Predicting three-dimensional target motion: how archer fish determine where to catch their dislodged prey

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Summary

On locating an insect prey on a twig above the water surface, a group of archer fish can shoot it down using powerful jets of water. The insect, dislodged by one of the shots, falls on a ballistic path towards the water surface, where it is devoured by the first fish to arrive. We report that the archer fish can predict the point where the dislodged prey will later hit the water surface and move in a straight line towards that point, thus enabling it to arrive as fast as possible. Only about 100 ms after prey is dislodged, the fish initiate a quick turn that aligns their body axis right towards where the prey will later land, and not to the actual position of the prey at that moment. In contrast to other known examples of three-dimensional target interception in man and animals, archer fish can head straight to the predicted point of catch without the need of any further visual feedback. Moreover, archer fish can predict the point of incidence of a target, regardless of the angle at which the prey takes off with respect to the initial orientation of the fish. To perform this remarkable task, archer fish extract a minimum set of independent variables that fix the point of incidence, but do not extrapolate the target's spatial trajectory.

Key words: prediction, 3-D target motion, vision, outfielder problem, archer fish, *Toxotes jaculatrix*.

Introduction

Animals that hunt for rapidly moving prey need to predict efficiently their target's future positions from its past motion. This can be achieved simply when the target motion is effectively restricted to two dimensions and constant speed. The prediction can then be based on velocity cues, which suffice to compensate the delay inherent in the processing of the stimulus that elicits the motor response. An elegant way to achieve this was demonstrated recently (Berry et al., 1999). Surprisingly, there are only a few studies of predictive ability in animals, and in each case the target motion was of the restricted type. Velocity cues suffice for praying mantids, which can perform head-saccades that place the image of the moving target on the mantid's fovea (Rossel, 1980). In a most interesting study, male hoverflies were shown to intercept rapidly flying females, using a simple mechanism in which two retinal variables suffice (Collett and Land, 1978). The saccades performed by the human eye as it tracks a moving target are also predictive and based on velocity cues (for a review, see for example, Carpenter, 1988).

To predict the position of a target that is free to move in three dimensions requires not only that its velocity but also its distance be taken into account. Though many hunting animals must evidently be efficient at doing this, and though their time-tested solutions are likely to stimulate technical applications, we are surprisingly ignorant of how animals predict complex three-dimensional motion.

A large number of studies have analysed how humans perform in various three-dimensional interception tasks (see, for example, Regan, 1997; van der Camp et al., 1997; Shaffer and McBeath, 2002). These studies demonstrated various closed-loop strategies in which continuous visual feedback guided the subject to the point of interception. However, these closed-loop strategies did not allow the pursuer to head directly to the point of interception. For instance, baseball outfielders that catch a fly ball (known as the 'outfielder problem'; e.g. Chapman, 1968; Shaffer and McBeath, 2002) move in such a way as to restrict the retinal slip to an upward straight line, which means that they follow a curved path towards the point of catch (McBeath et al., 1995). Recently an analogous closed-loop strategy has been demonstrated in dragonflies, which are able to intercept their prey in flight. In doing so, dragonflies steer so as to minimize retinal slip of their prey's image (Olberg et al., 2000). So far we know of no evidence that humans or other animals can derive the point of interception from the target's initial flight path in advance, and head straight to this point, without further visual feedback being required.

In this report, we demonstrate a three-dimensional predictive ability in an animal with a most remarkable hunting technique: the archer fish (Lüling, 1963; Dill, 1977). These fish are able to shoot down insects that sit on a twig above the water surface by a precisely aimed jet of water. Dislodged by the shot, the insect falls on a ballistic path towards the water surface, where it is caught either by the shooter or by one of the bystanders,
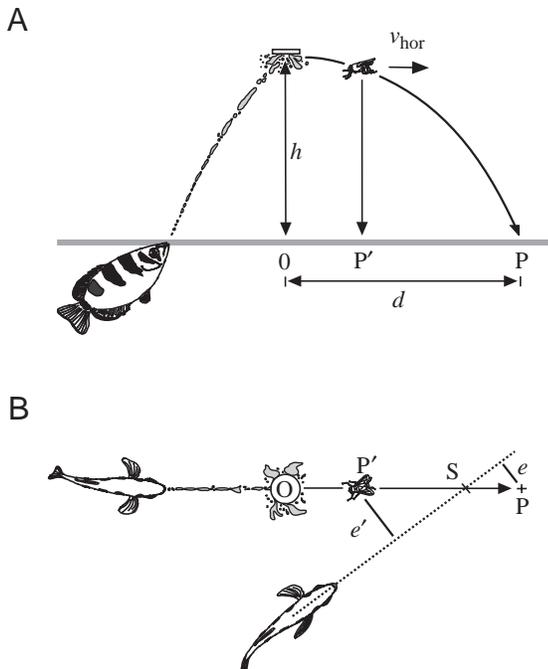
A

B

Fig. 1. Experimental situation and variables used. (A) A dead fly is attached to the lower side of a disk at height h above the water surface. When dislodged by the powerful water jet of an archer fish, it takes off passively at a horizontal speed v_{hor} and will hit the water surface at point P in a horizontal distance d. (B) The same situation as in A viewed from above, showing another archer fish nearby. After a quick initial turn the second fish has aligned itself in the direction indicated by the dotted line, on which it will then rapidly accelerate. At this time the fly is still on its ballistic path above the water surface. Two errors e and e' were analyzed in order to determine whether the fish rushes in the direction of either the later point of impact P or of point P′, the horizontal projection of the target's position at the end of the turn. $e(e')<0$ if distance O–S<O–P(P′), where O is the initial target position and S is the point of intersection between the path of the fish and the fly (horizontal projection).

whoever manages to arrive first. We show here that archer fish are able to predict the point of incidence of the dislodged prey to the water, requiring the fish to solve a complex three-dimensional task in which speed, direction and distance all need to be taken into account.

Materials and methods

Experiments were performed on a group of six juvenile *Toxotes jaculatrix* (Pallas) (size 6–8 cm) in a tank (120×50×50 cm; length×depth×height) filled to a height of 22 cm with brackish water (conductivity 4 mS cm^{-1}; temperature 26°C). Each individual could be recognized from the details of its stripe pattern. Five of the fish responded in all experiments with approximately equal frequency and the present analysis was thus based on their pooled responses. Prey items were dead flies (*Lucilia* sp.; mass when wet approximately 50 mg). A fly was wetted and stuck on the
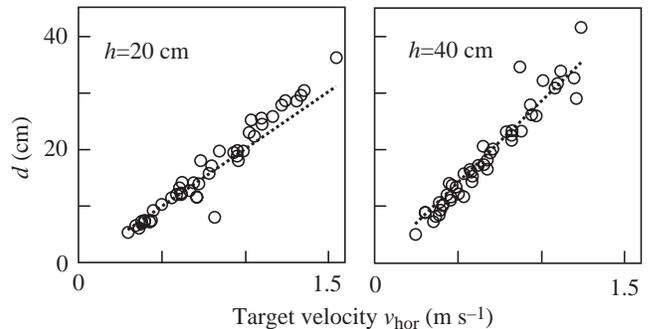

Fig. 2. Evidence that the path of the dislodged prey followed the rules of simple ballistics, with negligible air resistance and initial vertical velocity. For each of the two initial prey heights h used in this study, $h=20$ cm (left; $N=43$ shots) and $h=40$ cm (right; $N=50$ shots), the horizontal distance d travelled by the prey is plotted as a function of its initial horizontal velocity v_{hor}. Dotted lines show the distance $d=v_{hor}(2h/g)^{1/2}$ ($g=9.81$ m s^{-2}) predicted, assuming that there were no frictional effects and no initial vertical velocity.

bottom side of a white disk (diameter 20 mm) hung in the middle of the tank, so that prey could be presented in a height of either 20 or 40 cm above the water surface (Fig. 1). In our experiments, prey dislodged by a water jet from one of the archer fish fell on a ballistic trajectory in which any effects of air resistance and initial vertical velocity were negligible.

The falling prey, as well as the shooting and surrounding fish, were videotaped from above (at 20 ms intervals between successive frames). At each actual height of the falling prey, its position was projected to the water surface, the plane of the hunting fish, taking into account the known distortion in perspective for that height. The motion of the dislodged prey followed simple ballistics rules (Fig. 2), and thus the actual height of the falling prey could be accurately calculated from the time of falling. The response times of the fish were deduced by counting the number of frames between the one in which the prey was first dislodged from its supporting disk (frame 1) and frame m, in which the fish assumed a different position or orientation from that in the preceding frames. The response time was then taken as $(m-1)\times20$ ms. The time to complete the turn was similarly defined, but with frame m being the one in which the fish first assumed its final heading direction. We only evaluated responding fish (i.e. those that were the first to initiate a turn) that were not blocked in their turning by nearby conspecifics and whose body axis initially deviated by at least 10° from the direction of the falling prey (so that the start and end of the quick initial turn could be defined precisely). The initial horizontal velocity of the dislodged prey was derived from the horizontal path of the prey during the first 100 ms of its flight.

We analyzed three situations in which dislodged prey either (i) fell freely, (ii) was fixed to its substrate by a thin filament (white cotton filament diameter 0.8 mm, length 5 cm) so as to stop and reverse its motion after a short initial interval of falling freely, or (iii) moved only horizontally. The latter was achieved by placing the prey on a horizontal glass screen. As
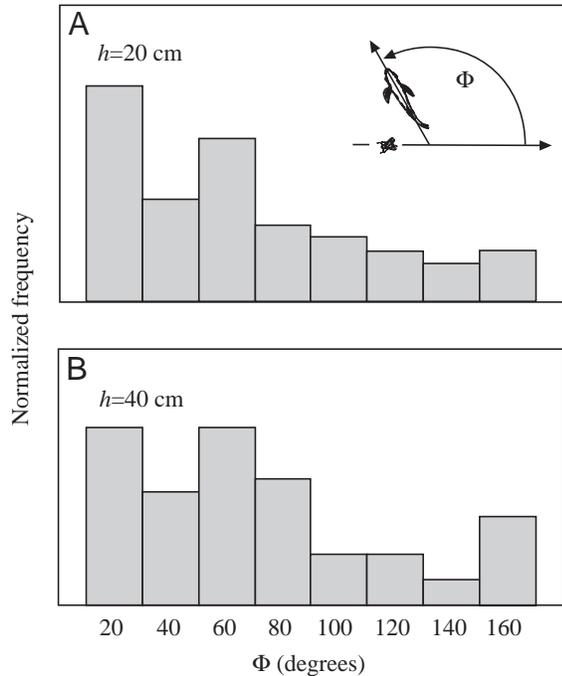
Fig. 3. Archer fish respond over a large range of angles between their initial orientation and the take-off direction of the dislodged prey. Distribution of the absolute values of angles Φ (inset) between take-off direction of the prey and the initial orientation of the responding fish. Angles were sampled at 20° intervals (starting at 10°; see Materials and methods) and accumulated in histograms normalized so that the total frequency equalled 1. (A) $h=20$ cm, $N=60$ responses; (B) $h=40$ cm, $N=64$ responses. Histograms are based on the responses analyzed in Figs 4–6.
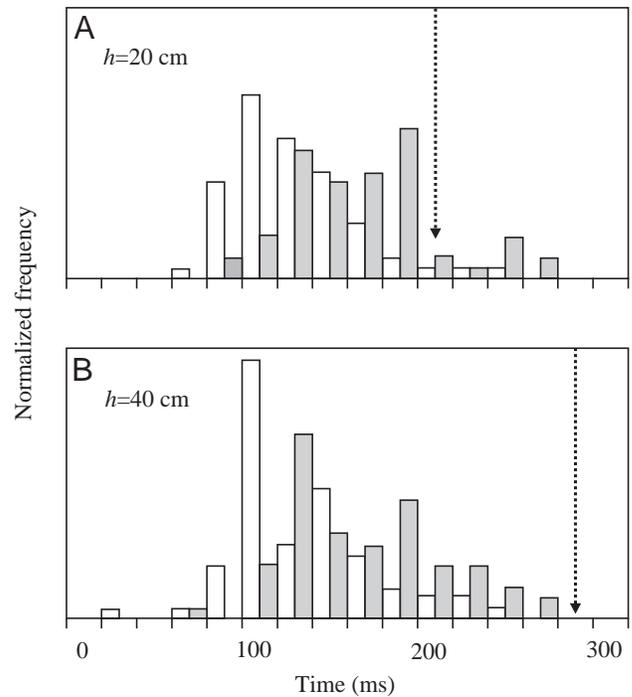

Fig. 4. Evidence that fish initiate their rapid turn within approximately 100 ms and are aligned while the prey is still on its ballistic path. The time intervals from when the prey was dislodged until the initiation of a turning maneuver (open columns) and until turning was completed (filled columns) were sampled at 20 ms intervals and accumulated in histograms normalized so that the total frequency equalled 1. The results obtained at both prey heights h are shown and the time to prey hitting the water surface (i.e. $(2h/g)^{1/2}$, where $g=9.81$ m s^{-2}) is indicated by the dotted lines. (A) $h=20$ cm, $N=60$ responses; (B) $h=40$ cm, $N=64$ responses.

soon as a water jet hit the target, the experimenter directed a stream of air from a thin blast pipe onto it so that it slid along the screen at a speed within the range of normally observed speeds of the dislodged prey. In these experiments the *virtual point of impact*, at which the prey would have hit the water if it had been allowed to fall, could be calculated from simple ballistics (see Fig. 2).

Results

In a first series of experiments, we analyzed the responses of a group of archer fish when prey fell freely. The fish that did not themselves score the hit were oriented over a large angular range with respect to the flight direction taken by the prey (Fig. 3). These fish generally responded with rapid turning maneuvers. Also the shooter that scored the hit often made a quick turn when a prey hit asymmetrically took off in a direction different from that of the shot. The turning maneuvers were performed very rapidly. Following turning, fish headed straight in the chosen direction. Fig. 4 shows the distribution of response time and time to completion of the turning maneuvers, as obtained at the two presentation heights of prey. Within 0.1 s after dislodging the prey, the responding fish initiated a turn that normally ended long before the prey

hit the water surface, before heading straight in the chosen direction.

At what point was the quick turn aimed? One possibility is that the fish can turn directly to the point at which the dislodged prey will later hit the water surface. As a simple alternative, the fish could turn to the position assumed by the prey after completing the turning maneuver, although in most cases the fish would then not directly aim at the later point of incidence and would need to correct this error later. The error might be small enough, however, to justify using this simple approximating mechanism. To test whether the fish turned directly towards the predicted point of incidence or used a simpler mechanism we analyzed two types of errors: (i) the error e, made with respect to the later point of incidence of the prey, and (ii) the error e', made with respect to the prey's horizontal position at the end of the turning maneuver (Fig. 1). If archer fish were able to turn to the true point of incidence, then the error should be minimized with respect to that point, i.e. errors e should scatter around zero and errors e' should be positive. By contrast, if the fish turned to the actual target position at the end of the turning maneuver, then the error e' should be minimized, i.e. errors e' should be distributed around
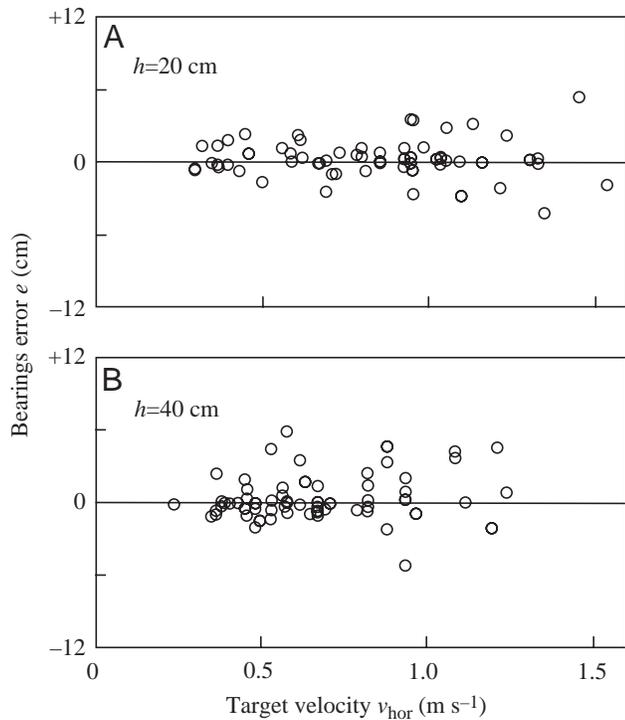
Fig. 5. Archer fish turn so as to minimize the error e with respect to the later point of incidence of prey (see Fig. 1). Evaluation of turning maneuvers in response to prey naturally dislodged by a shot from an initial height h=20 cm (A) or 40 cm (B), which was at the upper boundary of the natural shooting range of the fish. The responses are the same as in Fig. 4. For each response the error is plotted against the horizontal take-off velocity v_{hor} of the prey. The mean of the errors e made with respect to the later point of incidence was not significantly different from zero (t-test).

Fig. 6. Evidence that archer fish do not use an approximate strategy in which they minimize the error e' with respect to the prey's position at the end of their turning maneuver. Plot of the error e' (see Fig. 1) against the horizontal take-off velocity v_{hor} of the prey, as derived from the same responses as in Fig. 4, in which the times until initiation and completion of the turning maneuver are shown. In contrast to the error e made with respect to the true point of incidence (Fig. 5), the mean of the error e' was significantly larger than zero (P<0.01; t-test) at both heights h=20 cm (A) and 40 cm (B).

zero, and errors e should be negative. Note that it suffices to consider the best approximate strategy. In the event that the fish used a less-adequate, approximate strategy, i.e. turning towards the target position at the initiation of the turn, this would become evident by positive absolute values of both errors, i.e. abs(e)>abs(e')>0. Figs 5 and 6 show our results obtained for both target heights studied and over the full range of take-off speeds of prey. The data clearly show that fish minimized the error e made with respect to the true point of incidence and not the error e' made with respect to the prey's actual position when the fish had finished its turn. Thus, the archer fish were capable of predicting the future point of incidence of dislodged prey at all naturally occurring take-off speeds and within the natural range of heights at which they shot at prey.

This conclusion was confirmed in a further series of experiments in which the natural motion of the dislodged prey was altered. A thin filament was attached to the prey so that it could only fall freely during an initial period of slightly more than 100 ms, before being stopped abruptly and the motion reversed. In the 80 responses analyzed, the archer fish still showed their quick turns and accelerated straight in the direction assumed at the end of their turn. Turning aligned the
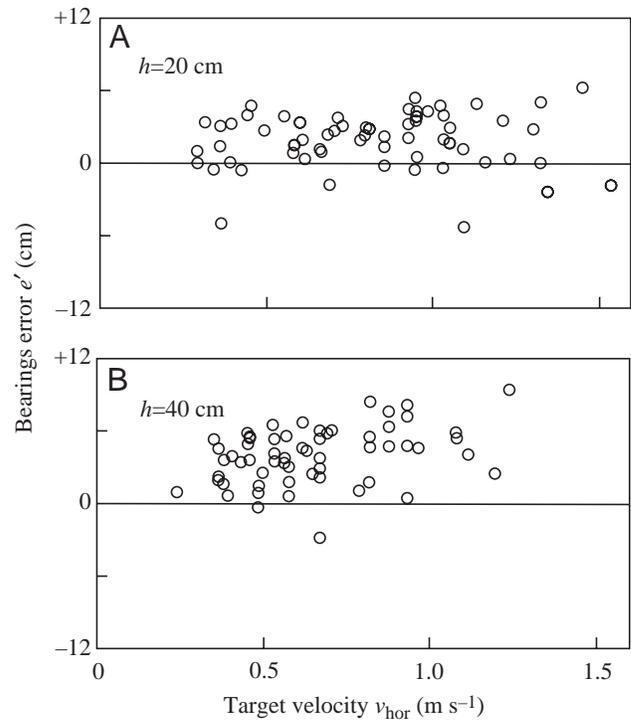
fish's axis towards the point at which prey would have hit the water surface if it had simply continued its initial path (40 analyzed responses at height 20 cm; 40 at height 40 cm; data not shown). This clearly shows that archer fish base their rapid turning maneuver on information deduced from the initial motion of the dislodged prey, and then accelerate in the chosen direction, even when the motion of the prey has been reversed by the filament. Continuous visual feedback was apparently not used during the turn and the initial acceleration phase, and necessary corrections were only seen much later. Rather, the angle of turning seems to be preprogrammed and based on information that is extracted during the initial 100 ms of the prey's ballistic motion.

On what information did the fish base their prediction of the spot at which dislodged prey would hit the water surface? In principle, the fish could have extrapolated the spatial trajectory of the falling prey. Alternatively, they could have determined the speed, direction and height variables, that completely fixed the trajectory in the present experiments. Whether archer fish use such a minimum set of variables and do not extrapolate the spatial trajectory could be tested by fooling them in a simple way, by confronting them with
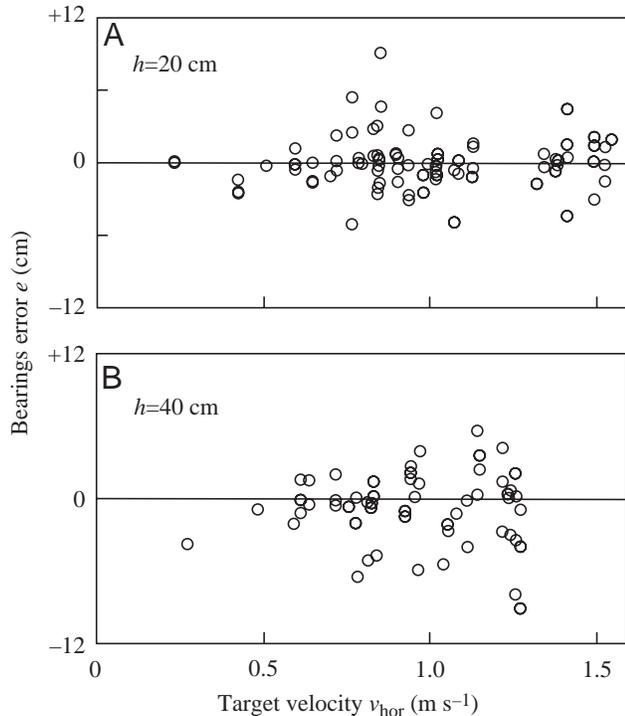
Fig. 7. Demonstration that archer fish base their prediction on an extraction of the horizontal speed and direction of dislodged prey and not on an extrapolation of the spatial trajectory. Fish were confronted with prey that moved only in a horizontal plane. Yet the fish turned towards the virtual point of incidence at which a natural prey of the same take-off speed and direction would have hit the water surface. This is shown for both heights, h=20 cm (N=83 responses) (A) and 40 cm (N=58 responses) (B) by displaying the errors e made with respect to the virtual point of incidence. At both heights the means did not deviate significantly from zero (t-tests). Prey velocity was adjusted to be within the naturally occurring range at the two heights (see Figs 4 and 5).

targets that move exclusively in a horizontal plane and are prevented from falling. If the fish were using a minimum set of variables, then the archer fish should still perform their rapid turn and head towards the *virtual* point at which a target of the same horizontal velocity and initial height would have hit the water surface if it had been allowed to fall freely. By contrast, extrapolation of the initial trajectory of such a target would place the predicted point of incidence at an infinite distance. We tested these predictions by placing a prey object on a transparent horizontal glass screen (either 20 or 40 cm above the water surface). When a water jet from one of the fish hit the prey, it was moved at a speed within the naturally occurring range (see abscissae of Figs 5 and 6) by directing a flow of air from a blast pipe onto it. Surprisingly, all fish responded to this artificial motion of 'dislodged' prey just as they did when the prey fell freely. At both the initial heights analyzed and over the full range of take-off velocities that occur during natural shots at these heights, the errors made by the fish with respect to the *virtual* point of incidence were centered at zero (Fig. 7). This shows clearly that the fish based

their predictive turning maneuvers on horizontal velocity and initial height of their target but not on an extrapolation of its spatial trajectory.

Discussion

In heading to the spot at which a dislodged insect prey will hit the water surface, archer fish are able to solve a three-dimensional prediction task in which direction, speed and target distance need to be taken into account. After one of their shots had dislodged their insect prey, all the fish in a group were able to initiate, within a period of less than 100 ms, a turn that aligned their body axes to the spot where the prey would later hit the water surface. Being thus properly aligned they headed straight towards the future point of impact. Archer fish are able to predict this point accurately within the full range of naturally occurring target heights as well as take-off velocities and directions. To our knowledge this finding is the first demonstration that animals are able to head straight to a point of interception that is predicted from an initial observation of the three-dimensional movement of a target. Interestingly, archer fish do not base their prediction on an extrapolation of the spatial trajectory. Rather, they extract from the first 0.1 s of the prey's flight the minimal amount of information that is needed to determine the point of incidence, i.e. initial height, speed and direction.

At present we do not know (i) how archer fish extract the required variables and, (ii) how these (or related) variables are combined in order to allow the fish to turn directly towards the point where the prey can eventually be caught. In aiming their shots, archer fish have an exquisite ability to judge the height of their prey above the water surface. Precise information about the height of their targets is required in the archer fish's ability to correct for both the light refraction at the air–water interface and the ballistic bending of their water jet (Dill, 1977; S. Schuster and S. Rossel, manuscript in preparation). Our current research indicates that archer fish can precisely estimate distance, even under monocular conditions, but we do not know how the fish perceive the initial velocity of their dislodged prey. In doing so the fish must gauge the perceived changes in the retinal image with the distance of the target. In the extensively studied problem of estimating the 'time-to-collision' (e.g. Lee, 1976) of a directly approaching target, retinal image changes can be used directly, and knowledge of the target's absolute velocity is not necessary. However, archer fish are able to predict accurately the point of incidence regardless of the initial direction of a dislodged prey, and therefore must use much more refined solutions than the time-to-contact approaches that have been discussed previously. Being able to predict a complex three-dimensional path of their dislodged prey clearly helps archer fish to arrive as quickly as possible at the later point of catch, perhaps more quickly than other, less attentive predators, and long before a downed fly would be on the wing again.

Interestingly we have found no evidence for bystanders (that generally have to make larger turns) performing less accurately than the fish that fired the successful shot. Moreover, current

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research in our laboratory indicates that the success of a given fish in the group in actually taking the catch is only determined by its distance from the point where the prey will hit the water: for any given distance, the hunting success of bystanders and successful shooters appears to be the same. So bystanders are apparently just as effective as successful shooters in predicting the point of catch.

We do not yet know whether the fish would also be efficient in predicting more complicated paths in which, for instance, the target initially moved upwards before falling down. In natural situations the fish need to cope with a broad spectrum of targets and heights, whereas in our experiments the ballistic properties of the target were constant, as was the height range at which the targets were presented. Given the remarkable ability of the fish demonstrated here, we suggest that archer fish may provide an excellent opportunity to study how organisms efficiently predict three-dimensional target motion.

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