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Colour vision in billfish

Kerstin A. Fritsches^{1*}, Julian C. Partridge², John D. Pettigrew¹ and N. Justin Marshall¹

¹*Vision, Touch and Hearing Research Centre, Department of Physiology and Pharmacology, University of Queensland, Brisbane, Queensland 4072, Australia*

²*School of Biological Sciences, University of Bristol, Woodland Road, Bristol, BS8 1UG, UK*

Members of the billfish family are highly visual predatory teleosts inhabiting the open ocean. Little is known about their visual abilities in detail, but past studies have indicated that these fishes were likely to be monochromats. This study, however, presents evidence of two anatomically distinct cone types in billfish. The cells are arranged in a regular mosaic pattern of single and twin cones as in many fishes, and this arrangement suggests that the different cone types also show different spectral sensitivity, which is the basis for colour vision. First measurements using microspectrophotometry (MSP) revealed a peak absorption of the rod pigment at 484 nm, indicating that MSP, despite technical difficulties, will be a decisive tool in proving colour vision in these offshore fishes. When hunting, billfish such as the sailfish flash bright blue bars on their sides. This colour reflects largely in ultraviolet (UV) light at 350 nm as revealed by spectrophotometric measurements. Billfish lenses block light of wavelengths below 400 nm, presumably rendering the animal blind to the UV component of its own body colour. Interestingly, at least two prey species of billfish have lenses transmitting light in the UV waveband and are therefore likely to perceive a large fraction of the UV peak found in the blue bar of the sailfish. The possible biological significance of this finding is discussed.

Keywords: colour vision; teleost; ultraviolet; anatomy; microspectrophotometry

1. INTRODUCTION

The family of billfish (Xiphiidae) comprises the marlin, sailfish and swordfish. As pelagic predators living in a clear-water habitat, billfish appear to rely strongly on their visual sense (Davie 1990). Irrespective of the time of day, marlin, and probably also sailfish, appear to spend most time within the first 10 m of the water column interrupted by short deep dives, while swordfish are known to hunt at greater depths than this (Holland *et al.* 1990; Block *et al.* 1992).

Two previous studies on colour vision in marlin, using both visual pigment extraction techniques (Munz & McFarland 1975) and recordings of the electroretinogram (Kawamura *et al.* 1981), have concluded that these animals are monochromats. Billfish are important targets of commercial and recreational fisheries, hence the issue of colour vision in these species might also have implications for catching strategies. Increased knowledge about fishes' colour vision has accumulated in recent years and improved techniques have led us to revisit the question of colour vision in billfish. Since the studies mentioned above, correlations between cone morphology and spectral sensitivity are more thoroughly understood. We therefore reinvestigated the cone distribution in the billfish retina and also attempted microspectrophotometry (MSP).

Billfish are capable of extremely rapid colour change and when hunting often show a striking blue coloration. This coloration is derived from exposed iridophores

mediated by adrenergic stimulation (Davie 1990). We aimed to measure billfish body coloration to characterize the blue colour using objective colour measurement techniques. We also investigated the possibility of ultraviolet (UV) vision in billfish by quantifying the transmission of their ocular media to establish whether the UV waveband is of importance for their visual system.

2. METHODS

The animals studied were caught by recreational game-fishermen and the animals sacrificed immediately after capture. For this study specimens of blue and black marlin (*Makaira nigricans* and *Makaira indica*) as well as sailfish (*Istiophorus platypterus*) were used. The difficulty in accessing these animals did not allow us to conduct all sets of experiments in every species. For the anatomical examination of the photoreceptor distribution, the retina was isolated from the eye before fixation and the pigment removed before submersing the retina in a fixation solution (4% paraformaldehyde–0.1% glutaraldehyde in 0.1 M phosphate buffer) for 2 h. The retina was then flat-mounted as a whole on a microscope slide with the photoreceptor layer pointing upwards, and examined by light microscopy. MSP was attempted with one sailfish specimen. Samples of the retina were removed from the eye and immediately frozen in a cryoprotectant. MSP measurements were performed at the University of Bristol, UK (for methods see Hart *et al.* 1998).

Measurements of the reflectance of billfish body colours and the transmission of light through the fishes' optical media were undertaken with a custom-built spectrophotometer. Details of the measuring procedure and analysis are described in Siebeck & Marshall (this issue). Transmission was measured through the

* Author for correspondence (k.fritsches@vthrc.uq.edu.au).

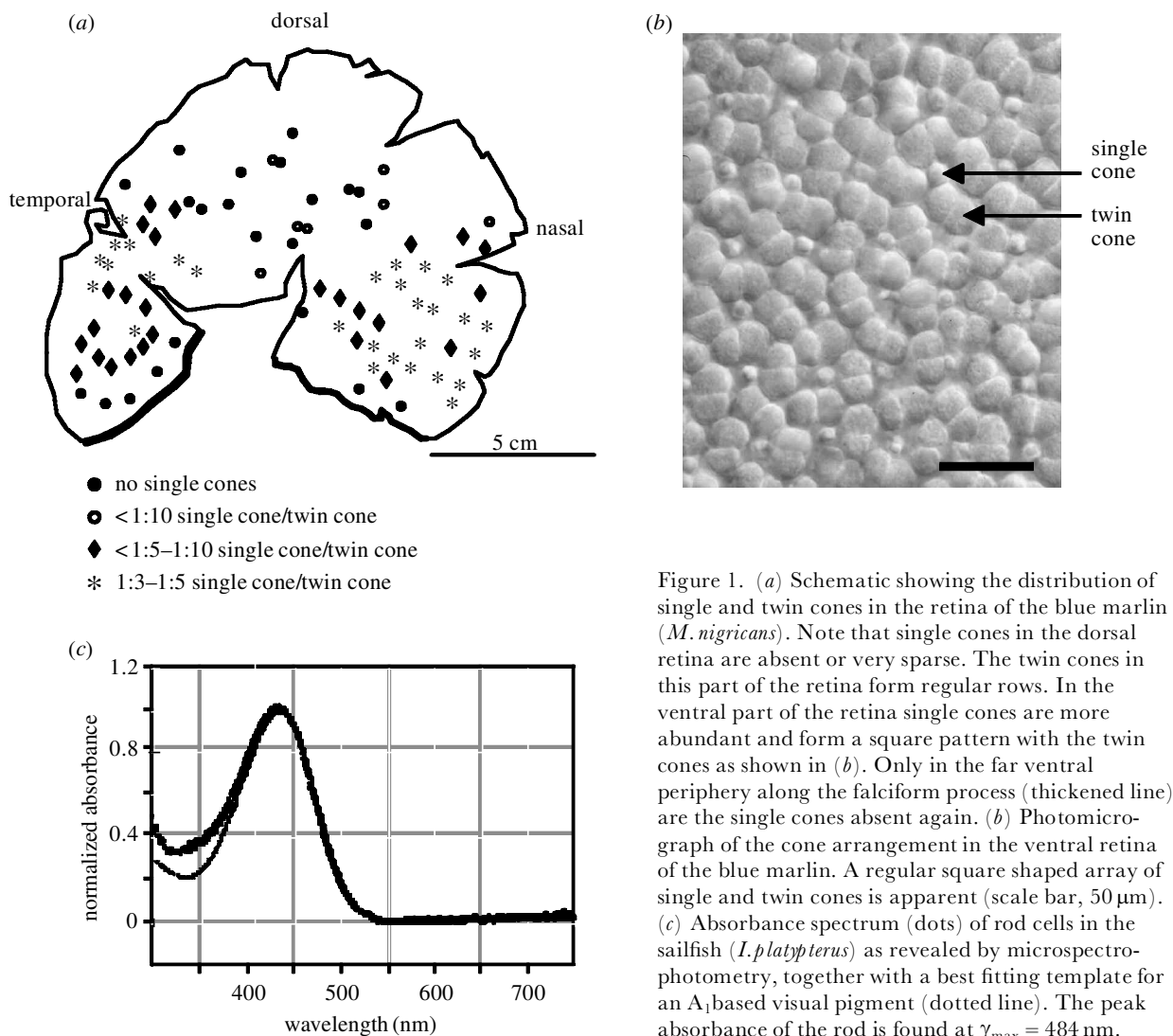


Figure 1. (a) Schematic showing the distribution of single and twin cones in the retina of the blue marlin (*M. nigricans*). Note that single cones in the dorsal retina are absent or very sparse. The twin cones in this part of the retina form regular rows. In the ventral part of the retina single cones are more abundant and form a square pattern with the twin cones as shown in (b). Only in the far ventral periphery along the falciform process (thickened line) are the single cones absent again. (b) Photomicrograph of the cone arrangement in the ventral retina of the blue marlin. A regular square shaped array of single and twin cones is apparent (scale bar, 50 μm). (c) Absorbance spectrum (dots) of rod cells in the sailfish (*I. platypterus*) as revealed by microspectrophotometry, together with a best fitting template for an A_1 -based visual pigment (dotted line). The peak absorbance of the rod is found at $\gamma_{\text{max}} = 484 \text{ nm}$.

isolated lens, the data normalized to 100% at 700 nm and the wavelength determined at 50% transmission. In order to measure the reflectance spectra of the body colours, small areas of skin were immersed in a solution of adenosine (Sigma-Aldrich, Castle Hill, Australia; 10^{-4} M), a treatment which triggers the exposure of the colour iridophores (for methods see Kasukawa *et al.* 1987).

3. RESULTS

Three types of photoreceptors can be identified in the retina of the blue and black marlin and the sailfish: rods, twin cones and single cones. Twin cones are the predominant cone type, consisting of an equal pair of large cones with exceptionally long outer segments (up to 120 μm), joined at the inner segments. In the whole-mount preparation, which provides a tangential point of view of the retina, smaller single cones are also visible. The blue marlin shows a regional variation in the number of single cones in relation to twin cones. While in many parts of the dorsal retina single cones are absent or very sparse, the ratio of single cones to twin cones increases to 1:3–1:4 in the ventral part of the retina, revealing a dorsoventral gradient (figure 1a). The occurrence of single cones increases rapidly within a narrow band in the nasal and

temporal periphery while few single cones are found in the fundus. Single cones are also absent in the ventral periphery of the retina along the falciform process.

In most teleosts single and twin cones are distributed in regular patterns that are arranged in row or square mosaics (Ali & Anctil 1976). The blue marlin shows regional differences in the distribution of the pattern in that row mosaics can be found predominantly in the dorsal retina while square mosaics occur in the ventral retina. The row mosaic is formed by twin cones that are orientated in one direction, with occasional single cones interspersed (figure 1b). However, these do not interrupt the regular row pattern of the twin cones. Square mosaics in the ventral retina are formed by neighbouring twin cones arranged at approximate right angles to each other, usually with a single cone at the centre of a formation of four twin cones. Unlike cone mosaics in many other teleosts (Ali & Anctil 1976) the mosaic in the marlin retina does not appear to be perfectly square. The long axis of the twin cones is slightly rotated within the square formation, although this could be an artefact of the whole-mount preparation.

The spectral sensitivity of photoreceptors in the sailfish retina was measured using MSP. Initially it was unclear whether this technique was possible in billfish since these

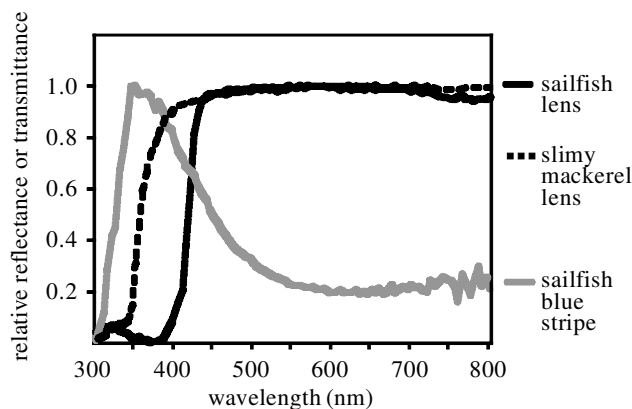


Figure 2. Reflectance spectrum of the blue stripe of the sailfish (grey line), and transmittance spectra for the lenses of the sailfish (black line) and the slimy mackerel (dashed line), a prey species of sailfish. The UV peak of the skin colour of the sailfish appears to be better matched to the visual system of its prey rather than that of the sailfish.

fishes can only be caught in the light, hence pigment regeneration had to be induced *in vitro*. Furthermore the tissue was frozen and airtailed from Australia to the University of Bristol, UK, a procedure that can diminish the quality of the preparation. The samples, however, led to precise absorbance spectra (figure 1c), indicating high quality measurements of visual pigment sensitivity. The sampling technique in this initial study restricted the measurements in that only rods could be investigated. The spectral sensitivity of the measured rods is found to have a peak absorbance at a wavelength (γ_{\max}) of 484 nm.

When excited, billfish show brilliant blue bars along their body. Measurements of the reflectance of these bars in sailfish *in vitro* reveal a strong peak located at 340–350 nm in the UVA band (315–400 nm) (figure 2). A major indicator of the ability to see in the UV waveband can be found by testing the transmission through the optic media of an eye. These measurements in two species of billfish indicate that the lenses block light at wavelengths shorter than 400 nm. The 50% cut-off for a lens is found at 415 nm in the black marlin ($n=2$ lenses) and 419 nm in the sailfish ($n=5$), respectively. These billfish are therefore not sensitive to the major component of their own body colour (figure 2). A competing predator, the mahi mahi (*Coryphaena hippurus*), has an even higher cut-off point at 436 nm ($n=4$). However, one of the major prey fishes of billfish, the slimy mackerel (*Scomber australasicus*), shows a cut-off at 357 nm ($n=3$) and is thus likely to perceive most of the UV colour displayed by the sailfish (figure 2). Another prey fish, the horse mackerel (*Trachurus* sp.), also perceives the upper part of the UVA spectrum, revealing a 50% cut-off value at 389 nm ($n=2$).

4. DISCUSSION

(a) Evidence for colour vision

The topography of cone distribution in the blue marlin reveals the presence of two morphologically distinct cone types, single cones and twin cones. In fishes, morphologically different cone types in a single retina usually have different spectral sensitivities, providing the foundation for colour discrimination

(Loew & Lythgoe 1978). The mosaic arrangement of twin and single cones found in billfish resembles that of dichromatic fishes (Lythgoe 1984). Some species show different spectral sensitivities in the two outer segments of the twin cone, hence trichromacy is also possible with this mosaic (Levine & MacNichol 1979). MSP data measured from the rods of sailfish reveal a peak absorption at 484 nm, a finding which supports previous measurements using pigment extraction (Munz & McFarland 1975). The paucity of suitable tissue did not allow further experiments to identify the spectral sensitivity of the different cone types, and this will be addressed in a future study.

Munz & McFarland (1975) measured spectral sensitivity of cones in billfish by extraction of visual pigment but they found only one identical pigment for both rods and cones. Although the authors recognized that pigment extraction of cones is very difficult, their finding of two different cone pigments (γ_{\max} at 521 nm and 469 nm) in the retina of the mahi mahi suggests potential differences in colour vision between the two species. Comparisons of anatomical investigations show that mahi mahi have an even distribution of single and twin cones throughout the retina (Tamura & Wisby 1963). In billfish, in contrast, single cones are only present in the ventral retina (Tamura & Wisby 1963; this study). The concentration of single cone pigment in a pigment extract would therefore be lower in billfish, possibly too low for detection.

Billfish, like other pelagic fishes, are faced with the difficult task of detecting prey against a uniform background of changing light intensity. Dichromacy in these animals is thought to have evolved to enhance the contrast of light and dark objects against the space light (for a review, see Lythgoe 1984). However, this system is only beneficial if enough light of different wavelength is available to the animal (Levine & MacNichol 1982). Billfish appear to have optimized their eyes to this constraint by developing two cone types in the ventral retina, which looks up into the bright light. The dorsal retina, which points downwards into the darker water below the animal, predominantly shows twin cones and therefore appears to be specialized for sensitivity rather than hue discrimination. A similar split between dorsal and ventral retina has been found in several species of clupeids (Engström 1963) and possibly also in the skipjack tuna (*Euthynnus pelamis*) and the amberjack (*Seriola dumerili*) (Tamura & Wisby 1963). Mahi mahi show sexual dimorphism in their body coloration and hue discrimination might be relevant in a social context. This could explain the need for colour vision in all parts of the eye, reflected by an even distribution of single and twin cones throughout the retina.

(b) The role of UV in billfish vision

Our results show that billfish lenses do not transmit light at wavelengths shorter than 400 nm, hence the UVA spectrum is unlikely to play a role in the colour vision of these fishes. Consequently these animals are not capable of seeing the UV component of their own colour bars. This is not unusual in fishes, many of which have developed lenses blocking UV, possibly to protect the eye from UV damage. The lens of the slimy mackerel, and to a certain extent the horse mackerel, does, however, transmit light at short wavelengths. This prey fish is therefore

likely to perceive the full reflectance spectrum of the billfish coloration, which would enhance the signal given by the billfish bar to the mackerel. It is thus possible that the sailfish might have developed its UV coloured bars for the visual system of its prey. In this respect two advantages for prey capture can be envisaged for the billfish. First, the brightly coloured bars could be used to break up the large dark silhouette of the approaching billfish, disguising an attack. Second, the presence of conspicuous coloration on the flanks of sailfish circling a prey fish school might confuse the schooling fishes. Conspicuous patterns in other predators have been shown to have a destabilizing effect on schooling fishes (Wilson *et al.* 1987) and billfish might follow a similar strategy, using strong signals to disrupt fish schools.

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