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What a predator can teach us about visual processing: a lesson from the archerfish

Mor Ben-Tov[1], Ohad Ben-Shahar[2,3,6] and Ronen Segev[3,4,5,6]

The archerfish is a predator with highly unusual visually guided behavior. It is most famous for its ability to hunt by shooting water jets at static or dynamic insect prey, up to two meters above the water's surface. In the lab, the archerfish can learn to distinguish and shoot at artificial targets presented on a computer screen, thus enabling well-controlled experiments. In recent years, these capacities have turned the archerfish into a model animal for studying a variety of visual functions, from visual saliency and visual search, through fast visually guided prediction, and all the way to higher level visual processing such as face recognition. Here we review these recent developments and show how they fall into two emerging lines of research on this animal model. The first is ethologically motivated and emphasizes how the natural environment and habitat of the archerfish interact with its visual processing during predation. The second is driven by parallels to the primate brain and aims to determine whether the latter's characteristic visual information processing capacities can also be found in the qualitatively different fish brain, thereby underscoring the functional universality of certain visual processes. We discuss the differences between these two lines of research and possible future directions.

Addresses
[1] Department of Neurobiology, Duke University, Durham, NC 27710, United States
[2] Computer Sciences Department, Ben Gurion University of the Negev, Israel
[3] Life Sciences Department, Ben Gurion University of the Negev, Israel
[4] Zlotowski Center for Neuroscience, Ben Gurion University of the Negev, Israel
[5] Biomedical Engineering Department, Ben Gurion University of the Negev, Israel

Corresponding author: Segev, Ronen (ronensgv@bgu.ac.il)
[6] Equal contribution.

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Introduction

While at first sight the archerfish appears unassuming, this fish has one of the most remarkable hunting strategies in nature. It is best known for its ability to hunt either static or dynamic (moving) insects above the water level, either by knocking them down with a jet of water from its mouth (Figure 1a) or by jumping well above the water's surface to bring down food [1–3]. Equally impressive is the archerfish's capacity to learn to distinguish and shoot at artificial targets presented on a computer screen in controlled laboratory experimental settings (Figure 1b,c), a behavioral feature that makes it possible to monitor its overt attention [4,5••,6••]. In this sense, the archerfish provides a relatively straightforward equivalent of monkey or human subjects, whose psychophysical decisions can be documented verbally or behaviorally. For these reasons, controlled complex experimental procedures on the archerfish have been growing steadily.

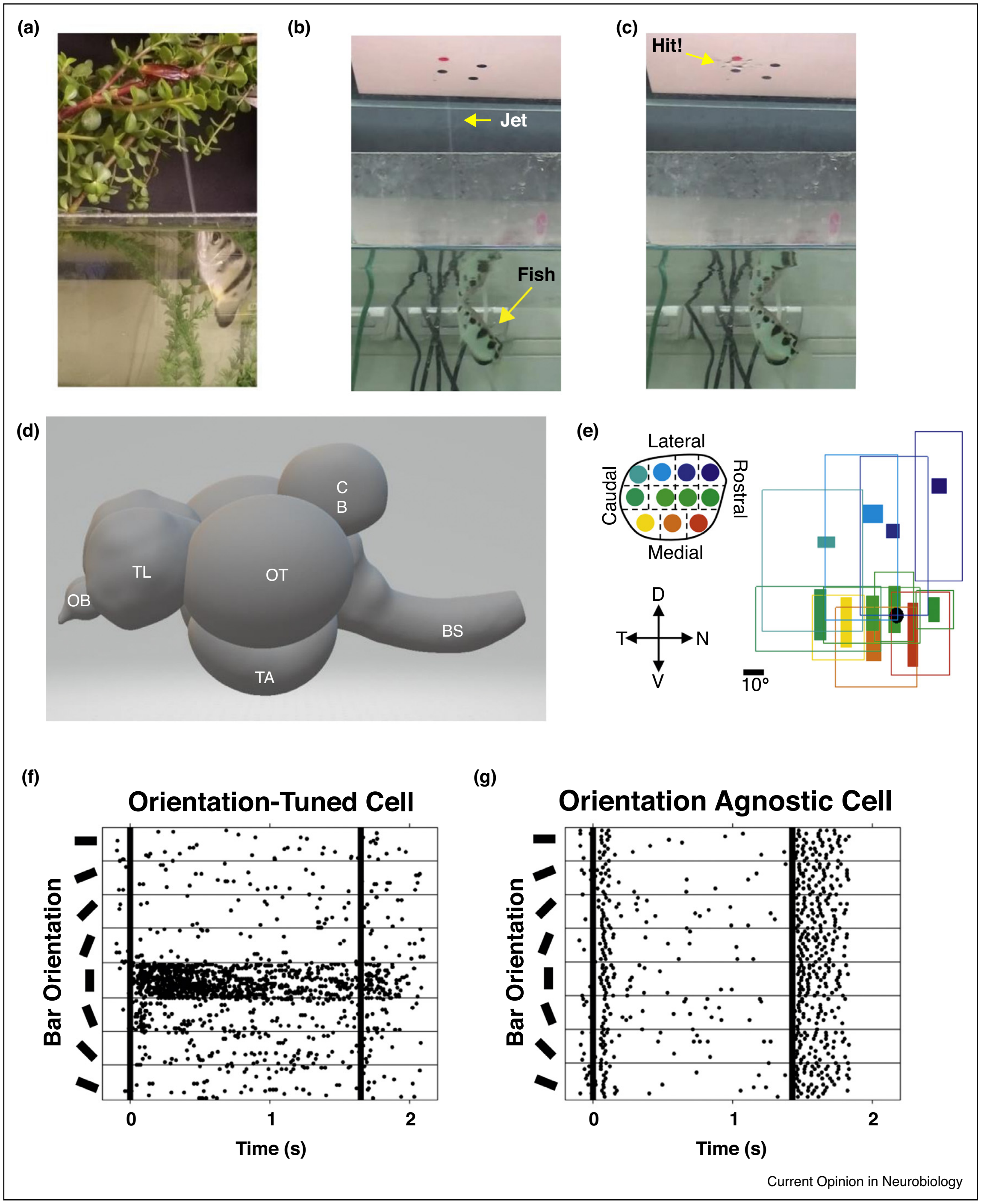
In this review, we describe recent progress in understanding visually guided behavior in archerfish. In particular we examine the ability of the archerfish to predict target trajectories during hunting behavior [7•,8], visual search behaviors that parallel those exhibited by mammals, where they are thought to be computationally supported by the cerebral cortex [6••,9••,10], and higher visual capacities such as face recognition [11••]. We conclude with some possible directions for future research.

Basic architecture of the archerfish visual system

As in any other animal, vision in the archerfish starts in the retina, which is characterized by a non-uniform distribution of photoreceptors over the retinal surface. The distribution of rods and cones is correlated with the spectral differences in aquatic and aerial fields of view [12]. The area centralis — a 6° retinal patch with the highest receptor density and maximal resolving power [13•,14•] — is located in the temporal retina and is aligned with the preferred spitting angle. The visual acuity in this region is approximately 0.15° and closely matches the predicted resolution by photoreceptor spacing. Given that the archerfish can shoot targets of 1 cm in size up to 2 m above the water level [2], this corresponds to a target spanning two photoreceptors on the retina.

As could be expected from a highly visual animal, the archerfish's largest brain region is the optic tectum, where much of the visual and sensory integration functionalities take place (see Figure 1d, redrawn from Ref. [15•]). While

Figure 1



The archerfish. **(a)** An example of an archerfish shooting at a cockroach sitting on leaf above the water level. The fish's mouth protrudes from the water while the fish (and in particular, its eyes) remains underwater. **(b,c)** The archerfish can be trained to shoot at targets displayed on a computer monitor. This makes well controlled behavioral experiments feasible. Here we depict the shot moment (b) and the readout of the success (c). **(d)** The archerfish brain is characterized by a large optic tectum, which is a major sensory processing region. (*Abbreviations*: OB, olfactory bulb; OT, optic tectum; TL, telencephalon; BS, brain stem; TA, thalamus.) **(e)** Retinotopic mapping of the optic tectum on the visual field. The mapping is from a dorsal view of the optic tectum (top left panel). The different locations on the optic tectum are mapped according to the color-coded rectangles. The solid rectangles represent the average receptive field location and size. Contour rectangles around the solid represent the area into which all the receptive fields belonging to the same grid fall. **(f,g)** Two examples of cells recorded from the optic tectum of the archerfish showing orientation tuning and orientation agnostic response profiles. (Panel d redrawn from Ref. [15•], panels e–g redrawn from Ref. [16•].)