# Motion Parallax as a Source of Distance Information in Locusts and Mantids

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*This review article is devoted to results on distance measurement in locusts (e.g., Wallace, 1959; Collett, 1978; Sobel, 1990) and mantids. Before locusts or mantids jump toward a stationary object, they perform characteristic pendulum movements with the head or body, called peering movements, in the direction of the object. The fact that the animals over- or underestimate the distance to the object when the object is moved with or against the peering movement, and so perform jumps that are too long or short, would seem to indicate that motion parallax is used in this distance measurement. The behavior of the peering parameters with different object distances also indicates that not only retinal image motion but also the animal's own movement is used in calculating the distance.*

## INTRODUCTION

The relatively simple principle discussed by Helmholtz (1866) that nearer objects shift at a larger angle than distant ones is used by the insect visual system in distance perception. Due to their immovable eyes, insects are not able to make use of such spatial cues as are provided by convergent eye movements or accomodation with the lens. Further, in contrast to human beings, the usually small interocular distance and the generally slight or nonexistent binocular overlap give insects little or no access to stereoscopic mechanisms. This means that even insects whose eyes have a relatively high capacity for spatial resolution and a relatively large binocular visual field, such as the praying mantis (Barros-

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Pita and Maldonado, 1970; Horridge and Duelli, 1979; Rossel, 1979), probably
have stereoscopic vision only in a range of a few centimeters [e.g., Pfaff and
Varjú (1991); the stereoscopic area might be somewhat greater than the calcu-
lations indicate, especially when movement is involved; see Collett (1987)].

Then, in insects, there is the matter of the characteristics of their compound
eyes: when there are a number of objects in the binocular visual field at the
same time, distance estimation with a stereoscopic mechanism would hardly be
possible, as the density of object images would lead to equivocal object posi-
tions. A possible solution may be given by motion parallax, but only under the
assumption that it is not a matter of a positional mechanism (see below) (Hor-
ridge, 1977, 1986, 1987; Cloarec, 1986).

All in all, motion parallax ought to be an important, if not the most impor-
tant spatial orientation aid in insects. As Demoll wrote back in 1909 about
distance measurement in some moths, "If it is a matter of an immovable object,
the speed with which the image moves over the actual receptors can permit
reception of the absolute distance, as long as the animal's own speed stays close
to constant."

## PEERING MOVEMENT

In some insects, special scanning or peering movements can be observed;
these can be definitely object related. The peering movement sequence can vary
considerably from one insect species to the next. Huber (1961) observed that
when the sphecid wasp *Mellinus arvensis* orients itself visually to jump at an
object of prey, before it jumps, it moves its body somewhat to the right and
left, but without changing the position of the legs; the forward end of the body
performs the maximum lateral movement while the abdominal end is nearly
immobile. Similar peering movements were also seen in the tephritid fruit fly
*Rhagioletis cerasi* shortly before it took off on an aimed flight toward a cherry,
where it lays its eggs (Wiesmann, 1937). Peering was also seen, e.g., in *Tetrix*
grasshoppers, which jump readily and move the head 1–2 mm laterally, and in
the wood cricket *Nemobius sylvestris* (Goulet *et al.* 1981; Jeanrot *et al.* 1981;
Lambin, 1984). Peering can be observed especially well with the naked eye in
gregarious locusts (Kennedy, 1945; Ellis, 1953; Wallace, 1958, 1959) and in
some praying mantids (Zänkert, 1938; Horridge, 1986); these animals show
significant translatory pendulum movements of the head or body of some mil-
limeters in the horizontal plane which can be directed toward an object that is
the target for a strike or jump.

Poteser (1995) used video analysis of praying mantids (*Polyspilota* sp.,
*Tenodera sinensis*) for a detailed study of the motion sequence for object-related
peering just before an aimed jump at a stationary object. The findings show that
peering is a quite variable movement. The basic movement program seems to

be highly variable and is adjusted according to the position and distance of the target (see Fig. 1). The lateral shift of the median–sagittal head axis is not always a straight line but often has forward- or backward-moving components depending on the position of the animal with respect to the target. The lateral component of the peering movement is, however, always dominant.

Peering was first described by Wallace (1959) in the juvenile locust *Schistocerca gregaria*; the locust nymphs often swing the anterior portion of the body some 5 mm from one side to the other, while each of the animal's six legs remains firmly planted on the ground. The lateral movement is produced by extension of the first and second legs on one side of the body and flexion of the first and second legs on the other side of the body; the head and body, however, do not tilt. The dorsoventral body axis remains vertical and the tip of the abdomen does not change position, so that the body long axis turns around a point (the tip of the abdomen) almost like a compass.

Collett (1978) used film recordings to study the precise course of the peering movement in fourth-instar *Schistocerca gregaria*. The findings are shown schematically in Fig. 2. It was found that the insect responds to optomotor stimuli with the attempt to keep the image shifts on the lateral retina as small as possible. Collett concluded from his studies that head turning is controlled by visual inputs in the lateral parts of the retina. During peering, the lateral retina is the only part of the eye that shows no image shifts, meaning that image
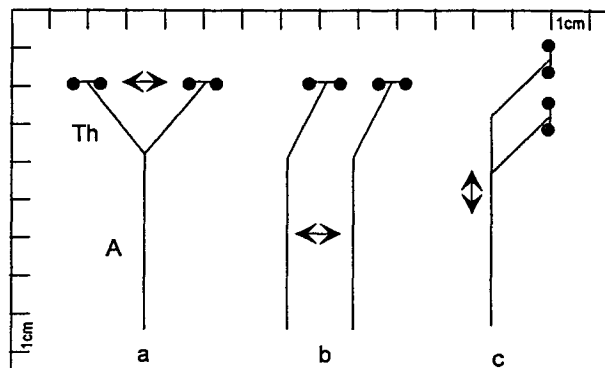


**Fig. 1.** Schematic representation of the isolated various movement elements involved in peering amplitude, as observed during peering toward a stationary object in ninth-instar praying mantis *Polyspilota* sp. Th, thorax; A, abdomen. The peering movement consists equally of a shift in the posterior thoracic joint (a) and a lateral shift of the entire body (b). In some cases, peering at the edge of the object requires a shift along the abdominal long axis (c). The average percentage of components is 51% of a, 42% of b, and 7% of c in peering amplitude.
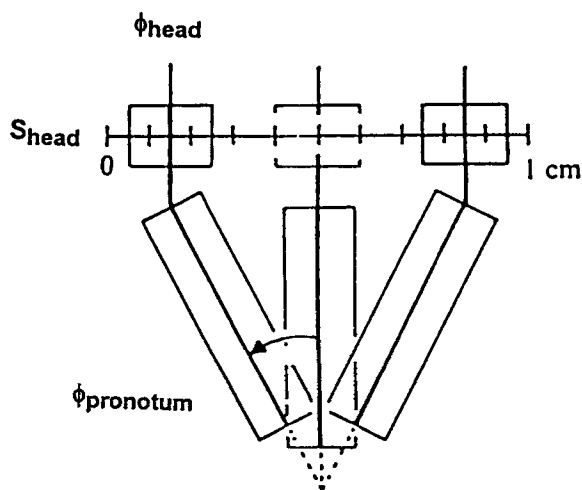
**Fig. 2.** Schematic diagram of peering in *Schistocerca gregaria* locusts. The head moves to compensate for turning of the pronotum ($\phi_{pronotum}$), so that its angular orientation in space remains constant ($\phi_{head} = 0°$) and there are only horizontal head shifts around path S. [From Collett (1978), with permission from The Company of Biologists Limited.]

shifts in these parts of the retina would give immediate information on any head turning. Of course, all this is true only when the surroundings are stationary.

In this context it should be mentioned that peering movements must not always be object related; they can also occur spontaneously, even when there is no visual input (locusts: Chapman, 1955). In both locusts and mantids, peering can even be observed in the dark, which in this case indicates that peering can be triggered by an endogenous peering generator (Collett, 1978; Horridge, 1986).

## DISTANCE MEASUREMENT USING MOTION PARALLAX

Assuming that peering movement gives nearer objects greater retinal relative movement than more distant ones, Wallace (1959) tried to trick desert locusts (*Schistocerca gregaria*) into perceiving a false object distance by moving a square black object in front of a white, unstructured background synchronously but counter to the peering movement (such horizontal object movements cannot be observed in natural environment). The movement of the object counter to the peering movement artificially increased the amplitude and speed of image movement, which was intended to give the peering locust the impression that

the object was nearer than it actually was. The locust in fact let itself be fooled and underaimed its jump; thus Wallace (1959) had the first convincing experimental evidence that locusts could use motion parallax for distance measurement. But his work also made clear that motion parallax can be used for absolute distance measurement only when the target is stationary.

Sobel (1990a,b) took up this subject and had the advantage of modern video technology for precise quantification of the peering-jump behavior in juvenile locusts (*Schistocerca americana*). He used the takeoff speed, which is monotonically dependent on object distance, as a measurement for the accuracy of this distance measurement; he was thus able to demonstrate and to quantify precisely under- and overestimation of distance with lateral movement of the object with or against the peering movement (Fig. 3). If the object was moved very precisely with the peering movement to simulate a very distant object, the locust lost interest in the object, turned away, and looked for a new object.

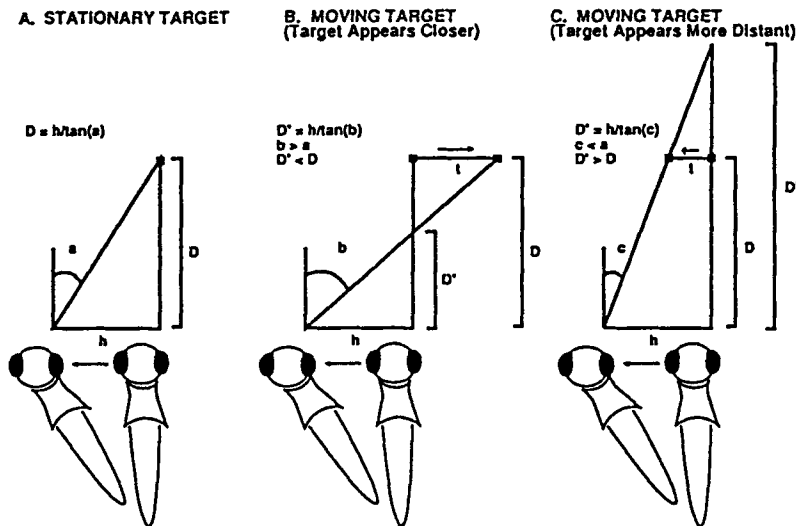It was recently shown that young mantid larvae (*Tenodera sinensis, Polys-*



Fig. 3. (A) Locust *Schistocerca americana* makes a peering movement *h* toward the left in front of a stationary object at distance *D*. The angular position of the object changes from the original 0° to angular position *b*. (B) While the locust is making a peering movement amounting to *h* to the left, the object is moved in the opposite direction. Due to the greater change in angular position, the final angle is *b* degrees and the object appears to be nearer (*D'*) than it actually is. (C) While the locust makes a peering movement amounting to *h* to the left, the object is moved in the same direction, but by the smaller amount *t*. The slighter change in the angular position results in a smaller final angle of *c* degrees and the object is accordingly perceived as being farther away than it actually is. [From Sobel (1990), with permission from Springer-Verlag.]

*pilota* sp.) with distinct peering-jump behavior, i.e., the ability to determine jump distance precisely, tended to perceive distances incorrectly when a square black object is moved laterally during the peering movement (Poteser and Kral, 1995). Based on the actual jump distance, a conclusion was drawn as to the accuracy of distance estimation. Movement of the object against the direction of peering could lead to jumps that were too short, while movement of the object in the same direction as peering could produce jumps that were too long (Figs. 4 and 5, Tables I and II). Countermovement of an object that was well outside of the jumping range could also induce the animal to jump. As was to be expected, the result was a too-short jump that ended in the moat (see Figs. 4 and 5). This was the first definite indication that mantids can also use motion parallax for distance measurement. But it was also found that motion parallax apparently can be used only from a certain distance onward, and only for objects with relatively large contrast limits. Mantids like *Tenodera sinensis* and *Polyspilota* sp. rarely show distinct peering movements at objects (stationary or mov-
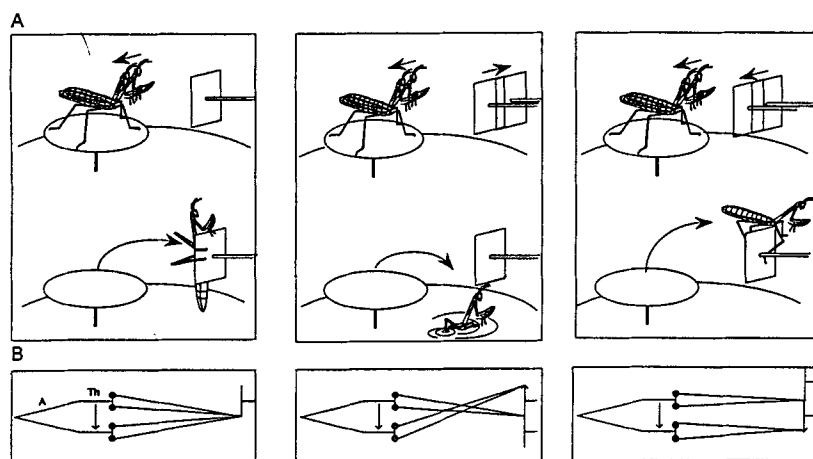


**Fig. 4.** (A) Semischematic diagram illustrating peering-jump behavior of third-instar praying mantis *Tenodera sinensis* with three object conditions. Left: With a stationary object, the mantid lands safely on the vertical edge. Middle: With object movement counter to peering movement, the mantis underjumps and lands in the water. Right: If the object is moved with the peering movement, but at a somewhat lower speed, the mantid overestimates the distance and can just manage to grasp the edge of the object while jumping over or past it, and is usually flipped behind the object. (B) Schematic diagram of the changes in angle with sightline from the edge of the object to the eye. The body positions (head with eyes, thorax, Th; abdomen, A) correspond to the beginning and end of a single peering movement, respectively. The radial organization of the eye makes the amount of change in the visual angle a measure of image shift. When the object is moved counter to the peering movement, the angle in one eye increases compared to peering toward a stationary object. When the object is moved in the same direction, the angle and thus the image shift are smaller.

A

Target distance of 3.0 cm
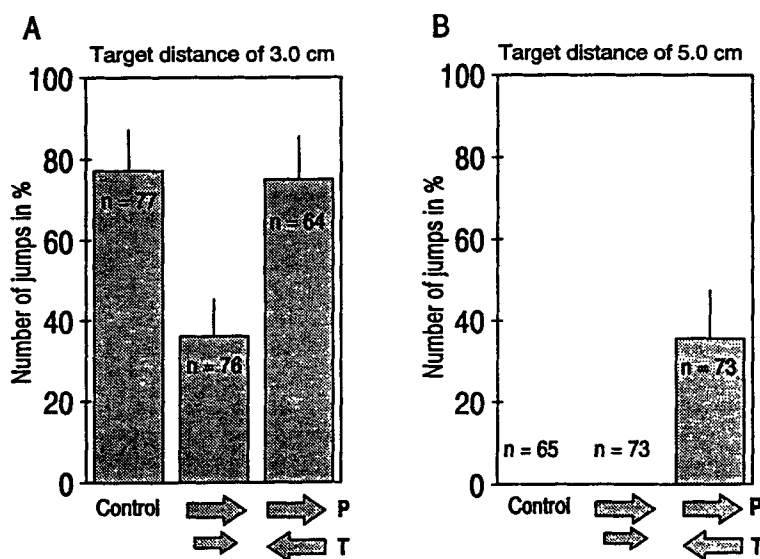
B

Target distance of 5.0 cm

Fig. 5. The diagrams show the average number of jumps towards an object as a percentage (+SD) after the third-instar praying mantis *Tenodera sinensis* has peered at an object that may be stationary (no arrow), or that was moved against peering movement (arrow in opposite direction), or that was moved in the same direction (arrow in same direction). (A) Object within jump range; (B) object outside of jump range. The vectors indicate direction and speed of movement. [After Poteser and Kral (1995), with permission from The Company of Biologists Limited.]

ing) in their immediate vicinity, i.e., within striking range. Here stereopsis may play a decisive role, but it seems that it is limited for localization of moving prey (Rossel, 1983a,b, 1986).

The findings for locusts and mantids lead to the question whether both eyes

Table I. Jump Distance with Movement of Object Counter to Peering Movement in Third-Instar Praying Mantis *Tenodera sinensis*

| | Mean ± SD (mm) | |
|---|---|---|
| Target distance | Jump distance[a] | Difference between jump distance and target distance |
| 42.9 ± 2.24 | 35.4 ± 5.02 | 7.5 ± 3.6 (17.8 ± 8.9%) |

[a]Video analysis shows that the ballistic course of the aimed jump is interrupted by the elevated object, while a misjump ends only when the animal touches the surface of the water. Accordingly, the intended jump distance is somewhat shorter than that measured here (the direct line between takeoff point and water landing).

Table II. Jump Behavior with Movement of the Object in the Same Direction as Peering
Movement in Third-Instar Praying Mantis *Tenodera sinensis*[a]

| Mean target distance (mm ± SD) | Hard landing on edge of object[b] (%) | Landing behind object[c] (%) |
|---|---|---|
| 42.9 ± 2.24 | 47.4 (=9 jumps) | 52.6 (=10 jumps) |

[a]$N$ = 19 animals.
[b]Overestimation of distance.
[c]Distinct overestimation of distance.

are required for distance measurement using motion parallax, or whether a mon-
ocular measurement would be possible. Wallace (1959) showed that locusts with
one occluded eye were nonetheless able to use peering to identify positively the
nearer of two target objects. This led the author to believe that the motion-
parallax mechanism was monocular. Sobel (1990a,b), however, demonstrated
a distinct distance overestimation due to increased takeoff speed in locusts with
one occluded eye [the lateral eye region had to remain free; in this context see
Collett (1978)]. There are contradictory findings from studies of grasshoppers
(*Phaulacridium vittatum*) in a natural environment which were fully blinded in
one eye and in spite of their handicap made aimed jumps (Eriksson, 1980).

Sobel (1990a,b) draws the simple conclusion from his findings that locusts
with one eye receive less motion-parallax information, and the motion parallaxes
in both eyes are either added or averaged (Fig. 6). The author sees in this
plausible explanation of a binocular interaction of the motion-parallax signals
the advantage that sensitivity is increased even for the slight image shifts that
occur with large object distances. But it could also be that the visual system is
calibrated to use information from both eyes since the information is there under
natural conditions. Walcher and Kral (1994) followed this question up in mantids
by studying the peering-jump behavior in larvae that were completely blinded
on one side, or frontally on both sides, or laterally, or whose foveae had been
destroyed. It was found that mantids who had undergone anyone of these treat-
ments were still capable of a relative distance measurement as shown by the
fact that they could localize the narrowest site between the platform and the
wall of the arena (the rate of flight reactions—forward stretching of the body—
at the narrowest site was greater with frontal visual input than with lateral visual
input). But mantids were not able to jump, which suggests that they were not
capable of making absolute distance measurements. Apparently, both locusts
and mantids need two fully intact eyes for absolute distance measurement. The
possibility of binocular processing of motion-parallax signals has also been dis-
cussed for the bulldog ant *Myrmecia nigriceps* (Eriksson, 1985).

The morphology alone of the visual systems of locusts and praying mantids
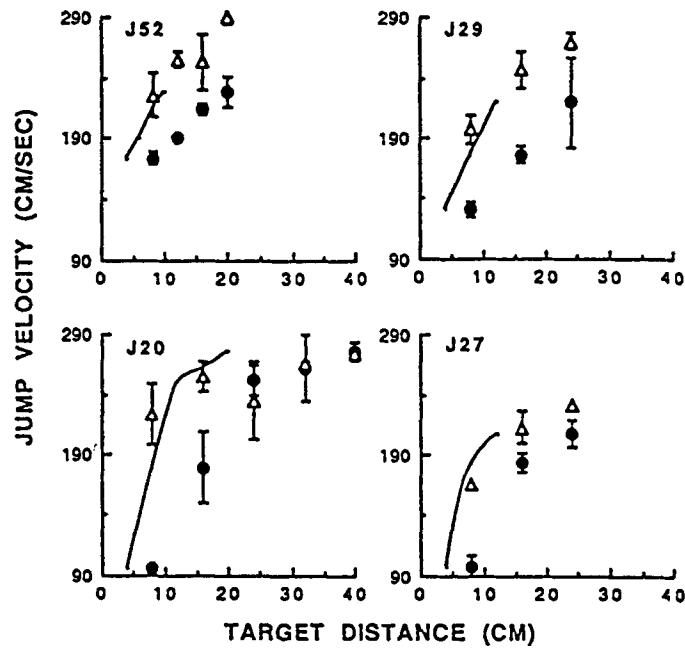
**Fig. 6.** The diagrams show the relationship of jump velocity to object distance in monocular *Schistocerca americana* locusts. J52—frontal region of left eye totally occluded; J20, J27, J29—frontal area of right eye occluded. The filled circles show the reference data for visually intact locusts; the open triangles are for the monocular animals. All symbols stand for a mean of three jumps ±1 SE. The lines represent the jump velocity that would be expected if the hypothesis mentioned in the text were true that the motion parallax signals from both eyes are added or averaged. [From Sobel (1990), with permission from Springer-Verlag).]

suggests binocularity in distance measurement, even if locusts do not at first glance give this impression, having as they do the distinctly sideward-directed eyes found in most herbivorous insects rather than the remarkably large, extremely forward-looking eyes found in predatory mantids (Maldonado and Barros-Pita, 1970; Rossel, 1979; review by Land, 1981; Köck *et al.*, 1993). Both insects have a distinctly binocular visual field and in both (i.e., in locusts as well, even if the homogeneous facet pattern does not suggest this), the frontal ocular region is equipped with greater spatial resolution (interommatidial angles $\Delta\phi$: 0.6° vertically, 1.8° horizontally), whereas in locusts, the fovea is vertically extended on the horizontal equator in accordance with the narrow frontal ocular region [this can be seen well with the pseudopupil; *Schistocerca gregaria* (Land, 1981; see also Autrum and Wiedemann, 1962)]. But this may have nothing to
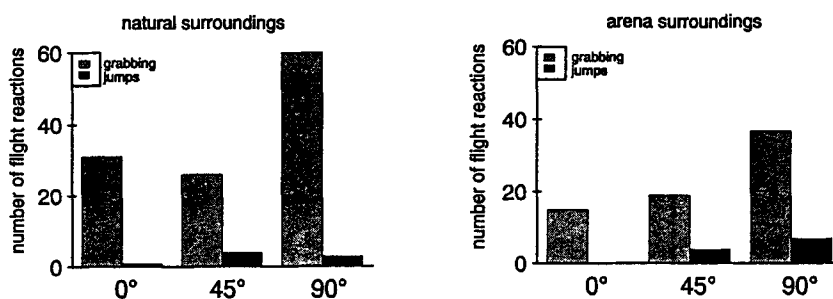
Fig. 7. Peering and flight activity in praying mantis (*Mantis religiosa*) with respect to horizontal, diagonal, or vertical patterns on stationary targets. Trials lasted for 45 min for all animals. In the field (highly structured background in constant motion) there is a tendency to favor the vertical objects; this is seen in the frequent grasping movements. Jump behavior was hindered by wind (last larval stage and adult stage; 18 animals). Under laboratory conditions with a homogeneous white background, attractiveness generally depended on the inclination of the object seen in the increasing number of jumps and also in the number of grasping attempts with inclination (adult stage, 11 animals).

do with peering; it may rather be for detecting events on horizon or because during flight less vertical than horizontal image motion occurs. In mantids the fovea forms a distinct mediofrontal region, $\Delta\phi = 0.6°$ (Rossel, 1979).

The similarities and differences in design and in the optical qualities of the eyes are seen to some extent in the peering behavior. The significance of the lateral ocular region as a stabilizing area for peering movements in locusts was mentioned above (Collett, 1978). In praying mantis as well, the lateral ocular region seems to have a certain significance in this respect, as animals with laterally occluded eyes are not capable of absolute distance measurement and do not jump (Walcher and Kral, 1994). As far as binocular input is concerned it seems that both locusts and mantids, when they have fixed a target object whose contours usually have a vertical orientation (see mantid; Fig. 7), perceive it with both eyes simultaneously and attempt during the peering movement to keep the object completely or as far as possible in the binocular visual field (Fig. 4B, left). In locusts, this is true only at greater distances owing to the position and form of the eyes and the related characteristic degree of binocular overlap; in mantids, in contrast, this holds only for the nearer distances, but outside of the optimal stereoscopic region, i.e., somewhat more distant than the length of the striking arms (see sketch in Fig. 8). Object-oriented locusts do in fact often jump more than 20 times their body length, while the maximum for mantids is about 5 body lengths.

As far as special regions with greater spatial resolution in the frontal ocular region in insect species are concerned, it can be said for mantids that the frontal eye region (fovea) apparently plays a crucial role in distance measurement
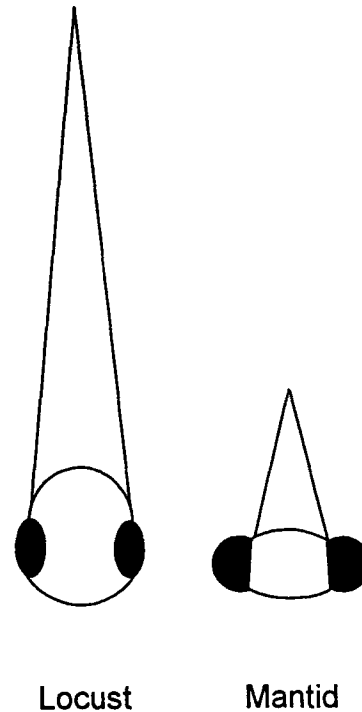
Fig. 8. Schematic diagram should illustrate that the
minimal *binocular* object distance is greater in locusts
than in mantids (not true to scale).                    Locust        Mantid

involving motion parallax. Animals whose fovea was destroyed through pho-
todegeneration with sulforhodamine (Leitinger, 1994; Leitinger *et al.* 1994)
were no longer capable of absolute measurement of the distance to a stationary
object via peering movements. These animals did not make object-related jumps.
Remarkably, this was also true for mantids whose foveas had partially regen-
erated after molting (Walcher and Kral, 1994). As yet, there are no comparable
studies on the acute zone in the frontal ocular region in locusts.

## DISTANCE–MEASUREMENT STRATEGIES USING MOTION PARALLAX

The question arises as to possible strategies used to obtain distance mea-
surement via motion parallax. Here we find three basic possibilities: (i) with
uniform peering movement, retinal image movement changes with object dis-
tance; (ii) peering movement so changes with distance to the object that the
retinal image movement has the same value for every distance; and (iii) when
peering speed is constant and peering amplitude changes continuously with dis-

tance, and vice versa, both the retinal image speed or retinal image displacement and the animal's own movements are computed.

In the jumping range (up to 30 or 40 cm) of locust larvae, both Collett (1978) and Sobel (1990a,b) found a modest increase in peering amplitude and peering speed with object distance, especially when peering preceded a jump (Fig. 9). Collett noticed here that during a peering series (up to 11 peering movements), the amplitude usually increased during the first few peering move-
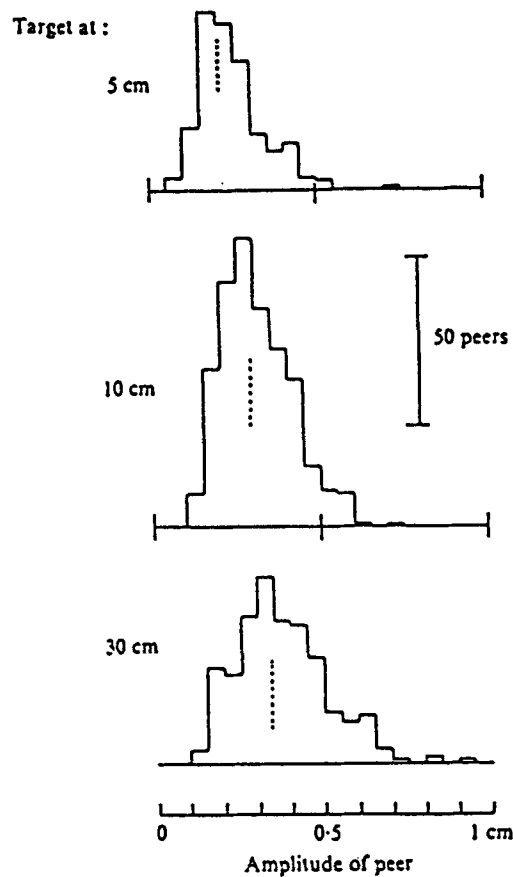


Fig. 9. Effect on object distance on peering amplitude in
fourth-instar *Schistocerca gregaria* locusts. The diagrams
show an increase in the mean amplitude of 0.21, 0.29,
and 0.35 with object distances of 5, 10, and 30 cm. [From
Collett (1978), with permission from The Company of
Biologists Limited.]

ments and then remained constant. This led the author to assume that locusts might measure the retinal image speed during a peering movement and, when it is too small, increase the amplitude of the next peering movement. The possibility arises that distance is not measured via an image shift that is created by a certain head movement but, rather, via the amplitude that is elicited by the largest peering movement. An increase in peering amplitude could also lead to a signal improvement.

If distance was to be measured as a function of peering amplitude, then image motion should be constant. However, Sobel (1990a,b) found both a
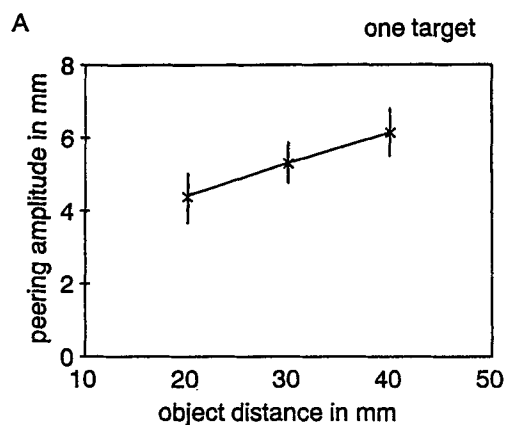


Fig. 10. These diagrams show, in the third to fifth-instar of praying mantis *Tenodera sinensis*, the dependence of the mean amplitude ($\pm$SD) of peering immediately before a jump on the distance to a stationary object (A) within jump range (modified after Poteser and Kral, 1995). (B) Relationship of the peering amplitude and the distance to stationary objects well beyond jump range. (C) Dependence of the peering velocity on the distance to stationary objects well beyond jump range. In both cases, maximum (max) (without extreme values), average (m), and minimal (min) values are shown. The upper diagrams show the results from a series in which two objects were offered at different distances, where the smaller of the two was always 5 cm. The lower diagrams show the results from trials in which only one object was presented. One or two objects were used in an experiment to show up any differences with simultaneous or successive distance comparison. With two objects, an immediate distance comparison is possible, which could have had an effect on peering parameters. The courses of the parameters with increasing distance did not, however, tend to deviate, which indicates that distance measurement does not require the simultaneous presence of a reference object.

decrease in image motion and an increase in peering amplitude so that the computation requires knowledge of both sensory input and motor output.

Our own work on third- to fifth-instar praying mantis *Tenodera sinensis* shows that within the jumping range (about 5 cm), there is a correlation between the peering amplitude immediately before a jump and the object distance, i.e., the peering amplitude increases with distance (Fig. 10A). But at this range there is no significant relation between peering speed and object distance, i.e., about the same peering speed was always measured for different object distances. Within jumping range, however, peering amplitude changes not only with object distance, but also when the object is so moved as to simulate a different distance (Poteser and Kral, 1995). Moving the object against the peering movement to simulate a lesser distance leads to a decrease in amplitude. It is our opinion that when mantids use movement parallax to measure the distance to the target object
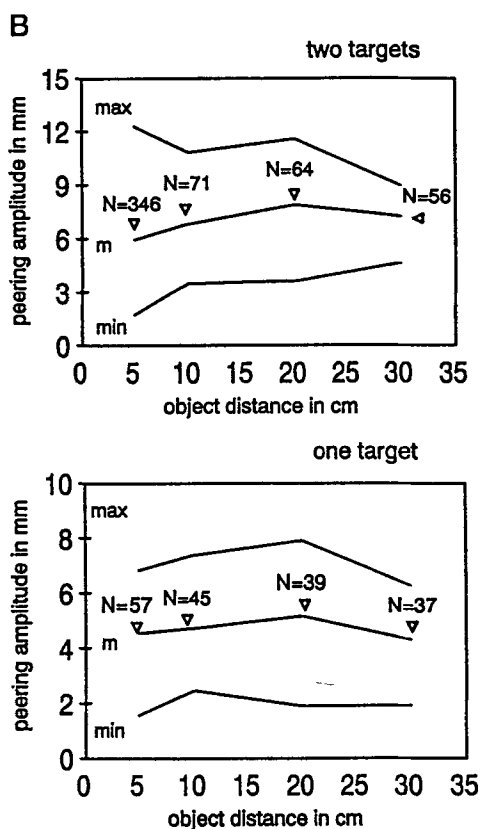


Fig. 10. Continued.
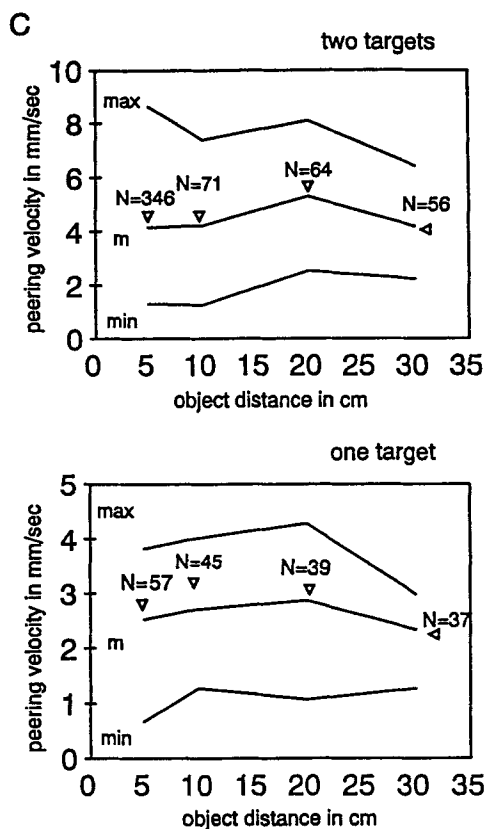
C

two targets



one target



Fig. 10. Continued.

of a jump, both the retinal image speed and the animal's own movement are included in the calculation, whereby image movement (speed) may control peering movement (amplitude). This, however, would assume a complex regulatory mechanism that could involve the reafference principle (von Holst, 1969). To understand this, we need to know about the sensorimotor couplings and their hierarchies. Information from the proprioceptive system, such as from the neck hairs (Mittelstaedt, 1957; Liske and Mohren, 1984), would also have to be taken into account.

If we look at the relationship in third to fifth *Tenodera sinensis* instars of peering parameters to the distance to stationary objects that are not within jumping range but at a middle or greater distance, we see the following, which is summarized in the diagrams in Figs. 10B and C: the minimal peering amplitude (peering speed) turns out to have relatively sharp limits, while the maximal

parameters are variable. This could be because the lower limit of the peering parameters is determined by physiological parameters, while the upper limit is determined by the animal's motivation. The explanation for the course of the maxima and minima and in turn of the average parameters could be as follows: to permit the peering mantid a minimal retinal image shift, the minimal peering amplitude is raised in the middle distance range (>5–15 cm). But from a certain distance on, an increase in peering amplitude, no matter how great, will not produce any real change in the image shift (Fig. 10B) (exponential decrease in image shift with increasing distance). This is probably why the minimal peering amplitude and peering speed stay about constant at the elevated level with large object distances (>15 cm). The decrease in maximal peering parameters with large distances could possibly be due to decreasing motivation; the more distant objects no longer have any significance as means of escape. All in all, this should lead to the measured narrowing of the range of peering parameters with large distances (Figs. 10B, C). It can hardly be expected that peering at the objects offered here at distances greater than 20 cm, i.e., well beyond jumping range, would provide the mantid larvae with detailed information on distances, but peering could place objects at this distance range in the "background," which probably begins at about 15 to 20 cm in the third to fifth instar. Figure 11 is a schematic graphic summary of the relationship between peering movement and *stationary* object contours that are offered in target objects in the near, middle, and remote distance ranges. In this context, we do not have any evidence that peering is needed for judging distance to moving prey.
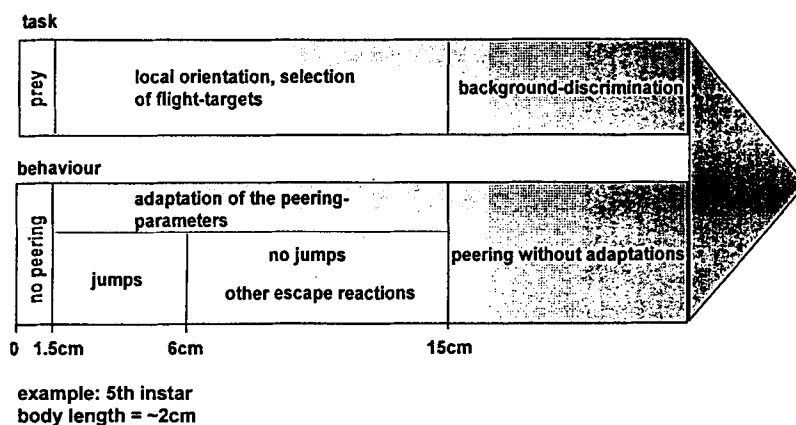
task

| | | |
|---|---|---|
| prey | local orientation, selection of flight-targets | background-discrimination |

behaviour

| | adaptation of the peering-parameters | | |
|---|---|---|---|
| no peering | jumps | no jumps<br>other escape reactions | peering without adaptations |

0  1.5cm            6cm                              15cm

example: 5th instar
body length = ~2cm

Fig. 11. Schematic diagram of the relationship between peering and object distance range in the fifth instar of *Tenodera sinensis* praying mantis.

## FIGURE-GROUND DISCRIMINATION USING MOTION PARALLAX

An important point that has not yet been discussed in connection with motion parallax as an aid to orientation is figure-ground discrimination, which is a necessary ability for locomotion in a structured environment if obstacles are to be avoided and landing targets safely reached. Collett and Paterson (1991) were the first to tackle this problem in locusts, *Schistocerca gregaria*. Their main findings were that (i) locusts can unambiguously recognize the edges of a stationary object located in front of an identically structured stationary background based alone on the speed contrast that develops during the peering movement through the difference in the retinal image speed of object and background, and (ii) locusts can use motion parallax to determine object distance independent of the relative motion between object and background.

We were recently able to show that praying mantids also have this ability. Peering mantids could identify a black, square object in front of a black-and-white striped background even when the object and background were identical with respect to contrast, brightness and contours. Under these same conditions, the animals were also reliably capable of finding the nearest of a number of identical objects simultaneously present in the visual field. We did not attempt to determine whether under these conditions mantids would also be able to determine the absolute distance to more remote objects.

## OUTLOOK

The findings presented here on the peering behavior of locusts and mantids indicate that many questions remain to be answered before anything definitive can be said about the motion-parallax mechanism. Some of these questions, such as binocularity, were touched upon briefly.

Another open question is whether the parallax measurement is based on positional mechanism or speed [see honeybee (Srinivasan *et al.*, 1991)]. As we have said, the relevant parameters for the peering movement are amplitude, duration, and speed. For the calculation to obtain the value for distance (probably taking the animal's own movement into account), these parameters must be transformed into neuronal activity patterns. This would be possible, on the one hand, if the persistence of the image of the edge of the object was measured in the different regions of the eye (positional mechanism); on the other hand, the compound eye is already divided into individual parts by the visual angle of the ommatidia. The information on parallax thus could be contained in the time that elapses between the activation of the sensory cells of neighboring ommatidia or rows of ommatidia.

Mantids seem to use at least two cues in visual processing of spatial infor-

mation, namely, stereopsis and motion parallax: the former for detecting moving objects such as prey and the latter for stationary targets.

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