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A spitting image: specializations in archerfish eyes for vision at the interface between air and water

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Archerfish are famous for spitting jets of water to capture terrestrial insects, a task that not only requires oral dexterity, but also the ability to detect small camouflaged prey against a visually complex background of overhanging foliage. Because detection of olfactory, auditory and tactile cues is diminished at air–water interfaces, archerfish must depend almost entirely on visual cues to mediate their sensory interactions with the aerial world. During spitting, their eyes remain below the water's surface and must adapt to the optical demands of both aquatic and aerial fields of view. These challenges suggest that archerfish eyes may be specially adapted to life at the interface between air and water. Using microspectrophotometry to characterize the spectral absorbance of photoreceptors, we find that archerfish have differentially tuned their rods and cones across their retina, correlated with spectral differences in aquatic and aerial fields of view. Spatial resolving power also differs for aquatic and aerial fields of view with maximum visual resolution (6.9 cycles per degree) aligned with their preferred spitting angle. These measurements provide insight into the functional significance of intraretinal variability in archerfish and infer intraretinal variability may be expected among surface fishes or vertebrates where different fields of view vary markedly.

Keywords: fish; *Toxotes chatareus*; acuity; colour vision; opsin; chromophore

1. INTRODUCTION

Visual ecology is the study of how visual systems have adapted to their visual tasks and light environments. In aquatic systems, light environments are heavily dependent on the optical properties of water and suspended particulate matter therein, which greatly affect the distance over which vision may be useful and alter the transmission of light at different wavelengths. When fishes from different habitats are compared, there is a general correlation between the spectral position of their cone pigments and the background spectral environment, with the correlation being strongest for double cones (Bowmaker *et al.* 1994; Lythgoe *et al.* 1994; McDonald & Hawryshyn 1995; Cummings & Partridge 2001). The adaptive value of spectral tuning has been further supported by examples where visual pigments change within a single species as they move between habitats (Carlisle & Denton 1959; Wood *et al.* 1992; Shand 1993; Loew *et al.* 2002; Temple *et al.* 2008*b*). But what about eyes that simultaneously look at two different spectral environments?

It has been observed in some fishes (Levine *et al.* 1979; Bridges 1982; Burkhardt *et al.* 1983; Takechi & Kawamura 2005; Temple *et al.* 2006), amphibians (Reuter *et al.* 1971), lizards (Bowmaker *et al.* 2005), birds (Bowmaker 1977; Hart *et al.* 2006) and mammals (Ferree & Rand 1919; Szel *et al.* 1992; Röhlich *et al.* 1994; Panorgias *et al.* 2009) that different parts of the retina employ different visual pigments or proportions thereof, or spectral filters that differentially tune spectral sensitivity. This poorly understood phenomenon—which we will hereafter refer to as 'intraretinal differential spectral tuning' a form of intraretinal variability—is potentially a powerful tool for explaining the role of specific sets of visual pigments within an animal eye. However, explaining the functional significance of different sets of visual pigments within any eye has proved challenging because we often know too little about the visual tasks and selective pressures that drive eye evolution. This is exemplified by our own eyes, in which proportions of the three cone types (red, green and blue) in the retina differ with eccentricity for which there, is as yet, no clear explanation (Ferree & Rand 1919; Szel *et al.* 1996; Mullen & Kingdom 2002). We demonstrate that archerfish also employ intraretinal differential spectral tuning, and we propose a model to explain the spectral position of the visual pigments in different parts of the eye by correlating the spectral sensitivity with the visual tasks associated with each visual axis.

The hunting tactic of archerfish (family Toxotidae), which spit jets of water to knock terrestrial prey down to the water's surface, was first brought to the attention of Western science nearly 250 years ago in *Philosophical Transactions of the Royal Society London* (Schlosser 1764). Since then research on archerfish has focused on

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