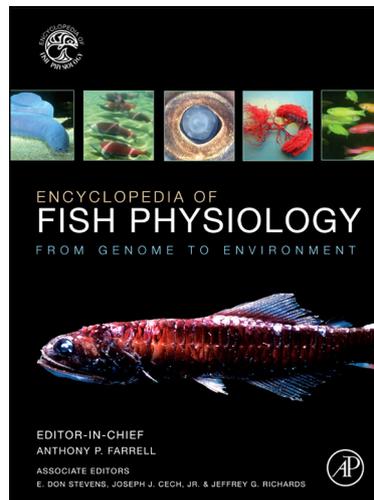


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## Behavioral Assessment of the Visual Capabilities of Fish

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### Glossary

**Color constancy** The capability to assign a unique color to an object, regardless of the spectrum of the illuminating light.

**Dorsal light reflex** A response to light in which fish try to tilt so as to keep the sun upright.

**Heart rate conditioning** If an electric shock that slows down heart rate is repeatedly paired with a stimulus, the stimulus alone will slow down heart rate.

**Optokinetic nystagmus** When the eyeball rotates to track a moving extended pattern.

**Optomotor response** When an extended visual pattern moves, animals often reduce retinal image motion by moving themselves.

**Size constancy** Assigning the absolute size of an object, irrespective of its distance from the eye.

**Template matching** A simple recognition strategy that lacks viewpoint invariance.

**Two-alternative forced choice** A paradigm in which the animal unequivocally selects between two options.

### Introduction

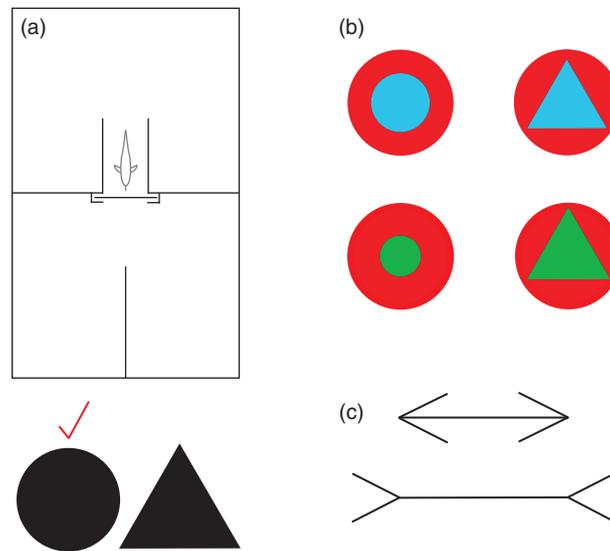
With more than 30 000 species inhabiting nearly every aquatic environment on earth, fish provide a rich source for studying fundamental aspects of visual processing (see also **Sensory Systems, Perception, and Learning: Communication Behavior: Visual Signals and Vision: Vision in Fishes: An Introduction**). Many fish show highly sophisticated visual behaviors that often allow the analysis of unique visual specializations. Furthermore, most fish can readily be trained. This was masterly used to dismount the claim that lower vertebrates and invertebrates could not see color. Interestingly, later Nobel laureate Karl von Frisch first succeeded to show this in fish, before his famous work on bees. In this article, we will illustrate a number of behavioral approaches that have been used successfully to tackle most aspects of fish vision. We hope that our brief survey is both stimulating and useful for scientists wishing to study the visual capabilities of their particular species.

Many methods can simply be adapted to study vision in the species that have not yet entered the laboratories and are certain to hold great discoveries in store. Some of the methods can easily be adapted to any species of fish and even to their larvae. Others require sophisticated learning capabilities of the fish and even more so of the

investigator. Sometimes methods can be tailored to particular species, elegantly making use of sophisticated naturally occurring behavior that relies on vision. Here, we present these methods on the way through a brief overview of the visual capabilities of fish. We are well aware of the many excellent accounts on visual behavior and visual capabilities of fish and have therefore focused on a few examples and more recent discoveries.

### Recognizing Objects

The first studies on learning in fish addressed their ability to recognize visual objects. Two-alternative forced-choice tasks were most commonly used. In these, the fish views two different objects (or two-dimensional images of objects) and has to decide which object to approach. Often, the objects are placed outside the tank to provide no other than visual cues for the task. Sometimes a divider between the possible paths is used to really force the choice (see e.g., **Figure 1(a)**). The approach to one of the two objects is rewarded. Many species of fish have been trained this way, providing a great wealth of data not only on the spatial resolution and representation of shape and color, but also on the way fish represent more abstract features such as the texture of a



**Figure 1** Two-alternative forced-choice tasks can be used to study visual pattern recognition. (a) Setup (top view) used to train the electric fish *Gnathonemus* to select one of the two visual patterns – in this case a circle – from a fixed vantage point. The fish views the patterns from its shelter and is rewarded upon moving to the circle. (b) Evidence suggesting simple template matching in *Gnathonemus*. Although successfully trained to a circle, fish chose both figures (top pair, blue) when they equally matched a putative snapshot (red) taken of the training circle. A triangle was preferred when it better matched the putative snapshot (bottom pair, green). (c) Several fish share the Müller–Lyer illusion with human observers. Though both horizontal lines are of equal length, the lower one is considered longer.

pattern or the number of elements in a pattern (e.g., the number of vertical lines). Some earlier studies even attempted to demonstrate a representation of more abstract topological features such as the closeness of a line.

While fish certainly have highly sophisticated capabilities to represent visual patterns, it is always important to keep Ockham's razor sharp and to look for the simplest explanation. A study on pattern recognition in a nocturnal electric fish, *Gnathonemus petersii*, reminds us that fish can discriminate shapes without necessarily using a concept of shape. In a typical two-alternative forced-choice arrangement, *Gnathonemus* viewed two visual patterns, a set distance away, through a transparent screen from its daytime shelter. When the screen was lifted, the fish swam to one of the patterns to receive a reward or to be driven back into the shelter (Figure 1(a)). It was possible to train the fish to discriminate visual patterns but specifically the visual (as opposed to e.g., electrosensory) training worked only at low ambient light intensities of about 10 lx and when the patterns subtended angles larger than about 3°. After the fish were able to discriminate visual patterns, transfer tests were run in which the training patterns were replaced by other patterns (Figure 1(b)). This way the features could be identified that the fish had used to discriminate the patterns. Surprisingly, the results of such tests suggested an extremely simple way of storing the rewarded pattern: template matching. In this strategy (whose use is much better documented in insects), the fish stores the view of

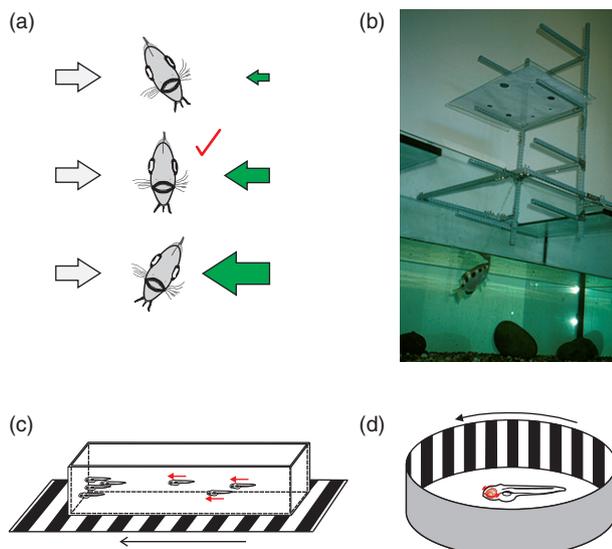
the rewarded pattern from its fixed vantage point and then chooses that one of the two other patterns whose retinal appearance best matches the stored view. These experiments may illustrate the power of a forced-choice arrangement: with fixing the decision point and suitably arranging transfer tests, much can be learned about the way and accuracy in which fish represent visual patterns.

Nonetheless, most fish use much more sophisticated visual representations and seem even to share certain visual illusions with us. The Müller–Lyer illusion, for instance, has been repeatedly demonstrated by Herter in the 1930s and the 1950s in minnows (*Phoxinus phoxinus*), sunfish (*Lepomis* sp.), and in the Siamese fighting fish (*Betta splendens*). He trained fish, for instance, to select the longer of the two stripes and then tested them with a Müller–Lyer pair of figures that were of equal length but appear to have different lengths for a human observer (Figure 1(c)). Herter ran two important controls to support his conclusion: in one the total lengths were equal, whereas in the other the lines were just changed in length so as to make the figures appear of equal length to a human observer. The outcome fully supports the equivalence of humans and fish as far as the Müller–Lyer illusion is concerned. It will be a very interesting future research direction to further probe the degree to which the visual system of fish parallels human performance. To our knowledge no work has specifically been done to disclose the number of images that can be stored over extended periods of time. Early work on acoustically trained fish in the laboratory of

Karl von Frisch suggests that acoustical memories last up to 1 year. Perhaps the visual system of some fish parallels that of the primates also in terms of the number of objects that can be stored during the lifetime of these fish.

## Detecting Color Spectral Sensitivity

The range of wavelengths, that stimulate the eye, can be probed, in principle, by testing which wavelength composition is capable of eliciting a particular visually mediated behavior (see also Vision: Photoreceptors and Visual Pigments). An interesting behavior that has been used is the dorsal light reaction of most teleosts (shared also by other swimming or flying animals) – a reflexive tendency to tilt about the longitudinal axis to keep the sun directly overhead. **Figure 2(a)** shows how it can be



**Figure 2** Making use of spontaneously occurring behaviors. (a) Many fish show a dorsal light reflex in which they partly turn their dorsal side toward the light. By shining reference light (constant, gray) from one side and probing monochromatic light (intensity varied, green) of wavelength  $\lambda$  from the other, it is possible to use this response to make the fish tell when both the light stimuli are equal. (b) Size constancy, and how it is acquired, can be analyzed using the natural shooting behavior of archerfish that requires no coupling between reward and target. The fish receives a reward only upon selecting, regardless of presentation height and its own horizontal distance from the target, a disk of fixed absolute size. (c) A way in which the optomotor response can be used for screening zebrafish larvae for visual defects. When a stripe pattern moves on the ground of the tank, fish with intact vision (and locomotion) follow it and can be collected on one side. (d) The optokinetic nystagmus (OKN) has profitably been used in zebrafish larvae. A larva is embedded in agar and follows the movement of a grating with its eyes. (b) Adapted from Fig. 1 in Schuster S, Rossel S, Schmidtman A, Jäger I, and Poralla J (2004) Archer fish learn to compensate complex optical distortions to determine the absolute size of their aerial prey. *Current Biology* 14: 1565–1568.

employed as a typical null method in which the animal is made to compare two stimuli. The fish receives light from two sources. One provides reference light, which is kept constant, whereas the other provides a probing light of known spectral range and intensity. This probing light is adjusted in intensity such as to balance the fish: if the probing light is too strong, the fish will tilt its dorsal part toward the probing light; if it is too weak, it will tilt to the reference light. This simple and clever method avoids a large number of problems one would run into if spectral efficiency were measured with only one light source and the angle of tilt being the measure of sensitivity. This approach is instructive as an example of how easy it can be to interrogate a fish about matching stimuli.

## Discriminating Colors

Many more methods have been employed to measure the action spectrum of various behaviors, that is, the efficiency of different wavelengths to drive the behavior. None of these *per se* demonstrates the capability of the animal to discriminate color. For color vision, circuitry is needed that compares the output of at least two photoreceptors with different spectral absorption peaks (see also Vision: Photoreceptors and Visual Pigments and Optic Tectum). Such circuitry is useful for detecting objects against a differently colored background in very much the same way as circuitry for detecting coherent movement aids in figure–ground discrimination. Perhaps for this reason, all major taxa use color for detecting and discriminating objects. In fish, color vision was demonstrated by von Frisch and ever since many clever behavioral experiments have been performed to test for color vision in fish. In the following, we describe a set of particularly carefully designed experiments by Neumeier and colleagues that demonstrated tetrachromatic color vision in goldfish (*Carassius auratus*).

In a typical two-alternative forced-choice training, Neumeier's goldfish first had to choose between the two test fields that were homogeneously illuminated with monochromatic light of different wavelength. For some fish, the task was to select that one of the two test fields which had the shorter wavelength. Other fish had to select the field with the longer wavelength of the two. For a given training wavelength, these experiments yielded the minimum difference,  $\Delta\lambda$ , the two wavelengths needed to have so that not less than 75% choices were correct. By then shifting the training wavelength in small steps – eventually through the complete spectrum – Neumeier was able to determine the wavelength dependency of the required difference,  $\Delta\lambda$ , the so-called  $\Delta\lambda$ -function. Interestingly, wavelength discrimination was best (i.e., the required difference in wavelengths,

$\Delta\lambda$ , was lowest) at 400, 500, and 600 nm. The high discrimination ability in the ultraviolet (UV) range was surprising because only three cone types were known before, with maximum absorption at about 450, 530, and 620 nm, but not in the UV range. The behavioral finding, thus, was compatible either with a new fourth cone type with an absorption maximum in the UV range or with a secondary absorption peak in the sensitivity curve of the long-wave cone type.

Neumeier settled this question in elegant color-mixing experiments. Suppose the long-wave cone had a (previously unnoticed) secondary UV absorption peak so that UV discrimination could be mediated by an interaction of the long-wave and a short-wave cone. If that is the case, then it should be possible to create a mixture of blue light (absorbed by one of the two players, the short-wavelength cone) and far-red light (absorbed by the other player) with just intensities matched so that the mixture excites the two cones exactly so as presenting monochromatic light of 404 nm would. In other words, there should be a suitable mixture of blue and red light that the goldfish should not be able to discriminate against monochromatic light of wavelength 404 nm. However, no such mixture could be found – at every intensity combination tested, the goldfish always detected the monochromatic light. A second set of color-mixing experiments tested directly if an UV receptor mediated the goldfish's performance. In this case, 404 nm should not be distinguishable from a suitable mixture of blue and UV. This was indeed found to be the case. Therefore, in very simple but well-designed behavioral experiments and with some patience, it was possible to discover a new UV receptor.

### Color Constancy

An important challenge in color vision is that the spectrum of the illuminating light can change dramatically. To label an apple and a banana unequivocally with the attribute color requires independence of the label with respect to these changes. The ability of our visual system in achieving this is impressive: when the illumination is changed such that now a banana reflects more red light than was previously reflected by a nearby apple, we basically perceive the colors unchanged. This property is described by the term color constancy. In primates, the visual cortex is thought to mediate color constancy. Nonetheless, in fish – that lack a cortex – color constancy was demonstrated not long after the von Frisch's discovery of color vision in fish. More recently, a thorough study by Neumeier and colleagues has probed in great detail the full extent to which color constancy of the goldfish parallels that of the humans. Such findings are important and can, taken together, suggest that color constancy is a

rather basic trait that does not rely on a visual cortex but can be realized with the circuitry at hand (see also **Vision: Optic Tectum**).

### Spatial Vision

Knowing the distance of objects can be decisive in the selection of an adapted behavior: How close is the predator – is it better to hide or to escape? Is the prey close enough to launch an attack (see also **Sensory Systems, Perception, and Learning: Spatial Orientation: How do Fish Find their Way Around?**) When food (or being fed on) is involved in an interesting visually guided natural behavior, it often can be used to characterize information about distance that the visual system provides. A good example is the archerfish (*Toxotes* sp.) that is famous for shooting water at aerial prey to dislodge it from its substrate and to catch and devour it at the water surface. Because these fish do not fire from directly below their prey, they cannot simply send their shot straight up. Rather the fish must set angle and speed of the water jet, depending on their vertical and horizontal distance from their target, so that it passes through the target location. Because in well-trained fish the jet is sharp and because the fish can hit from large vertical and horizontal offsets, this requires the fish to have precise distance information. The fish also use information on distance to infer the absolute size of their aerial targets, regardless of their horizontal and vertical distance (**Figure 2(b)**). Archerfish learn this in surprisingly efficient ways and achieve accuracy in estimated absolute size of at least 1 mm for targets presented 80 cm above the water surface, thereby fully accounting for the fact that the judging eye is under water while the target is in air. Training of the fish is easy because their natural feeding behavior requires neither identity of the reward with the object they fire at, nor strict temporal congruency of shot and reward. Furthermore, the fish are opportunistic and can be made to fire at anything that is rewarded. Thus, the spontaneous firing behavior of this fish can readily be used to assay size constancy. For archerfish, having size constancy is very useful to set the caliber of their shot: the maximal attachment force of prey tends to increase linearly with absolute size. Therefore, knowing size is useful for scaling the investment. Size constancy has also been shown in goldfish in a less dramatic setting without the complications introduced by a water–air boundary. Using a two-alternative forced-choice training, it was possible to show that size constancy in goldfish does not even require binocular vision. This suggests that the distance information is already provided by monocular cues (at least when binocular cues are absent).

## Detecting and Analyzing Movement

### Large Field Motion

When a fish drifts in a stream, the image of its surroundings moves coherently across its retina. Fish can compensate for drift by detecting this coherent motion and adjusting their forward speed so that the image motion vanishes. This is the basis of the so-called optomotor response (OMR) shown by most fish, but widely distributed among animals and is also present in humans. A standard paradigm used to characterize motion vision is to place the fish in the center of a rotating drum. The drum is lined, for instance, with a vertical grating of alternating black and white stripes. Using a suitable projector, the drum can also display a moving computer-generated pattern. If the eyes of the fish do not move themselves, the fish then attempts to move so as to minimize image motion. Ideally, this would make the fish circle at the pattern's angular speed. Many variations of this setting have been used. A very convenient method is, for instance, to project a computer-generated pattern on the bottom of the tank (**Figure 2(c)**). The movement can then be just in one direction or swinging back and forth.

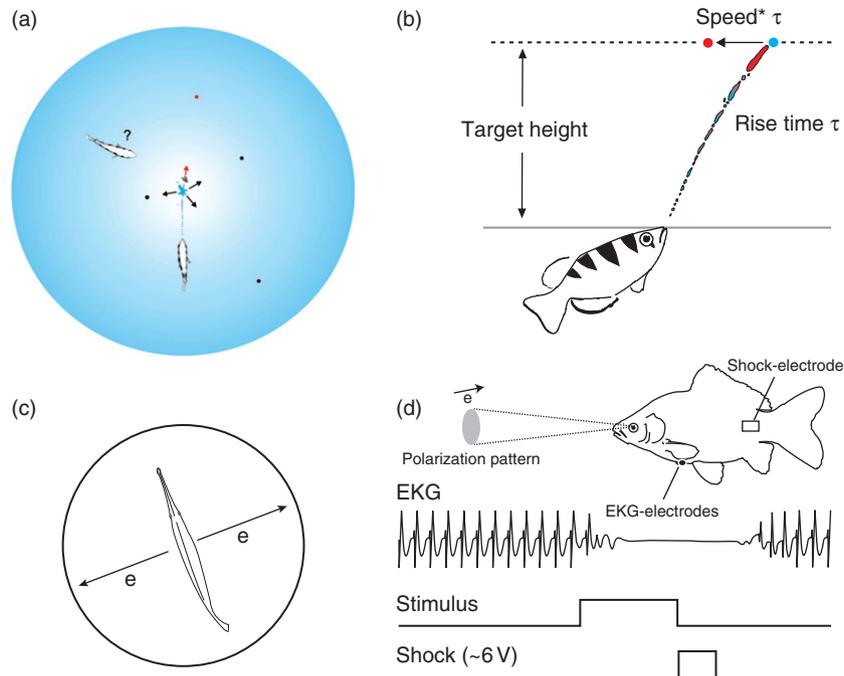
A second useful behavior in response to visual large field motion is the optokinetic nystagmus (OKN; **Figure 2(d)**). Here, the large-field retinal image motion is not compensated by moving the whole body but by following the moving pattern with the eye. Obviously, this cannot go on forever. The typical OKN therefore consists of periods in which the eyeball rotates to track the pattern motion and brief intervals when the eyeball is rapidly rotated back. Both the OMR and the OKN can be done noninvasively, do not require training, and can be probed over extended periods of time. This makes these methods very useful for probing the time course of light adaption, the spectral input to the pathways that drive the OMR/OKN, or the robustness of large-field motion detection with respect to floating particles (visual noise) in the foreground. The OMR has also been useful to probe functional specializations in species such as the four-eyed fish (*Anableps anableps*) that views its aerial and underwater world with different pairs of eyes and in which the OMR is predominantly driven by aerial motion. In light of all its advantages, it should not be forgotten that fish are not reflex machines that are under the strict command of moving stripe patterns. Fish use their OMR as a tool serving an intended movement but not preventing it. In intended locomotion from one location to another, the function of the OMR is to stabilize the chosen path through a stream. It is therefore important to check the readiness of the chosen species to cooperate in the given setup. Our lab has, for instance, failed in demonstrating and using an OMR in seahorses (*Hippocampus reidi*).

Nevertheless, OMR and OKN work well for most fish and, most surprisingly, even in some larvae. In zebrafish larvae (*Danio rerio*), this helps to assay genes important for retinal function and for assembly and maintenance of postretinal processing. With the visual system fully developed already 5 days after fertilization, the larvae already show visually guided behaviors. Because many techniques can readily be applied to larvae but not to adults, it is important to see which features of the fully developed system in adults are already functioning in the larva. Zebrafish larvae respond to visual motion very early on. Surprisingly, they not only detect the so-called first-order motion in which a pattern is defined by a spatial intensity gradient (e.g., in the case of the classic grating). The larvae even detect second-order motion of contours that are defined by changes in texture or flicker but leave the spatial distribution of luminance constant. Detecting such more elaborate ways of movement is – in primates – often considered a task for the visual cortex in which separately processed information on first- and second-order motion is combined. It is an exciting finding that the zebrafish larva is already fully equipped to detect second-order motion. This suggests that the computations can be done much more peripherally and, perhaps, even within the retina.

### Small Field Motion: Perceiving the Speed of Objects

Fish can also assess the speed of objects but little is known on how accurate they are. A good alternative to starting a forced-choice training setup is to look for naturally occurring behaviors that rely on information about speed. A particularly rewarding subject in this regard is the archerfish whose unique hunting technique requires it – in at least two ways – to represent the speed of small target objects. Archerfish can learn to hit moving aerial targets (**Figure 3(a)**) that travel considerably during the rise time of their shot. This requires the fish to adjust their shots to target speed. In the respective experiments, target motion was shown only in a small area. Surprisingly, fish that had been trained exclusively with horizontal motion also fired appropriately when the target had a vertical component of speed whose neglect would have been experimentally detectable. This suggests that they can represent three-dimensional speed, at least in ways that can readily be used to set the appropriate combination of shooting angle and horizontal distance from the target that is required to hit.

A different context in which it is important for the fish to judge the speed of small objects is in their predictive start. Archerfish launch a rapid start toward their prey's later impact point as soon as they estimate the direction and speed of their dislodged prey (**Figure 3(b)**). They can estimate speed well enough in an impressively short



**Figure 3** Naturally occurring behavior and classical conditioning. (a), (b) Two naturally occurring behaviors that help to assess how fish represent the motion of small objects. (a) Top view of prey catching in archerfish. The moment a shot is fired the fish do not know at what speed and in which direction its prey is going to move when dislodged. Archerfish therefore monitor initial motion and then turn and start so as to be at the right time at the inferred later point of catch. This behavior involves accurate representation of speed and direction. (b) Representing speed also is needed when the fish learn to hit a target that moves, in a restricted area, at constant speed. Depending on target height the fish must learn to account for the speed-dependent displacement of their target during the rise time of their shot. (c, d) Using behavior to demonstrate that fish detect polarized light. (c) *Zenarchopterus* spontaneously orient their body axes according to the e-vector of linearly polarized light. (d) Heart-rate conditioning: by pairing a visual stimulus with a mild electric shock fish eventually suppress their heart-beat activity when stimulated with polarized light. The conditioned response can then be used to obtain threshold levels and to correlate them with photoreceptor distribution in that spot of the retina that has been stimulated. (a) Adapted from Fig. 1 in Schlegel T and Schuster S (2008) Small circuits for large tasks: High-speed decision-making in archerfish. *Science* 319: 104–106. (b) Adapted from Fig. 1(a) in Schuster S, Wöhl S, Griebisch M, and Klostermeier I (2006) Animal cognition: How archer fish learn to down rapidly moving targets. *Current Biology* 16: 378–383.

interval of time. Experiments in which the fish are confronted with falling objects of novel sizes, in which the background behind the objects has a novel distance and in which novel vertical speed components are added to the movement currently, suggest that archerfish use an estimate of absolute speed to drive their predictive start.

### Detecting Polarized Light

Behavioral methods have also demonstrated that fish can detect the polarization of light. This was surprising because in vertebrate eyes the morphological foundation of this sense is less conspicuous than in the compound eyes of the arthropods: chromophores in the disks of vertebrate photoreceptors are not aligned as they are in the microvilli structures of arthropod rhabdoms and can move freely within the disk membranes in the outer segments. The first evidence came from orientation behavior of *Zenarchopterus dispar* and *Z. buffoni* under illumination with linearly polarized light. *Zenarchopterus* preferred

heading directions perpendicular or parallel to the e-vector (Figure 3(c)). This and other results disclosed the ability of fish to detect the polarization of light and to use this attribute for orientation. Furthermore, contrast enhancement, for example, for prey detection, was suggested as a further advantage of polarization vision in fish (see also Vision: Photoreceptors and Visual Pigments and Adaptations of Photoreceptors and Visual Pigments).

Behavioral studies also revealed the morphological basis of polarization vision in fish. One successful approach used the so-called heart-rate conditioning. In this classical conditioning method, fish are trained to associate a stimulus, in this case a polarization pattern (conditioned stimulus) with a harmless electric shock (unconditioned stimulus). Fish respond to mild shocks (about 6 V) by a short interruption of heart activity (Figure 3(d)), mostly combined with suppression of respiration activity. Monitoring the electrocardiogram of trained fish thus offers the possibility to measure precise thresholds of polarized light detection. By comparing the sensitivity thresholds for polarized light with the

absorption spectrum and the arrangement of double cones in the retina of the sunfish (*Lepomis cyanellus*), it became evident that the double cones are responsible for polarization vision in at least some fish.

## Conclusion

A rich repertoire of behavioral approaches is ready for use for future discovery. It is important, however, to keep in mind the simple fact that behavioral approaches elucidate those aspects of visual information that are fed into the behavior at hand. To demonstrate color vision, for instance, one must select a behavior that (if the fish has color vision at all) would probably be driven based on color information. For example, using the OMR would be a bad choice here: in goldfish, the OMR is colorblind. However, suitable training of the fish readily reveals its tetrachromatic color vision. Similarly, placing an archerfish into rotating stripe drums would not allow us discovering its many exciting capabilities.

We predict that behavior will continue to play an important role in the future of fish vision:

1. A promising direction is comparing visual capabilities of fish with those of primates. Such studies can show that many apparently complex tasks can be solved quite early by comparatively simple circuitry. Zebrafish larvae, for instance, readily detect second-order motion and may use circuitry right within their retinæ to detect this more abstract form of motion.
2. Exploiting the visual behaviors in the larvae of zebrafish will continue to be a promising direction for future research that provides key factors required for the assembly and higher functions of the visual system.
3. The behavioral analysis of visually specialized species will provide further surprises in visual information processing that force us to reconsider our notions on basic physiological processes.
4. Finally, vision is not simply a prerequisite of behavior but is tightly interwoven with it: fish move to obtain visual information, modulate incoming sensory information during intended movements, and integrate vision with other sensory information to most efficiently pursue their goals. In fish, these aspects are well accessible to behavioral dissection.

See also: **Sensory Systems, Perception, and Learning: Communication Behavior: Visual Signals; Spatial Orientation: How do Fish Find their Way Around?. Vision: Adaptations of Photoreceptors and Visual Pigments; Optic Tectum; Photoreceptors and Visual Pigments; Vision in Fishes: An Introduction.**

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