

RESEARCH ARTICLE

Rapid depth perception in hunting archerfish. II. An analysis of potential cues

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ABSTRACT

Based on the initial movement of falling prey, hunting archerfish select a C-start that turns them right to where their prey is going to land and lends the speed to arrive simultaneously with prey. Our companion study suggested that the information sampled in less than 100 ms also includes the initial height of falling prey. Here, we examine which cues the fish might be using to gauge height so quickly. First, we show that binocular cues are not required: C-starts that either could or could not have used binocular information were equally fast and precise. Next, we explored whether the fish were using simplifying assumptions about the absolute size of their prey or its distance from a structured background. However, experiments with unexpected changes from the standard conditions failed to cause any errors. We then tested the hypothesis that the fish might infer depth from accommodation or from cues related to blurring in the image of their falling prey. However, the fish also determined the height of 'fake flies' correctly, even though their image could never be focused and their combined size and degree of blurring should have misled the fish. Our findings are not compatible with the view that archerfish use a flexible combination of cues. They also do not support the view that height is gauged relative to structures in the vicinity of starting prey. We suggest that these fish use an elaborate analysis of looming to rapidly gauge initial height.

KEY WORDS: Visual depth perception, Binocular vision, Motion parallax, Accommodation, Distance vision

INTRODUCTION

Archerfish use jets of water to dislodge aerial prey from twigs or leaves (e.g. Smith, 1936; Lüling, 1963; Dill, 1977; Gerullis and Schuster, 2014). The shots typically transfer vertical and horizontal speed to prey, and small prey falls ballistically towards the water surface where it then can be caught (e.g. Rossel et al., 2002; Reinel and Schuster, 2016). In the wild, archerfish must outcompete other surface-feeding fish and use their predictive C-starts to secure prey. The archerfish predictive starts are launched quickly when prey has started to fall and make the fish arrive at the point of catch at the right time (Rossel et al., 2002; Wöhl and Schuster, 2006; Schlegel and Schuster, 2008). In the wild, the predictive starts were found to secure prey in a remarkable 98% of cases despite severe competition with sympatric halfbeaks (Rischawy et al., 2015). However, in the dark – when archerfish can still down prey but can no longer launch predictive starts – all downed prey would be lost to the competitors

(Rischawy et al., 2015). Though kinematically equivalent to high-power escape C-starts (Wöhl and Schuster, 2007), the predictive C-starts are tuned in both their kinematic phases (i.e. the initial bending and the subsequent straightening phase) so that they end with the fish aligned right toward the later impact point of prey (e.g. Rossel et al., 2002; Wöhl and Schuster, 2007; Schlegel and Schuster, 2008; Rischawy et al., 2015) and so that the fish has an optimal level of speed to arrive in time and at full speed (Fig. 1) (Wöhl and Schuster, 2006; Reinel and Schuster, 2014).

Surprisingly, archerfish select their predictive C-starts on the basis of motion cues sampled during less than 100 ms and do not require prior information sampled, for instance, during the shooting behaviour that precedes the ballistic falling of natural prey. This was shown in experiments in which accuracy and latency of the C-starts were compared in situations in which the fish either could or could not use information sampled before prey actually started to fall (Schlegel and Schuster, 2008). In the 'natural' condition, the fish could see the prey and set it into motion with their shots. They thus could determine, for instance, when and where motion would start. They could also observe the incoming shot and from this might predict the direction and initial speed of the initial movement of prey. In the 'deprived' condition the fish had no access to such cues. Rather, prey was located on top of a non-transparent disc and blown off any time by an airflow with initial speed and direction of prey selected randomly by the experimenter. Interestingly, the starts were selected with equal latency and accuracy (Schlegel and Schuster, 2008). Moreover, even when prey fell from a position that was displaced horizontally from the one to which the fish were cued and looking, this did not affect the quality of the start decision. These and all later experiments, however, do not allow us to conclude whether the fish use prior information about the initial height from which prey starts falling. In the 'deprived' condition of Schlegel and Schuster (2008), the starting positions were all at the same height level, so that the fish could, in principle, have set their C-start circuitry to just that fixed level of initial height. By extending the approach of Schlegel and Schuster (2008) to allow prey to be blown off from various height levels and by analysing the accuracy of the turns made by the fish as well as their take-off speed, we showed that the fish did not select their predictive starts on the basis of 'expected' height, the height at which they were looking and occasionally firing shots (Reinel and Schuster, 2018). In principle, the fish could have simplified the problem by (1) recognizing that movement starts from a location other than the expected one, (2) detecting which other location is close to where prey movement started and then (3) informing the C-start circuitry with the stored height level of that location. Our experiments, however, did not show the expected learning effects and showed no difference between setups that differed in the variability of the height levels of the landmarks. Moreover, storing the height of landmarks would not work in the wild, where water levels can fluctuate rapidly and remarkably irregularly (S.S., unpublished).

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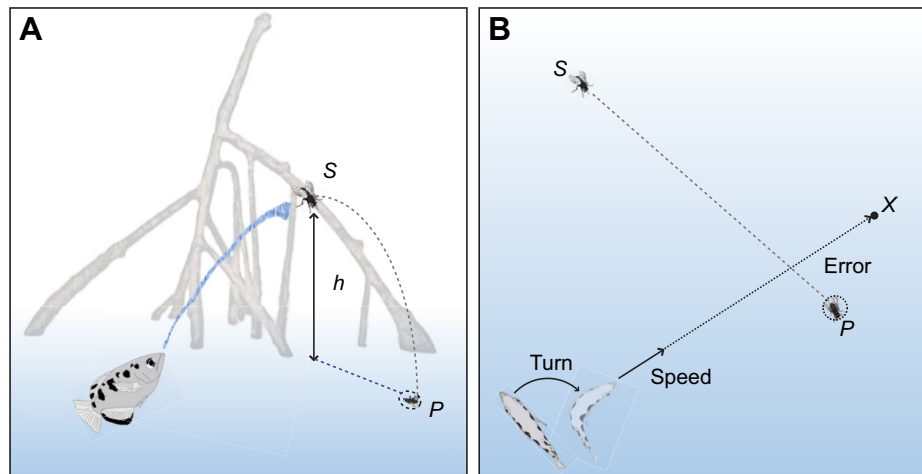


Fig. 1. Separate information on target height is used for shooting and to drive the archerfish predictive C-starts. (A) Archerfish use information on target height h to aim, select an appropriate amount of water fired depending on absolute size of prey and shape their jets to increase force transfer on their prey. (B) After prey is dislodged, the fish produce a rapid C-start that turns the fish toward the later impact point P and ends at a speed that, when kept, would make the fish arrive simultaneously with their prey. Because the landing point P will be farther away from the starting point S if initial height h is larger, the C-starts require information about height h . Surprisingly, C-starts do not use the information available for shooting (A) but use an independent estimate, obtained rapidly when prey starts to fall. The accuracy of bearing and linear speed assumed immediately at the end of the C-start can be used as a convenient assay of how the removal of a potential cue compromises the ability of the fish to produce appropriate C-starts. In that case, the distribution of errors made should be shifted and/or broadened relative to the situation with the cue available. In the start shown in B, continuing the movement in the direction and at the speed given by the C-start would make the fish arrive at point X when prey lands at point P . The fish would have made an error in its aim but also in its speed, having started too fast.

Our companion study (Reinel and Schuster, 2018) thus raises the possibility that the fish also derive initial height during the brief (less than 100 ms) initial falling phase of prey. For most mechanisms of depth vision, it would be quite challenging to gauge distance in so little time and from arbitrary initial distances and orientations. The present study therefore aims to explore which of the potentially available cues could allow archerfish to so quickly estimate three-dimensional distance with sufficiently high accuracy. First, we examined the use of binocular cues by comparing trials in which the fish either could or could not have seen the movement with both eyes. We next examined a range of potential monocular cues, such as accommodation. This cue is used by fish (e.g. Andison and Sivak, 1996; Land, 1999; Frech et al., 2012), but the available evidence suggests a typical time scale that would still seem to be slower than that required for the archerfish predictive starts. Given the demonstration of clever simplifications (e.g. Collett and Land, 1978) and of the role of figure-ground cues to gauge distance (e.g. Bland et al., 2014), we also examined the importance of fixed absolute size of falling prey objects or a fixed distance relative to a structured background. In technical systems, image blur is a potent and rapid cue used to gauge distance (e.g. Chaudhuri and Rajagopalan, 1999) and evidence suggests that it also is used in animals (e.g. Nagata et al., 2012). We therefore also ran experiments to test the importance of image blur or accommodation-related changes in image blur as possible cues used to gauge distance. Finally, we examined whether the fish might use context-dependent combinations of several of these cues.

MATERIALS AND METHODS

Animals

Archerfish were kept as described in the companion paper (Reinel and Schuster, 2018). The relevance of binocular cues was analysed using the recordings obtained in that study. However, the present study also involved additional groups of fish. The relevance of prior information on size and background distance was tested in a new group of 20 juvenile archerfish [13 *Toxotes jaculatrix* (Pallas 1767)

and seven *Toxotes chatareus* (Hamilton 1822); body size ranged from 5.4 to 9.0 cm; see remark on mixed groups in the companion paper (Reinel and Schuster, 2018)]. The ‘fake fly’ experiments (to test blur-related cues and accommodation) involved three *T. chatareus* with body sizes between 13.0 and 14.0 cm. To identify responses that could only have used monocular (or that would surely have allowed binocular) information, we used 15 fish (eight *T. chatareus* and seven *T. jaculatrix*) with body lengths within the range of the animals used in our previous behavioural experiments (Reinel and Schuster, 2018) and housed under the same conditions. The fish were killed with an overdose of the anaesthetic MS-222 and measurements were then immediately started and finished within less than 1.5 h.

Setup and procedures

Finding responses with and without access to binocular information

To determine monocular views, a euthanized fish was fixed in the centre of a transparent dish (diameter 23 cm, height 10 cm; bottom covered with 4 cm wax). A spacer of 70 cm length, aimed at the midpoint between the eyes, was used to constrain the observer’s viewpoint to the surface of a sphere. The dish itself was centrally placed – in a constant position – in a polar chart scaled in intervals of 5 deg. To mimic our experimental situation as closely as possible, the fish’s eyes were submerged (2 cm) in the same (brackish) water used in the experiments. Large stainless steel needles rigidly fixated the fish so that its orientation and length axis remained stable when we explored the effect of changes in the orientation of the eyes. Eyes were rotated and the eyeballs were fixed in the test position by means of small insect needles.

Testing unexpected changes in prey size and distance of a background

In these tests, performed with a new group, a simple setup (as in Reinel and Schuster, 2014) was used with only one opaque circular disc (polyvinyl chloride, diameter 34 mm), located centrally at a height of 40 cm above the water surface. In the experiments on size, a dead fly (*Calliphora* sp.; size 10 mm) or only its head (size approximately

2 mm) was put on the upper side of the disc and then dislodged by an airstream controlled by the experimenter. Speed and direction were randomly chosen from trial to trial ('deprived' condition as described previously by Schlegel and Schuster, 2008; Reinel and Schuster, 2014). In the majority of the 570 tests, complete flies were used as prey. However, in 17% of the tests only the head of a dead fly was used. To test the use of prominent structures in the background as cues, we constructed a structured background with thick (1 cm) black lines drawn in a random orientation on a transparent plexiglass board (size 1.3×1.3 m). The board could be placed at one of two preset height levels, either 42 or 62 cm above the water surface. Apart from the stripes, the plexiglass was transparent, so that the camera could still monitor the responses from above. Note, however, that apart from the camera lens, the background behind our structured plexiglass plate was homogeneously white. Data were derived from a total of 360 trials.

Performing the 'fake fly' experiments

For the 'fake fly' experiments, we used the setup of the companion study (Reinel and Schuster, 2018) but prey always came from one of the platforms of the central tube. In the majority of tests prey started from 55 cm above the water, but in some tests carefully prepared 'fake flies' (see below) were launched from the highest (65 cm) or the lowest (35 cm) platform. The tests were run over 9 weeks with 45 trials per day. We presented six 'fake flies' on each day, three from the highest and three from the lowest height. The remaining 39 presentations of each day were with normal flies launched from 55 cm initial height.

Evaluating image blur as a potential cue to gauge distance

To explore a (arbitrary) model situation in which blur would be a useful cue, we took photographs (Nikon D300S, focal length 105 mm, aperture 5.6, exposure time 1/30 s) of a total of 54 flies with the camera focused on a fly at 55 cm height. Distance of the fly from the lens was chosen based on the analysis of the position of the eye of the fish relative to the target in $n=186$ responses obtained in the companion study (Reinel and Schuster, 2018; distance $d=70.02\pm 0.01$ cm, elevation $\epsilon=54\pm 11$ deg; means \pm s.e.m.). A fly was put on a white plexiglass plate illuminated from the bottom (by adjusting two halogen lamps of 200 W each) so as to produce a Michelson contrast of 0.92. Starting from the camera's focus point (at 70 cm distance), we moved the fly to a higher or lower height and took photos to determine image blur at various deviations from the focus point. Blur was quantified on the basis of the maximal slope in a Boltzmann fit (OriginPro, version 7.5, OriginLab Corporation, Northampton, MA, USA) to the intensity profile in the boundary of the image. Slope at the focal point was set as the reference and blur was quantified as percentage deviation from the blur at height 55 cm. Blur increased significantly (linear regression: $R^2=0.996$, $F>683.953$, $P<0.001$) both for increasing and decreasing distance between the fixation point and the observer (Fisher z -transformation: $z=0$, $P=1$). Additionally, we measured changes in image size. Measurements were calibrated with $n=192$ arbitrarily chosen flies (1.09 \pm 0.05 cm, mean \pm s.e.m.).

Creating 'fake flies'

Two types of 'fake flies' were produced: one, to be presented at 35 cm height, was intended to mimic a fly at a much higher initial height; the other, to be launched from 65 cm height, was intended to mimic a much closer fly. Neither type should allow a focused image. The preparation started with half of a fly's thorax and ended when it was coated with 13 layers of agarose, each with its specific amount of black dye (agarose gel: Carl Roth GmbH, Karlsruhe, Germany; 3 g per 200 ml of distilled water; dyestuff: Pelzer Baits Boilie Colors

distributed by Mosella, Platten, Germany; 1.08 g finely ground per 18 ml of distilled water). The amount of dye in the respective layers was 900, 800, 700, 600, 500, 400, 300, 200, 100, 80, 60, 40 or 20 μ l of the dye-water mix per 15 ml of agarose gel. For coating, the fly's thorax was fixed on a needle and dipped into the appropriate agarose. After the layer had dried, the next layer was applied. For each experimental day, fresh 'fake flies' were prepared and quality-checked (by photographing them and running Boltzmann fits to check their degree of blurring).

Recording

All experiments employed digital high-speed video (HotShot 1280M, NAC Image Technology, Simi Valley, CA, USA; operated at 500 frames s^{-1}) as described in the companion study (Reinel and Schuster, 2018). In the experiments with changes in prey size and background distance, which involved a different group of fish, the illumination was different. Here, four halogen spots of 500 W each illuminated the tank from below. The distant white sheet above the tank was illuminated by four halogen spots (two of 250 W and two of 500 W). In these experiments, the Michelson contrast was 0.39 between the falling prey (48.0 $cd\ m^{-2}$) and the background (108.9 $cd\ m^{-2}$; averages of $n=10$ measurements). In the 'fake fly' experiments, conditions were comparable to those of the experiments of the companion paper (Reinel and Schuster, 2018), with a Michelson contrast of 0.88 between the prey (4.9 $cd\ m^{-2}$) and the background (75.1 $cd\ m^{-2}$).

Data analysis and statistics

The evaluation of data was as described in Reinel and Schuster (2018). Additionally, azimuth σ was determined by taking the angle between the line defined by the fish's snout and its centre of mass and the line between the snout and the horizontal projection of the fly's starting point. Elevation ϵ was taken as the angle from the horizontal plane and a line connecting the fish's snout and the fly's starting position.

Statistical analyses were run in SigmaPlot (version 12.5, Systat Software, San Jose, CA, USA) and OriginPro (version 7.5, OriginLab Corporation, Northampton, MA, USA) and were always performed two-tailed with an alpha level of $P=0.05$. First, we checked normality of data employing Shapiro-Wilk tests, Q-Q plots and histograms. If data were normally distributed, we performed Levene's tests to verify equal variances and one-sample t -tests to check distributions around zero mean. Two-sample t -tests or one-way ANOVA were used to compare differences among two or more data sets. Paired data (e.g. levels of take-off speed) were checked using either paired t -tests (two data sets) or one-way repeated-measures ANOVA (more than two data sets). Otherwise, if data were not normally distributed, we employed Brown-Forsythe tests to check equality of variance. One-sample signed rank tests were run to confirm distributions around zero mean. Mann-Whitney or Kruskal-Wallis tests were applied for differences among two or more data sets. Paired data sets were checked with Wilcoxon signed rank tests (two data sets) or Friedman repeated-measures ANOVA on ranks (more than two data sets). Pearson correlation (parametric data) or Spearman rank correlation (non-parametric data) were used to analyse correlations. Fisher z -transformations were employed to test the quality of two correlation coefficients. Boltzmann fits were employed to analyse blur and size of flies and fake flies.

RESULTS

Identifying conditions under which targets could only have been seen monocularly

In the first part of our study (Reinel and Schuster, 2018), we introduced a setup in which prey could be released from positions that

were offset horizontally and vertically from the one at which the fish were looking. Our aim now was to identify positions in which (1) the responding fish could only have used monocular information or in which (2) binocular cues definitely would have been available. The analysis is most conveniently done by translating the orientation and position of the responding fish relative to its prey into spherical polar coordinates as illustrated in Fig. 2A. Here, angle σ denotes the azimuthal deviation from the fish's length axis and elevation ϵ denotes the position of the target on the surface of a circumscribed sphere. The diagram shows the actually occurring combinations in all responses analysed in Reinel and Schuster (2018). Note that only elevations above the so-called Snell's angle (42 deg in our experiments) are relevant. At this critical angle (the arcsine of the ratio of refractive indices; e.g. Born, 1981), refraction of light causes light from underwater sources to travel along the water–air boundary. Conversely, the angles under which aerial objects can be seen is compressed to angles smaller than Snell's angle.

Our task then was to decide (1) whether a given combination of σ and ϵ could only have allowed monocular vision ('monocular always') or (2) whether it would definitely have allowed binocular vision ('binocular always'). The basic idea of this analysis is

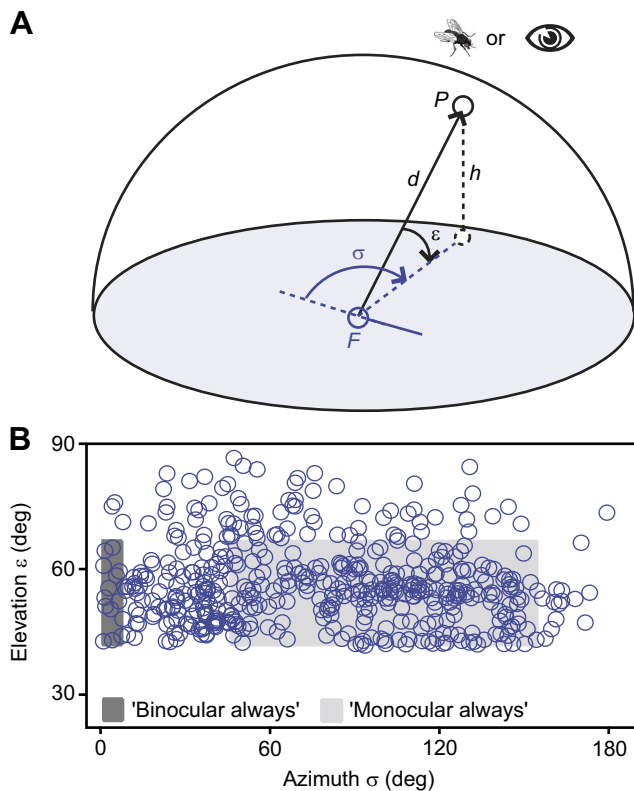


Fig. 2. Identifying C-starts with and without access to binocular information. (A) In the behavioural experiments of the companion paper (Reinel and Schuster, 2018), prey motion could be started from various positions P and heights h in the visual field of responding fish F . Orientation and distance d relative to the initial position of falling prey (indicated by fly icon) were quantified, for each response, as azimuth σ and elevation ϵ . Later we determined (indicated by eye icon) in suitably prepared fish whether prey could have been seen binocularly. (B) Blue circles show the combinations of σ and ϵ for all $n=472$ responses in the behavioural experiments. Grey areas mark the combinations of azimuth σ and elevation ϵ in which fish could only use monocular cues ('monocular always', light grey) or could definitely have used binocular cues ('binocular always', dark grey) irrespective of the various ways in which the eye could be rotated relative to the head. Respective combinations ($n=104$), verified in 15 fish, are shown. An elevation of 42 deg corresponds to Snell's angle in our experiments.

illustrated in Fig. 2A. The experimenter (marked with an eye icon) now took the place of prey (given by σ and ϵ). In 15 appropriately fixed fish (see Materials and methods), we looked in the direction defined by angle ϵ and then noted if it was possible to see the pupils of both eyes or of only one eye (a procedure successfully used in many studies: e.g. Schneider, 1954, 1957; Trevarthen, 1968). When we applied this method in goldfish, we could reproduce the binocular field as described by earlier studies (Trevarthen, 1968; Charman and Tucker, 1973; Easter and Johns, 1977), suggesting that the method provides robust estimates of the visual field (data not shown). When we could see only one pupil, we rotated both eyes of the subject in order to find out whether there would be a combination of eye positions that could potentially have allowed binocular vision. This step was necessary because our high-speed recordings of responding fish contained no detailed information on the orientation of the eyes. Therefore (and because we had many suitable recordings available; Fig. 2B, blue circles), we excluded all cases (i.e. σ, ϵ combinations) in which any combination of eye orientation would potentially have allowed binocular vision. Only combinations were labelled as 'monocular always' in which only one pupil was visible for all possible combinations of rotation of the two eyes. A similar evaluation was also needed to identify those responses that surely could have used binocular information. Here we took only σ, ϵ combinations in which both pupils were seen at all possible orientations of the eye (Fig. 2B). This strict selection left only a small (but sufficient) number of cases for subsequent analyses. As illustrated in Fig. 2B, the regions that we confidently could label as definitely monocular ('monocular always'; Fig. 2B, light grey) were conservatively chosen as $42 < \epsilon < 67$ and $42 < \sigma < 156$. The regions in which we were confident that prey could always be seen with both eyes ('binocular always'; Fig. 2B, dark grey) were chosen as $42 < \epsilon < 67$ and $\sigma < 10$ (with Snell's angle as the lower boundary value for ϵ).

Rapid assessment of depth without binocular cues

Based on the analysis described above, we identified $n=33$ (prey height $h=35$ cm), $n=91$ ($h=55$ cm) and $n=148$ ($h=65$ cm) 'monocular always' responses and $n=9$ ($h=35$ cm), $n=23$ ($h=55$ cm) and $n=7$ ($h=65$ cm) 'binocular always' responses (Fig. 3). This allowed us to compare, for each height level, whether the 'monocular always' and the 'binocular always' responses differed in accuracy and/or latency. However, at all height levels we were unable to detect any differences between the monocular and the binocular groups. For each starting height, the average errors in aim e were equal (t -tests: $P > 0.325$) and not statistically different from zero mean (one-sample t -tests: $P > 0.093$). Also, the distribution of the errors e was not statistically different (Levene: $P > 0.412$) (Fig. 3B, Bi–iii). Furthermore, the correlation between the required and the actual turn size was always tight (linear regression: $R^2 > 0.76$, $F > 21.65$, $P < 0.002$; data not shown) and not better when binocular cues could have been used. Hence, the availability of binocular cues had no effect on the accuracy of the fish's aim. This also held for the temporal aspects of the response: speed attained at the end of the C-starts correlated equally well under monocular and binocular conditions with the ('virtual') speed that would have been needed to arrive in time, given the remaining time until impact and the distance the fish needed to cover (linear regression between actual and 'virtual' take-off speed: $R^2 > 0.493$, $F > 6.808$, $P < 0.035$; Fisher z -transformation to compare the regression in monocular versus binocular responses: $P > 0.105$; data not shown). The errors made in setting the appropriate level of take-off speed (error in speed Δv ; Fig. 3C, Ci–iii) did not differ between the 'binocular always' and 'monocular always' conditions

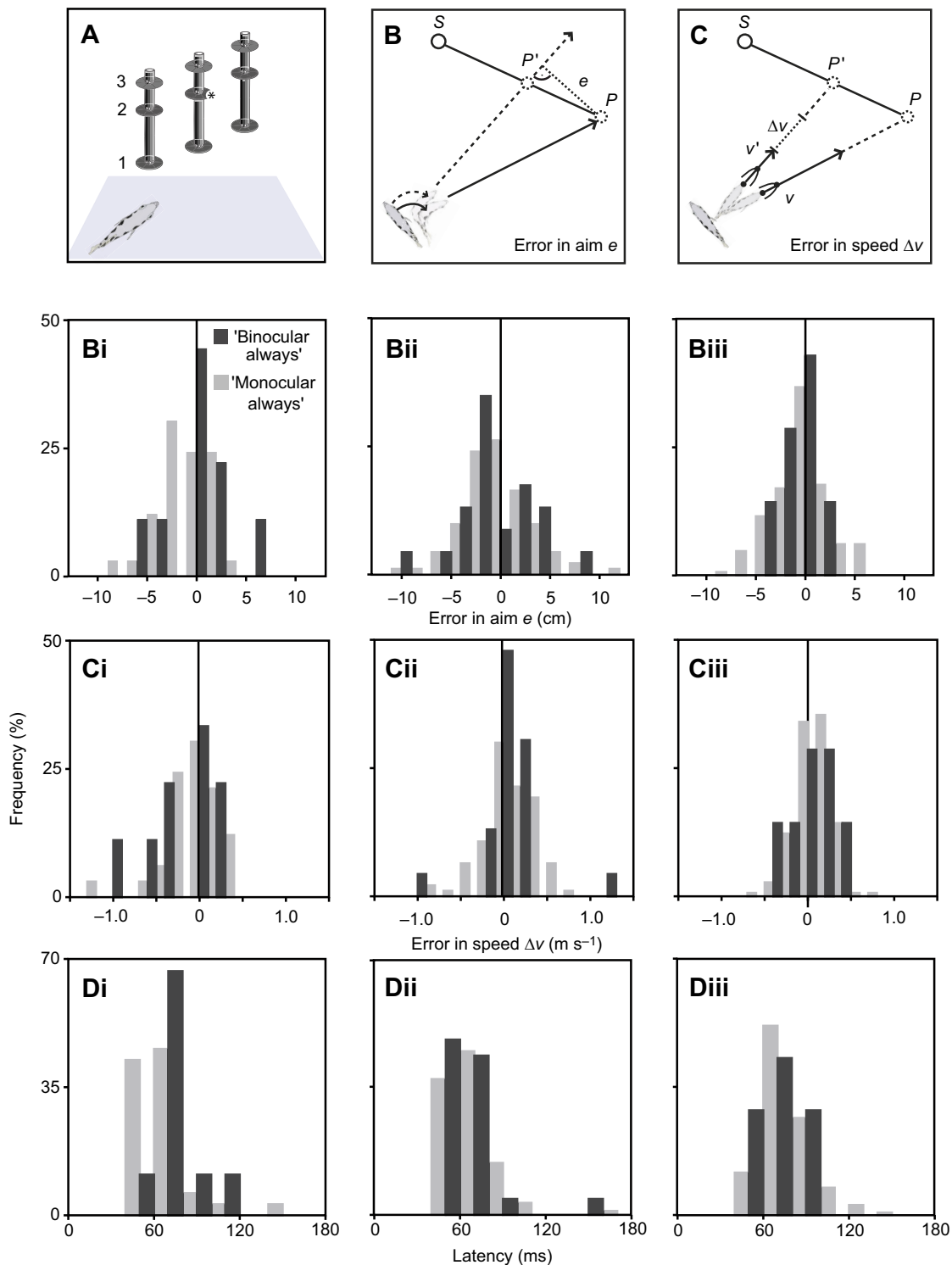


Fig. 3. Accuracy of the start decisions that could and that could not have used binocular information. (A) Sketch of setup with expected starting point indicated by asterisk and height levels denoted by numbers 1–3. (B) Error e assesses aim immediately at the end of the C-start in a way that is invariant against changes in geometry and orientation of fish from one test to the next. It allows determination of whether aim was, for example, to point P or P' . S is the starting point, projected to the water surface. (C) Error in speed Δv assesses whether speed immediately at the end of the C-start is set to distance to P or P' . (Bi–iii) Distribution of the error e in aim (at the end of the C-start) when prey was launched from height levels 1–3 as indicated in A and when binocular cues would have either been available ('binocular always', dark grey) or unavailable ('monocular always', light grey). At no height level did accuracy in aim differ under monocular versus binocular conditions (t -test: $P > 0.325$). (Ci–iii) Distribution of the error in speed Δv directly taken after the fish took off. Error in speed was taken as the difference between actual take-off speed v' and the 'virtual' speed v needed to arrive simultaneously with prey. Accuracy in setting the appropriate level of take-off speed also did not differ depending on monocular or binocular conditions (Mann–Whitney: $P > 0.187$). (Di–iii) Response latency, the time from onset of falling of prey to onset of the C-start, also did not differ, at each initial height, under binocular versus monocular conditions (Mann–Whitney: $P > 0.119$). All histograms are based on $n=33$, 91 and 148 (monocular) and $n=9$, 23 and 7 (binocular) responses for initial heights $h=35$, 55 and 65 cm. Bin widths are 2 cm (error in aim), 0.2 m s⁻¹ (error in speed) and 20 ms (latencies).

(Mann–Whitney: $P > 0.187$). We also note that distance to cover was not significantly different between the ‘binocular always’ and the ‘monocular always’ responses (difference in distributions: Levene, Brown–Forsythe: $P > 0.069$, difference among mean, median values, respectively; two-sample t -test, Mann–Whitney: $P > 0.155$, data not shown). Hence, the fish were equally able to set the angle of their turn and take-off speed under binocular and monocular conditions. We also found no effect on response latency: at each given level of initial height, median latencies and the distribution of latency did not differ significantly in the monocular and the binocular responses (Mann–Whitney: $P > 0.119$; Brown–Forsythe: $P > 0.473$). Median latency increased with target height under both monocular and binocular conditions (Mann–Whitney: $P < 0.001$). Furthermore, the minimal latencies observed (40 ms) were the same (Fig. 3Di–iii).

These analyses suggest that monocular information was sufficient to select an appropriate predictive start. However, one could still object that responses classified as ‘monocular always’ may not have remained monocular throughout the decision time. Falling prey might have initially been seen monocularly but then might have moved – in the brief 40 ms decision time – to a binocular position. We checked this by selecting cases in which we could be sure that prey had remained in the monocular (or binocular) region. The findings (see Fig. S1) support the conclusions drawn so far: (1) average accuracy in aim (two-sample t -test: $P > 0.425$; Fig. S1B), (2) accuracy in setting speed (Mann–Whitney: $P > 0.128$; Fig. S1C) and (3) median latency (Mann–Whitney: $P > 0.114$; Fig. S1D) did not differ in the monocular and the binocular conditions. Also, the distributions were equal [(1) Levene: $P > 0.570$; (2) Brown–Forsythe: $P > 0.318$; (3) Brown–Forsythe: $P > 0.662$]. These analyses are based on $n = 29$ ($h = 35$ cm), 91 ($h = 55$ cm) and 115 ($h = 65$ cm) responses under the ‘monocular always’ condition and $n = 8$, 18 and 3 responses under the ‘binocular always’ condition.

The start decisions do not require a priori information on absolute size

Knowing the absolute size of prey would allow a quick judgement of initial height from the size of the retinal image. To test this

possibility, we challenged a different group of archerfish (see Materials and methods) that had exclusively experienced flies of fixed size (10 mm) during several months before actual testing began. In the majority of experiments, normal-sized flies were launched, but in some experiments only fly heads, approximately one-fifth of the size of a fly, were blown off from the platform (Fig. 4). By accumulating responses to normal-sized and to unexpectedly (much) smaller prey, we could then test whether the change in size would cause systematic errors or more variability in the fish’s aim. However, mean errors in aim did not differ in the ‘expected size’ and ‘unexpected smaller size’ conditions [Mann–Whitney: $P = 0.666$, based on $n = 224$ (fly, grey bins) and 57 (head, red bins) responses; Fig. 4A]. Latency was longer for the unexpected small prey (Mann–Whitney: $P < 0.001$; Brown–Forsythe: $P < 0.001$; Fig. 4B). This could be because smaller prey requires the archerfish to sample more information to select an equally accurate predictive start. At any rate, the choices were equally accurate and the fish were not fooled, for instance, by assuming that smaller prey came from larger initial height levels. This view will be confirmed below in experiments in which both size and image blurring were co-varied.

Do the fish use a priori information about the distance of reference objects?

Knowing the distance of reference objects in the background could also be helpful in quickly judging the distance of a close object. For instance, the motion of falling prey relative to objects in the background would be faster the closer it is to the water surface (i.e. the greater its distance from the background). To test the relevance of such cues, we provided intersecting black background stripes as potential reference objects. Note that these experiments were carried out with a different group of fish that faced only one platform at 40 cm height (see Materials and methods). In an initial adjustment phase, the background always was placed 42 cm above the water surface, 2 cm above the platform from which prey was launched (Fig. 5). When the distance between the prey and the background was subsequently increased by 20 cm by placing the background

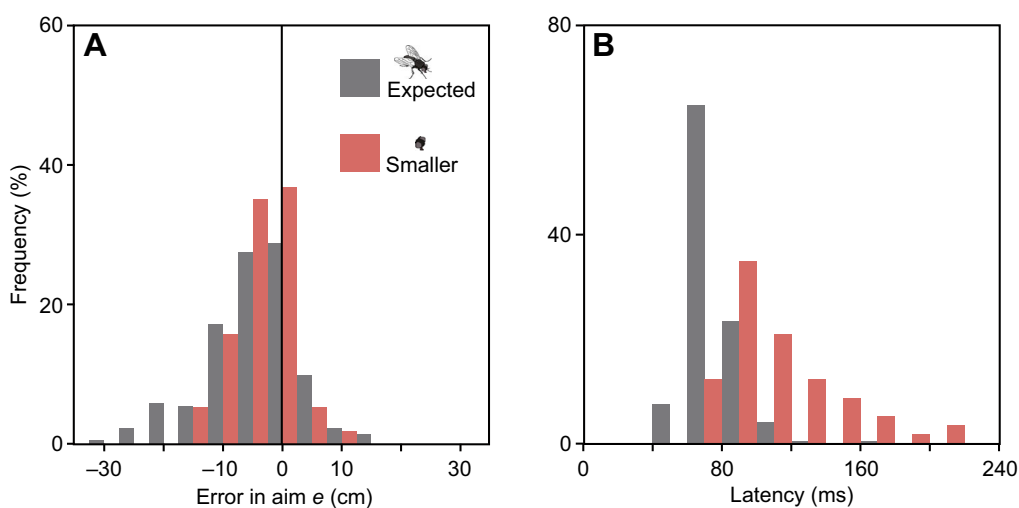


Fig. 4. The effect of unexpected changes in absolute size of prey. After being exclusively fed with flies approximately 1 cm in size, either these flies (‘expected size’) or, occasionally, fly heads (about 0.2 cm; ‘smaller size’) were blown off from a non-transparent platform, 40 cm above the water surface, and errors in aim e were determined (A) as well as latency (B). Regardless of whether size was as expected or much smaller, errors did not differ (A; Mann–Whitney: $P = 0.666$). Should the fish have estimated initial height above the water from a retinal image, then substantial and systematic errors should have occurred. (B) Although accuracy was constant, response latency was increased for the smaller objects (Mann–Whitney: $P < 0.001$; Brown–Forsythe: $P < 0.001$). Histograms are based on $n = 224$ responses to flies and on $n = 57$ responses to heads. Bin widths: 5 cm (errors), 20 ms (latencies).

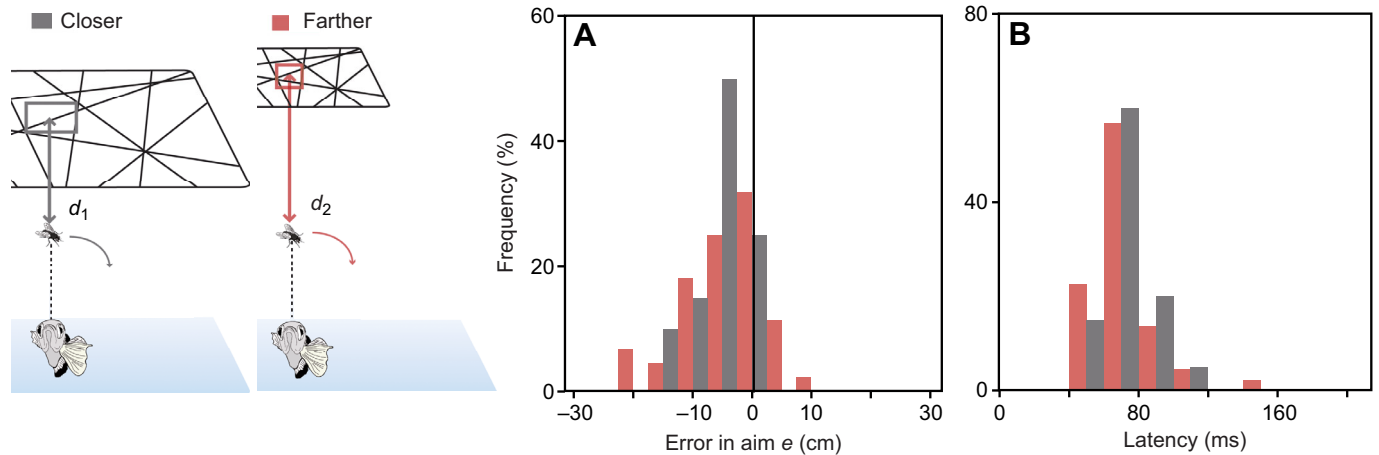


Fig. 5. The effect of changes in the distance of suitable reference structures in the background. Archerfish could view the movement of prey against a background composed of black lines (1 cm thick), as indicated. Prey was blown off from a platform at 40 cm height above the water surface. The background could be positioned either 42 cm above the water surface, i.e. $d_1=2$ cm above the fly's starting point – the 'expected closer distance', to which the fish were cued – or 62 cm above the water (i.e. $d_2=22$ cm from the fly). (A) The aim of the C-starts did not differ regardless of changes in the distance of the background (Mann–Whitney: $P=0.473$). Strong shifts in mean error would have been expected should the fish have measured speed relative to the background. (B) The distribution of response latency was also not affected by the changes in background distance (Mann–Whitney: $P=0.337$; Brown–Forsythe: $P=0.580$). Histograms are based on $n=44$ (background distance 42 cm) and $n=20$ (background distance 62 cm) responses. Bin widths: 5 cm (errors), 20 ms (latencies).

62 cm above the water surface (but leaving prey height at 40 cm), no deviation in the distribution of errors could be detected in the aims taken by the fish. Errors in aim (Fig. 5A) and response latency (Fig. 5B) were not statistically different from the values obtained in the initial condition (Mann–Whitney: $P>0.337$; Brown–Forsythe: $P=0.580$) and showed no systematic trend during the trials that followed the switch in background distance (linear regression: $R^2<0.187$, $F<0.152$, $P>0.057$; $n=20$).

'Fake flies': the relevance of image blur and accommodation

Another quick way of assessing distance monocularly could be based on the degree of blurring in the image, an approach of great importance in machine vision (e.g. Chaudhuri and Rajagopalan, 1999) but also demonstrated in animals (e.g. Nagata et al., 2012), and the basis for depth from focus, as used for instance in the eye of the chameleon (e.g. Ott and Schaeffel, 1995). Consider the experimental situation in which the fish are looking at the platform at middle height, from which prey typically falls. By appropriately focusing its eyes to produce a sharp image of the middle platform and the food that emanates from it, the fish could, in principle, create a situation in which a fly launched from the higher platform would be out of focus, at least initially, and could appear both blurred and smaller. Similarly, a fly launched from the lowest platform could appear blurred and larger. The fish could then derive height from (1) how much accommodation is needed to focus the image, (2) the rate of change in focusing (which might be a faster way) or (3) simply the degree of blurring itself, combined with the size of the image. Evidently, these options are purely hypothetical and would require the optical apparatus (and also the temporal resolution at which falling flies are seen) to be set appropriately. For some guidance on how such a mechanism could work, we first took photographs of flies with the camera focused on the expected distance (Fig. 6A) so that blur in the image varied systematically with distance from the focus point. Next, we created two types of 'fake fly'. Neither could be focused, and in both the combination of image size and image blurring was set to be a misleading cue to distance. One type of 'fake fly' was designed to be launched from the lower platform but to mimic a greater initial height. The other

type was designed to be launched from the top platform but to mimic (in terms of blur and size) a much closer fly. This approach was chosen to produce the largest possible error in predicting the landing point, given our uncertainty of what the actual optics were in the responding experimental fish. It turned out that both types of 'fake fly' could actually be produced. This involved a rather elaborate process that required coating the thorax of a fly with several layers of black agarose (Fig. 6F). The resulting 'fake flies' (shown in Fig. 6F on the right) fell just as normal flies would (e.g. linear regression between travelled distance and target velocity: $R^2>0.76$, $F>159.83$, $P<0.001$, data not shown). Because they actually fell into the water, they also had to be edible. This was achieved with such considerable success that each of the carefully produced and photographically calibrated 'fake flies' was gone after a test. The 'fake flies' that mimicked the distant flies but were launched from 35 cm initial height were chosen to be 9–17% smaller in size and the slope of the intensity change was reduced by a factor of five. 'Fake flies' launched from 65 cm initial height were 17–35% larger in size with an intensity gradient that was reduced by a factor of 13 (Fig. 6D–F). Note that both types of 'fake fly' did not allow a sharp image to be formed and so should interfere with accommodation-based mechanisms, predicting considerable scatter in the distribution of bearing errors of the predictive C-starts.

However, we found no differences in the bearing errors regardless whether real flies or occasionally interspersed 'fake flies' were launched. Under each condition, errors in aim were centred around zero mean [Kruskal–Wallis: $P=0.759$; mean \pm s.e.m. = -1.4 ± 0.4 , 1.0 ± 0.2 and -0.4 ± 0.4 cm based on $n=68$ ($h=35$ cm, red), $n=175$ ($h=55$ cm, grey) and $n=62$ ($h=65$ cm, blue) prey starts, respectively; Fig. 7A]. The distribution of errors also showed no significant differences (Brown–Forsythe: $P=0.125$). Furthermore, with all types of fly, 'fake' or real, latency increased similarly with increasing initial height (Mann–Whitney: $P<0.001$; Fig. 7B). Hence, providing 'fake flies' with only blurred images and changing the degree of blurring as well as absolute size did not cause any systematic errors or an increase in variability. The experiments thus failed to support the idea that accommodation or other evaluations of image blurring could explain why the

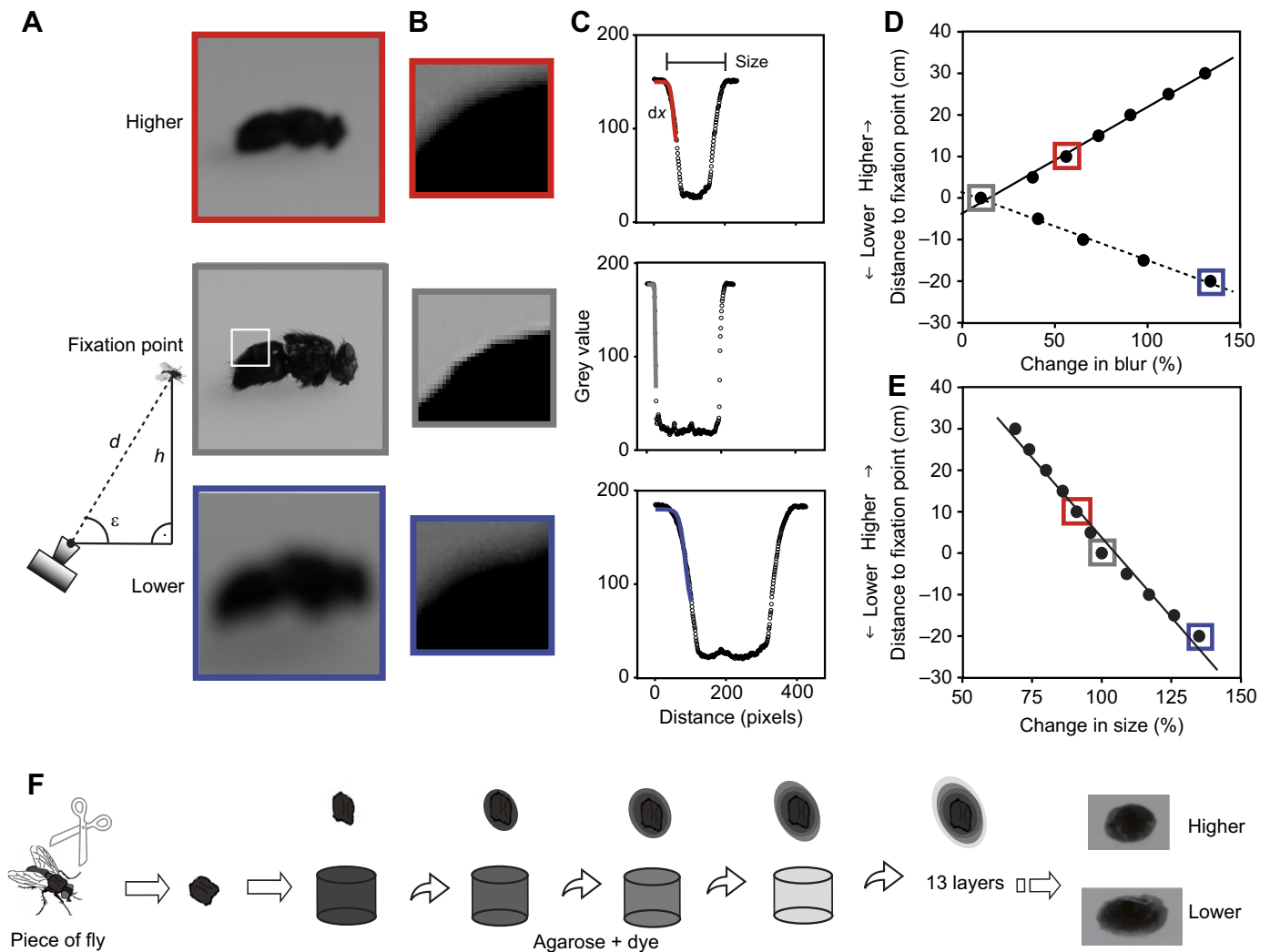


Fig. 6. Producing 'fake flies' to test the potential relevance of cues related to image blur. (A) In principle, the optics could be set so that the image of a falling object would be sharp at an expected height but blurred for higher or lower height. Either the blur itself, the speed of accommodation or accommodation could then potentially provide useful cues for the initial distance, when used together with image size. This is illustrated by a series of photographs (A,B), with B showing a detailed view of the fly's boundary. (C) Quantitative evaluation of the degree of blurring and image size. As illustrated, blur is derived from the slope of Boltzmann fits in the boundary region indicated with colour and label 'dx' and normalized to zero blur at the focus point. (D,E) Change in blur (D) and image size (E) with distance from the focus point for the (arbitrary) camera setting. (F) Schematic illustration of how 'fake flies' were created that mimicked the degree of blurring and size that would be appropriate for higher and lower height and in which focusing would not be possible and hence provide no depth cues. 'Fake flies' launched from 35 cm mimicked flies that fell from a higher height; they were 9–17% smaller and blurring was increased by a factor of five. 'Fake flies' launched from 65 cm mimicked flies that fell from a much lower height; they were 17–35% larger and blurring was increased by a factor of 13. Coloured frames (red, grey, blue) highlight corresponding distances in the images and in the later analysis.

archerfish predictive C-starts are so quickly informed about initial prey height.

DISCUSSION

When confronted with a situation in which archerfish expect prey to come from a cued location at a certain height but in which the prey starts from somewhere else and from a different height, the fish respond with C-starts that are chosen according to the actual initial height but not according to the height of the platform they were facing and occasionally shooting at (Reinel and Schuster, 2018). Here, we examined which cues might be involved in informing the circuitry that selects the appropriate C-start so quickly about initial height. Our findings exclude binocular and also major monocular cues (e.g. Gibson, 1979; Collett and Harkness, 1982; Land and Nilsson, 2002). Our tests would have caused detectable changes in accuracy and speed of the predictive starts, should the fish have used

accommodation or image blur to derive height, or should they rely on expected prey size or on expected distance from a background. Furthermore, we were unable to detect any difference in the starts made when one or both eyes could see the falling prey. Because the archerfish predictive starts allow even small errors in speed and turn angle to be detected (e.g. Krupczynski and Schuster, 2013; Reinel and Schuster, 2016), we could have detected both systematic errors as well as slight increases in variability. Our findings suggest that the C-start circuitry receives accurate information on target height rapidly and in a way that appears to be rather unusual.

Would a combination of cues explain our findings?

It would seem that, in principle, our pattern of results could be explained if the fish used a combination of several cues to infer target height. When only one individual cue is no longer helpful – as it was the case in each of our experiments – then the fish would

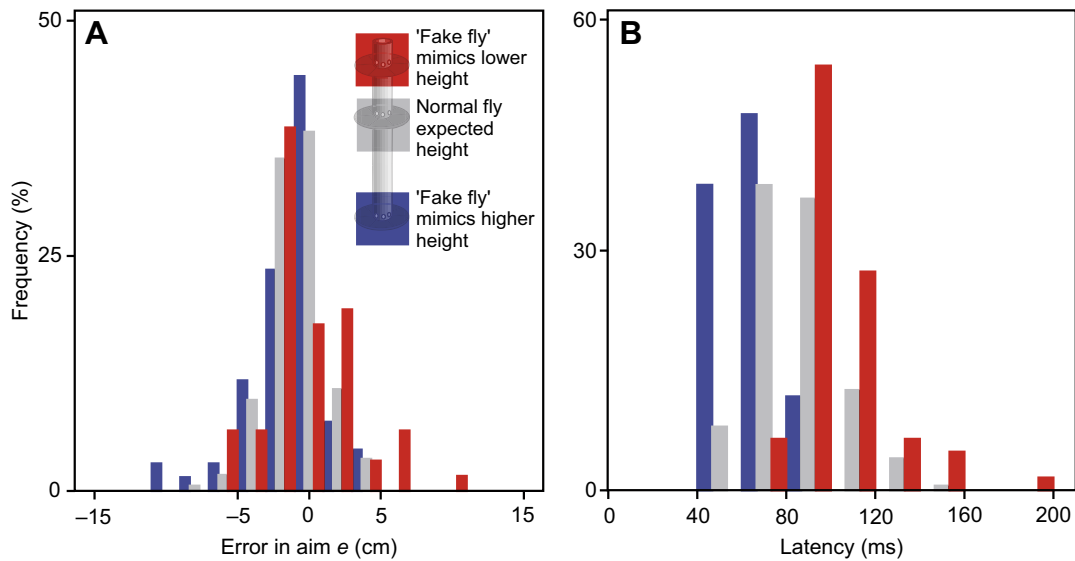


Fig. 7. Results of 'fake fly' experiments conducted to test the importance of accommodation and image blurring. (A,B) 'Fake flies' were created (see Fig. 6) to cause a divergence between actual and perceived initial height of prey. 'Fake flies' either appeared to be close but were launched from the highest initial height (65 cm) above the water surface ('mimics lower height', red), or appeared to be far away but were launched from the lowest initial height (35 cm) ('mimics higher height', blue). Additionally, normal flies were launched from 55 cm (expected height) above the water surface (normal fly, grey). (A) Errors in aim toward the actual impact point were not different, regardless of whether a divergence was present, and regardless of whether the outline was blurred (Kruskal–Wallis: $P=0.759$). (B) Latencies differed significantly, but in the same way as they would for normal objects with increasing starting height levels (Kruskal–Wallis: $P<0.001$). Histograms are based on $n=68$ ($h=35$ cm) and $n=62$ ($h=65$ cm) responses to 'fake flies' and $n=175$ responses to real flies ($h=55$ cm). Bin widths: 2 cm (errors), 20 ms (latencies).

'simply' switch to the other cues. Many animals have several cues available to gauge distance and can use the ones that are most useful (e.g. Collett and Udin, 1988; Douglas et al., 1988; Olberg et al., 2005; Collett et al., 2013; Bland et al., 2014). For instance, desert ants *Cataglyphis bicolor* can switch from landmarks to sun-related cues to find the entrance of their nest after a long foraging trip (Wehner and Menzel, 1969). Moreover, both counting steps and optic flow are used to measure the distance travelled, and ants that are carried (by another ant) are not misled by their own step count, but switch to use optic flow to monitor their position (Pfeffer and Wittlinger, 2016). Landmarks, when available, are preferred over sun-related cues (e.g. Wehner and Menzel, 1969), and closer to the nest, the ants can successfully use olfactory cues (e.g. Steck et al., 2009).

In the archerfish predictive starts, however, the situation is much more difficult. Consider, for example, the 'fake fly' experiments or the experiments in which the fish were confronted with prey items that were smaller than expected. In both experiments, the changes occurred not successively, but infrequently, so that the fish would have to rapidly assess (in less than 100 ms) whether – in the present situation – 'blur' or 'size' should be used to infer height. During the time to make the decision, no feedback can be used to identify which cues need to be excluded. Feedback could be obtained by keeping track of the errors made over several starts, but it is not clear how the fish could determine which of the cues is responsible for large errors. Most importantly, the idea of feedback from errors is not supported by our findings. We did not find any trend indicating that errors would change over time after the start of any of the experiments in the present study (linear regressions: $P>0.138$ for all experiments; regressions not shown), but this would be expected should the fish evaluate errors to identify and exclude a misleading cue. Still, the fish could be using other ways to exclude the effect of unreliable cues and these may not even require the fish knowing which cue was unreliable. Suppose the fish used many cues and

averaged the resulting landing points (and time of flight) predicted by each individual cue. If this was the case, then small but detectable errors should still have occurred in our experiments. Their absence suggests that such a mechanism is not likely. Alternatively, the exclusion of cues could work simply by picking as the landing point the one that is supported by the majority of cues. However, this also would not be supported by our findings: in some of our experiments, several of the cues were affected simultaneously (e.g. absence of binocular information as well as of accommodation- and image blur-related signals) and yet no changes in error were seen. Taken together, it appears unlikely to us that 'simply' combining all cues and excluding specific ones could explain our pattern of findings.

Ultimate and proximate aspects that could preclude the use of specific cues in the archerfish predictive starts

Ecological constraints might explain why so many cues cannot successfully be used to drive the archerfish predictive starts. For instance, binocular cues could be helpful for the shooting fish but perhaps not for a bystander that responds late to the falling motion of dislodged prey: by the time it takes to turn so that the prey could be seen binocularly, the food would have landed and been snatched by a competitor. So, a solution would clearly be preferable that does not require binocular information and perhaps works only with monocular cues. The latter seems to be the case in the archerfish predictive start, in which adding binocular information does not affect the quality of the start or the decision time. In the wild, archerfish shoot at a large variety of prey animals (e.g. Schlegel et al., 2006; Rischawy et al., 2015) from flies to small lizards (e.g. Smith, 1936). It would therefore seem very useful if the predictive start circuitry could handle a large spectrum of prey sizes and be able to deal with unpredictable variations in prey size from one C-start to the next. Although the responses could still have profited from prior knowledge of size, such additional information appears not to be helpful to increase the precision of the C-start decision. We found a

similar situation when binocular cues could have been used or when information on the distance of potential reference objects in the background was available. Surprisingly, the availability of such additional information could not be used to increase the precision of the C-starts any further. It is difficult to understand this purely from an ecological perspective. But it is unclear which proximate factors could prevent the fish from (1) feeding the available information on height into the C-start circuitry (Reinel and Schuster, 2018) and (2) exploiting cues that work well in other fish (Andison and Sivak, 1996; Douglas et al., 1988; Easter and Johns, 1977; Frech et al., 2012; Land, 1999; Pettigrew et al., 1999, 2000). We suggest that both aspects might have a common reason: the (unknown) circuitry that drives the rapid archerfish predictive C-starts. If this circuitry faced similar constraints as the (kinematically identical) escape C-starts, then it might be biased to use sensory cues that are similar to those used to elicit and direct escape C-starts. Archerfish might use looming, the apparent expansion of a rapidly approaching object, as such a cue. Adult zebrafish determine the distance of flight using looming cues, and a classic study showed that looming cues predicted their distance of flight (Dill, 1974). Dill's idea was that for a directly approaching predator, a prey zebrafish could determine the distance d of the predator from size S , speed v and rate of change $k=d\alpha/dt$ of visual angle α via:

$$d = \sqrt{\left(\frac{vS}{k} - \frac{S^2}{4}\right)}. \quad (1)$$

The success of his prediction also implied that other cues did not play a role – at least in the settings of his experiments. A prominent role of looming cues for escape responses has been firmly established in many species across the animal kingdom [fish (e.g. Dill, 1974; Preuss et al., 2006; Temizer et al., 2015); amphibians (e.g. Ishikane et al., 2005; Nakagawa and Hongjian, 2010); birds (e.g. Sun and Frost, 1998); mammals (e.g. Schiff et al., 1962; Yilmaz and Meister, 2013; Shang et al., 2015) and arthropods (e.g. Hatsopoulos et al., 1995; Holmqvist, 1994; de Vries and Clandinin, 2012)]. Based on these studies, escape circuitry of many, even taxonomically unrelated animals might share computations to derive flight distance from an analysis of looming.

Do the archerfish predictive starts use an elaborate version of 'distance from looming'?

An earlier study suggested that archerfish might be using looming cues to adjust their predictive C-starts to the initial vertical speed of prey (Reinel and Schuster, 2016), and looming could also be the missing cue that informs the archerfish predictive start about target height. The analysis of looming would, however, clearly have to be more elaborate than that of Eqn 1, and would need to provide a way of deducing target height independently from viewpoint for objects of different absolute size, perhaps by using a set of independently operating different looming detectors. Unfortunately, the behavioural experiments needed to directly test any involvement of looming cues are technically demanding and presently not possible. In our view, they require a system in which archerfish are stimulated via a monitor and in which the fish are rewarded as precisely as possible at the predicted time and position. In this setup, objects could be mimicked that move across the monitor but in which looming can be added to mimic different initial height levels as well as an initial vertical component of speed. Because the analysis of looming cues would have to be very rapid (to be useful for the quick predictive starts), monitors are needed that combine high refresh rates with high spatial resolution (to display the minute

changes in size). It will therefore take a while before our hypothesis can be tested in a straightforward way.

Conclusions

We show that the archerfish predictive C-start decisions operate exclusively on the basis of cues that are sampled in a brief interval after prey starts falling. This includes a rapid estimate of the initial height from which prey is falling. We suggest that the fish do not use stored height levels of characteristic landmarks in the vicinity of falling prey but derive height from an analysis of looming-related cues. These cues – and not others – might have been used in the evolution of the predictive C-starts because information on looming was already available in the C-start network to elicit appropriate escape responses.

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Competing interests

The authors declare no competing or financial interests.

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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Supplementary information

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