities, there are many other possibilities as concerns what stimulates mantis response. To differentiate between these possibilities, we need examine the effects of rectangle and line parameters on rates of fixation and strike responses. This examination will clarify what mantises respond to during fixation and strike of the nonlocomotive model. For example, if parameters of the rectangle have little effect on strike rate, it is suggested that mantises respond only to lines during strike. One of the purposes of the present study is this examination, which assists us to consider the mechanism underlying fixation and strike behaviors.

Even if prey or models are nonlocomotive, mantises may receive locomotive visual stimuli because mantises occasionally show "peering" movements before striking prey (Rossel 1980; Prete 1993). Especially, when prey is not walking, peering of the mantis is sometimes observed (Yamawaki 1999). In the mantis, peering movements involve swaying its body from side to side (or back and forth) and sweeping the target image across the retinae (see Kral

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and Poteser 1997 for review). Peering movements are often observed before jumping and are used to estimate the distance between the mantis and the object that it aims to jump onto. Although the mantis exploits binocular disparities to judge prey distance (Rossel 1983, 1986), the stereopsis is presumed to be available only in a range of a few centimeters because of small interocular distance and low spatial resolution. Hence, the mantis exploits motion parallax during peering to estimate the distance of an object that is far from the mantis. However, peering movements may also allow the mantis to assess several critical stimulus parameters of prey such as size, configuration, and direction (Prete 1993). Jumping spiders "scan" the target by moving their eyes during fixation, and scanning appears to be important to identify objects (Land 1969). Thus, peering movement in the mantis also appears to be important in recognizing nonlocomotive prey.

However, the prey model parameters that are important for eliciting peering movements have not been determined. Tethering the mantis prevents this voluntary movement, so free-moving mantises should be used to study peering. In the present study, we presented free-moving mantises with a "body-and-leg" model, a static rectangle with two lines oscillating regularly at its sides, generated on the computer display. The luminance and size of the rectangle and angular velocity of the oscillating lines were varied to examine their effects on rates of fixation, peering, and strike responses.

Materials and methods

Animals

Adult females of the mantis *Tenodera angustipennis* were used. The egg cases were collected at Uji City in Kyoto Prefecture, Japan, in April 1997. Hatched insects were reared individually to prevent cannibalism. They were kept on a fixed light/dark cycle (light, 0700–2100; dark, 2100–0700) at an ambient temperature of 25°C. Each mantis was fed on one live nymph of the cricket *Gryllus bimaculatus* every day. After 1 day of food deprivation, each experiment was carried out between 1300 and 2100. The subjects ($n = 24$) were 64.34 ± 4.25 mm (mean ± SD) in body length and 7.29 ± 0.42 mm in head width (at the widest point).

Apparatus

During presentation of prey models, the mantis was mounted on a columnar styrofoam bar (5 cm in diameter, 40 cm in length), facing a 13-in. cathode ray tube display (67 Hz, Apple BCGM1212; Fig. 1). The bar was placed on the styrofoam platform, which was precut to fit the bar. The display and bar were surrounded with paper walls (30 cm in height) to prevent visual disturbance from the observer. Experiments were performed under the illumination of fluorescent lamps (60 Hz).

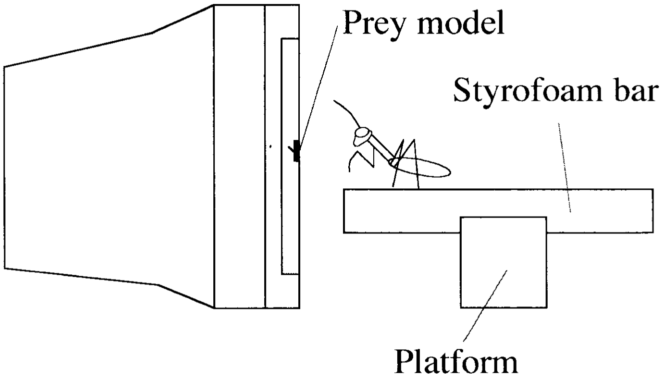


Fig. 1. Lateral view of apparatus

Prey models were generated on the screen of the display by computer (PowerBook 5300, Apple) with Tcl/Tk programing language. The center of the prey model was positioned 2.5 cm above the bar.

The brightness of the prey model and background on the screen was expressed as light intensity value, which was set between 0 and 255. Four colorations of the models and background – black (light intensity value = 0), gray (128), light gray (192), and white (255) – were depicted on the screen. The luminance of these colorations were measured with a luminance colorimeter (BM5A; Topcon) under the illumination of fluorescent lamps. Black, gray, light gray, and white had a luminance of 4.98, 35.15, 69.52, and 109.8 cd/m^2, respectively.

Prey models

Prey models were generated on a white background. In the first experiment, the mantises were shown three types of model varied in composition to confirm that the entirety of a "body-and-leg" model is necessary for eliciting strike behavior (Fig. 2). (1) The "leg" model, two black lines (3.6 mm in length, 0.36 mm in width) separated at a distance of 3.6 mm, appeared. The exterior ends of lines were oscillating bilaterally at an angular rate of 260°/s; The amplitude of oscillation was 120°. (2) The "body" model, a black rectangle (3.6 × 3.6 mm) appeared; it did not move at all. (3) The "body-and-leg" model, a rectangle identical to the body model, and two lines, identical to the leg model, appeared simultaneously. The lines oscillated in the same way as the leg model.

In the next four experiments, to examine the effects of parameters on recognition of a body-and-leg model, four sets of three body-and-leg models were presented to mantises. Within sets, three models varied in the following parameters: rectangle luminance (black, gray, and light gray; Fig. 3a), rectangle height (0.72, 3.6, and 18 mm; Fig. 3b), rectangle width (0.72, 3.6, and 18 mm; Fig. 3c), and angular velocity of oscillating lines (65, 260, and 1040°/s; Fig. 3d).

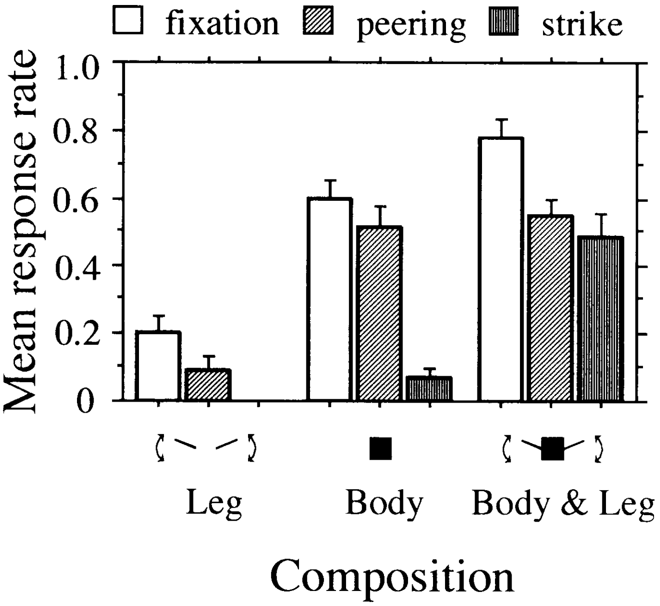


Fig. 2. Mean rates of fixation, peering, and strike responses to the "leg," "body," and "body-and-leg" models. Models are diagrammed under the columns. *Bars*, 1 SE

Experimental procedure

The mantis was carefully removed from its home cage, and the first session was started by placing the mantis on the bar. When the mantis settled down on the end of the bar, the bar was carefully mounted on the platform so that the distance between the mantis and the display was approximately 4 cm. When this operation succeeded, the first trial was started. (If not, it was tried again.) Each trial was initiated with the appearance of the prey model on the screen. The prey model was presented for 10 s in each trial. One session consisted of five trials with intertrial intervals of approximately 1 s. When the mantis moved away from the bar during the first trial, the session was reinitiated from the beginning. However, when the mantis moved away from the bar after the first trial, the session was continued to the last trial, and the next session was started by placing the mantis on the bar.

When the mantis was motionless on the bar after the end of the session, the next session was started by shifting the bar so that the distance between the mantis and the display was approximately 4 cm. The occurrences of fixation, peering, and strike were recorded for each session: fixation is defined as rapid orienting to the direction of the prey model, peering is defined as at least two successive movements of body swaying from side to side, irrespective of its amplitude, and strike is defined as a rapid grasping movement of the forelegs toward the prey model.

In each experiment, the same 24 mantises were used. For each prey model, each mantis received five sessions continuously at intersession intervals of more than 1 min. Each mantis was exposed to three types of prey models at intervals of more than 10 min in an experimental day. To avoid any order effect, the mantises were divided equally into six groups, and the order of model presentation was varied among groups within each experiment so that each group was assigned one of the six possible orders. The response rate of each mantis to each model was defined as the number of sessions, in which fixation, peering, or strike behavior was observed per number of total sessions (i.e., five).

Effects of composition and parameters of models on response rates were analyzed for each experiment with Friedman two-way analysis of variance by ranks. Multiple comparison tests were made using the Wilcoxon paired-sample test. The tests were performed by StatView-J4.11 for Macintosh. The experiment wise error rate was set at 0.05. The significance level of individual comparisons was approximately 0.0166, according to the Bonferroni method (Sokal and Rohlf 1995).

Results

Peering movements were often observed just after the mantis fixated on the model, after making a few steps forward, and before striking. The mantis sometimes struck the model without peering (23% of total strikes). The amplitude of peering seemed to be much smaller than that before jumping.

Rates of fixation, peering, and strike differed significantly among the "leg," "body," and "body-and-leg" models (Fig. 2; Table 1). Rates of fixation and peering in response to the leg model were significantly smaller than to the body and body-and-leg models. The strike rate for the body-and-leg model was significantly larger than for the leg and body models. Hence, the body and body-and-leg models elicited fixation and peering at a similar high rate, but only the body-and-leg model elicited strike effectively.

Rates of fixation, peering, and strike differed significantly among the models varied in rectangle luminance (Fig. 3a; Table 1). The black model elicited significantly higher rates of fixation, peering, and strike than the gray and light gray models, and the gray model elicited significantly higher rates of fixation and strike than the light gray model.

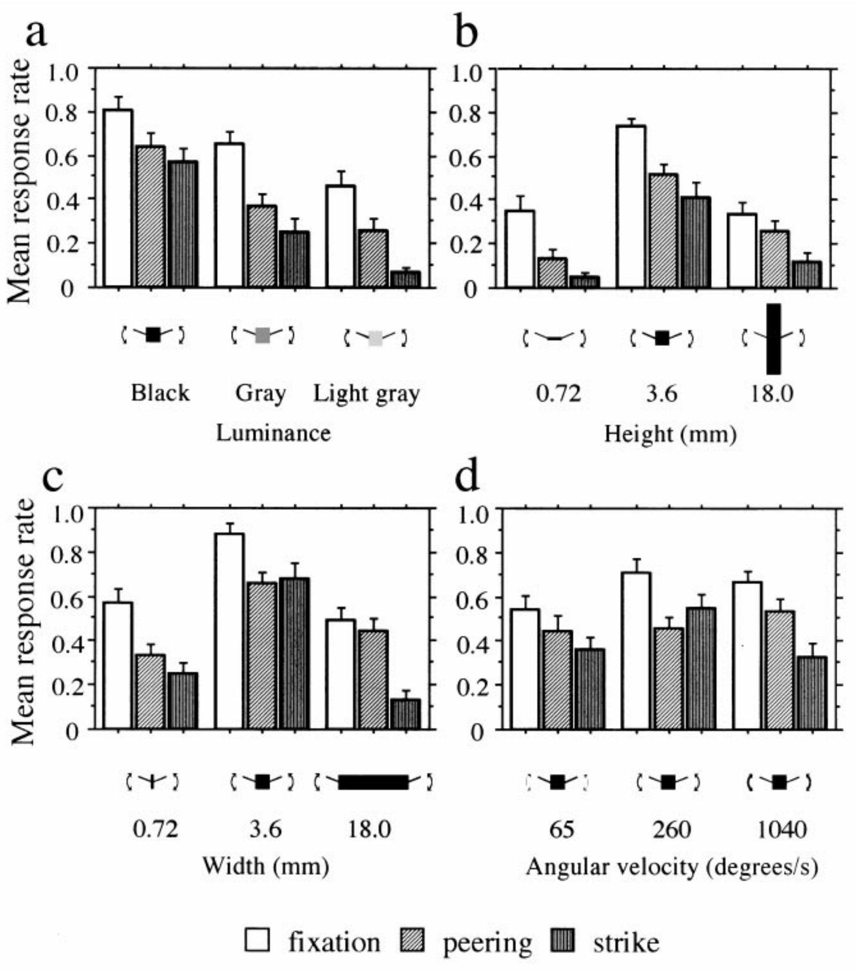
Rates of fixation, peering, and strike differed significantly among the models that varied in rectangle height (Fig. 3b; Table 1) and rectangle width (Fig. 3c; Table 1). Rates of fixation, peering, and strike in response to the medium models in both height and width were significantly larger than to the large and small models.

Strike rate was altered significantly depending on angular velocity of oscillating lines, but we did not find a significant effects on fixation and peering (Fig. 3d; Table 1). Strike rate in response to the model of medium angular velocity was significantly larger than to the large and small models.

Discussion

The higher response rate of strike to the body-and-leg model than to the leg and body models indicates that the combination of a static rectangle and moving lines is effec-

Fig. 3a–d. Mean rates of fixation, peering, and strike responses to four sets of three "body-and-leg" models varied in rectangle luminance (**a**: black, gray, and light gray), rectangle height (**b**: 0.72, 3.6, and 18 mm), rectangle width (**c**: 0.72, 3.6, and 18 mm), or angular velocity of oscillating lines (**d**: 65, 260, and 1040°/s). Models are diagrammed under the columns. *Bars*, 1 SE



tive for eliciting strike behavior of the mantis. It is presumed that the body-and-leg model represents a stationary prey moving some parts, such as a fly cleaning its legs or a grasshopper moving its antennae. If mantises could respond only to locomotive prey, they would lose, for example, a fly that landed on the ground. Because a prey animal is not always walking or flying, the ability to respond to such a stationary prey is considered to be useful to increase the capture efficiency of the mantis.

Using locomotive prey models, Prete and McLean (1996) showed that the decreasing the luminance of the moving rectangle increases the strike rate of mantises (*Sphodromantis lineola*). This result agrees with our finding that a model consisting of a dark static rectangle with oscillating lines elicited a higher response rate of strike than a light one. Hence, irrespective of whether the model is locomotive or not, a dark prey model seems to be most attractive.

Many systematic behavioral studies have been reported the effective size of prey on prey recognition in the mantis (Rilling et al. 1959; Holling 1964; Iwasaki 1990; Prete 1990; Prete and Mahaffey 1993). The conclusion drawn from these studies, ours included, is that prey models that are either too large or too small are ineffective to elicit mantis strike. Not only size but also configuration of model is important for eliciting strike (Prete 1993). For example, when the model moves toward the mantis, the "worm" model elongated parallel to its direction of movements elicits a higher rate of strike than the "antiworm" model elongated perpendicularly (Prete 1992). In this case, the strike rate in response to the worm model is similar to that to the square model, although the long edge of the worm model is about four to five times as long as the edge of the square model. In the future, it may be worthwhile to test configuration effects on recognition of nonlocomotive models by comparison between the response rates to square, vertically oriented rectangle, and horizontally oriented rectangle models of equal area. Prete (1993) showed that the configuration preferences in the mantis are affected by direction of model locomotion and location of retinal image of the model, but the effects of both direction and location cannot be examined in studies using nonlocomotive models and free-moving mantises.

The high response rate to the model of medium angular velocity suggests that mantises strike the body-and-leg model when the angular velocity of oscillating lines is similar to that of moving legs or antennae of actual prey animals. To test this supposition, the angular velocity of legs or antennae of stationary prey animals should be measured.

Although the experiments were carried out with free-moving mantises, results of the present study were similar to those of previous studies in which tethered mantises were

Table 1. Analysis of the differences in rates of fixation, peering, and strike among models by Friedman two-way analysis of variance by rank

Varied parameter	Behavior					
	Fixation		Peering		Strike	
Composition	$\chi^2 = 29.8$	$P < 0.0001$	$\chi^2 = 23.2$	$P < 0.0001$	$\chi^2 = 36.0$	$P < 0.0001$
Le < Bo	$z = -3.91$	$P < 0.0001$	$z = -3.88$	$P = 0.0001$		NS
Le < B&L	$z = -4.05$	$P < 0.0001$	$z = -3.95$	$P < 0.0001$	$z = -3.84$	$P = 0.0001$
Bo < B&L		NS		NS	$z = -3.84$	$P = 0.0001$
Luminance	$\chi^2 = 17.4$	$P = 0.0002$	$\chi^2 = 21.2$	$P < 0.0001$	$\chi^2 = 29.4$	$P < 0.0001$
LG < G	$z = -2.77$	$P = 0.0056$		NS	$z = -2.81$	$P = 0.0041$
LG < B	$z = -3.35$	$P = 0.0008$	$z = -3.62$	$P = 0.0003$	$z = -4.04$	$P < 0.0001$
G < B	$z = -2.47$	$P = 0.0136$	$z = -3.37$	$P = 0.0008$	$z = -3.31$	$P = 0.0009$
Height	$\chi^2 = 22.8$	$P < 0.0001$	$\chi^2 = 24.7$	$P < 0.0001$	$\chi^2 = 27.3$	$P < 0.0001$
S < M	$z = -3.78$	$P = 0.0002$	$z = -3.76$	$P = 0.0002$	$z = -3.54$	$P = 0.0004$
L < M	$z = -3.74$	$P = 0.0002$	$z = -3.24$	$P = 0.0012$	$z = -3.66$	$P = 0.0002$
S vs. L		NS		NS		NS
Width	$\chi^2 = 20.8$	$P < 0.0001$	$\chi^2 = 16.0$	$P = 0.0003$	$\chi^2 = 22.7$	$P < 0.0001$
S < M	$z = -3.45$	$P = 0.0006$	$z = -3.66$	$P = 0.0003$	$z = -3.76$	$P = 0.0002$
L < M	$z = -3.84$	$P = 0.0001$	$z = -3.21$	$P = 0.0013$	$z = -3.91$	$P < 0.0001$
S vs. L		NS		NS		NS
Angular velocity	$\chi^2 = 5.29$	$P = 0.0709$ (NS)	$\chi^2 = 1.31$	$P = 0.5203$ (NS)	$\chi^2 = 7.25$	$P = 0.0266$
S < M					$z = -2.63$	$P = 0.0085$
L < M					$z = -2.82$	$P = 0.0048$
S vs. L						NS

NS, not significant; Le, leg model; Bo, body model; B&L, body-and-leg model; LG, light gray model; G, gray model; B, black model; S, small model; M, medium model; L, large model

χ^2 and P values shown; results of multiple comparison tests (z and P values of Wilcoxon paired-sample text) also shown if significant differences were present

presented with locomotive models (Prete and Mahaffey 1993; Prete and McLean 1996). This agreement suggests that it is possible to use free-moving mantises for qualitative analysis of prey recognition. It would be better to use a free-moving animal in experiments, if the animal showed voluntary movements of its body during perception and the voluntary movements are considered to be important for perception, because it is possible that tethering prevents the normal responses of animals.

We discuss what mantises responded to during fixation and strike when presented with the body-and-leg model. Because the effects of model parameters on peering were similar to those on fixation, we may consider fixation and peering together. All the parameters of the rectangle (luminance, height, and width) affected the rates of fixation and strike. The low fixation rate in response to the large, small, and gray models was presumably responsible for the low strike rate to them. In other words, it is presumed that mantises rarely struck these models because they did not notice them. However, even after fixating on the models, rectangle parameters were presumably important for eliciting strike because the strike/fixation ratio (strike rate per fixation rate) to the large, small, or gray model seemed to be smaller than to the medium and black model (Table 2). On the other hand, the line parameter (angular velocity) only affected strike rates. Hence, we concluded that mantises respond to the rectangle in deciding whether to fixate and to both the rectangle and the lines in deciding whether to strike after fixation. Fixation behavior is presumably mediated by the visual system, which is selectively responsive to the flicker or motion of small target (see following).

Table 2. The strike/fixation ratio of each model for each experiment

Composition	Le	0.00	Bo	0.11	B&L	0.62
Luminance	B	0.70	G	0.38	LG	0.15
Height	S	0.14	M	0.56	L	0.35
Width	S	0.44	M	0.77	L	0.27
Angular velocity	S	0.66	M	0.78	L	0.49

What is the biological function of peering movements during prey recognition? The results of the present study indicate that a black rectangle of medium size with two oscillating lines is effective for eliciting fixation and peering irrespective of the angular velocity of oscillating lines, but that too large, too small, or gray rectangles are not effective. Hence, it seems that the mantis has already assessed the size and luminance of the prey model before fixation and peering. The function of peering may not be assessing the size or luminance of the prey. One possible function of peering during prey recognition is distance estimation, which is the function of peering before jumping. However, in the present study, the amplitude of peering before striking seemed to be too small to estimate distance using motion parallax.

The main function of peering before striking may be detection and orientation of prey. It may be easy to orient to a locomotive prey because of its noticeable motion. Because the amount of motion of a nonlocomotive prey is smaller than that of locomotive prey and the position of moving parts of a nonlocomotive prey is not exactly congruent with the center of the prey, it may be difficult to orient to a nonlocomotive prey. By sweeping the target image across the retinae, peering may assist the orientation. Even though prey shows no movement after fixation, mantises can detect it by peering. However, peering is not necessary for eliciting strike behavior, because the mantis sometimes approached and struck the model without peering. Not only peering, but also approaching, may play an important part in the detection and orientation of prey. During approach, the mantis will receive the image motion on the retinae, and this apparent motion may be useful for detection and orientation of prey.

Finally, let us consider the neuronal mechanism underlying prey recognition in the mantis. Prete and McLean (1996) hypothesized that a movement detector (MD) system similar to that in other orthopteromorph insects exists in mantises. The MD system can explain some but not all our results. In acridid grasshoppers, the MD system mediates escape or defensive responses by recognizing preferentially small-field luminance decrements as objects moving in the environment (O'Shea and Rowell 1976; Rowell and O'Shea 1976a,b; Rowell et al. 1977). The lobular giant movement detector cell (LGMD) in acridid grasshoppers is selectively responsive to the motion of small targets. In addition to LGMD, visual interneurones that selectively respond to small-field motion have also been found in other insect species (Collett 1971; Olberg 1981; Egelhaaf 1985a–c). The small-field motion-sensitive system may explain the previously published data on mantis recognition of locomotive stimuli. In addition, this system is presumably important for fixating a stationary target before peering (Kral 1998) and for detecting prey during peering before striking.

However, it is not clear what mechanism can explain the effects of angular velocity of oscillating lines on strike in the present study. We may suppose a modified system that is sensitive to small-field motion adjacent to the low luminance and appropriate size region in the visual field.

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