Current Biology, Vol. 14, 1565–1568, September 7, 2004, DOI 10.1016/j.cub.2004.08.050

Archer Fish Learn to Compensate for Complex Optical Distortions to Determine the Absolute Size of Their Aerial Prey

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Summary

Many animals, including humans, can visually judge the absolute size of objects regardless of changes in viewing distance and thus despite the resulting dramatic differences in the size of the actual retinal images [1–5]. For animals that have to judge the size of aerial objects from underwater views, this can be a formidable problem; our calculations show that considerable and strongly viewpoint-dependent corrections are needed to compensate for the effects of light refraction. Archer fish face these optical difficulties because they have to shoot down aerial insects over a wide range of horizontal and vertical distances [6, 7]. We show here that these fish can learn to acquire size constancy with remarkable precision and are thus fully capable of taking complex viewpoint dependency into account. Moreover, we demonstrate that archer fish solve the problem not by interpolating within a set of stored views and distances but by learning the laws that connect apparent size with the fish's relative position to the target. This enables the fish to readily judge the absolute sizes of objects from completely novel views.

Results and Discussion

In the course of this study we examined a total of 13 archer fish, *Toxotes jaculatrix*, which ranged in length from 6 to 16 cm. In all experiments reported here the fish were kept individually in large tanks (1.2 × 0.5 × 0.5 m). In each experiment an assembly of eight black disks with diameters ranging from 2 to 30 mm in steps of 4 mm was presented at one of four preassigned heights, from 200 to 800 mm above the water surface (Figure 1). The disks were printed black on white paper. Each experimental assembly shown was drawn at random from an ensemble that comprised all possible spatial arrangements of the differently sized disks on the edges of an imaginary octagon with 9 cm sides. When shown the assembly, fish generally swam straight to their shooting position and immediately fired a precise shot at one of the eight targets. In contrast to earlier claims [8], fish never shot from directly below the target. Rather, they chose viewing angles that varied over a broad angular range from about 60° to 88° with respect to the water surface with a median angle of about 79°, which was unrelated to target size or height. As a consequence, during the shot the selected target appeared at an average horizontal distance of 39 to 156 mm. At this time, however, the other targets appeared at much greater horizontal distances ranging from 79 to 391 mm. Note that these distances apply only to the situation in which the fish has already made its choice. The actual choice must be based on views taken somewhere on the way from the fish's starting position to its final shooting position. Note that the initial distance was random with respect to target size and that the spatial offset of the disks enforces a minimum spatial separation that adds to this initial distance; this yields a range of about 160 to 630 mm from any of the targets. Thus, selections are made over a large range of horizontal distances between the fish and its potential targets.

To demonstrate the difficulties of size constant vision through a media boundary, we considered a visual system with size constancy in one medium and asked which corrections such a system would have to make to achieve size constancy in the presence of the interface as well. Figure 2A illustrates this approach: by calculating the paths of rays [9] that emanate from a target point and enter the eye of the fish (4 mm below the water surface; pupil diameter was 0.4 mm, exact value is not critical), one can infer the corresponding virtual target. For a purely horizontal object, the virtual image is curved upward and has a horizontal (dxv) and also vertical (dyv) size. Figure 2B shows the apparent horizontal size (dxv of Figure 2A) of a horizontally oriented disk 10 mm in diameter for the spatial configurations that apply in our archer fish experiments. The deviations between real and apparent horizontal size are substantial, and the required corrections would be even larger if the system incorporated the Euclidean size rather than only its horizontal component. Moreover, the strong viewpoint dependency can even cause changes in the size relations among the disks. For instance, if the fish makes its selection while close to a large disk, the apparent size of a more-distant small disk can be larger than that of the close large disk. In principle, the fish could overcome these problems by scanning the targets and taking a view of each target from the same horizontal distance. However, this is clearly not what the fish did; as soon as the objects were shown, the fish swam straight to their shooting position and fired.

Do inexperienced archer fish spontaneously determine the absolute size of their prey? A first set of experiments tested the performance of "naive" fish, which were always rewarded with a *Lucilia* fly no matter the size of the disk they shot at. Surprisingly, in this naive state in which size did not determine the reward, all 13 fish showed clear size preferences at all presentation

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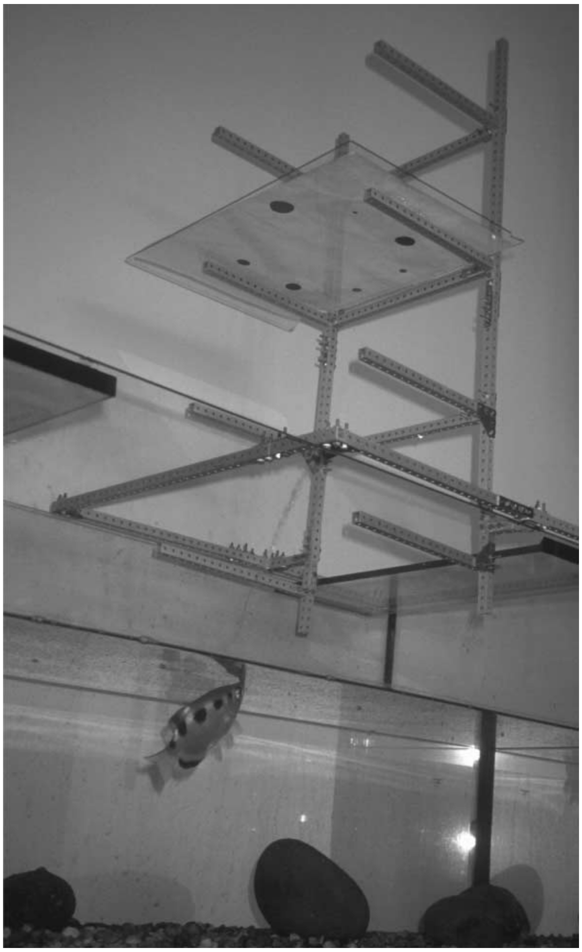

Figure 1. Experimental Arrangement

An archer fish fires at one out of eight differently sized disks, presented behind a glass plate at one out of four heights above the water surface.

heights. However, the preferred size generally shifted toward larger sizes as target height above the water surface was increased. Figure 3 demonstrates this with results from three of the 13 fish. With two exceptions (in which the fish apparently chose the same objective size at all heights), objective size did not govern the fish's preference. At the greatest heights, the fish often preferred to shoot at targets that would have been too large to be swallowed. In summary, all naive fish had clear size preferences, but these were not based on objective target size.

Can archer fish learn to compensate for complex optical distortions and judge the absolute size of prey items? To test this, we trained four fish (length 15–16 cm) to recognize a target (a disk 6 mm in diameter) at all vertical and horizontal distances only by its objective size. This task seemed hard for the fish; to attain the precision illustrated in Figure 4, the fish required 4–8 weeks of daily training, or approximately 500–1500 trials. During training only single disks were shown to the fish. In this way the fish were prevented from learning size relations; had they been trained with the eight-object assembly, they could have learned, for instance, to select the second-smallest target. Each disk shown during training was chosen at random from the eight differently sized disks and was presented at a height that was also randomly chosen from the four heights. If a correct choice occurred within 10 s, the fish was rewarded with a fly. Training success was tested by choice experiments with the assembly of eight objects as described above. All four fish mastered the task and selected the correct size at any height. The impressive precision attained, about 1 mm at a height of 800 mm, is illustrated in Figure 4 for one of the four fish.

In which way did the archer fish learn to make the complex corrections required for inferring absolute size from an underwater view? One possibility would be that the fish could have stored memory templates of previously rewarded situations, each template containing a rewarded combination of actual image size together with the target's vertical and horizontal distance. In a choice situation the fish would then select that target that comes closest to one of these stored combinations. In other words, during the learning stage the fish would simply assemble a table of reference of rewarded combinations and make its choices based on an interpolation within its table of reference. To test this hypothesis, we retrained two of the four fish to select a novel target size (10 mm). However, training to the new size was given only at two of the four possible presentation heights (200 and 400 mm). If the fish had been interpolating among stored rewarded combinations of apparent size and vertical and horizontal distance, then they would have selected the 10 mm disk only at the training heights of 200 and 400 mm and not at 600 and 800 mm. This is because at these greater heights rewarded combinations could previously have been stored only for the 6 mm target. Thus, when put to a test at the novel distances, the fish should have selected the old target size. Figure 5 first shows that our partial retraining to the 10 mm disk was successful (first two panels). Moreover, when put to the critical test the fish readily selected the novel size at the novel greater distances as well (Figure 5, lower two panels). This clearly disproves the interpolation hypothesis.

In learning the objective size of their targets, the archer fish thus had not simply learned combinations that were rewarded in the past but went beyond to acquire a concept of objective size that they later could readily apply to the novel views. This ability is remarkable in several respects. First, the optical effects require rather precise knowledge of spatial configuration (see Figure 2). The question of how the fish's visual system is able to provide this information is presently wide open. When fish aim their shots, for which precise distance information is also required, monocular cues suffice and binocular distance cues are not required. Whether stereo vision is also unnecessary for size constant vision cannot, however, be said at present. Second, the fish apparently is able to combine such spatial knowledge in a yet-unknown way with apparent size (or apparent locomotion-induced image transformations) to deduce a concept of objective size. Whatever sensory representation it uses, the fish evidently is able to form a concept of size that is tailored to the complex optics at the water-

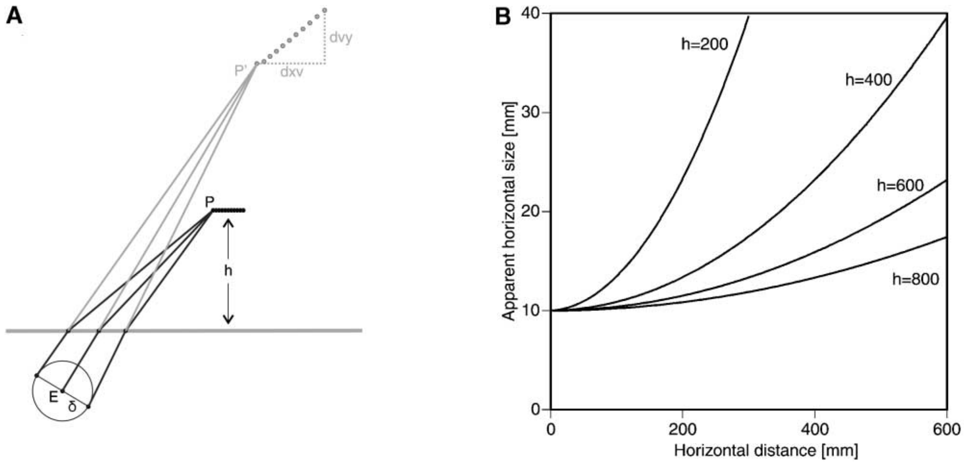

Figure 2. The Corrections a Size Constant Visual System Must Make to Account for Light Refraction

(A) An illustration of the virtual image of a horizontal disk (at height h above the water surface) as it would appear to a size constant visual system that is unable to account for the optical effects of the water-air interface is shown. The uncorrected apparent image has a larger-than-actual horizontal size (dxv) and also extends into the vertical direction (dyv). To quantitatively derive this a computer program calculates the virtual image point P′ for each point P of the real disk; it applies Snell's law [9] to the light rays within a bundle emanating from P and entering the eye's pupil (center at E, pupil radius δ) to do so.

(B) This panel shows how the apparent horizontal size of a disk of 10 mm diameter depends on height h and horizontal distance. Calculations are as illustrated in (A) for the experimentally relevant target heights 200, 400, 600, and 800 mm and for the horizontal distances (horizontal distance between E and P in [A]) that were assumed by the responding fish (see text). The impressive viewpoint dependency of the required corrections can equally well be demonstrated in terms of corrections to apparent distances and angles subtended by the images rather than sizes (results not shown).

air interface. Because this situation poses particularly rigorous requirements on the relation the animal must make between target localization and the apparent image, the fish is an attractive model to explore how animals learn to form concepts to bring order into their sensory experiences.

Received: June 24, 2004
Revised: July 8, 2004
Accepted: July 8, 2004
Published: September 7, 2004

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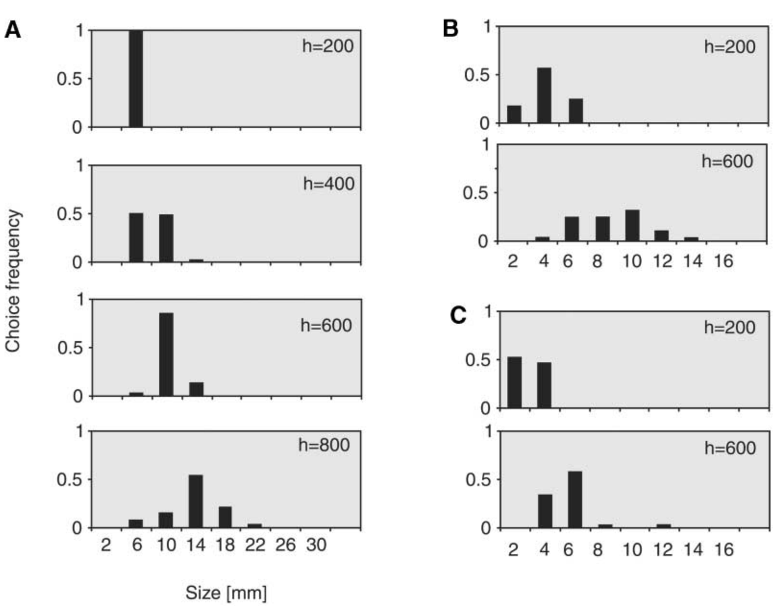

Figure 3. Naive Fish Do Have Size Preferences but Do Not Select Objects of the Same Absolute Size

(A) An example of results from a fish sized 15 cm is shown. The size of the preferred object increased about 2-fold as height h was increased from 200 to 800 mm (total of $n = 162$ tests).

(B and C) Experiments with two smaller fish are shown at a higher resolution. In these experiments disk sizes differed only by 2 mm (instead of the normal 4 mm). The choices of each fish are shown for two of the four heights (121 tests are shown).

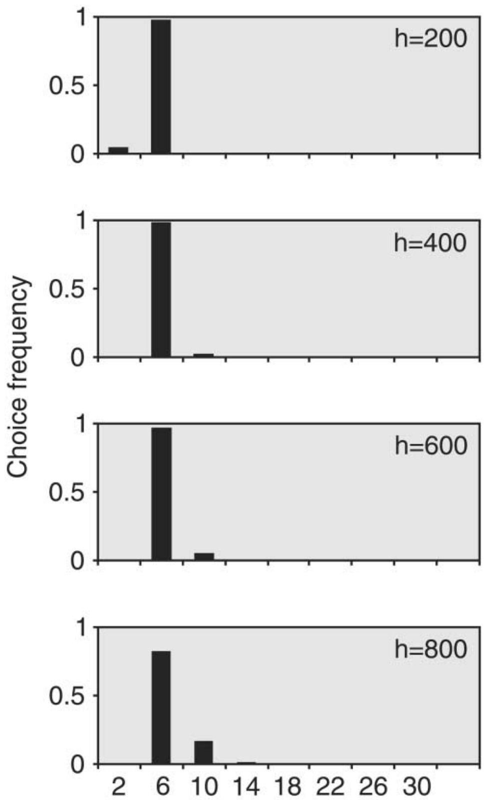

Figure 4. Trained Fish Can Acquire Size Constancy with Remarkable Precision

This is an example of tests with a fish (same as in Figure 3A) that had been trained to select an object of 6 mm absolute size at all heights h (200 to 800 mm) despite the viewpoint-dependent distortions in apparent size illustrated in Figure 2 (n = 270).

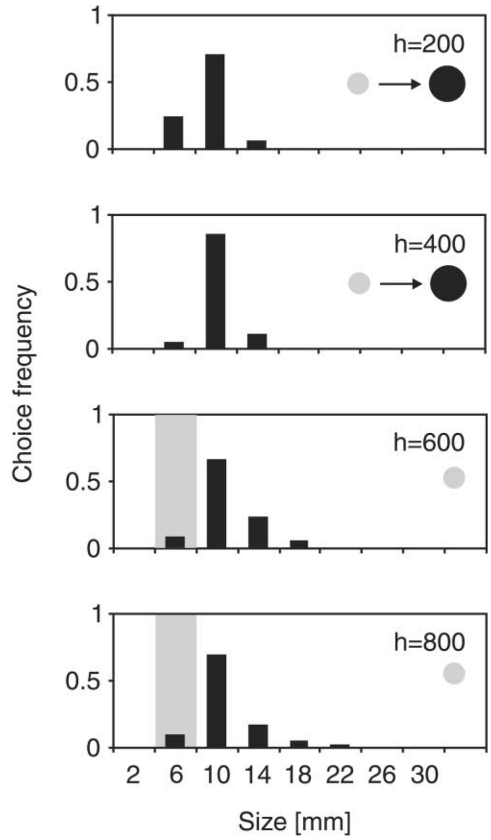

Figure 5. Archer Fish Form a Concept of Absolute Size Rather Than Interpolating Templates

This figure shows experiments we conducted with one of two fish to determine whether the fish had simply stored previously rewarded combinations of apparent image, viewing angle, and height ("templates") and based its choices on an interpolation among these templates. After having succesfully been trained to recognize a disk sized 6 mm (illustrated as a gray disk in the panels), the fish were subsequently retrained to select a novel target size (10 mm, illustrated as a larger black disk). However, only a partial retraining was given, at 200 and 400 mm. In subsequent tests carried out at all four heights, the fish chose the novel size at the two greater heights as well. This contradicts the template interpolation hypothesis that predicted the choice of the 6 mm disk (gray bar).

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