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

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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.

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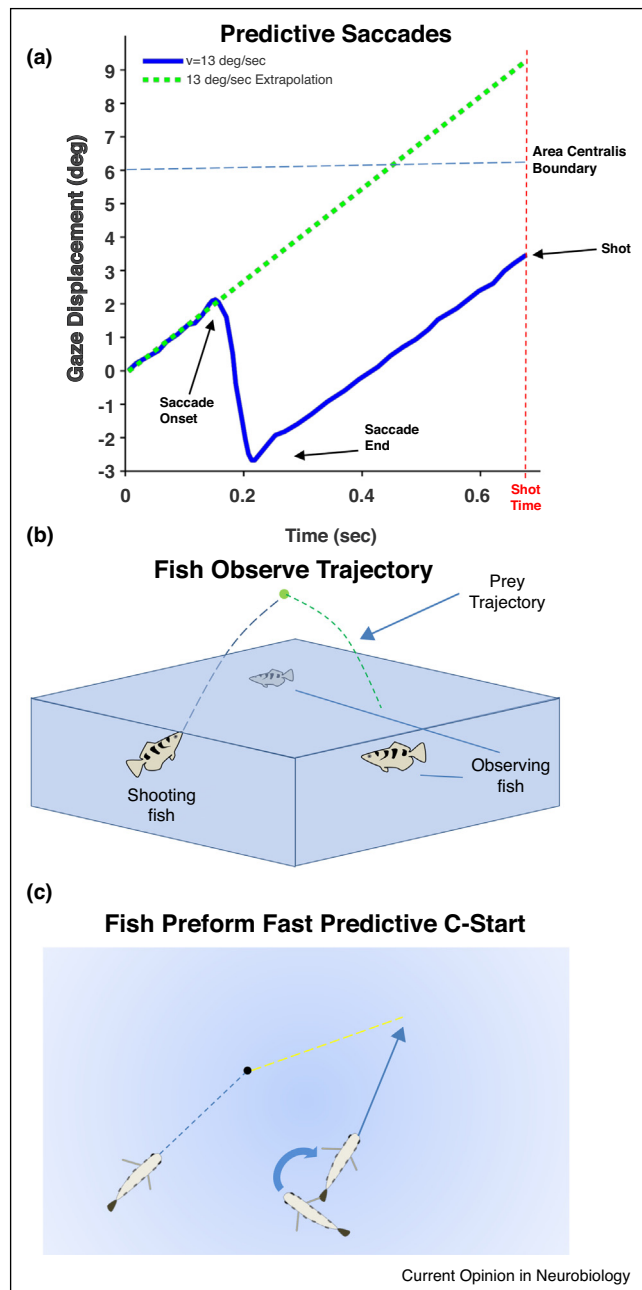
As could be expected from a highly visual animal, the archerfish's largest brain region is the optic tectum, where much of the visual and sensory integration functionalities take place (see Figure 1d, redrawn from Ref. [15•]). While

Figure 1
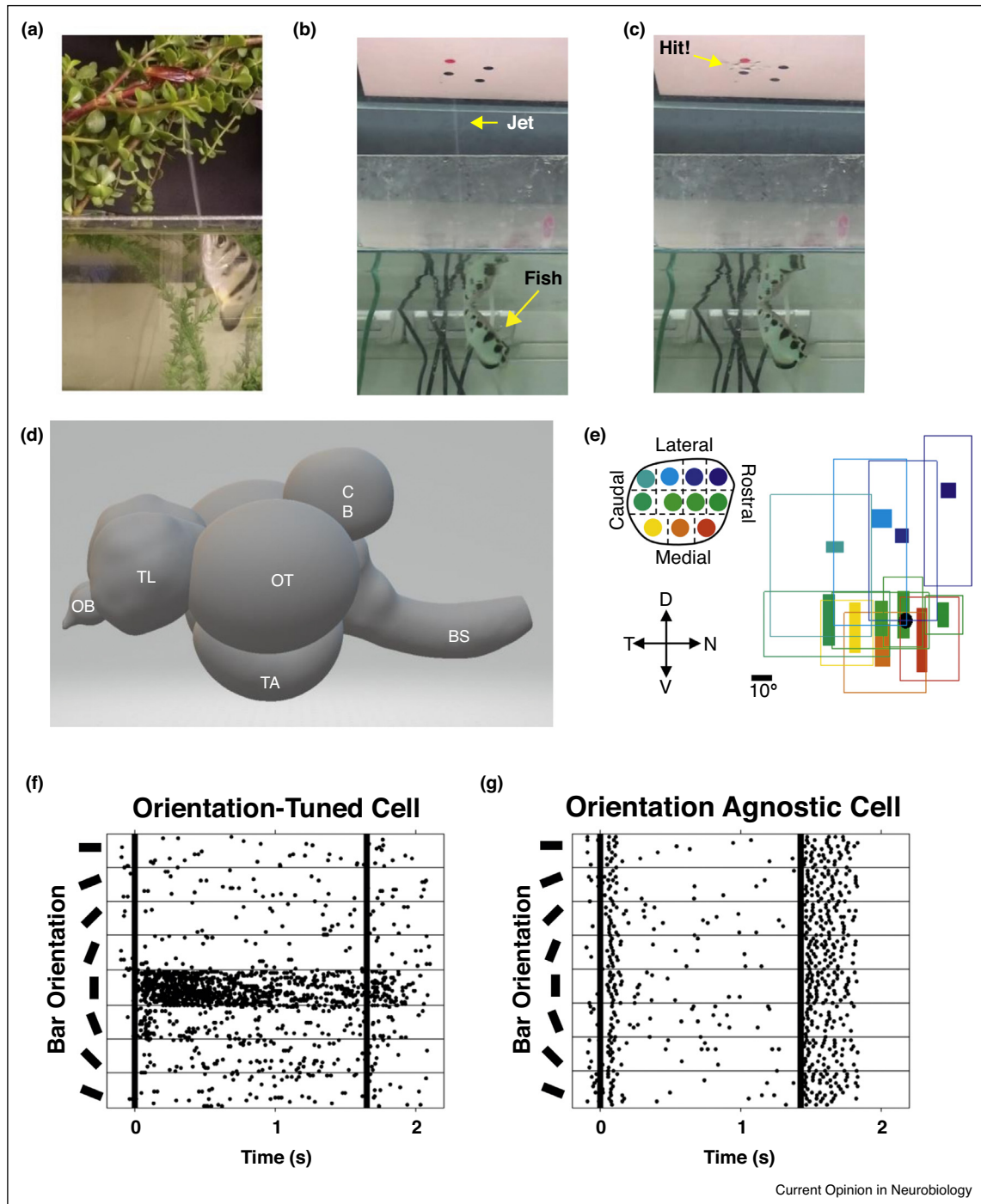
The archerfish. **(a)** An example of an archerfish shooting at a cockroach sitting on leaf above the water level. The fish's mouth protrudes from the water while the fish (and in particular, its eyes) remains underwater. **(b,c)** The archerfish can be trained to shoot at targets displayed on a computer 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*].)

Figure 2

(a) Predictive Saccades

(b) Fish Observe Trajectory

(c) Fish Preform Fast Predictive C-Start

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The archerfish uses fast prediction during visually guided behavior. **(a)** The archerfish is capable of shooting at moving targets by predicting the target's future location. To aim accurately at a moving target, the archerfish preforms a predictive saccade to a future location of the target. This is exemplified by extrapolating the target trajectory on the retina as if there is no predictive saccade. In this case (green curve), at the time of shot the target would have been outside of the area centralis boundary. The saccade overshoots (i.e. the gaze displacement on the retina goes blow zeros) such that at the time of the shot the target projection on the retina will be well inside the area centralis. **(b)** When archerfish hunt in a group, the shooting fish is not necessarily the one to grab the food. After the shot, bystander fish that watch the event can extrapolate the trajectory of the falling prey from the beginning of its ballistic trajectory up to the moment the prey lands on the water's surface. **(c)** Following the observation of the initial

the archerfish brain exhibits the general morphology of percomorphs, a large clade of teleost, or bony fish [15[•]], and its general anatomy is well mapped [15[•]], little is known about the connections between regions and the exact function of each.

The mapping from the retina to the optic tectum is organized in a way that preserves retinal topography [16[•]]. Specifically, the dorsal and ventral visual fields project to the lateral and medial parts of the optic tectum, respectively. Similarly, the nasal and temporal visual fields project to the rostral and caudal parts of the optic tectum (Figure 1e). Single visual cells in the optic tectum can be categorized functionally into orientation-tuned cells, direction-tuned cells, and direction-agnostic cells [16[•]] (see e.g. Figure 1f,g).

The archerfish uses fast prediction of the moving target during predation

While archerfish needs to compensate for the refraction at the water's surface for all targets, interception of fast-moving targets imposes an additional challenge to its visual system. If the fish cannot predict the target trajectory and position at the time of impact, the latency due to physiological and mechanical processing will cause overshoot or undershoot. However, the archerfish can indeed intercept targets high above water's surface, moving as fast as 25°/s (angular speed on the retina). This remarkable capacity is equivalent, in human terms, to a person hitting a target moving at 3 m/s from 6 m away with a racquetball approximately 6 cm in diameter. Clearly, to do so, the shooter needs to consider both the target's three-dimensional position and its displacement. Recent work indicates that archerfish do both [7[•]].

When archerfish shoot at moving targets, they must deal with an additional issue since unlike mammals, fish do not possess smooth pursuit eye movement [17[••]]. In humans, smooth pursuit makes it possible to lock the image of a moving object onto the fovea and thus avoids low-resolution vision during tracking (which would occur if the target was lost from the center of vision). Since the archerfish area centralis is about 6° in diameter, a fast-moving target can cross it in hundreds of milliseconds, leaving too little time for planning and executing the shot before the visual input reduces in quality. In the absence of smooth pursuit, archerfish have adopted a predictive saccade mechanism that shifts the center of gaze to the future location of the target in the visual field [17[••]]. These predictive saccades are initiated before the target leaves the area centralis, thus enabling its projection in high resolution for an additional duration (Figure 2a). If the fish fails to do so, the accuracy of the shot declines by a factor of two [17[••]].

trajectory segment, the archerfish can then initiate a fast swimming c-start directly to the landing location. (Panel a redrawn from Ref. [17[••]], panels b and c schematics following Ref. [42[•]].)

Visual prediction is not only crucial for greater shooting success but also in a social setting. This is because archerfish often hunt in the company of their conspecifics. Thus, prey that is shot by one fish in the school may be dislodged by another that was able to reach the falling prey faster once it hit the water. This fierce competition is often won by the fish that was able to predict the impact point and initiate a swimming maneuver to that location well before the prey hit the water. Careful investigation of such maneuvers in the lab reveals that archerfish observe the first ∼75 ms of the prey's ballistic trajectory after being hit (Figure 2b) and then initiate a fast swim directly towards the location where the prey will later land [8]. For their quickest response, archerfish use the fast C-start mode (Figure 2c) where the fish's body is bent into a C-shape that propels it forward extremely rapidly [8,18].

Visual search in the archerfish

Visual search is a visual behavior aimed at finding an object of interest within a background of distracting visual information (in the form of other objects or textures). This is one of the most critical tasks almost every visual system needs to perform quickly and accurately in diverse visual environments. In primates, there is a general consensus that there are two major modes of visual search: a parallel (and therefore fast) mode, and a serial (and therefore slower) mode [19–22]. These two modes are typically differentiated experimentally by measuring the dependency of the subject's reaction time (i.e. the time required to find the target object) and the number of distracting objects in the environment [19,23]. Since the mechanisms of visual search are considered to essentially be a *cortical* computation, it remained doubtful whether this visual behavior would be part of the non-mammalian visual toolkit. Research in the archerfish in the past decade has eliminated any such doubts.

Visual saliency in the archerfish

Often, especially in parallel visual search, behavior is guided by the saliency of items or stimulus parts. Capitalizing on the importance of orientation in human vision, a seminal work on fish vision saliency proved that archerfish experience the same type of orientation-based saliency as humans do [6••]. After being trained to shoot at oriented targets presented against the backdrop of anisotropic (i.e., non-oriented, Figure 3a) texture (all displayed on a computer screen over the fish tank), when confronted for the first time with *two* targets oriented differently, archerfish exhibited no preference for either target and shot at them with equal probability (Figure 3c). However, when the background texture became oriented (Figure 3b), the archerfish overwhelmingly preferred to shoot at the targets that were incongruent (i.e., orthogonal) to the texture (Figure 3c). In other words, all things being equal, targets with orientation that contrast with their background appear more salient to the archerfish, as is the case for humans [6••].

Pop-out, serial and conjunction visual search in the archerfish

With visual saliency established, at least based on orientation, later work extended this exploration to more elaborate settings using stimuli that are more complex and multiple items embedded in the display. Since the fish needs to select one item or target to shoot at, such scenarios inevitably involve some sort of visual search, a process that terminates with a decision of the preferred target to shoot at. The target can be defined by its saliency alone (as above) or by training the fish to prefer it in the first place by restricting the reward during training [6••]. Either way, by varying the number of non-targets (i.e., distractors), insights concerning visual search strategies (or behaviors) can be rigorously inferred, a methodology borrowed directly from human vision research [19,23].

This approach has yielded exciting new findings on archerfish vision in recent years. It was shown that archerfish vision exhibits the two modes of visual search found in humans, namely preattentive (i.e., pop-out or parallel) search and attentive (i.e., serial) search [11••]. More specifically, when a single-feature target defined by speed is embedded in a varying number of distractors (4, 6, or 8 [6••]), reaction time is characteristic of pop-out [6••]; in other words, it is independent on the number of distractors (Figure 3d,e). At the same time, when the target is defined by a unique combination of *two* features, in particular speed and width, this so called *conjunction search* task [19,23] yields a response time that grows linearly with number of the distractors [6••] (Figure 3f,g), just as found in humans.

The neural basis of pop-out in the archerfish

A central part of theories accounting for pop-out visual search performance is the notion of a *saliency map* — an internal neural representation of visual importance as a function of spatial location. This map is computed concurrently for the entire visual field, typically by evaluating local feature contrasts. Thus, the time it takes to generate this representation does not depend on field characteristics such as size, visual complexity, or the number of distracting objects present. In mammals, the neural correlate of a saliency map has been found in several brain regions such as the lateral intraparietal cortex, the frontal eye fields and the visual cortex [24–27,28••].

The combination of saliency map together with a winner-take-all mechanism may serve to detect the most active (i.e., salient) location on the map, which then pops-out to the observer [20,29,30]. If the saliency map cannot be computed or is too uniform (i.e., everything is equally salient or non-salient), the search process then reverts to the serial mode which forces attention to scan the visual scene item by item.

Figure 3
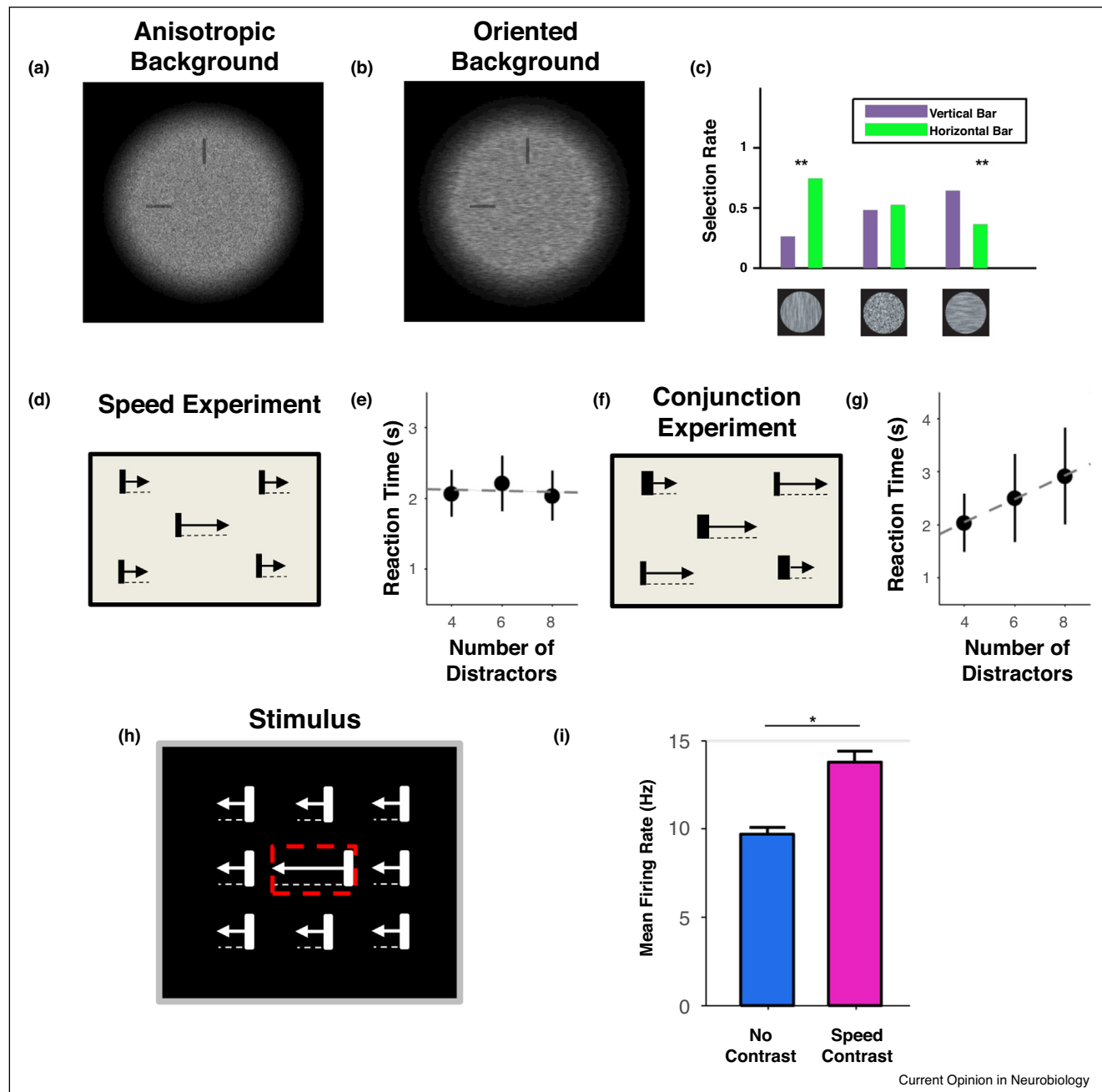
Saliency and visual search in the archerfish. **(a)** A control experiment where the two bars are presented on an isotropic (un-oriented) background can be used to eliminate any preference to orientation. **(b)** When an archerfish is presented with two bar targets that can be either congruent (parallel) or incongruent (perpendicular) with an oriented background, any preference for one target is indicative of orientation-based visual saliency. **(c)** The selection rate of all fish averaged for stimuli (left: vertical background, middle: anisotropic background, right: horizontal background). When the background was isotropic, no preference was exhibited for either target. When the background was oriented, however, the fish exhibited a strong preference for the incongruent target (regardless of the absolute orientation). **(d)** A speed-based example of a visual search task where the odd-ball target was faster than the distractors. **(e)** The reaction time in the speed-based visual search task does not increase with the number of distractors. This is an indication of pop-out in visual search. **(f)** An example of a visual search task where the target was defined by the conjunction of two visual features, width and speed. In this case, the fish had to select the thick fast target (central target in this example). **(g)** The reaction time in the conjunction visual search task increases with the number of distractors. This is an indication of serial visual search. **(h)** Neural correlates of the saliency map. A receptive field (RF) of a single cell in the optic tectum is first mapped (red dashed line). A fast target is then presented within the classical RF while additional targets are presented outside of it. **(i)** The average firing rate of an example cell in two conditions. The 'No contrast' relates to the condition where the bars outside the RF move in unison with the bar within. 'Speed contrast' represents the condition when the surround items move in the same phase but at double the speed relative to the RF item. The 'speed

Does the archerfish possess the building blocks for saliency maps to guide visual search? Since cells in the optic tectum of the archer fish are characterized by orientation tuning and sensitivity to bars moving across their receptive field [16•], the representation of feature contrast would require the modulation of their response to stimulation within the receptive field based on the stimulation outside it. Such contextual modulations, or non-classical receptive field properties, are exactly what was reported recently [6••]. In particular, the archerfish optic tectum appears to contain 'speed-contrast' cells that modulate their response to the optimal stimulus based on the speed of the stimulus in its surround. Specifically, the firing rate of such cells increases if the speed of a bar within the receptive field is higher than the bars in the surround (Figure 3h,i).

Inhibition of return

A practical aspect of any visual search strategy is a reasonable balance between exploration and exploitation, since otherwise attentional resources would be captured indefinitely by the most salient location in the visual field. Tagging recently attended locations or objects in the visual environment to avoid them in the near future, may facilitate the search for new, albeit less salient regions, a process known as 'inhibition of return'. Recent studies have suggested that this process is essential for the efficiency of visual search [31,32]. Furthermore, when we consider the evolutionary advantage of inhibition of return, one could expect to find this strategy in all species that employ visual search, the archerfish included (see [33••] for review).

To test for inhibition of return in the archerfish, Gabay et al. [9••] adapted Posner's exogenous cuing task [31] where a cue draws the subject's attention but provides no information on the position of a target that can appear in the same ('valid') or another ('invalid') location (Figure 4a). By measuring the detectability of the target as a function of the stimulus onset asynchrony (SOA) the effect of one fixation on a subsequent one can be assessed. The findings show that the archerfish exhibits both facilitation and inhibition of return. When the time interval between the cue offset and target onset was short (200 ms), the cue facilitated the detection of the target. However, when longer (1300 ms), performance switched to a pattern consistent with inhibition of return (Figure 4b).

Higher visual processing

Visual behavior in archerfish does not stop at low or intermediate level vision. Its capacity for higher level processing has also been studied. One of the best-known high level visual capabilities in humans is face recognition, and a recent study showed that it exists in archerfish as well [11••]. Clearly, it can be assumed that fish did not evolve to

recognize faces. Still, this study demonstrated that at the very least archerfish can process very complex visual stimuli since face recognition and discrimination requires analysis of intricate relationships between facial parts.

Another study exploring complex visual processing in the archerfish showed that they can compensate for size distortion of aerial targets. This size constancy capacity is particularly impressive since it must be acquired in the presence of the considerable distortion due to air–water refraction [3,34]. Other works have shown that the archerfish can estimate target distance and actively control their jet hydrodynamics [35].

Outlook

Recent studies on the archerfish as a unique model animal have produced exciting new behavioral and neurophysiological findings regarding its visual system. These studies fall clearly within the two major lines of research that appear to guide researchers in the field.

The first line of research considers the natural environment and habitat of the archerfish and how it interacts with visual processing. In this ethological approach, the goal is to understand the behavior of the archerfish in terms of the challenges imposed by its natural habitat and the fact that predation by shooting aerial food items is an important facet of its diet [36]. In research works, the native predatory behavior is modelled in experiments that mimic the natural habitat. Two notable examples in this line of research are the target motion prediction behaviors performed by the archerfish before [7•] and after [8] shooting.

The second line of research is driven by the parallels to the primate (or human) brain and examines whether the latter's characteristic visual information processing capacities can also be found in the qualitatively different fish brain, thereby further confirming the functional universality of certain visual processes. According to this approach, one harnesses the ability of preforming well-controlled experiments in the archerfish but attempts to analyze and understand the results in terms of its teleost brain anatomy, which is very different from the mammalian design. Specifically, studies that indicate that the archerfish can perform a particular task may lead to a better understanding of whether a specialized brain region in the mammalian brain is critical for this same task. A prototypical example of this agenda is the demonstration that archerfish can discriminate human faces [11••]. Since fish did not evolve to discriminate faces, finding such a capacity provides evidence that performing such a complex task accurately may not require a neocortex.

(Figure 3 Legend Continued) contrast' condition elicits a statistically significantly higher response, indicating the possible role of such a cell in representing the saliency map in the archerfish optic tectum. (Panels a–c redrawn from Ref. [5••], panels d–i redrawn from Ref. [6••].)

Figure 4
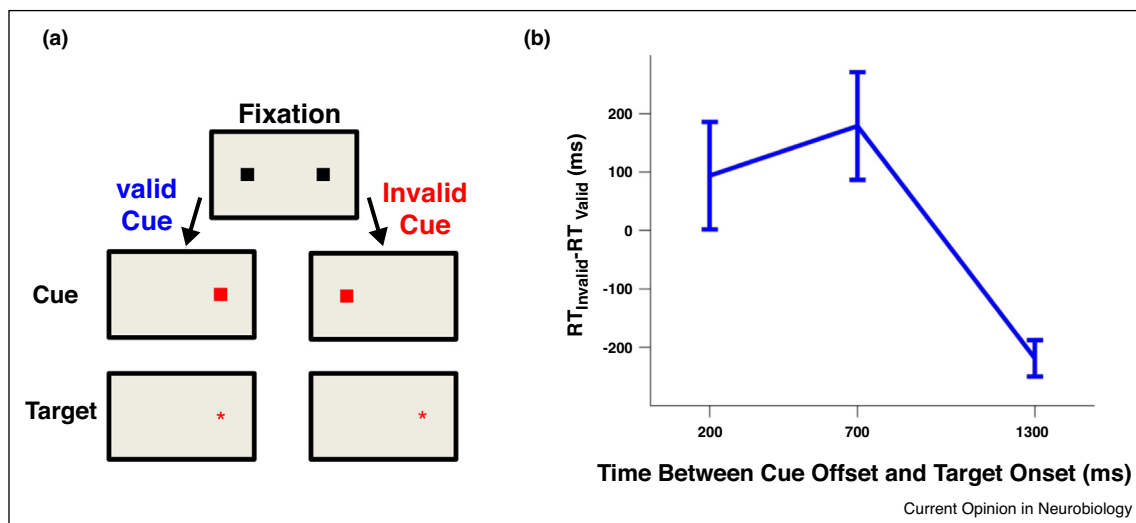
Inhibition of return in the archerfish. **(a)** Inhibition of return in the archerfish: a fixation display is presented followed by a cue to a future target that can be either valid (left) or invalid (right). **(b)** The average reaction time as a function of the time between the cue offset and target onset (SOA) shows facilitation for 200 ms and inhibition of return for 1300 ms. The time difference is defined as the reaction time of the invalid condition minus the reaction time of the valid condition. (RT, reaction time; panels a and b redrawn from Ref. [9••].)

Although these two lines of research have different agendas, they are not mutually exclusive. This is exemplified by the study of visual search, where the findings on pop-out and conjunction search [6••], together with inhibition of return [9••] are clearly critical component of the predatory behavior of the archerfish and as such share the two lines of research hallmarks.

The demonstration that archerfish can undertake what is considered sophisticated visual processing raises the question of what we can learn from studying visual processing in this model animal and how this can lead to future advances. Clearly, an important route for progress is the understanding of the neural mechanism governing the visual based behavioral capabilities of the archerfish. However, this requires further technical advances beyond recent achievements that make possible electrophysiological recordings from immobilized fish [16•] and record from shooting archerfish [37]. However, recording neural activity from freely behaving fish is both essential and a challenging technical task, given the constraints of the aquatic environment on the acquisition and transmission of these recordings. Crucial progress was recently made on a recording system for behaving goldfish [38], which might be adaptable to archerfish. In addition, more precise knowledge of archerfish anatomy is required; in particular, the main building blocks of the archerfish visual system and how they are connected. Lesion studies similar to those done in the goldfish [39,40], may help reveal more about this function–structure relationship. Finally, breeding the archerfish in captivity, which will make it possible to use molecular methods to manipulating neural activity, for example, optogenetics [41], should also lead to rapid progress.

Conflict of interest statement

Nothing declared.

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