RESEARCH ARTICLE

Archerfish use their shooting technique to produce adaptive underwater jets

Jana Dewenter*, Peggy Gerullis*, Alexander Hecker and Stefan Schuster‡

ABSTRACT

Archerfish are renowned for dislodging aerial prey using well-aimed shots of water. Recently it has been shown that these fish can shape their aerial jets by adjusting the dynamics of their mouth opening and closing. This allows the fish to adjust their jet to target distance so that they can forcefully hit prey over considerable distances. Here, we suggest that archerfish use the same technique to also actively control jets under water. Fired from close range, the underwater jets are powerful enough to lift up buried food particles, which the fish then can pick up. We trained fish so that we could monitor their mouth opening and closing maneuvers during underwater shooting and compare them with those employed in aerial shooting. Our analysis suggests that the fish use the same dynamic mechanism to produce aerial and underwater jets and that they employ the same basic technique to adjust their jets in both conditions. When food is buried in substrate that consists of large particles, the fish use a brief pulse, but they use a longer one when the substrate is more fine-grained. These findings extend the notion that archerfish can flexibly shape their jets to be appropriate in different contexts and suggest that archerfish shooting might have been shaped both by constraints in aerial and underwater shooting.

KEY WORDS: Animal tool use, Water jet, Animal cognition, Biomechanics, Evolution

INTRODUCTION

Archerfish are renowned for their ability to down aerial prey with precisely aimed shots of water (e.g. Dill, 1977; Schuster, 2007). Although impressive, the behavior has long appeared to lack an essential component of true tool use (Beck, 1980; Barber, 2003; Bentley-Condit and Smith, 2010; Seed and Byrne, 2010): a capability of the fish to adaptively modify their water jets. To consider archerfish shooting an instance of tool use, the fish should be able to adapt their jets in similar ways as, for example, a New Caledonian crow would modify a stick to help it access an insect larva (e.g. Hunt, 1996; Hunt and Gray, 2004). In recent years, it has become clear that archerfish shots are not simply all-or-none. Rather, the fish adjust the amount of force transfer to target size by shooting more water at larger prey while keeping the jet's speed and impact time constant (Schlegel et al., 2006). Interestingly, the fish manage to adjust key hydrodynamic properties of their water jets to engage aerial targets over a large range of distances (Gerullis and Schuster, 2014). This ability is

Department of Animal Physiology, University of Bayreuth, Universitätsstrasse 30, 95447 Bayreuth, Germany.
*These authors contributed equally to this work

‡Author for correspondence (stefan.schuster@uni-bayreuth.de)

ⓘ S.S., 0000-0003-0470-9802

related to the fish using their mouth as an 'active muzzle', i.e. a muzzle of continuously changing cross-section that opens slowly (compared with the duration of the shot) and starts closing as the jet is just being formed. By adjusting the dynamics of the opening and closing phases, the fish modify lifetime and time of focus of their water jets to adjust them to the target distance. The relationship between the effective target range and the timing precision required to adjust the opening and closing maneuvers are remarkably similar to that in human throwing. In this celebrated 'uniquely human' maneuver, precise temporal control of the release of the projectile is the key to the ability to forcefully hit distant targets (e.g. Calvin, 1983; Bingham, 1999; Schoenemann, 2006; Gerullis and Schuster, 2014). The findings available so far show that archerfish do modify their water jets in a task-dependent manner and justify the notion that archerfish use their jets as tools.

Many aquatic animals show forms of hydraulic jetting (e.g. Brown, 2012; Mann and Patterson, 2013; Marshall et al., 2014) and all of the archerfish tested in this study produced jets under water to lift up insect larvae buried in sand or mud (Movie 1). The simultaneous occurrence of both aerial and underwater jets in one species allows researchers to explore whether the fish use similar maneuvers in both contexts and whether the capability to modulate aerial jets might also extend to the underwater jets. Because recordings of the mouth opening and closing maneuvers of suitably trained archerfish are available for shots fired at aerial targets in various distances (Gerullis and Schuster, 2014), our goal was to obtain similar data for underwater shooting.

MATERIALS AND METHODS
Animals and training

Initial observations of shooting angle, distance and the extension of the sand cloud in underwater shooting involved one *Toxotes jaculatrix* (Pallas 1767) and one *Toxotes chatareus* (Hamilton 1822) (8 and 10 cm snout to peduncle length, respectively) kept in tanks 80×35×40 cm (length×depth×height) at 26±1°C (conductivity 3.6–3.8 mS cm^{-1}). The main body of results, including all measurements on the time course of mouth opening and closing, was obtained in a group of five further *T. chatareus* (8.2–9.7 cm, snout to peduncle length), kept in a large tank (127.5×127.5×55 cm) under a 12 h:12 h light:dark regime in brackish water (temperature 24±1°C; conductivity 3.5–3.7 mS cm^{-1}, height of water level: 26 cm). All five fish of this group successfully hit aerial prey but were not used in previous studies on aerial shooting. Taking photographs of each of the five fish from various angles allowed us to quickly tell the individuals apart (from differences in the pattern of their stripes and dots, size and shape), which was necessary because the individuals did not equally contribute to the tasks. To monitor aspects of the underwater shooting in more detail we trained the fish to shoot from restricted positions. We started by placing food particles (defrosted black mosquito larvae or Sera Cichlid Sticks) on top of fine-grained sand (particle size: 0.1–0.5 mm). The

sand was contained in a glass bowl (69 mm diameter, 35 mm high) located at the bottom of the tank. Once the fish had learned to take food from the bowl, we only presented food items that were buried under the sand. After a phase in which the fish bit into the sand, all fish eventually used water jets to uncover the food particles. At this stage, the fish were free to fire from anywhere. However, once they regularly used their underwater jets, we confined them such that we could eventually record the time course of their mouth opening and closing maneuvers orthogonally to the camera view. The bowl was therefore placed between a wall (polyvinylchloride) and the front of the tank. Initially the wall was distant from the front side. As the fish grew more confident in approaching the food bowl, the distance of the wall and the front of the tank was gradually decreased to a final distance of 12 cm. The fish then approached and left the test area from left or right and were sufficiently well oriented for the present analysis. Bowls with substrate and food were covered with a glass plate and placed at the recording site. Each trial was started by lifting the cover. In the initial part of the study, we exclusively used fine-grained sand as substrate. We later changed the substrate to coarse-grained shell sand (particle size: 1.3–6 mm) and then mangrove mud (particle size: <0.05 mm).

Recording, image analysis and statistics

The first measurements of shooting positions, angles and extensions of the sand clouds (Fig. 1A) were based on recordings made at 25 frames s^{-1} (Sony TRV 270 E). All other recordings with the group of five fish were made at 500 frames s^{-1}, using a Fastcam APX RS (Photron, San Diego, USA) that monitored the area around the feeding bowl with a spatial resolution of 0.14 mm pixel^{-1}. Illumination came from a 150 W halogen spotlight. Not all five fish

participated equally in the different experiments, so their contributions could not simply be pooled (see Table S1) and the statistical treatment had to account for possible individual-specific effects. All recordings were processed using ImageJ (v.1.47d). To derive the normalized mouth opening, we took the coordinates of three distinct points in each frame (Fig. 1B): the tip of the snout (P_1), the tip of the lower jaw (P_2) and the corner of the mouth (P_3). Mouth opening at the given frame was then calculated as the height h of triangle $P_1P_2P_3$ between side P_2P_3 and point P_1. Two measures were taken immediately at the end of the 'loading' phase, when the bottom of the fish's mouth is maximally depressed (and will subsequently be moving inwardly as the shot is being released): (1) shooting distance was measured as the distance between point P_1 and the impact point at the substrate and (2) shooting angle was measured as the deviation of the line from P_1 to the middle of the caudal peduncle from the vertical (Fig. 1A).

Statistical analyses were run using SigmaPlot 11.0, OriginPro 7.5, R-studio (v.0.99.892) and R (v.3.2.3). First, we checked for individual shooting behavior by performing two linear mixed-effects models (total shot duration ∼ fish and shooting angle ∼ fish) using the 'glmer' function of the package 'lme4' in R (R Development Core Team, 2015). To take into account the fact that each fish shot several times onto different substrates, the substrates were added to the models as a random factor. The models were assessed by means of a test of variance (ANOVA) and a *post hoc* test (Tukey test). To evaluate the influence of the three different substrates on the duration of four different phases of the shot (A, shot duration; B, pre-shot to maximum; C, pre-shot to onset; D, minimum before onset to minimum after shot) we built generalized linear mixed-effects models (GLMMs) with a Poisson data family (e.g. shot
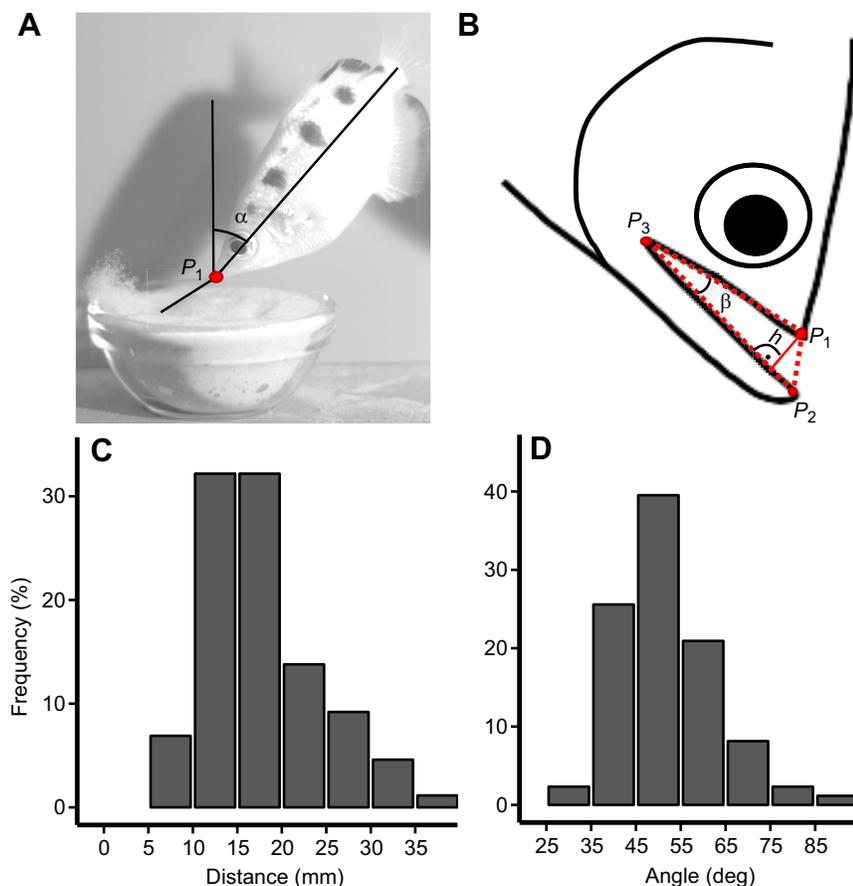

Fig. 1. Archerfish shoot under water to expose hidden prey. (A) An archerfish using a jet to expose food hidden in sand. Shooting angle α and tip of snout P_1, used to define range, are indicated. (B) Schematic illustration of how mouth opening was derived during the underwater shots. Red dots labeled P_1, P_2, P_3 show the points used to calculate mouth opening. Angle β is needed to calculate the height (h) of the triangle. (C) Underwater jets are only produced at close range (n=87 shots; N=6 individuals; distance as indicated in A). (D) Shooting angle α (indicated in A) varies over a broad range (total of n=86 shots from N=6 individuals).

duration ∼ substrate). In order to account for potential individual differences among the five fish, we added identity to the models as a random factor. The model (variable ∼ substrate | fish identity) was fitted three times, i.e. for variable B, variable C and variable D as the response variable. For variable A (shot duration), we fitted a linear mixed-effect model (shot duration ∼ substrate | fish identity). Another linear mixed-effect model was used to examine a potential influence of the shooting angle of the fish and the substrate on the duration of the shot. The random factor 'fish' and an interaction between substrate and angle were added to the model (e.g. shot duration ∼ substrate | angle). All variables were analyzed using ANOVA and Tukey's range tests when there was a significant difference.

RESULTS

Underwater shooting is limited to close ranges

All fish aimed underwater jets at the sand bowls with hidden food particles. In fine-grained sand (particle size: 0.1–0.5 mm) the underwater jets caused a sand cloud that typically extended from about 14 mm to 29 mm. A closer analysis of the sand cloud in one fish (sized 8 cm) showed that the cloud extends 22.1±5.1 mm (mean±s.d.; n=23 shots). All shots we observed were released from positions very close to the substrate, at distances from 6 mm to a maximum of only 40 mm (Fig. 1C; 18.±6.4 mm; mean±s.d.; random selection of n=87 shots from N=6 fish). This contrasts remarkably with aerial shooting where the fish engage targets over much larger distances from 0.2 to more than 2 m (e.g. Rischawy et al., 2015). The orientation of the shooting fish, however, appears to be equally variable as it is in aerial shooting (Fig. 1D). The body angle of the shooting fish (i.f. called 'body angle') varied from 28 to 89 deg (51.2±11.3 deg; mean±s.d.; n=89 shots). The variations in body angle appear not to be related to how distant the shooting fish is from the substrate (r^2=0.095; P=0.0038; n=86). Furthermore, we found no indication that the 'effectiveness' of the shots, as measured by the extension of the sand cloud, varied with either distance (r^2=0.078; P=0.196; n=23) or body angle (r^2=0.044; P=0.335; n=23). Maximum firing rate appears to be different between aerial and underwater shooting. In aerial shooting, archerfish can fire several shots within 1 s (e.g. Schlegel et al., 2006) but we never observed similarly high repetition rates in underwater shooting although the fish did generally have to produce several shots in our trials until they located and displaced a food particle. It is therefore interesting to note that the shortest delay we recorded between successive attempts was 10 s, which is considerably longer than the minimum interval between aerial shots.

Similar markers can be used to align aerial and underwater mouth opening maneuvers

Our goal was to obtain similar measurements on the time course of the fish's mouth opening and closing to those available for aerial shooting (Gerullis and Schuster, 2014). In aerial shooting, the onset and detachment of the jet can conveniently be used to align the time courses obtained in several experiments, to average them and to quantify their variability. In the absence of a directly visible jet we explored various possible reference points that might potentially have been useful in aligning several recordings and in enabling a simple comparison with the measurements available for aerial shooting. Fig. 2A schematically illustrates major landmarks that are apparent in the recordings of aerial and underwater shots. In aerial shooting (top trace) the shot is preceded by a phase in which the bottom of the mouth is continuously lowered and its 'bulging' out is readily detectable. The onset of the jet coincides with the onset of levation of the mouth bottom. The end (=detachment) of the jet
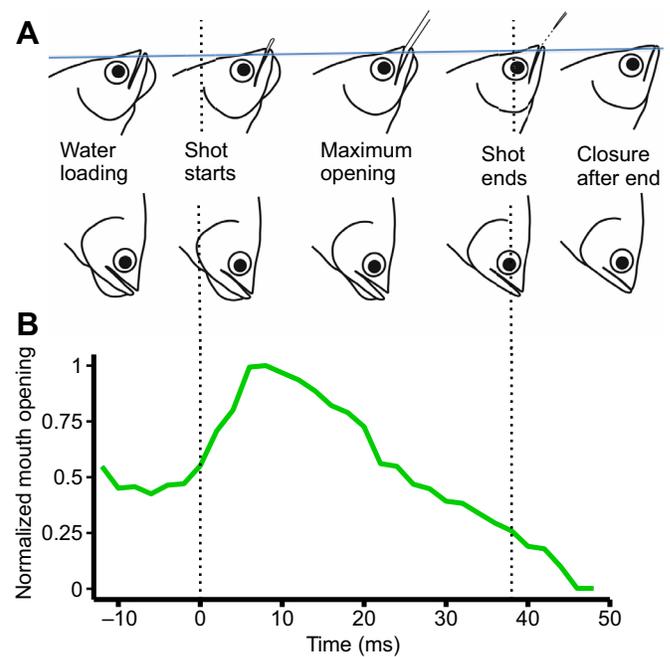

Fig. 2. Temporal markers to align mouth opening maneuvers in aerial and underwater shooting. (A) Schematic comparison of characteristic markers in aerial (top) and underwater (bottom) shooting. In aerial shots, an additional effect (besides the jet) can be used to precisely assign an onset and end of a shot: the movement of the bottom of the mouth. 'Onset' of the underwater shots (first dotted vertical line) was defined as the time in which the levation of the mouth bottom started and the 'end' as the time when the bottom of the mouth first is flat (second dotted line). (B) A time course of mouth opening as recorded in a fish (filmed from the side) that exposed a food particle hidden in fine sand. It was possible to average several such time courses (as in Fig. 3) because an 'onset' could be detected precisely enough to align the individual time courses.

coincides with the moment at which the bottom of the mouth first becomes flat again. This means, at least for aerial shots, that two events could be used as markers for the onset and end of the jet: the jet itself or the movement of the bottom of the mouth. Because the mouth bottom moves similarly in the underwater shots it can also be used – in the absence of an easily detectable jet – to tentatively define an 'onset' and an 'end' of the underwater shot. Fig. 2B provides an example of a time course of normalized mouth opening, aligned to the 'onset' of the shot (first dotted line). The 'end' of the shot (second dotted line) occurs 38 ms later. In this example, the mouth opened fully within 14 ms and closed over a time course of 30 ms (maximum to 'shot ends') to a width of 26%. During the subsequent 40 ms, it was fully closed. The conclusions that can be drawn at this stage are that accuracy is enough to analyze the time course of mouth opening in the underwater shots and that markers are available to align recordings made in different shots.

Using alignment to the 'onset' of the shot, we next obtained averaged time courses for all five individuals. It turned out that the courses were remarkably robust, suggesting that the alignment procedure was useful and the onset as defined in Fig. 2 provided an accurate marker. Furthermore, the courses were remarkably well conserved among the five individuals. Fig. 3 illustrates this by showing averaged time courses obtained with fish 1 and fish 4 as they shot at fine sand. Note the small jitter in each individual and the similarity of the basic pattern in the two individuals. Not only were the general time courses comparable between individuals, the absolute values of mouth opening were also similar. For instance, in two fish that were of identical size, the maximum width of mouth
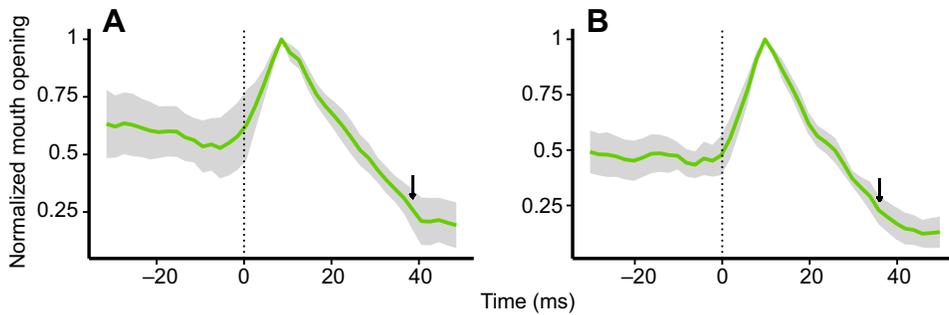
Fig. 3. The kinematic pattern is robust within and across individuals. The time course of normalized mouth opening is shown for two different individuals [fish 1 (A), n=11 shots; fish 4 (B), n=18 shots] as they exposed food buried in fine sand. Mouth opening was recorded from the side at 500 frames s^{-1} and normalized to the maximum opening width in the recording. Graphs report means±s.e.m. of normalized opening at distinct time points before and after the onset of the shots (as defined in Fig. 2). Arrows indicate the end of the shots.

opening (means 2.63 and 2.33 mm; t-test, P=0.071) was also not statistically different. However, shooting durations, the interval between onset and end (defined in Fig. 2), differed significantly among the five individuals (ANOVA, χ^2=17.204, d.f.=4, P<0.01; see Table S1) and these differences could not be attributed to differences in fish body length [Pearson product moment correlation coefficient (PPMCC), P=0.940; N=5].

Archerfish adapt their underwater jets

The consistency of the opening and closing maneuvers in the underwater shots (Fig. 3) suggested that it might be possible to detect small variations in the basic pattern that the fish might make if they faced ground of different constitution. After sufficient recordings of shots at fine sand were available, we therefore switched the substrate to coarse-grained sand (shell sand). We allowed 1 day of acclimatization in which several trials would allow the fish to familiarize themselves to food buried in the new substrate, but started sampling immediately on the next day. As soon as enough recordings were available, we then switched to a further new substrate, mangrove mud. Here, we allowed the fish just three preparatory trials but then immediately started sampling. The approach thus tested an ability of the fish to switch their patterns in the absence of extended learning and would fail to detect any difference in the mouth opening patterns should their adjustment require extended learning. However, the approach was surprisingly successful. As shown in Fig. 4, the fish used the same basic time course of mouth opening for all three substrates. All time courses are similar to those reported for aerial shots fired at targets 20 cm above the water surface (Gerullis and Schuster, 2014). It is also evident that the courses could be recorded with equal accuracy for all substrates – although the apparent slight variations of the basic course indicate that the fish did slightly vary their patterns. This suggests that most samples were obtained when the changes to a slightly modified pattern had already been made. Scrutiny of Fig. 4 suggests that the duration of the maneuver was changed in response to the change in substrate.

To examine this more closely, Fig. 5 reports a more quantitative analysis of several temporal characteristics that differed among the time courses shown in Fig. 4. Shot duration was shortest for the coarse-grained substrate and increased with more fine-grained substrate (Fig. 5A; ANOVA, χ^2=6.38, d.f.=2, P<0.05). Other temporal characteristics of the maneuver also changed with the roughness of the substrate: (1) the time from minimal pre-shot width until the mouth opened maximally was longer for shots directed at mud and shorter for sand (Fig. 5B; ANOVA, χ^2=112.88, d.f.=2, P<0.001); (2) the time from when the mouth was maximally closed before the shot to the onset of the shot was also longer for mud than for fine- and coarse-grained sand (Fig. 5C; ANOVA, χ^2=189.11, d.f.=2, P<0.001); (3) the interval between the first pre-shooting

minimal mouth opening width and the subsequent after-shot minimum was shorter for the coarser substrates (Fig. 5D; ANOVA, χ^2=29.861, d.f.=2, P<0.001). Apart from these changes in duration of the mouth opening and closing, the fish also modified the angle at which they released their underwater shots. The fish fired from flatter angles to expose prey hidden in mud than they did when they encountered fine or coarse sand (ANOVA, χ^2=14.996, d.f.=2, P<0.001; Tukey test, substrates: coarse sand vs fine sand, P=0.880; mud vs fine sand, P<0.01; mud vs coarse sand, P=0.001). Note, however, that the variations in shooting angle did not explain the different temporal characteristics of the mouth opening and closing maneuver (ANOVA, χ^2=0.16, d.f.=1, P=0.685) but the interaction between substrate and shooting angle (ANOVA, χ^2=9.46, d.f.=2, P<0.01) explained the duration of the shots better than the substrate alone (ANOVA, χ^2=8.55, d.f.=2, P<0.05). Normalized mouth opening at start was the same for all three substrates (one-way ANOVA; P=0.284) and the absolute maximal mouth opening width also did not depend on the substrate (one-way
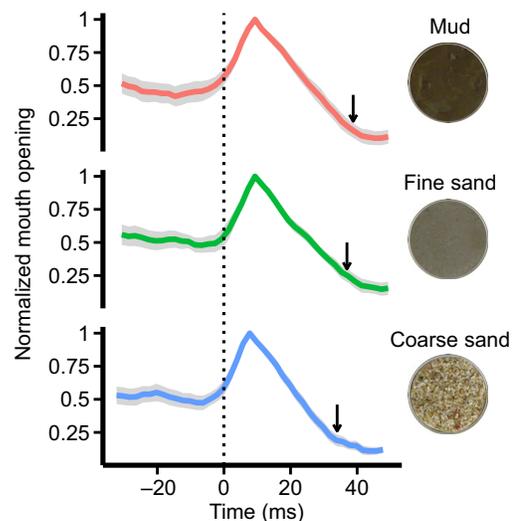

Fig. 4. Archerfish underwater shots after switching the substrate in which food was buried. Mouth opening maneuvers as fish exposed food buried in different substrates – from fine mud to coarse sand. Temporal order was from fine sand to coarse sand to mud and recordings were included that were sampled after only a few trials in which the fish gained experience with the new substrate (see text). Graphs report means±s.e.m. of normalized opening as determined from n=24, n=32, and n=38 shots at mud (red), fine-grained sand (green) or coarse-grained shell-sand (blue), respectively. For each shot, opening was normalized to maximum. Normalized opening was then averaged across shots at each substrate type. Time zero denotes onset and arrow indicates average end of shot (both as introduced in Fig. 2). Note the small variability even after the substrates were switched; small but conspicuous differences are observed in the time courses.
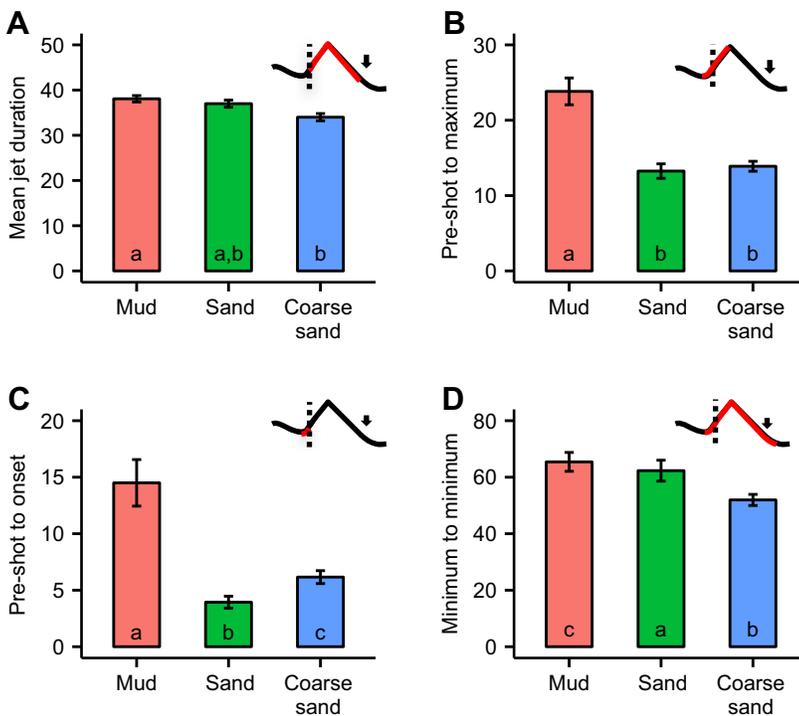
Fig. 5. Archerfish slightly shorten aspects of their underwater shots to engage coarse substrates. Quantitative analysis of time courses shown in Fig. 4 as fish shot at mud (red), fine sand (green) or coarse sand (blue). Various temporal characteristics are shown, as indicated by red lines in the insets. Insets all mark onset of shot as a dotted vertical line and the end of the shot as an arrow. (A) The time from onset to end of shot significantly decreases as grain size increased ($P<0.05$). (B) Time from the pre-shot minimum opening width to average maximum opening width shortens significantly ($P<0.001$) for coarse substrates. (C) Duration from minimum pre-shot opening width to 'onset' of shot at time zero decreases significantly ($P<0.001$) for coarse-grained substrates. (D) The time between the two minimal opening widths also decreases significantly from fine-grained to coarse substrates ($P<0.001$). Columns report means±s.d. of independent measurements of the respective variable in each shot fired at the indicated type of substrate. Significant differences are indicated by different letters in columns.

ANOVA; $P=0.084$) [conclusions based on $n=38$ (coarse), $n=32$ (fine) and $n=24$ (mud) shots].

How quickly were the adjustments made?

The changes in the opening and closing maneuvers (Figs 4 and 5) cannot simply be explained as a tendency of the fish to generally increase or decrease the duration of their shots over the course of our experiments. Suppose the decrease in shooting duration upon switching from fine to coarse sand was due to such a temporal drift, this would then have predicted similarly short (or shorter) durations in the subsequent switch to mud. However, duration was not shortened but was increased. Further evidence against a temporal drift could be obtained using the shots of fish 4, which produced a sufficient number of shots at all substrates to correlate (PPMCC) shot duration and trial number after a switch to a new substrate. No significant correlation ($P=0.15$) between shooting duration and trial number occurred during the experiments with fine sand. When sampling started after the substrate was switched to coarse sand, there was also no correlation between shot duration and trial number ($P=0.99$). Even with mangrove mud – with a minimal preparation phase – no significant change of duration with trial number could be detected ($P=0.09$). In summary, our findings cannot be explained by substrate-unrelated drifts and appear not to be confounded by ongoing changes in the time courses. Although we cannot rule out further much slower changes that would involve learning, the lack of a clear correlation between shot duration and trial number suggests that there is at least a rapid component in the adjustments that does not require extended immediate experience and works with limited amount of feedback. Because the fish were imported from Thailand they could potentially have relied on earlier experience from the wild, gained at least 1 year before the present experiments, to enable such rapid switching.

DISCUSSION

We argue here that archerfish use their adjustable mouth opening and closing maneuvers not only to shape aerial jets, but also to form and to adapt underwater jets. In our experiments, this enabled the fish to adapt their shots to different ground material that the fish explored for buried prey items.

The same basic time course is used in aerial and in underwater shooting

Fig. 6 examines more closely the striking similarity of the basic maneuver used in aerial and underwater shooting. Fig. 6A shows the time courses obtained in the present study for the underwater shots (Fig. 4), together with similarly analyzed shots obtained in an earlier study on aerial shooting (Gerullis and Schuster, 2014). Because the durations of the maneuvers differ for all time courses shown in Fig. 6A, they are plotted so that all maxima coincided (at time zero). The courses obtained in the underwater shots correspond best to that in aerial shots aimed at targets in 20 cm height, whereas shooting duration in aerial shots fired at more distant targets is clearly longer. To demonstrate how similar the underwater patterns were to the aerial ones, we ran analyses in which we correlated normalized opening at corresponding points in time for any possible pairing between the aerial and the underwater shots. This is illustrated in Fig. 6B,C in which the opening values for underwater shots on mud and coarse sand, respectively, are correlated with those obtained at the same time – before or after maximum opening – for aerial shots at a target 20 cm high. The degree of correlation is striking and linear regression yielded $r^2=0.975$, $P<0.0001$ ($n=20$) (Fig. 6B) and $r^2=0.962$, $P<0.0001$ ($n=18$) (Fig. 6C). But every other possible pairing of conditions also yielded highly significant correlations ($P<0.0001$). This strengthens our conclusion that archerfish use one basic maneuver in all contexts but vary it slightly to adapt it to a particular context, either to target height (in the aerial shots) or the substrate (in the underwater shots).

Adapting underwater jets

Our demonstration of an underwater jet being varied in response to a change in ground composition raises a number of questions. First, if archerfish are capable of modifying their underwater jets do they
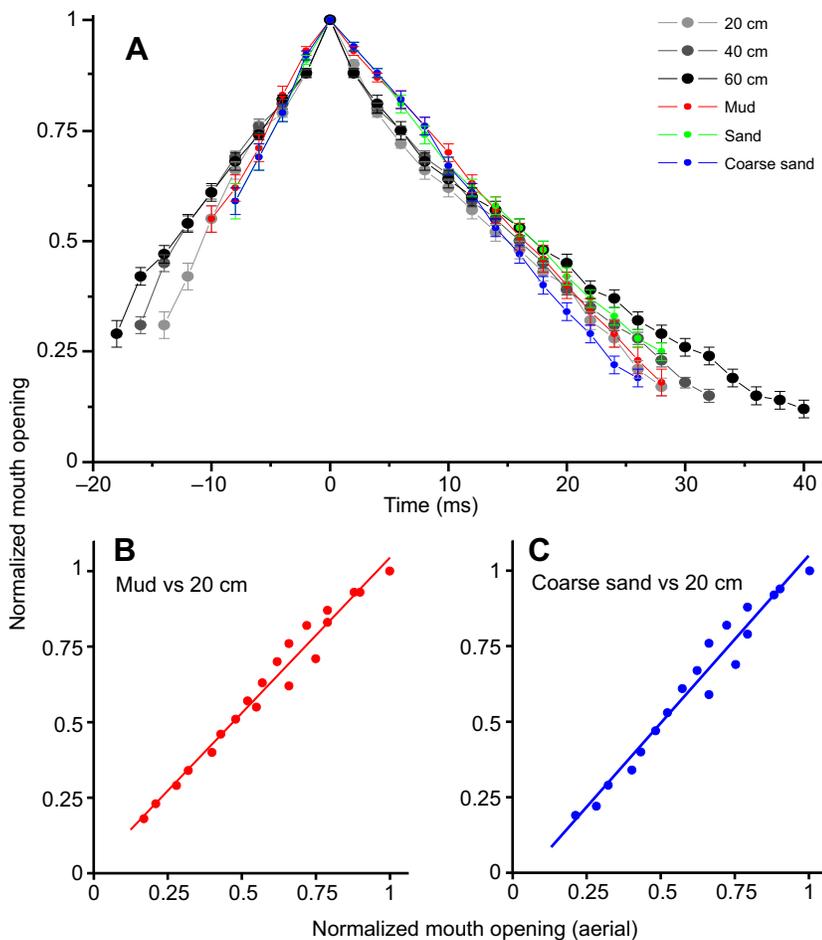
Fig. 6. Archerfish use the same basic kinematic pattern of mouth opening and closing in aerial and underwater shots. (A) Comparison of the time courses (means±s.e.m.) measured in this study (Fig. 4) with those obtained by Gerullis and Schuster (2014) for aerial shots fired at targets in various height, as indicated. Note that the duration of underwater shots corresponds best to that of aerial shots at low (20 cm) target height. Although all individual traces were aligned to shot onset before averaging, the resulting averaged normalized courses are shown so that their maxima coincide. This makes it easier to compare the respective durations. (B,C) Examples of direct correlation at respective times before or after the maximum of normalized mouth opening in underwater shots and aerial shots fired at targets in 20 cm height. Comparison relates to underwater shots aimed at mangrove mud (B) or at coarse sand (C). Correlation is highly significant in both cases ($P<0.001$) and slopes are not significantly different from unity. Offset of C (but not of B) significantly different ($P<0.01$) from zero.

also use such a capability in contexts other than for uncovering hidden prey? In the shots produced to probe the substrate for hidden prey what kind of feedback 'told' the fish which pattern to use for a given substrate type? How could the patterns be adapted so quickly to a new type of ground substrate? How can the rather small variations around a basic pattern possibly influence the effect a jet has on the various ground materials? All these questions would profit from the availability of direct force measurements. Pioneering work on how to infer force transfer in water (or air) from an analysis of the flow field (e.g. Dickinson and Götz, 1996; Drucker and Lauder, 1999; Dabiri, 2005) and many studies made possible after the advent of digital particle-image velocimetry (DPIV) suggest that this should be possible (e.g. Drucker and Lauder, 1999; Peng et al., 2007). Moreover, a range of impressive studies, performed with fish (e.g. Higham et al., 2006a,b; Day et al., 2015) and biorobotic models (e.g. Kenaley and Lauder, 2016) have successfully coupled such DPIV measurements with detailed analyses of head kinematics during specific feeding maneuvers. The basic concepts and techniques would therefore be available to work out how the small changes in the mouth opening patterns affect the force at the target region. Furthermore, these much more detailed techniques would allow us to explore which other variables (apart from mouth opening) may contribute to the formation and adjustment of the underwater jets. Such studies would also give us an idea of how much invention it takes to operate an apparatus capable of such elaborate maneuvers as suction feeding (e.g. Lauder, 1980; Day et al., 2015) so that it could produce the adaptive jets of archerfish.

Implications for the evolution of aerial shooting

The documented 2 m range (e.g. Rischawy et al., 2015) of the aerial jets of archerfish and the large amount of force transferred (40–500 mN depending on prey size; Schlegel et al., 2006) is impressive and probably unique among fish. In the few other documented examples of aerial 'shooting', the ranges appear to be restricted to a few centimeters (e.g. see Vierke, 1973, 1975). In contrast to aerial shooting, underwater jets appear to be far more common among fish (and other aquatic species). One of the most elaborate cases of underwater shooting occurs in the trigger fish *Pseudobalistes*. These fish access the soft ventral parts of sea urchins by first tipping them over with a jet of water ejected from their mouth (Fricke, 1971). Lionfish (*Pterois*) have been described to direct water jets at prey fish presumably to align them and then to take them head on (Albins and Lyons, 2012). Also, sharks and rays use water jets during foraging (e.g. Hueter et al., 2004; Kuba et al., 2010). It is therefore tempting to speculate that the more widespread capability of producing jets under water might have been the basis for the evolution of aerial jet production. But why should archerfish be using the same kinematic patterns in aerial and underwater shooting? Given that water jets in air and water face very different constraints, one could imagine that evolution would have quickly split the maneuvers used for aerial and underwater shooting. In aerial shooting, the cohesion of the jet and its focusing are important, whereas long-range underwater shots could profit from long-lived far-ranging vortex rings (see e.g. Hanke and Bleckmann, 2004). Nevertheless, our findings suggest that archerfish are not using a specialized technique for shooting under water, at least not

in the context of uncovering food. Archerfish seem rather to have settled for a strategy that simultaneously serves in both contexts. This adds an interesting aspect to the evolution of archerfish shooting. While shooting could have originally occurred in just one context (aerial or underwater) its application in the other context could then have reshaped it, which would then, in turn, affect its use in the original context and so on. In such a scenario, improvements achieved in one context could be used in the other one. For instance, it is conceivable that the temporal control of the mouth opening maneuvers – which is important to increase the effective range of the archerfish's aerial shots (Gerullis and Schuster, 2014) – could potentially have been shaped even in the absence of aerial prey because it was also useful in underwater hunting.

Supplementary information
Supplementary information available online at
http://jeb.biologists.org/lookup/doi/10.1242/jeb.146936.supplemental

References
Albins, M. A. and Lyons, P. J. (2012). Invasive red lionfish *Pterois volitans* blow directed jets of water at prey fish. *Mar. Ecol. Prog. Ser.* **448**, 1-5.
Barber, C. (2003). *Cognition and Tool Use: Engagement in Human and Animal Use of Tools.* London: CRC Press.
Beck, B. B. (1980). *Animal Tool Behaviour: the Use and Manufacture of Tools by Animals.* New York: Garland STPM Publishing.
Bentley-Condit, V. K. and Smith, E. O. (2010). Animal tool use: current definitions and an updated comprehensive catalog. *Behaviour* **147**, 185-221.
Bingham, P. M. (1999). Human uniqueness: a general theory. *Q. Rev. Biol.* **74**, 133-169.
Brown, C. (2012). Tool use in fishes. *Fish Fish.* **13**, 105-115.
Calvin, W. H. (1983). A stone's throw and its launch window: timing precision and its implications for language and hominid brains. *J. Theor. Biol.* **104**, 121-135.
Dabiri, J. O. (2005). On the estimation of swimming and flying forces from wake measurements. *J. Exp. Biol.* **208**, 3519-3532.
Day, S. W., Higham, T. E., Holzman, R. and Van Wassenbergh, S. (2015). Morphology, kinematics, and dynamics: the mechanics of suction feeding in fishes. *Integr. Comp. Biol.* **55**, 21-35.
Dickinson, M. H. and Götz, K. G. (1996). The wake dynamics and flight forces of the fruit fly *Drosophila melanogaster*. *J. Exp. Biol.* **199**, 2085-2104.
Dill, L. M. (1977). Refraction and the spitting behavior of the archerfish (Toxotes chatareus). *Behav. Ecol. Sociobiol.* **2**, 169-184.
Drucker, E. G. and Lauder, G. V. (1999). Locomotor forces on a swimming fish: three-dimensional vortex wake dynamics quantified using digital particle image velocimetry. *J. Exp. Biol.* **202**, 2393-2412.
Fricke, H. W. (1971). Fische als Feinde tropischer Seeigel. *Mar. Biol.* **9**, 328-338.
Gerullis, P. and Schuster, S. (2014). Archerfish actively control the hydrodynamics of their jets. *Curr. Biol.* **24**, 2156-2160.
Hanke, W. and Bleckmann, H. (2004). The hydrodynamic trails of *Lepomis gibbosus* (Centrarchidae), *Colomesus psittacus* (Tetraodontidae) and *Thysochromis ansorgii* (Cichlidae) investigated with scanning particle image velocimetry. *J. Exp. Biol.* **207**, 1585-1596.
Higham, T. E., Day, S. W. and Wainwright, P. C. (2006a). Multidimensional analysis of suction feeding performance in fishes: fluid speed, acceleration, strike accuracy and the ingested volume of water. *J. Exp. Biol.* **209**, 2713-2725.
Higham, T. E., Day, S. W. and Wainwright, P. C. (2006b). The pressures of suction feeding: the relation between buccal pressure and induced fluid speed in centrarchid fishes. *J. Exp. Biol.* **209**, 3281-3287.
Hueter, R. E., Mann, D. E., Maruska, K. P., Sisneros, J. A. and Demski, L. (2004). Sensory biology of elasmobranchs. In *Biology of Sharks and Their Relatives* (ed. J. C. Carrier, J. A. Musick and M. R. Heithaus), pp. 325-368. Boca Raton: CRC Press.
Hunt, G. R. (1996). Manufacture and use of hook-tools by New Caledonian Crows. *Nature* **379**, 249-251.
Hunt, G. R. and Gray, R. D. (2004). The crafting of hook tools by wild New Caledonian crows. *Proc. R. Soc. Lond. B Biol. Sci.* **271**, S88-S90.
Kenaley, C. P. and Lauder, G. V. (2016). A biorobotic model of the suction-feeding system in largemouth bass: the roles of motor program speed and hyoid kinematics. *J. Exp. Biol.* **219**, 2048-2059.
Kuba, M. J., Byrne, R. A. and Burghardt, G. M. (2010). A new method for studying problem solving and tool use in stingrays (*Potamotrygon castexi*). *Anim. Cogn.* **13**, 507-513.
Lauder, G. V. (1980). The suction feeding mechanism in sunfishes (*Lepomis*): an experimental analysis. *J. Exp. Biol.* **88**, 49-72.
Mann, J. and Patterson, E. M. (2013). Tool use by aquatic animals. *Philos. Trans. R. Soc. B Biol. Sci.* **368**, 20120424.
Marshall, C. D., Wieskotten, S., Hanke, W., Hanke, F. D., Marsh, A., Kot, B. and Dehnhardt, G. (2014). Feeding kinematics, suction, and hydraulic jetting performance of harbor seals (Phoca vitulina). *PLoS ONE* **9**, e86710.
Peng, J., Dabiri, J. O., Madden, P. G. and Lauder, G. V. (2007). Non-invasive measurement of instantaneous forces during aquatic locomotion: a case study of the bluegill sunfish pectoral fin. *J. Exp. Biol.* **210**, 685-698.
R Development Core Team (2015). *R: A Language and Environment for Statistical Computing.* Vienna, Austria: R Foundation for Statistical Computing.
Rischawy, I., Blum, M. and Schuster, S. (2015). Competition drives sophisticated hunting skills of archerfish in the wild. *Curr. Biol.* **25**, R595-R597.
Schlegel, T., Schmid, C. J. and Schuster, S. (2006). Archerfish shots are evolutionarily matched to prey adhesion. *Curr. Biol.* **16**, R836-R837.
Schoenemann, P. T. (2006). Evolution of the size and functional areas of the human brain. *Annu. Rev. Anthropol.* **35**, 379-406.
Schuster, S. (2007). Archerfish. *Curr. Biol.* **17**, R494-R495.
Seed, A. and Byrne, R. (2010). Animal tool-use. *Curr. Biol.* **20**, R1032-R1039.
Vierke, J. (1973). Das Wasserspucken der Arten der Gattung *Colisa*, *Bonn. Zool. Beitr.* **24**, 62-104.
Vierke, J. (1975). Beiträge zur Ethologie und Phylogenie der Familie Belontiidae (Anabantoidei, Pisces). *Z. Tierpsych.* **38**, 163-199.