

RESEARCH ARTICLE

Archerfish coordinate fin maneuvers with their shots

Peggy Gerullis*, Caroline P. Reinel* and Stefan Schuster‡

ABSTRACT

Archerfish down a variety of aerial prey from a range of distances using water jets that they adjust to the size and distance of their prey. We describe here that characteristic rapid fin maneuvers, most notably of the pectoral and pelvic fins, are precisely coordinated with the release of the jet. We discovered these maneuvers in two fish, the jets of which had been characterized in detail, that had been trained to shoot from fixed positions at targets at different heights and that remained stable during their shots. Based on the findings in these individuals, we examined shooting-associated fin movement in 28 further archerfish of two species that could shoot from freely chosen positions at targets at different heights. Slightly before the onset of the water jet, at a time when the shooter remains stable, the pectoral fins of all shooters switched from asynchronous low-amplitude beating to a synchronized rapid forward flap. The onset and duration of the forward and subsequent backward flap were robust across all individuals and shooting angles but depended on target height. The pelvic fins were slowly adducted at the start of the jet and stopped moving after its release. All other fins also showed a characteristic sequence of activation, some starting ~0.5 s before the shot. Our findings suggest that shooting-related fin maneuvers are needed to stabilize the shooter, and that these maneuvers are an important component in the precise and powerful far-distance shooting in archerfish.

KEY WORDS: Motor control, Fins, Stability, Temporal precision, Neuroethology

INTRODUCTION

Archerfish use water jets to down aerial prey from considerable distances (e.g. Lüling, 1963; Dill, 1977; Elshoud and Koomen, 1985; Rischawy et al., 2015; Schuster, 2018). The forces transferred to targets, the mass of water ejected and the speed of initial water release have been measured by Schlegel et al. (2006) for prey of various sizes, and the major result was that the fish adjust the force transfer to prey size so as to keep a considerable safety margin above the maximal attachment prey of that size can attain (Schlegel et al., 2006). Height-dependent changes in force transfer were reported by Burnette and Ross (2015), but even at large height a considerable safety margin was found. Vailati et al. (2012) showed that focusing of water at the jet tip can arise as a consequence of speed changes that occur because water is released from rest, so that water that leaves first is slower. A surprising later discovery was that the time at which this focus occurs is not fixed, but is adjusted to target distance, so that the later parts of the jet catch up with the front right

before impact, maximizing force transfer (Gerullis and Schuster, 2014). Using fish that were trained to fire from fixed positions, it was possible to see that the distance-dependent adjustments made in the jets were linked to precisely controlled mouth-opening and -closing maneuvers during jet formation. Similar maneuvers have also been seen when archerfish use underwater 'jets' to uncover hidden prey from various substrates (Dewenter et al., 2017). During the analysis of high-speed videos of these trained fish (Gerullis and Schuster, 2014), we noted characteristic movement patterns of the fins of the shooter that appeared to be linked to shooting. Surprisingly, these movements appeared to set in just at a time when they would no longer seem to be required: they started just when the shooters had assumed and subsequently kept their stable positions during their shots. At this time, the recoil forces from the emerging jet start to act on the fish, and so a synchronized onset of fin movement would mean that the forces produced by these maneuvers might be needed to compensate recoil. We therefore analyzed the previous recordings with a focus specifically on the timing of the fin movements relative to jet release. For these recordings, the changes in the water jets with target height, as well as the stability of the shooter during the shot, had already been characterized (Gerullis and Schuster, 2014). After characterizing timing of the fin maneuvers in two trained fish, we next explored whether these findings extend to freely hunting archerfish of two species, *Toxotes jaculatrix* and *Toxotes chatareus*.

Over the past two decades, remarkable insight has been gained into the ways in which teleost fish operate smaller fins, such as their pectoral and pelvic fins, for braking maneuvers and for steering at high speed. By combining detailed three-dimensional kinematic analyses (e.g. Gibb et al., 1994; Lauder and Jayne, 1996; Drucker and Lauder, 1999; Standen and Lauder, 2005; Tytell, 2006; Lauder and Madden, 2007; Standen, 2008; Tytell et al., 2008; Flammang and Lauder, 2009), detailed measurement of the induced flow fields and force reconstruction (e.g. Drucker and Lauder, 2001a,b; Lauder and Drucker, 2002; Drucker and Lauder, 2003, 2005; Lauder and Madden, 2006; Peng et al., 2007; Han et al., 2020), as well as by critical verification with robotic models (Lauder et al., 2007; Lauder and Tangorra, 2015; Flammang et al., 2017; Gravish and Lauder, 2018; Mignano et al., 2019; Zhu et al., 2019), it has become possible to see that even minute details in the movement of these fins can play a role in generating precisely controlled forces at the right time. Particularly interesting are maneuvers with specific and demanding constraints; for instance, during prey capture it is essential that the attacking fish arrives at the right place at the right time and in an orientation that allows it to actually swallow its prey. Beautiful studies on this aspect include those of Standen and Lauder (2005), Higham et al. (2005) and Higham (2007). For a shooting archerfish, the situation appears to be far less dramatic than for a predator braking from a full-speed chase: when an archerfish releases its water jet, it has already moved to a favorable position and has oriented appropriately (e.g. Lüling, 1958; Dill, 1977; Timmermans, 2001; Gerullis and Schuster, 2014), and all that seems now required is to remain stable while the jet

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forms. This could be achieved simply by keeping the fins spread during the shot (as suggested e.g. by Lüling, 1958, 1963; Bekoff and Dorr, 1976), which might suffice to prevent any roll, pitch or yaw that might result from the recoil of jet release. Here, we demonstrate that, surprisingly, characteristic rapid fin-movement patterns are synchronized with shooting that even show similarities to those seen in braking fish (e.g. Higham et al., 2005; Higham, 2007).

MATERIALS AND METHODS

Animals

Fish trained to shoot from a fixed location

The initial analyses used recordings from two archerfish, *Toxotes jaculatrix* (Pallas 1767), that had been trained to reliably score perfect hits over a wide range of distances from a fixed position and under heavy illumination so that various aspects of jet production could be monitored closely using digital high-speed video (Gerullis and Schuster, 2014). These recordings were particularly valuable, because a number of important issues had already been analyzed: (1) all shots at all target height levels were perfect hits, (2) the position and orientation of the shooter were stable during jet formation, and (3) the adjustments made in the jets and in the mouth-opening and -closing maneuvers for changing target height had already been characterized. The recordings allowed us to analyze temporal aspects of fin activation of the shooter, specifically, how tightly any fin movement was associated with shooting, and whether shooting-related fin movement patterns might correlate with changes in the characteristics of the jets. Recordings were taken from the two most successful fish in the earlier study (Gerullis and Schuster, 2014). These were 13–14 cm in

length (snout to caudal peduncle) and were kept in a tank (1.2×0.5×0.5 m, length×width×height) filled to 25.5 cm with brackish water (temperature, 26±1°C; conductivity, 3.6–3.8 mS cm⁻¹; 12 h:12 h light:dark regime). To shoot, the fish had to swim into a channel (Fig. 1A) formed by suitable walls and covers above the water surface [polyvinyl chloride (PVC)] so that the fish could not jump or shoot successfully from positions outside the channel. Targets were small black spheres (polyethylene terephthalate; diameter, 5 mm, mass, 0.065 g) hung on filaments 20, 40 or 60 cm above the water surface. For each successful hit, the shooter was rewarded with a dead fly (*Calliphora* sp.).

Groups of fish in which individuals were free to shoot from any position

A total of 28 additional fish (length, 8–17 cm) of two species, *T. jaculatrix* (eight individuals) and *Toxotes chatareus* (Hamilton 1822) (20 individuals), of eight groups were evaluated that were filmed mostly (in some instances from below and from the side) from above at 500 frames s⁻¹ (see Movie 3). The groups were housed in tanks sized 1.0×1.0×0.6 m and 1.3×1.3×0.6 m as described earlier (e.g. Reinel and Schuster, 2018), under the same conditions as the two spatially trained fish.

Recording and image analysis

Trained fish

A Fastcam PCI R2 (Photron, San Diego, CA, USA; resolution, 480×512 pixels; Sony TV lens 1:1.8 f=16 mm) was used to record the fish from above and a Fastcam APX RS (Photron; resolution, 1024×1024 pixels; Micro-Nikkor-P.C. Auto 1:3.5 f=55 mm; Nikon GmbH, Düsseldorf, Germany) recorded the shooter from the side

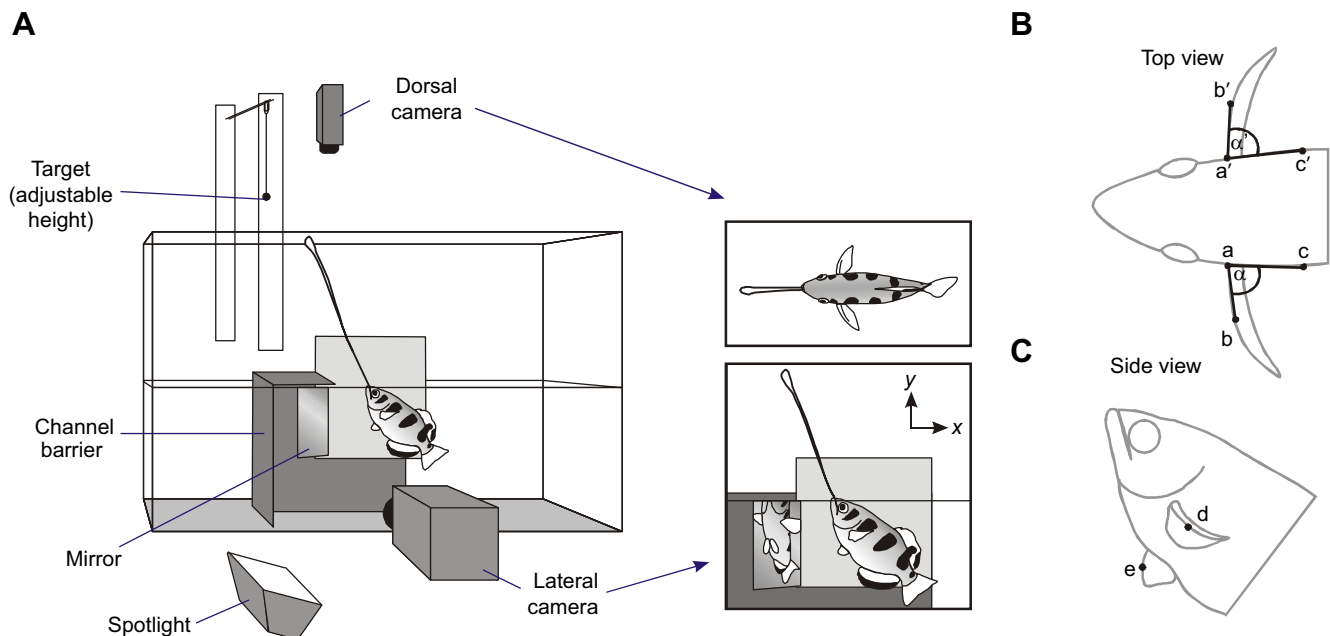


Fig. 1. Monitoring the timing of shooting-related fin movements in trained *Toxotes jaculatrix*. (A) A trained archerfish fires from a fixed position within a channel (formed by PVC plates) at a target at one of three pre-assigned height levels – either 20, 40 or 60 cm above the water surface. Dorsal and lateral views of the shooter and its fin movements are recorded by two synchronized digital high-speed cameras at 250 frames s⁻¹. An inclined mirror in the view of the lateral camera helps to monitor the ventral fins. For the events analyzed in this study, the height-dependent adjustments of the jets, precision of shooting and the stability of the shooters have already been characterized (Gerullis and Schuster, 2014). This allowed us to explore whether aspects of the timing of the fin maneuvers co-varied with the changes the fish made when they engaged targets at different heights. (B) Points digitized frame by frame in the top-view recordings for the left and right pectoral fin: one at the base (a,a'), one at the approximate midpoint of the leading edge (b,b') and one on the body (c,c'). (C) The side views – one direct, one in the mirror – were analyzed for the timing of pelvic fin action and, when possible, for roughly characterizing the vertical excursion of midpoints of the leading edges of the pectoral (d) and pelvic (e) fin.

(see Movies 1 and 2). Sufficient illumination came from a 1000 W spotlight, placed behind a diffuser plate below the tank (Fig. 1A). The two cameras were synchronized and operated at 250 frames s^{-1} . A small mirror (7.3×4.7 cm) placed in the channel at an angle of 45 deg to the shooter's length axis allowed the monitoring of the hidden fins in the side views (Fig. 1A). The horizontal component of the pectoral fin angle was taken from dorsal views (resolution, 0.3 mm $pixel^{-1}$; Fig. 1B). An additional vertical component was analyzed using the synchronized side view (resolution, 0.2 mm $pixel^{-1}$; Fig. 1C). The movement of the pelvic fins was monitored from side views. Recordings were evaluated using ImageJ (version 1.41m). To monitor the timing of the fast-forward flap of the pectoral fin from the top views, we tracked the front end (leading edge) of the pectoral fins frame by frame for all frames from 10 frames before to 20 frames after the shot, unless stated otherwise. In each frame, three positions were taken that were easy to find and that led to a robust estimate of fin angle: (1) the approximate midpoint (b,b' in Fig. 1B) on the front of the fin, (2) the base (a,a' in Fig. 1B) of the fin, and (3) a point on the body surface located ~1 cm caudally from the base of the pectoral fin (c,c' in Fig. 1B). Using these points, we derived an effective angle (α,α' in Fig. 1B) of the leading edge of the archerfish's pectoral fin. To estimate angular velocity, we simply considered the differences in angle from one frame to the next (i.e. in 4 ms), assigning it to the time of the later of the two frames. Because of the large distance from the lens (top view, 60 cm; side view, 75 cm), small vertical excursions could safely be ignored in the evaluation of the recordings from above. However, to get an impression of the relative coordination of the pectoral and pelvic fins we did also measure, as far as possible in the side views, two spots on the pectoral and the pelvic fins (d,e in Fig. 1C).

Freely ranging archerfish

Here, all recording was at 500 frames s^{-1} . In the analyses presented, recording was as described in Reinel and Schuster (2014) and involved a HotShot 1280M (NAC Image Technology, Simi Valley, CA, USA) that monitored the complete tank from above. To optimize contrast, four halogen lamps (200 W each) illuminated the tank's bottom through a diffuser plate (plexiglass, polymethyl methacrylate; transmission, 45%). Spatial resolution was 1.37 mm $pixel^{-1}$ (group of *T. chatareus*), 1.43 mm $pixel^{-1}$ (group of *T. jaculatrix*) and 1.48 mm $pixel^{-1}$ (recordings with three different target height levels). Wetted prey (dead *Calliphora* sp.) was stuck to the lower side of transparent disks, at fixed height above the water surface. For details of the arrangement, see Reinel and Schuster (2018). Qualitative aspects of any of the maneuvers could be seen in each of the recordings. In most, however, only parts of the complete maneuvers were clearly visible. To select maneuvers that were suitable for a quantitative analysis, we scrutinized a total of 5770 recordings and took those that fulfilled each of the following three criteria: (1) the onset of the shot could clearly be determined, (2) both pectoral fins were clearly visible throughout, and (3) recordings started early enough before the shot so that we could see the alternating beating of the pectoral fins of the later shooter. Additionally, two to 10 shooting events per individual were randomly selected and scrutinized for shooting-associated fin movement in eight more individuals (*T. chatareus*). Two of these were housed in a tank sized 1.2×0.5×0.5 m and filmed from the side, but with the same camera as described above. Six others were also *T. chatareus* and were members of three different groups. The other groups were kept in tanks sized 1.0×1.0×0.6 m (two groups) and 1.3×1.3×0.6 m and were filmed from below (also at 500 frames s^{-1})

using Photron Fastcam MC2 high-speed cameras (resolution, 512×512 pixel; Lensation 1/1.8" F1.6/4.4–11 mm).

Statistics

OriginPro (version 7.5) was used to estimate slopes and offsets of correlations between fin action of the left and right pectoral fin. All other tests (Kruskal–Wallis one-way ANOVA on Ranks and pairwise multiple comparisons using Dunn's Method; one-sample *t*-test, one-sample signed rank test and χ^2 test) were run using SigmaPlot (version 11.0) or custom written software (rank-based Brown–Forsythe and Fisher *z*-transformation).

RESULTS

The rapid forward flap of the pectoral fins

In none of the 278 recordings made of the two trained (and pre-characterized; Gerullis and Schuster, 2014) fish were the pectoral fins already spread before the onset of the jet; also in none was their position stable during the release of the jet. Before the onset of the shot, the pectoral fins were beating slowly and asynchronously (as will be detailed below). However, slightly before the onset of the jet, we always noticed a characteristic rapid forward flapping of both pectoral fins (see example in Fig. 2A and Movies 1 and 2) that quickly gained speed, so that the horizontal angular speed was ~1000 deg s^{-1} by the time jet release was started (means±s.e.m., fish 1: 1256.0±51.0 deg s^{-1} , $N=52$; fish 2: 1028.5±153.6 deg s^{-1} , $N=34$). Our first objective was to examine the degree of variation in the timing of the forward flap across different shots; specifically, how well its timing was synchronized with the onset of water release. For this, we aligned each individual time course of the pectoral fin angle to the onset of the jet, i.e. we always set time to zero when the jet was first visible. After aligning a total of $N=52$ (fish 1) and $N=34$ (fish 2) courses of pectoral fin angle (recorded during successful shots fired at a target at 40 cm height), we averaged the individual courses. Should the onset of the fin flap not be synchronized to the onset of the jet or should the fin flaps vary from one shot to the next, then considerable scatter around the mean angle should occur at each point in time. In addition, our rather crude way of simply following the approximate midpoint of the leading edge of the pectoral fin (Fig. 1B) could also introduce errors that would increase the degree of scatter. On these notes, it is remarkable how little scatter actually did occur when we averaged the individually aligned time courses of horizontal pectoral fin angle (Fig. 2B) and of angular speed (Fig. 2C). This analysis already suggests that the forward flap is rather precisely coordinated with the onset of the water jet. In the trained fish, this allows averaging times relative to the onset of the shots from several recordings, yielding a considerable temporal resolution for the means. The forward flap appears to follow a robust time course in which it reaches a maximal horizontal angular speed slightly after the onset of the jet. The rapid forward movement is kept during approximately the first third of the water release, when shooters are stable (Gerullis and Schuster, 2014), but speed declines after this time and, by the time the jet is fully released, the fins reverse direction to then move toward the shooter's body.

Changes made in the timing of the forward flap

The robust time course and alignment of the forward flap allowed us to explore whether it was kept or was adjusted when the fish changed their water jets to engage targets at different height *h*: the higher up the target, the longer is the interval of water released, the longer the lifetime of the jet and the later does water focus at the jet tip (Gerullis and Schuster, 2014). Jets aimed at different target

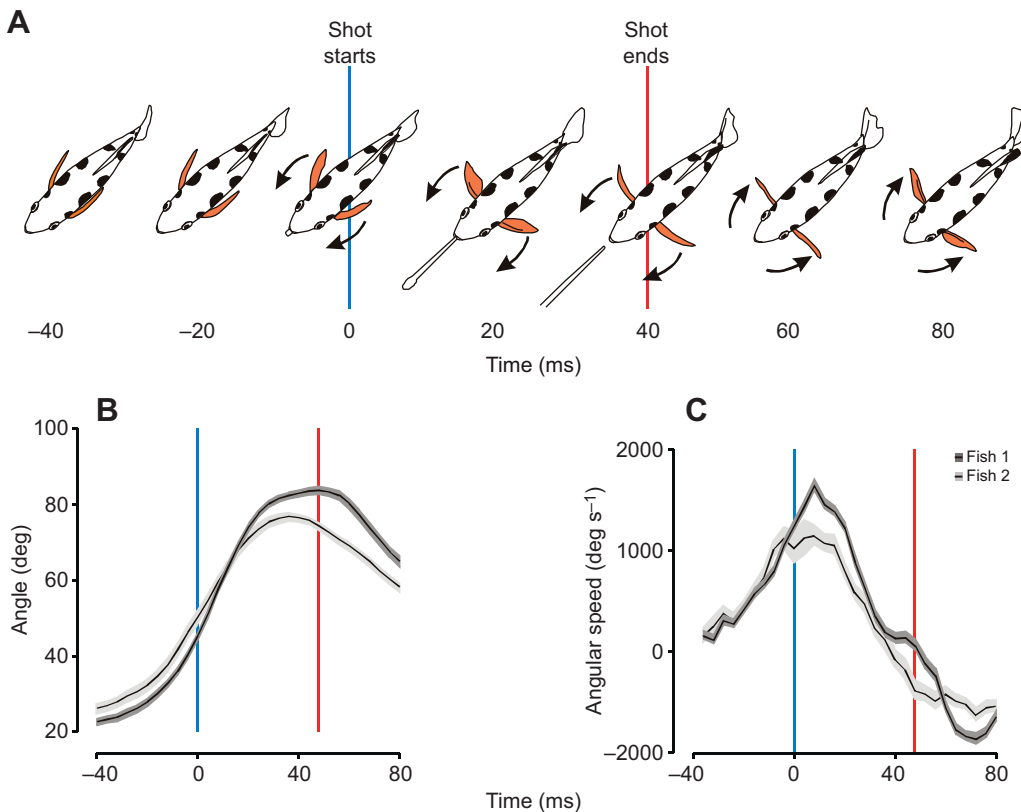


Fig. 2. The rapid forward flap of the pectoral fins in shooting *T. jaculatrix*. (A) The position of the pectoral fins (orange) every 20 ms during a shot fired by fish 1 at a target at 20 cm height. Release of the jet starts at time zero and is completed 40 ms later. (B) Individual recordings of the time course of the angle of the pectoral fin were aligned to the onset of the shot (blue line indicates time zero) and then averaged. Averaging this way indicates that the onset of the rapid forward flap is coupled to the onset of the shot. The forward flap starts slightly before onset of the shot and continues until the jet has been released completely (red line indicates the mean duration of shots). (C) Angular speed of the forward movement of the pectoral fin peaked shortly after onset of the shot and declines to zero by the end of the shot. Graphs in B and C report means \pm s.e.m. of fin angle and of angular speed of the right pectoral fin as recorded from above (Fig. 1B) in both trained fish (fish 1, $N=52$ shots; fish 2, $N=34$ shots) for a target height of 40 cm.

distance could therefore produce different disturbances to the shooter's position and compensating them might require different fin activation. To examine this, we again determined jet-onset-aligned mean horizontal angles for a given individual (as in Fig. 2) but now also for a lower ($h=20$ cm) and for a larger ($h=60$ cm) target height (Fig. 3A,B). This analysis shows that the forward flap varies slightly but systematically with target height. Maximal horizontal angular speed was reached later when the fish engaged targets at larger height [Fig. 3C; means \pm s.e.m., 3.8 ± 0.8 ms (20 cm; $N=51$); 8.9 ± 0.8 ms (40 cm; $N=52$); 8.1 ± 0.7 ms (60 cm; $N=66$); Kruskal–Wallis: $P < 0.001$]. Also, the absolute value of maximum angular speed was larger for more distant targets [1853.1 ± 40.9 deg s^{-1} (20 cm; $N=51$); 1932.6 ± 37.8 deg s^{-1} (40 cm; $N=52$); 2017.3 ± 25.9 deg s^{-1} (60 cm; $N=66$); Kruskal–Wallis: $P < 0.001$]. The maximal angular excursion of the pectoral fins was not significantly different [87.2 ± 1.5 deg (20 cm; $N=51$); 85.7 ± 1.1 deg (40 cm; $N=52$); 87.4 ± 0.7 deg (60 cm; $N=66$); Kruskal–Wallis: $P = 0.110$], but the maximal angle was reached earlier for more distant targets [Fig. 3E; 11.4 ± 1.3 ms after the end of the shot (20 cm; $N=51$); -4.0 ± 1.7 ms (40 cm; $N=52$); -7.8 ± 1.5 ms (60 cm; $N=66$); Kruskal–Wallis: $P < 0.001$]. For an estimate of the 'start' time of the forward flap, we used the time when both pectorals were moving in synchrony and at large angular forward speed (>500 deg s^{-1}). Using this estimate, we found that onset was significantly later when shots were fired at targets at larger height [Fig. 3D; -13.4 ± 0.8 ms before the onset of the jet (20 cm; $N=51$); -3.3 ± 0.8 ms (40 cm; $N=52$); -2.9 ± 0.7 ms (60 cm; $N=66$); Kruskal–Wallis: $P < 0.001$]. Also, the reversal of the synchronized pectoral fin movement occurred earlier for shots fired at more distant targets [Fig. 3F; 25.7 ± 1.2 ms after the end of the jet (20 cm; $N=51$); 7.9 ± 1.2 ms (40 cm; $N=52$); 2.9 ± 0.9 ms (60 cm; $N=66$); Kruskal–Wallis: $P < 0.001$]. Note that the precise coordination of fin

maneuvers with jet release and the resulting small standard deviations (e.g. <6 ms in Fig. 3D) allowed mean timing to be determined quite accurately (see the s.e.m. values reported above).

Preparing the forward flap: synchronization of the left and right pectoral fin

The forward flap sets in after a phase in which the two pectoral fins were beating slowly and in opposing directions. This is illustrated by the example in Fig. 4A in which the fins had been monitored for much longer than in the majority of our recordings. The alternating low-angle beating can clearly be seen, as well as the switch to synchronous movement when the two fins are at similar angles. The example also illustrates that pectoral fin beating is variable during the pre-shooting phase. However, this changes dramatically just before shooting, when the forward flap sets in. Here, the two pectoral fins appear to move in synchrony, achieving similar angles at each point in time. Fig. 4A also illustrates another remarkable aspect: the forward flap sets in when the pectoral fins had arrived at similar angles and levels of forward speed. The example illustrates aspects that were seen in each of the 278 recordings analyzed in this study in the two specifically trained sharpshooters (fish 1: $N=169$; fish 2: $N=109$). Specifically, there were no recordings in which (1) only one pectoral fin was moving, (2) the two fins moved in the same direction before the forward flap, and (3) the forward flap started when the two pectorals had largely different angles. We next examined the actual degree of synchrony between the two pectoral fins during the forward flap. For a quantitative measure of synchrony, we plotted, at each instant, the angular speed of the right pectoral fin against that of the left fin at the same point in time. Fig. 4B reports this for the complete interval from 40 ms before onset until the end of water release. Correlations between angular speed of the left and right pectoral fin were strong at all target height

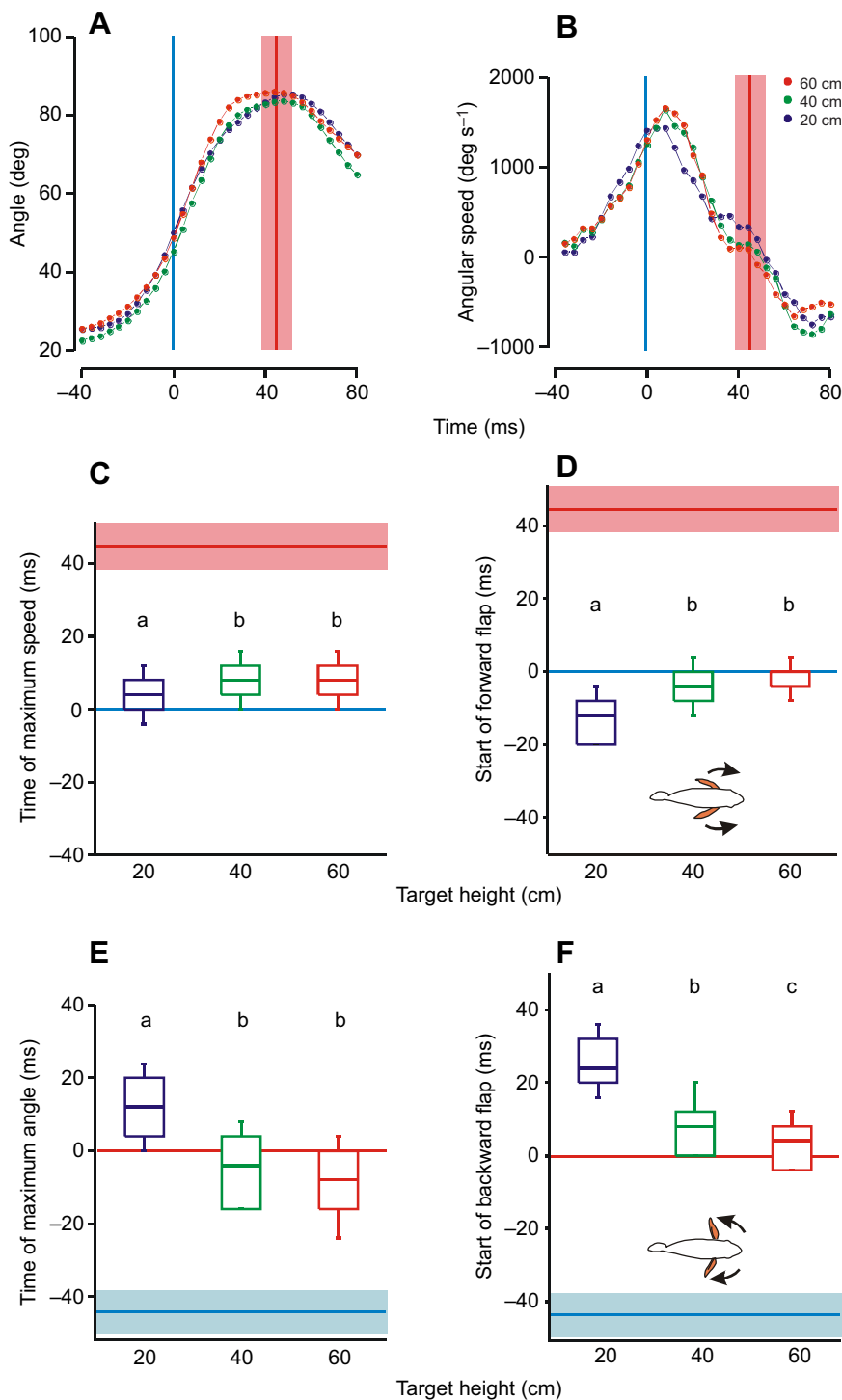


Fig. 3. Changes in the timing of the *T. jaculatrix* pectoral fin flap with increasing target height. When shots were fired at targets at different heights, the pectoral fins moved according to the same basic pattern but several aspects differed systematically. All data were collected during shots of fish 1 that all led to perfect hits ($N=51$, $N=52$ and $N=66$ at target height 20, 40 and 60 cm, respectively). (A,B) Plots report mean angle (A) and mean angular speed (B) of the pectoral fin as measured from top views (see Fig. 1B). Note the absence of scatter at onset (defined as time zero) but scatter around mean end (s.d. as indicated). (C) Maximum angular speed was reached later ($P<0.001$) and maximal levels were also different ($P<0.001$, data not shown). The blue line marks the onset of water release, the red line marks the end. (D) Forward movement started earliest at the lowest target height ($P<0.001$). (E) The time at which the maximal angle of the pectoral fins was reached differed across shooting events with different target height ($P<0.001$; maximum angles not significantly different, $P=0.110$, data not shown). At the lowest target height, the maximum extension was reached slightly after the end of the shot. To highlight the temporal relation to the end of the shot, in this and the subsequent plot (F), time is set to zero at the end of each shot (i.e. no scatter in red line but scatter in blue line). (F) The time of reversal of pectoral fin movement (adduction) also depended on target height ($P<0.001$) – it occurred latest (after the end of the shot) at the lowest target height. Box plots show median, 25(75)% and 10(90)% quartiles. Significant differences are indicated by differences in letters. All tests: Kruskal–Wallis.

levels (always $R^2>0.9$; $P<0.001$; correlation for line through origin), confirming our impression of synchrony in the forward flap.

Shooting-related movement of the pelvic fins

In contrast to the pectoral fins, the pelvic fins were already fully spread before the shot and remained so until the start of the jet. This was observed in each of the 278 recordings with at least one pelvic fin clearly visible for at least 40 ms before onset of the shot. The recordings in which the pelvic fin was monitored 600 ms (mean \pm s.e.m. 635.6 \pm 14.4, $N=10$) before onset of the shot confirm this and show that the pelvic fins are spread long before the onset of

the shot. The precise pattern of movement of the pelvic fins was much more difficult to assess from our recordings than that of the pectorals. However, it appears to be simply an adduction that starts with the release of the jet and that is not finished by the end of the shot (e.g. Movies 1 and 2). Synchrony between the two pelvic fins could be assessed in 236 of our 278 side-view recordings in which the movement of both pelvic fins could be clearly observed (i.e. in which the fin on the right side of the body could be seen in the mirror; Fig. 1A); only in 20 of these 236 recordings did one of the two fins start slightly later (one to maximally three frames, i.e. 4–12 ms) than the other. A simultaneous start of the two fins was

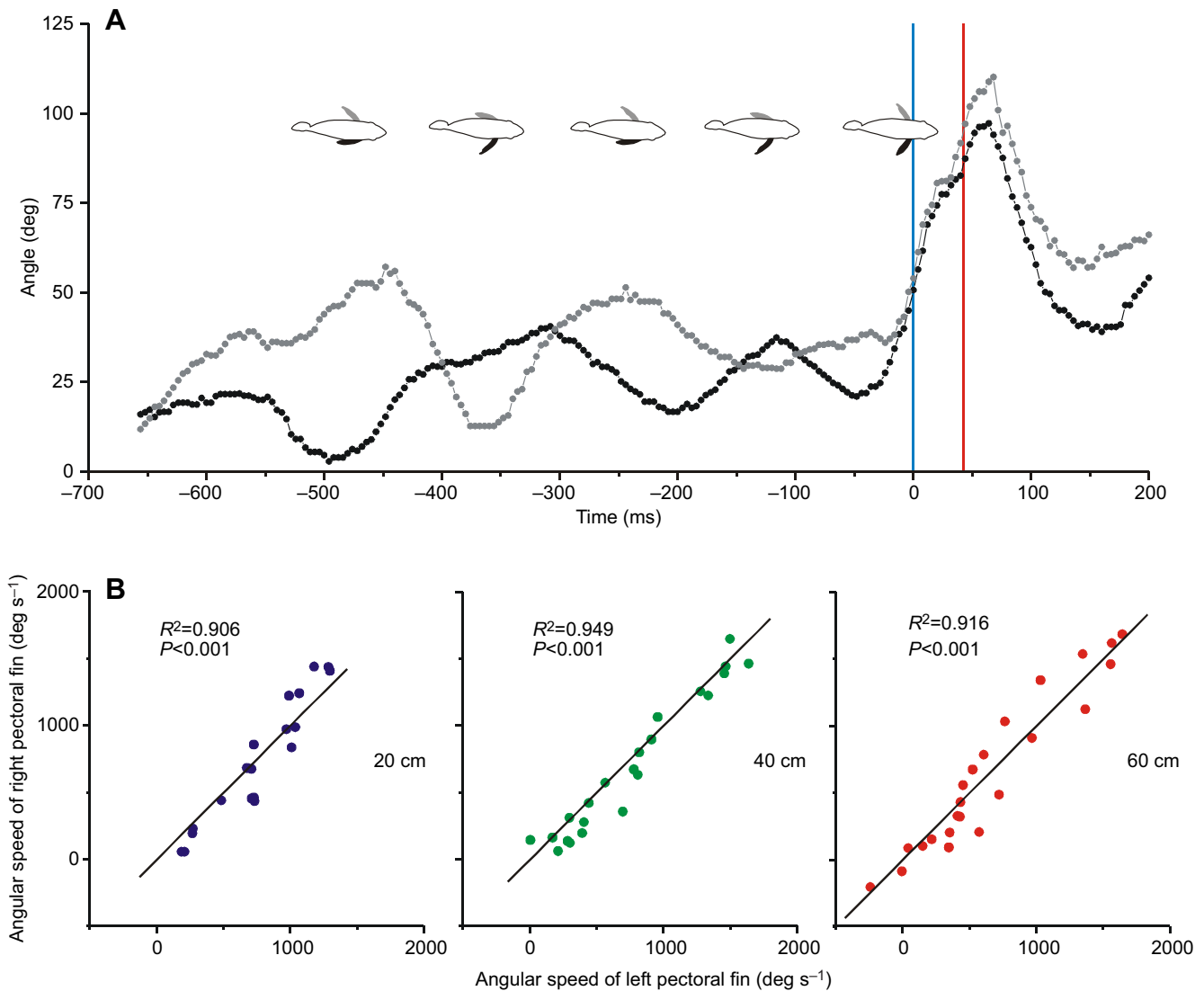


Fig. 4. Synchrony of the two pectoral fins during the *T. jaculatrix* forward flap. (A) Exemplary time course of angles (measured in fish 1 every 4 ms from top views, see Fig. 1B) of the left and right pectoral fin from a recording that started much earlier than usual and in which a shot was fired (at time '0', blue line) at a target at 20 cm height. The example illustrates that, before the shot, the left and right pectoral fins are beating out of phase. Shortly before the onset of the shot, the pectoral fins synchronize and the forward flap starts when the two pectoral fins have attained similar angles and angular speed. Synchrony is then maintained throughout the shot and at least 100 ms after its end (end of shot indicated by red line). (B) Fin movement was tracked during $N=51$, $N=52$ and $N=63$ shots at targets 20, 40 or 60 cm above the water surface, respectively. In all maneuvers, time was set to zero when the shot started and means \pm s.e.m. of angular speed (horizontal component) were calculated for the right and left pectoral fin at the same points in time from 40 ms before to the end of the jet, with 4 ms spacing between time points. Lines show expectation for perfect synchrony between left and right pectoral fin.

clearly seen in 216 of the 236 recordings. The recordings sufficed to test for systematic changes in the timing of the adductive movement when the fish adjusted their jets for target distance. Onset of pelvic adduction started approximately at the onset of the shot, with no robust trend for the onset of motion to occur later when target distance was increased [Fig. 5A; Kruskal–Wallis; fish 1: $P=0.004$; fish 2: $P=0.107$; means \pm s.e.m., fish 1 (fish 2): -11.14 ± 1.06 ms before the onset of the shot, $N=51$ at $h=20$ cm (0.1 ± 1.7 ms, $N=40$); -6.8 ± 1.1 ms, $N=52$ at $h=40$ cm (4.0 ± 2.4 ms, $N=34$); -6.6 ± 0.9 ms, $N=66$ at $h=60$ cm (4.9 ± 2.1 ms, $N=35$)]. At all target distances, the movement of both pelvic fins continued throughout the shot. The pelvic fins stopped moving earlier after shots fired at more distant targets [Fig. 5B; Kruskal–Wallis; fish 1: $P<0.001$; fish 2: $P<0.001$; means \pm s.e.m., fish 1 (fish 2): 101.1 ± 4.8 ms after the end of the shot, $N=40$ at $h=20$ cm (90.4 ± 6.8 , $N=40$); 60.6 ± 3.3 ms, $N=52$

at $h=40$ cm (78.2 ± 5.0 , $N=34$); 58.5 ± 1.9 ms, $N=66$ at $h=60$ cm (55.9 ± 4.0 , $N=35$)].

Relative coordination of the pectoral and pelvic fins

We next attempted to get a rough idea of the actual relative movement of the pectoral and pelvic fins. So far, we had only been looking at planar projections, which provided sufficient information to discover the temporal aspects reported this far. However, a closer analysis of the available recordings gave a good first impression of the spatial movement pattern. For this, we simply followed the trajectory of the midpoint on the trailing edge of the left-side pectoral and pelvic fins in a plane parallel to that of the shooter. In these analyses, we first aligned each individual recording to the onset of the shot and then calculated the mean positions measured at each point in time. Fig. 6 shows the mean position (\pm s.e.m.) every

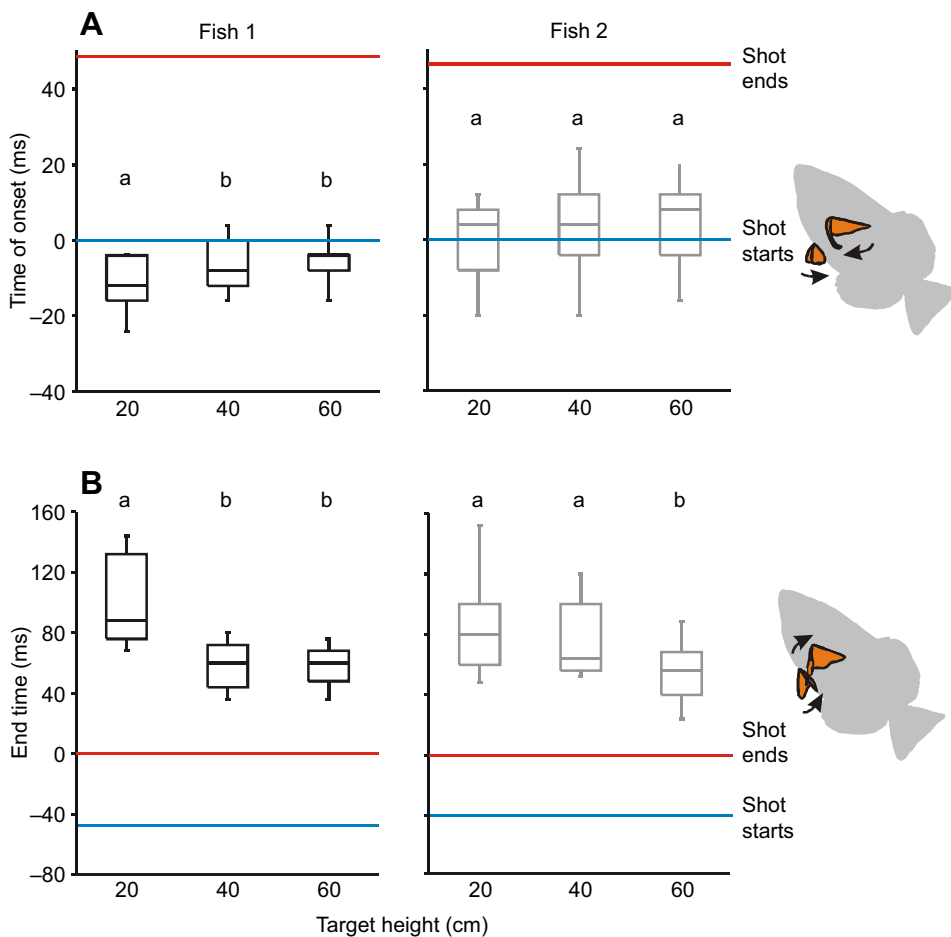


Fig. 5. Timing of *T. jaculatrix* pelvic fin movement during shooting. The pelvic fins are already spread before the shot and start being adducted towards the body at the onset of the shot (insets). (A) Adduction begins approximately at the onset of the shot (set as time zero, blue line). The mean end of the shots is indicated by the red line. (B) The adduction of the pelvic fins continues for ~60 ms after the end of the shot. To highlight this, time is set to zero at the end of each shot (red line). The corresponding mean time of onset is indicated by the blue line. Movement patterns in A and B recorded for successful shots at a target at 20, 40 and 60 cm height (fish 1, $N=51$, $N=52$ and $N=66$ jets, respectively; fish 2, $N=40$, $N=34$ and $N=35$ jets, respectively). Box plots show median, 25(75)% and 10(90)% quartiles. Significant differences (Kruskal–Wallis) are indicated by differences in letters.

4 ms after the onset of each shot for the pectoral (Fig. 6A) and pelvic (Fig. 6B) fins during shots fired by fish 1 at a target at 40 cm height. Given our crude way of obtaining these trajectories, it is remarkable how small the respective errors were. This suggests that the vertical component is synchronized to the shot and that it also follows a robust time course, at least for fixed target height.

We then tested for any systematic variation in the vertical component when target height was changed. The results of this analysis are shown in Fig. 6C and D, in which the trajectories obtained for target height 40 cm are shown as reference (gray shaded areas) and the means \pm s.e.m. for larger (upper graphs) and lower (lower graphs) target height are shown for the pectoral and the pelvic fins. The changes were clearly larger than the variations at any given target height, therefore suggesting that the fish adjust aspects of the relative coordination of their shooting-related pelvic and pectoral fin maneuvers.

Shooting-related movement of other fins

In all 278 recordings, the anal fin was clearly visible and was always erected before the shot, comparable to the pelvic fins. However, in contrast to the pelvic fin, the anal fin appeared to remain fully erected throughout the shots. In 202 recordings, the spiny anterior part of the dorsal fin was clearly visible (in the side views). In all these recordings, it was erected before the shot and appeared to remain erected throughout the shot. The soft posterior part of the dorsal fin was visible in the side views of 185 recordings and in each of them started to move during the shot. Although our recordings did not allow us to characterize its apparently rather complex

movement, they sufficed to show that it started at the onset of the shot with no apparent target height-dependent change in onset timing [means \pm s.e.m., 0.0 ± 4.7 ms ($N=24$ at $h=20$ cm height), 3.3 ± 1.8 ms ($N=46$ at $h=40$ cm), 2.8 ± 2.6 ms ($N=34$ at $h=60$ cm); Kruskal–Wallis: $P=0.169$]. The caudal and dorsal fins also appeared to be active during the shots: both fins could clearly be seen in 104 recordings (dorsal views). In all these recordings, the upper half of the caudal fin and the flexible posterior part of the dorsal fin both moved during the shot, always in opposing directions (e.g. Jayne et al., 1996 for data on sunfish). We also found a clear laterality in the movement of the dorsal and caudal fins. The flexible part of the dorsal fin moved significantly ($P < 0.001$, χ^2 test) more often (in 75 of 104 recordings) to the left side, and in all these recordings the upper part of the caudal fin then moved to the right side.

The forward flap in freely hunting archerfish of two species

We next examined to which extent the patterns monitored in the two highly trained fish that fired from a controlled position were typical for shooting archerfish. We surveyed 5820 additional digital high-speed video recordings made of a total of 28 archerfish, mostly during projects (Reinel and Schuster, 2014, 2018) that examined the predictive C-starts of the fish towards the later landing point of their prey (Movie 3). These fish were members of eight groups of archerfish that could hunt freely. All had extensive experience in downing prey from at least 30 cm height but were not especially trained for high hit rates. Most importantly, they were free to select the position from which they shot at prey. Three groups were filmed

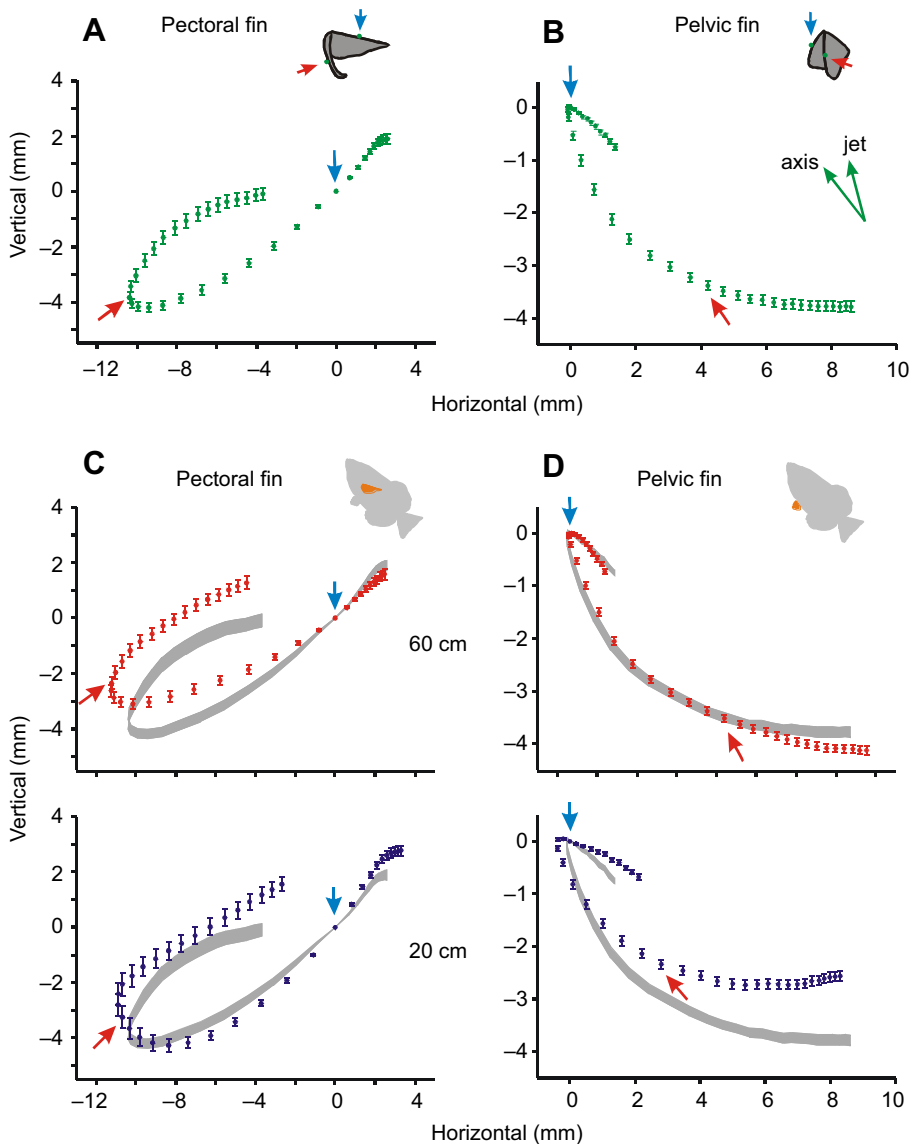


Fig. 6. Estimating target-height-related changes in *T. jaculatrix* fin trajectories. Two-dimensional representation of how the approximate midpoints on the leading edges of the pectoral and pelvic fins moved towards each other during a shot. Shown is the movement of the midpoint on the leading edge of the pelvic and the pectoral fin on the left side of the shooter. Position at onset of the shot ($x=0$, $y=0$) is indicated by a blue arrow. The red arrow marks the position at the end of the shot. (A) Mean trajectory (\pm s.e.m. of midpoint location; sampled between -40 ms and $+108$ ms relative to onset of the shot) for $N=52$ jets of fish 1 aimed at targets at medium height (40 cm). Note that the strong forward flap of the pectoral fin is also accompanied by a downward motion. (B) Trajectory of the midpoint on the leading edge of the left pelvic fin determined during the same shots analyzed in A. Note that the adduction of the pelvic fin is accompanied by vertical downward movement. Two green arrows shown on the right indicate the mean direction of the shooter's length axis and of its jet. Note that these directions also apply to A. (C,D) Data (means \pm s.e.m.) displayed as in A and B but with shots aimed at targets at higher (60 cm; red, $N=66$ shots) or lower (20 cm; blue, $N=51$ shots) height h , and with the data of A and B shown as gray areas for comparison. (C) The basic trajectory of the pectoral fins – with rapid forward and downward movement at the onset of the shot and slow adduction and upward movement at the end of the shot – is typical for all target heights. However, clear differences from the patterns observed at $h=40$ cm (gray area, data taken from A,B) are apparent. (D) Also the trajectories of the pelvic fins follow a basic trajectory but clear height-dependent variations are evident between the trajectories at $h=20$ cm and $h=40$ cm (gray).

from above at 500 frames s^{-1} and the movement of the pectoral fins could regularly be seen (see Materials and Methods). In eight additional fish (members of five further groups), 40 additional recordings were made from below (through the transparent bottom of the respective experimental tank) and 10 recordings from the side. The existence of the forward flap of the pectoral fins could be confirmed in all recordings. The pelvic fins could be seen clearly in at least 80 recordings. All these confirmed that the pelvic fins are extended before the shot and adducted during it. A number of recordings fulfilled all of the following criteria: the onset of both (1) the forward and (2) the subsequent backward flap could be determined accurately, (3) the prior transition from alternate beating of the pectoral fins to synchrony could be checked, and, most importantly, (4) the onset of the jet could be determined accurately. Fig. 7 presents the results of a quantitative analysis of such recordings in two groups of archerfish (Fig. 7A) that downed targets from 30 cm height. One group consisted of six *T. jaculatrix*, the other of six *T. chatareus*. For both species, the onset timing of the forward flap and of the backward flap (determined at target height 30 cm; Fig. 7C,D) lay in the ranges we had found in the trained fish at 20 cm and 40 cm (Fig. 3D,F), with no difference between the two

species (Brown–Forsythe: $P>0.084$). Estimates of the durations of the forward (Fig. 7E) and backward (Fig. 7F) flap also showed consistent timing, with no difference between species (Brown–Forsythe: $P>0.375$). Another remarkable finding is that the stability of the shooter's mouth during jet release (Gerullis and Schuster, 2014) is also seen in the freely hunting archerfish (Fig. 7G), again with no apparent difference between the two species (Brown–Forsythe: $P=0.490$). The variation in shooting positions selected in the freely hunting fish is shown in Fig. 7H. The distributions of horizontal distances d from prey showed considerable scatter but did not differ between the two species (Brown–Forsythe: $P=0.103$), and the same conclusion holds for the shooting angle ϵ (Brown–Forsythe: $P=0.150$; not shown). The variations in shooting position allowed testing of whether the timing (Fig. 7I) and duration (Fig. 7J) of the forward flap depended on horizontal distance from the target, but no correlations could be found (linear regression: $R^2<0.046$; $F<3.826$; $P>0.054$; no differences between both species, Fisher z -transformation: $P>0.333$). The same held for timing and duration of the backward flap (not shown; linear regression: $R^2<0.069$; $F<5.911$; $P>0.071$; no differences between both species, Fisher z -transformation: $P>0.423$) and also for the respective correlations

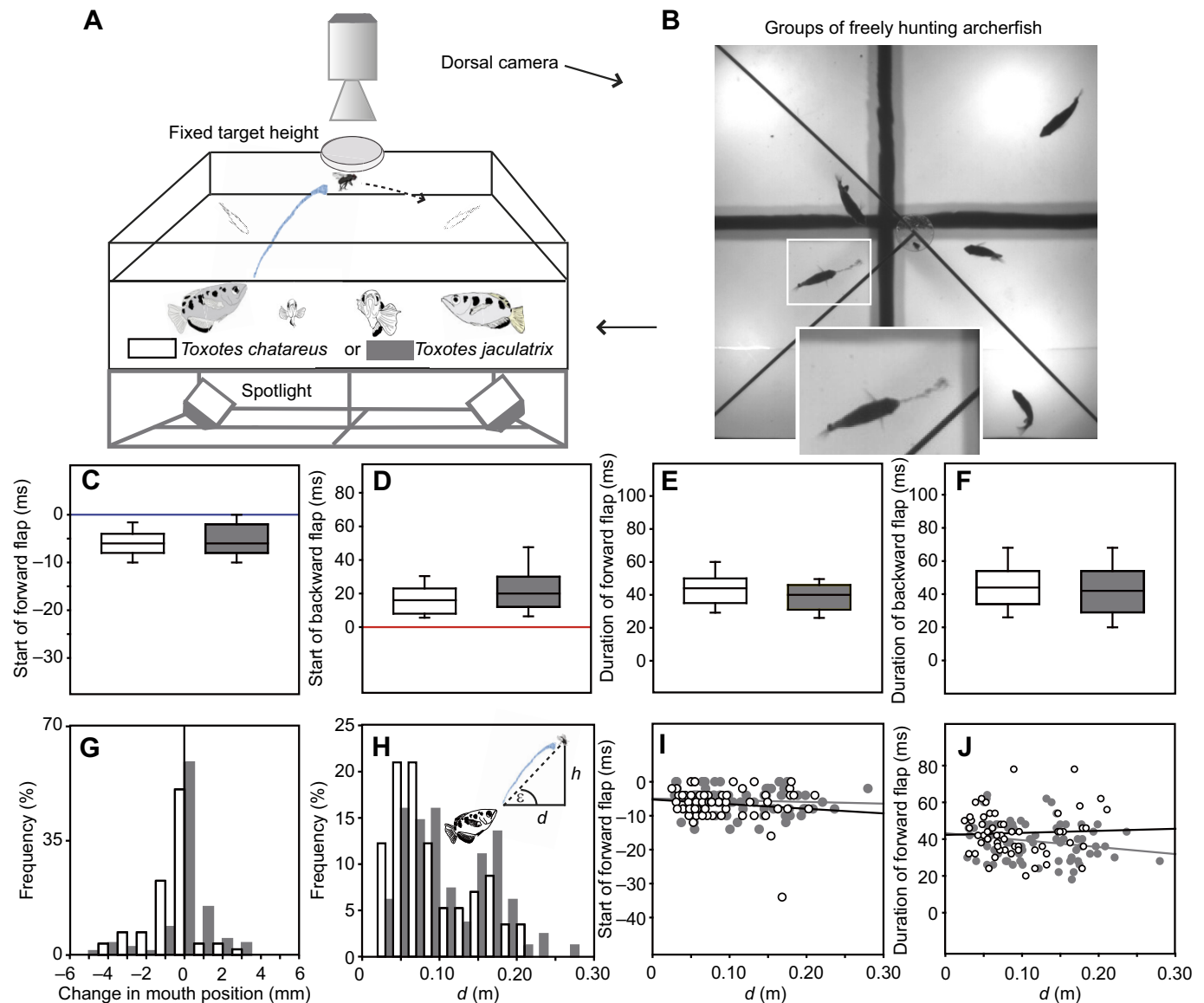


Fig. 7. The synchronized forward flap in unrestrained *T. jaculatrix* and *T. chatareus*. (A) Setup to monitor pectoral fin maneuvers during shots fired by groups of *T. jaculatrix* ($n=6$ fish; 1110 maneuvers recorded) and *T. chatareus* ($n=6$ fish; 1110 maneuvers recorded) during their natural hunting behavior. In each scene, a wetted dead fly was stuck on the lower side of a transparent disk, 30 cm above the water surface, and the shots and later prey capture were monitored from above (dorsal camera). (B) Example of one scene with one fish shooting and its pectoral fins abducted. (C,D) Times of onset of the forward flap (C) relative to the onset of the jet (at $t=0$; blue line) and subsequent backward flap (D) relative to the end of the shot (at $t=0$; red line) of the pectoral fin in the naturally hunting fish of both species show no difference between species (Brown–Forsythe: $P>0.084$) and closely match the findings reported in the two trained fish. (E,F) Durations of the forward flap (E) and backward flap (F) as determined in the maneuvers of freely hunting archerfish were in the range determined in the two trained fish and both showed no difference between species (Brown–Forsythe: $P>0.375$). (G) Stability of the shooter’s position. Shown is the maximal change in horizontal distance d of the mouth from the target during the jet release, positive when the change is away from the target. Stability was not different between the two species (Brown–Forsythe: $P=0.490$; bin width, 1 mm; first bin starts at -5.5 mm). (H) The variation in horizontal distances chosen by shooters did not differ between the two species (Brown–Forsythe: $P=0.103$; bin width, 0.02 m; first bin starts at 0.02 m). This also held for shooting angle ϵ (Brown–Forsythe: $P=0.150$; not shown). (I,J) No correlation between timing (I) and duration (J) of the forward flap with horizontal distance (linear regression: $R^2<0.046$; $F<3.826$; $P>0.054$; no differences between both species, Fisher z -transformation: $P>0.333$). Analyses in C–J are based on $N=57$ maneuvers during shots fired by *T. chatareus* and $N=81$ in *T. jaculatrix* (for criteria see Materials and Methods). Box plots show median, 25(75)% and 10(90)% quartiles.

with shooting angle (not shown; timing and duration of the forward flap: linear regression: $R^2<0.046$; $F<3.803$; $P>0.055$; no differences between both species, Fisher z -transformation: $P>0.291$; timing and duration of the backward flap: linear regression: $R^2<0.075$; $F<6.393$; $P>0.128$; no differences between both species, Fisher z -transformation: $P>0.450$; no differences between correlations with distance or shooting angle, Fisher z -transformation: $P>0.140$).

Target-height-dependent changes in the pectoral fin flap in freely positioned shooters

We next tested whether we could also detect height-dependent changes in the temporal characteristics of the pectoral flap in fish that downed targets from one of three possible heights, and whether such changes would also be independent from the shooter’s horizontal position from the target. An extensive analysis was made in a group that fired at targets at 35, 55 or 65 cm height (Fig. 8A).

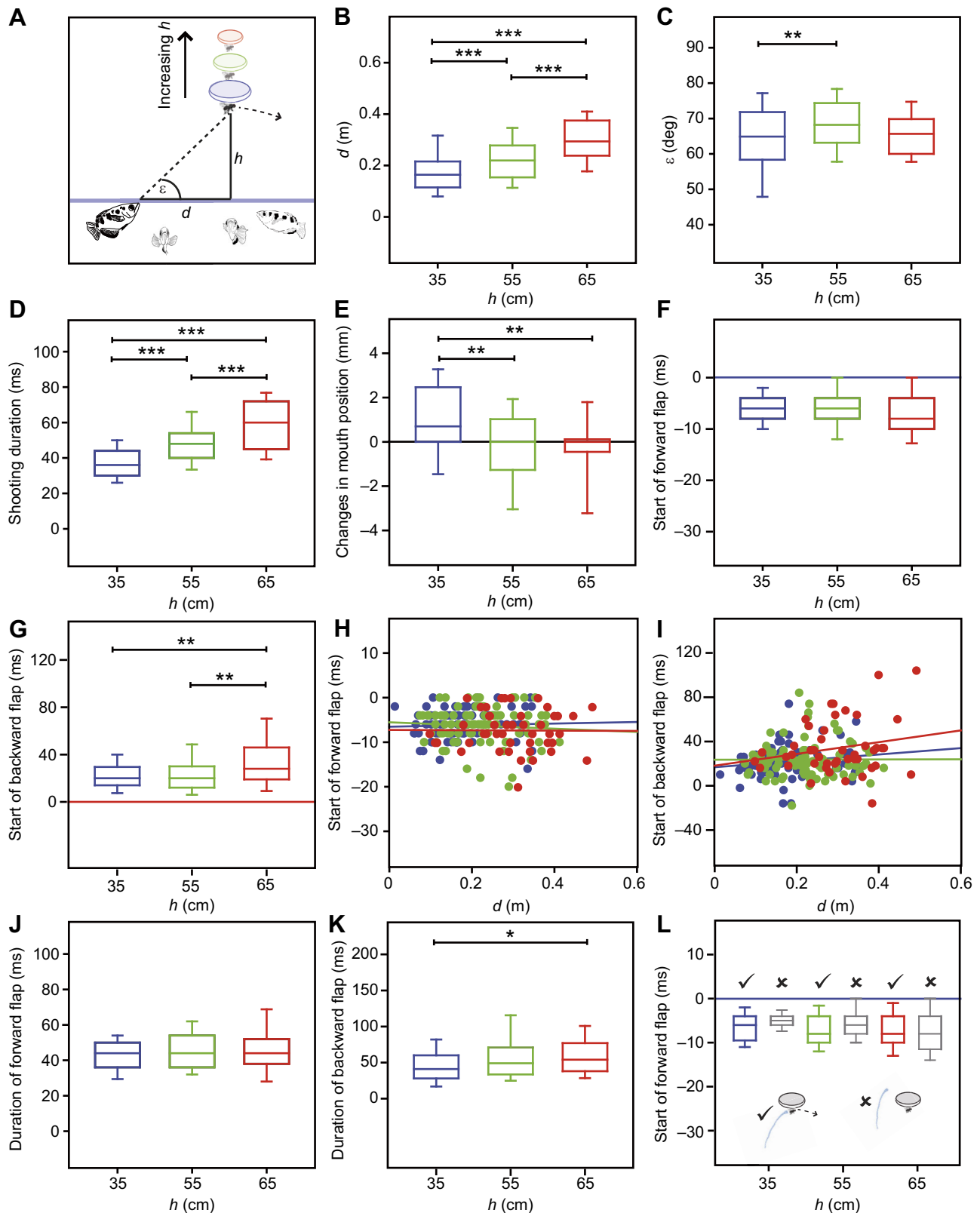


Fig. 8. See next page for legend.

First, we analyzed the horizontal distances assumed by shooters. They varied (as in Fig. 7H), but with an interesting trend: the mean horizontal distance chosen systematically increased with target height (Kruskal–Wallis: $P < 0.001$; Fig. 8B), whereas shooting

angles were approximately equal (only difference lowest versus medium level, Dunn's method: $P < 0.05$; Fig. 8C). Interestingly, shooting durations also increased systematically (Kruskal–Wallis: $P < 0.001$; Fig. 8D) with target height, as we had described

Fig. 8. Target-height dependence of the timing and duration of the forward flap in freely hunting *T. jaculatrix* and *T. chatareus*.

(A) Experiments in which freely moving shooters fired at targets at one of three possible height levels larger than 30 cm (h , colors as used to denote height in subsequent panels). Horizontal distance d and corresponding shooting angle ϵ are indicated. (B) Horizontal distances assumed by shooters vary considerably, but increase systematically with target height (Kruskal–Wallis: $P < 0.001$). (C) For the same events, approximately similar mean shooting angles were selected at each height (only difference lowest versus medium level, Dunn's method: $P < 0.05$). (D) Shooting durations increased systematically (Kruskal–Wallis: $P < 0.001$) with target height as in the trained fish (Gerullis and Schuster, 2014). (E) Stability of the shooter during jet release as quantified by the maximal change in horizontal distance from the target (positive for increasing distance). At the larger distances, mean change was not significantly different from zero (one-sample signed rank test: $P > 0.475$). However, at the lowest height, small changes away from the target were evident (difference from changes at other height levels, Kruskal–Wallis: $P = 0.002$; difference from zero mean, one-sample t -test: $P < 0.001$). (F) Start of the forward flap was again tightly linked to the onset of the jet (at $t = 0$; blue line), but no significant change in its timing could be detected when the target height changed (Kruskal–Wallis: $P = 0.373$). (G) Start of the backward flap (relative to the end of shot at $t = 0$; red line) depended on target height (Kruskal–Wallis: $P = 0.007$; Dunn's method: 35 cm and 55 cm versus 65 cm, $P < 0.05$). (H) Plot of time of onset of the forward flap versus horizontal distance of the shooter for all three height levels to show the absence of significant correlation (linear regression: $R^2 < 0.005$; $F < 0.414$; $P > 0.522$; no difference in R with height, Fisher z -transformation: $P > 0.740$). (I) Similar to H but plot of time of onset of the backward flap versus the horizontal distance. Lack of any significant correlation (linear regression: $R^2 < 0.040$; $F < 2.000$; $P > 0.161$; independence from target height; Fisher- z -transformation: $P > 0.289$) shows that changes in G were not due to changes in horizontal distance. (J,K) Duration of the forward flap (J) and the backward flap (K). The only significant difference among height levels was seen for the duration of the backward flap [(J) Kruskal–Wallis: $P = 0.596$; (K) Kruskal–Wallis: $P = 0.030$; Dunn's method: 35 cm versus 65 cm, $P < 0.05$]. (L) Example (for onset of the forward flap) of an analysis made to test whether the forward flap differed between hits (tick) and cases in which the jet missed the target (cross). No significant difference could be detected at any target height level (Kruskal–Wallis: $P = 0.269$). All analyses are based on $N = 207$ shots fired at three different target height levels [$h = 35$ cm ($N = 76$), $h = 55$ cm ($N = 86$) and $h = 65$ cm ($N = 45$)]. L is based on the same shots but sorted according to perfect hits ($N = 64$, $N = 37$ and $N = 14$, respectively) and failures ($N = 12$, $N = 49$, $N = 28$, respectively). Recordings were made in a group of two *T. jaculatrix* and six *T. chatareus*, different individuals than in the analyses of Fig. 7. Box plots show median, 25(75)% and 10(90)% quartiles. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

previously in specifically trained fish (Gerullis and Schuster, 2014). Furthermore, also in this group, the mouth position of the shooters was quite stable during jet release (Fig. 8E), particularly when they fired at targets at great height (change in position not significantly different from zero, one-sample signed rank test: $P > 0.475$), whereas small changes away from the target occurred at the smallest target height (one-sample t -test: $P < 0.001$). Start of the forward flap and of the backward flap were again tightly linked to the onset or end of the jet, respectively (Fig. 8F,G). Target-height-dependent changes could be seen at the onset of the backward flap (Kruskal–Wallis: $P = 0.007$; Dunn's method: 65 cm: $P < 0.05$). No changes in the time of onset of either the forward flap (Fig. 8H) or backward flap (Fig. 8I) versus the horizontal distance of shooter or versus the shooting angle (not shown) could be found at any height level [either horizontal distance or shooting angle; forward flap (onset and duration): linear regression: $R^2 < 0.044$, $F < 3.903$, $P > 0.051$ (R independent of target height; Fisher z -transformation: $P > 0.131$); backward flap (onset and duration): linear regression: $R^2 < 0.040$, $F < 2.327$, $P > 0.131$ (R independent of target height; Fisher z -transformation: $P > 0.289$)]. Durations of the forward flap (Fig. 8J) and backward flap (Fig. 8K) were comparable to the findings reported above, and significant

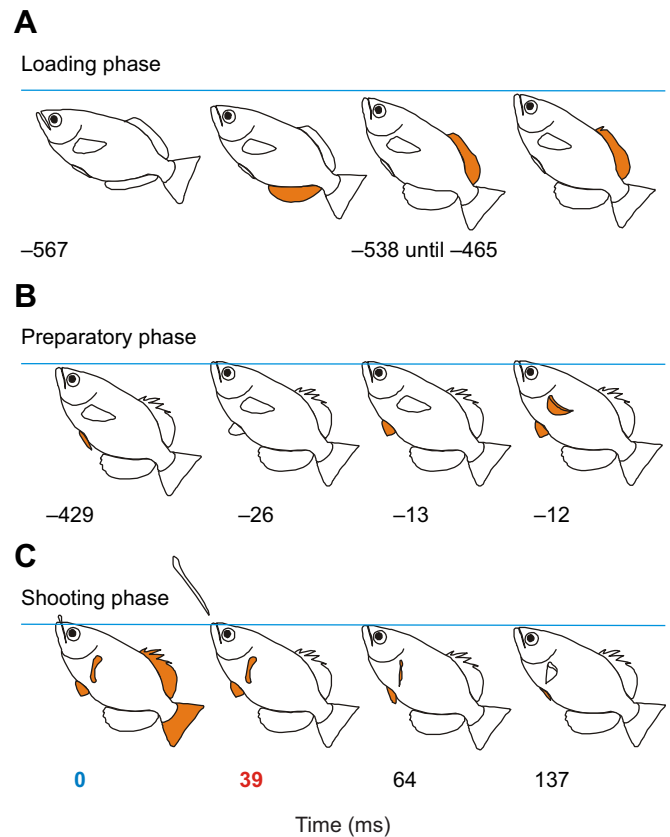


Fig. 9. Summary of fin maneuvers observed before and during shooting.

Frames depict characteristic episodes in which specific fins, highlighted in orange, are activated. Indicated times are means determined for a target height of 20 cm from $N = 10$ recordings in fish 1 in which recording time extended up to 700 ms before the start of the shot. Times change with target height (e.g. Fig. 8), but the sequence was confirmed for all 30 individuals examined in this study. Time zero is at the start of jet release. (A) During the water-loading phase, the mouth of the archerfish visibly opens and closes shortly thereafter. This phase preceded onset of the shot by about half a second (mean \pm s.e.m., -567 ± 37 ms). Around this time, the anal fin and the soft and spiny parts of the dorsal fin are erected while the body moves towards the water surface. At this time the pectoral fins still show alternate beating as shown in Fig. 4. (B) In the preparatory phase, the pelvic fins are erected (-430 ± 30 ms) and the tip of the mouth breaks through the water surface (-26 ± 3 ms). Both pelvic fins then slowly start to be adducted towards the body (-13 ± 2 ms), whereas the pectoral fins synchronize to start their rapid forward flap (-12 ± 2 ms). (C) In the shooting phase, the mouth opens slightly to release the jet (0 ms, blue), and the pectoral and pelvic fins continue their movement. Meanwhile, the soft part of the dorsal fin and the caudal fin beat horizontally (see text). After release of the water jet (39 ± 1 ms, red), the pectoral fins remain in synchrony but reverse their movement direction (64 ± 3 ms), while the pelvic fins complete their movement (137 ± 9 ms).

changes in the duration of the backward flap with target height could be seen (Fig. 8K; Kruskal–Wallis: $P = 0.030$; Dunn's method: 35 cm versus 65 cm, $P < 0.05$). Finally, we checked whether we could detect any differences between shots that were perfect hits and shots that missed their target. However, the start of the forward flap, for instance, did not differ between hits and failures (Fig. 8L; Kruskal–Wallis: $P = 0.269$) and the same held for duration of the forward flap, as well as onset and duration of the backward flap, along with changes in mouth positions during jet release [Kruskal–Wallis: $P < 0.002$ but all pairwise comparisons (Dunn's method) $P > 0.05$; data not shown].

DISCUSSION

In this study, we show that a number of fin maneuvers are tightly associated with shooting in archerfish. Most notable is the rapid and synchronized forward flap of the two pectoral fins that is precisely coordinated with the onset of the water jet. The fin maneuvers could conveniently be studied in fish that had been specifically trained to shoot from a fixed position. These fish could be filmed from two angles, and aspects of their jet production and stability had already been characterized, as these fish reliably scored perfect hits from a fixed position at targets at different distances (Gerullis and Schuster, 2014). It is striking that some of these fin maneuvers, most notably a rapid forward flap of the two pectoral fins, set in just when the shooter had already achieved its shooting position and perfectly maintained it. During this time, the beginning recoil from the onset of the jet starts to act, and so forces are needed to stabilize the shooter. The synchronized forward flap could equally well be seen in all freely moving 28 individuals of the two archerfish species – *T. jaculatrix* and *T. chatareus* – that we analyzed additionally. Moreover, the onset and duration of the forward flap and of the subsequent backward flap were similar across all fish. Aspects of the timing depended on target height (but not horizontal distance) (Figs 3, 5, 6 and 8) and could therefore potentially be needed to account for the systematic changes in the water jets (Gerullis and Schuster, 2014). Our findings suggest that coordinated and precisely timed fin maneuvers are an important aspect of the archerfish's unique ability to fire powerful long-distance water jets and that they contribute to stabilizing the shooter against recoil during the release of its water jet.

Spatially restricted versus freely ranging fish

Using trained fish that reliably fired from a fixed spot made it convenient to monitor the timing of all fin maneuvers relative to the onset of the shots. The tight synchrony with jet onset made it possible to measure mean timings with great accuracy (despite a rather low frame rate used in the trained fish). Height-dependent changes occurred in the timing of the pectoral (Fig. 3) and pelvic (Figs 5 and 6) fins. During an extensive survey of 28 additional archerfish, filmed during their natural hunting behavior as they positioned themselves freely below their targets, we found that the rapid forward flap was seen in each shooting maneuver. The most noteworthy aspects found are as follows: (1) the mouth position of the shooters was stable during the shot (Fig. 7G and Fig. 8E), suggesting that this might indeed be important for all fish that manage to hit distant targets (Gerullis and Schuster, 2014); (2) the increase in the duration of jet release with increasing target height (Gerullis and Schuster, 2014) could also be confirmed (Fig. 8D); (3) the shooters fired from a horizontal distance from prey as described previously by many authors (e.g. Timmermans, 2001). By varying target height we show that the fish seem to favour a specific angular range but not a specific distance. (4) The considerable variation around the preferred shooting position (or angle) allowed us to rule out that changes in the temporal characteristics of the forward and backward flap of the pectoral fins changed as a result of changed position relative to the target (Fig. 8H,I). Most importantly, however, the survey showed that the synchronized rapid forward flap and backward flap can be seen in every shooting maneuver of 28 freely moving archerfish of two species and, where results could be analyzed quantitatively, showed the basic characteristics observed in the two highly trained fish. On this basis (Figs 7 and 8), we conclude that the fin movements we describe here appear to be representative for shooting archerfish, at least for individuals that have learned to hit distant targets.

Comparison with braking maneuvers – what is the forward flap compensating?

The rapid synchronized forward flap of the pectoral fins (and its being accompanied by pelvic fin action) is strongly reminiscent of the rapid forward movement of the pectoral fins seen in braking fish as they prepare for a catch or avoid colliding with an obstacle (e.g. Drucker and Lauder, 2002; Standen and Lauder, 2005; Lauder and Madden, 2006; Lauder et al., 2007; Higham et al., 2005; Higham, 2007; Kane and Higham, 2011; Higham et al., 2016). A large body of detailed evidence on braking maneuvers has been obtained in the sunfish, which, also being a perciform fish, shares with archerfish similar shape and location of the pectoral fins. However, in contrast to braking, the rapid forward flap of shooting archerfish sets in just when the shooter is already at a stable shooting position and then holds it. Because the rapid fin action thus does not cause any changes in the movement of the fish, the question obviously is which other forces balance their effect. Clearly, and based on the synchrony with onset of the jet, the recoil forces of the jet would be chief among them. Or, reversing the argument, the 'braking-like' maneuvers would seem useful in stabilizing the shooter against the recoil of its jet (~100 mN for prey of the sizes presented here; Schlegel et al., 2006). The forces produced during the forward flap must produce sufficient lift to keep the shooter at the surface, which would clearly be possible (e.g. Breder, 1926; Harris, 1937; Webb, 1973; Blake, 1983; Walker and Westneat, 1997). None of our recordings allowed us to reconstruct the complexity of the changes in shape, orientation and rigidity of the fins that was clearly evident (e.g. see Movies 1 and 2); however, a number of observations could be made. During the forward flap, the shape and orientation of the pectoral fins underwent massive changes. In 236 of the 278 recordings, the plane of the pectoral fins could be seen both from the side and frontal views (i.e. also using the mirror that was placed in front of the shooter, see Fig. 1A). In all these events, the area of the pectoral fin was not constant. The images shown in Fig. 2A provide a good illustration: the visible area of the pectoral fins changes during the fin flap so that, at the end of the shot, its major area is actually orthogonal to the water surface. There is thus a clear rotatory component in the movement of the more trailing parts of the pectoral fins. Our finding that timing and duration of the pectoral flap did not change with shooting angle implies that these aspects (and not timing) might be important to provide the appropriate amount of lift required for the various shooting angles.

Preparatory aspects and coordination of fin maneuvers with shooting

All fins are activated to prepare the shooter, some long before the jet actually starts and with different degrees of synchrony to jet release (Fig. 9). About half a second before onset of the jet, when the shooter takes up water, the anal fin, the soft parts of the dorsal fin and the spiny parts of the dorsal fin get erected (Fig. 9A). The exact timing and temporal order of these maneuvers varies considerably, particularly when compared with later maneuvers (Fig. 9B). Here, the pelvic fins first start to be spread, allowing then the precisely timed onsets of pelvic and pectoral fin maneuvers. The forward flap also involves preparation, i.e. the pectoral fins must change from an alternating pattern to synchrony (Fig. 4), allowing the forward flap to then set in. Hence, coordination of the pectoral fins with the shot must set in already before the shot starts.

Conclusion

All 6098 shooting maneuvers scrutinized in this study in a total of 30 archerfish showed the characteristic rapid shooting-associated

forward flap of the pectoral fins. Wherever other fins could be seen during shooting, they followed the pattern that we had discovered in the two specifically trained fish. On this basis, we conclude that shooting-associated fin maneuvers are an integral aspect of shooting in archerfish and their timing relative to the expected recoil forces from the jet suggests that they are needed to keep the shooter stable.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: P.G., C.P.R., S.S.; Methodology: P.G., C.P.R., S.S.; Software: C.P.R.; Validation: S.S.; Formal analysis: P.G., C.P.R., S.S.; Investigation: P.G., C.P.R.; Resources: S.S.; Data curation: P.G., C.P.R.; Writing - original draft: P.G., S.S.; Writing - review & editing: C.P.R., S.S.; Visualization: P.G., C.P.R.; Supervision: S.S.; Project administration: S.S.; Funding acquisition: S.S.

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