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DISTANCE AND SIZE DISCRIMINATION IN A WATER STICK INSECT, *RANATRA LINEARIS* (HETEROPTERA)

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SUMMARY

The role of vision in distance, position and size discrimination in prey capture has been investigated in normal adult water stick insects (*Ranatra linearis* L.: Heteroptera) and in ones with one eye covered.

Both monocular and intact *Ranatra* were able to discriminate between two targets subtending the same angle but presented at different distances. They usually chose the target nearer to their foreleg claws. Although monocular subjects undershot more often than controls, they could still estimate distance correctly.

When presented with two different-sized targets at the same distance, both monocular and intact subjects usually preferred the larger target within a 1°–10° range, even though monocular animals chose the larger object less consistently. They were able to distinguish between two targets differing in size by only 1°.

Asymmetrical presentations of two identical targets stressed the importance of the central position. Intact animals always preferred the target nearer their midline.

These data also revealed the unexpected ability of *Ranatra* to strike accurately at two targets or prey items simultaneously. When two identical targets were presented simultaneously and symmetrically, aims were directed at both targets, and one was grasped by each raptorial foreleg, thus indicating an absence of confusion.

INTRODUCTION

Many insects, particularly predators, use vision to orientate towards small targets (e.g. *Aeshna*, Baldus, 1926; Hoppenheit, 1964; Etienne, 1969; Mokrushov & Frantsevich, 1973; *Cicendela*, Friederichs, 1931; mantids, Maldonado, Levin & Barros-Pita, 1967; Maldonado, Benko & Isern, 1970; *Ranatra*, Cloarec, 1979, 1984a). Precise estimation of predator–prey distance is necessary to ensure enough successful captures. Binocularity, assuming it has the same function in depth perception in insects as in vertebrates, has been thought to play an important role in adjusting aims correctly to the predator–prey distance. However, only recently has clear evidence been given for mantids that binocular disparity provides depth information over short distances (Rossel, 1983). It has been questioned for distance

Key words: insect, *Ranatra*, vision, distance estimation, angular size, predatory behaviour.

estimation in other situations (Horridge, 1977). For example, depth perception in *Nemobius* (Goulet, Campan & Lambin, 1981) goes well beyond the potentialities of binocular triangulation and, in this case, constant angular size seems an important cue for correct orientation.

Most monocular insects cannot strike their prey correctly, but monocular cues are available in some cases. Monocular bulldog ants snapped at the same mean target distance as binocular animals, although only 14% of the ants tested responded when one eye was occluded (Via, 1977). Monocular *Ranatra* were still able to seize prey items, although their predatory performance was impaired (Cloarec, 1979). Crickets use motion parallax rather than binocular vision to judge the distance of a vertical pole onto which they jump (Eriksson, 1980); monocular crickets exhibited accuracy similar to that of controls but hesitated longer.

The water stick insect, *Ranatra linearis*, is a sit-and-wait ambush predator which strikes with its raptorial forelegs at potential prey items that come within reach. Foreleg movement varies in amplitude according mainly to the distance and position of the target (Cloarec, 1980). Before striking, *Ranatra* may turn or rise slightly towards the target if necessary, without moving its posterior legs, so that the potential prey is usually within 30° of the predator's midline. Previous observations showed that unilateral blinding impaired predatory performance in *Ranatra*. Monocular animals showed a lower level of striking and hitting, a shorter maximum reactive distance, a lower capture rate, a longer delay between arousal and striking than intact animals (Cloarec, 1979, 1984a). However, when monocular animals did strike, they were still able to estimate predator-prey distances correctly. Thus, *Ranatra* must be able to exploit monocular cues to estimate depth. It is likely that intact insects usually use binocular cues as the theoretical limits of binocular vision, calculated for the first four nymphal instars using Burkhardt, Darnhofer-Demer & Fischer's (1973) formula, coincide with maximum reactive distances (Cloarec, 1984a).

Size is often a limiting factor in prey selection, and many predators such as mantids (Maldonado *et al.* 1970) are able to estimate the size of objects and to distinguish between potential prey and objects to be avoided. Monocular mantids seem to lack total depth perception as their reaction to predators beyond 15 cm was impaired. However, the way distance and retinal image size interact to determine a predator's behaviour is a topic which has remained largely unexplored in insects.

The aim of the experiments presented here was to investigate size and distance discrimination in adult *Ranatra*. Comparisons were made between the performance of intact subjects and unilaterally blinded animals when two targets were presented simultaneously.

MATERIALS AND METHODS

Animals

Adult water stick insects, *Ranatra linearis* (Heteroptera, Nepidae), were either reared in the laboratory from eggs or collected, as adults, from local ponds. They

were kept individually in small glass containers (10×20×15 cm). A glass rod 1 cm in diameter and inclined at 45° was provided for support. Water was at room temperature (20 ± 2°C). These insects were placed near a large window and received no extra artificial lighting. During experiments they were given abundant chironomid larvae at weekends and then starved for at least 24 h before testing started.

Blinding

Monocular subjects were blinded unilaterally by covering their right eye with layers of red nail varnish mixed with carbon black and diluted if necessary in acetone. *Ranatra* were never tested the day the varnish was applied. The varnish was inspected regularly under a binocular microscope and tests were validated only if the varnish was still intact.

Targets

A series of 21 spherical targets was used. Targets were glass balls covered with red varnish and attached to transparent glass rods. This type of dummy had previously proved to be very attractive (Cloarec, 1969). Diameters ranged from 0.09 mm to 17.7 mm so as to have a range of targets viewed under angles of 1° to 10° at distances varying from 5 mm to 100 mm. Different predator-prey distances were tested: 5 mm, 10 mm (both very close to the head), 15 mm (optimal reactive distance for monocular subjects), 20 mm (optimal reactive distance for controls), 25 mm (maximum foreleg reach), 50 mm and 100 mm (both far out of reach).

Test procedure

Ranatra were tested at irregular intervals, but at least 1 h was allowed to elapse between two tests with the same animal. A minimum of 20 reactions (strikes or hits) were recorded for each test situation. Each *Ranatra* was tested in its own tank several times, but never twice for the same situation and not necessarily for each situation as there were up to 50 subjects at one time. Individual records were not kept. Targets were always presented by hand. External factors were controlled as far as possible and the experimental environment was made homogeneous. As good contrast enhances detection, targets were presented in front of a uniform background of white paper stuck on the outside of the individual tanks. Simultaneous presentations were made by holding one target in each hand and by giving the targets a vertical downwards movement (Fig. 1A). Speed varied with distance from the predator so that angular speeds remained roughly constant (Fig. 1B). If an insect did not react immediately, the targets were moved up and down a few times, then, in the rare cases where there was still no reaction, they were removed. Angles were measured using a transparent protractor 17 cm in diameter, placed over the tank with its centre on the vertical line above the subject's head. Additional marks under the tank helped to evaluate angles.

Internal factors linked with particular physiological states can also influence animal performance. Foreleg posture has previously proved to be a good indicator of

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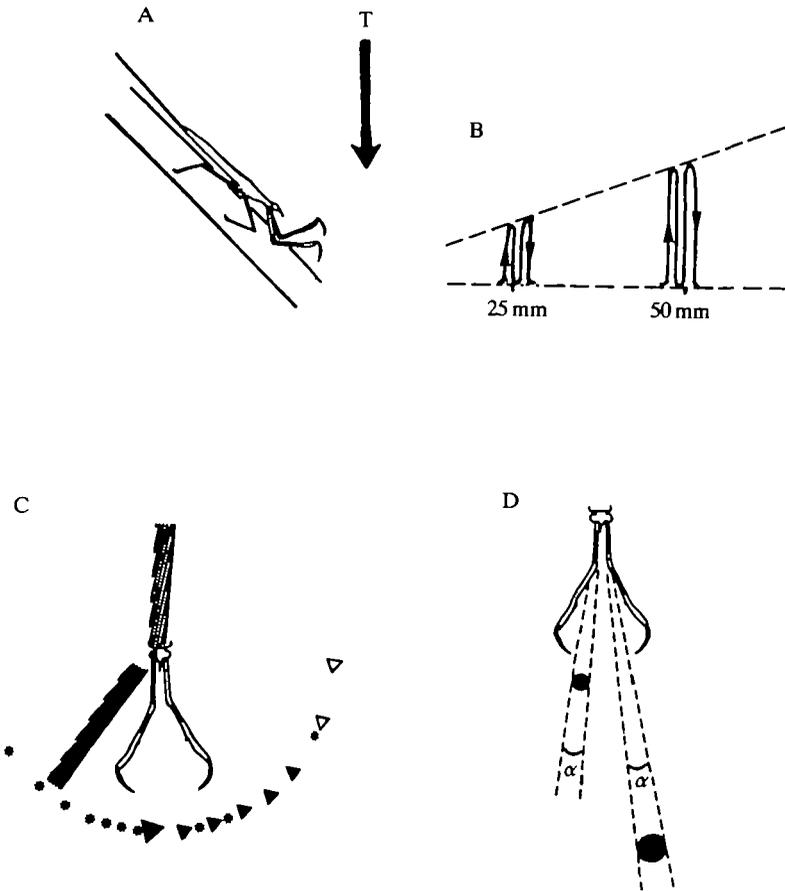


Fig. 1. Target presentation. (A) Side view of a *Ranatra* in the capture posture with arrow indicating direction of presentation of target T. (B) Example of movement of two targets of same angular size presented simultaneously, one at 25 mm, the other at 50 mm, from the head. (C) Presentation of two identical targets at same distance from the head. Stars, positions of symmetrical presentations; triangles, positions of asymmetrical presentations; black triangle, fixed position; shaded area, limits of visual field of left eye. (D) Distance discrimination: presentation of two targets of similar angular size ($\alpha = 5^\circ$ here).

internal digestive states and of potential reactions to alimentary stimuli in *Ranatra* (Cloarec, 1974). Therefore only subjects in capture posture – thus indicating that their alimentary tract was void and their reactivity to alimentary stimuli at a maximum – and with their bodies parallel to the glass rod were tested.

Only complete strikes (including hits and misses) were recorded. These predatory aims were either *oriented* towards one target or *non-oriented*. The category of non-oriented aims included *double strikes* directed towards both targets simultaneously, therefore indicating absence of preference, and *undirected* strikes occurring near the midline when targets were more lateral.

Selection index

A standard index was used:

$$S = \frac{|T1 - T2|}{T1 + T2},$$

where T1 represents the number of predatory movements directed towards one target, and T2 the number of movements directed towards the other target. S varies between 0 (= no choice) and 1 when all movements are oriented towards one target.

RESULTS

Target size

In preliminary tests, one target was presented at a time vertically along the insect's midline, at different distances from the subject's head in order to decide which sizes of targets should be used in subsequent experiments. The distances at which different reactions occurred were recorded for different-sized targets (Table 1). Maximum distances and sizes are given in Table 1, even if that reaction was recorded only once. However, hungry animals reacted similarly in over 90% of the trials. Intact insects reacted to targets which subtended angles ranging between 0.3° and 30°, although angles between 1° and 20° were preferred. Objects subtending too large an angle (more than 35°) were always avoided whatever the distance. Most predatory strikes occurred when the target moved close to the claws of the forelegs (15–25 mm from the head). Monocular animals reacted differently. They struck most at targets which subtended angles between 5° and 6°.

When targets out of reach elicited strikes, the aims of both monocular and intact subjects were directed towards the target, but claws closed far from it as *Ranatra* can only seize prey items which come within reach (i.e. nearer than the length of the foreleg). However, more monocular subjects undershot under these conditions.

It would thus seem that predatory performance is primarily controlled by the distance of the target in intact insects, which judge range more correctly, and by target size in monocular animals.

As targets with angular dimensions between 5° and 6° seemed particularly attractive whatever the distance, it was decided to present targets at both these angles (5° and 6°), as well as at much smaller angles (1° and 2°), or bigger angles (10°) at different distances from the head, either near maximum reactive distance or much closer and much farther away in order to test further whether real size and position, as well as angular size, influenced the behaviour of monocular and control animals. Angles of both 5° and 6° were tested to investigate the possibilities of distinguishing an angular difference of 1°, which is much smaller than the average interommatidial angle of 4° in adults.

Reactivity

During the experiments reported here reactions were timed and capture rate (number of items seized in relation to the total number of attempts) and reactivity

(number of reactions – strikes or hits – in relation to the number of presentations) were estimated. The present data confirmed previous results indicating that in *Ranatra* reactivity of both monocular and intact animals as well as capture rate decreased as predator–prey distance increased (Cloarec, 1979): the nearer the prey item, the higher the probability that *Ranatra* would strike at and grasp it (Fig. 2). No differences between the performance of monocular and intact subjects were found when targets were presented very near the head, but otherwise monocular subjects usually showed lower levels of reactivity than controls and longer delays before any predatory movement (arousal, strike or hit). Exceptionally, monocular subjects were more responsive than intact subjects for large objects far out of reach.

Table 1. *Reactions of monocular and control subjects to different targets*

Target diameter (mm)	Intact animals			Monocular subjects		
	Presentation distance (mm)	Reaction	Angular size (degrees)	Presentation distance (mm)	Reaction	Angular size (degrees)
0.10	≤ 20	strikes	≥ 0.3	≤ 6	strikes	≥ 1
0.45	≤ 25	strikes	≥ 1	≤ 20	strikes	≥ 1.2
2	≤ 50	strikes	≥ 3	≤ 50	arousal	≥ 2.3
				≤ 20	strikes	≥ 5.7
5	≤ 60	strikes	≥ 4.7	70–50	strikes	5.7–4
10	≤ 29	avoidance	≥ 19	100–150	strikes	3.8–5.7
	≤ 100	no reaction	≥ 5.7			
14.5	≤ 25	strikes	≥ 30	≤ 200	strikes	≥ 4.1
30	≤ 50	avoidance	≥ 30	200–250	strikes	6.8–8.5

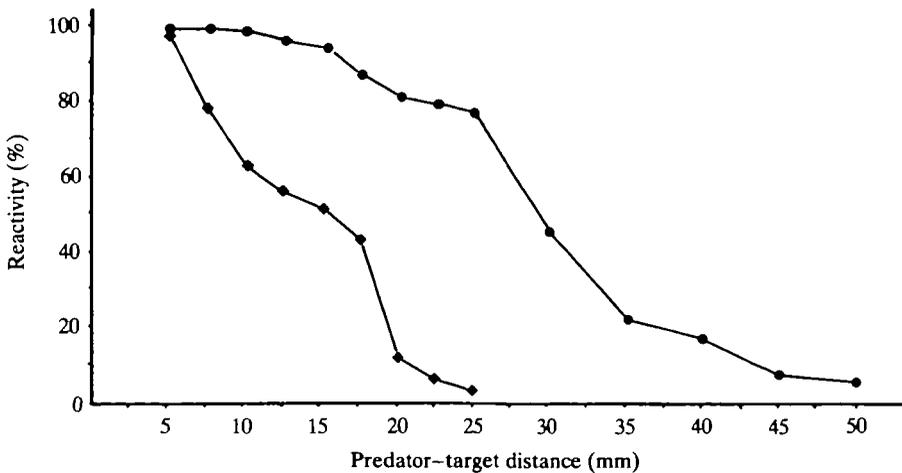


Fig. 2. Reactivity of monocular and intact *Ranatra*. Reactivity (i.e. percentage of number of strikes in relation to number of presentations of a 5° target) in relation to predator–target distance. Black circles, intact subjects; black diamonds, monocular subjects.

Reactivity also decreased as targets were presented at greater lateral distances from the midline.

Symmetrical identical targets

To make sure that the presentation was unbiased and that subjects had no preference for one side, two identical 5°-targets were presented symmetrically at 20 mm (optimal reactive distance for controls) from the eyes. The angle formed by the centres of the targets and the subject's head varied from 10° to 120° (Fig. 1C).

Controls

In this case a particular reaction was observed. When aiming at a prey item, the adult usually moves its forelegs simultaneously (the femurs subtend an angle of 60° between each other at rest) thus bringing the femur tips closer to each other and nearer to the prey item. When two targets were presented symmetrically and simultaneously, the forelegs again moved simultaneously but they stayed apart: each foreleg was directed towards one target and each claw often closed over a target, then both targets were seized simultaneously, one in each claw. When this happened, subjects were considered to make no choice.

Controls aimed significantly more often at both targets simultaneously when the targets were only 10°, 20° or 30° apart than towards only one target. These subjects aimed strikes at one target as often as at both targets at the same time when targets were further apart (40°–90°) and significantly more towards one target when they were 120° apart (Table 2A).

When aims with both forelegs were directed towards one target only, controls never chose significantly between the two targets. The selection index (S, Fig. 3) is close to 0 for all presentations, with a maximum of 0.35 when the two targets are 30° apart.

Monocular subjects

With small angular separations, monocular animals struck simultaneously at both targets. This tendency decreased as the angular distance between the targets increased. Both targets were rarely seized simultaneously when they were more than 40° apart. Monocular subjects could still perceive both targets with one eye as they have a 45° frontal binocular overlap; that means that the left eye can see up to 45° right of the midline and should be able to perceive simultaneously two targets presented symmetrically up to 90° apart (Cloarec, 1984b).

However, another category of strikes could be observed, particularly when targets were more than 40° apart: forelegs were brought closer together and strikes were directed near the subject's midline, far from the targets. These movements have been called 'undirected strikes' and were recorded under these test conditions only for monocular subjects. Intact animals never showed similar behaviour, in this or in subsequent tests.

Significantly more predatory movements were oriented towards one target than towards both or towards neither when targets were more than 40° apart. When

Table 2. *Symmetrical presentation of two identical targets*

Angular separation	10°	20°	30°	40°	50°	70°	90°	120°
A CONTROLS								
Number of aims								
L target	3	3	2	5	5	5	9	8
R target	3	2	4	8	8	6	8	11
Both targets	16	17	16	13	14	15	13	2
Total	22	22	22	26	27	26	30	21
L/R <i>P</i>	NS	NS	NS	NS	NS	NS	NS	NS
O/NO <i>P</i>	<0.05	<0.02	<0.05	NS	NS	NS	NS	<0.001
B MONOCULAR SUBJECTS								
Number of aims								
L target	6	9	10	9	17	16	15	15
R target	0	0	0	0	0	0	0	0
Both targets	14	12	10	11	0	1	0	0
Undirected					3	4	5	5
Total	20	21	20	20	20	21	20	20
L/R <i>P</i>	<0.02	<0.01	<0.01	<0.01	<0.001	<0.001	<0.001	<0.001
O/NO <i>P</i>	NS	NS	NS	NS	<0.01	<0.01	<0.05	<0.05

O/NO: comparison between the number of strikes aimed at one target implying a choice and at either both targets simultaneously or at neither (undirected aims), thus indicating no choice. X^2 , 1 d.f.

L/R: comparison between number of aims at the left target (L) on the intact side and at the right target (R) on the blinded side for monocular subjects. X^2 , 1 d.f.

NS, not significant.

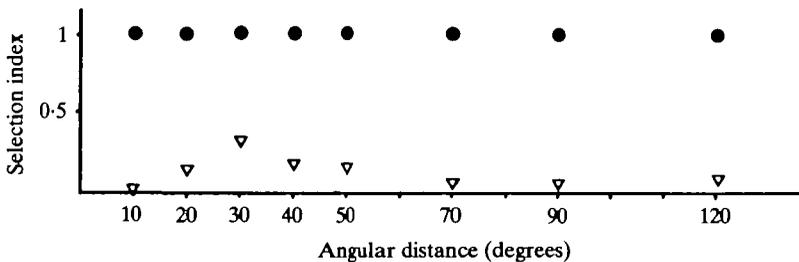


Fig. 3. Symmetrical presentation of two identical targets. Selection index, *S*, for different angular distances between the two targets for controls (triangles) and for unilaterally-blinded subjects (circles).

strikes by both forelegs were directed towards one target, monocular subjects always aimed at the left target (on their intact side). The selection index, *S*, is at its maximum and equal to 1 for all angular distances (Table 2B; Fig. 3).

Comparisons between controls and monocular subjects

One important feature of these results is the high proportion of simultaneous captures, even by monocular animals. Monocular subjects oriented more towards

one of the targets when they were 50°, 70° or 90° apart and performed more undirected aims. Controls never chose significantly between the two targets whereas monocular subjects always did.

Asymmetrical identical targets

The importance of the relative positions of the targets was tested by presenting two identical targets, both seen at an angle of 5°, at different angular distances from the midline (Fig. 1), but at the same distance from the head (20 mm). The right-hand target was presented along the midline so as to remain well within the visual field of monocular subjects, and the angular distance between the two targets was varied by presenting the left-hand target at different angular distances laterally.

Controls

The insects aimed significantly more often at both targets simultaneously when they were only 10° apart. This situation was similar to that in the previous experiment. However, differences were observed for the other angular distances. When targets were 20° apart, *Ranatra* aimed as often at one target as at both simultaneously; and they always aimed at only one target when these were more than 30° apart.

When strikes by both forelegs were aimed at one target, the centre target was chosen significantly more often than the lateral one when they were 30° or more apart. In fact, controls never aimed at the lateral target when the angular distance between targets was more than 30° (Table 3A; Fig. 4).

Monocular subjects

They aimed significantly more often at one target when these were 40° or more apart; at smaller separations they aimed at both targets simultaneously as often as at only one target.

These results differ from those reported in the previous test mainly for the situation where targets were 40° apart: significantly more strikes were aimed at one of the targets when they were presented asymmetrically than when they were presented symmetrically. No undirected strikes were recorded.

When strikes by both forelegs were aimed at one target, monocular subjects showed no preference for one of the targets when they were 10°, 30°, 40° or 50° apart. However, they chose the left-hand target when it was at 20° and the right-hand target only when the left-hand one was presented at 70° and at 90° (Table 3B).

Comparisons between controls and monocular subjects

Controls oriented more often towards one target; monocular subjects still seized both targets simultaneously when they were 40° and 50° apart, whereas controls

never did under those conditions. Choice of centre target was more pronounced in controls when targets were 30° or more apart.

Size discrimination

Size discrimination was tested by presenting symmetrically and simultaneously two targets with different angular values at the same distance from the predator's

Table 3. *Asymmetrical presentation of identical targets*

Angular separation	10°	20°	30°	40°	50°	70°	90°
A CONTROLS							
Number of aims							
L target	2	5	1	0	0	0	0
R target	2	6	16	20	20	20	20
Both targets	17	47	23	0	0	0	0
Total	21	21	22	20	20	20	20
L/R <i>P</i>	NS	NS	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
O/NO <i>P</i>	< 0.01	NS	< 0.02	< 0.001	< 0.001	< 0.001	< 0.001
B MONOCULAR SUBJECTS							
Number of aims							
L target	5	12	11	9	5	2	0
R target	2	2	4	9	13	18	20
Both targets	66	30	35	18	10	0	0
Total	21	20	23	22	20	20	20
L/R <i>P</i>	NS	< 0.01	NS	NS	NS	< 0.001	< 0.001
O/NO <i>P</i>	NS	NS	NS	< 0.01	< 0.001	< 0.001	< 0.001

See Table 2 for details.

Right target was always presented 5° right of midline (see Fig. 1).

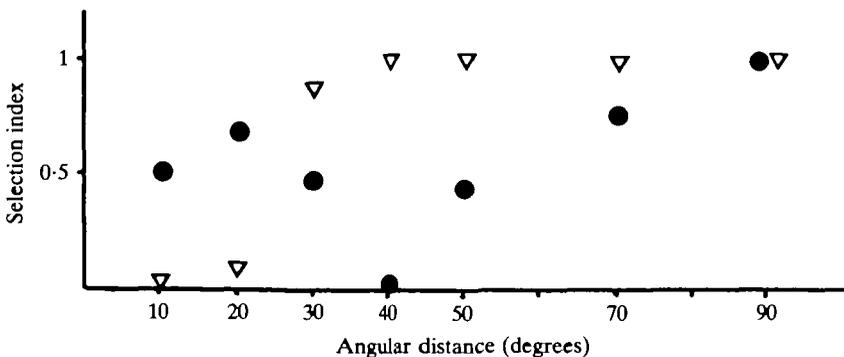


Fig. 4. Asymmetrical presentation of two identical targets. Selection index, *S*, for different angular distances between the two targets for controls (triangles) and for unilaterally-blinded subjects (circles).

head. The angular separation of targets was between 10° and 15° . Different predator–target distances were tested (see Materials and Methods; Fig. 1D).

Controls

In most cases, controls aimed at one of the targets. Only when both targets were presented at 100 mm were unoriented aims significantly more numerous than oriented aims, whatever the angular size of the targets (Fig. 5).

Controls discriminated between different-sized targets and aimed nearly exclusively at the larger target (Fig. 6). The only exceptions concerned the 5° – 6° pair, and even then more strikes were aimed at the larger target, although the difference was not significant.

As very few predatory movements were really oriented towards one target when pairs were presented at 100 mm, the preference for the larger target was rarely significant.

Monocular subjects

In 30 cases out of a total of 70 there were significantly more non-oriented than oriented aims (Fig. 5). At 50 mm and at 100 mm, most pairs elicited significantly more non-oriented aims, but the difference was statistically significant only once. Only at 5 mm did the number of oriented aims tend to be higher than the number of non-oriented aims. Monocular subjects chose the larger target when choice was significant, but they chose less consistently than controls did (Fig. 6). The data revealed an absence of choice between the following pairs: 1° – 2° ; 5° – 6° ; 5° – 10° for all distances.

Comparisons between controls and monocular subjects

Statistical comparisons made case-by-case revealed that, except at the shortest (5 mm) and at the furthest (100 mm) distances, aims of controls were usually significantly better oriented towards the targets than those of monocular subjects (Fig. 4). Both intact and monocular insects preferred the larger of the two targets and chose it with nearly the same precision.

Distance discrimination

Distance discrimination was evaluated by presenting two different-sized targets simultaneously and symmetrically. They were presented at different distances from the subject's head so that they subtended the same angle.

Controls

In most cases, most aims were oriented towards one target. However, subjects rarely aimed precisely at a target when both were out of reach (at 50 and 100 mm) or when both targets were at maximum distance from the optimal reactive distance

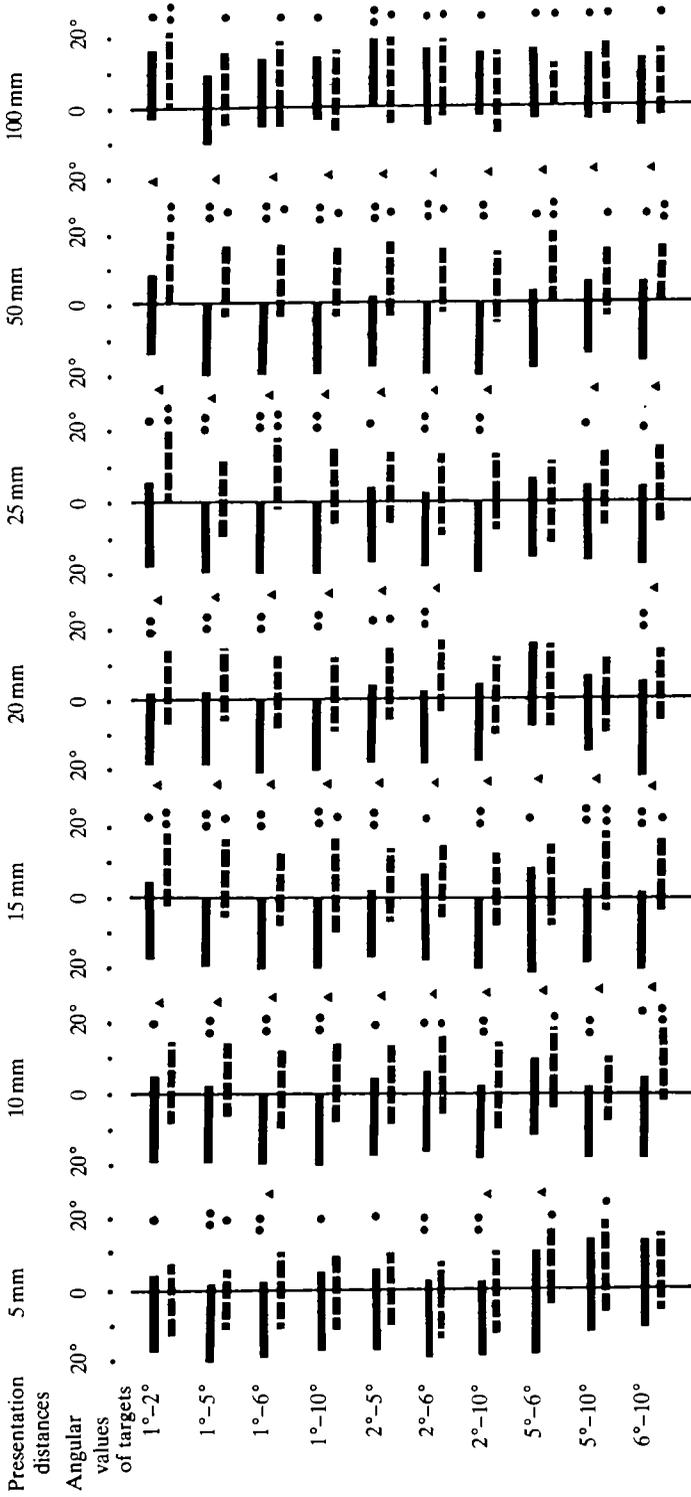


Fig. 5. Orientation in size discrimination experiments. Number of unoriented predatory movements (on the right of the 0 lines) and of movements oriented towards one of the two targets (on the left of the 0 lines) of different angular values (left column) presented simultaneously and symmetrically, at different distances (top line) for controls (solid bars) and monocular subjects (broken bars). Dots in first column indicate significant differences between the number of oriented and of unoriented movements for a group. Triangles in the second column indicate significant differences between performance of controls and of monocular subjects for a given test situation. ●, $P < 0.05$; ●●, $P < 0.001$; ▲, $P < 0.05$.

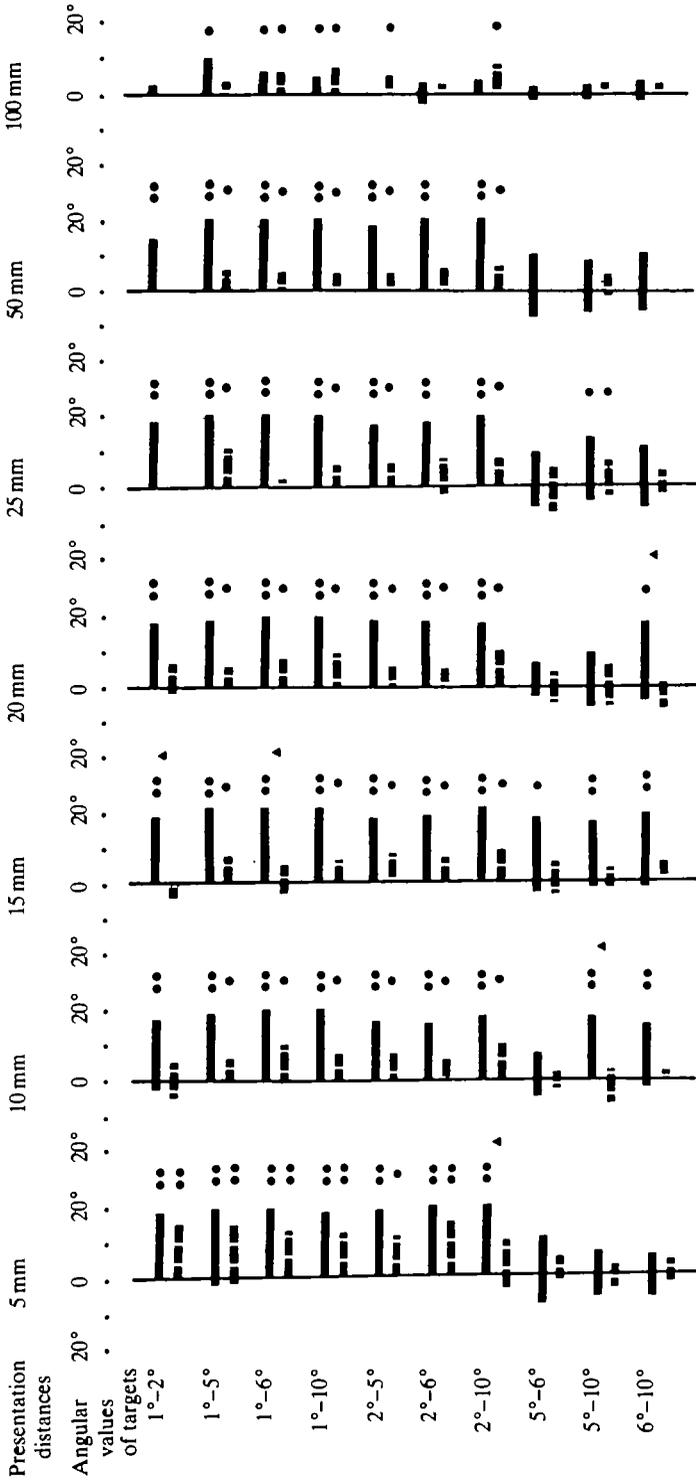


Fig. 6. Size discrimination. Number of predatory movements aimed at the larger (on the right of the 0 lines) and at the smaller (on the left of the 0 lines) of the pair of targets (left column) presented simultaneously. Dots in the first column indicate a significant choice between targets. Other details as in Fig. 5.

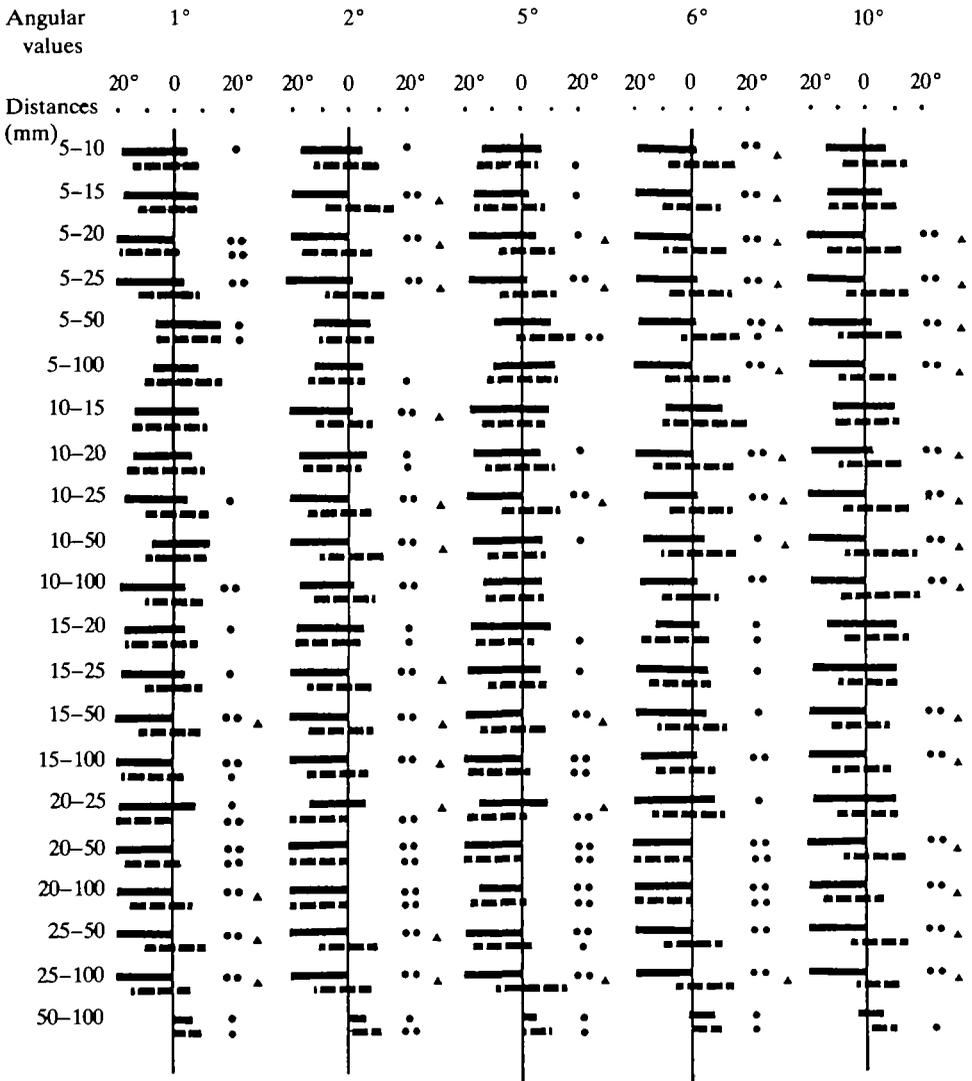


Fig. 7. Orientation in distance estimation experiments. Number of oriented predatory movements (on the left of the 0 lines) and of unoriented movements (on the right) towards one of the two targets presented simultaneously at different predator-prey distances (left column) but seen at the same angle (top line). Dots in the first row indicate a significant difference between the number of oriented and of unoriented movements for a group. Other details as in Fig. 5.

(5 mm-50 mm; and 5 mm-100 mm). Predatory movements were directed simultaneously at both targets when the difference between the predator-target distances was small (e.g. pairs 10 mm-15 mm or 20 mm-25 mm) (Fig. 7).

When predatory movements were oriented, controls always aimed at the target nearest to 20 mm (the optimal reactive distance), whether it was the further or the closer of the two. They directed about as many predatory movements towards the

closer as towards the further target when the choice was between 20 mm and 25 mm, 15 mm and 25 mm or 15 mm and 20 mm (Fig. 8).

Monocular subjects

In most cases there were as many predatory movements oriented towards a target as unoriented aims. Subjects never aimed precisely at a target when they were both out of reach (50 mm and 100 mm). Significantly more aims were oriented towards one target, often when one of them was presented at 15 mm (Fig. 8).

When predatory movements were oriented, monocular subjects, like controls, aimed more often at the target nearer their optimal reactive distance, which is 15 mm and differs from that of controls (Fig. 8).

Comparisons between controls and monocular subjects

Comparisons case-by-case indicated that controls oriented their predatory movements significantly more often than monocular subjects did, particularly when the targets were large (10°) or when one target was at 25 mm (except when the other target was at 15 mm). Significant differences in performance were observed between monocular subjects and controls. The two groups of *Ranatra* aimed at different targets when they were given a choice between 10 and 20 mm; 10 and 25 mm; 15 and 25 mm; 20 and 25 mm, whatever the angular size of the targets. Monocular subjects aimed more often at the closer target whereas controls aimed more often at the further target.

DISCUSSION

The experiments presented above aimed to investigate the role of visual discrimination of distance, position and size of targets in prey capture by *Ranatra*.

Distance estimation

Both monocular and intact *Ranatra* are able to discriminate between objects differing in absolute size but subtending the same angle, if they are presented at different distances from the head. Data presented here showed that *Ranatra* possess monocular mechanisms for judging depth: monocular subjects were able to aim correctly at different targets. Distance estimation was, however, somewhat impaired by unilateral blinding as these animals showed a higher proportion of non-oriented aims and of undershooting than controls.

Both monocular and intact subjects usually chose the target nearer to their foreleg claws and nearer to their optimal reactive distance (i.e. distance at which a prey item directly approaching a predator is most likely to elicit a strike). Previous data underlined discrepancies in optimal reactive distance between monocular and control subjects (Cloarec, 1979); it was significantly closer for monocular insects.

Our experimental conditions do not allow us to speculate about the type of monocular cues which are actually used. Nevertheless motion parallax would be a good candidate. Motion parallax, however, does not provide simple cues when the

object itself is in motion, and it is impossible to separate self- and object-induced components of image motion experimentally, because *Ranatra* only respond to moving targets. No self-induced movements of head or body comparable to the 'peering' movements made by locusts before jumping (Wallace, 1959) or the head saccades made by crickets while orienting towards a target (Lambin, 1984) were recorded before strikes. However, all these observations on *Ranatra* were made directly, and finer techniques may still reveal slight head movements.

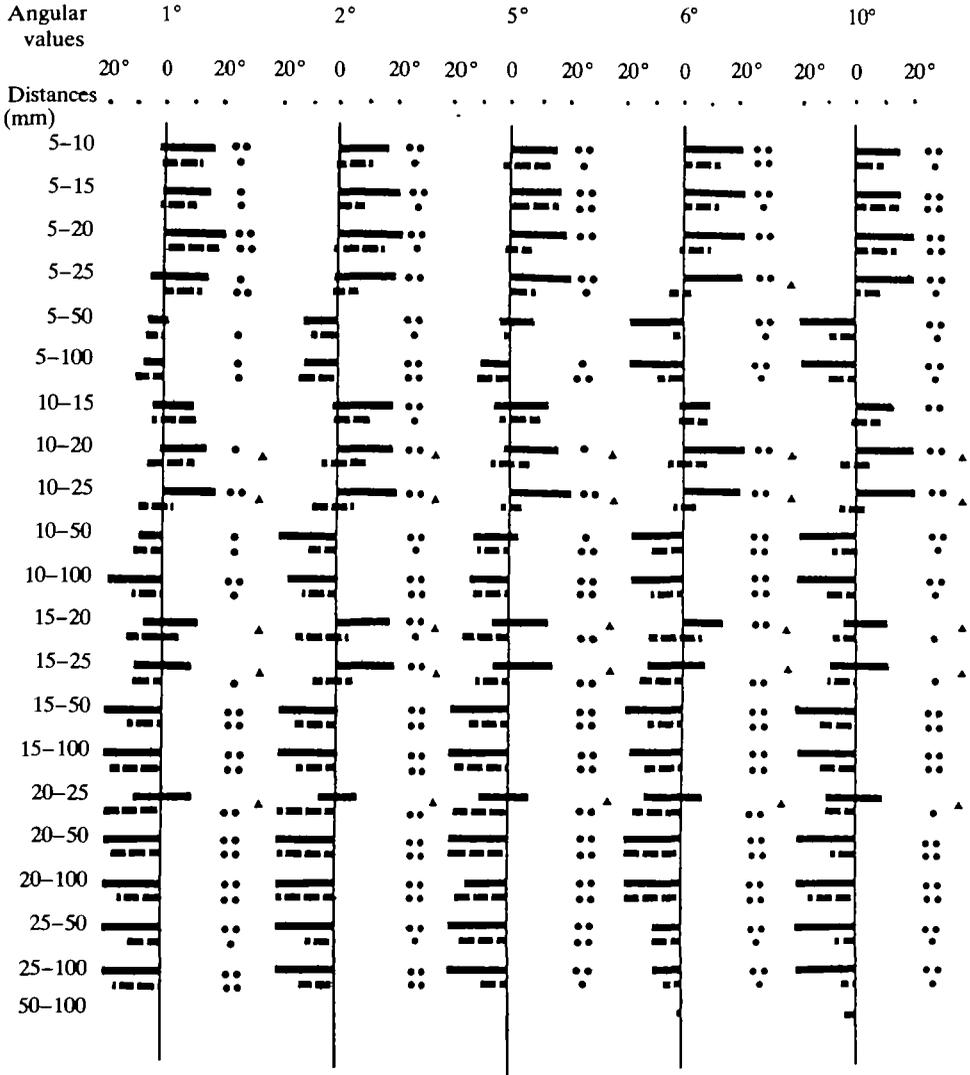


Fig. 8. Distance estimation. Number of predatory movements aimed at the nearer (on the left of the 0 lines) or at the further (on the right) of the pair of targets presented simultaneously at different distances but seen at the same angle. Dots in the first column indicate a significant choice between targets. Other details as in Fig. 5.

As the performance of intact subjects was significantly better than that of monocular animals, *Ranatra* probably normally use binocular cues in addition to monocular cues, although these experiments do not provide evidence that *Ranatra* possess binocular mechanisms for judging depth. Calculations applying Burkhardt *et al.*'s (1973) formula indicated that binocular cues could operate up to 31.5 mm from the head, along the midline (Cloarec, 1984a), and therefore beyond the tips of the forelegs (25 mm).

Relative position

Position of targets in relation to the animal's midline was also found to be an important factor. Although symmetrical presentations of two identical targets to controls revealed no preference for one side, asymmetrical presentations of two identical targets revealed the preponderance of the central position: controls always chose the target nearer to their midline. Unilateral blinding modified this choice: monocular subjects preferred targets presented between 20° and 40° on the side of their intact eye, even when the second target was nearer their midline, and well within their visual field. This emphasizes the importance of the specialized central acute zone of the eye within the binocular overlap involved in distance estimation. There is, however, no anatomical evidence for an acute zone in *Ranatra* eyes (Cloarec, 1984b). In comparison, in mantids (Maldonado & Barros-Pita, 1970; Barros-Pita & Maldonado, 1970; Levin & Maldonado, 1970), hoverflies (Collet & Land, 1975) and beetles (Bauer, 1981), for example, ommatidia in an area covered by the projection of a centred prey have the best depth perception.

Size perception

Data presented here also revealed that retinal image size is important in eliciting and controlling predatory behaviour in *Ranatra*. Both monocular and intact subjects usually preferred the larger target within a range from 1° to 10°, even though monocular animals chose the larger object less consistently. However, targets subtending angles of 5° or 6° were nearly as attractive as 10° targets whatever their presentation distance. This may be because a 10° target presented at 25 mm, that is at maximum catching distance, is difficult to handle with a 4.4 mm diameter compared to the 4.9 mm average length of a claw. It is therefore close to the maximum size that can be seized.

Although *Ranatra* can distinguish between targets differing by only 1° in diameter, there is no evidence that they can judge real size of objects in the way many vertebrates can. *Ranatra* do not seem to rely on image size to judge distance but image size remains an important determinant of target choice. It would seem that retinal image size and distance act as two independent parameters to control probability of striking.

Double strikes

The experiments show that *Ranatra* can strike accurately at two prey at once. A high proportion of predatory movements were aimed at both targets simultaneously

when they were presented symmetrically, whether they were of identical size or not. This occurred particularly when the angular distance between them was less than 60°. 60° corresponds to the angle formed by the two foreleg femurs when showing the capture posture (Cloarec, 1974). Each claw closed over one of the targets, even if *Ranatra* had to move its forelegs towards the midline. The same phenomenon was observed when the distance between the two targets was not important (≤ 10 mm). Complementary observations with live prey items proved that this was not an experimental artefact. When presented with two live prey items simultaneously under similar experimental conditions, *Ranatra* again caught both items simultaneously one in each claw, at about the same rate as the dummies.

If *Ranatra* were using disparity information, one would expect them to be confused by two identical targets presented simultaneously and symmetrically. The fact that they usually responded correctly and simultaneously to both targets, even when they were at different distances, if the difference did not exceed 10 mm, suggests an absence of confusion of the two targets or of their images and the use of additional mechanisms, probably parallax. It must be stressed that monocular animals were capable of seizing two targets simultaneously although they did it less frequently.

These tests did not reveal any conditions under which intact animals presented with two targets responded to apparent rather than real images. Curiously, only monocular animals misdirected strikes when two targets were presented simultaneously. All undirected strikes occurred along the animal's midline.

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