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Relationship between body size and spatial vision in the praying mantis – an ontogenetic study

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Abstract

Praying mantids determine prey-capture distances with the aid of binocular mechanisms and estimate distances to stationary objects such as jump targets with the aid of retinal image velocity. The latter mechanism makes use of the fact that the retinal image velocity resulting from translational self-motion (peering movements) is inversely proportional to the distance of the target object. The present study shows that for South African mantids *Polyspilota* sp., the interocular distance, an aspect of binocular vision, and the amplitude and velocity of peering movements, increase over the course of postembryonic development from 2nd instar to adult. In both cases there is a close positive correlation with body size. Calculated convergence angles and retinal image velocities indicate an improvement in absolute depth perception with increased body size. This is adaptive, because it allows the range of visual depth perception to increase with body size, strike distance and jumping capability, throughout the growth of the insect, from 2nd instar to adult.

Key words

praying mantis, *Polyspilota*, postembryonic development, body size, depth perception, peering, vision

Introduction

Body size varies with ontogeny and among individuals, and correlates with the size and capability of sensory organs. This is especially evident in the case of insect compound eyes, which typically increase dramatically in size through development (Zollikofer *et al.* 1995, Spaethe & Chittka 2003). Size disparity in the morphology and effectiveness of sense organs can influence fitness. If smaller conspecifics have a less effective sensory system due to smaller sense organs, the ability to perceive important environmental stimuli could be impaired. This could have negative effects on activities such as predator avoidance, finding food, prey detection and mate selection. For larger individuals, enhanced sensory perception due to larger sensory organs could aid survival. For example, larger bumblebees have a better visual system and ability to detect odors due to larger eyes and longer antennae. This results in greater food-gathering efficiency for larger individuals (Spaethe & Chittka 2003, Spaethe *et al.* 2007). Larger individual red wood ants have larger compound eyes, which improves foraging efficiency (Bernstein & Finn 1971). Likewise, larger *Pimpla* parasitoids are better able to locate hosts by means of vibration soundings (Otten *et al.* 2001).

Enhanced sensory performance could also be used to compensate for disadvantages associated with increased body size. For example, larger moths are detected earlier by bats. However, larger individuals are better able to hear bats, and hence compensate for greater

risk by enhanced hearing ability (Surlykke & Filskov 1999). There are also examples of smaller individuals that have greater sensory capabilities than their larger conspecifics. This is strikingly illustrated in the case of longicorn (Cerambycidae) beetles (Fukaya *et al.* 2004), where smaller males are more sensitive than larger ones to female sex pheromones. The authors hypothesize that this serves to compensate for the fact that the females prefer larger males.

Hemimetabolous insects increase in size with each molt, and this is associated with growth of their sensory organs. This is especially evident with regard to the compound eyes, as has been shown for instance, in cockroaches (Nowell 1981) and Hemiptera (Settembrini 1984). In the case of mechanosensory systems, the number of campaniform sensilla in cockroaches (Ridgel *et al.* 2003) and the number of hairs on hair plates in locusts (Newland *et al.* 1995) increase with each molt. Such increases are generally associated with enhanced sensory capabilities.

However, there can also be a negative correlation between body size and sensory performance, as illustrated by the escape behavior of crickets (Dangles *et al.* 2007). Younger, smaller individuals react more quickly to assailants than do larger, older conspecifics, due to shorter nerve pathways. However, age-related living circumstances modify the effect of the disparity: despite a better mechanosensory system, the survival chances of young crickets are no greater than those of their older conspecifics, because younger crickets have more predators. Overall, comparative findings indicate that the relationship between body size and sensory performance is not always based on simple principles, and that a complex interaction of physiological, developmental, behavioral, ecological, biogeographic and evolutionary factors must be taken into account (see Whitman 2008).

Predatory insects, including mantids, often determine prey-capture distances with the aid of binocular triangulation. In this mechanism, distance is computed by measuring the convergence angle formed by the lines-of-sight from ommatidia of the left and right eyes (Baldus 1926; Barrós-Pita & Maldonado 1970; Wehner 1981; Bauer 1981, 1985; Kral 1999; Kral *et al.* 2000). In contrast, locusts, grasshoppers and mantids usually estimate distances to stationary objects by means of peering (Collett 1978; Eriksson 1980; Horridge 1986; Sobel 1990; Collett & Paterson 1991; Kral & Proteser 1997; Kral 2003, 2008a,b, 2009).

Peering is a common behavior in orthopteroid insects, and consists of standing in one location while moving the head and forebody back and forth, usually laterally and horizontally, along a line transverse to a line between the insect and the distant object. However, a few insect groups may also move backwards and forward during peering, which can add a vertical component. This causes

an image of the target object, such as the point of a jump or of an item to be grasped, to move across the eyes. Due to the translational components of the peering movements, the velocity of image motion is inversely proportional to the distance of the object; this relationship is used by insects for distance determination.

In the present research, the relation between body size and distance determination using peering movements, and using the convergence angle between the two compound eyes, has been studied for the first time in praying mantids of different ages. Our goal was to investigate whether and in what way, increasing body size alters spatial vision during the course of postembryonic development, and to what extent this has biological relevance in terms of prey-capture and locomotory behavior.

Methods

Experimental insects and rearing conditions.— The present investigations were conducted with the praying mantis *Polyspilota nov. spec. ex: Natal* (determination by R. Ehrmann, see Ehrmann 2002). The individual mantids were kept in separate rearing containers, with a 12h:12h light-dark cycle, illumination of 800 to 1000 lux, relative humidity of 50% to 60%, and temperatures of 26 to 28 °C. Until the 5th instar the mantids were fed with live fruit flies (*Drosophila melanogaster*); subsequently they were fed with live common houseflies (*Musca domestica*), *Calliphora* flies, and nymphal and adult house crickets (*Acheta domesticus*). The interior surfaces of the container walls were sprayed with water daily.

Morphometry.— We defined body size as the body length, measured from the front of the head to the tip of the abdomen. The head width was defined as the distance between the most lateral parts of the curves of the two eyes; the line of measurement was perpendicular to the longitudinal axis of the body. The distance from the center of one compound eye to the center of the other was determined by measuring the distance between the most anterior parts of the curves of the two eyes (where the ommatidia are facing directly forward). This is defined as the interocular distance. The convergence angle (α) between the left and right compound eyes was calculated from the interocular distance and the target distance by using the formula $\alpha = 2\arctan(b/2d)$ (see Fig. 1A). All measurements were conducted on individuals anesthetized with chlorethane (= monochloroethane) 3 d after molting. Measurements were made with a precision of 0.1 mm, by using a stereo microscope (Wild M400, Heerbrugg, Switzerland) and an ocular micrometer, as well as calipers in the case of larger animals.

Behavioral investigations.— For the behavioral experiments we used mantids which had developed normally during the first 3 d following molting. We placed each animal separately on a round island in a circular white arena, located on a laboratory table. The following island and arena diameters were used: 2 cm and 22 cm respectively, for 2nd and 3rd instars; 3 cm and 33 cm for 4th and 6th instars; and 6 cm and 66 cm for the last (9th) nymphal stage and adults. The arena was evenly illuminated by a halogen lamp (~1500 lux). The island

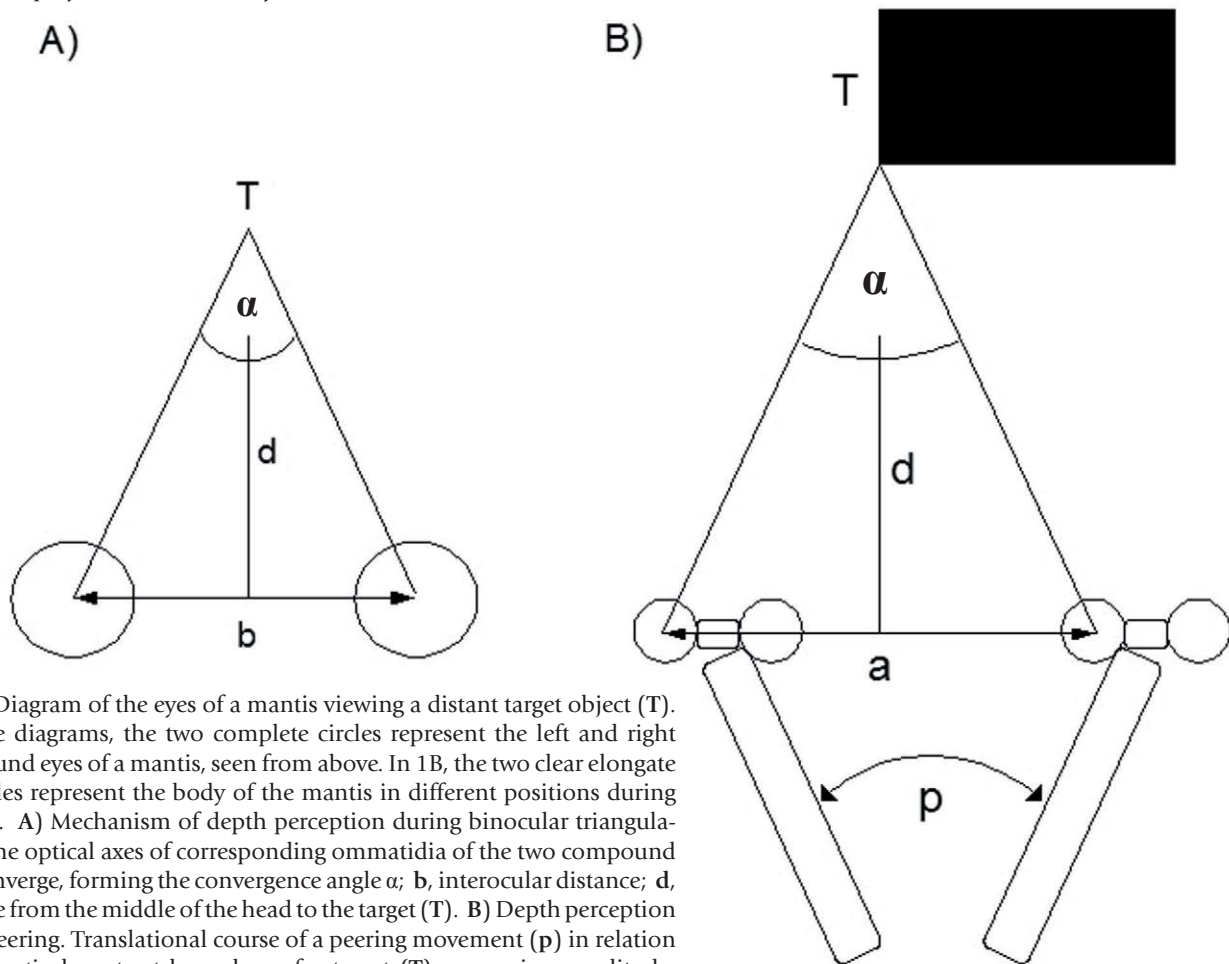


Fig. 1. Diagram of the eyes of a mantis viewing a distant target object (T). In these diagrams, the two complete circles represent the left and right compound eyes of a mantis, seen from above. In 1B, the two clear elongate rectangles represent the body of the mantis in different positions during peering. **A)** Mechanism of depth perception during binocular triangulation. The optical axes of corresponding ommatidia of the two compound eyes converge, forming the convergence angle α ; **b**, interocular distance; **d**, distance from the middle of the head to the target (T). **B)** Depth perception using peering. Translational course of a peering movement (**p**) in relation to the vertical contrast boundary of a target (T). **a**, peering amplitude; calculation of the retinal image velocity is described in the text.

was situated in a Petri dish filled with water, a dish that covered the bottom of the arena. The mantids could leave the island only by jumping. A black rectangular bar made of cardboard was provided as a target object against a homogeneous white background. When viewed from the edge of the island, the black bar had a horizontal extension of 67° and a vertical extension of 34° for all island/arena combinations.

After being placed on the island, each mantid began to scan its surroundings. The mantids usually quickly noticed the vertical black-white contrast boundary of the target object, as was evident from the fact that they positioned themselves at the edge of the island and executed precisely directed peering movements. The distance from the head of the mantid to the object (midpoint) was 15 mm to 50 mm, depending upon the age of the animal (see Table 2). Preliminary experiments were carried out in a 66-cm arena with 10 to 80-mm object distances, in order to determine the most suitable jump distances for the various age levels.

We recorded the peering behavior with a video camera (Sony CCD/RGD, Tokyo, Japan), using an S-VHS hi-fi recorder (SVO9620P, Sony). The recordings were displayed on a 14-inch color monitor (PVM-14440QM Sony) and a PC screen. The peering movements were analyzed based on the digitized video recordings. In order to determine the peering amplitude (in mm), we measured the distance between the turning points of the movement. Based on the recording speed in frames/second, we then calculated the duration of the peering movement by counting the corresponding frames in the video recording, which showed the lateral movement of the head from one endpoint to the other. The peering amplitude and duration were used to determine the peering velocity in mm/sec. In the case of repeated peering movements, the largest movement was always analyzed. We calculated the velocity of the retinal image motion of the target object (in deg/sec) from the convergence angle α and the peering velocity, by using the formula $\alpha = 2 \arctan(a/2d)$ (see Fig. 1B). A statistical analysis and a graphical representation of the data were carried out with the aid of GraphPadPrism, version 4 (San Diego, CA).

Results

General remarks.— Under our rearing conditions, *Polyspilota* sp. passed through nine nymphal stages to the adult stage in 3 mo. The 2nd, 3rd and 4th nymphal stages each lasted ~ 7 d. Subsequent nymphal stages were more prolonged, from 1.5 times longer to 3 times longer for the last nymphal stage. Morphometric data were obtained for all nymphal stages and adult animals, with the exception of the 1st nymphal stage, which lasts only a few minutes. However, we were unable to collect enough behavioral data for

statistical evaluation for the 5th, 7th and 8th nymphal stages, due to a general decrease of movement activity beginning in the 5th stage. Possible explanations for this lull in activity include the effects of weather conditions, intrinsic factors, or developmentally-related changes in the concentration of biogenic amines, which have been demonstrated for *Polyspilota* (Germ 1997).

Morphometric data.— From the 2nd nymphal stage to the adult stage, the average body length of *Polyspilota* increases eightfold. This is associated with an almost sixfold increase in head width. The increase in size varies from stage to stage (Table 1). The greatest increase in body length occurs between the 3rd and 4th nymphal stages, and between the last nymphal stage and the adult stage, while the greatest increase in head width occurs from the 2nd to the 5th nymphal stage. As head width increases, the interocular distance also increases fivefold (Fig. 1A). The relationship between head width and interocular distance varies for the different age levels. One reason for this is that the eyes, which are initially almost spherical, become flattened anteriorly in the last nymphal stage.

Behavioral data.— Video recordings confirm that peering movements took the form of side-to-side movements of the head and upper part of the body, performed while the mantid remained standing in one location without locomotion. The movements were translational in the horizontal plane, and directed toward only one vertical edge of a bar, or first to one and then to the other, vertical edge. During the peering movements, the line of sight was kept perpendicular to the direction of movement; this was achieved by means of compensatory counter-rotation of the head with respect to the prothorax. The pitch and roll angles of the head were also kept constant (see Fig. 1B).

From the 2nd nymphal stage to the adult stage, the mean peering amplitude increased 5.6 times, while the mean velocity of the peering movements increased ~ eightfold. The data relate to the mean jump distance in each case (Table 2). Both peering amplitude and peering velocity correlated with body length (Boltzmann sigmoidal curve: $R^2=0.998$, $R^2=0.999$ respectively). The relationships among these parameters vary in the different developmental stages (see data in Tables 1 and 2). Since the velocity of the peering movements increases as the amplitude increases, the duration of the movements remains largely constant throughout the entire course of postembryonic development.

Discussion

Our results confirm that in *Polyspilota* sp. mantids, the interocular distance increases over the course of ontogeny. This alters the

Table 1. Morphological dimensions of *Polyspilota* sp. in mm; $N=5$ animals per stage.

Instar	Mean body length (\pm s.d.)	Increase from previous stage	Mean head width (\pm s.d.)	Increase from previous stage	*Mean interocular distance (\pm s.d.)	Increase from previous stage
2	8.7 \pm 0.4	—	1.3 \pm 0.1	—	1.1 \pm 0.0	—
3	10.6 \pm 0.6	1.2	1.8 \pm 0.1	1.4	1.4 \pm 0.0	1.3
4	16.2 \pm 0.6	1.5	2.6 \pm 0.1	1.4	1.9 \pm 0.0	1.3
5	20.2 \pm 1.9	1.2	3.7 \pm 0.1	1.4	2.6 \pm 0.1	1.4
6	26.9 \pm 1.5	1.3	4.8 \pm 0.0	1.3	3.3 \pm 0.1	1.3
7	33.0 \pm 1.5	1.2	5.3 \pm 0.1	1.1	3.8 \pm 0.2	1.1
8	40.4 \pm 1.4	1.2	6.2 \pm 0.3	1.2	4.4 \pm 0.1	1.1
9	46.2 \pm 2.9	1.1	6.6 \pm 0.4	1.1	4.8 \pm 0.1	1.1
Adult female	70.6 \pm 1.7	1.5	7.6 \pm 0.5	1.1	5.5 \pm 0.1	1.1

*Distance between the most anterior parts of the curves of the two compound eyes.

Table 2. Behavioral measurements for *Polyspilota* sp. during peering.

Instar	Distance to target (mm)	Mean peering amplitude (mm \pm s.d.)	Increase from previous stage	Mean peering velocity in (mm/sec \pm s.d.)	Increase from previous stage	Number of animals (sample size)
2	15	2.78 \pm 0.66	–	1.57 \pm 0.63	–	25 (56)
3	20	3.47 \pm 0.96	1.24	1.94 \pm 0.57	1.23	9 (14)
4	20	3.84 \pm 1.28	1.10	1.92 \pm 0.48	0.98	7 (14)
*6	30	7.68 \pm 2.88	2.00	3.84 \pm 1.12	2.00	8 (14)
*9	40	14.08 \pm 3.84	1.83	9.92 \pm 1.28	2.58	10 (22)
Adult female	50	15.68 \pm 4.48	1.11	12.48 \pm 3.52	1.25	8 (20)

*Increase over two or three stages.

convergence angle between the left and right compound eye (Fig. 1A), which in turn, influences distance estimation (Barrós-Pita & Maldonado 1970, Kral 1999). The greater the interocular distance, the larger is the range of measurement where the lines of sight of corresponding ommatidia of the two compound eyes meet at the point of fixation (Fig. 2). As the object distance changes, different corresponding ommatidia (retinal areas) are stimulated, thus providing information to the visual nervous system that can be used for distance estimation.

A larger convergence angle for a given object distance also suggests greater spatial resolution (Fig. 2). For example, for an item of prey situated between the points of intersection of lines of sight of horizontally adjacent ommatidia of the left and right eyes, the position can be determined more accurately with increasing interocular distance, due to the smaller distance between points of intersection. However, the exponential curves indicate a rapid decrease in spatial resolution with increasing object distance (Fig. 2).

One factor not taken into account in our calculations is the developmentally related growth of the eyes themselves, clearly shown by the increase in the number of ommatidia from around 3,800 to 9,000. In general terms, increase in the number of ommatidia results in greater light sensitivity and a higher signal-to-noise ratio (Land & Nilsson 2002).

The anterior flattening of the eyes was also not taken into account. This leads to an increase in the number of ommatidia facing forward and slightly inward, resulting in an expansion of horizontal binocular overlap of $\sim 30\%$, and in the formation of a "fovea" (with

facets more than three times larger combined with interommatidial angles around three times smaller) for the binocular visual field (Rossel 1979, Köck *et al.* 1993). This means that both the binocular measurement range and the spatial resolution of older nymphs, and of adults in particular, can be expected to be significantly higher than indicated here by the convergence angles (Fig. 2).

If these aspects are taken into account, the behavioral findings for *T. sinensis*, which resembles *Polyspilota* (Köck *et al.* 1993), correspond well with our calculated data. Köck *et al.* found that the distance to an item of prey immediately before the strike was ~ 3 mm for the youngest nymphal stage, around 7 to 10 mm for the middle nymphal stage, and 25 to 28 mm for adults (*cf.* Fig. 2). These distances correspond to 45% to 50% of the length of the raptorial legs, and are thus clearly within the working range of the legs. For all age levels, prey-capture success was around 90% (Köck *et al.* 1993).

One question concerns the relationship between prey-capture distances and prey image size. In accordance with the values found for *T. sinensis*, our calculations for *Polyspilota* indicate that increase of both the prey-capture distance and prey size does not result in a retinal image of constant size. This is an interesting aspect, since the image size of the prey item could play a role in controlling the prey-capture distance. However, Rossel (1991) found that the evaluation of image size is based more upon a relative than an absolute scale, with the result that no direct relationship can be established between image size and object distance.

This means that even if they cannot use image size to determine the absolute distance of items of prey, mantids can distinguish between small and large prey based on the image size and possibly on the movement behavior of the prey. From our own experience with the breeding of mantids, we observed a direct relationship between the size of the mantid and the size of the preferred prey (see also our discussion in the Materials and Methods section, and Whitman & Vincent 2008). For successful prey capture, limiting factors include the relevant morphology, dimensions and biomechanics. For instance, for adult *Mantis religiosa* we observed that the males, which are smaller (body length 35 to 38 mm) and weaker, capture small houseflies, but no large flesh flies or honeybees, but that the larger (54 to 60 mm) and stronger females do capture large flies and bees. Here it would be of interest to carry out precise quantitative investigations, involving conditions found in the natural habitats of mantids.

In terms of the visual performance of *Polyspilota*, what is the significance of the increase in the amplitude and velocity of peering movements over the course of ontogeny? Does this also indicate that adults can see better than nymphs, particularly very young nymphs? Before answering these questions the following has to be clarified. With the aid of translational peering movements, mantids determine the distance to stationary objects, such as the black bar

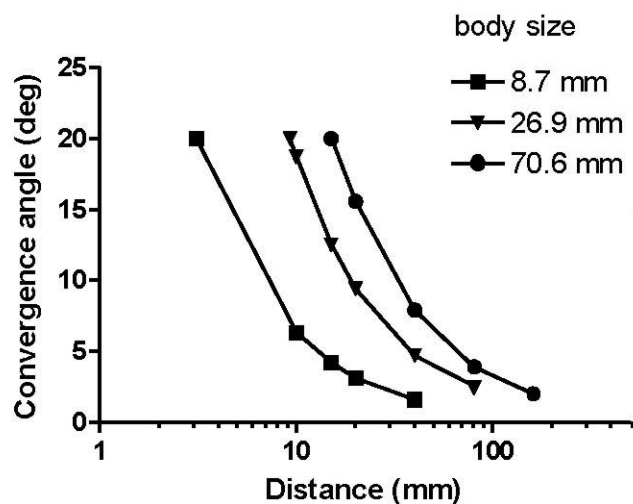


Fig. 2. Relationship between the convergence angle and the distance to the target object, for the 2nd and 6th nymphal stages and the adult stage of *Polyspilota*.

provided as a jump target in the present study. This method of distance determination makes use of the fact that during peering, the retinal images of closer objects move more quickly than do those of more distant objects (e.g., Poteser & Kral 1995). However, that only works when the velocity of the peering movement is constant, independent of the object distance, and hence has a fixed value during the measurement process. In this case, retinal image speed in conjunction with the velocity of the insect's own head movements (the amplitude can change) will determine object distance (Poteser *et al.* 1998).

Mantids could also use other strategies: 1) if peering velocity changes depending on the distance of the object, retinal image velocity could be the same for every distance; 2) the peering velocity could vary while the peering amplitude is kept constant, allowing the distance of the object to be estimated from the relationship between the peering amplitude and retinal displacement (Kral 1999). In studies of the relationship between peering behavior and object distance, for a range of object distances (up to 35 cm) extending beyond the jump range, no significant change in the velocity of the peering movements relative to object distance was found, provided that the object was relevant to the mantids (e.g., as an orientation target) (Kral & Poteser 1997). A decrease in velocity in the case of large distances was attributed to a decline in motivation.

In the present research, in preliminary experiments where all of the object distances (see Materials and Methods) were tested with all age stages in order to determine which distances were the most likely to result in jumps, it is important to note that the individual experimental animals executed peering movements with velocities of the same order of magnitude for every object distance that resulted in peering. For instance, adults exhibited the same peering velocity for objects at 15 mm and 50 mm. There were some fluctuations in peering amplitude, and sometimes a slight increase with increasing distance, as has also been found for locusts, where peering amplitudes increase with target distance (Collett 1978). Thus, these results suggest that the image velocity is inversely proportional to the object distance.

Since the peering velocity has a fixed order of magnitude in each age stage (Table 2) independent of object distance, peering movements with a greater velocity could be expected to be associated with a larger measurement range and more accurate measurements. In order to verify this, we calculated the velocity of the image motion (Fig. 1B) in relation to the object distance for various age levels (with different body lengths).

Our calculations show that retinal image velocity decreases exponentially with increasing object distance. This decrease is more pronounced in the case of greater initial image velocities. It should be noted that the initial values of image velocity are directly proportional to body size. In the case of distant objects, all image velocities remain at a low level over a relatively extensive range, gradually tending toward zero with increasing object distance (Fig. 3). Image velocities for distant objects are greater for individuals with a larger body size. The initial values for image velocity, defined in Figure 4 as half the maximum value, suggest that greater body size is associated with increased spatial resolution.

The positive effects of the increased size and flattening of the eyes, resulting in a greater signal-to-noise ratio and the strengthening of movement signals, were not considered in the calculation of retinal image velocity. Due to these factors, considerably better stimulus perception and higher retinal image velocities are to be expected in the last nymphal stage and the adult stage, than are indicated by the calculations. When these aspects are taken into account, the velocity ranges (Fig. 3) correspond to the observed jump distances of 15 to

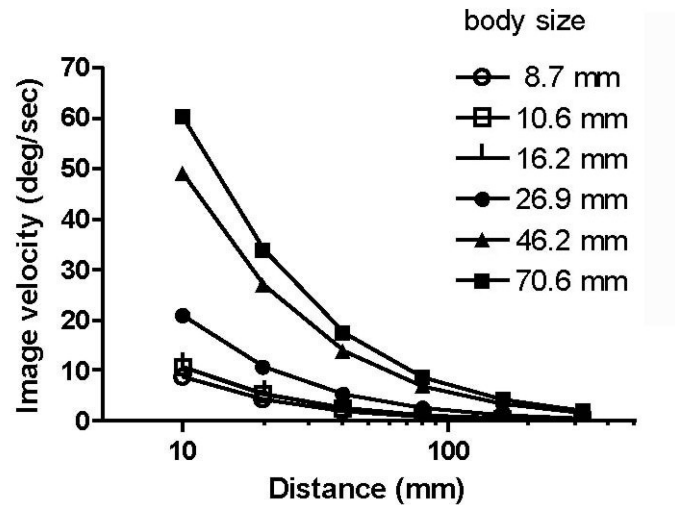


Fig. 3. Relationship between the retinal image velocity and the distance to the target object for *Polyspilota*, for all age levels studied.

20 mm for early nymphal stages, 30 mm for the middle nymphal stage, and 40 to 50 mm for the last nymphal stage and the adult stage. It should be noted that for every age level, the mantids only jumped at objects when the distance was within their capability range for achieving a safe landing.

In connection with this, it would be interesting to investigate spatial vision in relation to body length for distances greater than the jump distance. This could shed light on whether older nymphs and adults can use their compound eyes for greater distance ranges than is the case with young nymphs. If so, this would raise the question of the biological consequences of such a disparity. Due to the relatively low retinal image velocity values for objects beyond the jump distance, which change little as the distance increases (indicated by the asymptotic curve, Fig. 3), it is to be assumed that absolute distance determination is not possible for distances viewed beyond the jump distance. However, the retinal image velocity values should certainly still be sufficient for relative distance estimation. Mantids could thus detect low-contrast structures or objects against

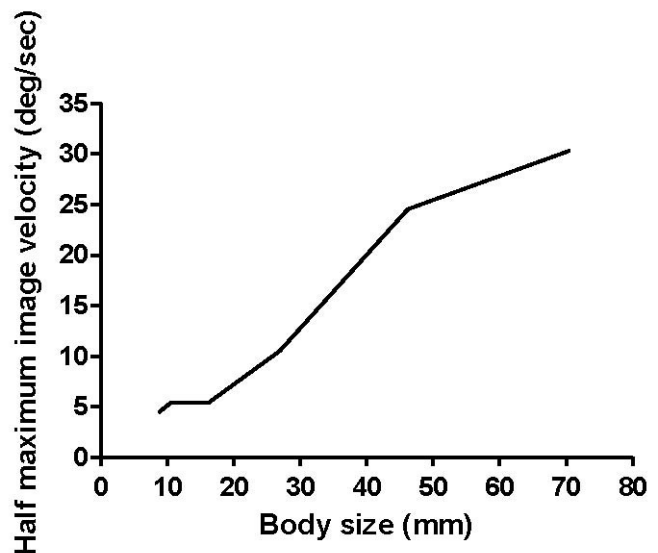


Fig. 4. Relationship between half the maximum retinal image velocity and body length for *Polyspilota*.

a structured background. However, figure-ground discrimination would only work with the aid of image velocity, which is robust with regard to pattern and contrast changes (Horridge 1986, Kral & Poteser 1997).

Finally, the present ontogenetic findings for the praying mantis clearly show that determination of the greatest distances with the most accuracy is achieved by the largest individuals, which have the largest eyes, the greatest interocular distance, and the most extensive peering movements; these levels are thus reached in the adult stage. Nevertheless, prey capture range is ultimately determined by interocular triangulation and jump range by image velocity, accomplished via peering. As such, it is interesting that in mantids, depth perception for two different functions (predation and jumping) is determined via two different mechanisms.

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