

Animal Cognition: How Archer Fish Learn to Down Rapidly Moving Targets

Stefan Schuster,^{1,*} Saskia Wöhl,¹ Markus Griebisch,¹ and Ina Klostermeier¹

¹ Universität Erlangen-Nürnberg
Institut für Zoologie II
Staudtstr. 5
D-91058 Erlangen
Germany

Summary

In extremely rapid maneuvers, animals including man can launch ballistic motor patterns that cannot immediately be corrected [1–3]. Such patterns are difficult to direct at targets that move in three-dimensional space [2–4], and it is presently unknown how animals learn to acquire the precision required. Archer fish live in groups and are renowned for their ballistic hunting technique in which they knock down stationary aerial insect prey with a precisely aimed shot of water [5–7]. Here we report that these fish can learn to release their shots so as to hit prey that moves rapidly at great height, a remarkable accomplishment in which the shooter must take both the target's three-dimensional motion as well as that of its rising shot into account. To successfully perform in the three-dimensional task, training with horizontal motion suffices. Moreover, all archer fish of a group were able to learn the complex sensomotor skill from watching a performing group member, without having to practice. This instance of social learning in a fish is most remarkable as it could imply that observers can “change their viewpoint,” mapping the perceived shooting characteristics of a distant team member into angles and target distances that they later must use to hit.

Results and Discussion

Archer fish hunt in groups and can shoot down stationary aerial insect prey over considerable distances by firing a precisely aimed shot of water at them [3, 5–8]. As the fish cannot correct their shot once released, they would need to account in advance for the spatial movement of both the target as well as of their released “projectile” in order to hit moving prey with their open-loop hunting technique. While archer fish excel in predicting the later point of impact of dislodged prey from a brief observation of its initial motion [3], only a few field observations indicate that the fish might use their excellent judgement of target motion to shoot at flying insects [8]. We found that this task is hard even for archer fish that are well-trained and proficient in shooting down stationary targets from great height. This became evident when we tested a group of ten fish that had been kept

under controlled conditions with regular training on stationary targets for at least 1 year prior to the experiments. All fish fired precisely aimed sharp water jets (diameter ≤ 3 mm) at stationary targets (sized 3–5 mm) that we presented within a height range from 15 cm to 60 cm above the water surface. In occasional tests, conducted rare enough so that the fish could not learn from them, a target object was moved. In these probing tests, all fish responded by following the target. However, in most cases they did not shoot or were unable to score hits with their sharp jets even when the target moved slowly. For instance, moving a target at a speed of only $u = 5$ mm/s at a constant height of 15 cm above the water surface cut the success rate to less than half the value obtained with the same target presented stationary.

To test how well the fish could learn to engage moving targets, we regularly trained the group with targets that moved horizontally at constant speed u at one of three selected height levels above the water surface. In order to score hits, the fish had to find a way to compensate for the distance the target travels in the time interval between release and advent of their shot (Figures 1A and 1B). The course of training is illustrated in Figure 1C. Training started at the lowest height and at low speed levels. After about 1 month of training, higher speed levels could be included. The same training program was then repeated at the second height, and after a maximum target speed appeared to be reached, also at the third height. Learning appeared to include a rapid initial step to low but significantly nonzero hit rates, but the further refining and extension to larger heights and target speed levels required extended practice. The apparent maximum rate of hits reached after extensive training of several weeks at all three height levels and for a large variety of target speed values is reported in Figure 1E. Evidently the trained fish were able to cope with considerable displacements the target would have travelled during their shot's rise time and reached large and reliable scores at target speed levels at which the rates predicted from the target's size (which equalled their shot's diameter, dotted lines in Figure 1E) should long have declined to zero.

Which strategies had the fish acquired to engage the moving targets so efficiently? For instance, had the fish learned to increase the speed of their shots to encounter moving targets? If so, they could reduce the target displacement during the shot's rise much below the expected values shown in Figure 1B. However, our high-speed video recordings clearly exclude this view: the rise time of the shots depended only on target height but not on target speed (see Tables S1 and S2 in the Supplemental Data available with this article online). High-speed video also revealed that the trained fish had not learned to encounter moving targets by broadening their jet's diameter. Another simple option that can be excluded would have been that the fish fire a bout of shots in rapid succession, using feedback from the preceding shot to correct their next one. However, even when the

*Correspondence: sschuste@biologie.uni-erlangen.de

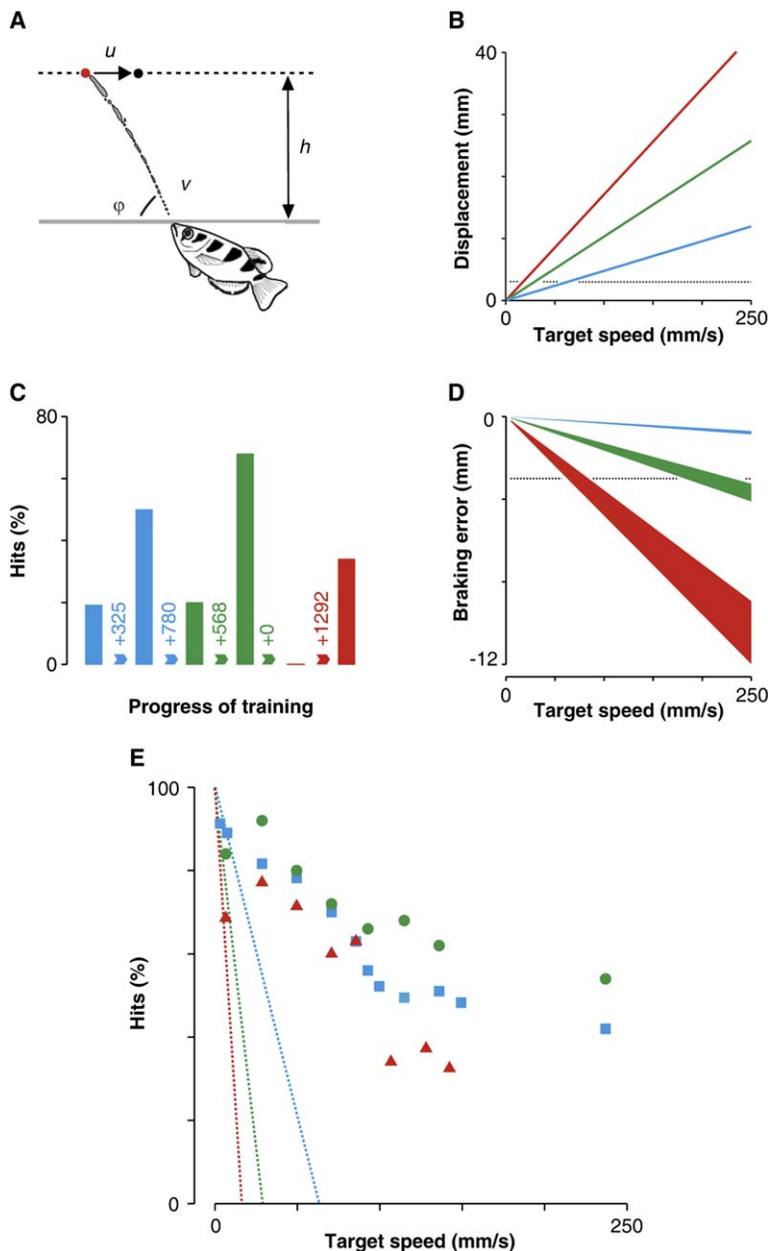


Figure 1. Archer Fish Learn to Account for Target Motion and Gravitational Braking of Their Shot

(A) While their shot (fired with speed v at angle ϕ) rises to target height h , a moving target (speed u) is displaced from the position it had when the shot was released (indicated by red circle).

(B) The target displacements expected in our experiments if the fish do not adjust the speed of their shots to target motion (see Table S1). Prediction appropriate for vertical velocity $v \sin \phi = 4$ m/s of the shot (see Figure S1A). Colors (in [B]–[E]) relate to different target height: blue, $h = 18$ cm; green, $h = 36$ cm; red, $h = 54$ cm. Distances traveled were large with respect to diameters of target and shot (both 3 mm, indicated by stippled horizontal line) and untrained fish were unable to account for them.

(C) Engaging rapid targets at large height requires extensive training. Hit rates at target speed $u = 115$ mm/s reached at various stages of training. Colored arrows indicate training progress at the respective (color-coded) height level with numbers reporting the total number of shots (at any target speed at this height) fired before and during determination of hit rate given in the subsequent column (hit rates determined from 26, 20, 20, 50, 100, and 47 presentations, respectively).

(D) If archer fish neglect the braking effect of gravitation, they should systematically undershoot the moving targets, depending on height and target speed. Three areas indicate the expected range of undershooting (braking error) at the three height levels. In each range, the lower boundary is for a shooting angle of $\phi = 70^\circ$, the upper boundary for an angle of $\phi = 90^\circ$. Errors are computed for an average $v = 4$ m/s of the shot (see Table S2 and Figure S1C). Target size is indicated by the stippled horizontal line.

(E) Percentage of hits after training at the three height levels as a function of target speed (total of 1692 shots). Stippled lines indicate, for each height level, rate of hits expected if the fish had not compensated for target displacement. Hit rate (in [C], [E]) is the proportion of presentations with at least one hit among those in which at least one shot was fired.

trained fish fired a series of shots, the first shot in the series was most likely to hit, showing that feedback from immediately preceding attempts was not required. Furthermore, fish were able to hit the moving targets at any place within the presentation area and did not require the target to assume a particular location.

Since the trained fish neither adjusted their shot's speed or diameter to target speed nor adopted other obvious tricks, they must have learned to release their shot so as to account for the target displacement during the shot's rise. The most prominent strategy the trained fish were using at all height levels was to assume a stationary position and to fire the shot a distance approximately $d = u \tau$ in front of the target's position at the time of release (with ± 3 mm tolerance), thus accounting for target speed u and rise time τ of their shot (Figures 2A and 2C). The range of target displacements d our trained fish were able to handle was more than 10 times the

diameter of shot and target. It follows already from inspection of Figure 1B that the fish could not simply hit with a constant amount of leading but rather must have adjusted the leading to the amount needed. This is directly confirmed in high-speed recordings of hits (Figure 2C).

Unlike the projectile fired by a human trap shooter, the shot of an archer fish is significantly slowed down on its way to the target. Because it rises against gravitation, the rise time τ of an archer fish shot is not simply proportional to distance but follows the relation

$$\tau = \frac{v_z - \sqrt{v_z^2 - 2gh}}{g}, \quad (1)$$

where v_z is the vertical component of the shot's velocity, h is the target's height above the water surface, and g is the acceleration due to gravity (9.81 m/s^2).

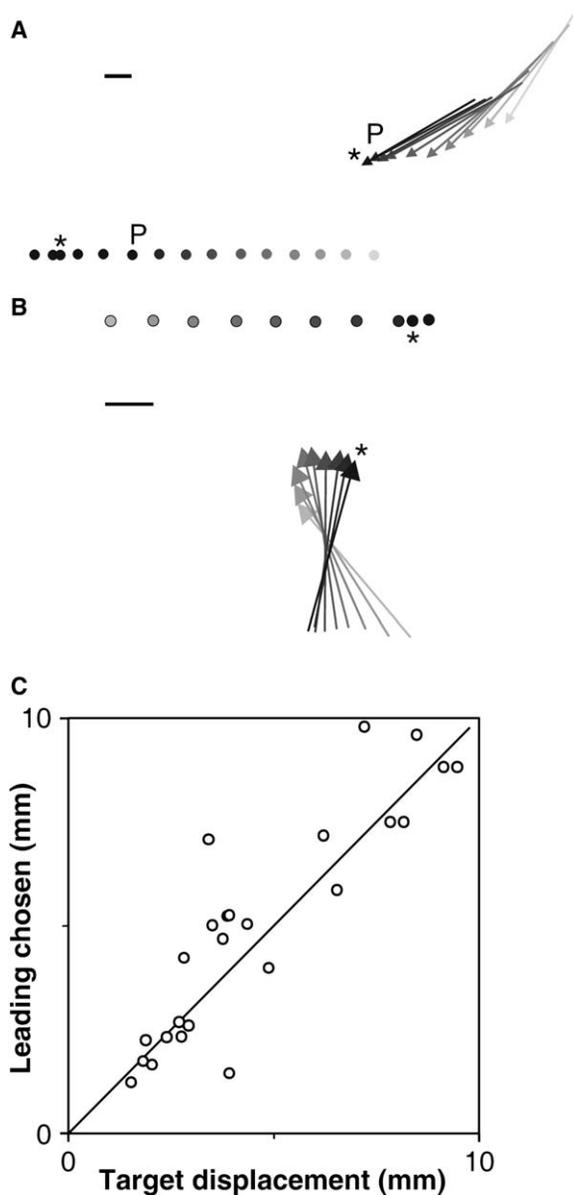


Figure 2. Trained Archer Fish Acquire Two Distinct Strategies to Hit Moving Aerial Prey

(A and B) Trained fish were imaged from above at 80 frames per second as they fired at a target that moved with speed $u = 85.5$ mm/s at height 54 cm (A) or 18 cm (B) above the water surface. Every tenth frame shown. Additional frames correspond to time of hit (last in each series) and release of the shot (indicated by asterisk). Arrows indicate orientation of fish, circles mark position of target (computed projection to the plane of the fish). Scale bar equals 10 mm.

(A) Leading strategy. Fish assumes final orientation toward future point of hit, but not toward actual target location, already at frame marked P. This strategy is used at all heights.

(B) Rotate and fire strategy, used as an alternative to leading at low target height. Fish does not shoot while stationary, aiming in front of the target's motion, but releases shot out of a rotating movement.

(C) Archer fish finetune the chosen amount of leading to the distance the target had travelled during the shot's rise. Scrutiny of randomly selected high-speed video recordings of hits that had been scored at various target heights and speed levels. The fish's length axis at the moment of firing was extrapolated and the point of intersection with the line of target motion (in plan view) was determined. "Leading chosen" by the fish is the distance this point of intersection has from the target's position at the moment of firing. Regression

Neglecting the braking effect of gravitation and aiming as if the shot would travel with its initial vertical velocity throughout the rise would cause the fish to undershoot the target by amounts in the range predicted in Figure 1D. At small height the predicted "braking" error ε rises proportionally to the square of height h and inversely proportional to the cube of the shot's vertical speed $v_z = v \sin \phi$, where v is the speed and ϕ is the angle at which the shot is fired with respect to the water surface. At the largest height used in our experiments and when target speed is higher than about 60 mm/s, the predicted amount of undershooting would have resulted in decreased hit rates. Nevertheless (red triangles in Figure 1E), the fish were still able to reliably score hits when neglect of gravitational braking would have led to detectable errors. This shows that the braking effect is sizable and that the fish can account for it. But to do this, the fish need not monitor speed and use equation 1. An attractive other way would be that the fish simplifies the problem by automatically adjusting the initial speed of its shot v to target height such that rise time either remains constant or increases in simpler ways with height. While the fish do indeed adjust the speed of their shots to height (see [6] for stationary targets), these increases are small and far from what would be needed to keep the rise time constant (see Table S2 and Figure S1). Though they reduce the problem of undershooting, they cannot completely remove it. Moreover, the same speed increases are observed in fish that never had to shoot at moving targets, which makes it more likely that speed is increased for other reasons, e.g., to increase the maximum height of the shot. Nevertheless, the slight increase of speed with height could be a part of the trick by which the fish solves the problem of gravitational braking.

Interestingly, the predictive "leading" strategy was not the only one the trained fish had acquired. At low target height, the animals could additionally use a second very different strategy: "turn and fire" (Figure 2B). In this maneuver, the shooter positions itself below the line of target motion and appears to approximately track the target. This forces the hunter into a rotating movement. When approximately level with the target, the fish releases its shot and stops tracking the target. Because the shooter's rotation is approximately matched to target motion, a released shot has about the correct horizontal speed to hit. The turn and fire strategy yielded hits only at the lowest target height (18 cm) at which it was used in about 60% of all shots. At the larger heights, where far more precision would be required, it was used only in 2% of all shots and never yielded a hit. This is reasonable because the error made in using this strategy is approximately the speed mismatch (between target speed u and the shot's horizontal speed $v \cos \phi$) multiplied by the shot's rise time τ . Thus, demands on a precise match in speed, and hence in the precision with which the firing fish must be able to match the rotation of its body to target motion, grow with height. Accordingly, the fish switch to their predictive leading strategy

analysis: $r^2 = 0.79$, $p < 0.0001$, $n = 25$; slope of the regression line (0.97 with a 5% confidence interval of 0.21) is not significantly different from unity (slope of the indicated bisector).

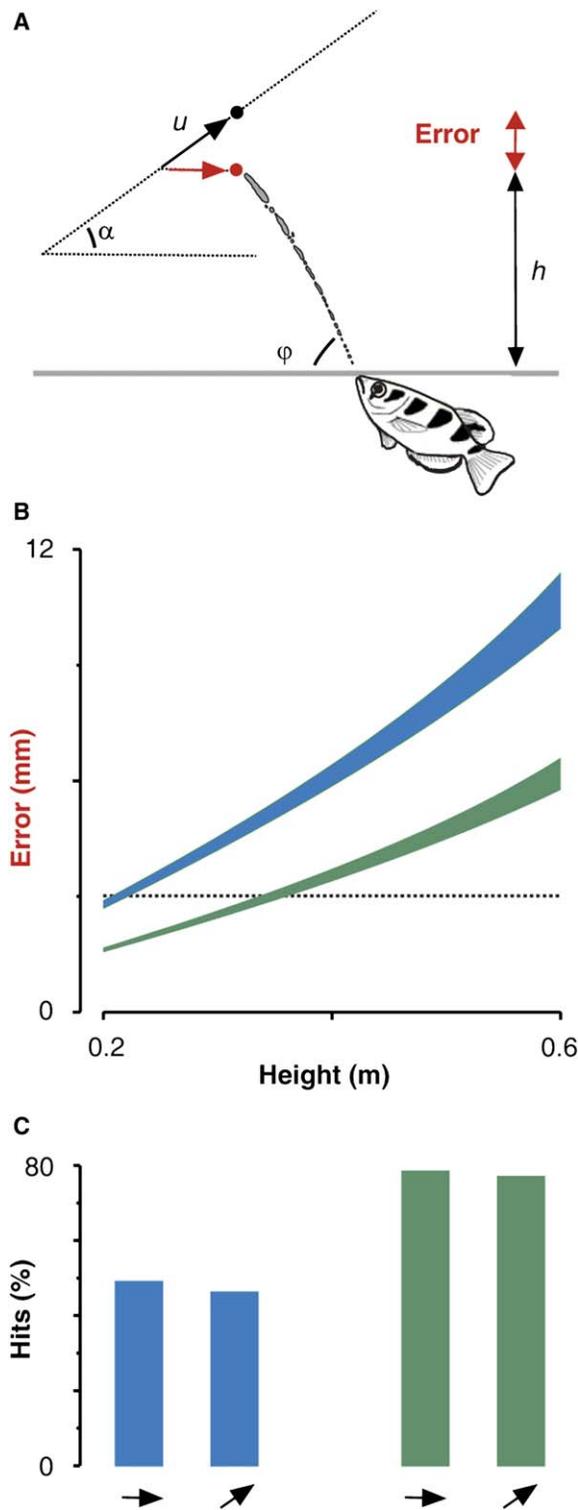


Figure 3. Three-Dimensional Movement Prediction
(A) Introducing a vertical component $u \sin \alpha$ to target motion should cause an error (indicated in red) in fish that had previously been exclusively trained with horizontal motion and engage targets solely based on horizontal speed.
(B) The range of errors predicted in the present experiments with two target speeds $u = 49.5$ mm/s (blue area) and 85.5 mm/s (green area) and an angle of inclination $\alpha = 36^\circ$. Diameter of target (same as shot) indicated by stippled line. Errors are computed for an average speed of $v = 4$ m/s of the shot (see Figure S1B). In each range, the upper

boundary is for a shooting angle of $\phi = 70^\circ$, the lower boundary for $\phi = 90^\circ$.

at large height, which seems to be better adapted to the high accuracy needed.
Throughout their training, all fish were exclusively shown targets that moved only horizontally. We therefore expected that the fish had, at this stage of training, acquired only a simplified solution in which they take only horizontal target speed into account. If so, then the trained fish should make predictable errors (Figure 3B) when tested with targets whose motion has an additional novel vertical component of sufficient size. In experiments to test whether the trained fish make these predicted errors, the target moved either horizontally in one of two heights (as in the training situation) or between the two heights, thus adding the novel vertical velocity component to the target's motion. Although the predicted errors would have been substantial at the speed values and the angle of inclination used in our experiments, the trained fish were still able to hit. Evidently, though trained in a simplified task, in which monitoring horizontal target motion was sufficient, the fish readily took the novel vertical motion component into account (Figure 3C). This has two major implications. First, archer fish evidently can estimate three-dimensional speed of an aerial object with sufficient accuracy despite the complex, strongly viewpoint-dependent metric distortions due to refraction at the water-air interface [7]. Second, during their training on the simplified two-dimensional task, the fish must already have acquired the general solution appropriate for target motion in space.

The impressive ability to generalize shown by our fish in learning the complex sensorimotor task is taken even further: evidence based on four fish of a group suggests that to learn the task, a shooter need not necessarily practice, since observational learning [9–11], watching a performing team member over an extended period, suffices. This is suggested by the following set of experiments. In a school of five motion-naïve fish that were initially all unable to hit moving targets, only one fish practiced. The four other group members were able to watch the performing fish and the target but did not attempt to enter a region from which they could shoot because they were chased away by the practicing fish. In none of the presentations did the observers attempt to shoot and they were never observed in maneuvers that would mimic the rotate and fire or leading of the model. After the performing fish had learned the task and reached a stable rate of hits at large height and speed levels, the other fish were allowed to shoot (by removing the dominant practicing fish), and their success in their first ~ 20 attempts was examined (Figure 4). Although the observers demonstrably had been unable to hit moving targets before, even at the lowest height and speed, and though they had never shot at the moving targets throughout the whole training, they readily reached

boundary is for a shooting angle of $\phi = 70^\circ$, the lower boundary for $\phi = 90^\circ$.

(C) Results of tests with a vertical speed component. In contrast to predictions from (B) (if fish had ignored the vertical speed component), hit rate did not decline substantially when vertical motion was present. First column in each pair (colors as in [B]) shows average hit rate for presentations with horizontal motion, second column for inclined motion. Although the fish had before been exclusively trained with horizontal motion, they readily took a vertical motion component into account.

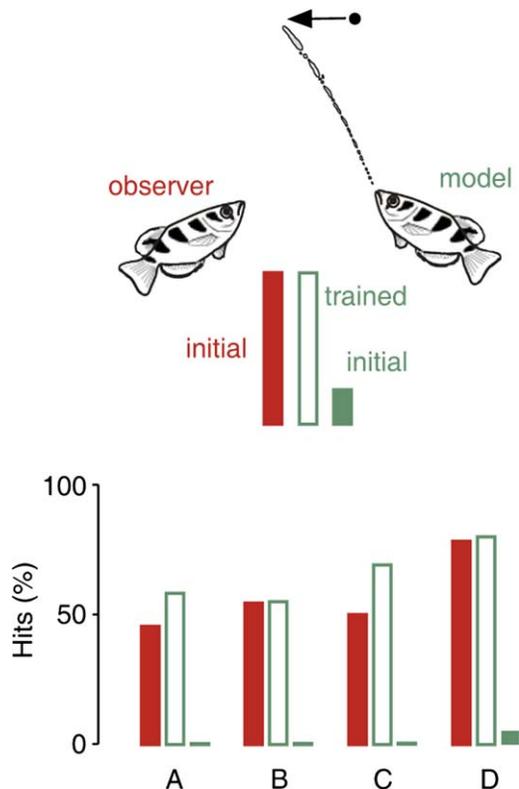


Figure 4. Observational Learning Enables Archer Fish to Hit Rapidly Moving Targets

Observer fish had before been unable to hit even slowly moving targets at low height. They were then allowed to watch the regular training and performance of a school member (model) over an extended period (more than 1000 shots), but were prevented from shooting themselves. Green columns: performance (% of hits) of practicing model fish in initial (filled, first 20 shots) and final (open) state of training. Red columns: initial performance of observers. (A)–(D) denote hit rate in first shots (16, 11, 20, and 23, respectively) of four observers. Target height 54 cm, target speed $u = 99.7$ mm/s (A), 85.5 mm/s (C), and 49.5 mm/s (D). In (B), u was randomly selected and h could be 54 cm or 36 cm with averages $h = 51$ cm and $u = 93$ mm/s.

high scores in their first tests. The initial performance of four of the four observers almost approached that of their long-trained model and, most importantly, was in each case clearly far above the score the practicing model was able to reach when it had started its practice. Thus, the observer fish must have been able to learn the task from extensively watching the performance of their practicing group member. Controls seem to make the view unlikely that observers need only to watch target motion and that learning does not require a social component: a group of four other control fish, each experienced in shooting down stationary targets, was regularly shown moving targets over the course of a month but the role the dominant fish had played in the other group was mimicked by gently moving them away if they were to take position to shoot. When these fish were subsequently allowed to shoot at moving targets, they were unable to hit moving targets in their first 20 trials (scores below 10%; scores for stationary targets were, in contrast, above 80%). Hence, the observational learning seems not simply triggered by watching target

motion but to involve a social component: monitoring the successful performance of a group member.

To appreciate the level of complexity of this form of social learning of a complex sensomotor task in a fish, consider the ballistics a fish must obey to score hits on moving targets with its leading strategy. No matter which way the fish solves the task, when releasing its shot with speed v its horizontal offset σ from the target and its shooting angle φ must be chosen conjoined to match the relation:

$$\sigma = \frac{\Delta v_x}{g} (\Delta v_y - \sqrt{\Delta v_y^2 - 2gh}), \quad (2)$$

where

$$\begin{aligned} \Delta v_x &= v \cos \varphi - u \cos \alpha \\ \Delta v_y &= v \sin \varphi - u \sin \alpha \end{aligned} \quad (3)$$

are the differences in horizontal and vertical speed, respectively, between shot and target. The velocities and angles of shot and target are denoted as v , φ , and u , α , target height is h , and g is the gravitational constant. Since observers were not noticed to imitate a performing group member but viewed their model from a distance and from all possible viewpoints, learning by observation requires that the observer must estimate at least the variables σ and φ from an observation of the distant model. In other words, in order to learn and act as if it itself had performed, an observer must be able to map observations between two three-dimensional frames of reference: its own egocentric system and the egocentric system of the model. Such an ability has, to our knowledge, never been shown before in a fish.

Conclusions

Generalization and prediction, key abilities of cognitive systems [12], allow a hunting animal, the archer fish, to efficiently engage spatially moving targets with a simple ballistic technique. In their natural mangrove habitat, archer fish could thus readily learn to hit insects that fly sufficiently straight for a few seconds or to down escaping prey that was missed in the first attempt. Archer fish live in schools and our surprising findings suggest that they can learn this complex sensomotor skill from their group members. This form of social learning in a fish would require that the observing fish can transform the angles and distances they view while observing a distant team member into values that they can directly use when shooting themselves. Very little is known in general about the information actually acquired and the neural mechanisms used in social learning [13–15]. The complex form of social sensomotor learning we report here in a fish is therefore potentially useful because it adds a system to the field in which it is not only possible to control the relevant sensory variables but that also holds a perspective to dissect the underlying circuitry by means of recording techniques primate models would not offer.

Experimental Procedures

Archer fish (*Toxotes jaculatrix*, length 8–11 cm) were held in groups of five in large tanks with brackish water (3.5 mS/cm, 26°C). A DC motor moved the target (a black sphere of 3 mm diameter) at

constant speed on a ropeway (nylon fishing line, diameter 0.3 mm, running through the center of the target) at one of three preselected height levels above the water surface. Targets were visible only within a small region that extended 275 mm perpendicular to the direction of motion. Time of visibility was, therefore, restricted to several seconds (minimum of 1.1 s at a speed of 250 mm/s), thus mimicking the limited response time hunting fish would have in the wild. In a presentation, the target moved once through the field of visibility. The direction of motion, the entering point in the field of visibility, target speed, target height, and inclination were selected at random from a set of preselected values. A digital high-speed video camera recorded target motion, the responding fish, release, and advent of the shot from above. The standard camera used (Basler A301f, with VideoSavant 4 software) provided 80 frames (658 × 494 pixels) per second. Additional recordings from above, measurements of the shot speed as well as close-ups of the diameter of the water jets, were made at higher temporal (250 frames per second) and spatial (1280 × 1024 pixels) resolution with a NAC hotshot camera. Digital images were processed with the public domain program NIH Image and custom-made software. Hit rate was defined as the proportion of presentations with at least one hit among the presentations in which at least one shot was attempted. Archer fish do not require the reward to be identical to their target [7], and this was made use of throughout this study: after a hit, targets remained stationary (in the preparatory phase with stationary targets) or continued their motion, but a small food pellet was thrown in the tank so as to mimic the ballistic falling of a dislodged target. Both shooters and bystanders executed rapid predictive turns and starts toward the later point of impact of the reward [3] and reached this ability already during the preparatory phase with stationary targets long before training with moving targets started.

Supplemental Data

Supplemental Data include one figure and two tables and can be found with this article online at <http://www.current-biology.com/cgi/content/full/16/4/378/DC1/>.

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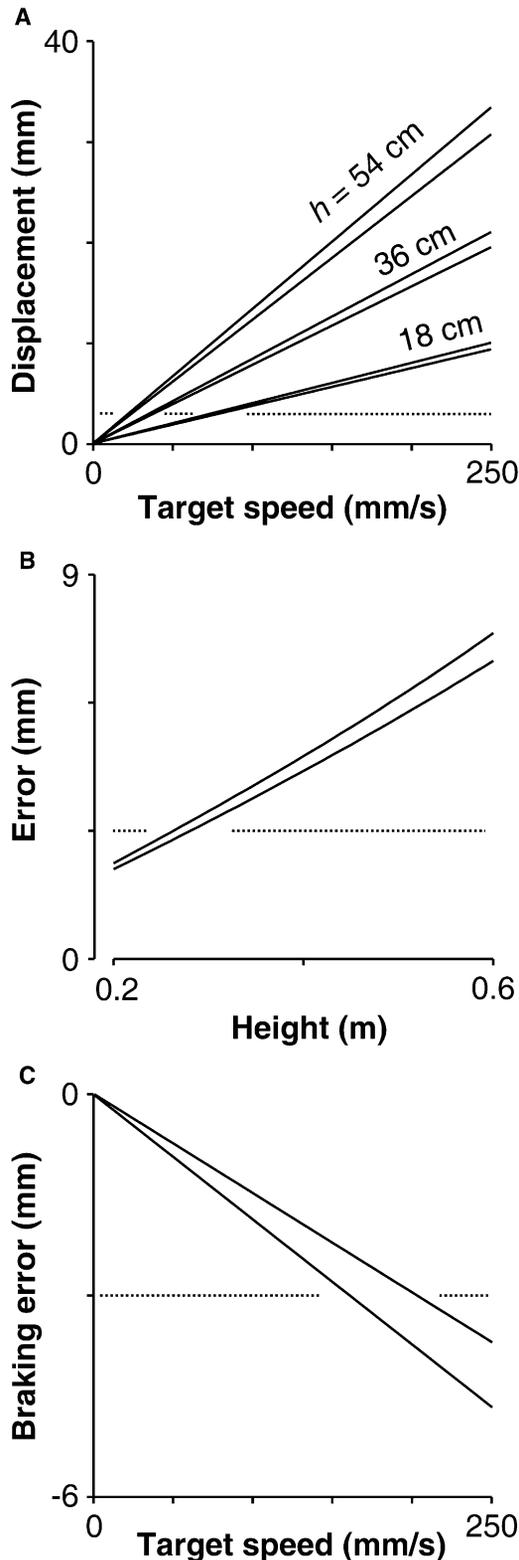


Table S1. Trained Archer Fish Do Not Reduce the Displacement of Moving Targets by a Decreased Rise Time of Their Shot

	Target Speed (mm/s)	
	$u = 0$	$u = 85.5$
Average rise time (ms)	48.0	44.3
SD (ms)	9.8	6.6
N	25	25

Hits at target height $h = 18$ cm. Camera frame rate 250 Hz (4 ms resolution).
Difference not significant ($t = 1.56$, $p = 0.13$, t test).

Table S2. Data Showing How Rise Time of the Shots Depended on Target Height

	Target Height h (cm)		
	$h = 18$ cm	$h = 36$ cm	$h = 54$ cm
Average rise time (ms)	54.2	89.6	132.4
SD (ms)	7.7	11.5	6.2
N	177	165	110

Data relate to model fish of Figure 4. For each height level, measurements over all experimental speed levels are pooled. Camera frame rate 80 Hz (12.5 ms resolution).

Figure S1. Variations in the Shot's Initial Speed Are Not Critical for the Conclusions Reached

The predictions of Figures 1B and 3B are robust against variations in the initial speed of the shot, and the gravitational braking problem (Figure 1D) is not completely solved by a speed increase with height. An average speed at all height levels was used in the text because interindividual differences in shooting speed v were in the same range as differences due to target height. To show that doing so does not affect the conclusions reached in Figures 1B and 3B, consider a shot fired with hypothetical speed of $v = 5$ m/s. Such a high speed was not observed in our experimental fish even for shots fired at targets at the largest height and serves merely to analyze robustness of the conclusions.

(A) Target displacements for the hypothetical shot with initial speed $v = 5$ m/s fired at either $\phi = 70^\circ$ (upper curve) or $\phi = 90^\circ$ (lower curve). Height level as indicated. Distances traveled were still much larger than diameters of target and shot (both 3 mm, indicated by stippled horizontal line) and would have caused substantial errors.

(B) The range of errors predicted for the hypothetical shot at $v = 5$ m/s in the experiments of Figure 3B for the larger target speed $u = 85.5$ mm/s (angle of inclination $\alpha = 36^\circ$). Diameter of target (same as shot) indicated by stippled line. The upper curve relates to a shooting angle of $\phi = 70^\circ$, the lower curve to $\phi = 90^\circ$. Errors in this experiment would have still been substantial even at this speed.

(C) Even if the fish increased its shooting speed to $v = 5$ m/s at the largest target height, this would still not fully resolve the problem of gravitational braking. The error would still be in the range of target and shot diameter, causing lower than measured hit rates at the largest speed and height levels. Lower curve is for a shooting angle of $\phi = 70^\circ$, the upper curve for an angle of $\phi = 90^\circ$.