Archerfish vision: visual challenges faced by a predator with a unique hunting technique

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Abstract

Archerfish are well-known for their ballistic hunting behaviour, in which they shoot down aerial prey with a well-aimed jet of water. This unique hunting strategy poses several challenges for visual systems. Archerfish face significant distortion to the appearance of targets due to refraction at the air/water interface, they search for prey against a complex background of foliage, they change prey targeting behaviour as conditions change, and they must make high speed decisions to avoid competition. By studying how archerfish have overcome these challenges, we have been able to understand more about fundamental problems faced by visual systems and the mechanisms used to solve them. In some cases, such as when searching for targets, the visual capabilities of archerfish are functionally similar to those of humans, despite significant differences in neuroanatomy. In other cases, the particular challenge faced by archerfish magnifies fundamental problems generally faced by visual systems, such as recognizing objects given strong viewpoint dependent changes to appearance. The efficiency of archerfish retrieving fallen prey to avoid kleptoparasitism, demonstrates that their visual processing excels in both speed and accuracy. In this review, we attempt to provide an overview of the many facets of visually driven behaviour of archerfish, and how they have been studied. In addition to their hunting technique, archerfish are ideal for visual processing experiments as they can be quickly trained to perform a range of non-ecologically relevant tasks. Their behavioural flexibility moreover, introduces the opportunity to study how experience-dependence and choice affects visual processing.

Keywords vision, cognitive ecology, behaviour, vertebrate, visual processing, sensory processing

Introduction

Teleost fish represent a large taxon of approximately 30,000 species [1] and demonstrate a huge range of diversity in terms of environment, ecology, physiology, and behaviour. One of the many aspects that make the study of fish vision so rewarding is the diversity in visual behaviour associated with the same general organization of the visual system. While some fish, such as cavefish, have lost functional eyes, others rely heavily on vision and have unique and impressive visual specialisations. As in all vertebrate systems, processing starts right in the retina, and later, sorting of information and processing for different tasks in various parts of the brain. While the eyes of fish follow the same general organization as in other vertebrate, the fish brain lacks a visual cortex [2], which is associated with higher order visual processing in mammals. Therefore we are able to ask how animals with very different brain architectures approach comparable challenges. This way we might be able to discover unique specializations but also similar computational mechanisms that might be shared across vertebrate (and perhaps also invertebrate) visual systems.

Archerfish inhabit tidal mangroves of the South Pacific and Indian oceans [e.g. 3, 4]. In the last twenty years, archerfish have increasingly been used as a model organism to study visual behaviour and processing associated with their unique hunting technique. Most studies use two regularly imported species of archerfish: *Toxotes chatareus* and *T. jaculatrix*. Archerfish are long known for their unique ability to use a jet of water spit from their mouth to dislodge aerial prey up to two meters above the water. When spitting, the fish press the rigid part of their tongue against the roof of their mouth to form kind of a gun barrel, take a large gulp of water, and then close their gill covers, building up internal pressure [5-7] that then is released by a tiny opening of the tip of the mouth (Fig. 1). As for water released from any pressure reservoir, the water that leaves first is slower than water that leaves later. This automatically causes the water jet to coalesce into a focused mass of water at the front tip of the jet. In archerfish, this would happen at a fixed closed distance of 10 cm [6]. However, it later turned out that the fish use precisely controlled variations in the way they open and close their mouth during jet release to adjust the distance after which the water mass coalesces, and to also modulate the lifetime of their jet to the range of target distances the fish are able to handle [8]. Archerfish can also match the force of their shot to the size and adhesive force of their target [9, 10]. They do so by adjusting the leaving speed of the water mass fired, and the interaction-time with the target remains roughly constant [9]. Interestingly, they can also apply their spitting behaviour underwater, using it to lift up sediment and find buried food particles, and also adjusting their mouth-opening and closing manoeuvers to the type of substrate [11]. The hunting technique of archerfish relies on a complex array of individual behaviours including prey detection and recognition, judging prey size, distance and reward-value as well as accurate aiming and spitting. Because archerfish share their habitat with a range of competitors, both intraspecific [12] and interspecific [13] their hunting also involves a rapid predictive start to retrieve falling prey.

Archerfish are easy to train using operant conditioning and can rapidly learn to spit at a variety of arbitrary targets presented to them. Although more sophisticated stimuli presentation methods have been used (see Fig. 1A for an example), it is impressive what can be learned by simply using objects printed on paper, presented at variable height above the fish. Early conditioning experiments showed that archerfish can rapidly learn to shoot at targets and ignore many other potentially distracting objects within view [14]. Moreover, it does not matter that the stimuli do not fall down when hit, that the stimuli don’t look like the reward, or that the reward comes after a significant and variable delay [14]. The complex behavioural repertoire and trainability of archerfish has been exploited to address a range of research questions including, neuroanatomy [e.g. 15, 16-18], biomechanics [e.g. 5-10, 19, 20, 21], cognition [e.g. 22, 23, 24], object recognition [e.g. 25, 26], social learning [14, 27, 28], and attention [e.g. 29, 30-34].

A number of studies on vision in archerfish have formed around the question how its lack of a cortex might cause its performance to differ from that of primates in comparable tasks [e.g. 25, 26, 29, 31, 33, 35]? This is a powerful question as it allows us to consider the evolution of mechanisms within the vertebrate visual system, determine the limits of non-cortical brains, and provides inspiration for the development of theories of vision that do not rely on complex neural circuitry. There is of course a caveat to the benefits of taking this anthropocentric point of view, and that is that the ability of species must be considered in the context of their own ecology as the observed behaviour may be shaped by brain structure or their ecology. One of the strengths of the archerfish model, is that its unique, visually based hunting strategy provides opportunities to ask mechanistic questions about the visual system, using tasks that are relevant to the species. While the majority of archerfish studies to date have been conducted in controlled laboratory environments where individual aspects of the archerfish hunting technique can be studied in isolation, these fish are also suitable for field studies which can examine their visual hunting behaviour amidst the considerable complexity of their mangrove habitat. In this review, we will discuss four aspects of the archerfish hunting strategy that make them particularly useful for studies on vision: view dependent object recognition, attention and searching, variable response to stimuli, and rapid decision making.

Archerfish visual pathway

The retina is the start of the visual pathway, and its organisation is generally similar in all vertebrates with lens eyes [36, 37]. In the archerfish, the eyes are significantly larger than their entire brain and they possess a thick optic nerve (Fig. 2). The distribution of rods and cones, and cone spectral sensitivity, appears to be tuned to the needs of hunting archerfish [38, 39]; cones in the dorsal and ventral-nasal retina are ideally suited to detecting and discriminating colours typically found underwater [e.g. see 40], while those in the ventrotemporal retina are tuned to light detection above water [38]. The archerfish has an area of increased retinal density, called the area centralis, onto which it can focus the image of its prey [38, 39]. Their acuity in this region is approximately 0.15° [41], which is much higher than in the commonly used model species, zebrafish (*Danio rerio*) [42] and goldfish (*Carassius auratus*) [43].

The organization of the archerfish brain is typical of the percimorph group and the optic tectum is the largest structure in the brain [16]. The optic tectum is the central unit of visual processing and receives signals directly from the retina as well as those relayed through pretectal layers [17, 44]. Cells within the archerfish optic tectum have three categories of visual receptive fields: orientation-tuned cells, direction-tuned cells, and direction-agnostic cells [17]. This structure is generally agreed to be homologous to the mammalian superior colliculus which plays a critical role in lower order visual processing, including visual detection of objects [45], edge detection and colour processing [46].

There is some evidence that the optic tectum is functionally analogous to the mammalian primary visual cortex [15, 41]. The primary visual cortex is composed of a series of layers that form multiple hierarchal pathways such that higher layers are successively responsive to increasingly complex and/or specific stimuli [47, 48]. There is no indication that the optic tectum of fish has the same hierarchal processing [46]. Although little is known about specific neural pathways for visual processing in the fish optic tectum, the cells are not arranged in columnar fashion and they can each respond to a variety of stimuli features [49]. However, the primary visual cortex and the optic tectum are both the primary site of visual processing and they share similar neural correlates of a saliency map [30]. In addition, the spatial receptive fields of cells in the optic tectum are similar to those in the primary visual cortex of mammals [15]. It has therefore been suggested that while the brain structures associated with higher order visual processing are different between fish and mammals, the function has been preserved and visual processing has migrated to other brain sections [15, 50]. Therefore, the pertinent question is, given the difference in brain structures between fish and mammals, do the differences in neural design cause limitations in visual processing, or can the brain of fish employ different mechanism to produce the same degree of behavioural complexity as seen in mammals.

Viewpoint dependent object recognition

Archerfish hunt at the interface between air and water, forcing them to account for complex, viewpoint dependent optical distortions when targeting prey. When archerfish fire a shot, their mouth is above the water level but their eye is just below [51-54]; the incoming light is refracted according to Snell’s Law and causes distortion to the appearance of objects, making them appear smaller, more distant, and in a different position (Fig. 3A, B) [14, 52, 55]. In addition, refraction can distort apparent shape (Fig. 3A), even adding a vertical component to a flat object [14]. Importantly, the degree of distortion is highly dependent on the viewpoint of the fish; small changes to the viewer’s position relative to the target, can lead to large changes to the targets appearance, particularly as the viewing angle increases (Fig. 3C). For example, if a fish is looking at an object directly above (0° viewing angle), there is no change to the apparent position of the target, but at 10° from the normal line to the water surface plane, then the difference between the real and apparent angle is about 3.4°, and at 48° the difference is about 10 times that, in freshwater. The fact that archerfish can accurately target prey, demonstrates that they are capable of adjusting for these optical distortions [14, 52, 56-58], but it is unknown exactly how they do so. Understanding how the brain recognizes objects regardless of viewing position continues to be of interest to vision scientists, and the aim is to determine how three-dimensional (3D) objects are represented in the brain based on two-dimensional retinal projections. Much of the work to date has focused on how this is achieved by primates and is considered in the context of the complexity of the visual cortex. However, this problem is faced by all mobile, visually oriented animals, regardless of whether they have a cortex or not, and this problem can be solved in more ways than one. Archerfish aerial vision presents a particularly interesting model because aiming at the target, recognizing objects, and adjusting shooting force, are sensitive to viewpoint based distortions. In addition, archerfish target prey above and below water, and therefore must switch between viewpoint dependent underwater vision, to aerial vision with added distortion.

Some of the earliest research on archerfish focused on how they accounted for the discrepancy between the apparent and actual position of a target [52, 54]. It was originally thought that archerfish position themselves directly below prey, possibly in an effort to reduce the effect of distortion [54]. However, later observations showed that archerfish typically position themselves at an angle to their prey ranging between 45°-110° from the water surface plane, with a mean of 75.5° [14, 52, 56, 58]. They will also alter their position between shots, even when targeting prey that is always in the same position, such as in laboratory experiments. Archerfish must therefore apply some form of correction for these optical distortions. This ability appears to be acquired either through learning early in development or through instinct, and archerfish do not require any continual external feedback to maintain accuracy [57]. However, extended practice is needed for the fish to learn to accurately hit moving targets [59].

There is evolutionary pressure on archerfish to identify the absolute size of their prey, as this allows them to adjust the volume of water they shoot at prey with different adhesive forces [9]. Archerfish demonstrate size constancy – i.e. the ability to recognize the actual size of an object regardless of changes in apparent size caused by distance in two ways. They can identify learned targets of a specific size, despite changes to the presentation height [14]. They can also adjust their on-target force to match the size-dependent adhesive forces of a target [9, 10]. Because of the viewpoint dependent nature of refraction at the surface, in order to assess absolute size, archerfish would theoretically need to know their position relative to the target, and then apply the appropriate refraction correction.

As the appearance of the target increases in complexity, distortion may alter more subtle features than just overall size. Archerfish can discriminate geometric shapes [e.g. 24, 60, 61] as well as highly detailed human faces [25]. Discrimination of these object classes can require the detection and differentiation of subtle cues as well as the spatial relationship between them. This is particularly true for human faces which all share the same basic components (i.e. two eyes above a nose and mouth). The non-linear nature of refractive distortion means some features will be distorted more than others, making the accuracy of archerfish when discriminating complex images rather impressive.

Archerfish can tolerate further viewpoint dependent changes to the appearance of complex objects as they have been shown to recognize objects which have been rotated. After training with only a single view of a human face, archerfish demonstrated spontaneous recognition of depth-rotated human faces [26]. Unlike in the size constancy experiments where only the size of stimuli changed [10, 14], in the experiments testing depth rotation, the features available for recognition were increasingly altered or entirely disappeared as the faces were rotated along the horizontal plane. Newport, Wallis and Siebeck [26] found that the fish could continue to recognize human faces rotated up to 90°, although there was a cost to both speed and accuracy. It should be noted that the fish were able to build a 3D representation of a human face from only a single learned view, despite relatively little experience and no evolutionary prerogative with this object class.

These combined results indicate that archerfish possess some form of flexible object recognition that can cope with viewpoint dependent changes to an objects appearance. This is similar, at least in terms of function, to other vertebrates, including primates. An interesting cause of optical distortion that has not yet been considered in laboratory experiments are surface waves, common in natural habitats [62]. The effect of refraction on the appearance of images, even targets that are moving, are predictable, and although the process is not trivial, it can be corrected following rules of refraction and trajectory. However, surface waves are stochastic and can be variable in both amplitude and length, making it difficult to learn a single rule to account for the distortion. Therefore, archerfish could provide a good model in which both systematic and stochastic events impact the sensory information underpinning an important behaviour.

Attention and searching

Given the ecological context of their hunting behaviour, archerfish are a fantastic species to study attention and searching behaviour. Scanning the richly-structured background of their mangrove habitats for potential aerial prey is a demanding problem for archerfish. Many twigs and leaves, as well as spots on them, look remarkably similar to potential prey [62]. In addition, archerfish hunt both above and below water, and these two visual environments have vastly different scene statistics [15].

Archerfish cannot simplify this problem and operate based on a fixed image of prey as they hunt a variety of prey in different sizes and orientations [13, 53, 62]. How archerfish search for and detect prey using only vision, has been the subject of many studies over the last decade. To mimic the search task in the wild, one study trained archerfish to consistently not shoot at objects they initially selected as targets. These objects were then shown as background objects together with a rewarded target. In these experiments, the median time to detect the rewarded target increased linearly with the number of background objects, as in a typical serial visual search [29, 62]. In a serial search, a focus of attention is thought to sweep from one object to the next. The hypothetical focus of attention then requires a fixed time to decide whether the current object is the target and the search can be ended, or whether it is a distractor. The search mechanism also is thought to have an internal memory for the objects that have already been scanned, thus preventing the revisiting of objects [e.g. 63, 64]. In experiments, the effective scan time per object increased when the search task was turned from 'simple' to 'complex' by increasing the number of novel and differently oriented background objects [29]. When humans were tested in a matching search task, the performance of the two species were the same. Neither the shape of the search-time distributions, nor the relative increase in the mean search time per object, were affected by the increase in complexity – hallmarks that are thought to restrain cortical architectures of attention [29, 62]. A number of earlier archerfish papers focussed on paradigms in which the target differed by one conspicuous stimulus category from the distracting other objects, for instance by its movement direction [30-32, 41] and in such instances 'pop-out' effects are often observed (i.e. detection time is independent of the number of objects shown in the scenery). A recent survey involving several stimulus attributes now also reports serial search characteristics and remarkable similarities between archerfish and humans [33], confirming the exceptional characteristics for efficient serial search in archerfish, that certainly involve nontrivial ways of allocating attention. The available evidence also suggests that archerfish may scan a scene segment-wise, starting with close areas [29]. Efficient search mechanisms may be found across several species of vertebrates and invertebrates, in species that have to be efficient in visually spotting important objects.

A surprising element of attention has also been discovered in the fast-start decisions archerfish make to retrieve their prey. As will be described in more detail below, the fish exclusively use visual information sampled during the brief interval about 40 ms after their prey has started falling to turn and take-off just so as to be at the later point of impact of their prey just when it also arrives there [34, 65-67]. When the fish are artificially challenged with two objects that simultaneously start falling ballistically with the same horizontal initial speed but in opposite directions, then archerfish base their fast-start decisions exclusively on the initial motion of one of the two objects, completely ignoring the other [34]. Moreover, they do not randomly pick one of the two moving objects, but tend to select the one for which the later landing point will be closer [34]. Attention does, however, not limit the spatial region in which target movement is processed. When the fish are cued to observe a particular spot but movement starts from a different location and height, then they neither take longer to respond nor is the accuracy of their predictive starts (i.e. how accurate the aim and initial speed is set to the position and time of later landing of prey) affected [34, 66, 67]. Therefore, archerfish can rapidly 'flag' a moving object anywhere within their visual field and specifically feed its movement characteristics in the circuits that drive their rapid predictive starts.

Competition pressure and high-speed decision making

Despite the many impressive aspects of their shooting behavior, archerfish would be rather unlikely to actually catch any of their downed prey if they waited until its splashing impact on the water surface. This is because they often have to compete with far more numerous and sensitive surface feeding fish that would readily steal their food [13]. An additional behavior is needed to ensure success of the archerfish's hunting technique: their so-called predictive starts [62, 68-70]. As soon as prey start falling on a ballistic trajectory, the fish, both shooter and bystander, turn rapidly and dash off towards where the falling item will later land. This response ensures that the archerfish arrive basically simultaneously with their prey, thus leaving no chance for their competitors. During daytime, this response ensures an impressive 98% success rate in the field, even in the presence of numerous competing surface feeding fish [13]. The archerfish predictive starts have several remarkable characteristics of which we only briefly highlight some that should be of interest in terms of the elaborate and yet fast visual processing involved. It has been shown that these starts not only turn the fish right into the direction of the later landing point [e.g. 34, 58] but also determine the speed of the approach in such a way that the fish, when maintaining that speed, arrives shortly after its prey, given the distance that's to be covered and the time that remains till impact [67, 70, 71]. Perhaps the most remarkable aspect of the predictive starts, is that they use independent channels of visual information but do not depend on information that would *a priori* be available or required to hit the target [34, 67]. For instance, the shooter must know the position and distance of its target to be able to adjust its jet and hit it. And yet, when experimentally challenged with prey starting at arbitrary times from some other positions [34], even from different height levels [67], the fish's start decisions were equally accurate. A number of studies have shown that the fish determine horizontal and even vertical speed of motion, direction, and initial height in the very short period (less than 100 ms) after onset of falling motion, and feed this information into the circuitry that drives the rapid predictive starts [34, 65, 67, 68, 72]. The visual analysis that is involved is impressive: On the basis of the behavioral findings assembled so far, the fish are able to judge movement direction, speed and initial height quickly and independently from each other and from any viewing angle in less than 100 ms. If viewing conditions get worse, for instance when there is insufficient contrast between the falling object and its background, lesser starts are triggered, but when predictive starts are released then these are always accurately aimed at the later landing point [e.g. 34]. A series of experiments on the information used to rapidly infer three-dimensional distance, suggest that the predictive starts do not use binocular cues but also none of the many common monocular cues, such as accommodation-related cues, relative movement parallax or image blur. Rather all evidence so far points to a specialized and highly sensitive evaluation of looming [65, 66]. Among the many interesting aspects of this behavior, we note its remarkable stability against fluctuations of environmental variables such as temperature. While all visual processing involved in driving the starts is strongly temperature-dependent, the predictive starts are not, and they are equally accurate after changes in environmental temperature [72]. Finally, it is interesting to note the competition that appears to have driven the evolution of the rapid predictive starts. In the dark, at light levels at which archerfish could still hit their prey in the laboratory, the visual information ceased to be able to support the predictive starts. In such experiments in the dark, it took even the successful shooters a long time to actually find its downed prey. The fact that their competitors in the field would be so much more efficient in the dark may explain why shooting in the dark was only seen in the laboratory but not in the wild or places with many nocturnally active competitors [13].

Cognitive flexibility and dynamic responses

The mangrove habitat of archerfish is highly dynamic and fish face a wide range of external forces that alter their ability to catch prey at varying temporal scales. For example, daily fluctuations in water level alters their proximity to prey and the suitability of particular hunting locations [62]. Wind and currents can cause increased distortion and can change the trajectory of their jets, while prey availability can shift over days and seasons [62]. Archerfish themselves add variability as both their hunting technique and prey choices are varied. While the ballistic hunting strategy has been the focus of most research to date, archerfish have three mechanisms for catching prey: underwater chasing, jumping out of the water [19-21], and finally shooting jets [52, 54, 69]. In addition, archerfish are opportunistic feeders and will target a wide array of prey items [3, 53]. Therefore, individuals must be able to alter their behaviour in response to external factors. For instance, archerfish experience significant kleptoparasitism from other archerfish [12] and when they have an audience of conspecifics, individuals will take longer to shoot and select prey that are closer [28]. They will also employ a range of behavioural counter-measures such as jumping and grabbing prey rather than waiting for it to fall, and increasing aggressiveness to force competitors out of range [12]. It is easy to imagine that in these conditions, errors in identifying the correct context and appropriate behavioural responses can be costly, but also that there is a benefit to exploration which may result in the discovery of new prey.

More recent experiments exploring how archerfish learn to shoot at a variety of artificial visual stimuli, indicates that they can indeed respond flexibly to stimuli based on context, even when the tasks have little basis in the natural ecology of the fish. They can easily be trained to discriminate a range of artificial and abstract stimuli (Fig. 1 C-E) when presented on a computer screen [e.g. 24, 26, 39, 61]. A four-alternative forced-choice test was used to explore how archerfish respond when presented with novel stimuli alongside previously learned ones [24]. It was found that archerfish are willing to select novel stimuli even in the presence of a known rewarded one, indicating a mechanism for exploration. It was also found that it was the learned unrewarded stimuli that had the greatest impact on whether the fish selected the known rewarded stimulus or a novel one. Archerfish can learn to avoid previously rewarded stimuli [29], indicating that decision strategies are not fixed but can change as the associated benefits of the target change. When presented with arbitrary stimuli, archerfish can learn differential reward values and make selections that maximize their food intake [61]. Therefore, it appears as though these fish do not have simple hardwired responses to visual stimuli, but can instead respond dynamically under changing conditions. However, archerfish learning appears to be limited to stimulus specific associations, as they have thus far been unable to solve tasks requiring abstract relational rules [22, 23].

These laboratory experiments show that the process of evaluating context and responding appropriately for archerfish can be controlled entirely by visual cues. Even when making a relatively simple choice between options, seemingly indirect cues are important to the decision making process. Therefore, archerfish present an interesting system to study the involvement of background information in making decisions about sensory input, and how context causes the fish to select one course of action over another. These questions are particularly pertinent to wild fish that are likely exposed to a significant amount of extraneous information.

Outlook

In this review, we have hopefully shown that the unique, visually guided hunting strategy of archerfish has already provided significant insights into how animals with non-cortical brains detect, identify, and target prey under demanding and dynamic viewing conditions. These studies have begun to address the broad question of whether ecology or brain anatomy shapes the mechanisms and functions required for archerfish hunting, particularly when considered in the context of similar studies with different species. There is growing evidence that some archerfish mechanisms, such as view dependent object recognition and visual attention mechanisms, are functionally comparable to that of primates. How archerfish are able to achieve similar behavioural outcomes with vastly different brain structures is a question that still needs to be answered. It is also worth asking whether some of the higher order behaviours we observe are shared by all fish or are specific to archerfish and their associated hunting strategy.

The vast majority of archerfish experiments have been hypothesis-driven, and the experimental tasks have been under controlled and simplified conditions. There are comparatively few studies that have actually taken place in the natural habitat of archerfish [but see 3, 13]. In many experiments, stimuli have been arbitrary shapes and colours, and fish have had to learn specific tasks in conditions with no predation or competition. In addition, the surrounding environment has lacked visual complexity and has been highly uniform (e.g. temperature, lighting). Controlled experiments such as these are of course an important part of experimental science, but looking at what archerfish must do in the wild will be helpful in at least two ways. First, by showing that the actual problems archerfish vision can solve are far more impressive and second, by helping to appreciate which behaviours that we study in the laboratory are heavily constrained ecologically and which are not. A prime example of this is the view-invariant object recognition capabilities observed when archerfish were given rotated human faces as stimuli [26]. Although observed recognition performance was similar to that of primates, there was a significant cost in terms of selection time and accuracy when archerfish were presented with faces that were increasingly rotated from the learned view. The accuracy of some individuals dropped to a frequency consistent with chance when the faces were rotated by 90°, and several individuals took significantly longer to make a decision (in one case it took on average <3.5 minutes more to make a decision between learned and novel views). While this experiment demonstrated that it is possible for archerfish to perform the task, it seems unlikely that individuals would take several minutes to determine the identity of a target in the wild when competition is high. There are clearly more questions that need to be answered before we can truly understand how archerfish cope with viewpoint dependent changes to the appearance of objects. Archerfish might use much more efficient mechanisms to recognise their prey in the wild or might use behavioural strategies to considerably simplify complex recognition tasks, thus reducing the processing burden on the optic tectum and increasing efficiency.

In the wild, archerfish are subject to significant variability and uncontrolled external factors (e.g. tides, prey location, lighting, weather, prey type, competition, wind), making their hunting strategy and visual capacities even more impressive [62]. While experiments thus far have honed in on individual skills, in reality, incoming visual stimuli can initiate multiple visual behaviours that require different mechanisms. For example, it is unknown which mechanisms allow archerfish to search so efficiently for a range of prey items against complex backgrounds and also use visual information from the scene to provide contextual cues. Therefore, archerfish present a compelling model to explore how animals respond when faced with multiple visual challenges and changing sensory information, as well as the potential trade-offs between response options.

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Figure captions

Fig. 1. (A) Video still of a stimuli presentation method on a computer monitor. Adapted from Newport, Wallis, Temple and Siebeck [24]. **(B)** Photograph of an archerfish shooting a jet of water (C. Newport). **(C-E)** Examples of experimental artificial stimuli which archerfish have been shown to discriminate. **(C)** Adapted from Newport, Wallis, Temple and Siebeck [24]. **(D)** Adapted from Karoubi, Leibovich and Segev [61]. Colours may not exactly match those used in experiments as specific colour information was not reported. **(E)** Images of morphed human faces adapted from Newport, Wallis and Siebeck [26]. Original images provided by the Max-Planck Institute for Biological Cybernetics in Tübingen, Germany [73, 74].

Fig. 2. Photograph suggesting the importance of vision for archerfish. Note the size of eyes relative to the fish’s brain. Dorsal view of the eyes and brain of an archerfish (*T. chatareus*), showing the eyes (EYE), olfactory bulb (OB), telencephalon (TC), optic tectum (OT) and the cerebellum (CB). The fish

standard length was 7.8 cm and the total length was 9.4 cm. The scale bar applies at the surface of the brain.

Fig. 3. Visualisations of the effect of distortion due to refraction at the air-water boundary on visual signals. **(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 on the real disk; it applies Snell's law to the light rays within a bundle emanating from P and entering the eye's pupil (centre 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 example target heights of 200, 400, 600 and 800 mm and for the horizontal distance (horizontal distance between E and P in [A]). (A) and (B) reprinted with permission from Schuster, Rossel, Schmidtmann, Jäger and Poralla [14]. **(C)** The change in target viewing angle according to Snell's Law. The lines i at 15°, is the average spitting angle of the fish. The lines ii at 45°, is the maximum reported spitting angle.

Fig. 4. The archerfish predictive start. **(A)** To secure downed prey, archerfish rapidly evaluate visual information to select a rapid start that turns the fish to where prey is later going to land. Additionally, the starts sets the speed so that the fish arrives just in time, when prey touches the water surface before competing halfbeaks [29, 72]. **(B)** Timestamps 1-3 highlight that the fish are already on their way when prey has begun falling [68].

References

[1] Nelson JS, Fishes of the world, J. Wiley, Hoboken, N.J, 2006.

[2] Northcutt RG, Understanding vertebrate brain evolution, Integr Comp Biol 42(4) (2002) 743-756. https://doi.org/10.1093/icb/42.4.743

[3] Simon KD, Mazlan AG, Trophic position of archerfish species (*Toxotes chatareus* and *Toxotes jaculatrix*) in the Malaysian estuaries, J Appl Ichthyol 26 (2010) 84-88. https://doi.org/10.1111/j.1439-0426.2009.01351.x

[4] Allen GR, *Toxotes kimberleyensis*, a new species of archerfish (Pisces:Toxotidae) from fresh waters of Western Australia, Rec Aust Mus 56 (2004) 225-230. https://doi.org/10.3853/j.0067-1975.56.2004.1423

[5] Elshoud GCA, Koomen P, A biomechanical analysis of spitting in archer fishes (Pisces, Perciformes, Toxidae), Zoomorphology 105(4) (1985) 240-252. https://doi.org/10.1007/BF00311967

[6] Vailati A, Zinnato L, Cerbino R, How archer fish achieve a powerful impact: hydrodynamic instability of a pulsed jet in *Toxotes jaculatrix*, PLoS ONE 7(10) (2012) e47867-e47867. https://doi.org/10.1371/journal.pone.0047867

[7] Milburn O, Alexander RM, The performance of the muscles involved in spitting by the Archerfish Toxotes, J Zool 180(2) (1976) 243-251. https://doi.org/10.1111/j.1469-7998.1976.tb04676.x

[8] Gerullis P, Schuster S, Archerfish actively control the hydrodynamics of their jets, Curr Biol 24(18) (2014) 2156-2160. https://doi.org/10.1016/j.cub.2014.07.059

[9] Schlegel T, Schmid CJ, Schuster S, Archerfish shots are evolutionarily matched to prey adhesion, Curr Biol 16(19) (2006) R836-R837. https://doi.org/10.1016/j.cub.2006.08.082

[10] Burnette MF, Ashley-Ross MA, One shot, one kill: the forces delivered by archer fish shots to distant targets, Zool 118(5) (2015) 302-311. https://doi.org/10.1016/j.zool.2015.04.001

[11] Dewenter J, Gerullis P, Hecker A, Schuster S, Archerfish use their shooting technique to produce adaptive underwater jets, J Exp Biol 220 (2017) 1019-1025. https://doi.org/10.1242/jeb.146936

[12] Davis BD, Dill LM, Intraspecific kleptoparasitism and counter-tactics in the archerfish (*Toxotes chatareus*), Behav 149 (2012) 1367-1394. https://doi.org/10.1163/1568539X-00003026

[13] Rischawy I, Blum M, Schuster S, Competition drives sophisticated hunting skills of archerfish in the wild, Curr Biol 25(14) (2015) R595-R597. https://doi.org/10.1016/j.cub.2015.06.005

[14] Schuster S, Rossel S, Schmidtmann A, Jäger I, Poralla J, Archer fish learn to compensate for complex optical distortions to determine the absolute size of their aerial prey, Curr Biol 14(17) (2004) 1565-1568. https://doi.org/10.1016/j.cub.2004.08.050

[15] Reichenthal A, Ben-Tov M, Segev R, Coding schemes in the archerfish optic tectum, Front Neural Circuit 12(18) (2018). https://doi.org/10.3389/fncir.2018.00018

[16] Karoubi N, Segev R, Wullimann MF, The brain of the archerfish *Toxotes chatareus*: A Nissl-based neuroanatomical atlas and catecholaminergic/cholinergic systems, Front Neuroanat 10 (2016) 106. https://doi.org/10.3389/fnana.2016.00106

[17] Ben-Tov M, Kopilevich I, Donchin O, Ben-Shahar O, Giladi C, Segev R, Visual receptive field properties of cells in the optic tectum of the archer fish, J Neurophysiol 110(3) (2013) 748-759. https://doi.org/10.1152/jn.00094.2013

[18] Kretschmer V, Kretschmer F, Ahlers MT, Ammermüller J, High speed coding for velocity by archerfish retinal ganglion cells, BMC Neurosci 13(1) (2012) 69. https://doi.org/10.1186/1471-2202-13-69

[19] Shih AM, Mendelson L, Techet AH, Archer fish jumping prey capture: kinematics and hydrodynamics, J Exp Biol 220(8) (2017) 1411. https://doi.org/10.1242/jeb.145623

[20] Khosronejad A, Mendelson L, Techet AH, Kang S, Angelidis D, Sotiropoulos F, Water exit dynamics of jumping archer fish: Integrating two-phase flow large-eddy simulation with experimental measurements, Phys Fluids 32(1) (2020) 011904. https://doi.org/10.1063/1.5130886

[21] Mendelson L, Techet AH, Multi-camera volumetric PIV for the study of jumping fish, Exp Fluids 59(1) (2017) 10. https://doi.org/10.1007/s00348-017-2468-x

[22] Newport C, Wallis G, Siebeck UE, Concept learning and the use of three common psychophysical paradigms in the archerfish (*Toxotes chatareus*), Front Neuro 8 (2014) 1-13. https://doi.org/10.3389/fncir.2014.00039

[23] Newport C, Wallis G, Siebeck UE, Same/different abstract concept learning by archerfish (*Toxotes chatareus*), PLoS ONE 10(11) (2015) e0143401. https://doi.org/10.1371/journal.pone.0143401

[24] Newport C, Wallis G, Temple SE, Siebeck UE, Complex, context-dependent decision strategies of archerfish, *Toxotes chatareus*, Anim Behav 86(6) (2013) 1265-1274. https://doi.org/10.1016/j.anbehav.2013.09.031

[25] Newport C, Wallis G, Reshitnyk Y, Siebeck UE, Discrimination of human faces by archerfish (*Toxotes chatareus*), Sci Rep 6 (2016) 27523. https://doi.org/10.1038/srep27523

[26] Newport C, Wallis G, Siebeck UE, Object recognition in fish: accurate discrimination across novel views of an unfamiliar object category (human faces), Anim Behav 145 (2018) 39-49. https://doi.org/10.1016/j.anbehav.2018.09.002

[27] Jones NAR, Webster M, Newport C, Templeton CN, Schuster S, Rendell L, Cognitive styles: speed–accuracy trade-offs underlie individual differences in archerfish, Anim Behav 160 (2020) 1-14. https://doi.org/10.1016/j.anbehav.2019.11.019

[28] Jones NAR, Webster M, Templeton CN, Schuster S, Rendell L, Presence of an audience and consistent interindividual differences affect archerfish shooting behaviour, Anim Behav 141 (2018) 95-103. https://doi.org/10.1016/j.anbehav.2018.04.024

[29] Rischawy I, Schuster S, Visual search in hunting archerfish shares all hallmarks of human performance, J Exp Biol 216(16) (2013) 3096-3103. https://doi.org/10.1242/jeb.087734

[30] Ben-Tov M, Donchin O, Ben-Shahar O, Segev R, Pop-out in visual search of moving targets in the archer fish, Nat Commun 6(1) (2015) 6476. https://doi.org/10.1038/ncomms7476

[31] Gabay S, Leibovich T, Ben-Simon A, Henik A, Segev R, Inhibition of return in the archer fish, Nat Commun 4 (2013) 1657. https://doi.org/10.1038/ncomms2644

[32] Mokeichev A, Segev R, Ben-Shahar O, Orientation saliency without visual cortex and target selection in archer fish, Proc Natl Acad Sci USA (2010). https://doi.org/10.1073/pnas.1005446107

[33] Reichenthal A, Segev R, Ben-Shahar O, Feature integration theory in non-humans: Spotlight on the archerfish, Atten Percept Psycho (2020). https://doi.org/10.3758/s13414-019-01884-4

[34] Schlegel T, Schuster S, Small circuits for large tasks: High-speed decision-making in archerfish, Science 319(5859) (2008) 104-106. https://doi.org/10.1126/science.1149265

[35] Saban W, Sekely L, Klein RM, Gabay S, Endogenous orienting in the archer fish, Proc Natl Acad Sci USA (2017). https://doi.org/10.1073/pnas.1700574114

[36] Joselevitch C, Kamermans M, Retinal parallel pathways: Seeing with our inner fish, Vision Res 49(9) (2009) 943-959. https://doi.org/10.1016/j.visres.2008.07.019

[37] Wässle H, Parallel processing in the mammalian retina, Nat Rev Neurosci 5(10) (2004) 747-757. https://doi.org/10.1038/nrn1497

[38] Temple S, Hart NS, Marshall NJ, Collin SP, A spitting image: specializations in archerfish eyes for vision at the interface between air and water, Proc R Soc B Biol Sci 277(1694) (2010) 2607-2615. https://doi.org/10.1098/rspb.2010.0345

[39] Ben-Simon A, Ben-Shahar O, Vasserman G, Ben-Tov M, Segev R, Visual acuity in the archerfish: Behavior, anatomy, and neurophysiology, J Vision 12(12) (2012) 1-19. https://doi.org/10.1167/12.12.18

[40] Zimmermann MJY, Nevala NE, Yoshimatsu T, Osorio D, Nilsson D-E, Berens P, Baden T, Zebrafish Differentially Process Color across Visual Space to Match Natural Scenes, Curr Biol 28(13) (2018) 2018-2032.e5. https://doi.org/10.1016/j.cub.2018.04.075

[41] Ben-Tov M, Ben-Shahar O, Segev R, What a predator can teach us about visual processing: a lesson from the archerfish, Curr Opin Neurobiol 52 (2018) 80-87. https://doi.org/10.1016/j.conb.2018.04.001

[42] Haug MF, Biehlmaier O, Mueller KP, Neuhauss SCF, Visual acuity in larval zebrafish: behavior and histology, Front Zool 7(1) (2010) 8. https://doi.org/10.1186/1742-9994-7-8

[43] Northmore DPM, Dvorak CA, Contrast sensitivity and acuity of the goldfish, Vision Res 19(3) (1979) 255-261. https://doi.org/10.1016/0042-6989(79)90171-8

[44] Vanegas H, Ito H, Morphological aspects of the teleostean visual system: A review, Brain Res Rev 6(2) (1983) 117-137. https://doi.org/10.1016/0165-0173(83)90036-X

[45] Yager D, Sharma SC, Grover BG, Visual function in goldfish with unilateral and bilateral tectal ablation, Brain Res 137(2) (1977) 267-275. https://doi.org/10.1016/0006-8993(77)90338-9

[46] Northmore DPM, Optic tectum, in: A. Farrell (Ed.), Encyclopedia of Fish Physiology: from Genome to Environment, Elsevier, Online, 2011, pp. 131-142.

[47] Grill-Spector K, Malach R, The human visual cortex, Ann. Rev. Neuro. Sci. 27(1) (2004) 649-677. https://doi.org/10.1146/annurev.neuro.27.070203.144220

[48] Rajimehr R, Tootell RBH, Organization of human visual cortex, in: A.I. Basbaum, A. Kaneko, G.M. Shepherd, G. Westheimer, T.D. Albright, R.H. Masland, P. Dallos, D. Oertel, S. Firestein, G.K. Beauchamp, M.C. Bushnell, J.H. Kaas, E. Gardner (Eds.), The Senses: A Comprehensive Reference, Elsevier, Oxford, UK, 2008, pp. 595-614.

[49] Nevin LM, Robles E, Baier H, Scott EK, Focusing on optic tectum circuitry through the lens of genetics, BMC Biol 8(1) (2010) 126. https://doi.org/10.1186/1741-7007-8-126

[50] Zhaoping L, From the optic tectum to the primary visual cortex: migration through evolution of the saliency map for exogenous attentional guidance, Curr Opin Neurobiol 40 (2016) 94-102. https://doi.org/10.1016/j.conb.2016.06.017

[51] Timmermans PJA, Souren PM, Prey catching in archer fish: the role of posture and morphology in aiming behavior, Physiol Behav 81(1) (2004) 101-110. https://doi.org/10.1016/j.physbeh.2004.01.010

[52] Dill LM, Refraction and the Spitting Behavior of the Archerfish (*Toxotes chatareus*), Behav Ecol Sociobiol 2(2) (1977) 169-184. https://doi.org/10.1007/BF00361900

[53] Smith HM, The archer fish, Nat Hist 38 (1936) 2-11.

[54] Lüling KH, The archer fish, Scientific American 209(1) (1963) 100-109.

[55] Temple SE, Effect of salinity on the refractive index of water: considerations for archer fish aerial vision, J Fish Biol 70(5) (2007) 1626-1629. https://doi.org/10.1111/j.1095-8649.2007.01432.x

[56] Timmermans PJA, Prey catching in the archer fish: angles and probability of hitting an aerial target, Behav Process 55(2) (2001) 93-105. https://doi.org/10.1016/S0376-6357(01)00172-3

[57] Timmermans PJA, Vossen JMH, Prey catching in the archer fish: does the fish use a learned correction for refraction?, Behav Process 52(1) (2000) 21-34. https://doi.org/10.1016/S0376-6357(00)00107-8

[58] Rossel S, Corlija J, Schuster S, Predicting three-dimensional target motion: how archer fish determine where to catch their dislodged prey, J Exp Biol 205(21) (2002) 3321-3326.

[59] Schuster S, Wöhl S, Griebsch M, Klostermeier I, Animal cognition: How archer fish learn to down rapidly moving targets, Curr Biol 16(4) (2006) 378-383. https://doi.org/10.1016/j.cub.2005.12.037

[60] Temple SE, Manietta D, Collin SP, A comparison of behavioural (Landolt C) and anatomical estimates of visual acuity in archerfish (*Toxotes chatareus*), Vision Res 83(0) (2013) 1-8. https://doi.org/10.1016/j.visres.2013.02.014

[61] Karoubi N, Leibovich T, Segev R, Symbol-value association and discrimination in the archerfish, PLoS ONE 12(4) (2017) e0174044. https://doi.org/10.1371/journal.pone.0174044

[62] Schuster S, Hunting in archerfish – an ecological perspective on a remarkable combination of skills, J Exp Biol 221(24) (2018) jeb159723. https://doi.org/10.1242/jeb.159723

[63] Wolfe JM, Visual search, Curr Biol 20(9) (2010) PR346-R349. https://doi.org/10.1016/j.cub.2010.02.016

[64] Wolfe JM, Horowitz TS, Five factors that guide attention in visual search, Nat Hum Behav 1(3) (2017) 0058. https://doi.org/10.1038/s41562-017-0058

[65] Reinel CP, Schuster S, Archerfish fast-start decisions can take an additional variable into account, J Exp Biol 219(18) (2016) 2844. https://doi.org/10.1242/jeb.136812

[66] Reinel CP, Schuster S, Rapid depth perception in hunting archerfish. II. An analysis of potential cues, J Exp Biol 221(14) (2018) jeb177352. https://doi.org/10.1242/jeb.177352

[67] Reinel CP, Schuster S, Rapid depth perception in hunting archerfish. I. The predictive C-starts use an independent estimate of target height, J Exp Biol 221(14) (2018) jeb177345. https://doi.org/10.1242/jeb.177345

[68] Schuster S, Fast-starts in hunting fish: decision-making in small networks of identified neurons, Curr Opin Neurobiol 22(2) (2012) 279-284. https://doi.org/10.1016/j.conb.2011.12.004

[69] Schuster S, Archerfish, Curr Biol 17(13) (2007) R494-R495. https://doi.org/10.1016/j.cub.2007.04.014

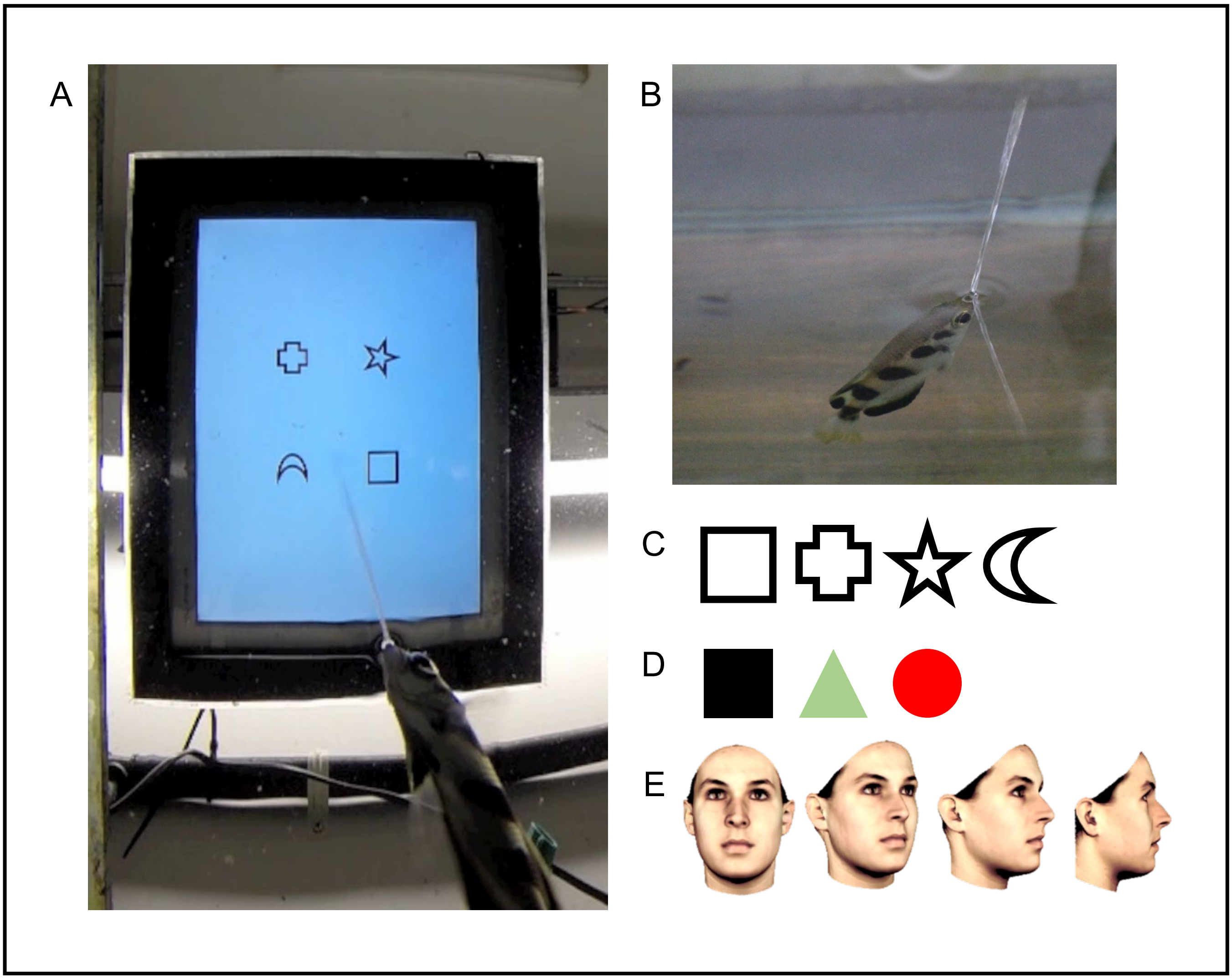
[70] Reinel C, Schuster S, Pre-start timing information is used to set final linear speed in a C-start manoevre, J Exp Biol 217 (2014) 2866-2875. https://doi.org/10.1242/jeb.105510

[71] Wöhl S, Schuster S, Hunting archer fish match their take-off speed to distance from the future point of catch, J Exp Biol 209(1) (2006) 141. https://doi.org/10.1242/jeb.01981

[72] Krupczynski P, Schuster S, Precision of archerfish C-starts is fully temperature compensated, J Exp Biol 216 (2013) 3450-3460. https://doi.org/10.1242/jeb.088856

[73] Troje NF, Bülthoff HH, Face recognition under varying poses: The role of texture and shape, Vision Res 36(12) (1996) 1761-1771. https://doi.org/10.1016/0042-6989(95)00230-8

[74] Blanz V, Vetter T, A morphable model for the synthesis of 3D faces, Proceedings of the 26th annual conference on Computer graphics and interactive techniques, ACM Press/Addison-Wesley Publishing Co., 1999, pp. 187-194.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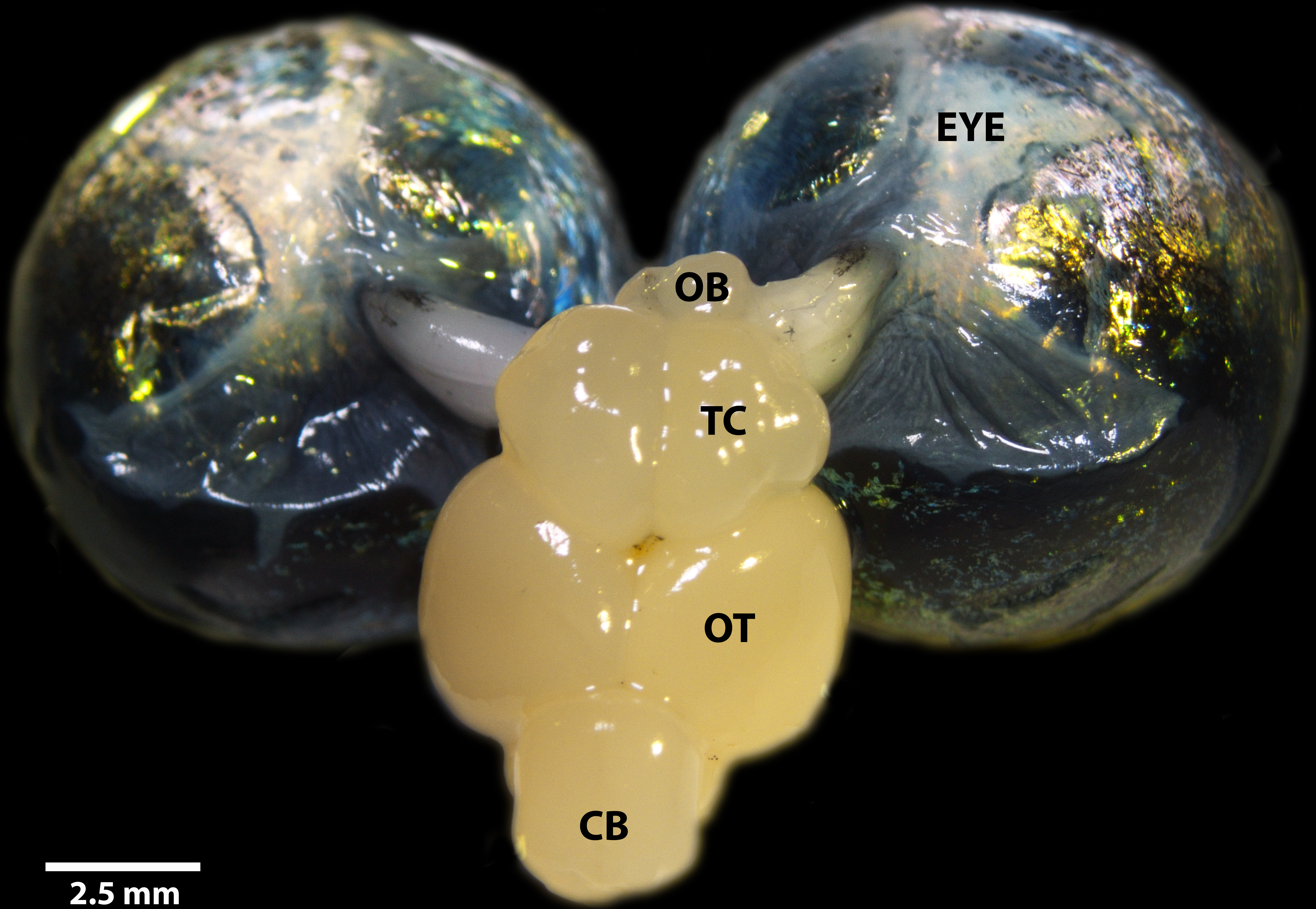
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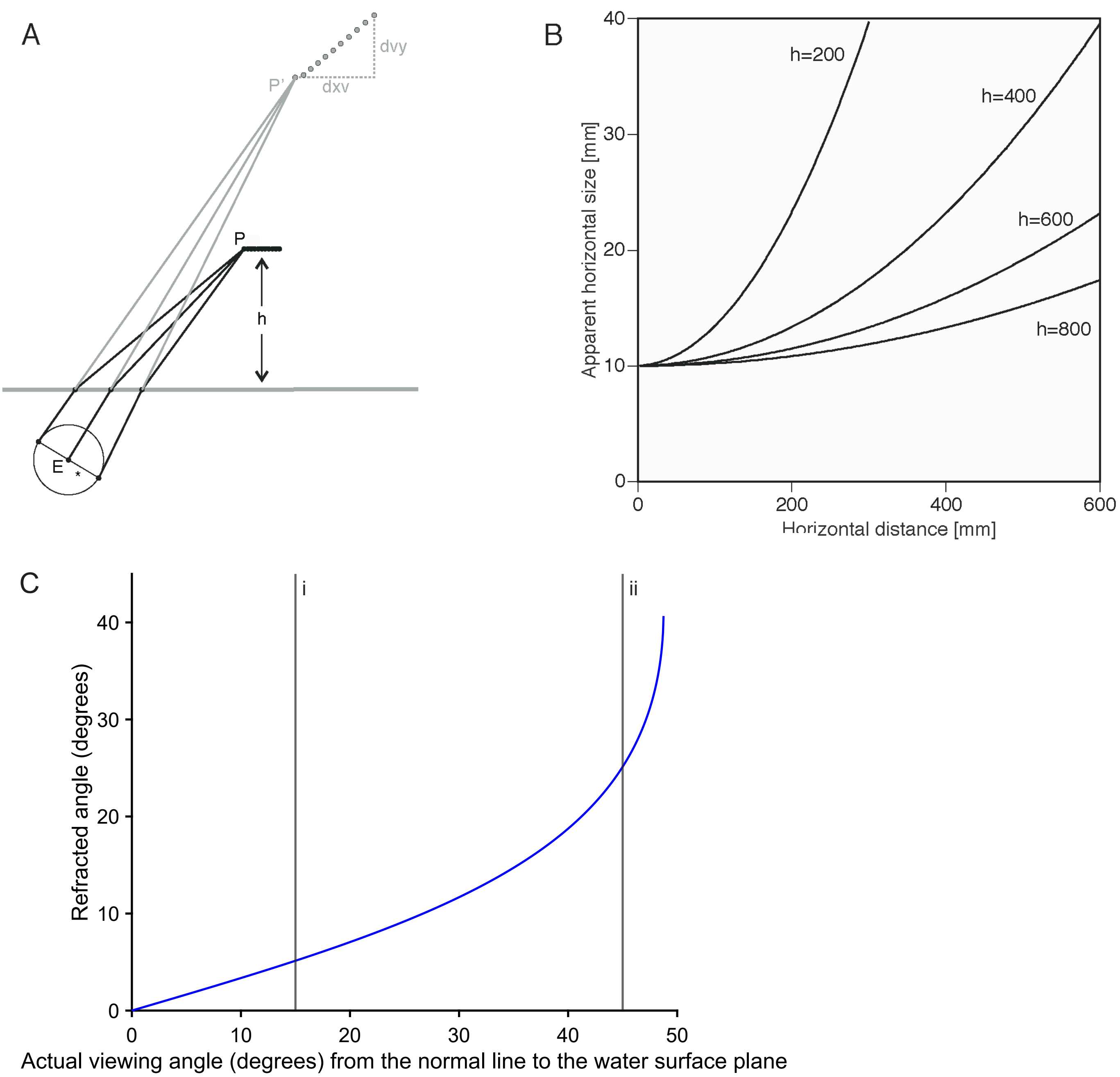
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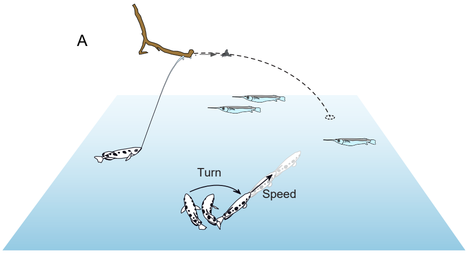
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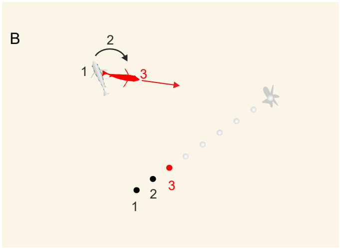
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