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A Fovea in the Praying Mantis Eye

I. Estimation of the Catching Distance

H. MALDONADO and J. C. BARRÓS-PITA
Centro de Biofísica y Bioquímica
Instituto Venezolano de Investigaciones Científicas (IVIC), Apartado 1827,
Caracas, Venezuela

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Summary. The possibility that a special area of the eye of the praying mantis *Stagmatoptera biocellata* was implicated in estimation of catching distance, was investigated.

1. The right eye of the female mantis was painted blinding only a restricted area of the eye. A special apparatus called the double-goniometer (Fig. 2 and 3) was used to obtain a coordinate system of reference and to determine, thus, which zone of the eye had been covered. The experimental device took advantage of the conspicuous pseudopupil of *Stagmatoptera biocellata*.

2. A simple projection map of the right eye (frontal part) with the isopseudopupil lines (Fig. 5) is presented to illustrate the different zones that were painted and their comparative sizes (Figs. 6—9).

3. 16 groups of animals with different blinded areas were used. Their hitting ability on a prey was measured in an experimental device described elsewhere (Maldonado, Levin and Barros-Pita, 1967) and compared with that of two control groups. One control group had both eyes free (the binocular group or group B) and the second control group had the whole right eye blinded (the monocular group or Group M). Animals of Group 15 (painted area is shown in Fig. 9; 15) performed as badly as the monocular mantids. Any other pattern of painting that did not include all the area of group 15, showed a number of successful strikes significantly greater than Group M. This finding proved to be true in spite that even more extense zones than those of Group 15 were blinded.

4. These results indicate that there exists an area in the female mantis eye that is, as a whole, necessary and sufficient for a fine estimation of catching distance. We call it a *fovea* by functional analogy with that of the eye of some vertebrates with great overlapping frontal fields.

Introduction

In previous work we have shown that if an eye of the praying mantis was blinded with a film of a special black paint, the animal strikes at a very low frequency (near zero) and a peculiar response called the *monocular cleaning reflex* was elicited when a fly entered its visual field (Maldonado and Levin, 1967). These facts were taken to indicate that a precise estimation of catching distance is accomplished in mantids by binocular method, based on some type of triangulation mechanism. The present series of papers intends to answer the following questions:

1. Are all the different areas of the eye equally responsible of the distance estimation or does only a "special zone" of the eye, with the complementary zone of the other eye, fulfil this function?

2. If a special zone really exists, has this area features that allow us to distinguish it from the remainder of the eye?

3. When a mantis is shown a fly, it moves its head as if it were trying to centre the prey. Is this a really centring process? If so, has it any connection with the hypothetical "special zone" for precise distance estimation?

This paper deals with the first question.

Material

Female mantids *Stagmatoptera biocellata* were employed. In all cases the specimens were kept in individual cages at a constant temperature of 29° C with relative humidity of 70%. Similar conditions of temperature and humidity were maintained in the experimental field described in Methods. In all the experiments the flies used to feed the mantids were *Parasarcophaga crassipes* of a carefully selected uniform size.

Methods

1. The Arena. The arena, i.e., the experimental field, and the fixation procedure of the insect on a plaster box have been described in detail elsewhere (Maldonado, Levin an Barrós-Pita, 1967). The arena consisted of a cylinder of thin bronze, diamater 30 cm, height 34 cm, with white painted walls, illuminated by a 60 watt lamp. The prothorax of the mantis was fixed on to a block of quick setting gypsum. The mantis-plus-block was fitted in an individual holder mounted on a small balance. The insect grasped the scale of the balance with its walking legs. The balance was used to compensate the weight of the animal. The individual holder with the mantid was placed in the arena fitting it in a central holder. A fly was stuck ventrally to a small magnet. Fly-plus-magnet were held on the internal face of the wall of the arena by the attraction of an external magnet which was joined to a bar. This bar could be moved by a central motor in such a way that the fly was passed around the entire perimeter of the cylinder. Both the mantid-fly distance, *cd*, and the height of the fly, *h*, could be modified at will (Fig. 1).

2. Values of cd and α (Fig. 1). The mantid-prey distance *cd* was an ideal straight line joining the main coxal articulatory point, i.e. the coxifer (Levereault, 1936), with the center of the fly. *CP* was the distance between the coxifer and the anterior end of the prothorax. A known value of *cd* was obtained by measuring the *CP* of each animal and modifying *PM'* (read on a horizontal rule of the arena). Hereafter, the *cd* values will always be expressed as a percentage of the foreleg length.

During the experiments, five values of *h*, namely 8, 14, 20, 26 and 32 mm were used and read on a vertical rule on the outside of the arena. For each *h*, three different values of *cd* were chosen, namely 100, 75 and 50% of the foreleg length. Combination of these two variables permitted us to distinguish three ranges of α_c:α_1, between 9° and 18°, α_2, between 21 and 35°; and α_3, between 38 and 63°.

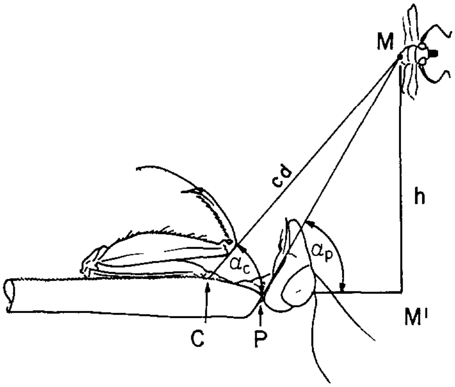

Fig. 1. Angles. α_p: angle formed by *PM* (line joining the tip of the prothorax with the centre of the fly) and the longitudinal axis of the animal. *cd* the mantid-prey distance, i.e. a line joining the coxifer *C* with the centre of the fly. α_c: angle formed by *cd* with the longitudinal axis of the animal. *h*: height of the fly

3. Choice of Animals. The mantids were mounted 10—12 days after being imago. A strict criterion of selection was adopted. The animals had to fulfil the following three conditions: 1) They should have a foreleg length between 48 and 52 mm; 2) they should have no corneal scars or malformations in the arrangement of the ommatidia; 3) the right eye should fit an "idiotype" which will be explained below.

4. Programme of Trials. The programme of trials was started 8 days after the animal was mounted. A trial consisted in running a fly twice round the entire perimeter of the cylinder: firstly counter clockwise, and clockwise the second time. The tangential speed of motion of the fly was 20 mm/sec. The programme consisted of 15 sessions of 3 trials. Each session combined one height of the fly out of the five possible values of *h* and one mantis-fly distance out of the three possible values of *cd*. The animals were subjected to 5 sessions a day over a 3 day period. The experimenter could see the animal reactions through a mirror system placed on the arena. Five possible kinds of responses were computed: 1) a *hit*, i.e. an attack in which the mantid actually caught the fly; 2) an *unsuccessful strike*, i.e. when the mantid missed the prey; 3) *a gaze*, i.e. a steady look at the prey; 4) *preparatory movements*, i.e. motions of foreleg from a normal position with the tibia tightly retracted against the femur to a "ready-attitude" in which tibia and femur formed an open angle; 5) a *monocular cleaning reflex* (MCR), i.e. a very neat response elicited when the prey entered the mantis visual field. It consisted of a sequence of three different actions: wetting of the foreleg tibia-femur by passing them between the mouth appendages, then "brushing" of the non-painted eye and finally cleaning of the foreleg tibia-femur. The intervals between trials of one session were of 1 minute and those between sessions of 5 minutes. The latter intervals were longer whenever a hit resulted because mantids were allowed to eat the fly they had caught. A trial was repeated when the mantid did not look at the prey and was given a rest for half an hour after a second failure. After a third unsuccessful attempt the sessions were postponed until the following day. If then the animal did not even gaze, it was definitely discarded.

5. A Coordinate System of Reference. The Double Goniometer. Several groups of animals had only a part of the right eye painted (see below). A coordinate system of reference was indispensable to determine which area of the eye had been blinded.

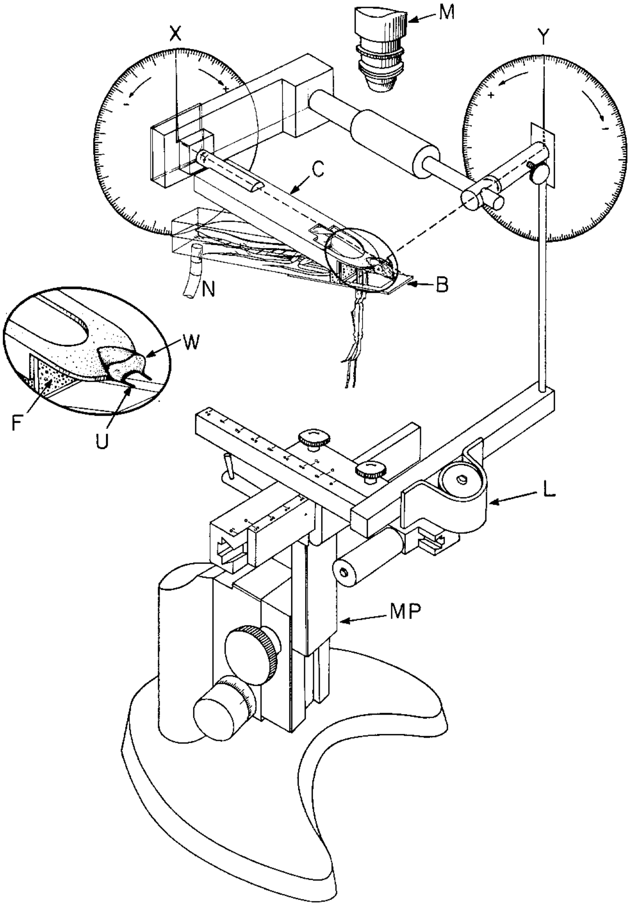

Fig. 2. *The double goniometer. C* a Perspex chamber where an anaesthetized mantis was placed. *N* tube for nitrogen supply. *X* goniometer where rotations around the *x*-axis were read. *Y* goniometer where rotations around the *y*-axis were read. *B* a barrier that prevented the mantid from any movement to remove the paint placed on its eye. *M* objective of light microscope Wild M 20. *MP* a micromanipulator to centre easily the pseudopupil within the optical field. *L* a spirit level. The insert shows the interior part of the chamber without animal. *W* a wax cast to fit the mantid's head. *F* a plastic foam pad. *U* a *U*-fork. The combined pressure of *F* and *U* guaranteed head immobility and its perfect fitting against *W*

To establish this system of reference, we took advantage of the exceptionally clear-cut mantid pseudopupil. A special apparatus called the double-goniometer was used (Figs. 2 and 3). It consisted of a Perspex chamber *C* where an anesthetized mantis was placed. Its head was perfectly fitted against a wax cast *W*. The combined pressure of a plastic foam pad *F* and of a *U-fork U* guaranteed head immobility and its perfect fitting against the wax cast *W*. Nitrogen could be supplied *at lib.* through tube *N*.

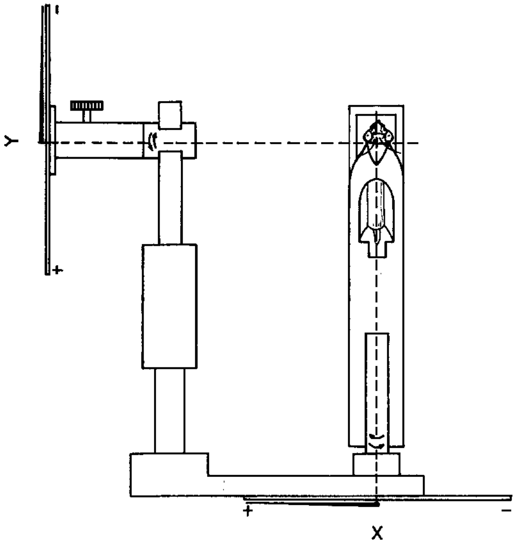

Fig. 3. Top view of the double-goniometer, *X* and *Y* as in Fig. 2

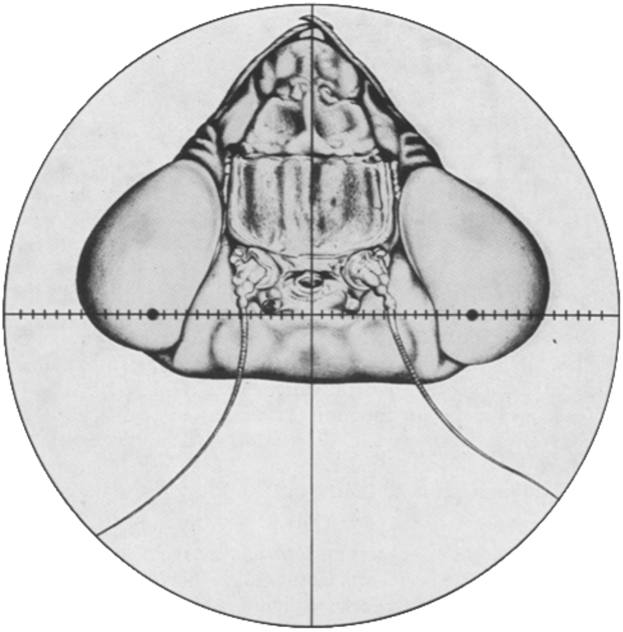

Fig. 4. Female mantid's head observed with a non-magnifying objective (1 ×) and with an eye-piece (12.5 ×) provided with a filament cross. The mantid had been placed in a double-goniometer ($y = 0$, $x = 0$)

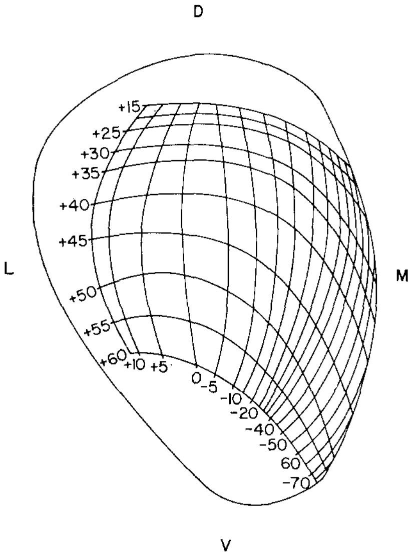

Fig. 5. Simple projection map of the right eye of the female mantid with isopseudopupil lines. Position of head in the double-goniometer $y=30$; $x=0$. Figure on the left-hand side stand for the numbers of the y-isopseudopupil lines. Figures on the bottom for number of the x-isopseudopupils lines. *D* dorsal, *V* Ventral; *L* lateral, *M* medial

The chamber had two possible axes of rotations. *X*-rotation: around a longitudinal axis that belonged both to the sagittal plane of the animal and to the coronal plane of the head so placed in the apparatus. *Y*-rotation: around an axis that was perpendicular to the x-axis and belonged to a plane that passes through the extreme end of the prothorax. One pointer on the x goniometer and one of the y goniometer, were fixed to accompany the rotation movements. A light microscope Wild M 20, M, was used. The microscope stage was removed and replaced by the double goniometer. A micromanipulator *MP*, permitted an easy centring of the pseudopupil. It was indispensable to employ a non esteroscopic microscope to ensure that the observation axis was parallel to the axes of the ommatidia of the pseudopupil.

To establish the zero of both scales the following method was used (Fig. 4). The head was observed with an objective (non-magnifying, 1 ×) and with an eye piece (12.5 ×) provided with a filament cross. The chamber was rotated until a position was attained that fulfilled simultaneously the following four conditions: 1) the horizontal thread of the cross passed through both pseudopupils; 2) the horizontal thread was tangential to the posterior border of both lateral ocelli; 3) both pseudopupils were placed equidistant to their corresponding ocular ridge; 4) the vertical thread bisected the medial ocellus.

When these conditions were satisfied, the x and the y pointers were set at zero and the microscope magnification was increased to 40 fold (objective: 2 ×, eye piece: 20 ×) so that both eyes could no longer be seen at the same time. The right eye was placed at the centre of the field and the microscope focused on the cornea. To every combination of x and y corresponded only one characteristic position

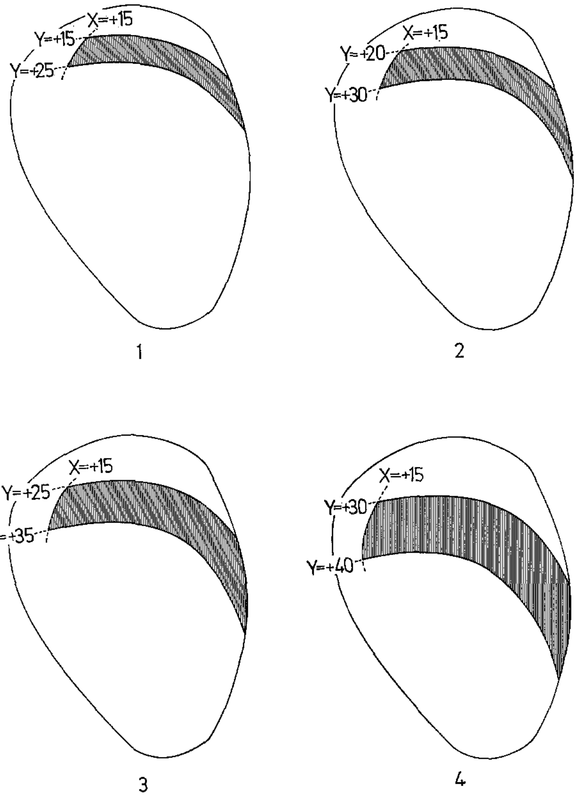

Fig. 6. Outlines of the right eye of the female mantid. Position of the head in the double-goniometer: $y=30$ and $x=0$. Shaded areas correspond to the zone painted in each group of animals. x and y-isopseudopupil lines that limit the areas are given. Boundaries of the zones are indicated by x and y-isopseudopupil lines, but it must be understood that the paint covered also the corresponding bands of the limits. A number below each outline stands for the corresponding group of animals

of the pseudopupil. Rotations around the x axis that moved the pseudopupil from zero towards the ocular ridge, were conventionally assigned negative values and rotations in the contrary direction, positive values. Rotations around the y axis that moved the pseudopupils backwards with respect to the lateral ocelli, were assigned negative values and rotations in the contrary direction, positive values.

The eye was illuminated obliquely by a bifurcated Fiber-lite (model 150, Dolan-Jenner, Mass.) with the two branches symmetrically placed at both sides.

To have a first panoramic view of the different possible positions of the pseudopupil on the frontal part of the eye, we drew a simple projection map with isopseudopupil *lines* (Fig. 5). To trace each y-isopseudopupil line the following method was adopted. The double goniometer was set at a fixed value of y, the x was moved from $+15$ up to the ocular ridge and every 5° the pseudopupil was covered with paint. A photograph of this isopseudopupil band was taken with the double-

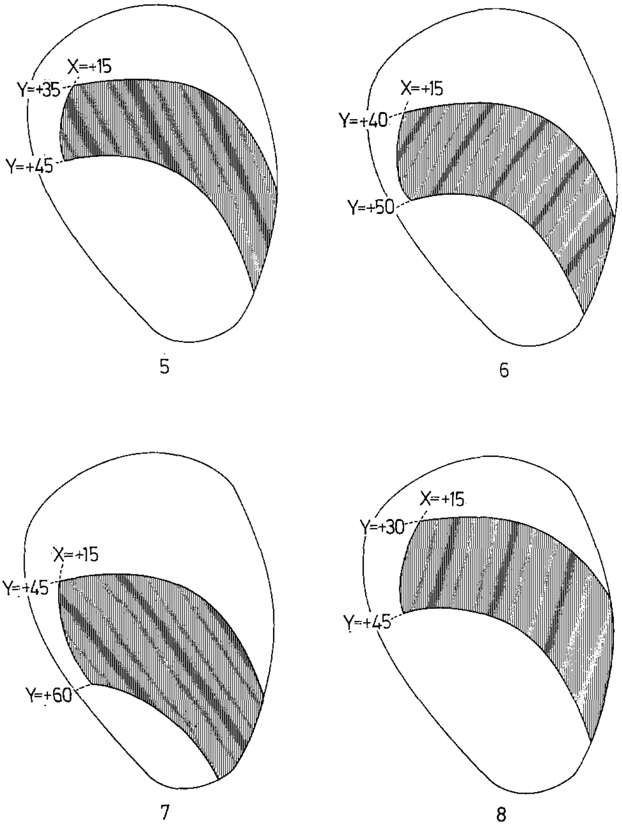

Fig. 7. Symbols as in Fig. 6

goniometer set at position $x = 0$, $y = +30$. Then the band was erased and a new one was painted at a different value of y. Repeating this procedure at every 5° for y and at every 5° for x, and combining the photos and drawing a mid-line for every band, the projection map was obtained.

6. The Idiotype. Before accepting a female mantis for experimentation, the double-goniometer was placed with $x = 0$ and $y = +30$. The perimeter of the right eye and the position of the pseudopupil were compared through a camera lucida, with the drawing of an idiotype. This idiotype corresponded to a sort of eye that proved to be the most usual in the female mantis population of the vivarium. Any disagreement both in the perimeter or in the position and shape of the pseudopupil led us to reject the animal.

7. Method Used to Paint the Eye. If the whole right eye had to be blinded, the animal was placed in the double-goniometer only to check under the microscope if the black film covered all the ommatidia. But if only a restricted area of the eye was to be blinded, the role of the double-goniometer was to determine every necessary x-y combination that included the zone to be covered. The chamber was rotated to reach a desired x-y values and, then, the pseudopupil was painted. The

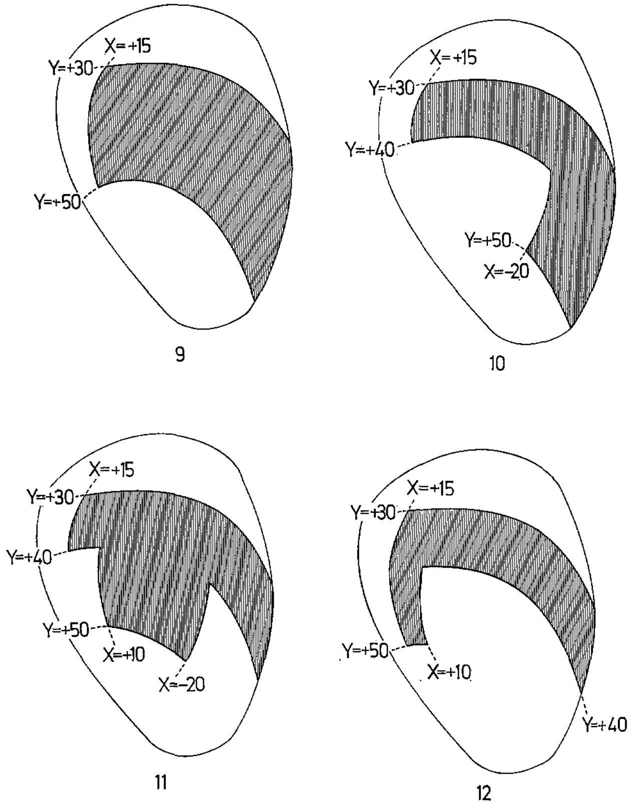

Fig. 8. Symbols as in Fig. 6

operation was repeated with different *x*-*y* associations until all of the zone had been coated. The pseudopupils were observed at 40× magnification. The paint was a mixture of equal parts of Sudan black B dissolved in ethyl acetate plus a solution of celluloid in ethyl acetate until adequate viscosity was obtained. To apply the mixture, a 5λ-Hamilton syringe mounted on a micromanipulator, was used. Small and precise amount of paint could be delivered by moving the plunger with a micrometer screw. Mantids tried to take the paint off only immediately after the paint has been applied. The barrier *B* in the chamber (Fig. 2) prevented an animal from this possible action if the effect of the anesthesia wore off during painting.

8. Animal Groups. 18 groups of animal were used.

Group B (binocular group): 76 mantids without painting. *Group 1:* 9 mantids. Painted area as in Fig. 6.1. *Group 2:* 11 mantids. Painted area as in Fig. 6.2. *Group 3:* 7 mantids. Painted area as in Fig. 6.3. *Group 4:* 16 mantids. Painted area as in Fig. 6.4. *Group 5:* 16 mantids . Painted area as in Fig. 7.5. *Group 6:* 16 mantids. Painted area as in Fig. 7.6. *Group 7:* 10 mantids. Painted area as in Fig. 7.7. *Group 8:* 13 mantids. Painted area as in Fig. 7.8. *Group 9:* 8 mantids. Painted area as in Fig. 8.9. *Group 10:* 8 mantids. Painted area: that coated in group 4 plus one

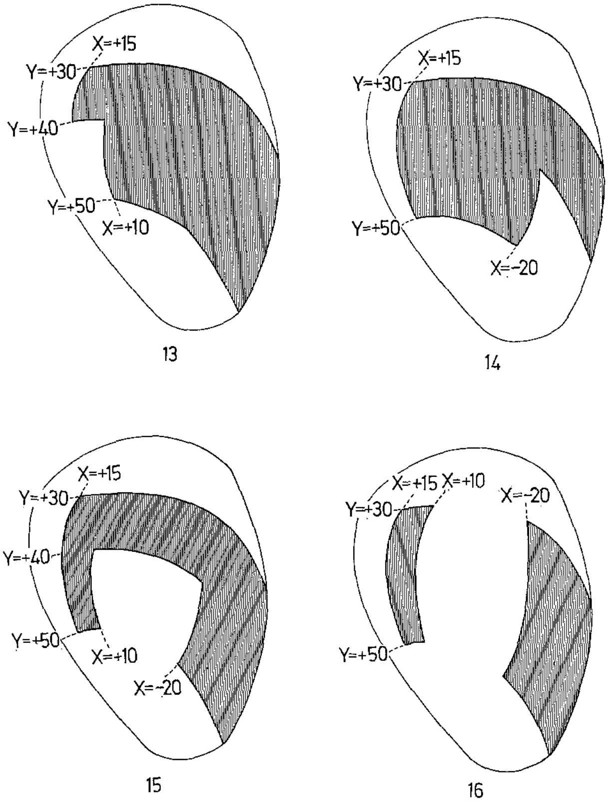

Fig. 9. Symbols as in Fig. 6

additional zone, Fig. 8.10. *Group 11:* 9 mantids. Painted area: that coated in group 4 plus one additional zone, Fig. 8.11. *Group 12:* 10 mantids. Painted area: that coated in group 4 plus one additional zone, Fig. 8.12. *Group 13:* 10 mantids. Painted area: that coated in group 4 plus one additional zone, Fig. 9.13. *Group 14:* 9 mantids. Painted area: that coated in group 4 plus one additional zone, Fig. 9.14. *Group 15:* 21 mantids. Painted area: that coated in group 4 plus two additional zones, Fig. 9.15. *Group 16:* 9 mantids. Painted area as in Fig. 9.16. *Group M* (monocular group): 10 mantids. Right eye completely painted over.

All the groups underwent the same programme of trials (item 4, above). But the painted groups, including the monocular one, had to pass through a double control. Before being painted they were subjected to a 4 trials at a distance of 50%-α_3 and 4 at 75%-α_3. If they did not hit 3 out of every 4 times at 50%-α_3 and 2 out of every 4 times at 75%-α_3 they were not accepted. The same control was performed when sessions were finished and after the paint had been removed. If they failed to maintain their former record, the results were not considered.

9. Statistical Methods. Since the data did not meet the assumptions of parametric statistics, the Mann-Whitney *U* test was used in the analysis (one-tailed). In graphs, however, performance value of the different groups were expressed in terms of arithmetic means. If the median had been chosen for illustration purposes, the reader would have been led to believe that for the same groups extreme values did not occur, because of the skewness in data dispersion. It was convenient that graphs did not conceal the small but real differences between groups. Only in Table 2, the *t*-test was used for comparison, since data seems to meet parametric requirements.

Results

1. The Binocular Group (*Group B*). Fig. 10 shows a summary of the result with group B (binocular). The abscissa represents three different classes of mantis-prey distance, expressed in terms of the foreleg percentage. The three possible α angles are shown for each distance.

The optimal hitting was achieved at a distance that represented 50% of the foreleg extension whatever the α angle. Hitting at 50% was greater than at 75% ($p < 0.001$). Hitting was exceptional at 100%. The angle α_3 proved to be optimal for hitting within each distance. At 75%-distance the performance was better for α_3 than for α_2 ($p = 0.013$) and for α_2 better than for α_1 ($p < 0.001$). At 50% distance, the performance between α_3 and α_2 did not differ significantly but at both angles they were superior to that at α_1 ($p = 0.014$).

Similar results could be obtained if all strikes are pooled, i.e. without distinction between hits and unsuccessful strikes.

If efficiency was estimated from the ratio of hits to hits and misses added together, mantids placed at 50% distance were also superior to those placed at 75% ($p = 0.017$). This means that at 50% distance they did not only strike more but more successfully. At 75% the efficiency was greater for α_3 than for α_2 ($p = 0.037$) and for α_2 than for α_1 ($p = 0.014$). But at 50% there was no significant difference between angles.

At 100% distance there were many preparatory movements.

2. Comparison between Groups. Two comparison criteria were chosen to confront performances between groups: a) number of hits over trials by 100, at distances 50 and 75%; b) number of preparatory movements over the sum of number of preparatory movements plus number of gazes, at distances 75 and 100%. These two types of responses elicited when a mantid is shown a fly are, in fact, good indicators of its ability to estimate distance. But according to results of Group B, no advantage would have been gained by including results at 100% distance with the first comparison criterion or results at 50% with the second one.

a) Hitting at all Angles. Fig. 11 depicts the hitting ability in the different groups (the figure should be examined in the context of Figs. 6 to 9). Four sets of groups could be distinguished according to the strategy we followed to find an area for precise estimation of catching distance.

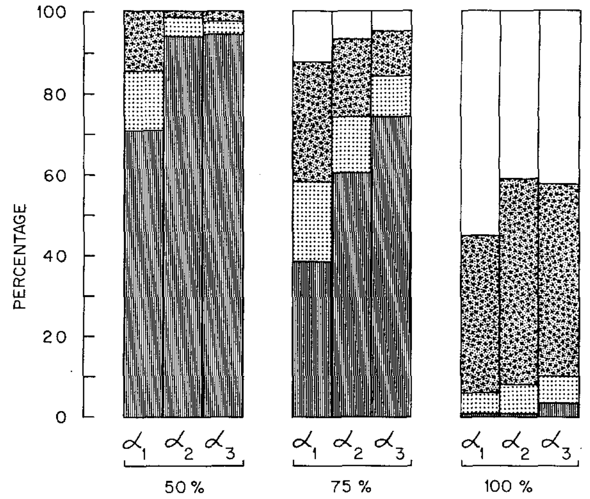

Fig. 10. Performance of the binocular group. Ordinate: mean values as a percentage of the number of trials. Abscissa: three different mantid-prey distances expressed as percentage of the foreleg extension (50, 75, and 100%). Within each distance the three possible α_c angles (α_1, α_2, and α_3) are given. Histograms: vertical stripes stand for hits; mottled, for unsuccessful strikes; heavily mottled, for preparatory movements; and white stands for gazes

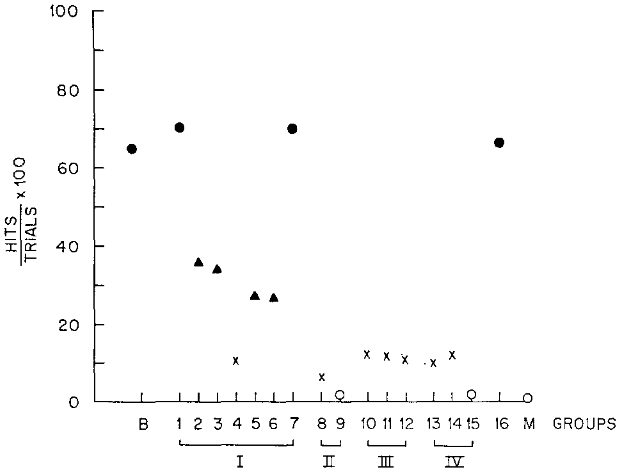

Fig. 11. Hitting performance, at all α_c angles, of the 18 groups of animals. Ordinate: mean values of hits as percentage of the number of trials. Abscissa: the 18 groups of mantids. For I, II, III, and IV see text. Closed circles: performance as that of group B, the binocular mantids; black triangles: the performance was significantly lower than in Group B but higher than in Group 4; X: performance insignificantly different from that of Group 4; open circles, performance insignificantly different from that of Group M

Table 1. *Mann-Whitney U test prob-*

	(1) Fig. 11			(2) Fig. 12a		
Angle	All			α_1		
Groups	B	4	M	B	4	M
1	NS	<0.001	<0.001	NS	<0.001	<0.001
2	<0.001	<0.001	<0.001	<0.001	NS	0.0202
3	<0.001	<0.001	<0.001	<0.001	NS	0.0202
4	<0.001	—	<0.001	<0.001	—	NS
5	<0.001	<0.001	<0.001	0.0057	0.0179	0.008
6	<0.001	<0.001	<0.001	<0.001	0.0418	0.0162
7	NS	<0.001	<0.001	NS	<0.001	0.001
8	<0.001	NS	<0.001	<0.001	NS	NS
9	<0.001	NS	NS	<0.001	NS	NS
10	<0.001	NS	<0.001	<0.001	NS	NS
11	<0.001	NS	<0.001	<0.001	NS	NS
12	<0.001	NS	<0.001	<0.001	NS	NS
13	<0.001	NS	<0.001	<0.001	NS	NS
14	<0.001	NS	<0.001	<0.001	NS	NS
15	<0.001	<0.001	NS	<0.001	NS	NS
16	NS	<0.001	<0.001	NS	<0.001	<0.001

Set I (Groups 1 to 7) was the first series of groups designed to asses the importance of the horizontal bands, $+30$, $+35$, and $+40$ in distance estimation. Groups 1 to 6 had three horizontal painted bands with a common feature: all them had covered at least one of the three bands of groups 4. Group 7 had four bands painted but none of them was shared with those of Group 4. *Set II* included groups 8 and 9 that added one and two horizontal bands, respectively, to those of Group 4. *Set III* (groups 10 to 12) contained the areas of Group 4, plus one additional zone that extended ventrally but that was different for each group. These additional zones covered horizontal bands $+45$ and $+50$, but restricted to certain x-values. *Set IV* (groups 13 to 15) was similar to set III in that the painted areas contained that of group 4 plus an *additional zone.* However, the additional zones of this set were more extensive than those of set III. Group 13 joined the additional zones of groups 10 and 11; Group 14 put together those of groups 11 and 12; and group 15 combined those of groups 10 and 12.

Group 16, out of any set, was built up *a posteriori* knowing the results of the former sets, to asses the importance of the dorsal "bridge" of group 15.

All groups were compared with Group B, Group 4 and M. Table 1, column 1, summarizes the Mann-Whitney U-test probability values for the different comparisons.

ability values corresponding to

(3) Fig. 12b			(4) Fig. 12c			(5) Fig. 13		
α_2			α_3			preparatory movements		
B	4	M	B	4	M	B	4	M
NS	<0.001	<0.001	NS	<0.001	<0.001	NS	<0.001	<0.001
<0.001	0.0139	<0.001	NS	<0.001	<0.001	NS	<0.001	<0.001
<0.001	0.0132	<0.001	NS	<0.001	<0.001	0.0212	<0.001	<0.001
<0.001	—	0.0087	<0.001	—	0.0125	<0.001	—	0.0262
<0.001	NS	0.0016	0.0023	NS	<0.001	<0.001	<0.001	<0.001
<0.001	NS	0.0023	<0.001	NS	<0.001	<0.001	<0.001	<0.001
NS	<0.001	<0.001	NS	<0.001	<0.001	NS	<0.001	<0.001
<0.001	NS	0.0119	<0.001	NS	0.0129	<0.001	NS	NS
<0.001	0.0217	NS	<0.001	0.03	NS	<0.001	0.0054	NS
<0.001	NS	0.0016	<0.001	NS	0.0019	<0.001	0.025	NS
<0.001	NS	0.0409	<0.001	NS	0.0116	<0.001	NS	0.0256
<0.001	NS	0.0082	<0.001	NS	0.0495	<0.001	NS	0.0281
<0.001	NS	0.0035	<0.001	NS	0.0202	<0.001	NS	0.0495
<0.001	NS	0.0219	<0.001	NS	0.0041	<0.001	NS	0.0427
<0.001	0.0129	NS	<0.001	0.0294	NS	<0.001	0.0035	NS
NS	<0.001	<0.001	NS	<0.001	<0.001	NS	<0.001	<0.001

Results with Set I indicate that the performance of Group 4 was the worst in spite of the fact that groups 1, 2, 3, 5 and 6 had the same number of horizontal bands painted and that Group 7 had one more. The latter group behaved as the binocular group. Set II shows that, by painting two additional bands (Group 9) to Group 4, the mantids hit at a level as low as that of Group M. Results with Set II and IV indicate the hitting abilitity improved with any diminution of the zone covered in Group 9, with the important exception of Group 15. These mantids behaved as monocular animals. Animals of Group 16 with an area similar to that of group 15 but with the dorsal "bridge" broken, performed as binocular ones.

b) Hitting as a Function of the Angle α. Fig. 12 shows the hitting performances of the groups depicted as in Fig. 11, but at the three different α angles. Only the results at 50% distance are presented, but they essentially parallel the findings for 75%. The greatest percentate of hits was obtained at 50% distance.

In Fig. 12a, open circles include an X when the performance were not significantly different from that of Group 4 or Group M. Columns 2 to 4 of Table 1 summarize the corresponding Mann-Whitney U-test probability values for the different comparisons. All groups were compared with Group B, Group 4 and Group M. With every angle mantids of groups 1, 7 and 16 behaved as Group B, and Group 4 showed the

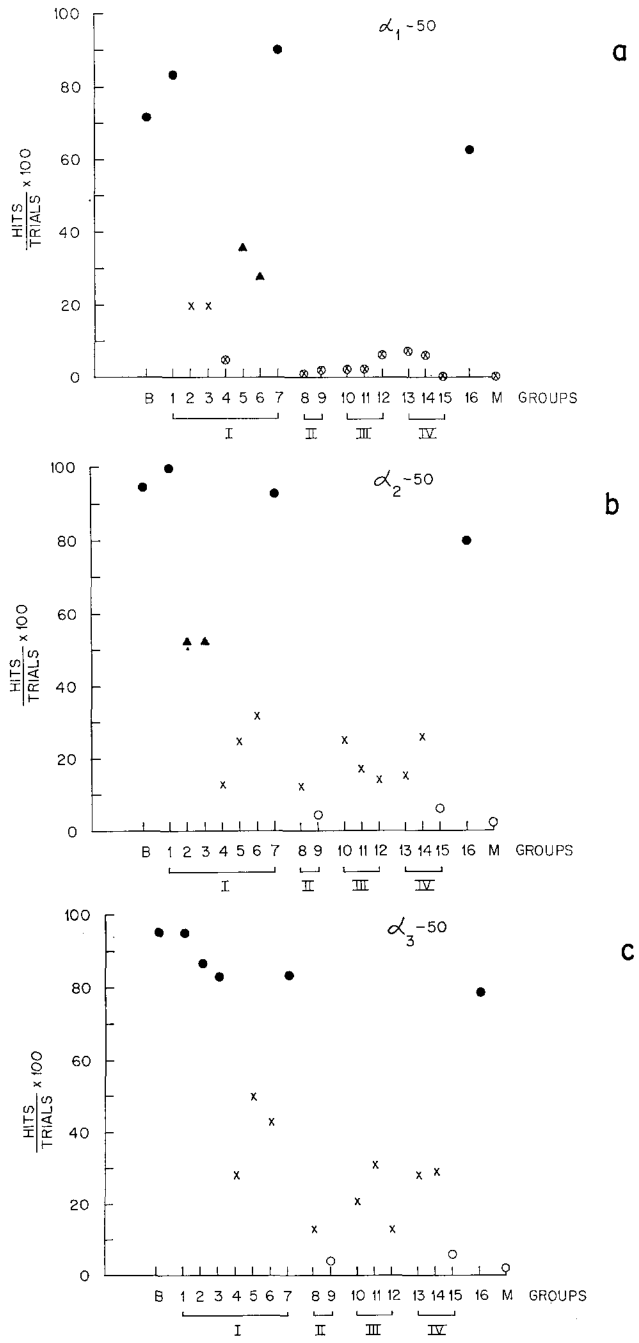

Fig. 12a—c. Hitting performance at 50% distance of the 18 groups of animals. a) at angle α_1; b) at angle α_2 and c) at angle α_3. Ordinate, abscissa and symbols as in Fig. 11

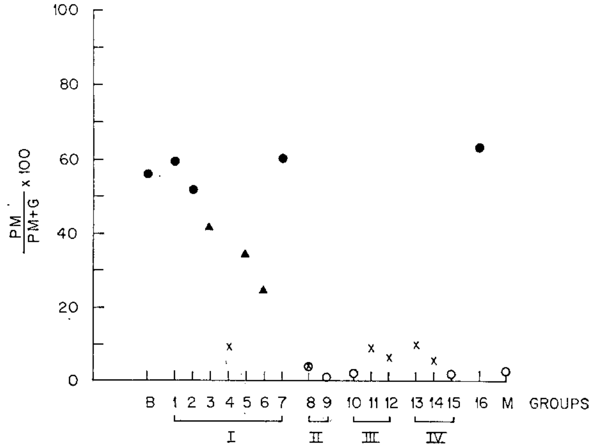

Fig. 13. Number of preparatory movements of the 18 groups of animals. Ordinate: mean number of preparatory movements (*PM*) as a percentage of number of preparatory movements plus number of gazes (*G*). Abscissa and symbols as in Fig. 11

worst performance of Set I. With angle α_1 (Fig. 12a) the hitting ability of all those animals in which horizontal bands +30, +35 and +40 had been painted (i.e. groups 4, 8, 9, 11, 12, 13, 14 and 15) performed as Group M. A striking difference can be observed when attention is paid to groups 2, 3, 5 and 6. With angle α_1 (Fig. 12a) groups 2 and 3 hit less than groups 5 and 6 (the former ones did not perform better than Group 4). With angle α_2 (Fig. 12b) groups 5 and 6 hit less than Group 2 and 3 (the former ones did not perform better than Group 4) i.e. with α_2 the relationship was inverted as regards α_1. This tendency was emphasized with α_3 (Fig. 12c): groups 2 and 3 behaved as Group B and groups 5 and 6 as Group 4.

c) Preparatory Movements at all Angles. Fig. 13 shows number of preparatory movements as a percentage of number of preparatory movements plus number of gazes, computed at 75 and 100% distance and Table 1, Column 5, summarizes the statistical comparisons between groups. It may be seen that results, in general parallels those of the hitting ability.

3. Number of MCR's. Table 2 presents number of MCR's over trials by 100 for each group. One MCR was computed when the three successive steps that characterize the sequence were accomplished. Thus, more than one MCR could occur during a trial. Group B, 1, 7 and 16 did not present any MCR's at all. Group M showed a high percentage of MCR's. Group 9 presented a percentage of MCR's that is lower than that of group M ($p = 0.001$) but higher than that of Group 4 ($p = 0.025$) (t-test,

Table 2. $\frac{\textit{Number of MCR's}}{\textit{trials}}$ × *100 (mean values)*

Groups								
B	1	2	3	4	5	6	7	8
0.00	0.00	2.96	2.96	11.5	5.90	6.20	0.00	9.70

Groups								
9	10	11	12	13	14	15	16	M
21.30	8.30	9.40	10.70	12.00	10.50	9.80	0.00	71.00

one tailed). The values of all remaining groups with significant figures did not differ statistically from those of Group 4 (*t*-test, double-tailed).

Discussion

1. The Pseudopupil. The precise system of reference used to identify different areas of the eye was based on the conspicuous pseudopupil of *Stagmatoptera biocellata.* The eyes of this mantid are not deeply pigmented and their pseudopupil fields fade out sharply enough to permit an observer to distinguish their boundaries. In other insects the pseudopupil can hardly be observed, so that eye colour mutants had to be employed, e.g. white chalky mutant of *Callyphora erythrocephala* (Burkhardt, de la Motte, and Seitz, 1966; Seitz, 1968) and white mutant of *Musca domestica* (Kirschfeld, 1967).

2. The Binocular Group. 75% of the foreleg extension was established as a maximum limit for catching distance. Maldonado, Levin and Barrós-Pita (1967) showed that there is a relationship between the optimum distance to hit, on the one hand, and the salient anatomical features of the grasping mechanism and the length of the forelegs, on the other hand. At 100% distance there were very few hits but many preparatory movements. Mantids must have an accurate system for catching distance estimination, since the different between 75 and 100% foreleg extension distance is very small as compared with the animal size.

Whatever the distance, the angle α_3 was the optimal angle for hitting, while α_1 was the worst. This may be explained as follows. The optimum angle for hitting would be attained in free animals by moving the prothorax. In our experimental conditions the prothorax was immobilized so that the animal could show their maximum ability only when the fly *was placed* at that angle (α_3). The reasons for adopting this angle, however, are not completely understood. A first explanation may be that with more acute angles (i.e. the α_1) the grasping mechanisms of the foreleg could not be displayed normally. This became evident when the prey was placed within a catching distance but at an angle $\alpha \overset{=}{<} 0$. Under these conditions mantids cannot hit the fly and they miss frequently and show preparatory movements. An alternative or additional explanation could be that mantids adopt that optimum angle because they need to centre the prey in a certain area of the eyes. This possibility is discussed by Levin and Maldonado (1969) and is directly related with the central hypothesis of this series of papers.

3. A Specialized Area for Estimation of Catching Distance. Three horizontal bands were painted in groups 1 to 6, covering the same extension between x-bands. However, the performance between groups was very different. Group 1 behaved as the binocular mantids while the hitting ability of the remaining groups was impaired. Group 4 performed the worst. Results with Group 7 were dramatic: four horizontal bands were painted instead of three but these mantids behaved as binocular. A first conclusion is that the three y-isopseudopupil bands $+30$, $+35$ and $+40$ were decisive for correct hitting. When they remained uncovered (i.e. groups 1 and 7) mantids behaved normally, but painting only one of the three bands was enough to lower the efficiency. The efficiency diminished greatly when all the three bands were painted.

Group 4, however, performed significantly better than the monocular group. When two painted bands were added ($+45$ and $+50$ i.e. Group 9) the mantids behaved as the monocular ones.

But, were these two additional bands necessary in all the x-extension to lower the performance to that of the monocular group? A trial and error method was used to answer this question. It consisted in adding to the three y-isopseudopupil bands of Group 4, two other y-bands, i.e. $+45$ and $+50$, but with a more reduced x-extension. Groups 10—14 showed that the hitting ability of Group 4 was not impaired because of these conditions. But when the supplement was that of Group 15, mantids behaved as Group M. This zone had an inverted U-like shape.

If the "bridge" of the inverted U was broken (Group 16) mantids performed as normal ones.

These results rule out the possibility that the eye was working, for a correct distance estimation, based on a mass-action principle, i.e., it is not true that the larger the blinded area of the eye, the poorer the ability. There is no correlation between the extension of the blinded area of the eye and hitting ability. For example (a) Group 7 (4 bands covered) behaved as the binocular group and Group 4 (3 bands covered) showed a very poor performance; (b) groups 13 and 14 seem to have had areas equal to or more extended than those of Group 15, but only the latter behaved as Group M; (c) the painted pattern of Group 15 coated an area clearly smaller than that of Group 9, but both of them performed as monocular animals; (d) an apparently small change in the pattern of Group 15, as that tried with Group 16, did not only improve the performance but brought it up to the level of binocular mantids.

Hitting level and number of preparatory movements were taken as a measure of the ability of the animals to accurately estimate distance. Thus, there exists an area in the female mantis eye that is, as a whole, necessary and sufficient for a precise estimation of catching distance. We call it a fovea by functional analogy with that of vertebrates, specially that of man; i.e. an area that works coordinately with the complementary zone of the other eye, for precise spatial discrimination. The zone agrees with the painted pattern of Group 15. This represents an upper limit for this area. The real area could be even smaller.

4. Equipotentiallity and Mass-Action in the Fovea. — Results suggest that neither all the areas of the fovea have the same importance for estimation of catching distance nor their importance is the same at different angles.

It appears that some parts of the fovea can take over the whole function of the remaining blind ones, e.g. the "bridge" not painted in Group 16.

Nevertheless, Fig. 12a—c show that when α was an acute angle (i.e. α_1) horizontal bands +40 and +35 were more important for distance estimation than horizontal bands +40 and +45. When α was greater (i.e. α_2) the latter bands increased their importance. With the maximum α angle (i.e. α_3) the most dorsal y-isopseudopupil bands did not seem to play any role (groups 2 and 3 behaved as the binocular ones). But with the same α_3, the most ventral bands of the fovea maintained a great "weight" on distance estimation, i.e. when horizontal bands from +40 to +50 were covered (groups 5 and 6) mantids behaved as Group 4. These results seem to indicate that there is specialization i.e., non-equipotentiallity, for certain zones of the fovea. However, there could be an alternative interpretation, which at present seems far fetched. Fixation impeded mantids from combining movements of the prothorax with those of the head in order to allow them an ample range of positions. It was possible, for instance, that when α was wide (α_3) and y-bands 40 and 45 were painted, sharp fall in the hitting level occurred because more dorsal areas of the fovea could not take over the function. Mechanical and anatomical limitations could have prevented this from occurring because pitching of the head was not enough to permit dorsal areas to "look at" the prey. (A complementary discussion on this matter in Levin and Maldonado, 1969.)

For some areas it seems that the mass-action principle is relatively valid, e.g. the increasing effect of adding some horizontal bands in groups of Set I and II (Fig. 11).

5. Relationship between the Fovea and Two Different Types of Distance Estimation. In the foregoing considerations it was emphasized that when the fovea was painted, animals showed a level of hitting and a number of preparatory movements as low as those of the monocular group. A conclusion from these findings was that painting the fovea proved to be enough to eliminate the mantids skill for estimation of catching distance. Nevertheless, it cannot be concluded that painting areas other than the fovea will not impair the mantid's ability for *any kind* of distance estimation. It is convenient to distinguish here, as it is done concerning the sense of touch and temperature discrimination, between an *epicritic* estimation which enables the animal to appreciate very fine distinctions of distance, and a *protopathic* estimation which enables only coarse discriminations.

Maldonado and Levin (1967) showed that the monocular cleaning reflex served as additional evidence for the hypothesis that distance estimation implicates a binocular method. The MCR occurred because "without binocular vision every object-mantid distance becomes equal to zero". But in the present results, Table 2, the number of MCR's of group 15 (i.e. with painted fovea) was significantly smaller than the monocular group. Two relevant observations are in order. a) Number of MCR's were recorded without computing the distance at which a response was elicited. Fly-mantid distance changed continuously during a trial, so that MCR's came about both at very long distance, i.e., at the extremes of the drum perimeter, and at very short distances, i.e. at catching distances. b) The hypothesis put forward in this paper is that the fovea is a specialized area for estimation of catching distance, i. e. for an epicritic estimation, but not necessarily for a long distance estimation, i.e. for a protopathic estimation. For the latter, binocular vision seems to be also indispensable (Maldonado and Rodriguez, manuscript in preparation) but it is possible that more extense areas than the fovea are implicated. A sharp fall in number of strikes (hits and misses) and in the number of preparatory movementes indicate that the ability for an epicritic estimation has been lost. But MCR's are elicited either when the mantis is presented a fly at catching distance and the mechanism for epicritic estimation has been interferred with (i.e. the fovea has been painted) or when mantid is presented a prey at greater distances and the mechanism for protopathic estimation has been impaired (i.e. areas more extensive than the fovea have been painted). This difference accounts for the finding that Group 15 parallels Group M *only* concerning hitting ability and numbers of preparatory movements.

A similar distinction is presented by Wallace (1959) concerning the jump of the locust nymph.

6. Possibility of Suppletory "Cues" for Epicritic Distance Estimation. It is necessary to point out that the statement that the mantid will be unable to hit the prey when the fovea is covered, is valid under the present experimental conditions. Further studies with unfixed mantids are necessary. Yawing and pitching of the prothorax or swinging of the body would be an additional mechanism for depth perception. A monocular movement parallax may play a suppletory role for short distance estimation. Redundancy of mechanisms, i.e. redundancy of "cues" (Helmholtz, 1924) is well known in visual space perception for different animals including man (Graham, 1965). Therefore, the possible finding of monocular cues in mantids would not contradict the conclusions of this paper. A specialized zone exists in each mantis eye that elicits epicritic spatial discrimination on the basis of binocular vision.

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References

Burkhardt, D., de la Motte, I., Seitz, G.: Physiological optics of the compound eye of the blow fly. In the functional organization of the compound eye, p. 51—62. Oxford: Pergamon Press 1966.

Graham, C. G.: Visual Space perception. In Vision and visual preception, p. 504—547. New York: John Wiley & Sons 1965.

Helmholtz, H. L. F. von: Treatise on physiological optica. New York: Opt. Soc. Amer. 1924.

Kirschfeld, K.: Die Projektion der optischen Umwelt auf das Raster der Rhabdomere im Komplexauge von *Musca*. Exp. Brain Res. **3**, 248—270 (1967).

Leverault, P.: The morphology of the *Carolina mantis*. Univ. Kansas Sci. Bull. **14**, 205—259 (1936).

Levin, L., Maldonado, H.: A fovea in the praying mantis eye. III. The centring of the prey. Z. vergl. Physiol. **67**, 93—101 (1970).

Maldonado, H., Levin, L.: Distance estimation and the monocular cleaning reflex in praying mantis. Z. vergl. Physiol. **56**, 258—267 (1967).

— — Barrós-Pita, J. C.: Hit distance and the predatory strike of the praying mantis. Z. vergl. Physiol. **56**, 237—257 (1967).

Seitz, G.: Der Strahlengang im Appositionsauge von *Calliphora erythrocephala* (Meig.). Z. vergl. Physiol. **59**, 205—231 (1968).

Wallace, G. K.: Visual scanning in the desert locust *Schistocerca gregaria* Forskoal. J. exp. Biol. **36**, 512—525 (1959).

Dr. Héctor Maldonado
Dr. J. C. Barrós-Pita
Instituto Venezolano de Investigaciones Cientifícas (IVIC)
Apartado 1827
Caracas, Venezuela