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Pre-start timing information is used to set final linear speed in a C-start manoeuvre

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ABSTRACT

In their unique hunting behaviour, archerfish use a complex motor decision to secure their prey: based solely on how dislodged prey initially falls, they select an adapted C-start manoeuvre that turns the fish right towards the point on the water surface where their prey will later land. Furthermore, they take off at a speed that is set so as to arrive in time. We show here that the C-start manoeuvre and not subsequent tail beating is necessary and sufficient for setting this adaptive level of speed. Furthermore, the C-start pattern is adjusted to independently determine both the turning angle and the take-off speed. The selection of both aspects requires no *a priori* information and is done based on information sampled from the onset of target motion until the C-start is launched. Fin strokes can occur right after the C-start manoeuvre but are not required to fine-tune take-off speed, but rather to maintain it. By probing the way in which the fish set their take-off speed in a wide range of conditions in which distance from the later catching point and time until impact varied widely and unpredictably, we found that the C-start manoeuvre is programmed based on pre-C-start estimates of distance and time until impact. Our study hence provides the first evidence for a C-start that is fine-tuned to produce an adaptive speed level.

KEY WORDS: Decision-making, Time perception, Motor programme, C-start, Motor output space

INTRODUCTION

Archerfish are renowned for their hunting method, in which they use well-aimed shots of water to dislodge aerial prey from a substrate (e.g. Lüling, 1963; Dill, 1977; Schuster, 2007). Once a dislodged prey item starts its ballistic path towards the water surface, archerfish are able to determine the later impact point merely on the basis of a brief glimpse of the initial motion of the falling prey (e.g. Rossel et al., 2002; Wöhl and Schuster, 2007; Schlegel and Schuster, 2008; Schuster, 2012; Krupczynski and Schuster, 2013). After a very short latency in the range of 40–100 ms (e.g. Rossel et al., 2002; Schlegel and Schuster, 2008), they elicit their predictive starts, C-starts that turn the fish in the direction of the future landing point of their (still falling) prey (Wöhl and Schuster, 2007). To select the appropriate C-start based on the initial movement of prey, the fish do not need any prior information. Rather, they determine 'online' when, in which direction, at what speed and even from where dislodged prey starts to move (Schlegel and Schuster, 2008). Hence, the fish can be challenged with any random assembly of initial motion parameters and their ability to quickly select the most appropriate C-start

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manoeuvre – based on the information just gathered – can then be assayed with great precision (Schuster, 2012).

For some time, the C-start manoeuvres of fish have been viewed as reflex-like manoeuvres that are simply triggered by a threatening stimulus (for a review, see Korn and Faber, 2005). Nevertheless, C-start escapes have long been known to show considerable variability in their two phases – the initial bending into the shape of the letter C and the subsequent straightening – and it soon became evident that they are directed both with respect to the threatening stimulus and obstacles (e.g. Eaton et al., 1977; Eaton et al., 1981; Eaton et al., 2001; Eaton and Emberley, 1991; Foreman and Eaton, 1993; Preuss and Faber, 2003; Korn and Faber, 2005; Szabo et al., 2008; Sillar, 2009). However, it is difficult to fully appreciate the impressive degree of fine-tuning to which C-start manoeuvres are capable: efficient escapes need to be unpredictable – to predators and scientists alike. Unlike escape C-starts, the archerfish's predictive C-start considerably simplifies the situation: In this start the aim is known, the ecological constraints on aiming well are high and the information on which the decision is based can be fully controlled. The accuracy of the archerfish C-start decisions can be readily measured. These fish can set an appropriate turn with approximately 6 deg accuracy, i.e. the angle the minute hand of a watch covers in 1 min.

The goal of the present paper is to critically examine whether the fine-tuning of a C-start manoeuvre can extend one step further. Can the C-start manoeuvre itself – and not the immediately subsequent fin beating – fully account for take-off speed (Fig. 1)? It is already known that at the end of their C-starts, archerfish are not only turned right towards the future landing point of their prey, but also take off at a speed that is matched to the remaining distance between them and the landing point of their prey. This adjustment appears to be made so that the fish arrives at minimal travel cost slightly after their prey has landed (Wöhl and Schuster, 2006). The available evidence suggests that speed after the C-start is set based both on distance and remaining time until impact (Wöhl and Schuster, 2006; Krupczynski and Schuster, 2013). An adapted level of take-off speed – large if the distance to the landing point of the prey item is large and little time remains until impact – is attained rapidly and kept constant for at least the first 40 ms subsequent to the C-start (Wöhl and Schuster, 2006; Krupczynski and Schuster, 2013). Moreover, linear speed and acceleration during the C-start correlate with take-off speed (Wöhl and Schuster, 2007). Although these findings clearly demonstrate a role of the C-start manoeuvre for setting take-off speed, they do by no means rule out the possibility that post-start fin strokes, which can set in right after the C-start, contribute to or even play a major role in the fine-tuning of post-C-start speed. A range of post-C-start manoeuvres would be available to quickly contribute to take-off speed: among them would be suitable propulsive tail beats (Webb, 1975; Webb, 1976; Webb, 1977) or suitable body bends, whose efficiency has been beautifully described by the pioneering work of Gray (Gray, 1933a; Gray, 1933b; Gray, 1933c; Lauder and Tytell, 2004). Setting speed by post-C-start manoeuvres would have the
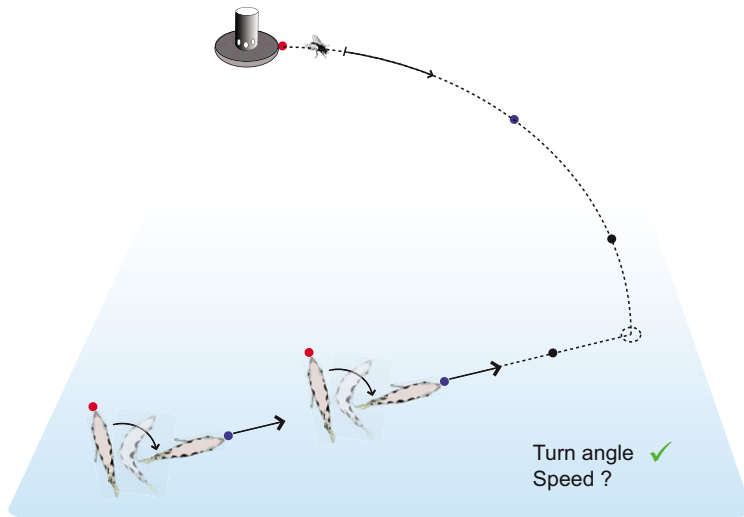
Fig. 1. Can a C-start manoeuvre set an adaptive level of speed? When initially invisible prey is catapulted from the top of a non-transparent platform (speed and direction of prey chosen at random), archerfish select an adaptive C-start based solely on information sampled during the initial movement of their falling prey. This manoeuvre turns the fish right towards the future landing point of its (still falling) prey. The question posed here is whether the C-start – and not other immediately subsequent propulsive mechanisms – fully determines take-off speed. If it does, then the archerfish's C-start manoeuvre must independently determine turning angle and linear speed. In the two cartoon fish, response timing and angle of turning would be the same, but the more distant fish would have to take-off faster. Time stamps (red, blue, black) denote successive positions of fish and prey.

added advantage that more information can be fed into the take-off speed decision than is available earlier when the C-start is selected. Furthermore, the archerfish predictive starts require speed and turning to be set independently from each other (see Fig. 1), and post C-start manoeuvres could be crucial in ensuring this independence.

In this study we demonstrate that the C-start manoeuvre is necessary and sufficient for setting take-off speed. We further demonstrate that, like turn size (Schlegel and Schuster, 2008), speed is also set solely based on the initial motion pattern of prey without any *a priori* information needed. Based on a large dataset of independent responses, we suggest a simple way in which the fish feeds timing information into the selection process of the appropriate C-start pattern.

RESULTS
Propulsion during the actual approach to the later point of catch

Our first aim was to see which non-C-start manoeuvres the fish could potentially use to set their take-off speed. We therefore examined in detail a total of 50 full approach paths from the initial

take-off until the fish's arrival at the point of prey capture. The examples provided in Fig. 2 illustrate the following general finding: on their paths towards where the falling prey is going to land, the fish generate propulsion with their caudal fin and by body bending. This movement fits very well into the so-called 'body and caudal fin transient' or 'periodic swimming' pattern (e.g. Blake, 2004) in which the stiff front end and centre of mass (CM; black circles in Fig. 2B) of the fish move on a line whereas the tip of the caudal fin (blue circles) moves approximately sinusoidally. Furthermore, our analysis shows, for all paths analysed, that the caudal peduncle (red circles) also moves sinusoidally, just as the fin tip, only phase-shifted and with reduced amplitude (linear regression between amplitudes: $r^2>0.45$, $P<0.01$ in each case; Fig. 2B). During their approach, archerfish thus propel themselves by beating their caudal fin. Fin beating can be assayed most easily and robustly by monitoring the position of the caudal peduncle. In doing so we took the angle between (1) the line through the tip of the mouth and the CM and (2) the line through the CM and the caudal peduncle. Because of its higher accuracy, this measure will subsequently be reported to explore whether non-C-start propulsion becomes
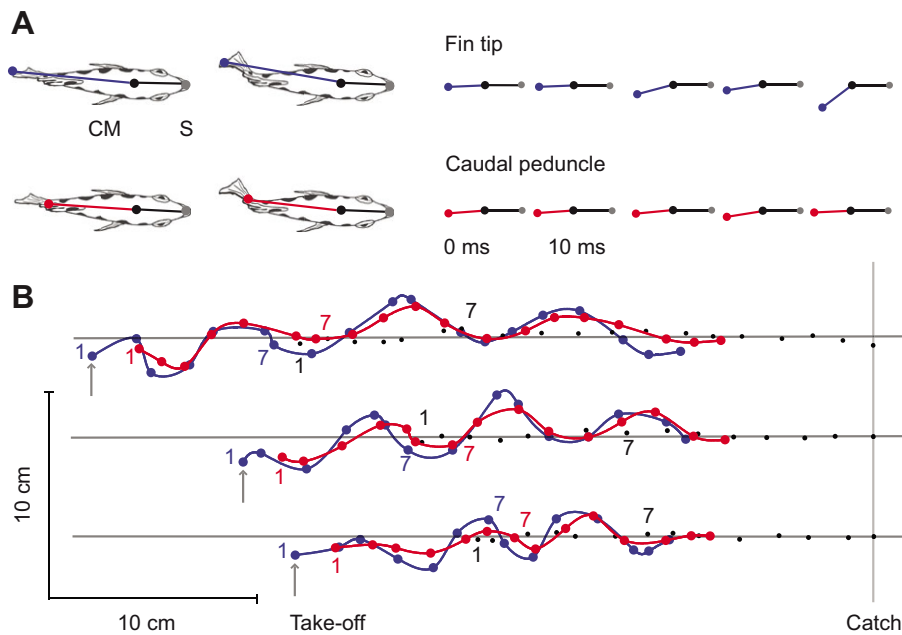

Fig. 2. Body bending and beating of caudal fin set in early after the C-start and are the major components of propulsion during the actual approach. To analyze how rapidly major en route propulsive mechanisms could act to set the archerfish's take-off speed we started by quantifying in detail onset and strength of bending and tail beating during full approach paths. (A) Successive positions of caudal fin tips (blue), caudal peduncle (red), centre of mass (CM; black) and tip of the mouth (S; grey) were derived from high-speed video and led to sequences shown on the right with angular excursions monitored every 10 ms. (B) Examples of full approach paths from take-off until prey capture illustrate the approximately linear movement of the CM (black dots) while the caudal body parts undergo large-amplitude oscillation. Successive positions of the fin tip, caudal peduncle and CM are shown. Note that bending can start rapidly and can occur immediately after the C-start. Grey arrows indicate the take-off and the vertical grey line the point of capture. Numbers in red, blue and black denote corresponding points of caudal peduncle, fin tip and CM, respectively, as seen in frames 1 and 7 of the video after take-off.
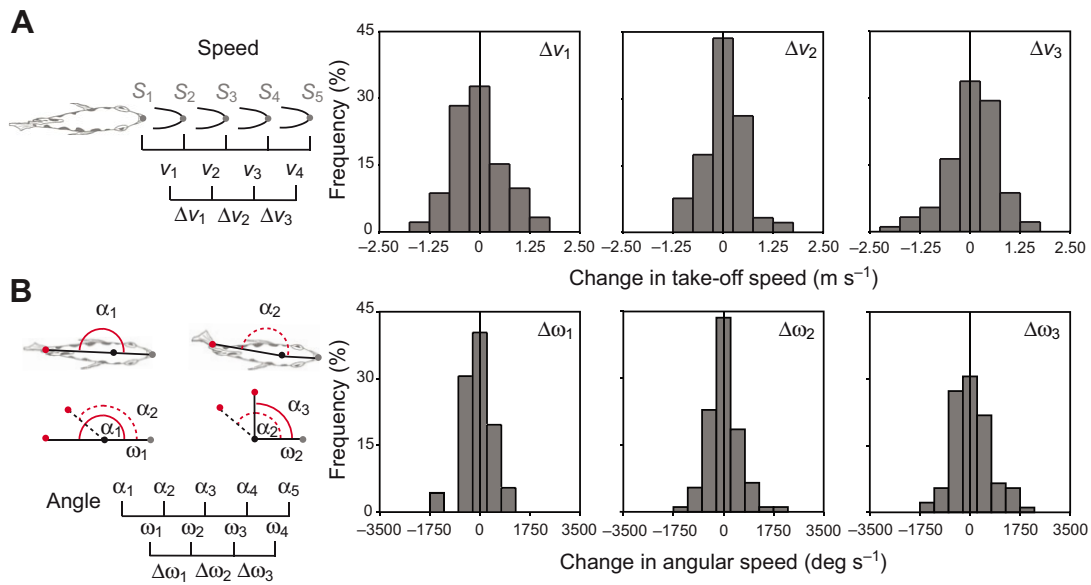
Fig. 3. No net acceleration during initial take-off. (A) Immediately after the fish has finished its C-start, four values of take-off speed (v_1–v_4) were obtained from the changes in position of the fish's snout tip (S_1–S_5) in four consecutive 10 ms intervals. The differences, Δv_1–Δv_3, are distributed normally with zero means, indicating the absence of linear acceleration. (B) Tail beating and body bending was quantified by our measure of bending. At each instance, three points [snout (grey), centre of mass (black) and caudal peduncle (red)] on the fish were measured and the angles α_1–α_5 were determined (illustrated for α_1–α_3). From the angular changes, bending (ω_1–ω_4) was determined and the changes in bending ($\Delta\omega_1$–$\Delta\omega_3$) were derived as outlined. As with linear acceleration (A), no net changes in bending speed could be detected. All changes in bending were distributed normally, with zero means. (A,B) All histograms are based on n=92 responses and normalised, so that each total frequency sums to 100%. The first centre bin in A is from −0.25 to 0.25, with a bin width of 0.50 m s^{-1}; the first centre bin in B is from −250 to 250, with a bin width of 500 deg s^{-1}. Solid lines indicate the expectation when acceleration is absent. All data are distributed normally (Shapiro–Wilk: P>0.06 in each case) with distribution around zero (one-sample t-test: all P>0.31) and there was no significant difference among the intervals [mean ± s.e.m. (A; in m s^{-1}): Δv_1: −0.05±0.07; Δv_2: +0.05±0.06; Δv_3: +0.04±0.05; one-way repeated measures ANOVA: P=0.56; (B; in deg s^{-1}): $\Delta\omega_1$: −54.19±52.53, $\Delta\omega_2$: +10.92±58.99, $\Delta\omega_3$: 43.23±67.38; Friedman repeated measures ANOVA: P=0.15].

activated early enough to contribute to take-off speed. As we will show, however, the conclusions are the same when the excursion of the tip of the caudal fin is directly measured.

No changes in speed and bending during the first 40 ms of take-off

Starting with the end of the C-start (denoted '0 ms'), we took four consecutive instances spaced at 10 ms intervals to determine whether constant take-off speed is paired with changes in post-C-start bending. This would be expected if speed was driven by post-C-start propulsive manoeuvres. In accordance with earlier findings (Wöhl and Schuster, 2006; Krupczynski and Schuster, 2013), take-off speed was attained already in the 10 ms that followed the end of the C-start and was maintained throughout the first 40 ms of take-off (Fig. 3A). As illustrated in Fig. 3A, this can be seen by analyzing, for each individual start, the differences between subsequent speed levels. For all consecutive intervals in the initial

take-off phase, the differences in speed level scattered around the zero mean (one-way repeated measures ANOVA: P=0.56). All differences are distributed normally with zero means (Shapiro-Wilk: P>0.19, one-sample t-test: P>0.40, n=92; see Table 1). Hence there is no more net acceleration 10 ms after the end of the C-start and throughout the subsequent 30 ms. Interestingly, this also held true for bending, the measure we used to quantify the major en route propulsion mechanism. Also, bending speed remained constant throughout the 40 ms phase of initial take-off (Friedman repeated measures ANOVA: P=0.59). When – again for each start – the differences were taken between two consecutive levels of bending speed ($\Delta\omega$, see Fig. 3B), no net changes could be found and changes in bending speed were normally distributed with zero means (Shapiro-Wilk: P>0.06, one-sample t-test: P>0.31; Friedman repeated measures ANOVA: P=0.15, n=92, mean ± s.e.m.: $\Delta\omega_1$=−54.19±52.53 deg s^{-1}, $\Delta\omega_2$=+10.92±58.99 deg s^{-1}, $\Delta\omega_3$=43.23±67.38 deg s^{-1}; Fig. 3B). It should also be noted that

Table 1. Take-off speed and changes in take-off speed of archerfish at various initial height levels of prey

Variable		Prey starting height		
		35 cm (n=92)	55 cm (n=94)	65 cm (n=120)
Take-off speed (m s^{-1})	v_1	1.391±0.06	1.297±0.05	1.186±0.04
	v_2	1.340±0.06	1.274±0.05	1.224±0.05
	v_3	1.387±0.05	1.342±0.05	1.249±0.04
	v_4	1.431±0.06	1.352±0.05	1.214±0.04
Change in take-off speed (m s^{-1})	Δv_1	−0.051±0.07	−0.023±0.04	0.033±0.04
	Δv_2	0.047±0.06	0.068±0.04	−0.013±0.03
	Δv_3	0.044±0.05	0.010±0.04	0.007±0.04

Data are means ± s.e.m.

an analysis using angles that were measured based on fin tips (rather than the position of the caudal peduncle) produced the same pattern of results (Shapiro–Wilk: $P>0.63$; one-sample t-test: $P>0.71$; one-way repeated measures ANOVA: $P=0.925$, $n=92$, mean ± s.e.m.:, $\Delta\omega'_1=64.92\pm173.13$ deg s^{-1}, $\Delta\omega'_2=-32.95\pm151.34$ deg s^{-1}, $\Delta\omega'_3=35.51\pm146.63$ deg s^{-1}). Taken together, these findings restrict any putative effect post-C-start manoeuvres might have on take-off speed to the very first 10 ms after the end of the C-start.

No differences in take-off with or without tail beating
It suffices thus to examine the putative role of non-C-start propulsive mechanisms during the first 10 ms after the C-start. Although there was no net change in bending ($\Delta\omega$), bending itself (ω, i.e. the change in angle α, see Fig. 3B for explanation) was nonzero and detectable already in the first 10 ms after the end of the C-start. The level of bending in this interval varied considerably – from basically absent (i.e. $\omega<0.1$ deg) to large (up to 20.2 deg) (Fig. 4C). However, this variation is not an adaptation to the speed level required in the take-off, as would be expected if bending contributed to take-off speed. The level of ω correlated neither with distance ($r^2=0.004$, $P=0.556$, $n=92$) from the later point of catch nor with 'virtual' speed (i.e. the speed needed to arrive in time) ($r^2=0.010$, $P=0.341$, $n=92$). However, the large variation in ω allowed a simple way of testing the effect of bending on take-off speed: the cases with almost no bending should be the ones with low take-off speed, whereas take-off speed should be high in cases with strong bending. To test these predictions, we considered take-off speed when bending was smaller than or equal to 3 deg ($n=31$) or larger than 3 deg ($n=61$). The two groups did not differ in take-off speed (two-sample t-test: $P=0.91$). Also, the changes in speed were not higher in the starts with larger bending (change in take-off speed: two-sample t-test: $P=0.93$). The same level of take-off speed is seen both with small (1.403 ± 0.09 m s^{-1}, mean ± s.e.m.) and large bending (1.414 ± 0.06 m s^{-1}) and also the changes in take-off speed were zero in both groups (-0.059 ± 0.11 and -0.046 ± 0.09 m s^{-1},

mean ± s.e.m.; Shapiro–Wilk: $P>0.08$; one-sample t-test: $P>0.59$). It is important to note that bending differed considerably among the two groups (no bending 1.69 ± 0.15 deg, bending 8.03 ± 0.57 deg, mean ± s.e.m.; Mann–Whitney: $P<0.001$; Fig. 4C), so that the lack of any effect on take-off speed is not simply due to the differences in bending being simply too small. Our analysis thus rules out a role of bending (i.e. the speed of change of ω) in adjusting take-off speed. It should also be noted that the same pattern of results is obtained if bending is analysed using the positions not of the caudal peduncle but of the fin tips (strong versus absent bending: two-sample t-test: $P=0.442$). In agreement with this clear result, a full typical fin beat, produced during the actual approach phase, lasts approximately 44 ms (with a range from 20 to 126 ms, $n=215$ cycles; Fig. 4D). The findings shown in Fig. 3, however, indicate that a contribution to take-off speed should have been achieved within 10 ms – just when the fin stroke has started. Furthermore, although the fin stroke has just begun, its effect on take-off speed would have to be gone after 10 ms (Fig. 3). Taken together, our data clearly show that the C-start alone determines take-off speed.

The role of timing information for setting take-off speed
When take-off speed is fully determined by the C-start manoeuvre then selecting the appropriate C-start requires additional information on timing. A previous assumption was that the fish set their take-off speed based on time and distance when their C-start is finished, i.e. when they are ready to head off (Wöhl and Schuster, 2006). However, in light of the present findings this view poses a problem: setting speed in this way would require the fish to predict how long its C-start manoeuvre will take and how far it will shift the fish's CM. This would be difficult because both quantities are not simply constant but depend on the particular C-start manoeuvre that is to be selected in the given situation, i.e. the angle (Wöhl and Schuster, 2007) and speed the C-start has to produce. So tackling this problem would require implementing a sort of iterative procedure. To address
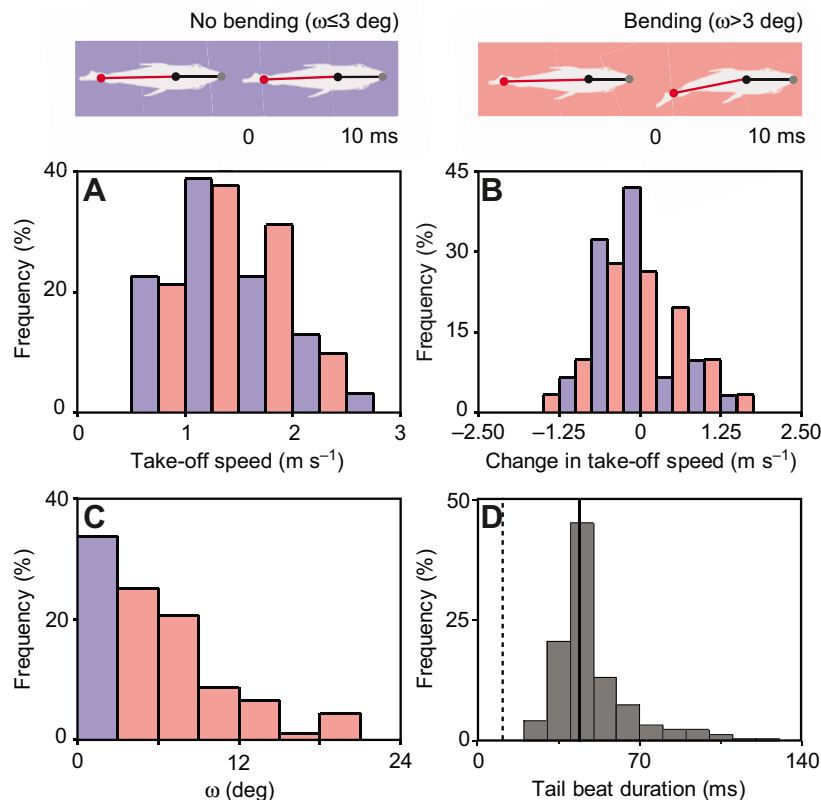

Fig. 4. Take-off speed is set by the C-start itself and not by subsequent tail beats. Tail beats can occur immediately at the end of the C-start but do not contribute to fine-tuning of take-off speed. Starts without (blue) and with strong (red) tail beating were classified according to body bending (see Figs 2, 3) (blue: tail beats ≤3 deg, $n=31$; red: >3 deg, $n=61$). Neither take-off speed (A) nor changes in take-off speed (B) during the first of 10 ms of the take-off were affected by tail beats or associated body bending (two-sample t-test: $P>0.91$). (C) The frequency of changes in bending angle during the first 10 ms of take-off (in which speed is set, see Fig. 3) (first bin from 0 to 3 deg, $n=92$), demonstrating the degree of bending in the strong bending group. (D) Distribution of tail beat duration in the subsequent approach phases that followed the initial take-off (total of $n=215$ strokes, bin width 10 ms, first bin from 20 to 30 ms). Note that typical stroke duration (solid line) is longer than the 10 ms (dashed line) during which take-off speed is already constant.
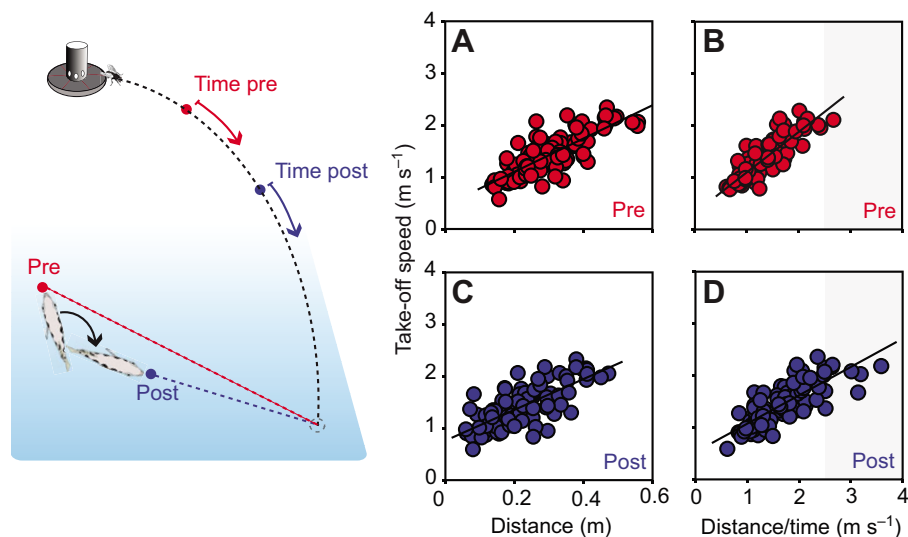
Fig. 5. Take-off speed is matched to distance and time as estimated before the C-start is launched. Initially invisible prey were blown off a platform (h=35 cm height) in a randomly chosen direction and at a randomly chosen horizontal speed. Take-off speed for a total of n=92 responses was measured and its correlation with either distance or distance per time was analysed. Distance and time were measured either before (pre-C-start; red) or after (post-C-start; blue) the C-start. All correlations were highly significant (P<0.001) but the best correlation was between take-off speed and distance per time measured pre-C-start (multivariate linear model: r^2=0.748, F=64.512, P<0.001). Grey areas in B and D show responses in which the distance/time ratio ('virtual' speed) exceeds the archerfish's actual speed limit corresponding to 15–25 body lengths s^{-1}.

this issue, we considered the capability of four models in explaining the observed levels of take-off speed in a variety of situations (Fig. 5). The models assume that the information used to set the take-off speed is based on either: distance (Fig. 5A) and distance/remaining time ('virtual' speed; Fig. 5B), both taken pre-start, or distance (Fig. 5C) and distance/remaining time (Fig. 5D) as determined at the end of the C-start. Because we analysed 92 C-starts in which the starting fish actually made the catch, we could be sure that the starts all came from highly motivated fish. Furthermore, it is important to stress that the variation in initial movement of prey (and landing points) led to considerable variation in the pre- and post-C-start measurements of both timing and distance, thus causing considerable differences in the predictions made by the four models. Because of the duration of the C-starts, a major difference existed between the average time until impact pre-C-start (219.6 ms) and post-C-start (136.6 ms). Similarly, the deviation in distance was also considerable, depending on whether pre- or post-C-start difference was used. Average pre-C-start distance was 0.30 m but average post-C-start distance was 0.23 m (Mann–Whitney: P<0.001, n=92 starts). Correspondingly, calculated levels of 'virtual' speed give significantly different predictions (average 'virtual' speed calculated with pre-C-start data: 1.39±0.05 m s^{-1}, post-C-start data: 1.66±0.06 m s^{-1}, mean ± s.e.m., n=92 in each case, Wilcoxon signed rank test: P<0.001).

The linear regression analyses shown in Fig. 5 provide a clear picture: although actual take-off speed correlated significantly with all four measures (P<0.001 with r^2=0.64, 0.74, 0.52 and 0.62 for A, B, C and D, respectively, based on the same n=92 responses), the best predictor of take-off speed is the ratio distance/remaining time taken before the C-start was actually launched (multivariate linear model: r^2=0.75, F=64,51, P<0.001). Besides being the best predictor, the resulting regression line also had a slope that was closest to unity and its intercept was closest to zero.

At this stage one could argue that the evidence for the use of pre-C-start timing and distance is artificial because it relies on the concept of 'virtual' speed and its connotation that the fish 'wants' to arrive simultaneously with its prey. In adopting this view we considered a measure in which the fish would hypothetically set a start according to how late it wants to be. Because all starts analysed actually led to a catch, the actual delays between arrival of prey and the fish were known in each individual case and the hypothetically 'correct' levels of 'virtual' speed are easy to provide. The major

result of this analysis is, simply, that the conclusion would still not change: the 'corrected' take-off speed is again best predicted by assuming that the fish uses pre-C-start information (multivariate linear model: r^2=0.83, F=103.92, P<0.001; slope of regression line between actual take-off speed and virtual speed 1.01±0.05; data not shown). Hence, all evidence available so far suggests that the fish use time and distance before their C-start to set the level of take-off speed. In particular, there is no evidence suggesting that the fish account for the fact that the C-start manoeuvre shortens the time until impact.

Testing the conclusions: increased time of falling
To test the generality of our conclusions, we challenged the fish by varying the initial height from which prey fell (h): 35, 55 or 65 cm. Because the initial positions of the responding fish are broadly distributed in the 1.3×1.3 m surface area of the tank, average distance from the point of catch is not largely affected by changing initial height. In contrast, falling time is systematically increased (by a factor of either 1.25 or 1.36), thus adding further variation in the time the fish have to cover their path towards the landing point. How would these further variations translate into the chosen levels of take-off speed? The first interesting finding is that at all height levels take-off speed was attained in the first 10 ms after C-start (Friedman repeated measures ANOVA: P=0.173 for h=35 cm based on n=92 responses; one-way repeated measures ANOVA: P>0.170 for h=55 and 65 cm based on n=94 and 120 responses, respectively; Table 1). Furthermore, at all height levels speed was again kept constant during the subsequent 40 ms (changes in take-off speed: one-way repeated measures ANOVA: P=0.558 for h=35 cm based on n=92 responses; Friedman repeated measures ANOVA: P>0.169 for h=55 and 65 cm based on n=94 and 120 responses, respectively; for further details, see Table 1). Fig. 6 shows how well 'virtual' speed pre- or post-C-start predicted the actual take-off speed levels of the starts. All differences between pre-C-start predictions and actual take-off speed were distributed around zero means (pre-C-start conditions: one-sample t-test or one-sample signed rank test: P>0.07 in each case; Fig. 6). In contrast, predicted and actual speed levels deviated systematically when post-C-start estimates of time and distance were used (post-C-start conditions: one-sample t-test or one-sample signed rank test: P<0.001 in each case; Fig. 6). Accordingly, the desired level of speed attained at the end of the C-start appears to be generally set based on pre-C-start distance and
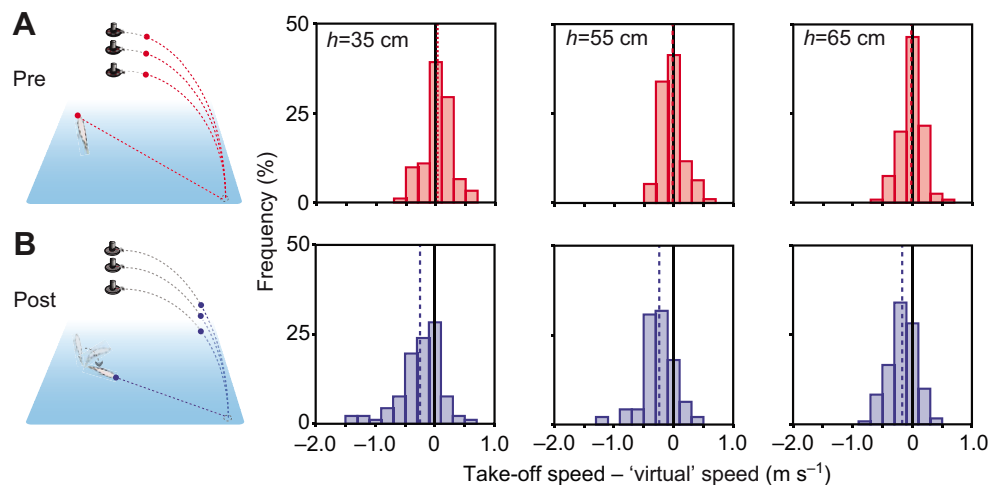
Fig. 6. When falling time is systematically increased, the fish again select an adapted take-off speed – matched to pre-C-start distance and time. To increase the variations in distance and timing further we systematically varied time of falling by randomly blowing prey off a platform at various initial height levels. Prey were initially invisible to the fish, which did not know when, from what initial height, in which direction and at what horizontal speed a prey item would be travelling. A and B evaluate each of the responses according to two interpretations: in A, the chosen speed ('virtual' speed) is calculated with pre-C-start distance and time, in B it is predicted based on post-C-start distance and time. Histograms from left to right denote the distribution of observed difference between actual and predicted speed levels. In A, all differences were symmetrically distributed around zero [one-sample t-test, one-sample signed rank test: $P>0.08$, means ± s.e.m.: $h=35$ cm: $0.03±0.02$ m s^{-1} ($n=92$ responses), $h=55$ cm: $-0.02±0.02$ m s^{-1} ($n=94$ responses), $h=65$ cm: $-0.02±0.02$ m s^{-1} ($n=120$ responses)]. In contrast, predictions based on the post-C-start constellation were systematically negative [one-sample t-test, one-sample signed rank test: $P<0.001$, means ± s.e.m.: $h=35$ cm: $-0.25±0.04$ m s^{-1}, $h=55$ cm: $-0.24±0.03$ m s^{-1}, $h=65$ cm: $-0.17±0.02$ m s^{-1}, same responses as in A]. All data are normalised, so that each total frequency sums to 100%; the first bin is from -0.01 to 0.01, with a bin width of 0.02 m s^{-1}. Solid lines show the zero mean expected by a full agreement between actual and predicted speed levels; dashed lines show the actual mean.

the time until impact that remained before the fish initiated its start. The analysis of Fig. 6 also gives an estimate of the considerable accuracy at which the fish were able to set the speed level required in the particular situation.

DISCUSSION

In this paper we show that the C-start manoeuvre of hunting archerfish not only turns the fish right towards the later landing point of its falling prey (Rossel et al., 2002; Schlegel and Schuster, 2008) but that it is also necessary and sufficient to generate the appropriate take-off speed to reach the later point of catch in time (Wöhl and Schuster, 2006). Although the major en route propulsion mechanisms can set in right at the end of the C-start, they do not contribute to fine-tuning take-off speed but rather to maintain the chosen speed level. Furthermore, under widely varying conditions the chosen levels of take-off speed were predicted by a model in which the fish selects its C-start based on estimates of the pre-C-start distance from the later point of catch and the remaining time.

The C-start completely determines take-off speed

Subsequent to its C-start the fish takes off straight, using body bending and strokes of the caudal fin as major propulsive mechanisms (see Fig. 2). However, the take-off speed not only is constant during the first 40 ms after the C-start, but it is already set in the first 10 ms. The speed levels observed in the first 10 ms after the C-start were adaptively selected in a wide range from 0.51 to 2.56 m s^{-1}, depending on the distance that the responding fish had to cover and how much time remained. Because typical fin strokes last much longer than 10 ms (Fig. 4D) but the adapted speed level is attained already in the very first 10 ms subsequent to the C-start (Fig. 3A), it is reasonable to suppose that the C-start manoeuvre itself determines speed. This is critically examined by contrasting take-off events in which the fish either showed considerable body

bending right after the C-start or not. This analysis failed to detect any effect of early post-C-start bending (and fin beating) on either the level of speed or acceleration during the first 10 ms of take-off (Fig. 4). Furthermore, these findings also extend to the full 40 ms of the take-off. Hence, take-off speed is solely determined by the C-start and later fin strokes seem to be only needed to maintain the chosen level of speed or to change it later during the actual approach. As will be detailed below, an analysis of the information used to set the adapted level of take-off speed fully supports this view: the fish simply use pre-C-start timing and distance and do not correct for the duration of the C-start manoeuvre. This causes the fish to start slightly but systematically too slow. A correction of this 'error' is made at a much later stage, when the fish are close to the point of catch and when their target has already landed (Wöhl and Schuster, 2006).

The archerfish predictive C-start can independently set speed and angle

In their predictive starts, archerfish can independently set the angle of turning and take-off speed (Wöhl and Schuster, 2006; Wöhl and Schuster, 2007; Krupczynski and Schuster, 2013). This independence is also fully evident in the C-starts analysed in the present study. That is, speed and angle varied widely but no correlation among the two variables exists ($r^2=0.019$, $P=0.191$; data from C-starts shown in Fig. 5). Because take-off speed is set completely by the C-start, this means that somehow the C-start manoeuvre must be programmed to independently set speed and angle. A simple view to explain this would seem to be much in line of Weihs' original views (Weihs, 1973). He considered stage 1 of the C-start (the bending phase) as determining the later angle of turning and stage 2 (the straightening phase) as the phase that determines speed attained at the end of the C-start. The analyses of the present and an earlier study (Wöhl and Schuster, 2007) both show that in archerfish significant correlations do indeed exist between aspects

Fig. 7. The second phase of the C-start appears to be important in determining take-off speed. Examples of predictive C-starts (imaged at 500 frames s^{-1}, every frame shown) that required a similar turn size of 43.3 deg (A) and 48.1 deg (B). In each case, in stage 1 (no shading) the archerfish had already turned the front end as needed (A: 42.0 deg; B: 42.3 deg) and in exactly the same interval of 30 ms. Examples A and B differ in the second phase, stage 2 (grey shading). Straightening occurred much slower in A, corresponding to a lower take-off speed in this C-start. Stage 2 durations of 30 ms (A) and 16 ms (B) led to straightening speeds of 1.39 deg ms^{-1} (A) and 2.64 deg ms^{-1} (B). Take-off speed was 1.42 m s^{-1} (A) and 1.98 m s^{-1} (B).

of stage 1 and bending on the one hand, and between stage 2 and take-off speed on the other hand (Fig. 7). In fact, archerfish are almost perfectly aligned to the future landing point of their (still falling) prey – right at the end of stage 1. Also, the turning angle correlates with the degree of stage 1 bending (r^2=0.85, P<0.001, based on n=50 randomly chosen responses). Moreover, the speed of straightening in stage 2 correlated well with take-off speed (r^2=0.24, P<0.001, based on the same n=50 responses) and even significantly better with 'virtual speed' (r^2=0.39, P<0.001, n=50 responses; multivariate linear model: r^2=0.39, F=14.98, P<0.001, n=50 responses, data not shown). However, it also clear that the correlations are much less tight than would be predicted based on Weihs' view. The advent of powerful imaging and computational methods has made the mechanics of force generation by C-start manoeuvres a flourishing field of study and suggests that Weihs' view is probably a major oversimplification (e.g. Tytell and Lauder, 2008). Nonetheless, our data suggest that it should not be abandoned altogether and is presently the best (to be correct: the only) model to explain how independence of speed and angle would be attained in the archerfish predictive C-start. With Weihs' views currently under heavy fire (e.g. Tytell and Lauder, 2008; Borazjani et al., 2012), it should be a rewarding challenge for studies of the mechanics of C-starts to show how independence of speed and angle can be attained without functionally separating the two phases of the C-start. Given the impressive advances in our understanding of the mechanics of the C-start manoeuvre (see Tytell and Lauder, 2008; Borazjani et al., 2012), it will be exciting to use the archerfish predictive start as a challenge of present views on how C-start kinematics generates force.

Which estimate of time is used to select the C-start?

A second line of evidence also supports the view that take-off speed is fully determined by the C-start. This emerged from an analysis of which variables would predict, for a given situation, the level of take-off speed that the fish chooses. Our experiments were run so that speed and direction of initial prey motion changed randomly from trial to trial (even initial height was variable in the experiments of Fig. 6). This produced large variations not only in distances from the later catching point and time until impact, but also between distance and time measured pre- and post-C-start. Because of this task-specific variation, we could make distinct predictions about the take-off speed the fish should select. These predictions clearly showed that speed was best accounted for by assuming that the fish

had done nothing other than using pre-C-start estimates of distance and time (Fig. 6).

A critical objection against this conclusion could be that the fish make their decisions based on other information that we had simply failed to consider. Fig. 8 presents results of analyses that we attempted to tackle this. In these, we allowed for a variety of models in which the fish selected speed based on: (1) the complete falling duration, (2) the time until impact measured pre-C-start, (3) the complete falling duration, corrected for the duration of the C-start but not for response latency, and (4) the time that actually remains after the C-start until impact (and that thus takes into account both response latency and duration of the C-start). Furthermore, in the analyses shown we also allowed for the possibility that the fish combines the times (1, 2, 3 and 4, above) with one of two measures of distance (pre- or post-C-start). Accordingly, for any given start we generate eight predictions of the level of speed the fish should choose. Summing the deviations between predicted and actual speed levels then gave us a measure of how well the models explain the archerfish's choices (Fig. 8). Among all models it was again the combination of pre-C-start distance and pre-C-start time that best predicted the chosen speed level (indicated by the lowest bin in Fig. 8B).

Previously the only model we considered was that the fish would be using the time and distance that remains once the C-start is finished (Wöhl and Schuster, 2007). Here we show that the fish use both pre-C-start distance and pre-C-start time, a finding that correlates well with the C-start itself being the sole determinant of take-off speed. Also note that our conclusion is robust and was also the best explanation of take-off speed when we relaxed the assumption that the fish started to arrive simultaneously with their prey. Using the known delays between fish and prey we could also analyse take-off speed under the assumption that the fish 'wanted' to arrive with a delay. Again, this analysis yielded the combination of pre-C-start distance and pre-C-start time as the best predictor of take-off speed. This finding also removes some unclear aspects in the previous analyses of take-off speed versus 'virtual' speed – (1) the 'offset', i.e. the actual speed at zero initial distance, was above zero, (2) the slope was not unity and (3) a large number of starts apparently occurred across a range of speed levels that the fish could not attain – and these data were excluded from an assay of the correlation of real and virtual speed. As evident from Fig. 5, for example, the new view does not require the exclusion of responses that would require speed above the limits (see grey area in Fig. 5B,D). Furthermore, slope is now closer to unity and the offset
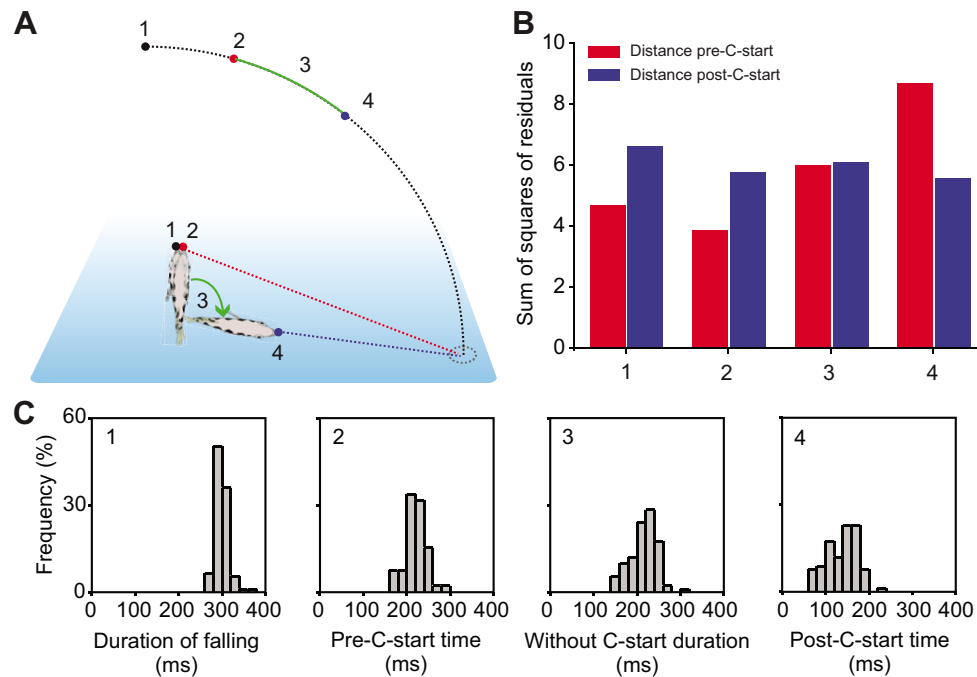
Fig. 8. Which estimate of time is used to select the C-start? (A) We evaluated which of the following four estimates of timing would best account for the take-off speed in a given situation: (1) the complete duration of falling, which depends only on prey height; (2) an estimate of the remaining time until impact, after a correction for latency but not for C-start duration (pre-C-start time); (3) the falling duration, with a correction for the time needed to complete the C-start but not for latency; or (4) the actual time, corrected for both latency and C-start duration (post-C-start time). For each of these four possibilities we assumed that the fish would combine its estimate of time with an estimate of either pre-C-start distance (red) or the actual distance from the point of capture at the end of the C-start (blue). (B) For each combination we calculated the 'virtual' speed that the fish would set in each situation and accumulated the residuals between the prediction and the actual speed. Bins show the sum of squares of residuals. Among all models tested the chosen speed levels in a given situation are best predicted (e.g. least residuals) by assuming that the fish simply use pre-C-start distance and pre-C-start time. Total of $n=92$ responses at height $h=35$ cm. (C) Histograms show the variation in the time estimate that the fish would be using in their responses according to the four models. Bin width=20 ms. For more details, see Table 2.

is close to zero [both are exactly as predicted if the actual delay (see Table 2) is included].

A major disadvantage for the fish's use of pre-C-start timing and distance would seem to be that the fish start too slow because they overestimate the time that remains until impact. However, this is what they actually do (Table 2) (Wöhl and Schuster, 2006). The adaptive value of starting slightly too slow is also evident. Suppose the fish selected a speed level that would make it arrive, on average, exactly simultaneously with its prey. With any variation in speed around this average setting or with slight variation in the falling time of prey, such a strategy would basically mean that the fish overshoots and hence probably loses its prey in 50% of the cases (Wöhl and Schuster, 2006). Another advantage of using pre-C-start

distances and time would be that eliciting a C-start could safely be suppressed if pre-C-start distance was already too large and/or pre-C-start time until capture too small.

Sensing time

So far we have emphasised the capability of the fish's C-start manoeuvre to provide adapted independent levels of speed and angle, based on information sampled in a brief interval of less than 100 ms. However, part of this is an impressive ability of the fish to estimate how much time remains until impact. This was evident from the experiments in which falling time was systematically varied (Fig. 6), but also from the large variations that existed in response latency (Fig. 8C). This implies that the fish either have a

Table 2. Performance characteristics of archerfish when prey was launched from various height levels

Variable	Prey starting height		
	35 cm (n)	55 cm (n)	65 cm (n)
Duration of falling (ms)	297.8±1.6 (92)	363.2±1.3 (94)	409.4±1.4 (120)
Time pre-C-start (ms)	219.6±2.6 (92)	290.2±2.6 (94)	323.2±2.0 (120)
Time post-C-start (ms)	136.6±3.7 (92)	185.5±5.0 (94)	226.0±4.2 (120)
Distance pre-C-start (m)	0.30±0.01 (92)	0.39±0.01 (94)	0.41±0.01 (120)
Distance post-C-start (m)	0.23±0.01 (92)	0.30±0.01 (94)	0.32±0.01 (120)
'Virtual' speed pre-C-start (m s^{-1})	1.39±0.05 (92)	1.34±0.05 (94)	1.26±0.03 (120)
'Virtual' speed post-C-start (m s^{-1})	1.66±0.06 (92)	1.56±0.06 (94)	1.40±0.04 (120)
Mean take-off speed (m s^{-1})	1.42±0.04 (92)	1.32±0.04 (94)	1.23±0.03 (120)
Time between prey landing and capture (ms)	30.3±2.56 (59)	22.4±2.74 (41)	22.0±2.40 (48)

Data are means ± s.e.m.

rather accurate sense of timing (e.g. Wittmann, 2013) or feed their C-start with information that happens to be tightly correlated with timing. Presently we know nothing about the substrates that mediate the fish's estimate of time. However, the search for the underlying mechanisms should be guided by an impressive constraint: the timing information that is fed into the C-start selection appears to be buffered against variations in temperature. Indeed, a previous study (Krupczynski and Schuster, 2013) suggests that the fish's choice of take-off is not affected by temperature because it is either temperature-compensated (much as in biological clocks) or acclimates rapidly. In contrast, without temperature compensation a given interval of time would appear longer at high temperatures (because internal rates are faster) than at cold ones, leading cold fish to select starts that are too fast and warm fish to select starts that are too slow.

Conclusions

We have shown that the C-start manoeuvres of archerfish set an adaptive level not only of turning but also of speed. They are thus remarkably complex decisions made with outstanding speed in a two-dimensional motor output space (because speed and angle are set independently). Moreover, the precision at which archerfish select angle and speed is most remarkable (see Fig. 6). C-start decisions are a superb and presently completely underrated model of decision-making and are very far from being simple triggered reflexes of primitive non-mammalian species (Wang, 2008).

MATERIALS AND METHODS
Animals

Experiments were run on a group of eight archerfish consisting of six *Toxotes chatareus* (Hamilton 1822) and two *Toxotes jaculatrix* (Pallas 1767). Working with a group is imperative because latency and performance of the archerfish predictive starts depend on competition being present (see Schlegel and Schuster, 2008; Schuster, 2010). The body lengths of the archerfish ranged from 8.2 to 13.4 cm (mean ± s.e.m.=10.6±0.2 cm) measured from the tip of the nose to the caudal peduncle. As their performance did not differ, data on all individuals were included. Fish were kept in a tank (1.3×1.3×0.6 m; length × depth × height) filled with brackish water to a height of 30 cm. Water level, temperature (27°C) and conductivity (3.5 mS cm^{-1}) were controlled every day and kept constant during the experimental period. The fish were adjusted to a 12 h:12 h light:dark photoperiod and all experiments started no earlier than 6 h after light onset.

Experimental setup

Fig. 1 illustrates the basic setup of our experiments. A dead fly (*Calliphora* killed by freezing, size 1.1±0.5 cm, mean ± s.d., fresh mass roughly 57.0 mg) was put on the upper side of a circular opaque disk (polyvinyl chloride, diameter 50 mm, thickness 14 mm) that was located centrally, a given height (35, 55 or 65 cm) above the water surface. A flexible tube (9/12 mm inner/outer diameter, 3 m long) with eight air valves (3 mm diameter each, spaced equally around the tube) 1 mm above the disc's surface and mounted centrally on the disc allowed the fly to be sent on a ballistic path by an airstream controlled by the experimenter. The direction and speed of the fly were randomly chosen from one trial to the next. This arrangement excludes the potential use of any information other than that available after the onset of prey motion (see Schlegel and Schuster, 2008). The initial height from which prey fell was kept constant during the first 560 presentations (10 days, 56 presentations per day), but subsequently height was varied to 35, 55 or 65 cm.

Recording

Responses were recorded using digital high-speed video (HotShot 1280M, NAC Image Technology, CA, USA) with a frame rate of 500 Hz and a spatial resolution of 0.18 cm per pixel. The camera was positioned vertically above the tank (height 1.7 m; lens Sigma 1:1.8 20 mm) to provide top views of the entire tank. To optimise contrast, four halogen lamps (200 W each)

illuminated the tank's transparent bottom through a diffusor plate (plexiglass, PMMA, transmission 45%) placed directly under the tank. The background above the tank – against whom the fish viewed prey motion – consisted of a white sheet sized 2.6×2.6 m, mounted 3 m above the water surface. This sheet was illuminated by two halogen lamps (500 W each) to achieve a high Michelsen contrast of 0.95 between the falling fly (reflected light 10.45 cd m^{-2}) and its homogeneously illuminated background (reflected light 397.98 cd m^{-2}).

Data analysis

The movies were analysed using ImageJ 1.42 (developed at the National Institutes of Health, USA) and custom-written software to evaluate times, distances, velocities and angles. To be informative, the responses that were evaluated had to fulfil the following set of criteria that have been described previously (e.g. Rossel et al., 2002; Wöhl and Schuster, 2007; Schlegel and Schuster, 2008): (1) to ensure that the fish's response was predictive and only driven by visual input, the fish had to be on its way before the fly touched the water surface; (2) to exclude the possibility that responses were driven or directed by the starts of other fish, only the responses of the group member that responded first were evaluated; (3) to exclude trivial cases in which the fish could simply follow the prey's motion, we required a minimum angle of 10 deg between the path selected by the responding fish and the horizontal projection of the path of the falling prey; (4) furthermore, the actual turn size, measured between the orientation of the fish before and after its C-start, had to be larger than 10 deg so that latency could be determined unequivocally; (5) moreover, the path to the future point of catch had to be free from any obstacles, e.g. other group members, because obstacles strongly influence the fish's take-off (S. Wöhl and S.S., unpublished); and (6) finally, in this study we additionally required that the first responding fish also had to be the one that actually caught the fly. This ensured two aspects that are important for the conclusions: first, that the responding fish were demonstrably motivated to make the catch, and second, that actual catching distance as well as time until catch could be measured. Taking all these six criteria into account led to a set of 92, 94 and 120 responses for the initial height levels of 35, 55 and 65 cm, respectively.

We generally analysed latency of the starts (i.e. the time between the onset of prey motion and the onset of the fish's predictive turn) and the bearing the fish had right at the end of the C-start. To determine take-off speed we measured the change in position of the fish's snout between four intervals of 10 ms beginning directly at the end of the C-start. To quantify the magnitude of propulsive tail beats we adopted the following procedure. The angle α between the fish's snout, CM and caudal peduncle was taken at the end of the C-start and every 10 ms later until 40 ms after C-start. This yielded a sequence of angular changes ω_1 to ω_4, with ω_i denoting the change in angle between the fish's bending from the (i–1)th to the ith picture. Both clockwise and anticlockwise bending was taken as positive. This is justified in the context of the present analysis because ω_i was monotonous during the initial 40 ms interval. We then considered the course of change in bending speed, i.e. $\omega_{i+1}-\omega_i$, to assess how bending changed during the initial take-off phase. Complete courses of speed during the actual approach to the later point of catch were obtained in 50 randomly chosen responses. In each of these the fish's position was determined every 10 ms until the fish made the catch. In the same responses we also determined the C-start kinematics: duration of both stages, the maximal bending at the end of stage 1 and the speed of straightening during stage 2 (e.g. Wöhl and Schuster, 2007). Tail beat duration was determined as the time of one stroke, e.g. from left to right (e.g. Videler and Wardle, 1991).

Statistical analysis

All testing was carried out using SigmaPlot (version 12.5, Systat Software, Inc. 2011) and performed two-tailed with an alpha level of P=0.05. In the first instance, normality of data was checked using Shapiro–Wilk tests and verified with Q-Q plots and histograms. Equal variance of parametric data was assessed by Levene's tests. Distributions around zero were confirmed with one-sample t-tests for normally distributed data or with one-sample signed rank tests for non-normally distributed data. To compare two or more data sets we used parametric tests such as a two-sample t-test or one-way ANOVA. To compare data obtained in the same response we used paired t-

tests (for two data sets) or one-way repeated measures ANOVA (for more than two data sets). For non-parametric (not normally distributed) data, Mann–Whitney (two data sets, unpaired), Kruskal–Wallis (more than two data sets, unpaired), Wilcoxon signed rank (two data sets, paired) or Friedman repeated measures ANOVA on ranks (more than two data sets, paired) tests were applied. Correlations were analysed with Pearson correlation (parametric data) or Spearman rank correlation (non-parametric data). Differences in slopes and intercepts were checked with a two-sample *t*-test. To determine which independent variable ('virtual speed' or distance alone) matched best with take-off speed, a multivariate linear model was used with take-off speed as the dependent variable and distance and 'virtual speed' as independent variables.

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