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RESEARCH ARTICLE

Rapid depth perception in hunting archerfish. I. The predictive C-starts use an independent estimate of target height

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ABSTRACT

Archerfish dislodge aerial prey with water jets and use their predictive C-starts to secure it. Their C-starts turn the fish to the later point of impact and set the speed so that the fish arrive just in time. The starts are adjusted on the basis of information on speed, direction, timing and horizontal start position of prey movement – sampled during less than 100 ms after prey starts falling. Presently, it is unclear whether one essential parameter, the initial height of prey, can also be determined during this brief sampling time. Shooters and probably also observing bystanders already know target height – used to hit and to shape their jets – and would simply have to feed this information into their C-start circuitry. We challenged archerfish by launching initially invisible prey objects either from the expected height level, at which the fish were looking and at which they fired shots, or from more lateral positions and a lower or higher initial height. The arrangement was designed so that an analysis of the direction and the linear speed chosen by the starting fish could determine whether the C-start information is based on the expected height or on the actual height, which can be detected only after hidden prey has begun falling. Our findings demonstrate that the fish quickly estimate initial height during the initial falling phase of prey and do not simply use the expected height level to which they were cued.

KEY WORDS: Depth vision, Visual perception, Predation, Fast-start, Decision making

INTRODUCTION

Archerfish dislodge aerial prey from twigs or leaves by a shot of water fired from their mouth (e.g. Smith, 1936; Lüling, 1963; Dill, 1977; Schuster, 2007). In natural situations, downed prey usually picks up both vertical and horizontal momentum and falls on a ballistic path towards the water surface. Only in the special case (mostly examined in the laboratory) in which prey is located on the lower side of a horizontal rigid surface is any upward motion blocked, and thus the average time to impact of the prey is determined by its initial height and the horizontal distance travelled by prey is given by the product of horizontal speed and time of flight (e.g. Rossel et al., 2002; Reinel and Schuster, 2016). To actually catch dislodged prey in the wild, hunting archerfish must outcompete other surface-feeding fish, particularly the more numerous halfbeaks (Rischawy et al., 2015). The archerfish's powerful predictive C-starts play a key role in efficiently securing downed prey under daylight conditions. Data obtained in the field in

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Thailand showed that during the day, the archerfish predictive starts help the fish secure 98% of ballistically falling prey in the presence of far more numerous competitors (Rischawy et al., 2015). In contrast, archerfish that successfully downed prey in the dark, but can no longer launch predictive C-starts, require seconds to find their prey, while their competitors catch it in less than 200 ms after impact (Rischawy et al., 2015). The archerfish predictive C-starts are kinematically equivalent to their escape C-starts (Wöhl and Schuster, 2007) but are precisely adjusted to when and where prey will impact on the water surface: they turn the fish right towards where their prey will later land (Rossel et al., 2002; Schlegel and Schuster, 2008) and release the fish at the linear speed needed to arrive just in time, when prey hits the water surface (Wöhl and Schuster, 2006; Reinel and Schuster, 2014).

To select the appropriate turn angle and take-off speed in a given situation, the underlying circuitry needs to be informed about how falling prey moves. Remarkably, this information is sampled in a brief interval (of less than 100 ms) after prey has started to fall (Schlegel and Schuster, 2008). This is surprising, because during hunting, a successful shooter controls when prey is going to fall and has detailed information about the spatial location of its prey. Initial height must be known particularly well by a successful shooter as this is essential to: (1) correct for the ballistic bending of the water jet (Dill, 1977), (2) judge target size and select the appropriate water dosage (Schuster et al., 2004; Schlegel et al., 2006), but also (3) shape lifetime and distance of focus of the water jet (Gerullis and Schuster, 2014). Moreover, it is conceivable that a shooting archerfish could estimate and perhaps even manipulate several other variables of how dislodged prey is likely to fall, such as its direction and speed. Some of this information could even be available to bystanders that watch the target and/or the shooter and might later shoot themselves. Experiments in which the fish were 'deprived' from using this potentially available prior information showed that the fish do not use prior information on speed, direction, timing and horizontal position. By hiding prey, cueing the fish to expect it from a certain position and releasing it from some other location, and decoupled from the fish's shooting behaviour, with direction and speed assigned randomly, it could be shown that the fish still selected their targets as quickly and accurately as when prior information was potentially available (Schlegel and Schuster, 2008). This remarkable finding allows easy experimental control over the decision-relevant parameters so that the fish can be challenged with combinations of the initial values of the trajectories that vary randomly from one test to the next. However, no conclusion could be reached on whether prior information on the initial height (required for successful shooters) also remained unused.

All experiments so far have shown that archerfish quickly judge the initial motion of ballistically falling prey (Rossel et al., 2002; Wöhl and Schuster, 2006; Schlegel and Schuster, 2008; Krupczynski and Schuster, 2013; Reinel and Schuster, 2016), and

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this has also been confirmed in experiments in the wild (Rischawy et al., 2015). When initial prey motion had a vertical speed component – the most likely situation in nature – the fish correctly took this added component into account (Reinel and Schuster, 2016). After the fish had initially experienced a long phase in which prey exclusively took off horizontally, they could, in principle, have learned that time of flight was only determined by the initial height from which prey fell. However, when the fish were tested with vertical speed added, they responded with equal accuracy already in the first trials, despite the substantial deviations in time of flight and the correspondingly large changes required in aim and take-off speed in the predictive C-starts (Reinel and Schuster, 2016). Hence, in this setting, the extensive experience with exclusively horizontal motion had not caused the fish to learn times of flight and to operate their C-starts on this basis.

The previous experiments have shown that all decision-relevant parameters are sampled during the short initial movement phase of prey, except for one essential parameter: the initial height from which prey is falling. Here, all previous experiments provide no conclusive evidence on when height information is obtained. Because initial height determines time of flight (generally in concert with initial vertical speed) of prey and how far it will travel, it is crucial that the C-start circuitry is informed about initial height. The very short sampling time of less than 100 ms in which all other decision-relevant variables are estimated makes it difficult to imagine that height could also be estimated within this interval. For most mechanisms of depth vision it would be a serious challenge to estimate distance in less than 100 ms. Stereopsis or accommodation would seem to be far too slow to allow estimating distance in less than 100 ms (e.g. see reviews of Collett and Harkness, 1982; Davies and Green, 1994). Furthermore, because the sampling interval is so

short, movement of the fish and of its eyes is also unlikely to provide any motion-related depth cues (see reviews of Collett and Harkness, 1982; Land, 1999) after prey motion has started. So it would seem that the C-start decisions might be based on depth information sampled earlier, before prey starts falling. It would then, however, be conveyed to the C-start circuitry in other ways as all other variables are.

With this background, it was the aim of the present study to critically examine whether fish use prior information about initial height. We used a novel setup to explore the possibility that the fish would be able to determine initial target height from a quick look at the initial falling motion of prey. To clarify this, we sent initially invisible prey objects on ballistic paths towards the water surface. In all tests, we cued the fish to look and shoot at a specific location (Fig. 1A, expected position; light grey) from which prey typically was released. Prey could, however, also be released from somewhere else and from either higher (red) or lower (blue) initial height. The spatial arrangement was chosen so that we could detect, from errors in aim (Fig. 1B) and in the final linear speed of their C-starts, whether the starts had been based on expected or actual height.

MATERIALS AND METHODS
Experimental animals
All experiments were carried out with a group of six archerfish [five *Toxotes chatareus* (Hamilton 1822) and one *Toxotes jaculatrix* (Pallas 1767)]. Mixed groups of these species are typical in the wild (Allen, 1978; Rischawy et al., 2015) and the two species launch predictive starts that do not differ, e.g. in their accuracy [e.g. error in aim, derived in $n=232$ (*T. chatareus*) and $n=209$ (*T. jaculatrix*) responses, Brown–Forsythe: $P>0.799$; C.P.R. and S.S., unpublished data]. Body size – measured between the snout and the caudal
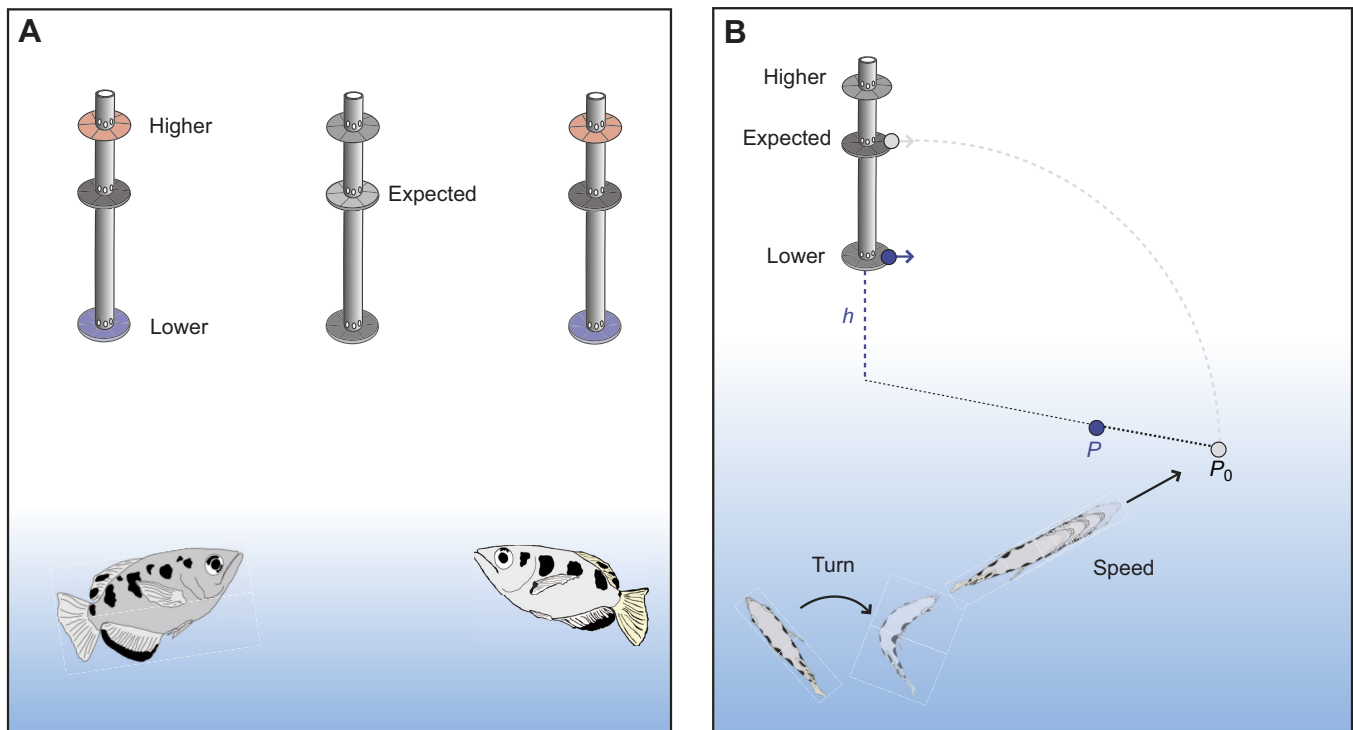

Fig. 1. Experimental design used to test whether archerfish use a prior estimate of height to predict the landing point of prey. (A) Fish are trained to expect flies being blown off from a specific platform (expected). However, in occasional tests a fly can be launched from one of the lateral platforms and at either a lower or higher initial height. (B) Bearing and speed attained immediately at the end of the predictive C-starts will disclose which height level (h) the fish were using in their prediction. Illustration of a situation in which prey fell from lower initial height, leading to actual landing point P. Using expected height, the fish would predict landing point P_0.

peduncle – ranged from 9.0 to 15.5 cm (12.0±1.5 cm, mean±s.e.m.) at the beginning and from 12.5 to 17.6 cm (13.9±1.9 cm, mean± s.e.m.) at the end of the study. Fish were kept in a large tank (1.3×1.3×0.6 m; length×depth×height) filled with brackish water and all experiments were conducted in this tank. Temperature (27°C), water level (30 cm) and conductivity (3.5 mS cm^{-1}) were kept constant during the complete experimental period. Archerfish were adjusted to a 12 h:12 h light:dark regime and all experiments began no earlier than 6 h after light onset. Dead flies (*Calliphora* sp. killed by freezing, size 1.1±0.5 cm, mean±s.d., fresh mass roughly 57 mg) were used as prey. Performance of the group members did not differ, and over an extended series of trials all individuals could respond equally well to dislodged prey. Therefore, data sampled from all individuals could be included in the analysis. It is interesting to note that in tests in which the fish were required to dislodge prey by their shots, the performance of shooters and bystanders differed neither in latency nor in accuracy [Mann–Whitney: $P>0.195$, based on $n=59$ (bystander) and $n=54$ (shooter) responses]. Of the six fish, at least three (two) fish responded with a C-start before target impact in 54% (88%) of all trials. Across trials, each of the six fish of the group could be the first to respond.

Experimental setup and procedures

All previous experiments were conducted such that the fish could have known that always only one constant height level was being tested (Fig. 2) (Rossel et al., 2002; Wöhl and Schuster, 2006; Schlegel and Schuster, 2008; Krupczynski and Schuster, 2013; Reinel and Schuster, 2014). The present setup now allowed us to intersperse tests in which initial height was unexpected. The actually used setup was chosen on the basis of experimental evidence gained with an initial setup (Fig. S1) in which initial height could not be set accurately enough, so that there was considerable variation around the average height levels. Although these variations were not appropriate for the present work, the findings obtained with the setup are instructive to later discuss the idea that the fish might have memorised time of flight. Fig. 3A shows the amended setup that was constructed on the basis of the evidence obtained with the previous setup and that was used in all experiments of the present study. On each of three vertically oriented pipes, four non-transparent circular discs (polyvinyl chloride, diameter 50 mm) were mounted above each other and connected to the supporting pipe (polyvinyl chloride, 14/16 mm inner/outer diameter, 34 cm long). This way we could position and later blow off prey from initial heights of 35 cm (blue), 55 cm (grey) or 65 cm (red) above the water surface. The platform at 45 cm height was just for decoy, and was not used to launch prey in the tests that were evaluated. On the upper side of each disc, a stream of air, pumped into the pipe via a flexible tube (9/12 mm inner/outer diameter, 3 m long), came out of each of eight valves in the pipe (3 mm diameter each, spaced equally around the pipe, 1 mm above the disc's surface), so that direction of prey motion could be varied between trials by placing prey in different positions relative to the valves. Variations in air pressure and distance from the valve were used to randomly vary the prey's initial speed. One of the pipes was above the centre of the tank; the two others were 20 cm to the left and to the right. As in earlier studies (e.g. Schlegel and Schuster, 2008), the setup was used to remove any *a priori* available information on the prey's initial speed and direction as well as information about the timing of movement onset. As shown in Fig. 3B, the discs were not transparent.

In the actual testing, height and starting positions were varied as follows. In most of the tests (2160 of 3240 starts, i.e. 66%), prey actually started from the median height level (55 cm) and from the

central platform. By mimicking a fly being placed on this platform, we always cued the fish to look at this particular platform before each test. However, actual movement did not always start from where the fish were looking (Fig. 3B). In some tests, movement started from a position randomly chosen out of four possibilities: the lower (35 cm; 17% of starts) or the higher (65 cm; also 17% of starts) position on either the left or the right side of the centre platform. Initial speed and direction were varied randomly in all trials, and independent of whether movement started from the expected or from a different height level. Not only were fish cued to the central disc, but tests were also triggered only when at least three of the six fish were looking at it. The first fish to respond with a predictive C-start was predominantly one of these three fish. It is important to note that before and between the tests, the fish would shoot at this platform but not at the others. These observations were the basis to call the height of this platform the expected height. All tests were conducted over a period of 12 weeks and comprised 60 days with 54 tests per day.

Pretests

The fish were first allowed to hunt naturally (by shooting) at the three height levels ('natural' condition; Fig. 2A, left). In each test, the fish faced only one of the three possible height levels (Fig. 2A, right; each level was kept for 10 days with 60 presentations per day). Subsequently, they were tested under conditions in which prey motion was controlled by the experimenter (the 'deprived' condition of Schlegel and Schuster, 2008; Fig. 2A, middle). This was achieved by placing prey on the upper side of a non-transparent disc (so that it was invisible to the fish) and by blowing it off from the platform at a time, direction and speed chosen randomly. These tests began with only one initial height (35 cm) and height was then increased to 55 cm and then 65 cm (each height level was kept for 10 days with 52 presentations per day).

After these experiments, an initial setup was used that allowed three platforms at three different height levels to be presented simultaneously (Fig. S1A,B). In this setup, the height of the platforms was not rigidly fixed. Rather, the heights and positions of the platforms could be rearranged between tests. Accuracy of setting the height levels was, however, insufficient to predict the hypothetical expected landing point with the required accuracy (Fig. S1D), and therefore the setup described above with 12 rigid platforms was built and used in the experiments of this study. However, the results obtained with the pre-setup showed that the accuracy of the predictive start decisions with respect to the actual landing point of prey was high – despite the variations in height and the substantial overlap in time of flight (Fig. S1C) between the different height levels (Fig. S1E–G).

Recording

C-starts were recorded using digital high-speed video (HotShot 1280M, NAC Image Technology, Simi Valley, CA, USA). Frame rate was 500 Hz (2 ms intervals between successive frames) and spatial resolution was 1.8 mm per pixel (lens Sigma 1:1.8 20 mm). The camera was mounted 1.7 m (height of lens) above the tank – its optical axis orthogonal to the water surface – to provide planar views of the complete experimental area. Four halogen spots (200 W), placed directly under the tank, illuminated the tank's transparent bottom through a diffusor plate (plexiglass PMMA, transmission 45%). Above the camera, at a height of 3 m above the water surface, we mounted a planar white sheet (2.6×2.6 m) and illuminated it with two halogen lamps (500 W each). These
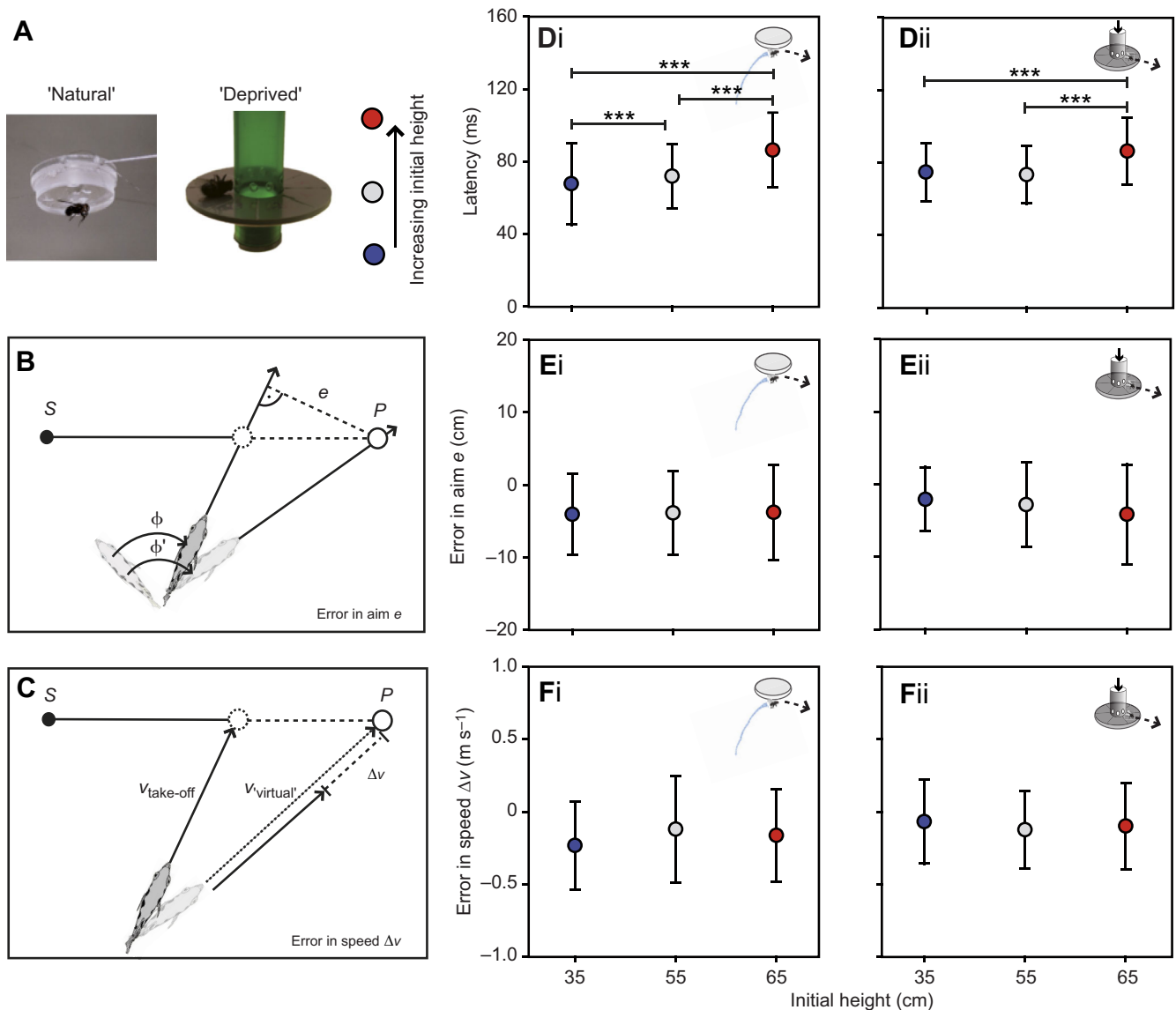
Fig. 2. Pretests to show equal errors and sufficiency of motion information in the full height range needed in the study. (A) The platforms used in the 'natural' and the 'deprived' conditions. During these tests, only one platform was present in one of the three indicated height levels (h=35 cm, blue; 55 cm, grey; 65 cm, red). (B) Illustration of how error in aim e was determined to compare responses with very different distances and orientations of responding fish. Error was taken as distance of a line along its orientation at the end of the C-start and the later landing point P. If the actual turn ϕ is made but ϕ' would be required to capture the prey, the error e as indicated would be made with respect to point P. Errors were defined as negative if the fish's actual orientation ran between the prey's starting (S) and landing point (P) (as in the given example above), otherwise the sign was positive. (C) Illustration of the error in speed Δv, the mismatch between actual take-off speed (immediately at the end of the C-start) and 'virtual' speed required to reach the impact point in time. In the 'natural' condition, neither errors in aim (Ei) nor errors in speed (Fi) differed in experiments with different initial height (Kruskal–Wallis: P>0.05; Brown–Forsythe: P>0.226). The only significant differences are in median latencies (Di; Kruskal–Wallis: P<0.001; Brown–Forsythe: P=0.146). Data are based on n=93, 134 and 46 responses for an initial height of h=35, 55 and 65 cm. Also, in the 'deprived' condition, errors in aim (Eii) and errors in speed (Fii) were not different at the different levels of initial prey height (Kruskal–Wallis: P>0.05; Brown–Forsythe: P>0.05). Median latencies also increase with increasing height (Kruskal–Wallis: P<0.001; Brown–Forsythe: P=0.394). Data are based on n=179, 265 and 245 responses for h=35, 55 and 65 cm. Distributions of errors in aim and speed did not differ among the three height levels, regardless of whether they were obtained under 'natural' or 'deprived' conditions (Brown–Forsythe: P>0.05).

were arranged to achieve – for all starting heights and positions of the responding fish – a Michelson contrast of 0.954±0.003 between falling prey (reflected light 9.31±0.55 cd m^{-2}) and its homogeneously illuminated background as seen by the responding archerfish (reflected light from background sheet 397.98± 15.49 cd m^{-2}; all data are means±s.e.m.). No significant differences could be detected among the contrast levels of flies launched from the various platforms (one-way ANOVA: P=0.453). This is required, because latency and probability to launch a C-start depend on contrast (Schlegel and Schuster, 2008).

Data analysis
All recordings were analysed frame-by-frame using ImageJ 1.42 (National Institutes of Health, Bethesda, MD, USA). As in earlier studies (e.g. Rossel et al., 2002; Reinel and Schuster, 2016), custom-written software was used to evaluate times, distances, velocities and angles of fish and falling prey and to account for different and changing horizontal and vertical distances from the camera lens. As also described in detail in earlier studies (Rossel et al., 2002; Wöhl and Schuster, 2007; Schlegel and Schuster, 2008; Krupczynski and Schuster, 2013; Reinel and Schuster, 2014, 2016), only starts were
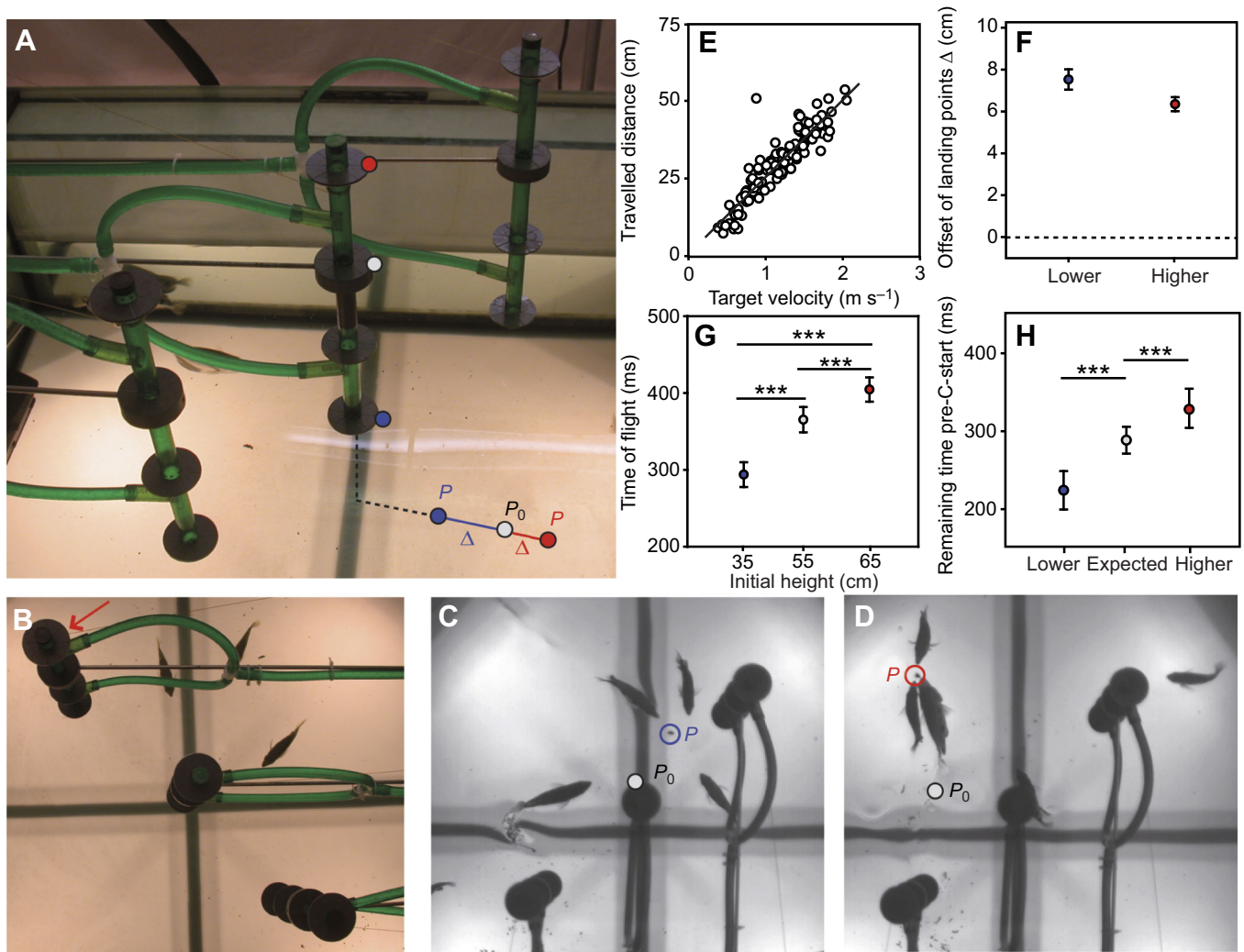
Fig. 3. Illustration of the experimental approach. (A) An initially invisible fly could be blown off from one of the horizontal discs (dark grey) placed on three vertical pipes (green). This setup allowed us to randomise the prey's initial speed, direction, position and initial height. For a given initial speed and direction, the predicted impact point depends on initial height (lower: blue; medium: grey; higher: red). Deviations (Δ) show the shift in the predicted landing points if the fish assumes prey to come from the median height (expected height; grey) but it actually comes from lower (blue) or higher (red) height. (B) The fish were cued to expect the fly's start from the disc in the middle from a median height level (55 cm). In some tests, initial height actually was lower (C: 35 cm, blue circle) or higher (D: 65 cm, red circle; also actual starting position in B indicated by the red arrow) than expected. (E) Correlation between initial velocity (target velocity) and the horizontally travelled distance of prey confirms simple ballistic motion and allowed computation of 'virtual' landing point P_0, predicted from expected height. (F) The deviations (Δ) between actual (P) and 'virtual' (P_0) impact point were large and equally detectable for the lower and higher conditions. (G) Time of flight of prey depends on initial height (Kruskal–Wallis: $P<0.001$). (H) The remaining time pre-C-start – measured between the onset of the C-start and the prey's impact – also differed (Mann–Whitney: $P<0.001$). (E–H) Data based on $n=114$, 186 or 248 tests for $h=35$ cm (blue), 55 cm (grey) or 65 cm (red). The apparent positions of the start platforms in B–D illustrate the importance of our carefully calibrated corrections for the distortions that are brought about by the different lateral and vertical distances (of fish, platforms, falling flies) from the camera lens.

included in the analysis that were informative for the questions at hand. To ensure that a C-start was only driven by visual input from the falling prey, only the first fish that responded was evaluated and its C-start had to be terminated at least 40 ms before impact of prey on the water surface. To accurately determine latency, a minimal turn angle of 10 deg was required. Finally, the path of the responding fish to the later impact point had to be free of other fish. Additionally, we excluded tests (1) in which the prey was hit by more than one shot, or (2) in which a fish fired at falling prey thereby changing its trajectory.

Aspects of prey motion

Time of flight was the number of frames (2 ms duration each) from the one in which the first displacement of the prey item could be seen and that of its impact (and/or catch), including this first and final defining frame. The initial speed of falling prey (target velocity) was derived from its horizontal distance covered within the first 20 ms after its start. Horizontal distance travelled by prey was linearly related to initial target velocity [linear regressions always $R^2>0.82$, $F>517.05$, $P<0.001$; $n=114$, 186 and 248 starts for $h=35$, 55 and 65 cm, respectively; for one example ($h=35$ cm), see Fig. 3E] so that our flies, artificially set into motion by streams of air (and not by archerfish shots), demonstrably fell ballistically with negligible frictional effects. This allowed us to compute in each test the 'virtual' landing point P_0 of prey (Figs 1 and 3). At this point the prey would hit the water surface, given its initial speed, direction and height level. Actual and 'virtual' distances travelled by prey differed significantly (Wilcoxon: $P<0.001$): the offset (Δ) between P and P_0

is 8 or 6 cm, for lower or higher actual initial height, respectively (Fig. 3C,D,F). For the design of the study it was crucial to know the accuracy at which we could determine this conceptually important point P_0. To obtain a measure of this accuracy, we evaluated trials in which prey actually had started from the expected height so that a real landing point was available that we could directly compare with the calculated 'virtual' landing point, predicted from our analysis of initial prey motion. In these trials, actual and inferred 'virtual' travelled distances did not differ significantly (Mann–Whitney: $P=0.851$, $n=186$ launches from $h=55$ cm, data not shown) and were tightly correlated (linear regression 'virtual' versus actual flight distance: $R^2=0.735$, $F=509.212$, $P<0.001$, data not shown). The distribution of the difference 'virtual'–actual was centred around zero mean (one-sample t-test: $P=0.689$, data not shown). Hence, our determination of the 'virtual' landing points introduced no systematic errors (in contrast to the earlier setup shown in Fig. S1).

Aspects of the responses

Latency was the number of frames from the first in which prey was seen displaced and the first in which the responding fish started its C-shaped bending (including these two frames). The accuracy of the fish's aim, taken immediately at the end of its C-start (when also the actual turn angle was measured), was determined as in earlier studies by considering the minimum deviation between a line that continued the fish's length axis (using the tip of mouth and centre of mass as landmarks, e.g. Reinel and Schuster, 2016) and the (actual or calculated 'virtual') landing point. As in earlier work, this error in aim was assigned a negative sign if the line ran between the starting (S) and landing point (P) of the prey (as illustrated in Fig. 2B), otherwise it was counted as positive. We additionally analysed the fish's initial take-off speed, which was attained immediately at the end of the C-starts (Fig. 2C) and compared it with the speed ('virtual' speed) that would be required to arrive simultaneously with the prey (i.e. the distance to the future landing point divided by the remaining time between onset of the C-start and prey impact). Error in speed (Δv) was defined as the difference between actual take-off speed and 'virtual' speed (Fig. 2C). As in earlier work (Reinel and Schuster, 2014), we first evaluated speed values v_1, v_2, v_3 and v_4 based on changes in the position of the fish's snout (S_1, S_2, S_3, S_4 and S_5) in subsequent intervals of 10 ms each immediately after the end of the C-start. Changes between two subsequent intervals (Δ_{ij}, i.e. v_j-v_i) were always calculated to confirm that initial speed was constant in a given C-start. Take-off speed was then calculated as the average across the four values.

Statistical analysis

All statistical tests used SigmaPlot (version 12.5, Systat Software, San Jose, CA, USA) and were performed two-tailed with an alpha level of $P=0.05$. We checked normality of data using Shapiro–Wilk tests and verified the results with Q–Q plots and histograms. For parametric data (normally distributed), equal variance was checked with Levene's test. Distributions around zero mean were confirmed with one-sample t-tests. Differences were tested with two-sample t-tests (two data sets) or one-way ANOVA (three or more data sets). Paired t-tests (two data sets) or one-way repeated-measures ANOVA (more than two data sets) were used to compare paired data sets (e.g. changes in take-off speed). If data were non-parametric, we used the following scheme: equal variances were checked with rank-based Brown–Forsythe tests and distributions around zero mean were confirmed with one-sample signed rank tests. For differences among data sets, we applied Mann–Whitney (two data sets) or Kruskal–Wallis tests (more than two data sets). For paired data sets,

we used Wilcoxon signed rank tests (two data sets) or Friedman repeated-measures ANOVA on ranks (more than two data sets). Correlations were analysed using Pearson's correlation (parametric data) and Spearman rank correlation (non-parametric data). Differences in slopes and intercepts of regression lines were checked with two-sample t-tests. Multivariate linear models were used to determine which independent variable (e.g. 'virtual' speed) best predicts a dependent variable (e.g. take-off speed). To compare two correlation coefficients, we used Fisher z-transformations.

RESULTS

Accurate C-starts require no prior information on timing, direction or speed of motion for all height levels of the study

The basic idea of the study was to create a situation in which the fish could be fooled if they informed their C-starts with the height of the platform at which they were looking. This required an arrangement in which the fish could be cued to expect prey at a certain height and in which it would be possible to launch prey from other height levels. This approach, however, has three prerequisites. First, evidence is needed that the fish are motivated to hunt and to launch precise predictive starts in the full range of initial height levels (i.e. 35 to 65 cm). Second, because the tests require prey items set into motion by the experimenter and not by an archerfish shot, it is necessary to extend to the novel height levels the earlier finding (Schlegel and Schuster, 2008) that the C-start decisions need no *a priori* information about all other cues. Third, we needed to show that the accuracy of the C-starts (both in speed and aim) was equal and sufficiently high at all initial height levels.

Once the fish were proficient in accurately dislodging prey ('natural' condition) from the three different experimental height levels (35, 55 and 65 cm), we analysed the accuracy of the aims taken immediately at the end of their predictive C-starts. We found no difference in the accuracy in aim (error in aim e) between the three initial height levels (Kruskal–Wallis: $P=0.951$; Fig. 2Ei). Also, the distribution of the errors was not statistically different (Brown–Forsythe: $P=0.669$) across the different height levels. Furthermore, at all height levels, the required turn angles (i.e. the ones that would orient the fish toward the later landing point) and the actual turn angles were equally tightly correlated (linear regressions: $R^2>0.895$, $F>375.327$, $P<0.001$; Fisher z-transformation: $P>0.056$; data not shown). In the respective datasets, turn angle always ranged from 0 to 180 deg. Hence the fish were equally capable of selecting appropriate C-starts over the full angular range at all three height levels (the distributions of actual and required turn angle did not differ at every height level: Brown–Forsythe: $P>0.133$; data not shown). Equal proficiency over the full range of height levels also held for how the fish adjusted the linear speed attained at the end of their C-starts. We confirmed, as in earlier studies (e.g. Reinel and Schuster, 2014), that take-off speed was constant for at least 40 ms after the end of the C-start and that speed changes did not occur (speed intervals: Friedman repeated-measures ANOVA, one-way repeated-measures ANOVA: $P>0.085$; speed changes: Friedman repeated-measures ANOVA, one-way repeated-measures ANOVA: $P>0.086$, one-sample t-tests: $P>0.133$, data not shown). Additionally, speed was equally distributed for all tested heights (Brown–Forsythe: $P>0.075$) and take-off speed was equally well adjusted to 'virtual' speed (linear regressions: $R^2>0.357$, $F>35.847$, $P<0.001$; Fisher z-transformation: $P>0.077$; data not shown). The resulting error in speed (deviation between take-off speed and 'virtual' speed) did not differ between the three tested height levels (Fig. 2Fi) (Kruskal–Wallis: $P=0.008$; Dunn's method: all $P>0.05$, Brown–Forsythe: $P=0.226$). Latencies

(Fig. 2Di) were also equally distributed (Brown–Forsythe: P=0.146), but, as shown in an earlier study (Reinel and Schuster, 2016), median latencies did increase with increasing target height (Kruskal–Wallis: P<0.001; Dunn's method: all P<0.05). These analyses are based on n=93, 134 and 46 tests with initial height h=35, 55 or 65 cm, respectively.

Next, we studied the performance of the fish when they did not shoot themselves but when prey motion was controlled by the experimenter (the 'deprived' condition of Schlegel and Schuster, 2008) so that the fish could not know when, in what direction and at what speed prey was going to fall. In these tests, prey was blown from one platform placed at 35, 55 or 65 cm height. Our findings confirmed that response latency as well as the accuracy of bearing and of setting speed were comparable, at all height levels, to those found when the fish had themselves dislodged prey. The errors in the accuracy of both aim (error in aim e; Fig. 2Eii) and speed (error in speed Δv; Fig. 2Fii) never differed significantly between the three experimental height levels, and also their distributions did not differ significantly (Kruskal–Wallis: P>0.05; Brown–Forsythe: P>0.05). Again, at all height levels, required and actual turn angles were equal and tightly correlated (linear regressions: R^2>0.948, F>3212.947, P<0.001; Fisher z-transformation: P>0.830, data not shown). Take-off speed was constant during the first 40 ms that followed the C-starts, the distribution of take-off speed showed no differences among tests in which height levels differed and take-off speed was adjusted to the required 'virtual' speed to arrive just in time (speed intervals: Friedman repeated-measures ANOVA, one-way repeated-measures ANOVA: P>0.05; speed changes: Friedman repeated-measures ANOVA: P>0.506; one-sample t-tests, one-sample signed rank tests: P>0.081; distribution: Brown–Forsythe: P=0.234; adjustment to 'virtual' speed: linear regressions: R^2>0.589, F>301.653, P<0.001; Fisher z-transformation: P>0.201, data not shown). Finally, although distributions were equal (Brown–Forsythe: P=0.394), median latencies increased with initial prey height also under the 'deprived' conditions (Kruskal–Wallis: P<0.001, Dunn's method: data h=65 cm, P<0.05; Fig. 2Dii). These analyses are based on n=179, 265 and 245 tests with initial height h=35, 55 or 65 cm, respectively.

Most importantly, the distribution of the errors both in aim and in setting speed did not differ significantly between the 'natural' (prey dislodged by an archerfish shot) and the 'deprived' condition (prey started by experimenter so that potential prior cues would be removed) (Brown–Forsythe: P>0.05). Moreover, at each given height level, the distribution of latency was also not statistically different between the 'natural' and the 'deprived' condition (Brown–Forsythe: P>0.05).

The C-start decisions are not based on the expected initial height

Suppose the fish were feeding into their C-start circuitry the height of the platform at which they were looking and occasionally firing shots. Instead, however, prey came from an actual height of 65 cm. Then, at the given speed and direction of prey in this trial, the landing point P would be farther out than the expected landing point P_0 (Fig. 4A), i.e. the one that would result from the standard height 55 cm being used instead of the actual height. To test which option the fish followed, we determined two types of errors: the error e made with respect to point P and the error e_0 made with respect to point P_0. In the next test (with a new speed and direction of prey), a new actual (P') and a new expected (P_0') landing point will occur and the responding fish (that will now have another orientation and distance with respect to P) will make errors e' and e_0', and so on. Whether the fish aimed at P_0 or at P can then be determined from

whether the fish minimised the error made to P or to P_0. Fig. 4B shows the averaged absolute errors $|e|$ and $|e_0|$ in our experiments: regardless of whether actual height was lower or higher than expected, the median errors $|e|$ were not significantly different (1.78 and 1.72 cm for the lower and higher initial heights, respectively; Mann–Whitney: P=0.924) and median errors $|e_0|$ were always much larger (4.63 and 4.04 cm for the lower and higher initial heights, respectively; Mann–Whitney: P<0.001). This clearly shows that the fish did not aim at the virtual points P_0 that should be inferred by simply using the 'expected' height of 55 cm.

For a closer look, we took into account the signs of the errors (Fig. 4C). Here, a negative sign indicates that the aim at the end of the C-start is to a position between the starting point S and the landing point P (which would be the case in the example shown in Fig. 2B). A positive sign indicates that the bearing is to a point shifted away from point P, in the direction of horizontal motion of prey. If the C-starts were indeed aimed at the real impact point P, based on actual height information, then the average error e_0 should be negative when initial height is lower than expected (because the actual landing point P is closer to S than P_0 is). However, when actual height is higher than expected, then the average error e_0 should be positive. Our results confirm this prediction. When actual height was lower than expected, the median error made to the virtual point P_0 was significantly negative (one-sample t-test: P<0.001; e_0=−2.49 cm; Fig. 4D). When the actual height was higher than the expected height, then there was again a systematic error with respect to P_0, but this time the error was positive (one-sample signed rank test: P<0.001; e_0=+3.32 cm; Fig. 4D). In contrast, the median errors e to the actual landing point P were significantly smaller than respective errors e_0 (Mann–Whitney: P<0.003) and did not change sign.

As a check for consistency, we also considered two measures for the impact point in those cases in which prey actually came from the expected height: the first with the impact point calculated from initial speed (and labelled P_0); the second directly measured as the real impact point (labelled P). The apparently 'obvious' result is that e and e_0 were not statistically different in these trials (Mann–Whitney: P=0.392; data not shown). The result is nonetheless important to note as it justifies our way (and accuracy) of calculating the 'virtual' point P_0 (which would not work with the setup shown in Fig. S1). In summary, we conclude that the bearing of the C-starts was such as to minimise error e but not e_0.

We next ran an analysis for the speed component of the C-start decisions. To select the proper take-off speed, archerfish need information about the distance that they have to cover and how much time they have. Both variables would differ largely, depending on whether the fish use the expected or the actual initial height [distance d to P versus distance d_0 to P_0: Wilcoxon: P<0.001; data not shown; actual remaining time t (i.e. the time from onset of the C-start till prey impact) versus expected remaining time t_0 (i.e. the time between onset of C-start and prey impact that would be expected based on an assumed height of 55 cm) Mann–Whitney: P<0.001; see Fig. 3H]. Using a multivariate model, we now checked whether the take-off speed of the C-starts matched the actual required speed (d/t; matched to the actual impact point P) or that based on expected initial height (d_0/t_0; matched to the hypothetical point P_0). This analysis showed that take-off speed correlated best with the speed predicted based on P and not P_0 (multivariate linear regression: R^2>0.546, F>66.810, P<0.001; data not shown). In summary, the analyses of both bearing and speed of the C-starts clearly demonstrate that the fish were using actual prey height and not the height of the platform at which they had been looking and firing shots.
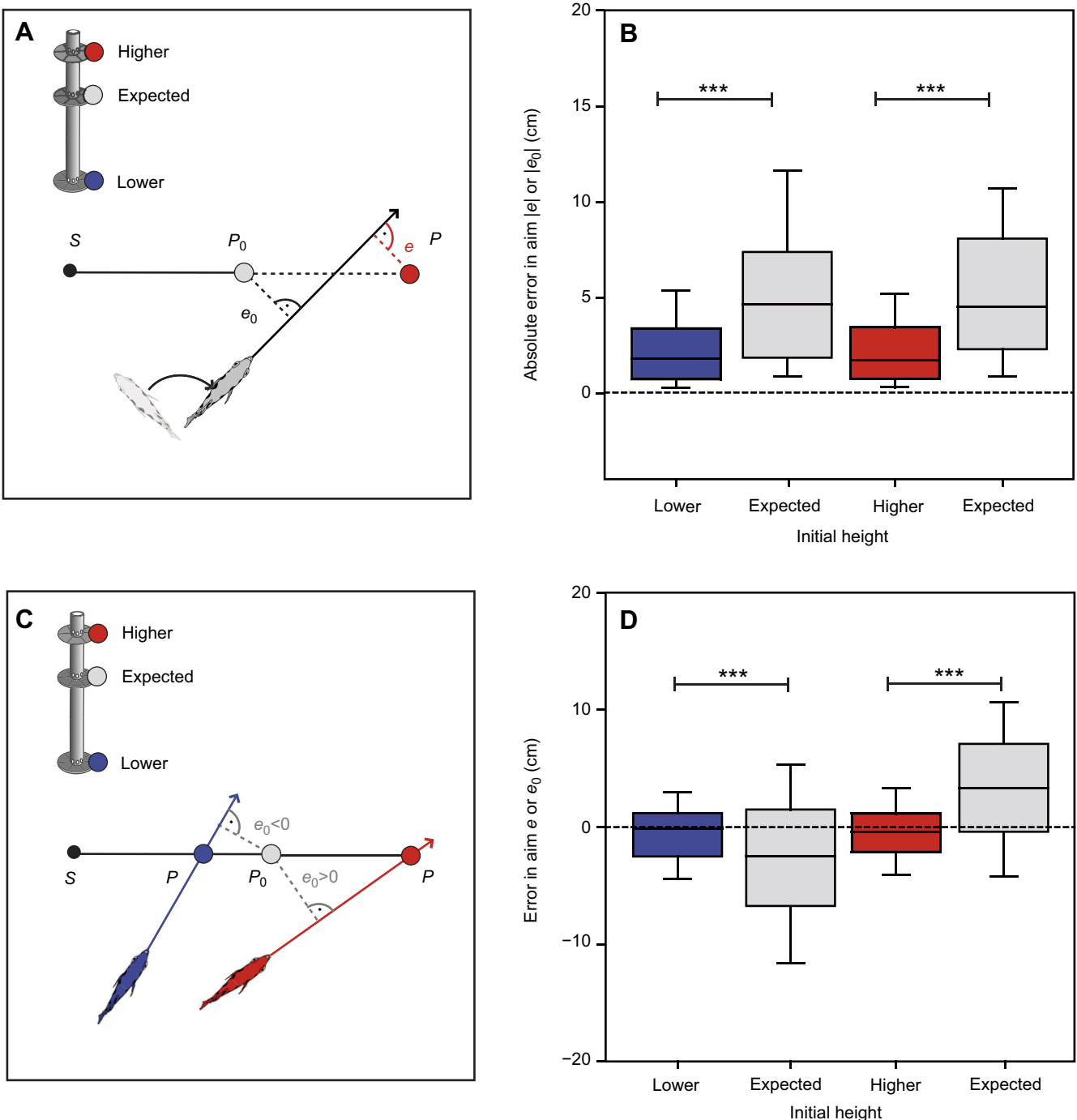
Fig. 4. Archerfish use actual and not expected initial height in setting the bearing of their C-starts. (A) Analysis to test whether archerfish minimised the error e made to the landing point P predicted from actual initial height or that predicted from expected height (P_0). The example illustrates an experiment in which prey came from a higher (red) than expected (grey) initial height and landed at point P (red). Two errors, e and e_0, denote the mismatch between the aim at the end of the C-start and either point P or point P_0. (B) The median of the absolute errors $|e|$ made with respect to the actual impact P (blue or red) did not differ when the actual initial height was lower or higher (Mann–Whitney: $P=0.924$). Moreover, the median of the absolute errors $|e|$ is significantly smaller than the median of the absolute errors $|e_0|$ (grey) made to the landing point P_0 predicted from expected height (Mann–Whitney: $P<0.001$). Additionally, the distributions of error $|e_0|$ are broadened (Brown–Forsythe: $P<0.001$). (C) Schematic to illustrate that errors e_0 should switch their sign if the C-starts did indeed aim at the true impact point. Errors e_0 should be negative for the lowest height and positive for the highest initial height. Blue and red fish indicate initial bearing after the C-start in experiments with prey falling from lowest (blue) or highest (red) initial height. (D) As predicted, errors e_0 do change sign whereas errors e did not.

Was the precision in bearing or speed different when actual and expected height differed?

The previous findings suggest that the fish did not use the expected height level. However, it could still be possible that their aim was less accurate when actual height deviated from that at which they were looking and firing shots between trials. To examine this possibility, we compared the distribution of the errors e made with respect to the actual landing point in cases where height either was as expected or was not. However, this comparison yielded no statistically significant differences (Kruskal–Wallis: $P=0.998$;

Brown–Forsythe: P=0.359; Fig. 5A–C). A closer look also revealed no differences in the relationship between the actual and the required turn angles (Fig. 5D–F), regardless of whether prey came from the expected or a lower or higher initial height. Firstly, at all height levels, turns occurred over the full angular range, and secondly, actual and required turns were equally tightly correlated with no statistically significant differences in the correlation coefficients at all height levels [Mann–Whitney: P>0.586; linear regressions: R^2=0.97 (Fig. 5D), 0.98 (Fig. 5E,F), F=3168.83 (Fig. 5D), 9669.31 (Fig. 5E), 15,430.93 (Fig. 5F), P<0.001, Fisher z-transformation: P>0.05].

Fig. 6A–C presents an analogous analysis but for the distribution of the speed errors. The difference between actual take-off speed and the speed that would be required in the given trial ('virtual' speed) was always distributed around zero mean with no significant difference between the distributions (Kruskal–Wallis: P=0.584; Brown–Forsythe: P=0.267), regardless of whether prey came from the expected or another height. A closer look at the relationship between required ('virtual') and actual take-off speed (Fig. 6D–F) also showed that responses covered comparably broad speed ranges and that the quality of the correlations did not differ between
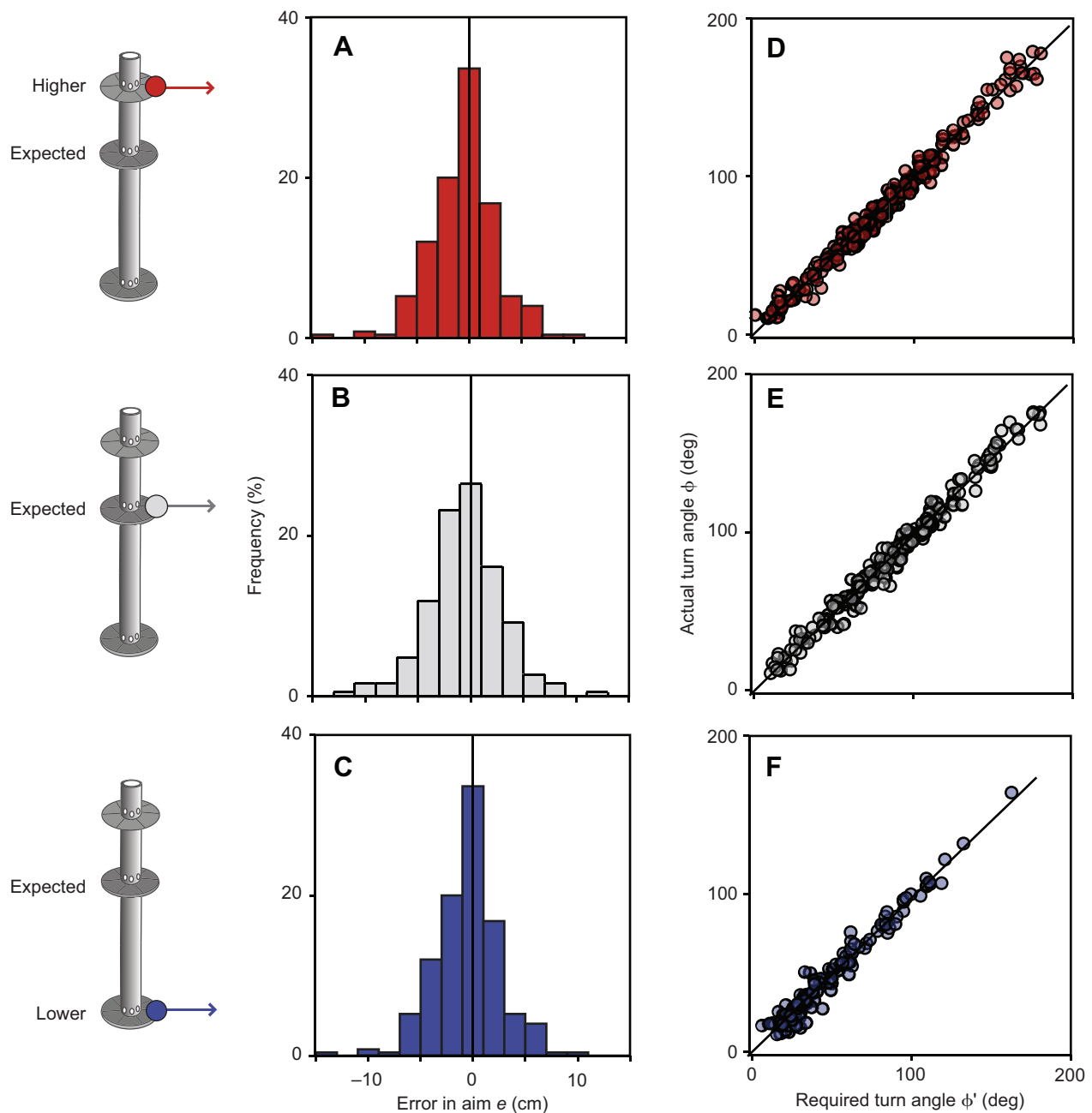

Fig. 5. Bearing is set according to actual but not expected initial target height. (A–C) The distributions of the bearing errors e made with respect to the actual impact point were not significantly different (Brown–Forsythe: P=0.359; Kruskal–Wallis: P=0.998), regardless of whether prey actually came from the expected (grey) or a lower (blue) or higher (red) initial height. Bins start at −15 cm, width is 2 cm. (D–F) shows that turns came from the complete angular range and that actual (ϕ) and required (ϕ') turn angles were always equally tightly correlated (linear regressions: R^2>0.97, F>3168.83, P<0.001; Fisher z-transformation: P>0.05). Note that bearing is determined at the end of the C-starts, typically 121 to 187 ms (depending on initial starting height) before the falling prey reaches the point of impact. Data are based on n=114, 186 and 248 responses for an initial height of h=35, 55 and 65 cm.
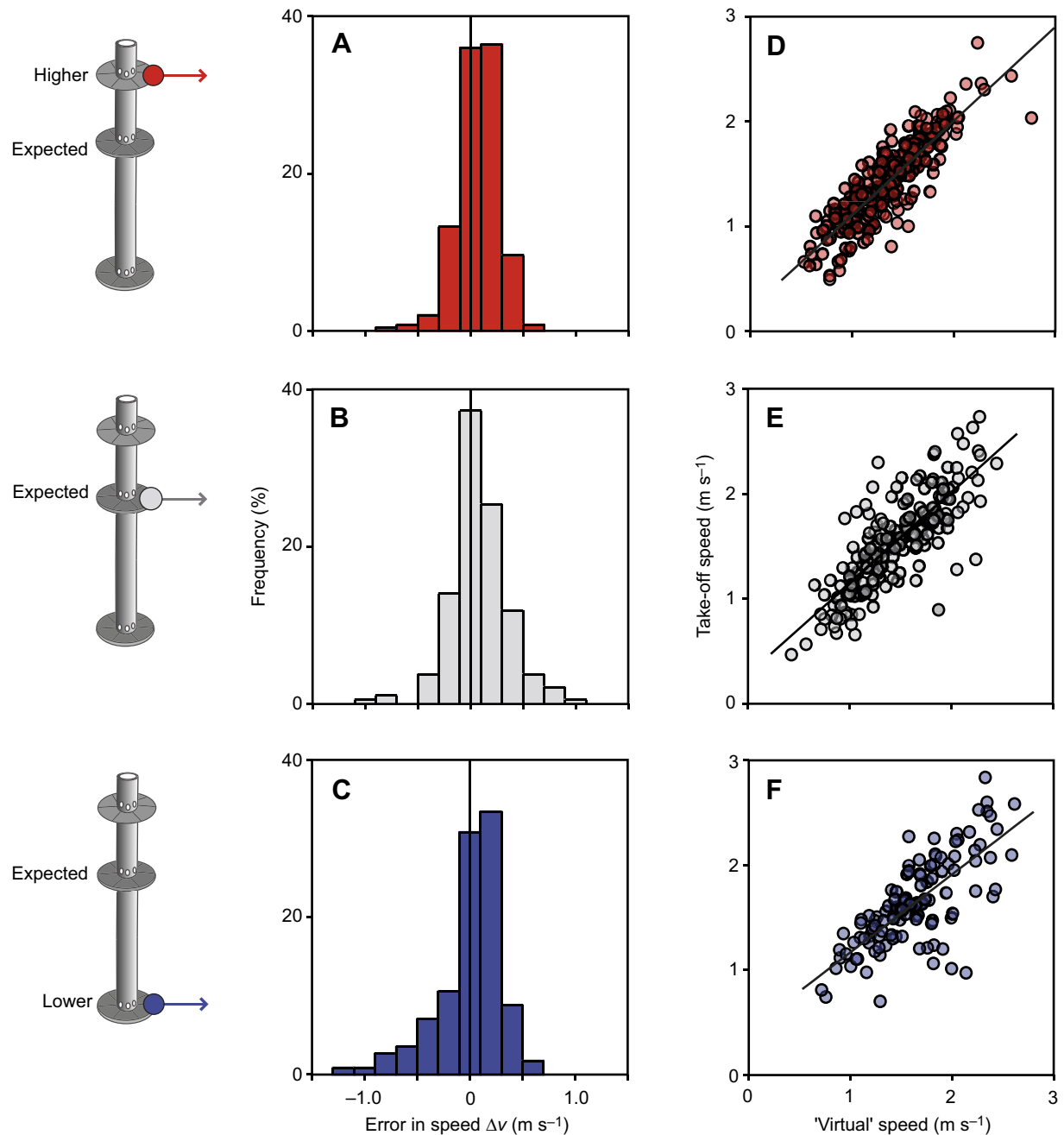
Fig. 6. Final linear speed at the end of the C-starts is set based on actual not expected initial target height. (A–C) Distributions of speed errors Δ*v* did not differ and were of similar shape (Kruskal–Wallis: *P*=0.584; Brown–Forsythe: *P*=0.267) regardless of whether initial height actually was as expected (grey) or lower (blue) or higher (red). (D–F) Plots of actual take-off speed (i.e. speed attained immediately at the end of C-start) versus required ('virtual') speed to reach the point of impact simultaneously with the prey. Correlation between actual and required speed was equally tight in all three conditions (linear regressions: R^2>0.58, F>156.52; P<0.001; Fisher *z*-transformation: *P*>0.276). Analyses are based on same C-starts as in Fig. 5.

instances where actual and expected height agreed and instances in which they differed (Fisher *z*-transformation: *P*>0.276). In summary, we found no indication that the C-starts were less accurate, either in aim or in setting the appropriate speed, when prey did not fall from the expected height level.

Latency changes only with height per se
Although errors were independent of height, latency was not (Kruskal–Wallis: *P*<0.001). This was already emphasised in Fig. 2 with experiments in which prey could fall from only one height level in any given test. Hence, the increase of latency with increasing

height needs to be taken into account in interpreting the data on latency (Fig. 7). Although median latencies were significantly smaller at each height level than in the (much earlier) pre-experiments with the group, the same trend of latency increasing with height can clearly be seen. Medium latency was significantly larger in the trials with higher than expected initial height (Mann–Whitney: *P*<0.001), but not in the trials where prey came from lower than expected height (Mann–Whitney: *P*=0.205). This was just as in the earlier trials of Fig. 2Dii ('deprived' trials; Mann–Whitney: *P*=0.247), where also no significant difference in latency was observed at the two lowest height levels. Hence, it is clear that the
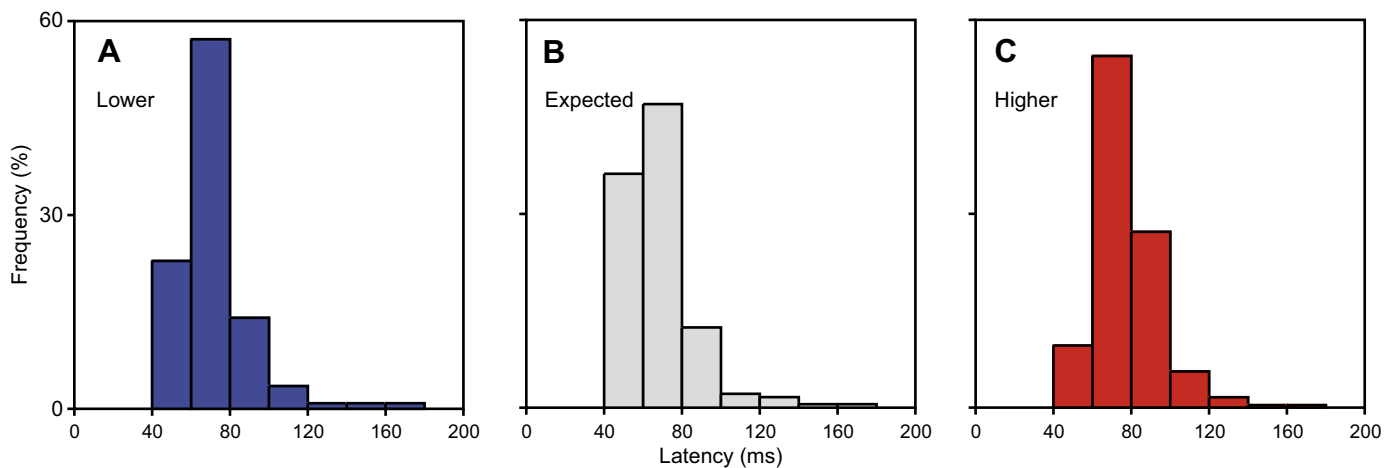
Fig. 7. Latency varies with time of flight not because of lacking information on height. Distribution of latency for the three initial target heights: actual height lower than expected (blue; h=35 cm), as expected (grey; h=55 cm) or higher than expected (h=65 cm). Median latency increased with increasing initial height (Kruskal–Wallis: P<0.001; Brown–Forsythe: P=0.034) in accord with the experiments shown in Fig. 2 (with only one target height in each test). However, minimal latencies were equal for all three height levels. Data are from the same responses as in Fig. 5.

mismatch between expected and real initial height had no effect on latency. Minimal latencies were in the range of 38–46 ms regardless of whether actual height was matching with the expectation. Moreover, regardless of whether height was lower, higher or as expected, no relationship existed between accuracy and latency (linear regression: R^2<0.04, F<7.49, P>0.007; data not shown).

Did learning occur during the extensive experimental series?
Because our experiments required a large number of trials, it is natural to think that the fish may have gained experience about which height levels could be encountered and which times of flight they might face. It is therefore important to note that there is no indication of any learning that would show itself in the quality and speed of the C-starts. Particularly noteworthy are the pretests in which the fish first encountered the target height levels they would later face so extensively. 'Training' would have started at h=35 cm, then height was switched to 55 cm and then finally to 65 cm. However, after each switch there was no indication of an effect on latency, error in aim or error in speed, and at each height level there was no significant correlation between any of these variables with trial number ('natural': R^2<0.025, F<3.133, P>0.079; 'deprived': R^2<0.122, F<3.314, P>0.058; data not shown). Even in the first tests, in which different height levels occurred at the same time (conducted with the setup shown in Fig. S1), neither latency, error in aim nor error in speed changed with extended experience (R^2<0.160, F<3.919, P>0.050; data not shown) and the same continued during the actual tests discussed here (R^2<0.026, F<3.022, P>0.085; data not shown). Thus, if the fish had learned anything about the height levels, this could not be used to improve any of the aspects of their predictive C-starts that we analyse here.

DISCUSSION
Our findings show that all variables that are relevant for the C-start decisions are determined after prey has started to fall. This also includes initial height, the only variable for which direct evidence so far has been missing. Presently, it is not known how information on height is gained so quickly and why the fish do not simply use the height of the pre-assigned spot to which they are looking and firing shots. Our findings add height to the list of cues

that archerfish determine 'online' in the brief interval after onset of prey motion. This finishes a series of papers (Schlegel and Schuster, 2008; Reinel and Schuster, 2014, 2016) that suggest that motion cues sampled in a very brief decision time of less than 100 ms are necessary and sufficient to drive the predictive C-starts of hunting archerfish.

Why is shooting-related information on height not used?
The most intriguing aspect of our finding is why the C-starts are independent of the height of the platform to which the fish are looking, at which they fired shots and from which they typically would receive prey. In a natural situation, all archerfish that dislodge prey need information on its height in order to hit the prey despite the effect of gravity on the jet (e.g. Dill, 1977), to estimate prey size (Schuster et al., 2004), to set the amount of water to be fired (Schlegel et al., 2006) and to adjust their jets (Gerullis and Schuster, 2014). Furthermore, bystanders can probably also judge the height of prey (Schuster et al., 2006). In the experiments of the present study, the archerfish were not controlling target motion with their shots. Rather, prey was blown off from any of the platforms at a timing and with a direction and speed that the fish could not know before. However, the fish regularly received food from one particular platform at one height and often fired at this but not at the other platforms. They also had exclusively received food from that platform many months before experiments started and during all feeding that occurred outside the experimental sessions. Most importantly, they could easily be cued to assemble below this platform, to be oriented toward it and to fire targeted shots at it. In fact, as noted in the Materials and methods, tests were launched only when at least three fish were looking at the cued platform. Although we expected that purely lateral displacements should not affect the C-starts (Schlegel and Schuster, 2008), we did expect at least some bias towards the expected landing point when prey came from a higher or lower initial height.

Our findings suggest that the information that guides where the fish are looking and firing shots is dissociated from the information that guides their C-starts. Such patterns are, however, not uncommon in ethology, and the renowned egg-rolling behaviour of oystercatchers is one example. Although these birds clearly can discriminate object sizes, the circuitry that drives egg-retrieval into

the nest apparently has no access to fine-grained size information, so that the birds desperately try to roll eggs into their nest that are far too large for the bird to sit on (e.g. Tinbergen, 1951). Such examples may point to the fact that the connections between brain centres that do or do not have access to certain information are subject to different evolutionary pressures. In the case of the oystercatcher, for instance, the occurrence of over-sized eggs outside the nest of a breeding bird was so rare that the circuits that drive egg-rolling behaviour need not have access to size information that would be available elsewhere in the brain. With respect to the archerfish predictive C-starts, the situation would seem to be very different. Here, we would expect strong evolutionary pressures to make height information that is available in the shooting-relevant brain areas also accessible to the circuitry that makes the C-start decisions. This would seem particularly important given the severe lack of time to determine height with sufficient accuracy in the very brief interval in which the decision must be made. At this stage, it is a mystery why archerfish do not 'simply' feed the information into the decision-making circuitry. In part, the answer might be that the construction of the circuitry does not allow simple connections to the shooting-related brain areas. It could also be that the major driving force was that bystander fish needed to add independent information into the C-start circuitry to be able to compete with the actual shooter and to achieve equally precise performance (see Materials and methods). Another explanation could be that archerfish use particularly clever cues that allow them to extract C-start relevant spatial information so quickly that no need has arisen to use the height information used for shooting.

The extent to which memory for the alternative platforms could have helped the fish to respond to unexpected height levels

In principle, a highly attractive alternative view to explain our results would be that the fish have learned time of flight or the height levels during the extensive experience they had gained during the long series of pretests. They would then still have to realise that prey took off from another platform than the one they were looking at and then not use the height to which they were cued. However, the problem of gaining a new estimate of height would be reduced to recognising from which of the rigid platforms prey came. With extensive experience, the fish could have stored the height levels of the active platforms, and the problem of gauging height would then be shifted to that of recognising the platforms. The stored height level of this platform would then be fed into the circuitry that selects the C-starts. Although this is an elegant hypothesis (and could be an effective method for territorial species with a small number of rigid landmarks), it would not work for archerfish in the wild and would also not be compatible with our data. Let us begin with the experimental facts. First, we noted that none of the hallmark variables used to assay the quality of the predictive C-starts depended on the availability of extensive experience. During all pretests, during the many tests with the insufficient setup with changing and variable height levels as well as positions and, finally, during the experiments presented here, the starts were equally accurate right after introduction of a new height or a change in paradigm (three or more heights presented simultaneously). Second, learning time of flight would be meaningless in a natural situation, where a vertical speed component will usually be present. This component will vary from shot to shot but will largely affect time of flight. The data assembled with the pre-setup of Fig. S1, which allowed insufficient control over prey height, show directly that overlap between times of flight (Fig. S1C) can occur between different height levels without having a detectable

effect on latency or on the errors in aim and speed (Fig. S1H–J). Third, learning of height levels would also have been difficult in the pre-setup (Fig. S1) because the height levels could only be set roughly and because the arrangement was changed from test to test. Nonetheless, the pattern of results was just as in the main experiments (Figs 5–7). This held even when we increased the number of height levels and positions (Fig. S1K–M). However, the major difficulty with this view is that it is bound to fail under the natural conditions in the archerfish's mangrove habitats. Suppose the fish knew the height levels of a set of strategic spots in the criss-cross of twigs and leaves in an aerial hunting area. Spotting that something falls down in the vicinity of one of these strategic spots would then feed the stored height level into the C-start circuitry and, in principle, solve the difficult problem of gauging height. Unfortunately, the height levels are not fixed because the water levels fluctuate rapidly and, most importantly, so irregularly that no simple corrections can be employed (in the sense of 'add 0.5 m to the stored values after 16.00'; S.S., unpublished). Briefly, this complexity arises because of the interaction of tidal water movement with the irregular inflow of freshwater from nearby rivers. This irregularity also prevents the fish from simply staying in a certain hunting area as it is often unpredictable at which time, if at all, that area will be accessible and thus may be why they do not need stored information of landmarks to simplify the visual search for stationary prey objects (Rischawy and Schuster, 2013). It does seem that their environment forced the fish to go the hard way.

Conclusions

With this study, we conclude a series of papers arguing that motion cues are necessary and sufficient for the C-start decisions of hunting archerfish. The present findings show that this also includes the judgment of initial height from which prey is falling. Any ecological reason why the fish do not simply use the height from which they expect prey to fall is presently unknown, and we suggest that it may be linked either to the difficulty of feeding this information into the unknown circuitry that selects the C-starts or to the occurrence of a rapid way of gaining distance information. The latter possibility will be examined in the companion paper (Reinel and Schuster, 2018).

Author contributions
Conceptualization: C.P.R., S.S.; Methodology: C.P.R.; Software: C.P.R.; Validation: C.P.R., S.S.; Investigation: C.P.R.; Data curation: C.P.R., S.S.; Writing - original draft: C.P.R., S.S.; Visualization: C.P.R.

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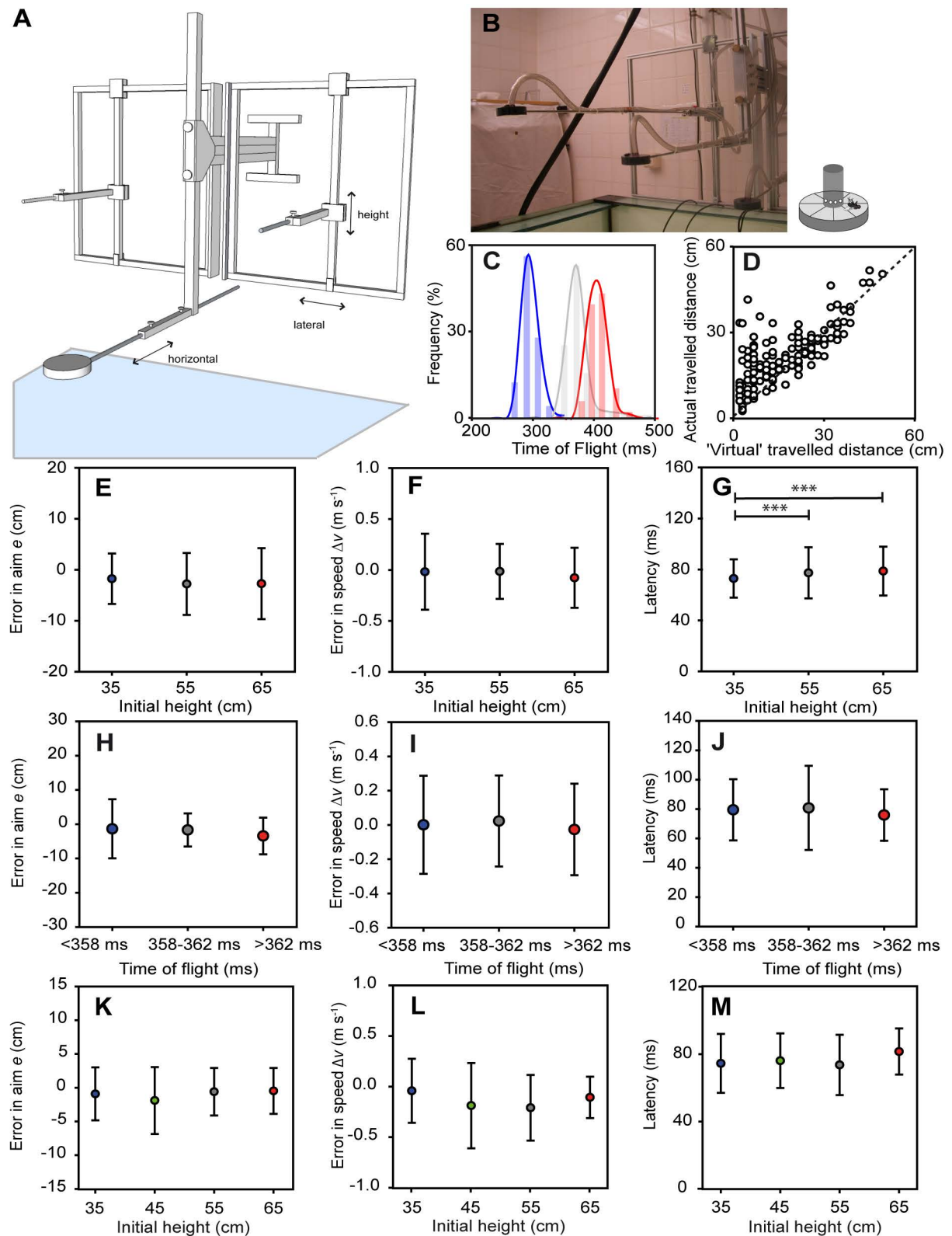
Fig. S1: Setup used initially to simultaneously present three platforms at different height levels.

(A) Arrangement to move each of three non-transparent platforms (only one shown) to the desired position. Each platform (polyvinyl chloride disks, diameter 50 mm, thickness 14 mm) was connected to a steel rod (length 80

cm) and its intended height above the water surface was either 35, 55 or 65 cm. Frame construction was rigidly fixed to wall of lab. (B) Side view of actual arrangement. Note flexible tubes (9/12 mm inner/outer diameter, 3 m long), each with eight air walves (3 mm diameter each, spaced equally around the tube and 1 mm above disk's surface; inset in B on the right) connected to each of the three platforms so that an airstream could send prey, located on the upper side of the platform, on a ballistic path. Control over the initial starting height of prey was insufficient, resulting in overlapping time of flight (C) and insufficient correlation between the calculated 'virtual' and the actual travelled distance when prey was dislodged from 55 cm initial height (linear regression: R^2=0.534, F=156.118, P<0.001). Most importantly, actual and calculated 'virtual' impact points differed significantly (Mann-Whitney: P<0.001, n=138) so that we could not determine a 'virtual' landing point as required in the analysis. The setup thus needed to be improved. However, an analysis of how accurate the starts made by the fish are suggests that the lack of precision in precisely setting the height levels and time of flight did not affect accuracy and latency: Neither errors in aim (E) nor errors in speed (F) made with respect to the actual later landing point differed significantly among height levels (Kruskal-Wallis, Dunn: P>0.05). Latency (G) increased – as in Figs. 2 and 7 – with an increasing starting height (Kruskal-Wallis: P<0.001). Analyses are based on n=294, 144 and 293 responses for h=35, 55, 65 cm and were carried out as in Figs. 5-7. (H-J) show an analysis of error in aim (H), error in speed (I) and latency (J) for starts made when prey took off from the expected platform in 55 cm height but in which time of flight overlapped with values found in the higher (i.e. > 362 ms; n=95) or lower (i.e. < 358 ms; n=28) height or did not overlap (i.e. 358-362 ms; n=21). All differences are not significant (Kruskal-Wallis: P>0.187).   (K-M) In additional series of experiments we increased the number of positions and possible height levels. Horizontal displacement of the lateral disks could be either 15 or 20 cm and we added an additional height of 45 cm. Analysis as in E-G. Again, error in aim (K), error in speed (L) and latency (M) did not differ (Kruskal-Wallis: P>0.164, based on n=20, 43, 45, 23 responses for h=35, 45, 55 and 65 cm). Data show means and SDs.