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Object recognition in fish: accurate discrimination across novel views of an unfamiliar object category (human faces)

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Accurate visual object recognition is essential to survival for a wide range of species across a wide range of evolutionary histories and visual requirements. However this task is solved, it is a major achievement because object recognition is far from simple. The appearance of an object can alter almost completely as viewing conditions change, not least under variations in lighting and orientation. Determining the recognition limits of a species is important to understanding its visual ecology and can help identify conditions under which recognition may fail. In this study, we tested whether a species of fish can recognize objects from an unfamiliar object class (human faces) across changes in viewing direction. Using operant conditioning, we trained archerfish, *Toxotes chatareus*, to discriminate between two frontal views of standardized human faces and, critically, tested whether they could continue to do so as the orientation in depth of the faces changed. All fish learned the initial discrimination task and could also recognize rotated forms. These results represent the first conclusive evidence that a species of fish can generalize recognition across views, speaking against a strict image-matching process. This ability rather speaks to the capacity of relatively simple brains to tackle the hard problem of view invariance and provides insight into the mechanisms employed in more complex organisms such as humans. Although we speculate that other fish species may demonstrate similar abilities, a visual system capable of recognition across changes in viewpoint may be especially important to the unique hunting strategy of archerfish.

Object recognition is fundamental to many complex visual behaviours (e.g. food detection, mate selection, individual recognition) and yet it is a far from trivial task because changes in viewing conditions (e.g. lighting or viewing direction) can drastically alter the two-dimensional (2D) image cast in the eye of the observer by the three-dimensional (3D) object. The underlying mechanisms of recognition can constrain performance in terms of accuracy, flexibility or speed, and have real consequences for the visual ecology of a species. Recognition that is robust allows for flexibility but may be slower than other systems and limited to animals with sufficiently sophisticated brain structures (Wallis & Bülthoff, 1999). Conversely, a view-dependent recognition system would require less processing power, allowing for faster recognition, but at the cost of reduced flexibility (Wallis & Bülthoff, 1999). The aim of this study was to test, for the first time, whether a species of fish is capable of view-invariant recognition of a complex object category. This should bring us closer to answering two things: how a fish might perceive visual stimuli in its environment, and the capabilities and limitations of the recognition system of a lower vertebrate with no visual cortex.

Experiments with primates (Logothetis & Sheinberg, 1996), rats, *Rattus norvegicus* (Alemi-Neissi, Rosselli, & Zoccolan, 2013; Rosselli, Alemi, Ansuini, & Zoccolan, 2015; Tafazoli, Di Filippo, & Zoccolan, 2012; Zoccolan, 2015; Zoccolan, Oertelt, DiCarlo, & Cox, 2009), sea lions, *Zalophus californianus* (Stich, Dehnhardt, & Mauck, 2003), domestic chicks, *Gallus gallus domesticus* (Mascalzoni, Osorio, Regolin, & Vallortigara, 2012) and horses, *Equus ferus caballus* (Hanggi, 2010) have all demonstrated that some mammals and birds can recognize objects from novel viewpoints. Conversely, some insects (Collett, 1992, 1995) appear to use 'active vision' in which they physically move until the image projected onto the retina matches a selection of less flexible, stored views to the object. The result is that recognition is slower and more error prone.

Even in species that demonstrate view-invariant recognition, the underlying mechanism may vary and result in significant

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differences to their object recognition capabilities. Both pigeons, *Columba livia*, and bees, *Apis mellifera*, for example, have been used to test how species lacking a neocortex recognize complex objects by testing whether they can identify rotated human faces after experience with a single orientation (Dyer & Vuong, 2008; Jitsumori & Makino, 2004). When bees were trained with frontal views (0°) of two faces, they were unable to discriminate between the two when rotated by 30°, but given experience with multiple views of the same faces (0° and 60°), the bees were able to recognize the rotated face (30°) albeit with reduced accuracy (Dyer & Vuong, 2008). As a result, the authors concluded that bees are most likely to be relying on a mechanism of image interpolation. Conversely, pigeons and chicks demonstrated true spontaneous view-invariant recognition with a single exemplar, suggesting that they are capable of using some form of image extrapolation (Jitsumori & Makino, 2004; Wood, 2013, 2015). One important lesson from this is that while bees are capable of performing many seemingly sophisticated behaviours (e.g. Avarguès-Weber & Giurfa, 2013; Biernaskie, xa, Walker, xa, & Michael, 2009; Howard, Avarguès-Weber, Garcia, & Dyer, 2017), it does not necessarily mean the underlying mechanisms or the functional limits are identical to those of other species. Therefore, it is worth exploring how a range of animals with different life histories perform the same tasks to understand the evolution of visual systems and complex behaviour.

Contrary to common misconceptions about fish intelligence, studies of the visual ecology and cognitive abilities of fish are providing increasing evidence that fish can have sophisticated visual repertoires and possess impressive visual systems (e.g. Champ, Wallis, Vorobyev, Siebeck, & Marshall, 2014; Cheney, Grutter, Blomberg, & Marshall, 2009; Cheney, Newport, McClure, & Marshall, 2013; Cheney & Marshall, 2009; Newport, Wallis, Temple, & Siebeck, 2013; Newport, Wallis, & Siebeck, 2014, 2015; Newport et al., 2017; Rosa Salva, Sovrano, & Vallortigara, 2014; Siebeck, Litherland, & Wallis, 2009; Siebeck, Parker, Sprenger, Mathger, & Wallis, 2010). Studies on the underlying mechanisms of their visual system indicate that despite their relatively small (Northcutt, 2002) and simple brain (i.e. no neocortex), fish demonstrate some sophisticated visual abilities that are comparable to those of humans (e.g. Rischawy & Schuster, 2013; Schlegel & Schuster, 2008; Schuster, Rossel, Schmidtmann, Jäger, & Poralla, 2004). We even know that fish can generalize recognition across some affine transformations, including changes in size (Douglas, Eva, & Guttridge, 1988; Frech, Vogtsberger, & Neumeyer, 2012; Schuster et al., 2004), indicating some recognition flexibility. That said, there are very few studies investigating a task as complicated as object recognition across changes in viewpoint.

Some of the earliest attempts to test recognition across more complex image transformations were reported by Schuster and Amtsfeld (2002), who used 2D shapes to explore whether weakly electric fish, *Gnathonemus petersii*, generalize between learned and novel stimuli based on similarity of the retinal image. The authors concluded that a template-matching recognition system explained the generalization behaviour of this species. Schluessel, Kraniotakes, and Bleckmann (2014) used 3D objects as stimuli for experiments with Malawi cichlids; however, the stimuli had features that were not affected by changes in orientation (e.g. overall colour and size) making the results difficult to interpret. In addition, the approach angle of the fish was not restricted, allowing it to view the objects from different angles, before making a selection.

In this study, we adapted methods and a set of visual stimuli used in primate and human testing to systematically investigate recognition generalization across rotation in depth in a species of fish. Our test species was the archerfish, *Toxotes chatareus*, which is known for its ability to hunt aerial prey by knocking them down with a jet of water spat from the mouth. Given the fish's proven ability to perform visual discrimination tasks (Newport et al., 2013, 2016; Temple, Manietta, & Collin, 2013) and its ecology, archerfish are a good candidate for testing. The stimulus set we chose was human faces as they offer a number of points of interest as a test set. First, they are not biologically relevant to the fish, making it unlikely that the fish is endowed with an innate ability to discriminate them. Second, recognizing faces is particularly taxing as their appearance changes dramatically as a function of viewing angle, and a very large set of similar-looking distractors exist, namely other faces (Wallis, Siebeck, Swann, Blanz, & Bülthoff, 2008). Third, while other stimuli can be used to test view invariance, previous studies on a range of taxa have used faces as a study set, permitting comparisons to be drawn. If fish can recognize novel views of human faces it would provide the first evidence of a remarkably robust recognition system in a fish, providing insight into its ecology and, in a wider sense, into the mechanisms that might underlie sophisticated recognition systems, since this fish does not possess a cortex.

METHODS

General Procedure

Six archerfish were used which is an adequate sample size for this type of experiment. To reduce the number of animals used, individuals were used in both experiments. Fish were purchased from commercial aquarium shops; commercial collection and handling of fish is regulated by governmental agencies in Australia. All fish were kept as described by Newport et al. (2013) in accordance with the University of Queensland Animal Ethics Committee approval (AEC approval number: SBMS/241/12) and all experimental protocols were approved by the same body. Experiments followed similar procedures to those described by Newport et al. (2016). Briefly, stimuli were displayed on a 15-inch (1024 × 768 pixels) LCD monitor (SyncMaster 153v, Samsung) with a Plexiglas housing, suspended above the aquaria. The archerfish were presented with a two-alternative forced-choice test (stimulus monitor coordinates: 0 −160, 0 160). Stimulus positions on the monitor were balanced so that the rewarded stimulus (S+) appeared equally often on the left and right and was further constrained to never appear in the same position on more than two consecutive trials. Archerfish selected a stimulus by spitting a jet of water at the stimulus on the computer monitor. The experimenter recorded the response of the fish, as the jet of water and the presented stimuli were clearly visible. The accuracy of the fish meant that the water jet hit within the area of only one stimulus and therefore there was no ambiguity in its choice. The fish received a food pellet as a reward (CichlidGold, Kyorin Co. Ltd., Tokyo, Japan) which was dropped in by hand by the experimenter when the correct stimulus was selected in training and reinforcement trials (frontal views). Selection of the distractor stimulus (S−) resulted in no food reward and an immediate termination of the trial. The experiment relied on operant conditioning through positive reinforcement. Training cannot be achieved without willingness on the part of the fish and ensuring healthy living conditions is necessary to preserve its motivation. Although this project does involve animal experimentation, the experiment was unlikely to have any adverse effects on the fish and in fact may serve as artificial enrichment for captive animals.

Stimuli

The images comprised 2D renderings of scanned human faces from the 3D Head Models Database created by researchers at the Max Planck Institute in Tübingen, Germany (Blanz & Vetter, 1999;