

PURSUIT AND PREDICTION IN THE TRACKING OF MOVING FOOD BY A TELEOST FISH (*ACANTHALUTERES SPILOMELANURUS*)

BY BETTY S. LANCHESTER AND R. F. MARK

*Department of Physiology, Monash University, Melbourne and
Department of Behavioural Biology, Research School of
Biological Sciences, Australian National University,
Canberra, Australia*

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SUMMARY

1. The path, eye and body movements of a teleost fish (the leather-jacket *Acanthaluteres spilomelanurus*) approaching and taking food were measured by cinematography.

2. Fixation of the food by movement of the eyes is an invariable feature of the approach. The eyes then remain aligned with the target while the body moves forward and round to bring the mouth to the food.

3. When pursuing pieces of food moving vertically at constant velocity through the water these fish normally trace out the pathway that can be calculated by assuming the fish aims constantly at the food. Predictive pathways that imply anticipation of the point of intersection with the food are not regularly seen.

4. Deviations from pursuit occur sporadically, usually in the direction of a predictive path, particularly when the fish approach falling food from below.

5. The geometry of the situation suggests that predictive paths may sometimes be generated if the alignment of eye and body during the pursuit of moving food can be delayed. In approaches from below this may be because forward movement of the fish would tend to stabilize the image of the falling food in the retina.

6. We suggest that a simple linked control system using both eye and body movements to fixate retinal images will on occasions generate predictive pathways without any need for the central nervous system to calculate them in advance.

INTRODUCTION

Most animals spend some or perhaps a good deal of their time in either pursuit or flight. Since the outcome is often sheer survival, it is an aspect of behaviour that should influence the design and function of the nervous system. However, few analyses have been made of the physiological mechanisms that have been developed for the capture of prey or the avoidance of predators. Exceptions are the work on orientation and striking towards prey objects in insects (Mittelstaedt, 1957) and jumping spiders

(Land, 1971, 1972), but so far they have not yielded direct information as to the brain processes required to carry out capture or avoidance.

In the vertebrates knowledge of the mechanisms of location, approach and attack which are required for prey capture still remains at the level of receptor identification (Grinnell, 1970; Kalmijn, 1971) and verbal description (Ingle, 1968, 1971). Even the simplest visuomotor abilities of the higher vertebrates are not well documented. One problem is that in a controlled laboratory situation it may be difficult to extract optimum performance from an animal (Fuchs, 1967; Barmack, 1970) and yet relaxing the conditions to give a naturalistic setting may make it impossible to obtain accurate observations.

We have tried to circumvent these difficulties and to present some cinematographic measurements of pursuit behaviour in a teleost fish, the common coastal leather-jacket of South Australia *Acanthaluteres spilomelanurus* (Quoy and Gaimard). It is a very suitable animal for this study. The eyes are large and have an elongated pupil which makes it possible to measure the direction of gaze. The body is flattened laterally and swimming is done by the wave-like action of two large dorsal and ventral fins which gives it a smooth arrowlike motion. A lively and voracious fish, the large mobile eyes are constantly searching for moving prey which is rapidly tracked down and eaten. The young, on which this study was done, are found in large numbers on warm sandy bottom weed-beds in sheltered water off the South Australian coast during the summer months. They survive well in an aquarium.

Eye and body movements made in the approach to stationary food particles were measured. The situation for the pursuit of moving prey was simplified to the tracking of a piece of food moving at constant velocity in a path initially at right angles to the movement of the fish. The movements allowed were kept effectively to two dimensions and incentive was maintained by adjusting the velocity of the food so that the fish was rewarded by capture of the food in about half the trials.

Performance on any task involving pursuit would be improved if the animal was able to predict the intersection of its own trajectory with that of the target, on the basis of knowledge of the movement of the prey gained through its visual system, compared with its own relative movement. If a predictive path is to be taken towards a target moving at constant velocity the overall mechanism is simple. The pursuer must sight the target and begin on a course that will keep the angular deviation of the target from the line of travel constant. This will allow a straight path to be followed to a point of intersection with the target, provided the velocity of the pursuer and target are proportional to the ratio of the distances of each from the point of intersection. The optimal angle will depend on the distances, the speed of the target and the speed of which the pursuer is capable. True prediction such as is needed in man for catching a ball (Chapman, 1968) demands the early choice of the best predictive path, and although the geometry is simple the same is not necessarily true of the neurological calculations.

If the pursuer catches a moving target by aiming directly towards it at every instant, the pathway of the pursuer, which will be longer than one with a predictive element, can be calculated, provided the position of the target and the speed of the pursuer are known. The experiment, therefore, was designed to discover to what extent the pursuing fish's pathway deviated from that calculated on the assumption

It was continuously pursuing the target and if the deviations were in the direction of a more economical predictive pathway.

METHODS

Animals

Leatherjackets (*Acanthaluteres spilomelanurus*) were caught by netting and kept in salt water aquariums. Those used were between 7 and 12 cm in length.

Cinematography

For observation of eye and body movements fish were housed in a tank 120 × 35 × 45 cm deep which had a vertical perspex divider making a narrow compartment at the front, the full depth of the tank but only 5 cm from front to back. A rectangular 1 in (2.54 cm) grid with numbered coordinates was drawn on the divider. The fish was tracked with a cine camera on a tripod about 2 m in front of the tank as it swam across in front of the grid. The camera was a Bolex 16 mm with zoom lens (17–85 mm focal length) and an electric film drive set at 48 frames/s. Two 1000 watt lamps in front of the tank served for illumination and Ilford Mark V black and white negative film (ASA300) was used.

Presentation of food

Stationary food was placed on a perspex table in the bottom of the front compartment or suspended from a wire in the water. Moving food was controlled with a viscous drag apparatus shown in Fig. 1. A small piece of beef liver was attached by a barbless shallow hook to the end of a glass rod which was rigidly connected to a cylindrical brass weight guided through a vertical stainless steel tube. The weight of these components was partially counter-balanced by weights on a scale pan and by the viscous drag produced by the motion of a small glass bottle through a large volume of treacle. Speed could be varied by adjusting the scale weights. Variations in velocity were reduced by adding a block and tackle pulley system to reduce the travel of the bottle through the treacle. A remote control trigger mechanism for the apparatus (see Fig. 1) consisted of a solenoid that worked a spring-loaded rocker with two plungers 7.5 cm apart which intercepted the fall of the brass weight. With withdrawal of the first plunger the food could be dropped from just above the water to just below the surface where it became visible to the fish. When the solenoid was turned off and the second plunger retracted the food began to descend through the water. The same switch was wired to start the electric motor of the cine camera. At the bottom of its travel the food passed through a small hole in a perspex box where the fish could not get it. The speed of descent of the food was adjusted so that by swimming across the tank at top speed a fish was rewarded on about half the trials. Each experimental run began with the fish excluded from the front compartment of the tank by a translucent plexiglass door worked by a string. The fish was admitted to the race by opening the door, food was released and the camera motor started together.

To obtain sufficient magnification the focal length of the cine camera lens was adjusted so that the fish filled about 1/3 of the frame. It was then tracked by the camera as it swam across the tank. At the completion of the run the fish was coaxed from the

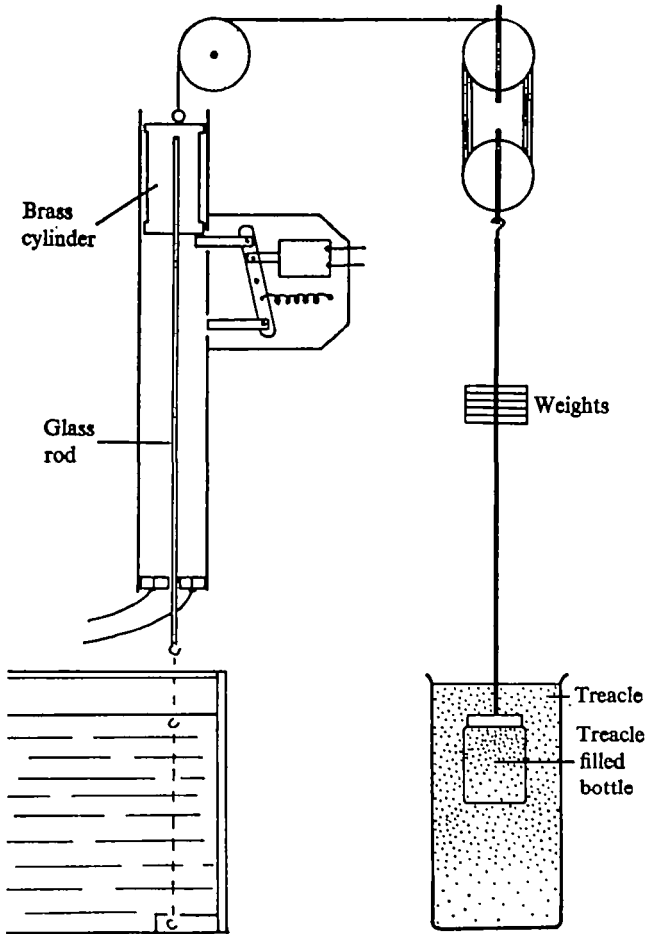


Fig. 1. Viscous drag apparatus for lowering food into the tank at constant velocity.
Description in the text.

front compartment and the various controls re-cocked for the next run. A fish would do up to 15 runs in one session lasting an hour or so.

Analysis of films and sources of error

All films were viewed at 16 frames a second, that is $\frac{1}{3}$ natural speed, to determine the runs that were most suitable for analysis. These were the ones in which the fish began its pursuit quickly and finally intercepted the food. A frame-by-frame analysis of the chosen run was made with a film reader. The nose and the eye positions in relation to the grid in the tank were plotted on large (63×48 cm) graph paper, usually every 3 or 5 frames, and the body and eye angles were measured (Fig. 2). Each frame was measured independently, and the numbered coordinates of the grid seen behind the fish were the only frame-to-frame reference. The body orientation was very easily determined from markings on the fish. Although the eye has an elongate pupil the direction in which it was pointing could not be measured with an accuracy of less than $\pm 5^\circ$.

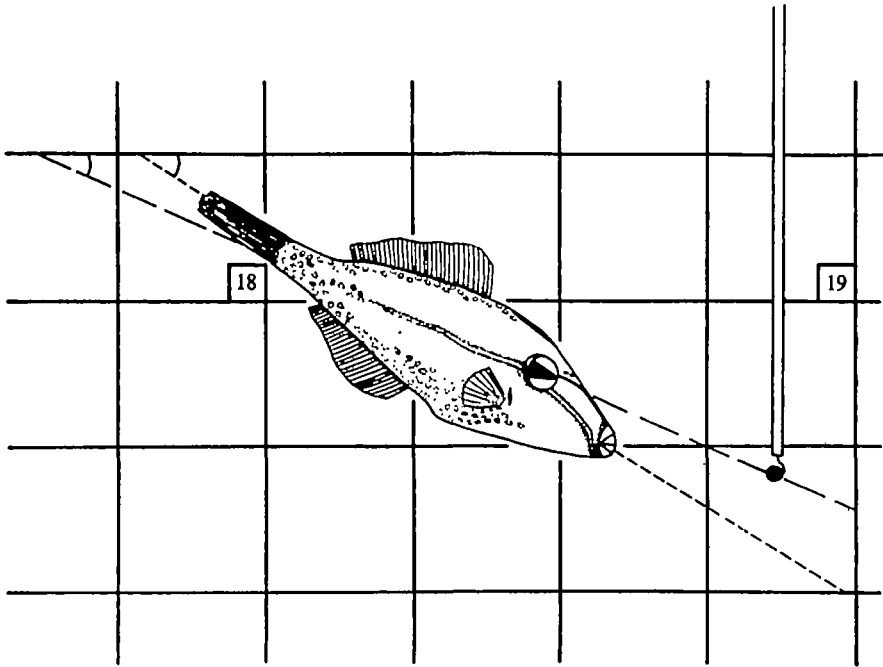


Fig. 2. Drawing of a fish as seen in the film against the grid on the back of the tank. The angle of eye and body were measured against the grid and the position of the nose plotted. The position of the food was also plotted when it appeared in the frame.

Since the camera was tracking the fish the position of the food had to be plotted separately from a filmed trial run, and compared with its position in the fish run, when it came into view. This allowed an estimation of the error involved in extrapolating the speed of the food. It was found to vary between zero and ± 1 frame. This error was mostly due to the starting of the camera motor. Once the camera was running smoothly, after at the most 10 frames, the food speed was found to be extremely constant, with no measurable error at slower speeds. At very fast speeds its velocity increased slightly during the fall, with a maximum increase of 10% by the bottom. This was not important, as the trial runs allowed it to be predicted so that the only error was that due to extrapolation from calibration run to intermediate points in the test run, and this was negligible.

Estimation of the pursuit pathway

If it is assumed that the fish points directly towards the food throughout its path and if the positions of fish and food at the beginning of the chase and the velocities of both fish and food are known then the pathway that would be followed by the fish can be calculated. The way in which this was done is given in the appendix. If the velocities of both pursuer and target are constant the problem is easy. In the experimental runs filmed, however, while variations in the velocity of the food were negligible the pursuing fish changed speed in unpredictable ways. It was necessary therefore to solve the pursuit equation for short segments of the chase, taking on new values for the speed of the fish each time. The computer program used plotted out the

pursuit pathway and also a number of other variables which changed during the trajectory. Full details of the computational methods are available on request to the authors.

RESULTS

(a) *The capture of stationary food*

Fish food grains of about 1 mm diameter were scattered sparsely over the perspex floor of the tank and individual fish were filmed while eating. Tame and hungry fish cruise a few cms above the bottom with their head down scanning the floor of the tank. The approach to a piece of food follows a stereotyped pattern. First both eyes rotate together in one flick movement so that the elongate pupil is pointing towards the food. Then the fish slowly swims down tilting to a more vertical position until the mouth contacts the food. The approach, in contrast to the initial movement of the eyes, is slow, taking several seconds. At the moment the food is taken the eyes flip in one very rapid movement back to an approximately horizontal position. The fish then usually backs off tail first and the body slowly reverts to a more horizontal position as the fish moves forward again to search a new area.

(i) *Trajectory analysis*

A frame by frame analysis was made of those filmed sequences in which the fish was photographed side on, normal to the camera. Movements can be represented graphically, with the time scale represented by the frame speed of the camera and the spatial coordinates by the grid on the back wall of the tank.

The first finding was the paths followed by the fishes' mouths in approaching the food was not constant. The path is the resultant of the gradual descent of the whole animal, which usually has some forward moving component, and the tilt of the body towards the vertical position. It may, therefore, have curves, sharp angles and even loops depending on the rate and the direction of the various movements, even though one's impression is that the fish approaches the food smoothly. No further analysis was made.

(ii) *Analysis of eye and body movements*

The rotation of the eyes within the body and the rotation of the body towards the vertical during the approach show some constant features. An example is shown in Fig. 3 in which are plotted the angle of the eye to the horizontal, the angle of the fish body to horizontal and the angle of the eye to the body, which is obtained by subtraction from the first two measurements.

The moment of fixation is near the beginning of the trace. The whole rotatory movement of the eye occurred within 3 frames, which means that it was completed in about 60 msec and it took the eye from a position of 70° above the position of alignment of eye and body to a position of 20° below. As the body slowly rotated during the approach to the food the eye counter-rotated back until at the moment of capture eye and body were aligned. After capture the pupil flicked up to a near horizontal position, also within 60 msec. All approaches to food on the bottom showed these features except that sometimes, when the body was pointing close to a food particle at the beginning of a run, the initial rapid fixation movement could not be discerned

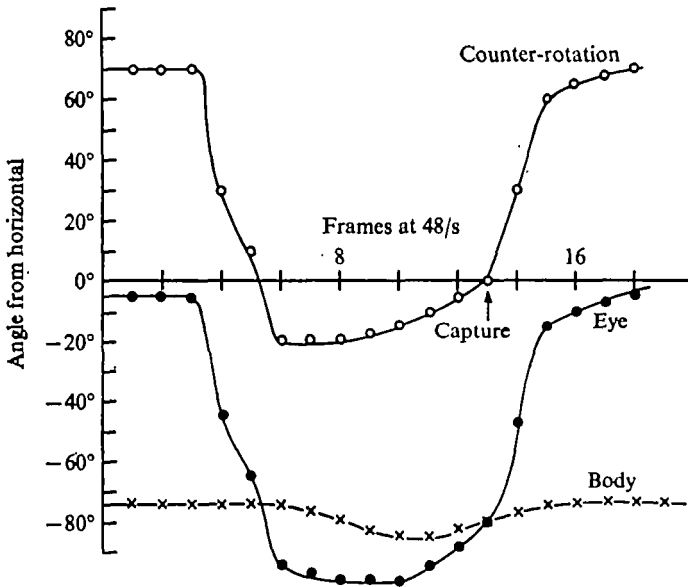


Fig. 3. Angles of body (\times) and eye (\bullet) to horizontal during an approach to stationary food. Open circles plot the angle of eye to body, that is ocular counter-rotation. The horizontal scale is time measured in frames of film at 48 frames/s. The fixation of food is shown by the abrupt rotation of the eyes at frame 3. The moment of capture is shown by the arrow. Note that eye and body are aligned so that counter-rotation is zero when the food is taken.

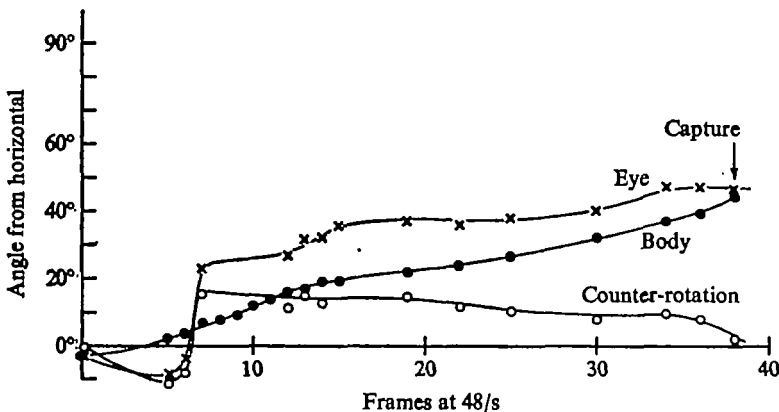


Fig. 4. Eye and body angles and counter-rotation during approach to a food particle on the surface. Symbols as in Fig. 3.

Movements towards food particles which were floating on or suspended below the surface were similar. The target was fixed by a rapid rotatory eye movement and ocular counter-rotation slowly reduced to zero during advance towards the food, with the body and eye aligned at capture (Fig. 4).

The following common features emerged from analyses of eye movement during approach to stationary food:

1. At rest the eyes are held close to the horizontal, irrespective of body angle.

2. The first sign of approach is a rotation of the eyes to direct the elongate pupil towards the target.
3. During the approach the eyes remain aligned towards the food, while the body aligns itself with the eyes.
4. At the moment of capture, eyes and body are always in line.
5. Upon capture the eyes flick back to an approximately horizontal position.

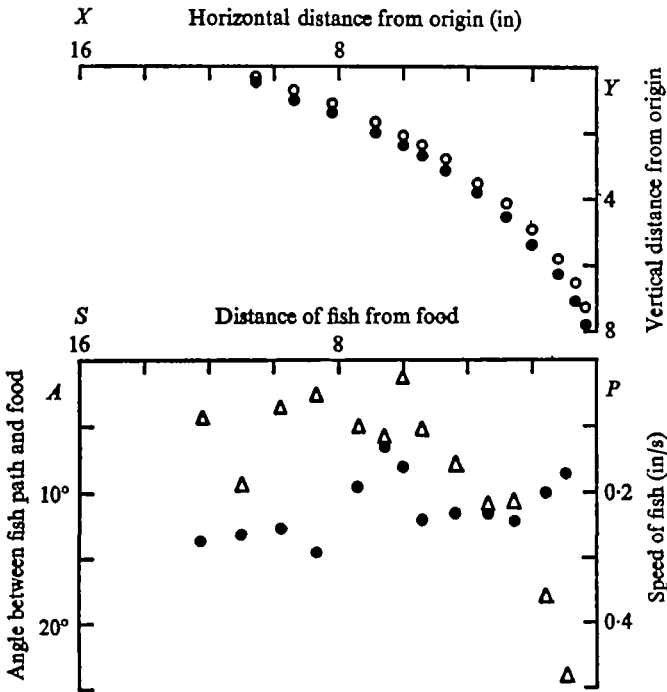


Fig. 5. Graphical representation of the trajectory of a fish chasing falling food. In the top graph open circles plot the pursuit path, calculated as in Methods; closed circles the actual path of the fish. Position is plotted every 3 frames at 48 frames/s so the spacing of points indicates speed. In the lower graph are plotted two variables derived from the original data. Velocity (closed circles, *P*) and the angle (open triangles, *A*) between the tangent to the fish's path and the position of the food.

(b) *Moving food*

(i) *Trajectory analysis*

The runs that we selected for analysis were those in which the speed and direction of the fish gave evidence of an intention to catch the food from the moment the fish entered the front compartment. The paths of the fish and food were then plotted out by frame-to-frame analysis and compared with the pathway generated by the pursuit equation as described in Methods. The paths were almost never longer than those estimated by the pursuit equation. Most trajectories followed the calculated pursuit paths quite closely but the variations were always in a direction of a more economical path which would be expected if the fish was predicting a point of intersection. However, there was great variation, from fish-to-fish and from trial-to-trial in the same fish on successive runs. Also in using the same fish on many occasions there was n

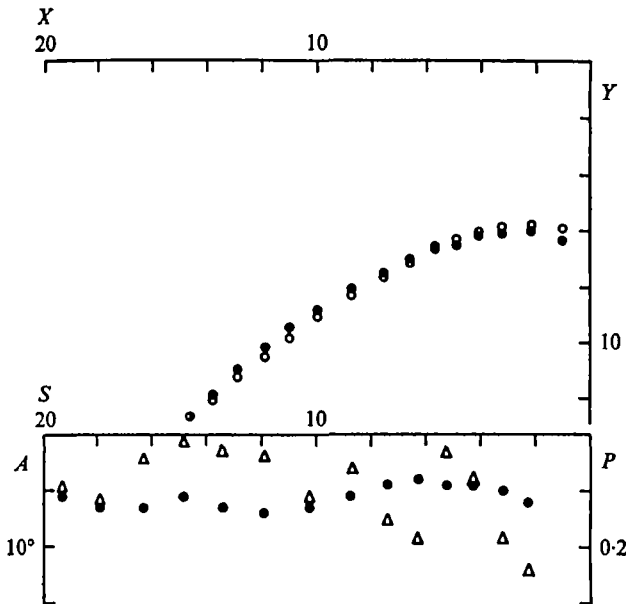


Fig. 6. As in Fig. 5.

noticeable tendency of fish to use a progressively more predictive pathway, in spite of the apparent advantage this would give them in securing food.

Our conclusion was that, although the tracking mechanism allowed the fish to improve upon the pursuit pathway quite frequently, these deviations could not be pre-selected and that the strategy could not be learned.

Examples of the kind of paths seen are presented in the following figures.

In Fig. 5, fish velocity is plotted against distance from the target (closed circles) and the angle between fish and target is plotted against distance from the food (triangles). For a predictive pathway velocity should be uniform and the angle should be set at some value greater than 0 early in the run and remain constant until near capture. For a pursuit path velocity could vary and the angle should be close to 0° all along. The same symbols are used in subsequent figures.

The pathway in Fig. 5 is very close to the theoretical pursuit path; the velocity shows a decrease in mid-path and a subsequent acceleration afterwards. The angle between the food and direction of travel is less than 10° until it suddenly increased at the end. Fig. 6 shows a pathway from below the food that almost fits that of pursuit. Velocity is constant throughout and the angular deviation is small until the very end. Fig. 7 however illustrates a run, also from below, that clearly deviates from the pursuit equation. Velocity is constant but angular deviation, the measure of a predictive path, gets progressively larger as the target is approached. In Fig. 8 the early part of the run is not distinguishable from that traced by the pursuit pathway but there is an increasing tendency for the fish to drift ventrally at the end, matching its speed to that of the food. This is mirrored in the two lower graphs where the velocity decreases as the angle between fish path and food direction increases.

The fish came from below in Fig. 9 and the pathway was clearly different from

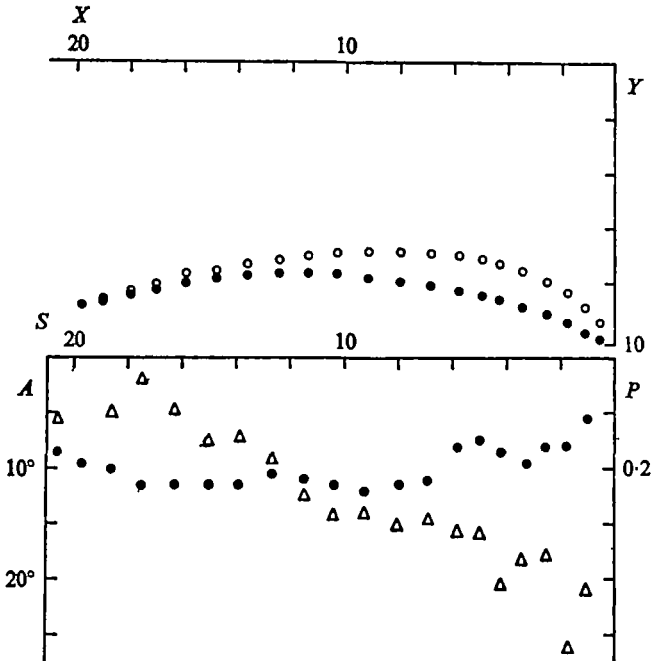


Fig. 7. As in Fig. 5.

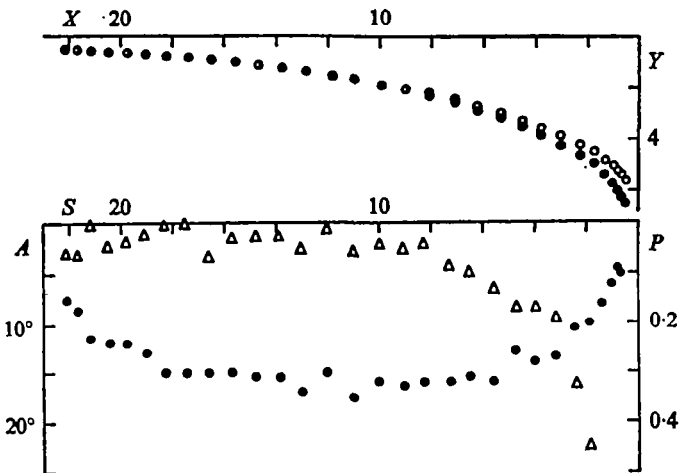


Fig. 8. As in Fig. 5.

that for instantaneous tracking. Here velocity was constant and the angular deviation was set early and maintained across the tank as would be expected from a predictive mechanism. Fig. 10 gives an example of a run where the fish did rather worse than constant tracking, recovered part-way through, and then passed below the theoretical path to intercept the food by a predictive path. Velocity decreased steadily until the change of course in mid path when the fish accelerated again to slow down at the end. The angular deviation increased sharply as the fish changed course. The last 3 run

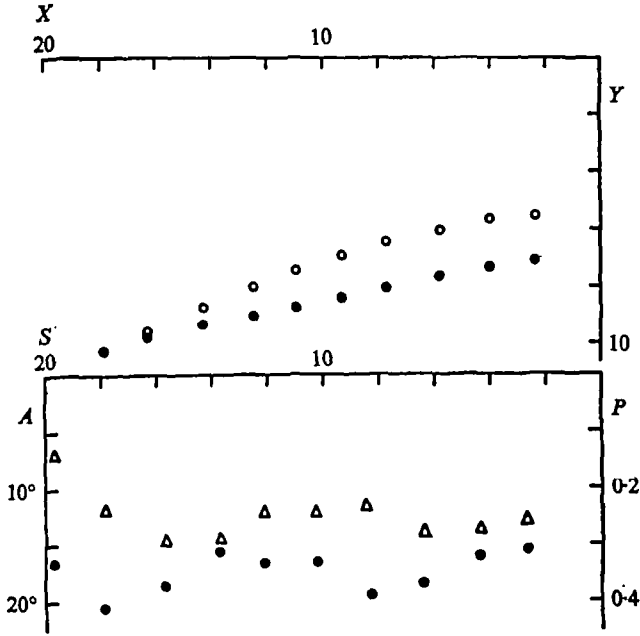


Fig. 9. As in Fig. 5.

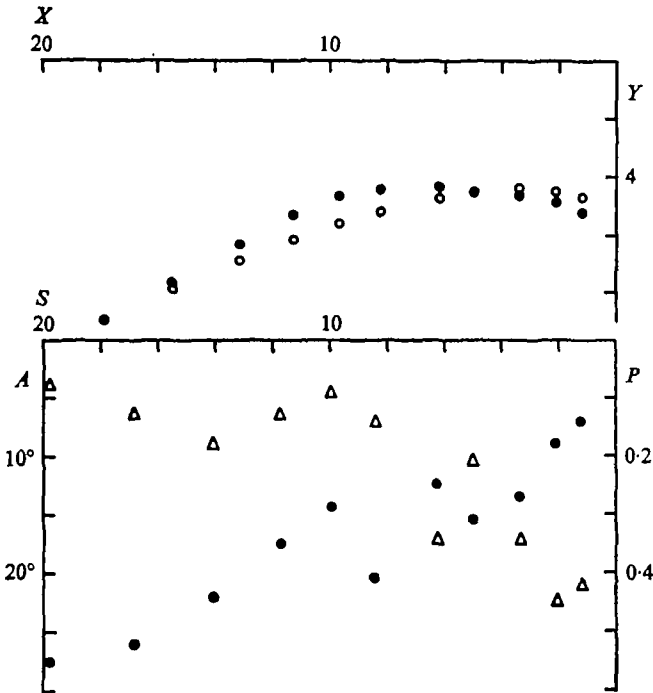


Fig. 10. As in Fig. 5.

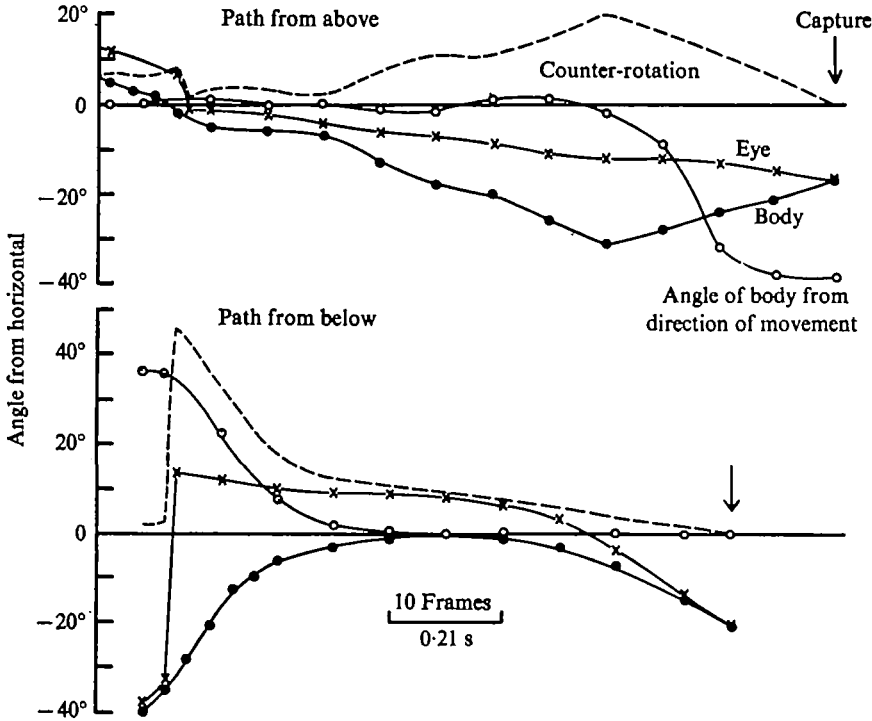


Fig. 11. Body and eye movements during two predictive paths, one from above (top graphs) and one from below. \times , eye angle; \bullet , body angle; ---, counter-rotation of eye; \circ , angle between body angle and direction of travel. Further description in the text.

illustrated were made by the same fish and photographed within a few minutes of each other. There was no tendency for this or any other fish to change or improve its tactics either during a session or between sessions on different days.

(ii) *Eye and body movements*

The eye direction was difficult to measure accurately especially when the movements were smooth and not detectable as such from frame to frame, as they were once the fish had set its course. An initial fixation movement, similar to that seen in the approach to stationary food, was often quite obvious at the beginning of a run. The flick of the eye towards the food was again fast, being completed in 1 frame (≈ 20 msec).

If it is assumed that the fish's eye follows the moving target smoothly throughout the run, as seems likely from the results with stationary food, then the inclination of the eye can be better estimated as the line drawn between food and eye, at successive positions of each. No significant deviations between this line and the apparent direction as given by the elongate pupil were ever noticed. Fig. 11 shows graphs of eye and body rotation measured in this way. If the fish is at the bottom when it sights the food the eye curve is a smooth decreasing line, the body angle and the eye angle converging just before the capture, and they appear to be together at the moment of impact. The pathway followed in this run was predictive, i.e. it traced a shorter more direct route to the food than that given by the pursuit equation.

Some runs from above the food, in which a predictive course was followed, differed from others in that the ocular counter-rotation did not slowly decrease up to the capture. Fig. 11 also shows a run from above in which sighting the food is indicated by a flick of the eyes towards it, which in fact lined up eye and body. Then, as the fish progressed, the downward angle of the body increased while the eye remained aligned to the target so the counter-rotation increased. As this reached a maximum the fish changed its direction and began to swim ventrally along with the falling food, while the body became aligned with the eye again at the moment of capture.

It was obvious in many runs to moving food that the fish need not be pointing its nose in the direction that it was moving. These fish are able to propel themselves in almost any direction, no matter which way they are oriented. Ocular counter-rotation is, therefore, not always the same as the angle between the fish's path and the target, as measured from the path analysis. However, in the main part of each run the line between successive nose or eye positions does correspond to the actual body direction. It is only while the fish is bringing its body onto course, or swinging around to capture the food that the body direction is very different from the direction of motion.

The eye and body movements of fish tracking moving targets were more varied than those for stationary food. However, the following common points could be distinguished.

1. While just swimming about the tank the eyes are normally held near the horizontal.
2. When attracted to the moving food in the periphery of the visual field the eyes are rotated towards the target.
3. The eyes appear to keep their orientation towards the moving food but the body does not always move towards this same direction until near the moment of capture.
4. In predictive runs from above the eye does not steadily align to the body. Ocular counter-rotation may increase before decreasing again to zero at the moment of capture.

DISCUSSION

Watching the approach to stationary food one can see that directing the eye towards the target is an essential part of the visual tracking mechanism in these fish. The eye direction never deviates from the target direction, as far as can be seen during the tracking process and the anatomical relationship between eye and mouth means that they must always be in line at the moment of capture. The fish does not track an object without the image being fixed on the retina and it does not eat without aligning eye and body. This being so one would expect the eye to have a well developed fovea, which is, in fact, true and it can be easily seen in routine histological sections of the retina (Lanchester, unpublished observations).

The path most commonly taken by fish pursuing moving food is quite close to that traced out by solving the equation for pursuit and allowing for varying fish velocity. Fish did not systematically predict an intersection with the food and follow a direct path towards it, in spite of the obvious advantage this would have given them. There was no sign of progressive improvement in prediction during one training session in one fish and no day to day improvement. The angle between the actual path of the fish and the momentary position of the target, which should be set at the beginning

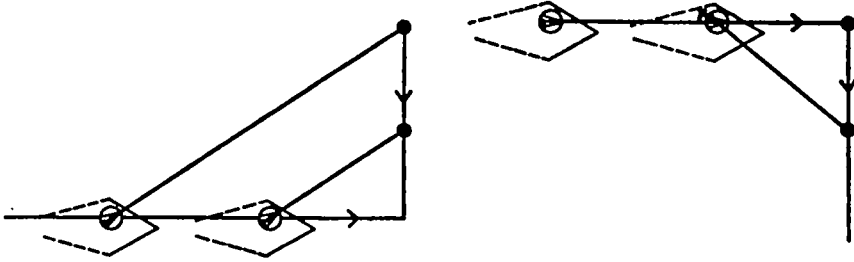


Fig. 12. On left, once the image of falling food is fixated, movement of the fish forward will tend to minimize displacement of the image on the retina. On the right, forward movement of the fish when the food is falling below the line of travel will accentuate movement of the image of the food on the retina.

of the run and held for a constant velocity predictive mechanism, showed this characteristic only occasionally. In most cases, even those which did show deviation from pursuit, the angle increased more or less steadily throughout the run. This suggests that the angle is varying with some other exigencies of the tracking mechanism and is not itself a controlling feature. The speed of the fish, was quite variable, sometimes remaining fairly constant throughout a run, sometimes accelerating and decelerating and sometimes slowing steadily to the point of capture. The mechanism of speed control is not known.

Yet the fish were clearly able sometimes to swim at an angle to the sighted position of moving food. Deviations from the path of continuous tracking are mostly in the direction of a more economical path that appears to be aimed at a future point of intersection rather than the instantaneous position of the food. Predictive paths were seen more often when the fish approached the food from below, whereas paths were closer to tracking when the fish approached from above. Thus the ability to swim at an angle to the target is enhanced when the fish is below it. Why should this be so and what mechanism could allow an apparently predictive path to emerge from a system that mainly operates by pursuit? Further consideration of the geometry of the situation shows why this may be so.

From measurement of eye position during the approach to food we know that the first noticeable event is a rotation of the eyes so they point towards the target. If the fish is swimming horizontally and the food is falling vertically, continued movement of the fish in the initial direction will have the effect of preventing movement of the image of the food on the retina (Fig. 12). The opposite occurs when the fish approaches from above. Continuation along the initial path sweeps the food image over the retina.

We suggest, therefore, that when the image of the food remains still on the retina the alignment of the body with the eye is delayed. When approaching from below this automatically generates the prediction because the fish may swim for a longer time at an angle to the food position with its forward motion stabilizing the retinal image. To generate a predictive pathway from above by this method, the body of the fish must overshoot its alignment with the eye, which would allow forward movement of the body to stabilize the retinal image in the same way. This does happen, but not regularly (Fig. 11).

The evidence is that predictive pathways, which are seen sporadically, do not seem

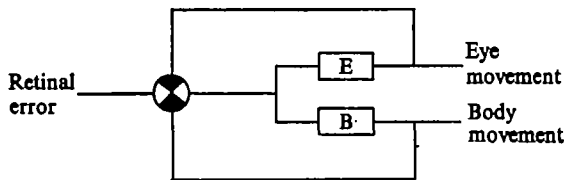


Fig. 13. A simple control system for visual fixation that can generate predictive paths. Description in the text.

to be trainable and are not calculated in advance, emerge because of a limited ability of the fish to swim at an angle to its eyes when the relative movement of fish and food are such that image movement on the retina is minimized. In cases where retinal image movement would be expected to occur the body moves round to align with the eye and the whole fish takes up a direction of travel that will minimize further movement.

All of the above observations can be accounted for by the assumption that the rotatory movements of the body were simply added to the rotatory eye movements as part of the tracking mechanism. A simple control scheme consistent with this behaviour has the structure shown in Fig. 13. Eye movements are known to be relatively rapid and since they operate on a low inertia system the controlling mechanism could afford to use a relatively low gain, which in turn confers stability (at the expense of some steady state error). The body movements are slower and operate on a high inertia system perhaps with higher gain. If rotation of eye and body depends on a simple position signal from the retina then the steady state error in the eye fixation loop could provide the input for the body loop.

This scheme is similar to the one postulated by Middelstaedt (1957) for prey capture in the mantid except that the second system (body in fish, fore-legs in the mantid) is a closed loop here but an open one in the mantid. No special efference copy mechanism is required to signal eye position relative to the head but neither do those observations exclude one.

There is no need to postulate a brain mechanism capable of calculating a predictive pathway for visuomotor tracking. In a behavioural situation such as that studied here two such linked tracking systems would quite often generate a pathway rather better than pure pursuit simply by allowing progression for a time at an angle to the sighted position of a target. Maybe one of the advantages of mobile eyes or a mobile head in predatory animals is that it enables this to be done with very little increase in the complexity of the central nervous system.

REFERENCES

- BARMACK, N. H. (1970). Dynamic visual acuity as an index of eye movement control. *Vision Research* **10**, 1377-91.
- CHAPMAN, S. (1968). Catching a baseball. *Am. J. Phys.* **36**, 868-70.
- FUCHS, A. F. (1967). Periodic eye tracking in the monkey. *J. Physiol.* **193**, 161-71.
- GRINNELL, A. D. (1970). Comparative auditory neurophysiology of neotropical bats employing different echolocation signals. *Z. vergl. Physiol.* **68**, 117-53.
- INGLE, D. J. (1968). Visual releasers of prey-catching behavior in frogs and toads. *Brain. Behav. Evol.* **1**, 500-18.

- INGLE, D. J. (1971). Prey-catching behavior of anurans toward moving and stationary objects. *Vision Res. Suppl.* 3, 447-56.
- KALMIJN, A. J. (1971). The electric sense of sharks and rays. *J. exp. Biol.* 55, 371-83.
- LAND, M. F. (1971). Orientation by jumping spiders in the absence of visual feedback. *J. exp. Biol.* 54, 119-39.
- LAND, M. F. (1972). Stepping movements made by jumping spiders during turns mediated by the lateral eyes. *J. exp. Biol.* 57, 15-40.
- MITTELSTAEDT, H. (1957). Prey capture in mantids. In *Recent advances in invertebrate physiology* (ed. B. J. Scheer), pp. 51-71. Eugene: Oregon University Press.

APPENDIX

All results were measured in a reference frame as Fig. 14 with the initial position of the food at the origin. This had no particular significance otherwise as the fish's decision to chase the food is usually some frames of film later. The initial position of the fish (x_0, y_0) is the first position relevant to the chase, usually once it has reached a fairly steady velocity.

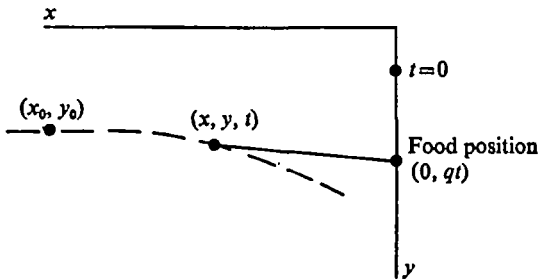


Fig. 14. Symbols used in deriving the tracking equation.

The following algebra derives an expression for y in terms of x , where (x, y) is the fish position at time t , p is the fish's speed, and q is the food speed. Since $t = 0$ when the fish is at (x_0, y_0) the distance between the origin and the food position at $t = 0$ is referred to as a constant G .

$$\frac{dy}{dx} = \frac{qt + G - y}{-x}$$

as y is increasing and x is decreasing, therefore

$$x \frac{dy}{dx} = y - qt - G.$$

Differentiating with regard to x :

$$x \frac{d^2y}{dx^2} + \frac{dy}{dx} = \frac{dy}{dx} - q \frac{dt}{dx}.$$

Putting $u = \frac{dy}{dx}$

$$x \frac{du}{dx} = \frac{-q}{dx/dt}. \quad (1)$$

An equation of the fish's motion is

$$\left(\frac{dx}{dt}\right)^2 + \left(\frac{dy}{dt}\right)^2 = p^2$$

therefore
$$\left(\frac{dx}{dt}\right)^2 + \left(\frac{dy}{dx} \frac{dx}{dt}\right)^2 = p^2$$

therefore
$$\left(\frac{dx}{dt}\right)^2 (1 + u^2) = p^2$$

therefore
$$\frac{dx}{dt} = \frac{\pm p}{(1 + u^2)^{\frac{1}{2}}}$$

In this case $\frac{dx}{dt}$ is a negative quantity at all times

$$\frac{dx}{dt} = \frac{-p}{(1 + u^2)^{\frac{1}{2}}} \quad (2)$$

From equations (1) and (2)

$$x \frac{du}{dx} = \frac{-q(1 + u^2)^{\frac{1}{2}}}{-p},$$

putting $r = \frac{q}{p}$

$$\frac{du}{(1 + u^2)^{\frac{1}{2}}} = r \frac{dx}{x} \quad (3)$$

Integrating equation (3):

$$\ln\{u + (u^2 + 1)^{\frac{1}{2}}\} = \ln Cx^r$$

where C is constant, therefore

$$u + (u^2 + 1)^{\frac{1}{2}} = Cx^r, \quad (4)$$

when $x = x_0$,

$$\frac{dy}{dx} = \frac{y_0 - G}{x_0} = u$$

therefore
$$\frac{y_0 - G}{x_0} = \left[\frac{(y_0 - G)^2}{x_0^2} + 1 \right]^{\frac{1}{2}} = Cx_0^r$$

therefore
$$C = x_0^{-r} \left(\frac{y_0 - G}{x_0} + \left[\frac{(y_0 - G)^2}{x_0^2} + 1 \right]^{\frac{1}{2}} \right) \quad (5)$$

From equation (4):

$$u + (u^2 + 1)^{\frac{1}{2}} - \frac{1}{u + (u^2 + 1)^{\frac{1}{2}}} = Cx^r - \frac{1}{Cx^r}$$

$$\frac{u^2 + 2u(u^2 + 1)^{\frac{1}{2}} + u^2 + 1 - 1}{u + (u^2 + 1)^{\frac{1}{2}}} = Cx^2 - \frac{1}{Cx^r},$$

therefore
$$u = \frac{1}{2} \left(Cx^r - \frac{1}{Cx^r} \right) = \frac{dy}{dx} \quad (6)$$

Integrating equation (6):

$$y = \frac{1}{2} \left(\frac{Cx^{r+1}}{r+1} + \frac{x^{1-r}}{C(r-1)} \right) + D, \quad (7)$$

where D is constant.

When $x = x_0, y = y_0$

therefore
$$D = y_0 - \frac{1}{2} \left(\frac{Cx_0^{r+1}}{r+1} + \frac{x_0^{1-r}}{C(r-1)} \right). \quad (8)$$

Therefore, with known values of x_0, y_0, p and q , the equation of the fish's theoretical tracking curve can be solved with equations (7), (5) and (8).

If the velocities p and q of fish and food were indeed constants throughout each run, then the above equations could be used to provide the theoretical values of y for given increments in x . However, the variation in the fish's speed during a chase is an obvious feature of all the results plotted in Figs. 5-10, and so a computer program was written to incorporate this variation into the solution for theoretical y values. Where enough measurements were possible, the food position was considered as a variable (i.e. q was also a variable in the program). However, in several cases there was no calibration run of the food's path, so q had to be calculated by interpolation of the positions of the food at the beginning and end of the run. This meant that two different programs were needed to deal with these two situations.

The following data was required for each type of program

(i) for constant q :

The experimental values of x in the coordinates of Fig. 14 (X)

the experimental values of y (EY)

the time interval between successive measurements, e.g. either 3 or 5 frames (TINT)

the calculated value of food speed (Q).

(ii) to deal with possible variations in q :

X as above

EY as above

the experimental food positions (FPOSN)

TINT as above.

The number of measurements of X, EY and FPOSN vary with the run. There are $N-1$ measurements for any particular run, and when $N=1$, $X=X_0$, $EY=Y_0$ and FPOSN has the value of the constant G in the calculations above. This constant is supplied to program type (i) as the frame no. at $t=0$ (N_2). The only units of time used are frames. The food is at the origin at frame no. 1.

Both programs are written to provide more information than just the theoretical tracking curve (TY). They calculate for each of the $I=N-1$ data points

TY(I)

P(I) fish speed

S(I) actual distance of fish from food

ANG(I) angle between tangent to fish's path and fish-food direction and where relevant in type (ii)

Q(I) food speed.

They also print out all the data that is supplied, tabulating X(I), EY(I) and FPOSN (I) with the above.

In order to use the varying values of fish speed, as each new value of X is considered, the previous X value and the previously calculated value of TY are substituted for X_0 and Y_0 , and P is given its new value. This means that the three

Equations (7), (5) and (8) only provide one set of results for each set of 'constants' X_0 , Y_0 , P and Q .

However, the equations derived above assume that when the fish is at (X_0, Y_0) the food is also at its initial position, although in fact after each calculation it has moved on by (i) $Q \cdot TINT \cong$ (ii) $FPOSN(I) - FPOSN(I - 1)$. This is accounted for by moving TY through this increment in the negative y direction at each step. When all points are calculated and stored, they are shifted appropriately to construct the theoretical curve.

A similar shift in the y direction must be made in type (i) only, to account for the constant $G = N_2 \cdot Q$ in the calculations.

