

## ESCAPE TRAJECTORIES IN ANGELFISH (*PTEROPHYLLUM EIMEKEI*)

PAOLO DOMENICI\* and ROBERT W. BLAKE

*Department of Zoology, University of British Columbia, Vancouver BC,  
Canada V6T 2A9*

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### Summary

Although fish escape trajectories are linearly related to stimulus direction, they vary considerably after the initial turn away from the stimulus. Past studies of escape trajectories in fish and other animals have been analysed by employing linear plots of stimulus angle *versus* body turning angle. Here, we define escape trajectories as a circular variable, with 0° as stimulus direction.

Angelfish (*Pterophyllum eimekei*) escape in non-random trajectories when the stimulus is presented laterally, within an angular zone of approximately 30–120° (discriminating zone). The circular plot of escape trajectories shows a bimodal pattern that cannot be revealed by linear analysis. Angelfish escape preferentially at 180° and 130° away from the stimulus, maximizing the distance covered from the stimulus and escaping at the limit of their discriminating zone, respectively. Angelfish correct their responses when turning towards the stimulus, suggesting that escape trajectories are modulated by sensory feedback.

Re-analysis of published work on other animals, by employing circular histograms of escape trajectories, reveals multimodal patterns which are also not apparent from the linear plots. We suggest that the presence of multiple preferred trajectories may be adaptive in preventing predators from learning any single fixed pattern of response and compensating for it.

### Introduction

Escape responses in fish have been studied from biomechanical (e.g. Weihs, 1973; Webb, 1976, 1978; Harper and Blake, 1990; Domenici and Blake, 1991a), physiological (e.g. Eaton *et al.* 1981, 1988, 1991; Faber *et al.* 1989; Covell *et al.* 1991) and behavioural (e.g. Dill, 1974a,b; Hurley and Hartline, 1974; Blaxter *et al.* 1981) perspectives. The ability of fish to escape predators may depend upon linear performance (velocity, acceleration) (Webb, 1976; Harper and Blake, 1990), accurate timing (Eaton and Hackett, 1984) and turning capabilities (Howland, 1974; Webb, 1982; Nissanov and Eaton, 1989; Domenici and Blake, 1991a).

\*Present address: Dunstaffnage Marine Laboratory, PO Box 3, Oban, Argyll, PA34 4AD, Scotland.

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Fish escape responses are commonly divided into two stages on the basis of kinematics (Weihs, 1973): a preparatory stage (stage 1) involving a strong, unilateral muscular contraction bending the fish into a C-shape, and a propulsive stage (stage 2) in which the tail bends in the opposite direction to that in stage 1. In angelfish, stage 2 may be a coasting phase ('single bend' escape responses; Domenici and Blake, 1991a). The initial contraction during stage 1 is usually initiated by a single pair of reticulospinal neurons (Mauthner cells), although alternative circuits may exist (Eaton *et al.* 1984; DiDomenico *et al.* 1988). A parallel network of neurons interacting with the Mauthner cells controls the extent of stage 1 contraction (DiDomenico *et al.* 1988).

Escape paths tend to be away from the stimulus, since the axial musculature contralateral to the stimulus contracts during stage 1, forming the C-bend (Blaxter *et al.* 1981; Eaton *et al.* 1981). It has been suggested that turning angles are preprogrammed at the onset of the escape response in fish (Nissanov and Eaton, 1989; Eaton *et al.* 1991) and other animals (Camhi and Tom, 1978; Camhi and Levy, 1988). Recently, Eaton and Emberley (1991) showed that escape trajectories are linearly related to stimulus direction. However, they vary considerably after the initial turn away from the stimulus (Eaton *et al.* 1981; Eaton and Emberley, 1991).

The analysis of escape trajectories in fish (Eaton *et al.* 1981; Eaton and Emberley, 1991) and other animals (Camhi and Tom, 1978; Comer and Dowd, 1987; Nalbach, 1990) has been performed by employing linear plots of stimulus angle *versus* body turn (defined as the angle between the animal's initial orientation and its orientation at the end of the response). Here, escape trajectory is considered as a circular variable, and is defined as the angle between the stimulus direction and the animal's swimming path at the end of the response. Our main result is that the circular distribution of escape trajectories of angelfish appears to be bimodal, not unimodal as linear analysis suggests.

### Materials and methods

Angelfish (*Pterophyllum eimekei*) of four group sizes (total length,  $L=4.9\pm 0.4$ cm; mean $\pm 2$ S.E.M.,  $N=4$ ;  $L=7.3\pm 0.4$ ,  $N=5$ ;  $L=10.9\pm 0.4$ ,  $N=4$ ;  $L=13.5\pm 0.6$ ,  $N=2$ ) were employed. Fish were kept as described by Domenici and Blake (1991a). A total of 62 escape responses (14, 20, 18, 10 for each size group respectively) was analysed. A 2.5cm reference grid was placed on the bottom of the tank. In all the escape responses analysed, the center of mass of any given fish was within a 7.5cm $\times$ 7.5cm square in the center of the experimental tank (60cm $\times$ 32cm $\times$ 30cm) and at least 1 body length away from the walls. Therefore, stages 1 and 2 of the escape responses were unobstructed by walls since angelfish escapes cover about half a body length (Domenici and Blake, 1991a).

Eaton and Emberley (1991) showed that the proximity of walls can influence the escape trajectories of goldfish when less than 0.6–0.7 body length away from the fish's center of mass. They suggested that escape responses in which the initial position of the fish was approximately 8.8cm (0.7–0.9 body length) from the side of the tank were influenced by wall effects, when compared to escapes in which the initial position averaged 13.2cm (1.0–1.3 body lengths) from the nearest wall. In our experiments, fish were startled when between 12.25 and 16cm from the nearest wall, which corresponded

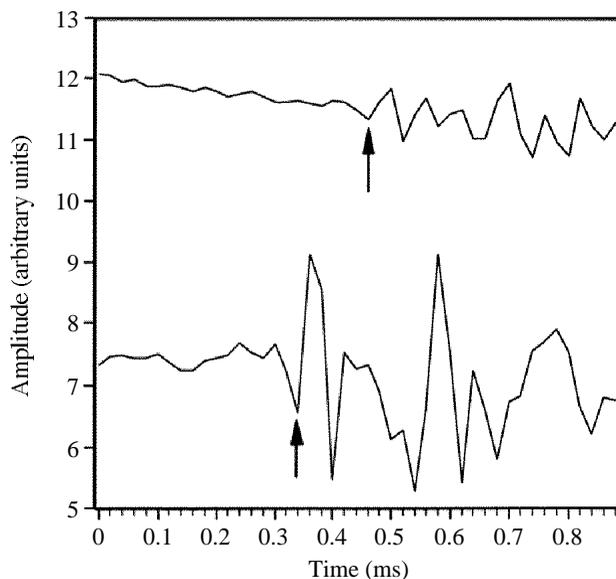


Fig. 1. Time delay in stimulus signal as perceived by two hydrophones positioned along the axis of stimulus direction. The distance between the hydrophones was 18cm. The bottom trace is from the hydrophone closer to the stimulus. Arrows show the first inflection of the sound signal for each hydrophone. Sampling intervals indicate 0.02ms. Six points (0.12ms) separate the two arrows. The y-axis represents amplitude in arbitrary units since the two hydrophones had different sensitivities.

to a minimum of 1 body length (for the largest fish) and maximum of about 3 body lengths (for the smallest fish). Although to be certain of the absence of any wall effects one should ideally operate in open water, we have only analysed trials in which wall effects should be minimal.

The experimental tank was placed on four rubber supports (diameter 5cm, height 2cm), one at each corner, and situated in the middle of a larger acrylic tank (240cm×120cm×45cm) surrounded by a black plastic screen. The fish could see neither the approaching stimulus nor the investigator. Fish were left in the experimental tank for at least half an hour prior to being startled. A mirror angled at 45° over the tank allowed the top view of the fish to be filmed. A plastic container filled with 1l of water was suspended at a fixed height of 1.5m over the edge of the tank. This container was lifted 1m away from the tank and swung against the side of the external tank to elicit the escape response.

In order to ascertain the directionality of the stimulus, two hydrophones (Sparton 60 CX 123, omnidirectional, with a flat response  $\pm 3$ dB from 50Hz to 80kHz), separated by 18cm along the axis of the stimulus direction (5cm and 23cm away from the wall closest to the stimulus, respectively), were placed in the middle of the experimental tank. Therefore, the separation line between the two hydrophones was bisecting the area of 7.5cm×7.5cm in the center of the experimental tank, in which the center of mass of any given fish was located when it was startled. The recorded time interval between the onsets of the sound signal for the two hydrophones was 0.12ms (sampled at intervals of 0.02ms;

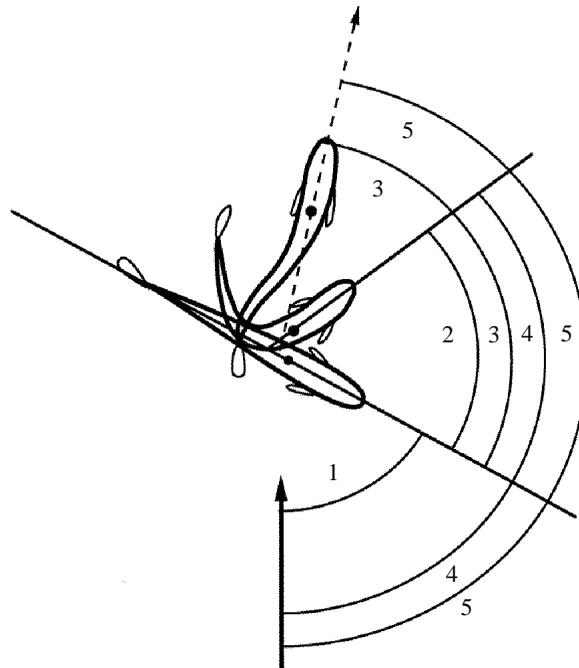


Fig. 2. Diagram illustrating angular variables. Solid arrow indicates stimulus direction, dashed arrow indicates escape direction. The straight fish indicates position at time 0, the fish bent into a C indicates position at the end of stage 1 (s1), and the swimming fish indicates position at the end of the escape response. Black dots indicate the fish 'stretched straight' center of mass. 1 indicates the angle representing initial orientation; 2 represents the angle of s1 turn; 3 represents the angle of escape turn; 4 represents the angle of s1 trajectory; 5 represents the angle of escape trajectory.

Fig. 1). The calculated delay for the speed of sound in fresh water at 20°C (1481 ms<sup>-1</sup>; Kinsler *et al.* 1982) is 0.124ms for an 18cm separation. The agreement of our measurement and the time delay calculated for a sound stimulus travelling along the distance between the two hydrophones showed that the stimulus presented to the fish was indeed directional along the separation line between the two hydrophones. This confirmed the stimulus direction that we have used in our analysis. If sound was travelling in any other direction, the delay between the signals received by the two hydrophones would have been shorter or reversed.

Escape responses were filmed at 400Hz (see Domenici and Blake, 1991a, for details). The position of the 'stretched straight' fish center of mass for the film analysis was determined by aligning a wire, marked at 0.37 body length (Domenici and Blake, 1991a), along the midline of the image of the fish. The center of mass and the tip of the head were recorded frame by frame. These points were later analysed on a digitizing pad (GTCO type, 0.61 m×0.91m) connected to a computer (80286 AT-compatible). Data were then transferred to an Olivetti M24 PC for further analysis.

The orientation of the fish relative to the stimulus direction was random (Watson  $U_n^2$  test;  $P>0.1$ ;  $N=62$ ). Responses to stimuli from the left and right were pooled as if the

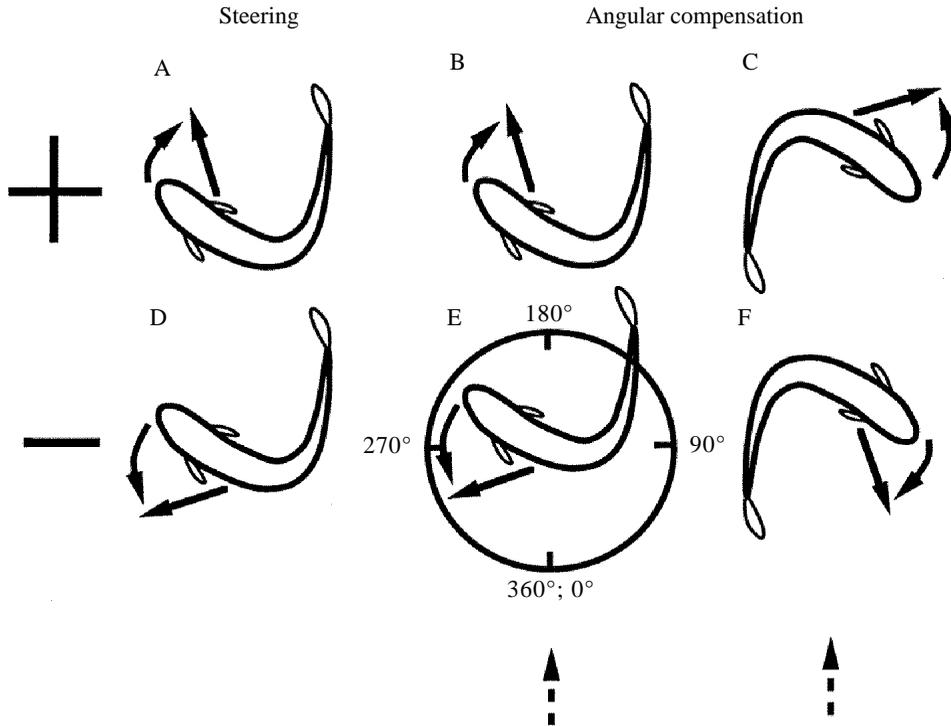


Fig. 3. The sign of steering and angular compensation. Fish position is shown at the end of s1. The top diagrams show positive steering (A) and positive angular compensation (B,C). The bottom diagrams show negative steering (D) and negative angular compensation (E,F). The angular orientation relative to the stimulus is shown in E. Steering (curved arrow) is positive when the escape turn (straight solid arrow) is in the same direction as the C-bend, and negative if *vice versa*. The sign of angular compensation (curved arrow) depends on the direction of steering relative to the stimulus (dashed arrow). Angular compensation is positive when steering is away from the stimulus, and negative when towards it. Since all the escapes were analysed as if the stimulus were on the right side of the fish at the onset of the response, the fish's initial orientation (not shown) is always between  $0^\circ$  and  $180^\circ$ .

stimulus were always on the right side of the animal. Stage 1 (s1) angle for the anterior part of the body was determined by measuring the angle between the straight lines passing from the center of mass to the tip of the head at frame 0 (one frame before the first detectable movement) and at the end of stage 1. A total escape angle was measured between the midline of the fish at frame 0 and the regression line considering seven positions of the center of mass about the end of stage 2 (stage  $2 \pm 3$  frames) (Domenici and Blake, 1991a). Here, these angles were redefined as s1 turns and escape turns when calculated relative to the midline of the fish at frame 0, and s1 trajectories and escape trajectories when relative to the stimulus direction (Fig. 2). Directionality of the response was indicated by the orientation of the C-bend relative to the stimulus (Blaxter *et al.* 1981). Therefore, escape responses were divided into 'away responses' and 'towards responses' when the fish was oriented away and towards the stimulus, respectively.

Initial orientation was defined as the angle between the midline of the fish anteriorly

and stimulus direction at the onset of the response (Fig. 2). Since responses to left and right stimuli were pooled, initial orientation spanned from  $0^\circ$  to  $180^\circ$ . An angle of  $0^\circ$  indicated the stimulus direction; therefore, a fish positioned at  $180^\circ$  was facing directly away from the stimulus. Angular measurements were made to the nearest degree. The discriminating zone was defined as the angular zone of initial orientation within which the fish responded to a stimulus by escaping in non-random directions.

Steering was defined as the difference between escape turn and s1 turn. Therefore, steering was positive if the fish continued the turn after s1, and negative if it reversed the turn direction (Fig. 3). Angular compensation was calculated as having the same absolute value as steering; however, its sign was negative if steering was directed towards the stimulus, and positive if away from it (Fig. 3). Steering and angular compensation have been determined for the semicircles  $0-180^\circ$  and  $180-360^\circ$  separately, since the signs of the two variables within each semicircle did not always coincide (see Table 1 and Fig. 3).

Circular statistics (Batschelet, 1981) were employed to analyse s1 and escape trajectories, since they could vary from  $0^\circ$  to  $360^\circ$ . Linear regression was used to analyse the relationship between s1 trajectories and steering, since each regression (A and B; Fig. 10) included only s1 trajectory values within  $40^\circ$ . When a circular variable is restricted to such a narrow interval, linear analysis is appropriate (Batschelet, 1981). All other angular variables were considered to be angular distances and were analysed employing linear statistics.

## Results

### *Effect of fish initial orientation*

The effect of the initial orientation on the randomness of the trajectories has been analysed by considering six arbitrarily defined 'orientation sectors' of  $30^\circ$  each ( $N=10, 9, 14, 10, 11$  and  $8$  for each sector from  $0^\circ$  to  $180^\circ$ ). For initial orientations of  $0-30^\circ$ ,  $120-150^\circ$ ,  $150-180^\circ$ , both s1 and escape trajectories are randomly distributed. For the remaining three orientation sectors ( $30-60^\circ$ ,  $60-90^\circ$ ,  $90-120^\circ$ ), s1 and escape trajectories are not random ( $P<0.01$ ;  $P<0.005$ ;  $P<0.005$  for each sector respectively; Watson's  $U_n^2$ -test). Therefore, the discriminating zone spans from  $30^\circ$  to  $120^\circ$ . Angular deviations of both s1 and escape trajectories in each orientation sector are shown in Fig. 4.

Initial orientation has an effect on directionality (away *versus* towards responses) of escapes. Away responses occur significantly more often than towards responses only for initial orientation sectors of  $30-60^\circ$  and  $60-90^\circ$  ( $P<0.05$  in both cases; binomial test; Fig. 5). When the initial orientation is near  $180^\circ$ , a towards response at a small angle of turn may actually mean that the fish is effectively swimming away from the stimulus. Therefore, escape trajectories within two semicircles ('away semicircle' *versus* 'towards semicircle') have been considered (Fig. 5). There are significantly more escape trajectories in the semicircle away from the stimulus ( $90-270^\circ$  sector, see inset in Fig. 5) than in the opposite semicircle when the initial orientation is  $90-120^\circ$  and  $120-150^\circ$  ( $P<0.05$  in both cases; binomial test; Fig. 5).

Circular-linear correlation of away responses shows that escape trajectories are

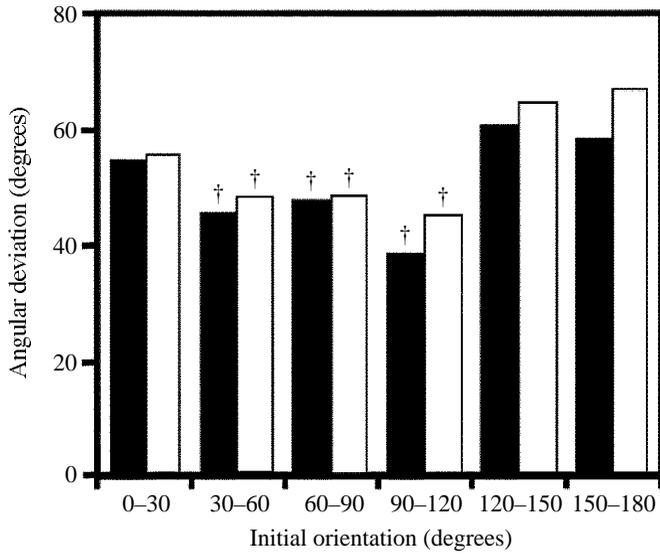


Fig. 4. Angular deviation of s1 and escape trajectories for different 30° orientation sectors. † indicates non-random distribution of trajectories. Filled bars indicate escape trajectories and open bars indicate s1 trajectories.

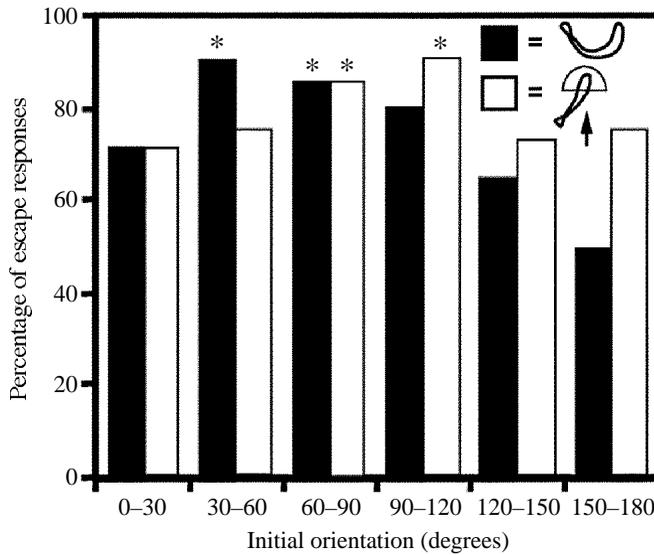


Fig. 5. Percentage of away responses for different 30° orientation sectors. \* means significantly different from random. Filled bars indicate away responses and open bars indicate responses in the semicircle away (90–270°) from the stimulus. The inset shows the orientation of the C-bend of the fish at the end of stage 1 for away responses (filled square) and the position of the fish for escape trajectories that are within the semicircle away from the stimulus (open square). Arrow indicates stimulus direction.

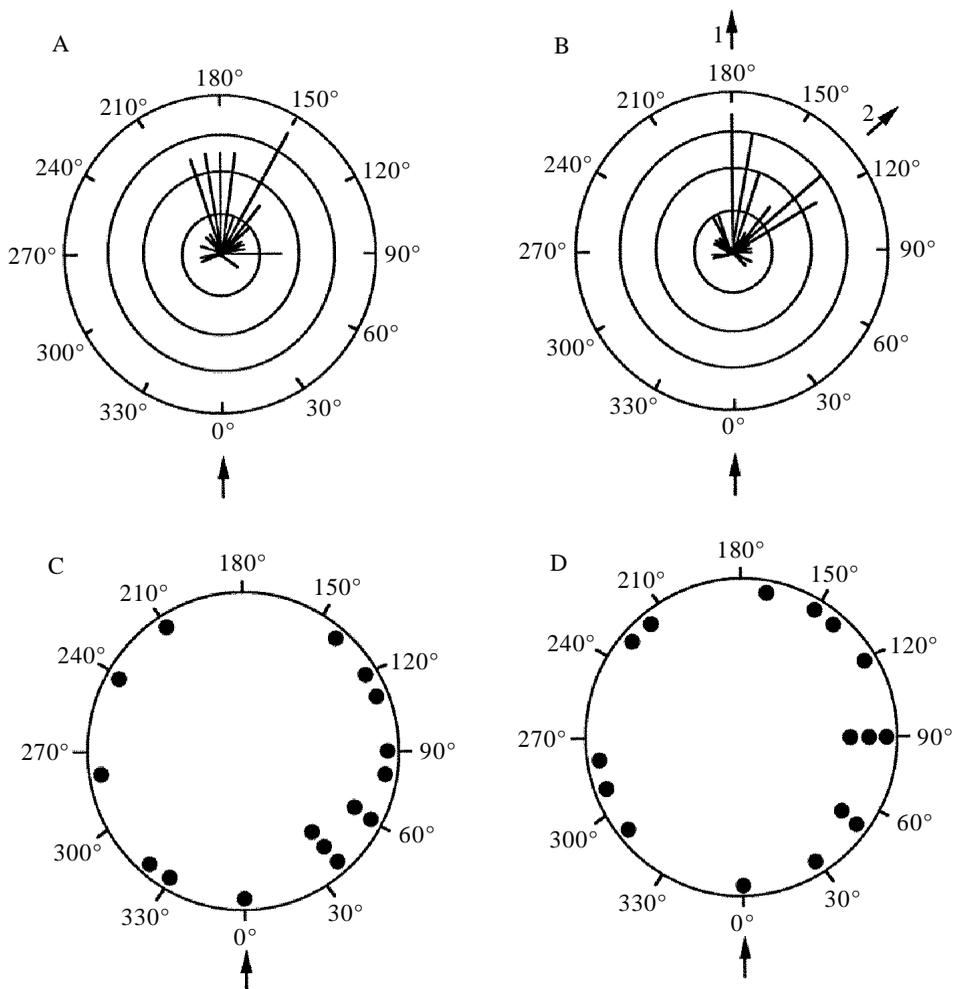


Fig. 6. Circular frequency distributions of s1 trajectories (A, away responses; C, towards responses) and escape trajectories (B, away responses; D, towards responses). Responses to left or right stimuli are plotted as if the stimulus were always on the right side of the fish. Frequency histograms (away responses) and scatter diagrams (towards responses) are shown. The frequency interval is 10°. In away responses, each concentric circle represents a frequency of 2. In B, two main modes, separated by 50°, are present: numbered arrows indicate trajectory 1 (180°) and trajectory 2 (130°).

independent of initial orientation ( $N=46$ ;  $P>0.1$ ; rank correlation test), whereas s1 trajectories are positively correlated to it ( $N=46$ ;  $P<0.01$ ; correlation coefficient  $D_n=0.4$ ; rank correlation test). Initial orientation has no effect on steering ( $N=46$ ;  $P>0.1$ ; linear regression test).

#### *Escape trajectory frequency distributions*

Fish size has no effect on s1 and escape trajectory distributions ( $N=62$ ;  $P>0.05$ ; Mardia–Watson–Wheeler test). Away responses occur significantly more often than

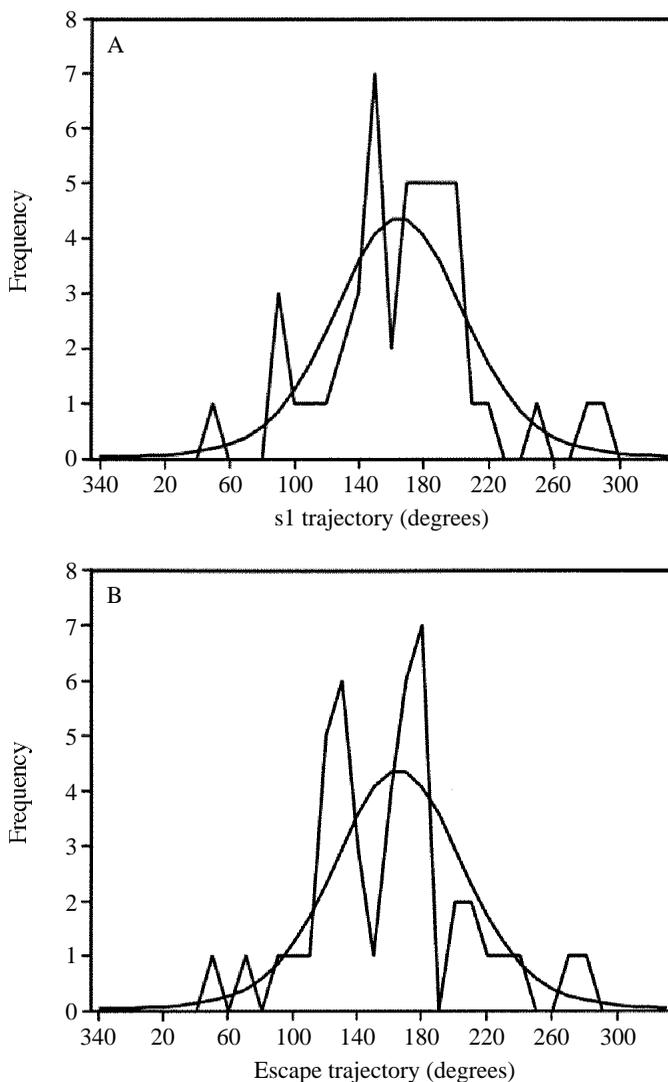


Fig. 7. Fitting a von Mises distribution to frequency polygons of s1 (A) and escape (B) trajectories. Frequency intervals are  $10^\circ$ . A does not differ significantly from a von Mises distribution, whereas B does ( $P < 0.05$ ).

towards responses (46 and 16, respectively; different from random;  $P < 0.001$ ; binomial test). The circular frequency distributions of both s1 and escape trajectories are non-random in away responses (Watson's  $U_n^2$ -test;  $P < 0.005$  in both cases; Fig. 6A,B) and random in towards responses (Watson's  $U_n^2$ -test;  $P > 0.1$  in both cases; Fig. 6C,D). The frequency distribution of the s1 trajectories of away responses is not statistically different from a von Mises distribution (Fig. 7A;  $N=46$ ;  $P > 0.25$ ;  $\chi^2$ -test), whereas that of the escape trajectories is (Fig. 7B;  $N=46$ ;  $P < 0.05$ ;  $\chi^2$ -test), with two peaks at  $130^\circ$  and  $180^\circ$ . Although we have not tested the significance of the two peaks (there is no standard

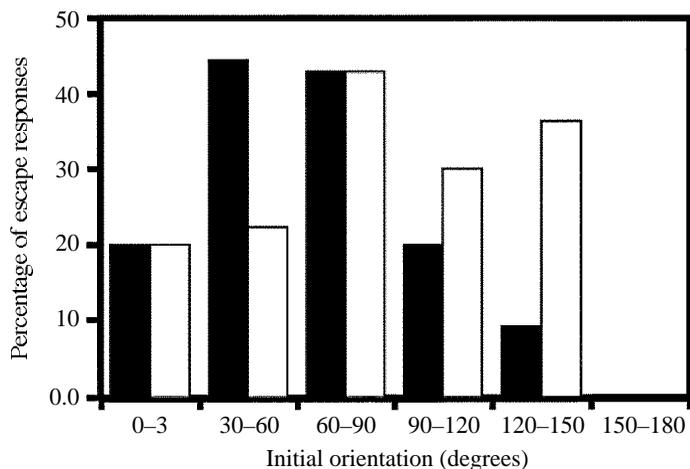


Fig. 8. Percentage of responses within 110–150° (filled bars) and 150–190° range of escape trajectories (open bars) for different orientation sectors.

method for this procedure), a bimodal pattern is apparent. To test whether the presence of the two modes is related to the initial orientation, we have separated escape trajectories into two groups (110–150° range and 150–190° range) that can be considered as representative of the two modes. Fig. 8 shows the percentage of responses within each 40° range of escape trajectories for different initial orientations. Initial orientation has no effect on the choice of escape trajectory (Mann–Whitney test;  $P > 0.1$ ).

In addition to circular statistics, we have employed a linear regression analysis of stimulus angle *versus* escape angle, following Camhi and Tom (1978) and later studies (e.g. Eaton *et al.* 1981; Nalbach, 1990). We define stimulus angle as the angle between the midline of the fish posteriorly and stimulus direction at the onset of the response (see inset in Fig. 9); escape angle corresponds to our definition of escape turn. Therefore, if escapes were always directly away from a stimulus, they would appear as a line passing through the origin at 45° in Fig. 9. The bimodal nature of the data visible when employing circular analysis is not apparent from the graph, although the linear regression is significant ( $P < 0.0001$ ;  $r^2 = 0.3$ ). Arguably, linear regression analysis is not appropriate because it assumes that for any given value of  $x$ , the values of  $y$  are normally distributed (Zar, 1984; Sokal and Rohlf, 1981). We have shown that this is not the case as the circular distribution of the data does not fit a normal circular (von Mises) distribution.

#### *Steering and angular compensation*

Steering in away and towards responses has been determined for the semicircles 0–180° and 180–360° separately. Steering in the two semicircles is not statistically different for away responses and the values have the same sign, whereas they have opposite signs and are statistically different in towards responses (Table 1). Pooled angular compensation values for away and towards responses differ ( $t$ -test;  $P < 0.001$ ), as do their absolute values ( $t$ -test;  $P < 0.05$ ). In addition, the initial orientation,  $s_1$  and escape turn of towards responses differ for the two semicircles (Table 1). In away responses,

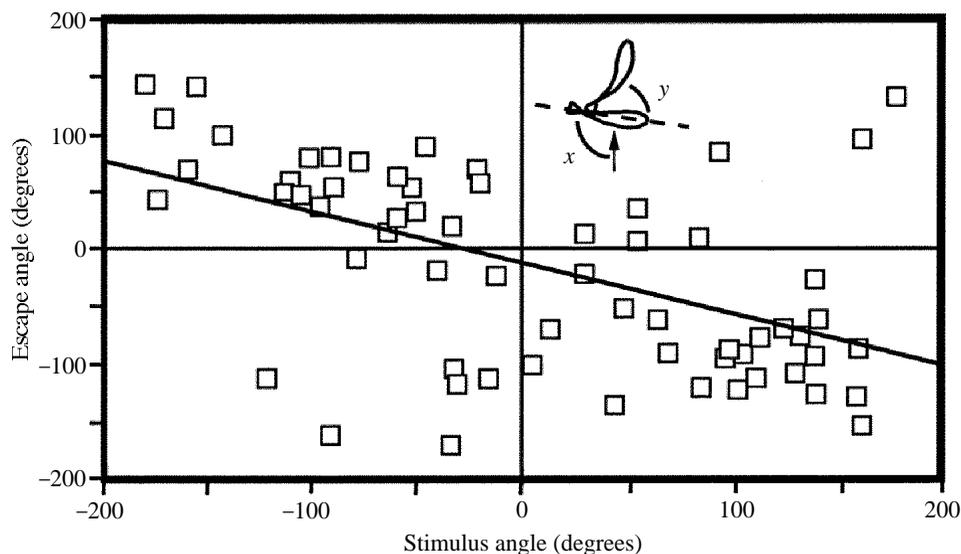


Fig. 9. Linear analysis of angelfish escape angle, following conventions established by Camhi and Tom (1978). Points in the right half of the graph show escape angles of trials in which the stimulus was on the right side of the animal. Points on the upper half of the graph indicate trials in which the fish's escape angle is on the right side of its midline. Therefore, points in the lower right sector or in the upper left sector indicate responses in which the escape angle was away from the stimulus.  $N=62$ ;  $r^2=0.3$ ;  $y=0.44x-12$ ;  $P<0.0001$ . The inset shows the position of the fish at time 0 (straight fish) and its midline (dashed line), and at the end of the escape response (curved fish). Arrow indicates stimulus direction. Curved lines ( $x$  and  $y$ ) indicate stimulus angle and escape angle respectively.

only initial orientation and angular compensation are statistically different for the two semicircles (Table 1).

The relationship between steering and s1 trajectory of away responses is shown in Fig. 10. The two regression lines include only responses that have escape trajectories within  $110\text{--}150^\circ$  (line A) or  $150\text{--}190^\circ$  (line B). These two ranges were chosen as representative of the two modes. The slopes of the two lines are not significantly different from each other, whereas their elevations are ( $P<0.001$ ).

## Discussion

### *Effect of initial orientation*

Angelfish discriminate the direction of a stimulus by escaping in non-random trajectories when the stimulus is presented laterally, within an angular zone (discriminating zone) that extends approximately between  $30^\circ$  and  $120^\circ$  of their initial orientation (Fig. 4). These results are confirmed by the left-right choice data (Fig. 5), both for directionality (left-right C-bend) and semicircle chosen.

Canfield and Eaton (1990) have shown that swimbladder acoustic pressure transduction initiates Mauthner-mediated responses, and suggest that the detection of particle motion ensures the directionality of the response. Although mechanical

Table 1. *Turning angles, angular steering and angular compensation in two semicircles for towards and away responses*

Semicircle	s1 turn (degrees)	Escape turn (degrees)	Angular steering (degrees)	Angular compensation (degrees)	Initial orientation (degrees)	<i>N</i>
Towards responses						
0–180°	62.3 (20.7)	45.7 (29.8)	–16.5 (11.3)	16.5 (11.3)	134.4 (17.0)	11
180–360°	116.4 (20.4)	127.4 (22.8)	11.0 (13.9)	11.0 (13.9)	34.0 (34.6)	5
Pooled	<i>P</i> <0.01 79.2 (20.0)	<i>P</i> <0.005 71.2 (28.8)	<i>P</i> <0.05 –7.9 (10.9)	NS 14.8 (8.7)	<i>P</i> <0.05* 103.1 (28.6)	16
Away responses						
0–180°	81.0 (12.2)	73.7 (14.4)	–7.3 (4.9)	–7.3 (4.9)	60.2 (13.0)	29
180–360°	84.5 (13.8)	78.2 (14.1)	–6.2 (7.6)	6.2 (7.6)	124.5 (15.0)	17
Pooled	NS 82.3 (9.2)	NS 75.4 (10.4)	NS –6.9 (4.3)	<i>P</i> <0.005 –2.3 (4.7)	<i>P</i> <0.001* 84.0 (13.1)	46

A *t*-test is used for all comparisons except \* (Mann-Whitney test).  
±2 S.E. of the mean are given in brackets.  
NS, not significant.

sensitivity is maintained for 360° around the fish (Hawkins and Horner, 1981), left–right discrimination should decrease when the stimulus is more in line with the longitudinal axis of the fish, because of limits in the angular discrimination between two sound sources (Schuijff, 1975).

The influence of initial orientation on the escape response is an important factor in the predator–prey interactions of fish. Webb (1986) suggests that a predator should attack in line with the anticipated escape trajectory of the prey. Since escape responses were thought to be fixed turns of 90°, Webb (1986) suggests that the strike angle should also be about 90°. However, escape turns are not fixed, but cover a wide range of angles (Domenici and Blake, 1991a; Eaton *et al.* 1991). In addition, the prey may optimize its positioning relative to a stalking predator.

To maximize directional sensitivity and visual acuity, the prey should orient itself perpendicular to a stalking predator. However, if readiness to escape is to be maximized, the prey should be oriented away from the predator, in order to minimize the time for turning away, while keeping the predator within its angular regions of directional mechanical discrimination and visual range. This corresponds to an orientation of about 130° away from the predator (Hall *et al.* 1986).

Webb and Skadsen (1980) report values of strike angle for pike attacking minnows. Although calculated as the angle subtended between the prey body axis and the strike path of the predator's snout, these values should approximate the prey's orientation, since

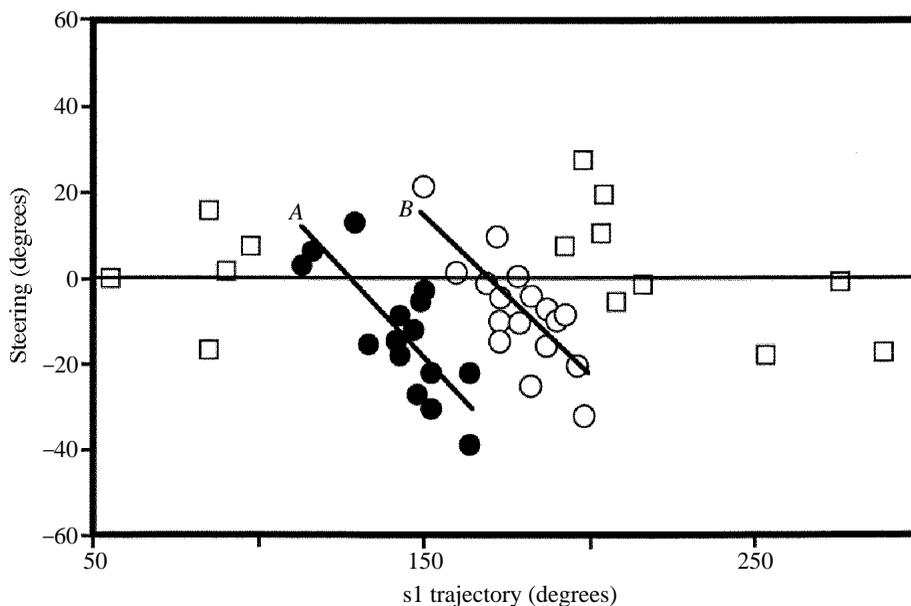


Fig. 10. Relationship between steering and s1 trajectories in away responses. The two regression lines include only escapes whose trajectory is within  $110\text{--}150^\circ$  (line A; filled circles) or  $150\text{--}190^\circ$  (line B; open circles). For A,  $y=94-0.75x$ ;  $r^2=0.59$ ;  $P<0.001$ ;  $N=15$ . For B,  $y=132-0.78x$ ;  $r^2=0.60$ ;  $P<0.001$ ;  $N=17$ . The slopes of the two lines are not significantly different from each other, whereas their elevations are ( $P<0.001$ ). Open boxes represent responses whose trajectory is less than  $110^\circ$  or greater than  $190^\circ$ .

strike paths were more or less straight. The frequency distribution of strike angles does not deviate significantly from normality (Webb and Skadsen, 1980). The mean angle is  $82^\circ$  and the highest mode is the  $80\text{--}100^\circ$  sector. This corresponds to a position approximately perpendicular to the predator. A second peak occurs at  $120\text{--}140^\circ$  (Fig. 3, Webb and Skadsen, 1980) regardless of strike pattern. This suggests an alternative prey strategy, corresponding to the position maximizing readiness to escape.

Initial orientation has no effect on escape trajectory of away responses and a positive effect on s1 trajectory. This may explain why the distribution of s1 trajectories does not show the distinct modes seen in escape trajectories (Fig. 7). With steering, swimming trajectories are brought to fixed directions away from the stimulus.

#### *Frequency distribution of escape trajectories*

As in previous studies (Blaxter *et al.* 1981; Eaton *et al.* 1981) away responses occur significantly more often than towards responses. In addition, towards responses are uniformly distributed around a circle (Fig. 6C and D), whereas away responses are not (Fig. 6A and B). Towards responses have been suggested to be due to errors of symmetry in the left–right decision (Eaton and Emberley, 1991).

Eaton and Emberley (1991) re-analysed the data of Eaton *et al.* (1981) by pooling left and right responses and found that the magnitude of both s1 and escape turns decreases linearly as the angle of the initial orientation increases. Arguably, comparing our data

with those of Eaton *et al.* (1981) and Eaton and Emberley (1991) is confounded by differences in methodology. In particular, in both studies on goldfish (Eaton *et al.* 1981; Eaton and Emberley, 1991), trajectories were measured at a fixed time after the initial movement. However, fast-starts can differ in duration by as much as 100%, reflecting differences in turning angle (Domenici and Blake, 1991a). For our measurement of escape duration (Domenici and Blake, 1991a), like that of Camhi and Tom (1978), Comer and Dowd (1987) and Nalbach (1990) for other animals, the escape response is considered to be over when the animal's turn stops.

When employing traditional linear methods of analysing escape angles *versus* stimulus direction (Camhi and Tom, 1978; Eaton *et al.* 1981; Nalbach, 1990), we obtain a significant linear regression for angelfish escapes (Fig. 9), suggesting a unimodal distribution of escape trajectories. However, a circular plot reveals a bimodal pattern that differs from normal circular distribution (Fig. 6B).

Multiple preferred trajectories may be adaptive in preventing predators from learning any fixed single pattern of response and compensating for it. Eaton *et al.* (1977) suggest that fish escape trajectories should be unpredictable for this same reason. However, a random distribution of escape trajectories would include, for instance, escapes directed straight towards the predator's mouth. Also, linear analysis (Fig. 9) suggests a normal unimodal distribution of escape trajectories, whereas circular analysis (Fig. 7) shows that angelfish do not employ a single (unimodal) direction of response. Multiple preferred trajectories may maximize the distance from the stimulus (trajectory 1; 180°; Fig. 6B) and, by following trajectory 2 (Fig. 6B; 130°), fish may maximize this distance while swimming just within their discriminating zone. Interestingly, the direction of visual avoidance responses in fish is just within their visual zone (Hall *et al.* 1986). Sensory feedback at these particular orientations (trajectories 1 and 2) may control the escape turns and angular steering. The choice of one preferred trajectory is independent of the initial orientation of the fish.

Eaton and Emberley (1991) found that the linear relationship between initial orientation and s1 turn was stronger than that between initial orientation and escape turn. They suggested that this is due to the variability of steering (stage 2 in Eaton and Emberley, 1991), and that this variability is due to the influence of nearby walls. Our results show that steering subsequent to s1 contributes to the bimodal pattern (Fig. 7 and Fig. 10). In our experiments, wall effect was minimal. Although there were differences in relative distance (body lengths) from the wall due to differences in fish size, the latter had no effect on the escape trajectory distribution. Therefore, varying the relative distance from the wall had no effect on the escape trajectory.

Fish size has no effect on s1 and escape trajectories. However, size has an effect on turning (Domenici and Blake, 1991b) and flexibility (Aleev, 1969). Smaller fish are more flexible about their center of mass than larger fish. For large fish, the angle required to set a particular trajectory from a given orientation may be too large for a single body contraction. A fish with limited flexibility may employ a continuation of the turn which extends s1 angle ('single bend' responses; Domenici and Blake, 1991a). This type of turn, however, compromises velocity (Domenici and Blake, 1991a) and, although bigger fish can achieve higher absolute velocity than smaller ones (Wardle, 1975), preferred

trajectories may limit their escape performance as far as velocity and acceleration are concerned.

#### *Steering and angular compensation*

A sensory feedback mechanism is suggested by the behaviour of fish during towards responses. When the towards responses are triggered at a large angle of initial orientation (Table 1), the fish minimize s1 turns, remaining within the 0–180° semicircle, and swim away from the stimulus by steering. In contrast, at a small angle of initial orientation (Table 1), correction of the turn does not occur before the fish orientation is 0° (facing the stimulus). After reaching an orientation of 0°, the fish continue their turn within the semicircle 180–360° and move away from the stimulus. The resulting s1 turns are large and are further increased by steering (Table 1).

In away responses, steering allows fish to reach the preferred trajectories as shown in Fig. 10. Although we were unable to make predictions as to which of the preferred trajectories the fish would follow, the animals never reached trajectory 2 (130°) when s1 trajectories were greater than 180°. This may reflect biomechanical constraints on stage 2 turning.

Angelfish are able to adjust their trajectories by steering away from the stimulus once they have committed an apparent tactical error by making a towards response. In addition, the different values of s1 towards turns for the two semicircles suggest that feedback may start before the end of s1. Although inhibition of the lateral line mechanosensory input lasts for approximately the duration of s1 (Russell, 1976), this would still allow sensory feedback to influence steering. However, Eaton *et al.* (1988) suggest that stage 2 is preprogrammed and not dependent on movement-induced feedback. Using electromyograms, they show that the contralateral muscular activity can begin before the escape response has started. Although preferred trajectories could be achieved without sensory feedback, it is difficult to explain correction of 'wrong turns' in its absence. Although the stage 2 contraction starts before the movement of the fish, its extent may partially be controlled by a feedback system. Further behavioural analysis of towards responses conducted together with physiological measurements are needed in order to establish whether, and to what extent, sensory feedback plays a role in determining fish escape trajectories.

#### *Escape trajectories in other animals*

Cockroaches evade wind puffs simulating a toad's tongue protrusion (Camhi and Tom, 1978; Comer and Dowd, 1987). Their escape is triggered by a threshold value of wind acceleration (Camhi *et al.* 1978), detected by sensory cercal hairs arranged in 14 rows (Dagan and Camhi, 1979). Hairs of a particular row have a preferred axis of pliancy which is excitatory in one direction and inhibitory in the other (Dagan and Camhi, 1979). Sensory information from these hairs is conveyed to giant neurons, which are also directionally sensitive (Westin, 1979). Re-analysis of four published data sets suggests that the circular distribution of the escape trajectories appears multimodal (Fig. 11B). We suggest that preferred escape directions correspond to particular orientations of the

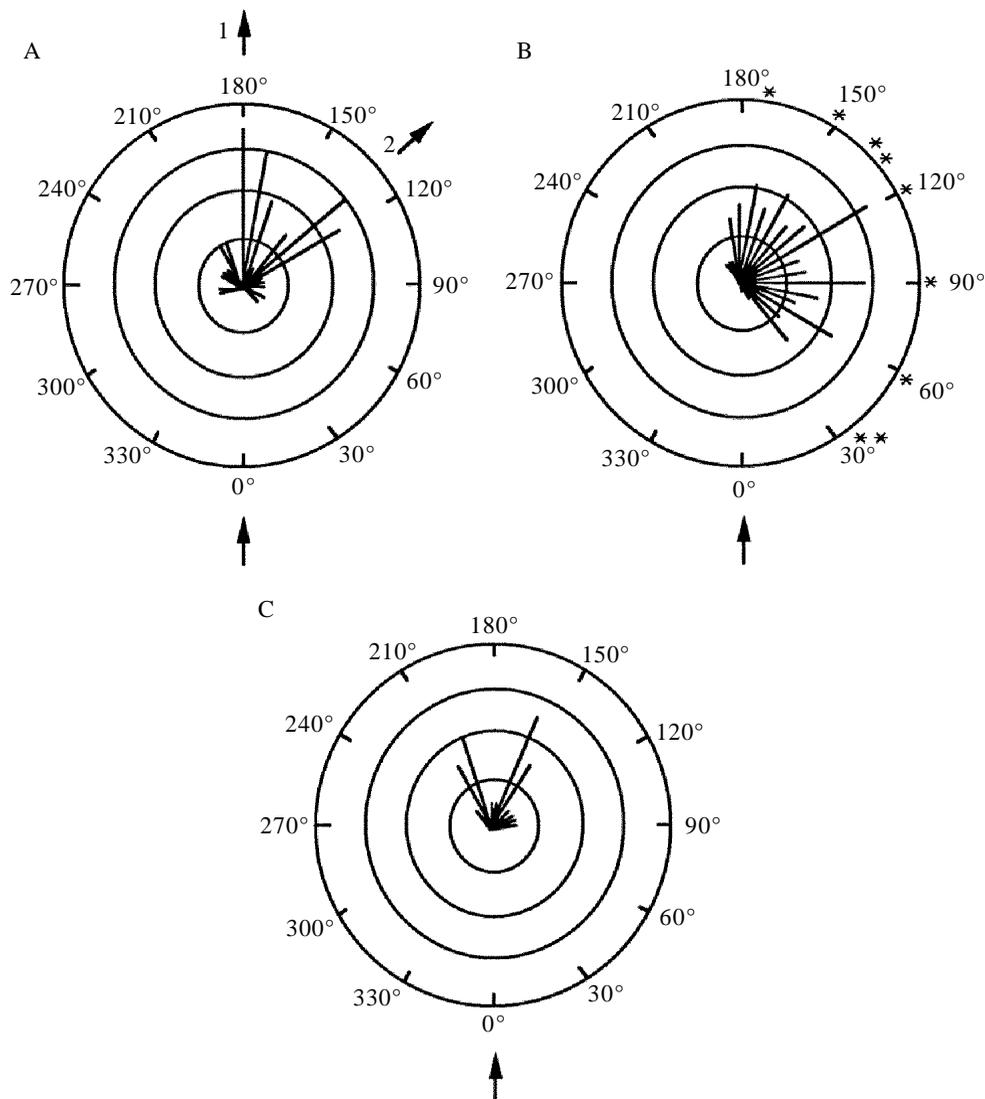


Fig. 11

sensory organs relative to the stimulus. Possible candidates controlling the cockroach escape trajectories are the preferred directions of pliancy of its sensory hairs (Fig. 11B) and the directional responses of the giant neurons (Westin, 1979). The mechanisms underlying the onset of the cockroach escape response are understood (Ritzmann, 1984; Camhi and Levy, 1989), but little is known about what determines the magnitude of its turn. The sensory hairs are not completely phasic receptors (Westin, 1979) and, in addition to detecting wind acceleration, should also be able to detect a more constant wind velocity such as that occurring later during the response (Camhi *et al.* 1978). As for fish, escape trajectories cannot be predicted from the initial orientation.

Soldier crabs walk forwards, unlike most shore crabs, and their escape responses are

Fig. 11. Circular frequency distributions of escape trajectories in response to a stimulus (arrow at the bottom of the graph). Only away responses are plotted. Responses to left or right stimuli are plotted as if the stimulus were always on the right side of the animal. The frequency interval is  $10^\circ$ . Each concentric circle represents a frequency of 2 (A, C) or 10 (B). None of the frequency distributions is random ( $U^2$ -test;  $P < 0.005$ ) and all of them are significantly different from normal circular (von Mises) distributions ( $\chi^2$ -test; A,  $P < 0.05$ ; B,  $P < 0.001$ ; C,  $P < 0.05$ ). (A) Angelfish (*Pterophyllum eimekei*). Escape trajectories in response to a mechanical stimulus. Responses away from the stimulus represent 74% of the total ( $N=62$ ; significant at  $P < 0.001$ ; binomial test). Two main modes, separated by  $50^\circ$ , are present, at  $180^\circ$  (arrow 1) and  $130^\circ$  (arrow 2). (B) Cockroach (*Periplaneta americana*). Escape trajectories in response to wind puffs. Data from Camhi and Tom (1978) and Comer and Dowd (1987). Four data sets are pooled (Figs 5A and 6A from Comer and Dowd, 1987, and Figs 5 and 6 from Camhi and Tom, 1978) (not statistically different;  $P > 0.05$ ; Mardia–Watson–Wheeler test). Responses away from the stimulus represent 83% of the total ( $N=408$ ; significant at  $P < 0.001$ ; binomial test). The inhibitory directions of hairs (Dagan and Camhi, 1979) from both cerci match closely with the modes and are shown as asterisks in the graph. (C) Soldier crab (*Mictyris longicarpus*). Escape trajectories in response to a visual stimulus represented by a walking person. Data from Nalbach (1990). Responses away from the stimulus represent 71% of the total ( $N=31$ ; significant at  $P < 0.05$ ; binomial test).

visually mediated (Nalbach, 1990). It has been suggested that they do not escape in a fixed direction relative to a stimulus, but rather within a fixed range of angles relative to their initial body orientation (Nalbach, 1990). However, a circular plot shows a bimodal pattern of escape trajectories, with modes either side of  $180^\circ$  (Fig. 11C). As in the previous examples, we suggest that the two preferred escape directions correspond to particular limits imposed by the crab's sensory organs. Soldier crab eyes have a limited field of view, which may be extended by the rotation of their eye stalks (Nalbach and Nalbach, 1987).

The common escape response, described above, involves a turn away from the stimulus (away responses). Escape responses may involve a turn towards the stimulus (towards responses), as discussed previously for angelfish. We have shown that the fish tend to correct their 'wrong turns', by steering away from the stimulus.

The cockroach's mean body turn in towards responses is small ( $29^\circ$ ) compared to that in away responses ( $52^\circ$ ). Comer and Dowd (1987) found that the magnitude of the turn was linearly related to the initial orientation in both towards and away responses. They suggest that this reinforces the hypothesis of absence of sensory feedback during the response. However, a linear relationship is significant only if towards responses ending in both semicircles ( $0-180^\circ$  and  $180-360^\circ$ ) are considered. As discussed for angelfish, when the stimulus is delivered almost frontally, the turn may continue away from the stimulus (in the  $180-360^\circ$  semicircle) after the animal has reached a frontal position. The mean value of the body turns in this case is  $90^\circ$ . When these responses are excluded, the mean body turn for towards responses is even smaller ( $17^\circ$ ) and has lower variance, making them highly predictable. Perhaps the animals are aborting these 'wrong' turns. This supports our suggestion of a sensory feedback mechanism occurring during the escape response. In soldier crabs, escape responses to a stimulus presented posteriorly (between  $160^\circ$  and  $180^\circ$ ) can elicit a towards response which allows the animal to reach its preferred trajectory of  $150-160^\circ$ .

The existence of preferred escape trajectories in animals has important implications for animal behaviour, physiology and ecology. Behaviourally, the presence of multiple preferred escape trajectories may be adaptive in preventing predators from learning any single fixed pattern of prey response and compensating for it. Physiologically, preferred escape trajectories imply mechanisms controlling the magnitude of the turn relative to a stimulus. This may be achieved through sensory feedback. Ecologically, the choice of a specific turning angle (regardless of size) may constrain important escape variables such as velocity (Domenici and Blake, 1991*a*). For example, although bigger fish can achieve higher absolute velocities than smaller ones (Wardle, 1975), they have lower turning capabilities (Domenici and Blake, 1991*b*) and are less flexible at their center of mass (Aleev, 1969). This may be a determinant of size-specific differential survival. In addition, the consideration of preferred escape trajectories may have practical implications, for example, in fish gear design (Wardle, 1986).

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