Hunting archer fish match their take-off speed to distance from the future point of catch

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Summary

Archer fish can shoot down insect prey with a sharp jet of water. Fish usually fire from positions that are not directly below their target so that a dislodged insect falls ballistically with a horizontal velocity component. Only 100 ms after the insect is on its path both the shooter and other school members can initiate a rapid turn and then head straight in the direction of the later point of impact of their falling prey. The quick turn and subsequent take-off are performed 'open-loop', based on the initial values of the falling insect's motion. We report here that archer fish can not only take off in the direction of the later point of impact but also predict its distance. Distance information allows the fish to adjust their take-off speed so that they would arrive within a narrow time slot slightly (about 50 ms) after their prey's impact, despite large differences in the size of the aligning turn and in the distance to be covered. Selecting a constant speed program with matched speed and catching the insect on the move minimizes frictional losses. The initial speed of starting fish is slightly but systematically too slow and is increased later so that the fish arrive 20 ms earlier than expected and often make the catch on a higher than take-off speed. The variability of later speed changes suggests a systematic 'error' in the take-off, as if the fish underestimated distance. However, this apparent deficiency seems well adapted to the fish catching their prey at a high speed: if later the fish had no possibility to correct an initial error then it is better to start slightly too slow in order to minimize the risk of overshooting the point of catch.

Key words: prediction, motor planning, open-loop start, animal cognition, archer fish.

Introduction

Archer fish are well-known for their impressive ability to shoot down aerial insect prey with a precisely aimed jet of water (e.g. Lüling, 1963; Dill, 1977). Thereby the fish fire from positions not directly below their target but displaced laterally from it (e.g. Dill, 1977; Timmermans, 2001; Rossel et al., 2002; Schuster et al., 2004) so that their shot transfers horizontal momentum to their target and makes a small prey item fall on a ballistic path towards the water surface. It then takes only about 100 ms from the start of the prey's ballistic motion till the shooter as well as other school members can initiate a rapid turn and then head off straight in the direction of the later point of impact of the falling prey (Rossel et al., 2002). The rapid turn and subsequent take-off in the chosen direction are performed 'open-loop', i.e. based only on information that the fish had sampled during less than 100 ms of the prey's initial motion. That the fish can operate without immediate sensory feedback is shown by experiments in which (i) a filament connecting a prey item to its starting position swung the prey back after an initial free flight phase and (ii) the fish responded to purely horizontal target motion with turns that were directed towards the virtual point of impact, which would be predicted on the basis of the initial values of motion (Rossel et al., 2002).

Though restricted to the plane of the water surface, to choose the appropriate turning angle requires the fish to solve a three-dimensional problem, in which three independent variables need to be correctly taken into account: the initial speed, direction and height of the falling prey. While there is convincing evidence that the fish solve this problem and predict the bearing of the future point of impact, it is not easy to prove our conjecture that the fish truly pinpoints the location of this point. This is illustrated in Fig. 1A. In principle, the fish's 'internal estimate' of the fly's later point of impact P could be anywhere within the area indicated in green (e.g. at P′ or P′′), and yet the fish is led to the point of impact. Here we provide direct evidence against this view by showing that (i) archer fish also predict the distance of the later point of impact and (ii) use this information to adjust their take-off speed to distance. The fish select a take-off speed that would allow them to arrive within a narrow time slot slightly after the prey's impact after travelling at constant speed. In their initial open-loop response to falling prey, hunting archer fish thus start with a predetermined turn size and take-off speed, which
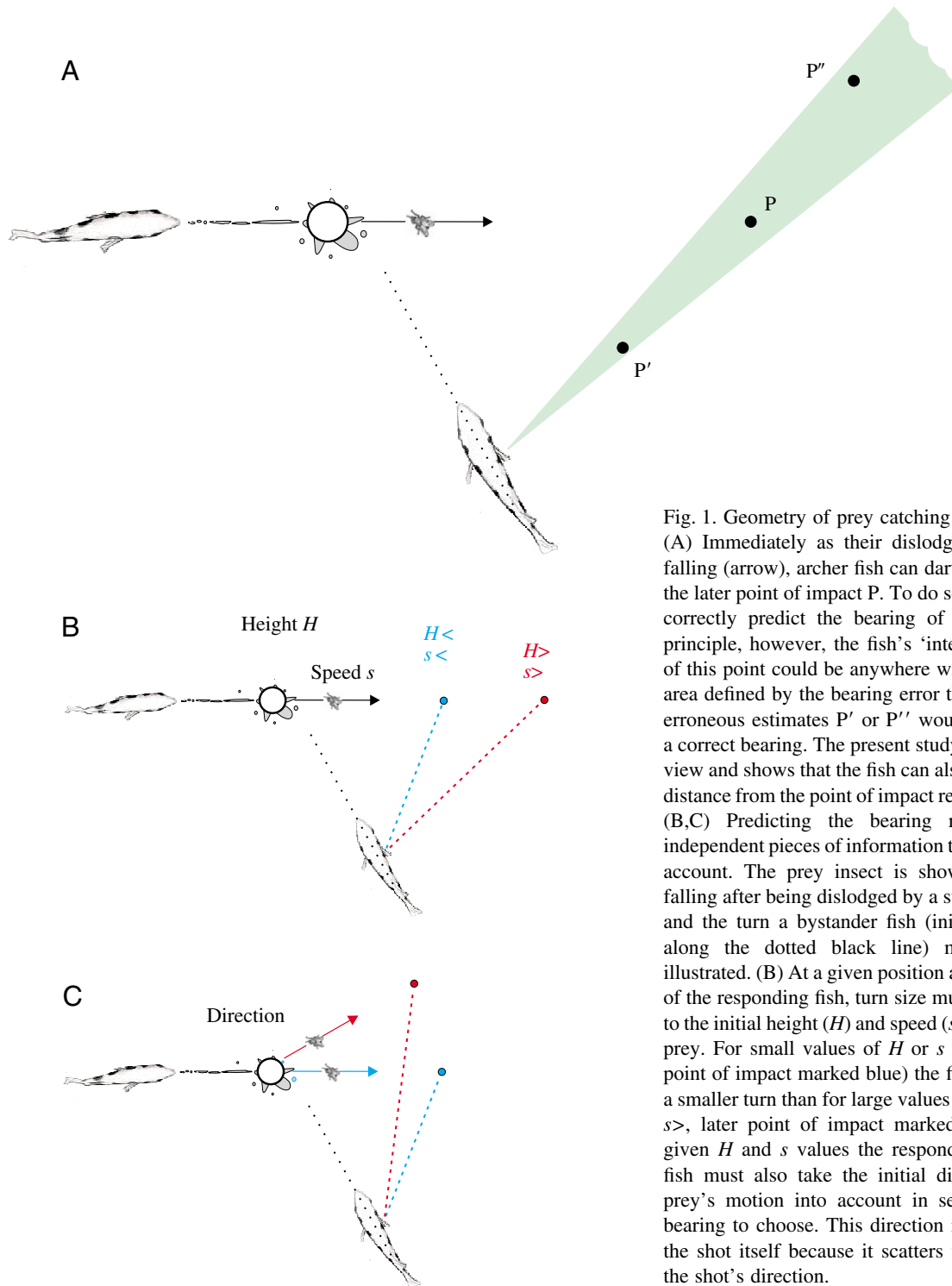
Fig. 1. Geometry of prey catching in archer fish. (A) Immediately as their dislodged prey starts falling (arrow), archer fish can dart right towards the later point of impact P. To do so the fish must correctly predict the bearing of this point. In principle, however, the fish's 'internal estimate' of this point could be anywhere within the green area defined by the bearing error the fish makes: erroneous estimates P′ or P″ would still lead to a correct bearing. The present study excludes this view and shows that the fish can also predict their distance from the point of impact reasonably well. (B,C) Predicting the bearing requires three independent pieces of information to be taken into account. The prey insect is shown at start of falling after being dislodged by a successful shot, and the turn a bystander fish (initially oriented along the dotted black line) must make is illustrated. (B) At a given position and orientation of the responding fish, turn size must be matched to the initial height (H) and speed (s) of the falling prey. For small values of H or s ($H<$, $s<$, later point of impact marked blue) the fish must make a smaller turn than for large values of H or s ($H>$, $s>$, later point of impact marked red). (C) At given H and s values the responding bystander fish must also take the initial direction of the prey's motion into account in selecting which bearing to choose. This direction is not cued by the shot itself because it scatters widely around the shot's direction.

they can set independently to match the solution of a complex three-dimensional predictive problem.

Materials and methods

Experiments were performed on two groups of 6 and 8 juvenile *Toxotes jaculatrix* Pallas 1767 (size 6–8 cm) kept in tanks (120 cm×50 cm×50 cm; length × depth × height) that were filled with brackish water (conductivity 3.5 mS cm^{-1}; temperature 26°C) to a height of 25 cm. All group members responded to dislodged prey and the present analysis is based on their pooled responses. The set-up was as described earlier (Rossel et al., 2002). Briefly, stationary prey items (*Lucilia*; killed by freezing) were wetted (wet mass was about 50 mg)

and stuck on the bottom side of a heavy white disk (diameter 20 mm) hung in the middle of the tank, so that prey could be presented at a height H of either 20 or 40 cm above the water surface. Captures were videotaped from above (with 20 ms intervals between successive half-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 dislodged prey followed simple ballistics so that the actual height of the falling prey could be derived from the time it had been falling.

Responses and analysis

We restricted the analysis to responses that fulfilled all of the following criteria. (1) Prey had to be still falling when the fish started to take off. This criterion ensured that the response was predictive and driven by visual input (and not e.g. mechanosensory input from the splashing prey). (2) The path to the later point of impact had to be free of obstacles such as fellow group members. This criterion is needed because obstacles strongly influence the fish's take-off (S. Wöhl and S. Schuster, manuscript in preparation). (3) Cases were excluded in which the fish could simply follow the prey's motion. This criterion was needed to check whether the fish also predicted bearing. A minimum angle of 10° was required between the path a responding fish would have to take towards the point of impact and the horizontal path of the prey. (4) To ensure that responses of sufficiently motivated fish are evaluated and to be able to exclude extremely slow responses on the basis of rigid criteria, the 5% responses with the largest arrival times after prey impact (some in the order of seconds) were not included in the present analysis.

A set of 90 responses (26 of the group of 8 fish, 64 of the group of 6 fish) was obtained that satisfied all criteria. Responses came from bystanders (*N*=36) and shooters (*N*=54).

The deinterlaced frames (50 s^{-1}) were analyzed with the public domain program NIH Image (developed at the US National Institute of Health) using custom-written software to extract coordinates, derive angles and distances and plot traces such as shown in Figs 8–10. Speed was determined from the change in position of the tip of the fish's mouth between successive frames and the speed value is assigned to the start of the second of the two frames. It should be noted that this is not a generally valid method as it confounds translational and angular speed during phases of turning. If independent estimates of translational speed had been required during extended phases of turning, then they would have been better based on the displacement of the center of mass. However, because the fish turn and accelerate and then take off in the chosen direction, our more convenient measure could safely be used. From the distance between neighbouring pixels in the deinterlaced images we expect our speed estimates to be accurate to about 0.05 m s^{-1}. Additional errors could occasionally result when the fish were not moving horizontally. Because archer fish take off so fast, these errors are of a size that does not affect the conclusions of this paper.

Results

The initial turn

Fig. 1B,C illustrates the geometry of the problem a responding archer fish must solve. The turn a responding fish at a given position and orientation must make needs to be tuned to three variables that vary independently from each other over broad ranges: the speed of the dislodged prey, its initial height and the horizontal projection of its direction of motion. In the present experiments the direction in which prey fell scattered widely within the full angular range around the direction of the incoming shot so that the direction of the shot itself did not provide *a priori* cues about the direction of target movement. Target height was selected randomly to be either 20 cm or 40 cm and the horizontal speed acquired by the target scattered widely in the range between 0 and 1.5 m s^{-1}. This section addresses two aspects that are prerequisites for the later analysis and shows that (i) responding fish in our dataset predict the bearing of the point of impact correctly and do not use an approximate mechanism and (ii) that responses occurred within a sufficiently broad range of distances and turning angles.

Fig. 2A introduces the error angles used to check whether the responding fish predicted the correct bearing. In the responses, the errors ϵ made with respect to the point of impact are distributed around a zero mean (Fig. 2B). In other words, the responses were so as to minimize the bearing error with respect to the later point of impact. This is, however, not yet proof that the responses were indeed predictive. An approximating strategy in which the fish turned to align themselves with the prey's position at the end of the turn could in principle mimic a true prediction. The findings reported in Fig. 2C exclude this view. In this figure the bearing error is evaluated not with respect to the later point of impact but with respect to the fly's horizontal position at the end of turning. The distribution of the respective errors ϵ' is systematically shifted towards positive values. Thus the responses we have gathered were indeed predictive, i.e. were directed at the later point of impact but not towards the actual sighting at the end of the initial turn.

An interesting aspect is that bystanders and shooters did not differ in their performance. For instance, their bearing errors did not differ significantly: means ± s.e.m. of ϵ (in degrees) were –0.04±0.93 for bystanders (*N*=36) and –0.78±0.73 for shooters (*N*=54). Also, if the errors are quantified by the minimum distance the fish's course has from the point of the later point of impact (as was done in Rossel et al., 2002), bystanders and shooters perform equally well.

The distances responding fish had to cover varied over a broad range from about 30 mm to 380 mm (Fig. 2D). Fig. 2E shows the distribution of time till prey impact that remained for the responding fish after they had finished their rapid turn and were ready to take off. In most cases the remaining time was long enough to potentially allow the fish to select an adapted motor program. The sizes of the turns responding fish made were also broadly distributed (Fig. 2F).
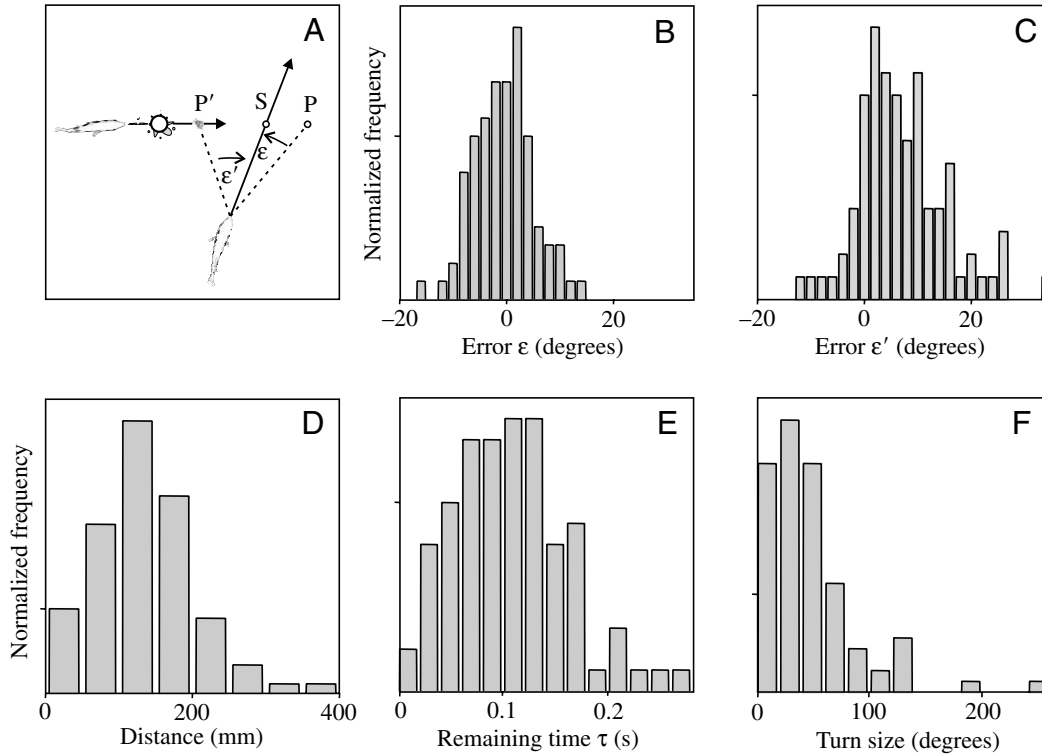
Fig. 2. Suitability of the responses analyzed in this paper. (A–C) Evidence that the responses were directed at the predicted later point of impact but were not based on an approximate mechanism. (A) Illustration of the errors analyzed. A shooter has dislodged a fly, which falls towards its later point of impact P. At the instant shown, a bystander has just finished its initial turn and starts to head off with a bearing indicated by the solid line. The actual position of the fly is at P′. The solid line crosses line of prey movement (from P′ to P) at point S. Errors ε and ε′ denote the angular deviations of the bystander's bearing with respect to either the later point of impact P or the actual position P′ of the fly (broken lines). Error ε (ε′) is positive when the respective reference point P (P′) is before S, otherwise the error is negative: in the situation shown ε′ is positive and ε is negative. (B) Bearing errors ε made with respect to the later point of impact are symmetrically distributed around zero. (C) In contrast, the distribution of errors ε′ with respect to the fly's actual position, is systematically offset towards positive values ($P<0.001$, t-test). Errors ε and ε′ are sampled in intervals of 2°. (D) Distribution of distances the responding fish had to cover from their initial position towards the later point of impact. Bin width 50 mm. (E) The time τ that remained till prey impact when the fish had sampled the necessary information about target motion, had finished their turn and were ready to take off. The histogram shows how remaining times τ, binned in 0.02 s intervals, were distributed in the set of responses. (F) The fish responded over a remarkably wide range of target-flight directions with respect to their initial orientation. The histogram shows the correspondingly wide distribution of turn sizes the responding fish made. Bin width is 20°. All histograms are based on the same $N=90$ responses and are normalized so that their total frequency equals 1, ticks on ordinate indicate 10% frequency.

Take-off speed scales with distance

After it has finished its turn and is aligned towards the later point of impact a responding fish accelerates very rapidly and reaches a high and approximately constant take-off speed already in the first video frame after take-off. Compared to the speed gained immediately at the end of the turning phase, the later speed changes in the first 60 ms of translation are negligible. This is shown in Fig. 3, which reports the differences in speed between subsequent intervals of 20 ms duration. A slight but systematic increase in speed of 0.05 m s^{-1} (Fig. 3A, 20–40 ms after start) and 0.07 m s^{-1} (Fig. 3B, 40–60 ms after start) occurred. Though these speed changes were significant ($P<0.01$ in each case, t-test), they are small compared to the speed of about 1 m s^{-1} on top of which they occurred. It therefore appears well justified to treat the take-off as a start with constant speed, with speed acquired

rapidly at the end of the turning phase. This view is confirmed by current high-speed video analyses in our laboratory. Maximum take-off speed was in the range of 1.2–1.6 m s^{-1} or about 15–25 fish lengths s^{-1}, which is remarkably fast and clearly in the upper range of values reported for other teleost fish (e.g. Gray, 1953; Bainbridge, 1960; Webb, 1973; Wardle, 1975; Nissanov and Eaton, 1989).

The speed measurements disclosed in a simple way that the fish must indeed have a measure of how far away the future point of impact is. This became evident when take-off speed was plotted against the distance the responding fish had to cover to the later point of their prey's impact. Fig. 4A–C report the speed values measured in the first (A) and the two subsequent (B,C) intervals (of 20 ms duration) of each take-off. Speed values determined in each of these intervals correlated highly significantly ($P<0.0001$) with distance.
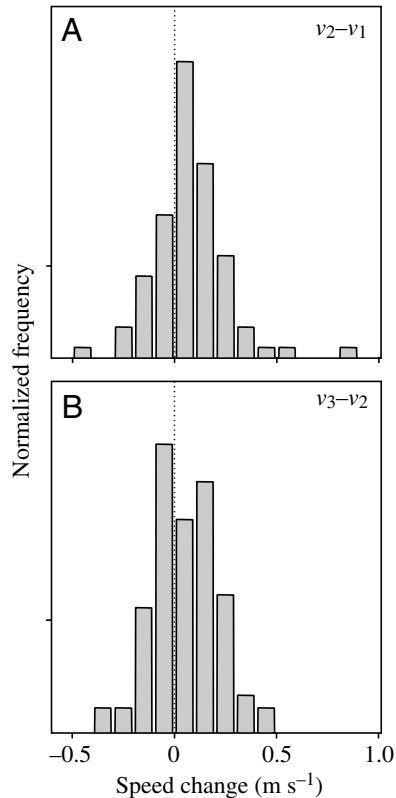
Fig. 3. Take-off speed is rapidly gained at the end of the turning phase and is changed only very slightly in the immediately subsequent translatory phase. For each of the N=90 responses, speed measurements v_1, v_2, v_3 were derived from changes in position during the first, second and third 20 ms interval, respectively, of the fish's initial translatory motion. The histograms show the distribution of speed differences between subsequent intervals. Distribution of (A) speed changes v_2–v_1, (B) v_3–v_2. Both distributions are systematically shifted towards positive values, but the shifts (0.05 m s^{-1} and 0.07 m s^{-1}, respectively, both P<0.01; t-test) are small compared to the basis speed level of about 1 m s^{-1} acquired during the final phase of the turn. Speed differences in A and B are sampled in intervals of 0.1 m s^{-1} and accumulated into histograms normalized so that total frequency is 1, ticks on ordinate indicate 10% frequency.
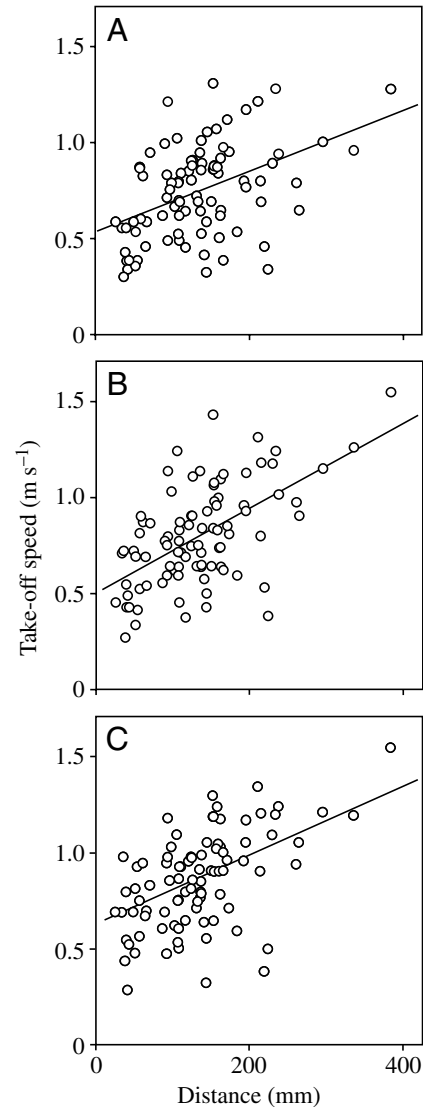

Fig. 4. Take-off speed correlates with distance from the later point of prey impact. (A–C) The speed values determined within the first (A), second (B) and third (C) 20 ms interval after the fish has executed its initial rapid turn and starts moving in the direction of the predicted later point of impact while the fly is still falling. In each case the correlation is highly significant (P<0.0001; r^2=0.20, 0.33 and 0.21 in A–C, respectively).

This shows that the fish must have a measure of their distance from the future point of impact, which allows them to adjust their take-off speed. However, it does not exclude the possibility that take-off speed could be based on a more complex measure that takes other information besides distance and motor constraints into account. If such other factors were important in setting take-off speed and if these factors varied independently from distance then they could potentially explain the scatter in the speed–distance relation in the plots of Fig. 4. They also could offer a simple explanation for why the intercepts of the regression lines predict a non-zero take-off speed, even if a responding fish is already at the point of capture. Of the many negative findings of our extensive search to identify such other factors, two are worth mentioning. (1) The turn that the fish must make might in principle limit which

speed level it can choose at start. For instance, after a large turn the fish might not be able to start slowly because the release of its strong bending could dictate a rapid start. In other words, if a responding fish had to turn much and then would have to start slowly because the point of impact were close it might not be able to set the required speed. Because turning angles of our responding fish varied largely (see Fig. 2F), we could test this notion by checking whether larger take-off speed levels tended to occur after large turns. However, we found no evidence for such a correlation. (2) We also found no convincing evidence that the fish would modulate their take-off speed in response to social factors

such as 'urgency' to be fast because competitors are close to the future point of impact.

How do the fish use distance information?

The search for a combined measure led to a better predictor of speed: take-off speed scaled better with the ratio 'distance/remaining time of flight' rather than distance itself. The meaning of this ratio is intuitively clear: it can be viewed as a 'virtual speed' that the fish would have to keep in order to arrive simultaneously with the fly after a travel at constant speed. Fig. 5A plots take-off speed against 'virtual speed', also including those virtual speed values that are far above the fish's (and all other known teleosts) speed limit (indicated by an arrow). In the range of attainable speed the concentration of
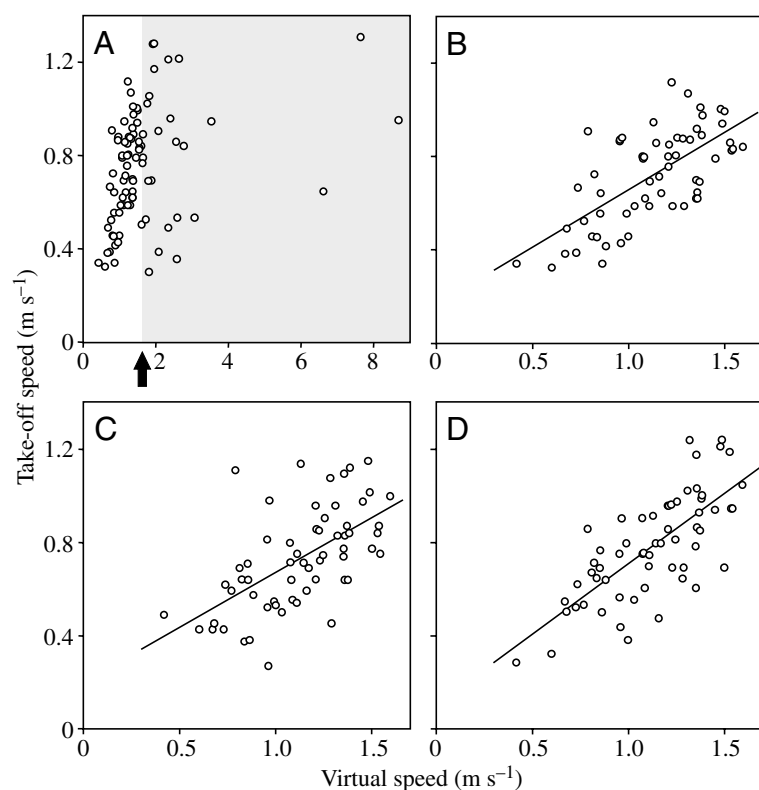
data points on a line is striking. Fig. 5B plots the responses for which the remaining flight of the target was long enough so that virtual speed was within the range of attainable speeds. Within this region the plots describe take-off speed remarkably well. Speed values determined in the first and third intervals of 20 ms duration after take-off (Fig. 5B,D) correlated significantly ($P<0.05$; Fisher z-transformation) better with virtual speed than with distance (Fig. 4A–C). For this analysis, the speed values of the same 60 responses of Fig. 5 were plotted against distance, yielding $r^2=0.14$, 0.24 and 0.22, respectively, for the three intervals. For the second interval the apparent better correlation (larger correlation coefficient) was not significant. It is interesting to note that the large speed predicted by the regression lines of Fig. 4 at zero distance is greatly reduced. For the regression lines against distance the intercepts ±5% confidence intervals in m s^{-1} were (A) 0.56±0.12, (B) 0.50±0.12, (C) 0.56±0.12 (using the $N=60$ responses of Fig. 5). Thus, intercepts were clearly (and significantly) larger than zero. In contrast, the regression lines against virtual speed (shown in Fig. 5) had intercepts (m s^{-1}) of (A) 0.17±0.16, (B) 0.20±0.20 (C) and 0.11±0.18, which are close to zero. Taken together, virtual speed (distance per remaining time till impact) explains the take-off speed better than distance alone.

Arrival times at the point of catch: predicted and actual

When did the fish actually arrive at the point of catch? Did they arrive too early, too late or exactly just when the fly also arrived? Fig. 6A shows when the responding fish arrived after (which is assigned positive values of t) their prey's impact (denoted as $t=0$) on the water surface. There was not one case in which the fish overshot the point of impact. In the majority of the responses fish managed to arrive within a narrow time slot of 20–40 ms after their prey's impact. This is remarkable as the responses were started from a wide variety of distances (ranging from 2.6 to 38.4 cm, see Fig. 2D) and required very different turning angles chosen out of a broad range (see Fig. 2F). It is interesting to note that bystanders and shooters also performed equally well in this respect (difference between the arrival times $P>0.2$, U-test).

A further remarkable fact is that the fish caught their prey while still at full speed. Fig. 7 plots the actual speed values at capture (as derived from the two frames that immediately preceeded the catch) as a function of the fish's speed at start. It is evident that the fish not only caught their prey while at full speed but that they had often even increased their speed to make the catch at higher than take-off speed. This seems to fit nicely with the finding that fish arrive slightly too late: even with a slight amount of scatter

Fig. 5. How take-off speed appears to be determined by distance plus remaining time of falling. (A–D) Plots of take-off speed *vs* 'virtual speed', i.e. distance (*d*) of responding fish from the predicted catching point divided by the time (τ) the prey has still to fall when the fish has finished its turn and is ready to take off. Virtual speed is the speed the fish would have to choose in order to arrive simultaneously with the prey after a course with constant velocity. (A) Plot that includes responses (within the grey area) in which virtual speed was above the actual speed limit of the fish (arrow), corresponding to 15–25 fish lengths s^{-1}. Take-off speed was determined from the first 20 ms of translation. (B–D) Plots of take-off speed *vs* virtual speed within the accessible range of speed values that the fish can potentially realize (*N*=60 responses). (B) Speed in the first 20 ms interval after take-off; (C,D) speed in the subsequent two intervals of 20 ms duration. In each case correlation coefficients are highly significant (*P*<0.0001; *r*^{2}=0.45, 0.35 and 0.54 in B–D, respectively) and higher than the corresponding correlation coefficients in the plots of take-off speed against distance (Fig. 4A–C).

in the arrival times it would not be useful to make the average arrival time coincide with that of the prey because this would cause a high risk of overshooting. Arriving slightly too late diminishes this risk. Moreover, the rapid availability and processing of mechanosensory cues (for reviews, see e.g. Bleckmann, 1993; Montgomery et al., 2002) of the splashing prey provide, even within the remaining short time interval, useful cues that could be used to fine tune the actual catch.

How well do the actual arrival times correspond to those expected from the take-off speed? Suppose the fish were to keep their initial speed to bridge the whole distance to the point of catch. It is then easy to predict the expected arrival times. Should the fish follow a constant speed program and should they be able to perfectly determine and set the speed that is appropriate to the predicted distance and remaining time, then the expected and actual arrival times should perfectly match. Discrepancies between the two times could result from deviations in any of the conditions mentioned above, i.e. that take-off speed cannot be set precisely enough or that the prediction of distance contains errors. The distribution of the expected arrival times (i.e. expected on the basis of a constant-speed strategy) is shown in Fig. 6B, to allow easy comparison with the distribution of actual arrival times (Fig. 6A). The two distributions do not differ dramatically; however, the distribution of expected arrival times is shifted towards slightly later arrival ($P<0.0001$, U-test). It is striking that the expected arrival times do not scatter much more than do the actual arrival times, so that the 'blur' in arrival time would not be much greater if the fish simply continued at their take-off speed. In other words, the take-off speed initially chosen by the responding fish was slightly but systematically too slow and was corrected later.

The course of speed and direction during the approach

To see how well fish held their initial settings of bearing and speed we randomly selected 40 of the responses for a detailed analysis of post-start changes. Fig. 8A shows an approach path in which a fish initially turned by about 30°, accelerated and took off at a speed of about 0.7 m s^{-1}. It then approximately kept its speed to arrive about 100 ms after the fly at full speed. Fig. 8B shows that speed increases slightly during the course but the major acceleration to take-off speed occurred at the rapid start. Fig. 8C shows that the bearing was kept to throughout the approach.

A high precision in the fish's initial choice of bearing is typical of all examples. The chosen direction was kept with deviations less than about 5–10°. In 3 of the 40 paths, corrections to the chosen bearing were made but were likely due to the fact that other responding fish were about to come into the way. In contrast to direction, speed was not nearly as constant. As far as our speed resolution permits us to say, there appears to be no fixed pattern according to which take-off speed is changed in an approach. Approaches with approximately constant speed were seen in 25 of the 40 cases. In several cases (about 7 of 40) the responding fish kept an approximately constant acceleration throughout its course. An
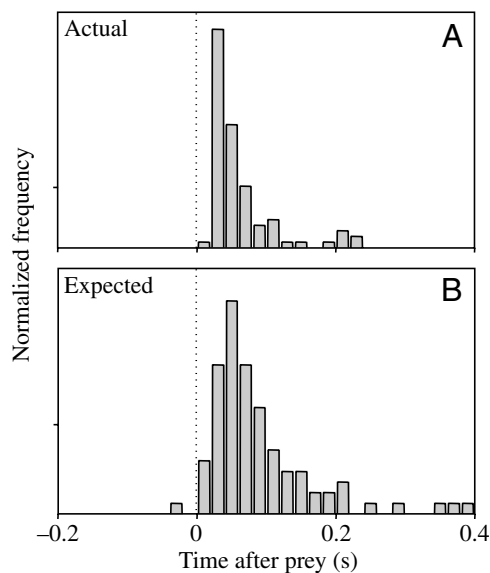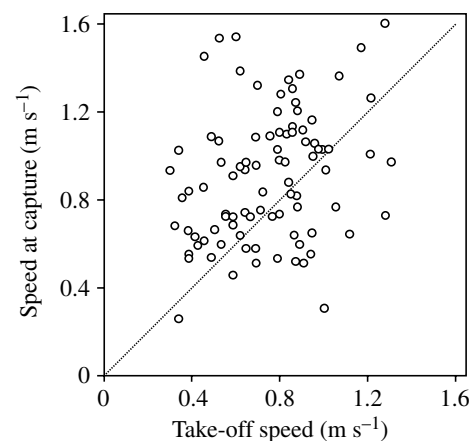

Fig. 6. With no immediate competition at the point of catch fish arrive very slightly after the prey has landed. (A) Actual arrival times at the point of catch. The histogram shows the distribution of actual arrival times with respect to prey impact (which occurs at time $t=0$). In this diagram $t>0$ means that the fish arrives after the prey has landed, $t<0$ means that fish arrives before prey. (B) Histograms of arrival times expected on the basis of the respective take-off speed and supposing that the fish would simply continue to move with this speed. This distribution corresponds well to that of actual arrival; however, systematically larger expected than actual arrival times show that take-off speed was chosen slightly too slow and that later speed corrections were made. Expected and actual times were sampled at intervals of 0.02 s and accumulated in histograms that were normalized so that the total frequency equalled 1. All $N=90$ responses, ticks on ordinate indicate 10% frequency.

Fig. 7. Prey is taken on the move. Plot of speed at capture *vs* speed at take-off shows that fish had no tendency to reduce their speed at the catching point but rather to increase it, making the catch at full speed. The line marks where speed at capture equals speed at take-off. All $N=90$ responses.
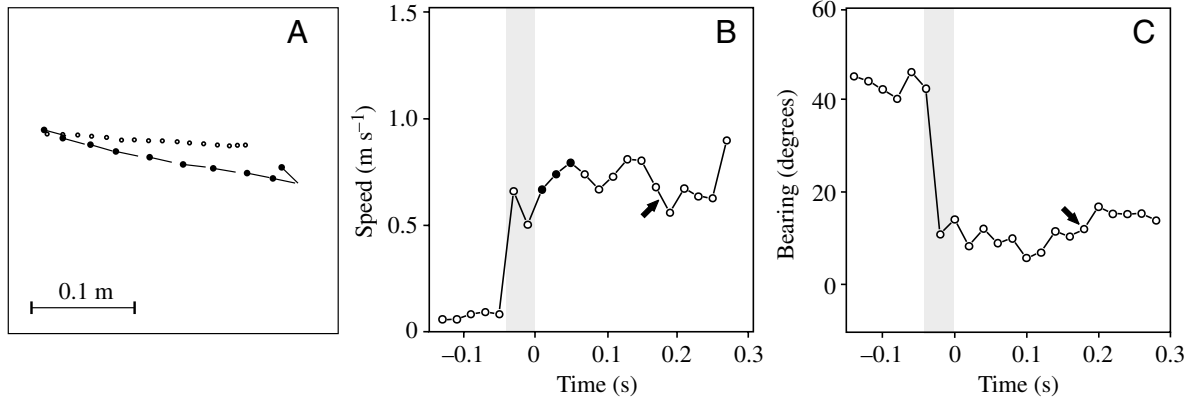
Fig. 8. Scrutiny of a constant-speed approach path towards the predicted point of impact. (A) Path of falling fly (open circles, calculated projection onto the plane of the water surface) and of responding fish (filled dot indicates the head) sampled every 20 ms. For the fish, only every second sample is shown. (B,C) The corresponding time course of (B) speed and (C) angle. The phase of rapid turning is shown by grey shading. Three filled dots indicate the speed determined in the first, second and third interval of 20 ms duration after take-off. The impact of the fly is indicated by an arrow. Sequence ends with the catch. In B, speed values report translational speed except for the phase of turning (grey shading) in which values report only the change of head position that was due to turning. During translation the speed is approximately constant. Note that speed could not be estimated better than about 0.05 m s^{-1}. (C) After an initial turn of about 30°, the bearing is maintained. A bearing of 0° denotes a course in the orientation of the scale bar in A (0.1 m).

example of this is shown in Fig. 9. In other cases the fish first accelerated to high speed and then decelerated, or first reduced their speed and then accelerated during the final phase that preceded the catch. An example of this latter situation is shown in Fig. 10.

Discussion

The major surprise of this paper is that archer fish not only predict the bearing of the future point of impact of their dislodged prey, but that they in addition choose a take-off that is adapted to how far this point will be away. In their open-loop start, archer fish thus drive their motor system with a predetermined turning angle and take-off speed that are both

matched to a computed point from which currently no signals emanate. In this regard the open-loop start of hunting archer fish clearly differs from many impressive examples of ballistic open-loop starts in other animals, such as jumping insects that can launch ballistic starts with just the right amount of speed to reach a potential landing site a certain distance away (e.g. Wallace, 1953; Heitler and Burrows, 1977; Sobel, 1990). The ability of archer fish to fine tune an open-loop start on the basis of three-dimensional movement prediction so far is unique. It differs remarkably from what sportsmen, such as baseball outfielders, do in comparable three-dimensional interceptive tasks in which the direction of target motion is not restricted within a narrow range (e.g. Chapman, 1968; McBeath et al., 1995; Regan, 1997; van der Camp et al., 1997; Shaffer and
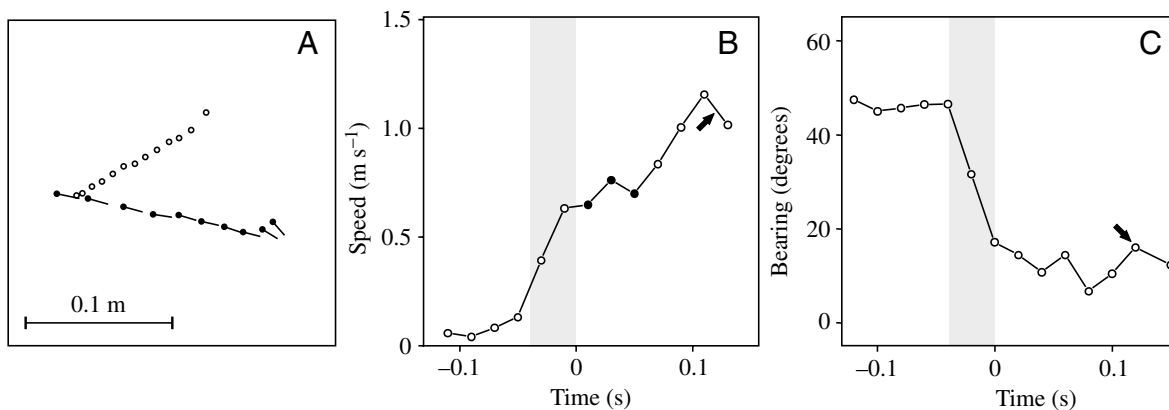

Fig. 9. Example of an approach path in which the fish did not hold a constant speed, but rather accelerated till the point of catch. (A) Path of falling fly (open circles, calculated projection onto the plane of the water surface) and of responding fish (filled dot indicates the head) sampled every 20 ms. Each sample is shown. Arrangement of panels A–C and the ordinate scale in B and C are as in Fig. 8. In contrast to speed (B), the bearing of the fish's movement (C) is kept rather constant.
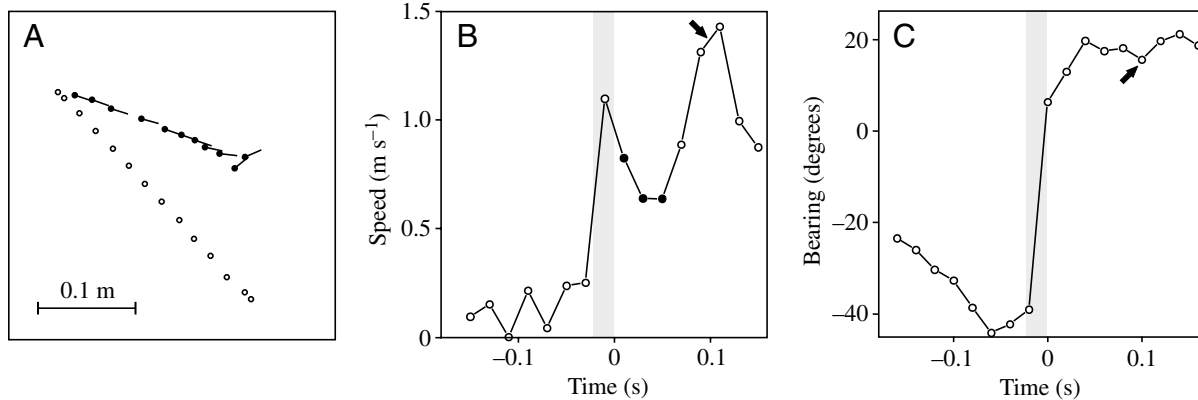
Fig. 10. Approach path with irregular velocity changes before the fly's impact at the water surface. Path of falling fly (open circles, calculated projection onto the plane of the water surface) and of responding fish (filled dot indicates the head) sampled every 20 ms. Each sample is shown. Arrangements of panels A–C and the ordinate scale in B and C are as in Fig. 8. Despite speed changes (B), the bearing (C) of the fish's movement is held throughout the approach.

McBeath, 2002). Outfielders have been convincingly shown to employ closed-loop strategies in which their movement is under continuous sensory control so that no precise match between the start direction and speed to the spatial location of the later point of catch is required.

How to set take-off speed?

What could be an advantage for the fish to adjust take-off speed to distance rather than simply heading off at maximum speed? This point is perhaps best addressed by considering two hypothetical strategies to reach the future point of catch. In the first strategy, the fish would accelerate very rapidly to a speed that then is kept throughout the approach and selected such as to make the fish arrive simultaneously with the prey at the point of impact. A fish that follows this strategy would choose a constant velocity $v_0 = d/\tau$, where d is its distance from the future point of impact and τ the remaining time of falling. An alternative second strategy would be to move at maximum speed, stop at the point of impact and wait for the prey to arrive. If the fraction of the prey's falling time during which the fish moves is denoted as the 'duty interval' δ, then a fish that follows this strategy would select a speed $v = v_0/\delta$. To choose the second strategy would, however, be more costly. The power a fish must invest in order to keep its speed v is expected to vary roughly proportional to v^3. In a beautiful experimental arrangement, Webb (1971) has experimentally shown the proportionality to be $v^{2.8}$ in freely moving trout. The roughly cubic dependency of power on speed explains why the second strategy is not clever: the saving made during the resting phase at the point of catch is far outweighed by the costs of moving faster during the previous translatory phase. Generally, the power P required for a path with duty interval $\delta < 1$ increases very rapidly as δ decreases below $\delta = 1$ (i.e. the first, constant-speed, strategy), according to the relation $P(\delta)/P(\delta = 1) = 1/\delta^2$. For instance, moving fast for the first half of the prey's falling time and waiting at the later point of impact for the remaining other half (i.e. $\delta = 0.5$) causes fourfold

higher costs than following the constant speed motor program ($\delta = 1$).

This argument does not, however, clarify whether moving at constant acceleration a would be better than moving with constant speed. It is easy to see that moving at constant speed is superior in terms of work lost to hydrodynamic friction. The argument goes as follows. In order to cover the distance d in the remaining time τ by means of a constant-acceleration motor program, the fish would have to set its acceleration to $a = 2d/\tau^2$. The power loss to frictional forces, P_a, would then be:

$$P_a = \eta \int_0^\tau a^3 t^3 dt = 2\eta d^3 / \tau^2 , \qquad (1)$$

where η is a constant. In contrast, to cover the distance d in time τ at constant speed v requires $v = d/\tau$ and the frictional power loss is:

$$P_v = \eta \int_0^\tau v^3 dt = \eta d^3 / \tau^2 , \qquad (2)$$

which is only one half of the loss P_a. Thus using a constant acceleration rather than a constant velocity strategy would double frictional costs.

Sensory and motor requirements

To profit from an optimal strategy requires that the fish is able to predict with sufficient accuracy its distance d from the future point of catch and the time τ that remains till prey impact. This prediction is not at all trivial (see Fig. 1) and the algorithm the fish uses is presently unknown. Deriving absolute speed, for instance, requires rather precise knowledge of the spatial relations between eye and target in order to correct for the strongly position-dependent refractional errors at the water–air interface (Schuster et al., 2004). Moreover, the time period that the fish have to sample visual information and to carry out the computations is very short (<100 ms) and would be expected to seriously limit the precision the fish can attain (e.g. see Bialek, 1990). It is thus likely that the fish can only use rough estimates of d and τ, which may even contain systematic errors. This will translate into deviations from

a constant-speed program. For instance, if the fish underestimated the distance d from the later point of impact then it would start too slow and would have to speed up later during the approach in order not to arrive too late.

However, despite these difficulties, archer fish must be able to derive at least some of the variables quite accurately. Otherwise they could not have set their bearing so well (e.g. see Figs 8–10). It is clear that the pressures on the yet unknown algorithm that predicts bearing are high because even slight bearing errors at take-off can cause large errors in the target region. For instance, to arrive within a region that lies not more than 10% of the true distance apart from the later point of impact already requires a precision of at least 5.7°, or about the angle a minute hand of a watch covers in 1 min.

On the other hand the motor system of the fish must also be able to translate the available estimates of distance, direction and remaining time into extremely rapid and well set angular- and translational acceleration phases that rapidly turn the fish precisely by the required angle and push it off at the required take-off speed. Clearly, failures to do so will also result in errors that the fish might have to correct later as it comes close to the point of catch. It is impressive how well the fish can set angle and speed independently from each other within an extremely short time interval of approximately 60 ms, and the linear and rotational accelerations involved are remarkable. This remarkable performance of the fish's motor system is currently analyzed using high-speed video techniques and our analysis so far strongly suggests that archer fish recruit their fast life-saving C-start network of identified reticulospinal neurones, common in teleost fish (e.g. Nissanov and Eaton, 1989), to drive their fine-tuned and extremely rapid open-loop starts to the point of catch (S. Wöhl and S. Schuster, manuscript in preparation).

The deviation between actual and expected arrival times

If a constant velocity strategy minimizes frictional losses, why then do the fish not simply keep their take-off speed constant throughout the approach and arrive exactly as expected? Is it because they do not intend to follow a constant speed approach because other constraints are more important than minimizing friction? Or is it due to sensory or motor limitations as discussed above? As shown in Fig. 6, fish started slightly too slowly, so that most take-offs would lead the fish to arrive about 20 ms later than they actually did. However, despite this the correspondence between expected and actual arrival times is rather close. The scatter in the expected arrival times (expected on the basis of constant speed) is not much larger than that observed in the actual arrival times and would still enable the fish to arrive within a narrow time slot, despite the broad range of preceeding turns and distances to cover (shown in Fig. 2D–F). This suggests that speed corrections are not so much needed to compensate an initial sloppiness, i.e. a broad distribution of take-off speed and hence of expected arrival times, but rather to correct for a systematic 'error'. The alternative interpretation, that the fish did not intend to follow a constant speed profile but another, for instance a slightly

accelerated velocity profile, seems not to fit two findings: (i) the close correspondence of actual and expected arrival, and (ii) the failure to observe a clear pattern of post-start speed changes that would have been indicative of another strategy the fish might be trying to use. We therefore suggest that the fish set a slightly erroneous take-off speed, which they correct later. This small 'error' need not be viewed as a shortcoming, but can be of adaptive value for an open-loop start that enables the fish to catch its prey at full speed. If a chance occurs to view the falling target during the actual approach, then the slow initial speed can readily be corrected. And in case no useful cues occurred after the start it is safe to set the initial speed slightly too slow – slow enough to minimize the risk of overshooting the target.

Conclusion: the potential of open-loop solutions

Archer fish can not only predict the bearing but also the distance of the later point of impact of their dislodged prey, and use this ability to predetermine an appropriate turn size and take-off speed in their open-loop start. This makes archer fish an attractive model to study how hunting animals use predictive abilities to match extremely rapid open-loop responses to non-trivial tasks. Given that such responses remove the heavy computational demand of continuous sensory-processing and -feedback to the motor system, we hope that this work will provide novel impetus on how open-loop strategies could help to make autonomous robots a bit faster than they currently are.

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