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Warm Eyes Provide Superior Vision in Swordfishes

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Summary

Large and powerful ocean predators such as swordfishes, some tunas, and several shark species are unique among fishes in that they are capable of maintaining elevated body temperatures (endothermy) when hunting for prey in deep and cold water [1–3]. In these animals, warming the central nervous system and the eyes is the one common feature of this energetically costly adaptation [4]. In the swordfish (*Xiphias gladius*), a highly specialized heating system located in an extraocular muscle specifically warms the eyes and brain up to 10°C–15°C above ambient water temperatures [2, 5]. Although the function of neural warming in fishes has been the subject of considerable speculation [1, 6, 7], the biological significance of this unusual ability has until now remained unknown. We show here that warming the retina significantly improves temporal resolution, and hence the detection of rapid motion, in fast-swimming predatory fishes such as the swordfish. Depending on diving depth, temporal resolution can be more than ten times greater in these fishes than in fishes with eyes at the same temperature as the surrounding water. The enhanced temporal resolution allowed by heated eyes provides warm-blooded and highly visual oceanic predators, such as swordfishes, tunas, and sharks, with a crucial advantage over their agile, cold-blooded prey.

Results and Discussion

Due to the large size of swordfishes, and their remote open-ocean habitat, we recorded electroretinograms (ERGs) from fishes caught live at sea on longline gear. The animals used in this study had body lengths ranging from 130 cm to 206 cm (jaw-fork length) and eye diameters of up to 90 mm (Figure 1A). Such large eyes suggest that swordfishes are highly visual predators, adapted to maximize visual performance in the dim down-welling daylight at great ocean depths. Using isolated retinal preparations for ERG recordings from swordfishes, we investigated the retina's response to sinusoidally modulated light stimuli of various intensities at different temperatures. We found that temperature had a pronounced effect on temporal resolution as measured by the flicker fusion frequency (FFF), the stimulus frequency at which the retina is no longer able to resolve the sinusoidally modulated light stimulus (Figure 1B; greater temporal resolution is equated with a higher FFF). The swordfish retina was exceptionally sensitive to temperature changes, showing an increase in FFF from 5 Hz or less at 10°C to over 40 Hz at 20°C (Figure 2A). Intact swordfishes maintain brain and eye temperatures between 19°C and 28°C [2], thus allowing a substantially higher FFF at low ambient temperatures (Figure 2A, gray shading).

The light-adapted swordfish retina showed a Q_{10} (the fractional increase in FFF per 10°C) of 5.1 ($n = 6$, $r^2 = 0.80$). This Q_{10} value was more than twice as high as those measured in two species of tunas, which we tested for comparison. The surface-living yellowfin tuna (*Thunnus albacares*) and the deep-diving bigeye tuna (*Thunnus obesus*) revealed Q_{10} values of 2.3 ($n_{\text{yellowfin tuna}} = 5$, $r^2 = 0.72$) and 2.5 ($n_{\text{bigeye tuna}} = 6$, $r^2 = 0.76$), respectively (Figure 2B). These results in tunas are comparable with the temperature sensitivity of visual function found in other studies [7–9]. Both bigeye and yellowfin tunas achieve whole-body warming using vascular countercurrent heat exchange interposed between the swimming muscles and the gills. This leads to improvements in a range of temperature-sensitive physiological processes such as locomotion, digestion, metabolism, and neural function [10]. For swordfishes it appears that no other physiological processes other than neural function require warming in order to allow thermal niche expansion [4]. This has led to the development of a heating mechanism devoted exclusively to the eye and brain, a mechanism fundamentally different to that found in the tuna. The exceptional temperature sensitivity of the swordfish retina described here might have driven the evolution of this unique adaptation, thus preventing a rapid deterioration of temporal resolution with decreasing temperature as the swordfish descends.

The temporal resolution of a visual system is not only affected by temperature; the FFF also decreases with decreasing light intensity [11] (Figure 3A). As the swordfish descends in clear water on a sunny day, light intensities reach starlight levels by 600–700 min depth [12, 13]. We translated our experimental light intensities into equivalent diving depths (see Experimental Procedures) to approximately correlate the FFF with light levels experienced by the fish when diving. Between depths of 100 m and 500 m and at a retinal temperature of 22°C, the FFF decreases from 40 Hz to 2 Hz (Figure 3A), which increases the signal-to-noise ratio and improves contrast discrimination by suppressing photon noise at

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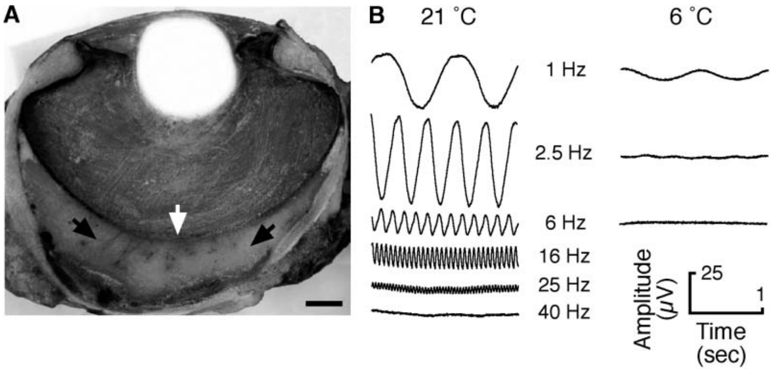

Figure 1. Longitudinal Section through a Swordfish Eye and Electroretinogram of Retinal Response to Sinusoidal Light

(A) Longitudinal section through a swordfish eye of 90 mm diameter, showing the bony eye cup and the thick layer of insulating fatty tissue (black arrows), which surrounds the blood vessels carrying warm blood from the heater organ to the retina [6] (white arrow; the scale bar represents 10 mm).

(B) Electroretinogram recordings of the retinal response to sinusoidal light stimuli of increasing frequency. At a temperature of 21°C (left column), this retina failed to distinguish stimulus frequencies above 32 Hz (i.e., the Flicker Fusion Frequency (FFF) is 32 Hz). When the same retina is cooled to 6°C (right column), the FFF occurs at 6 Hz.

temporal frequencies that are too high to be reliably resolved [14].

Despite the decrease in FFF due to decreasing light levels with depth, we have found that the ability to maintain elevated eye temperatures clearly provides a net benefit for diving swordfishes by increasing temporal resolution. This becomes particularly obvious in parts of the swordfish habitat where the water temperature rapidly declines in near surface water. In these areas, swordfishes can experience temperature declines (thermoclines) from 23°C to 10°C within the top 50 m of the water column [15]. Tracking studies have shown that in these conditions, swordfishes tend to remain in shallower depths down to a few hundred meters and even spend some time on the surface during the day [1, 2, 15]. If the animal did not maintain a warm retina, the drop in ambient temperature would lead to a dramatic deterioration of FFF, even at shallow and brightly lit depths (Figure 3B). In contrast, at 100 m, the swordfish retina is capable of maintaining an FFF twelve times higher than that attainable with a retina at ambient temperature, with a slow decrease in FFF due to decreasing light intensities as the fish descends. At 300 m, a common plateau depth for swordfishes [1, 2, 15], the FFF of a warmed retina is still seven times higher than that of an eye at ambient temperature. Only by 500 m, where light levels are close to starlight levels, are warm and cool eyes equally fast with an FFF of 2 Hz (Figure 3B). Thus, at common daytime depths encountered by swordfishes, their elevated retinal temperatures radically improve temporal resolution and, thereby, the detection and pursuit of fast moving prey. During descents below 500 m in clear water, the advantage of warm eyes is less obvious. For a swordfish swimming at 900 m [15], where light levels are 15 orders of magnitude lower than those experienced on the sunlit surface [13], a lower retinal temperature would be favored for minimizing thermal noise levels, thereby improving absolute light sensitivity [16]. However, there is no evidence that the swordfish

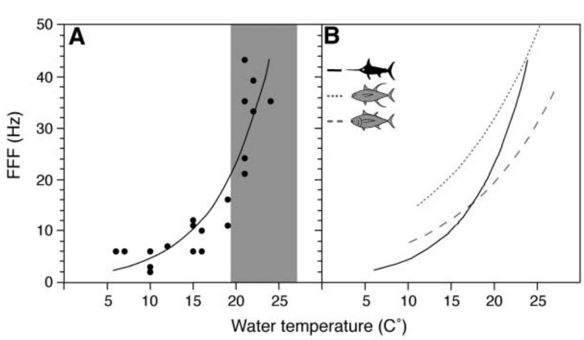

Figure 2. Effect of Temperature on FFF in Isolated Retinas of the Swordfish

(A) The effect of temperature on FFF in isolated retinas of the swordfish ($n = 6$). The gray shading indicates the temperature range within which the swordfish brain and eyes are maintained due to the heater organ [2].

(B) Comparison of temperature effects on FFF in swordfishes (black line, from [A]), bigeye tunas ($n = 6$, dashed gray line), and yellowfin tunas ($n = 5$, dotted gray line).

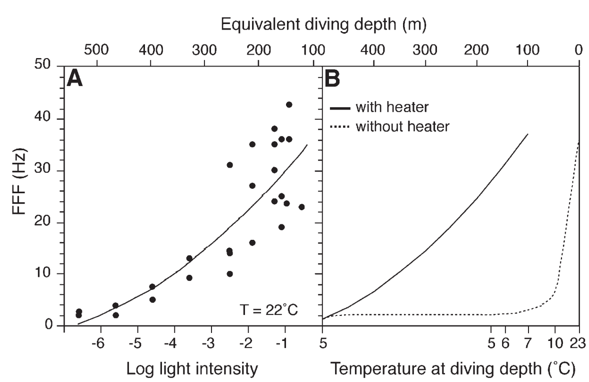

Figure 3. Relationship between FFF and Light Intensity in Swordfishes

(A) Relationship between FFF and light intensity in swordfishes ($n = 5$, curve fitted by eye). Stimulus light intensities were translated to light levels at equivalent diving depths in the ocean (upper horizontal axis; see Experimental Procedures).

(B) A model of the combined effect of light intensity and water temperature on temporal resolution using existing satellite tracking data from a swordfish [15] and the results presented in Figure 3A. Without warm eyes (dotted line), the swordfish FFF would be drastically reduced due to the thermocline present in the first 100 m Although experiencing a slow reduction in FFF due to decreasing light intensity with depth, a swordfish with an intact heater organ that maintains a constant eye temperature (solid line) has a substantially higher FFF than would be expected in an eye lacking a heating mechanism.

brain and eye heater is turned off at deeper depths. Indeed, a near-constant brain temperature might be crucial for maintaining active hunting behavior in swordfishes at all depths [5, 17].

The improved temporal resolution resulting from retinal warming that we have described for swordfishes is also likely to occur in other endothermic open-ocean predators, such as other billfishes [6], tunas [18], and mackerel sharks [19]. Their cold-blooded prey, on the other hand, will have eyes at the same temperature as the surrounding water and, thus, potentially much lower temporal resolution, diminishing their ability to visually avoid predation. Given the speed and maneuverability of the swordfish's cephalopod prey, such as large flying squids of the family *Ommastrephidae* [20, 21] (mantle length of up to 50 cm [21]), the large, fast, and sensitive eyes of swordfishes give them a crucial advantage in pursuing and intercepting fast-moving prey in the cold and dimly lit depths of the ocean.

Experimental Procedures

Source of Animals and Tissue Preparation

Swordfishes (*Xiphias gladius*, n = 10), bigeye tunas (*Thunnus obesus*, n = 6), and yellowfin tunas (*Thunnus albacares*, n = 5) were caught with standard commercial longlining gear on the National Oceanic and Atmospheric Administration (NOAA) research vessels *Townsend Cromwell* and *Oscar E. Sette* in the Pacific Ocean north of the Hawaiian Islands during 2001–2004. The fishes were sacrificed by direct brain destruction, and the retina was immediately removed. Small sections of the dorsal part of the retina (1 cm^2), with vitreous matter attached, were placed on a sponge perfused with aerated Fluorinert solution (FC77, 3 M). We used Fluorinert rather than teleost ringer for maintaining a moist retina due to its high oxygen solubility [22] and electrically inert properties, which were invaluable for low-noise recordings of the ERG in high seas. Isolated retinae continued to respond to light stimuli for several hours under these conditions.

Recording of the Electroretinogram

Multiunit recordings were obtained with Ag-AgCl electrodes. The retina faced the visual stimulus with its photoreceptor side upwards. The active electrode was placed on this surface of the retina and the reference electrode into the vitreous below the retinal piece. The retina, stimulus light source, and electrode apparatus were enclosed in an earthed light-tight metal box in order to maintain a dark-adapted state between stimulus presentations. The stimulus consisted of an array of white LEDs (light output = 7000 mCd, each) diffused to a single, uniform large-field circular light source that subtended 45° at the retina. At maximum illumination, the light source provided an intensity of 1.64×10^3 cd m^{-2}. The broad-spectrum white light LED ensured that both rods and cones were stimulated by the light source; however, the relative contribution of the two photoreceptor types to the ERG at different light intensities and different temperatures was not investigated here.

ERG Recordings at Different Temperatures and Light Intensities

For both sets of experiments, frequencies of sinusoidal light stimulation were varied from 0.4 Hz to 100 Hz in 0.2 log unit steps, with each frequency presented 5 times for 5 s each, and the responses averaged. Sinusoidal light stimuli had a peak-to-peak contrast of 1 between the brightest and the darkest phase (Michelson contrast [23] = $(L_{max} - L_{min})/(L_{max} + L_{min})$; L = luminance). Isolated retinae of swordfishes (n = 6), bigeye tunas (n = 6), and yellowfin tunas (n = 5) were used for the cooling experiments (Figures 1B and 2). A piece of the retina was mounted on a temperature-controlled plate with a control thermocouple placed immediately next to the retinal piece. At the beginning of each experiment, a response-intensity curve (VlogI curve) was recorded for determining an appropriate mean stimulus intensity for the subsequent temperature experiment. A mean stimulus intensity was chosen that gave a response amplitude that was 25% of the saturated response amplitude. A 25% response amplitude was always found to lie within the linear part of the VlogI curve. The response to the sinusoidal stimulus was first recorded at the highest retinal temperature (between 20°C and 25°C), and then at a series of temperatures reduced in steps of 5°C, acclimating the retina for a minimum of 20 min to each temperature. Following the coldest temperature tested (5°C–10°C), the retina was warmed to the initial temperature, and the recovery of response speed was confirmed (otherwise the recordings were rejected). For the second set of experiments (Figure 3), a piece of retina from swordfishes (n = 5) was maintained at a single warm temperature within the physiological range (average 22°C). The response to sinusoidal light stimuli at each stimulus frequency was then recorded for a series of increasing mean light intensities that varied over a 7 log unit range in 1 log unit steps (using both the lamp voltage and Kodak Wratten neutral density filters).

Determining the Flicker Fusion Frequency

The FFF was determined by analyzing the power spectrum of the averaged response at each stimulus frequency. The power at the stimulus frequency (signal) was compared to the standard deviation of the power of a neighboring frequency section (noise). The criterion FFF was defined as the frequency at which the power of the signal was five times larger than the power of the noise. Even though the FFF is a subjective value that depends on the method of measurement and relative noise levels in the preparation, we considered our criterion to be a conservative and reliable method for determining FFF in our experiments, since it was unaffected by differences in response amplitude between experiments. It also removed the experimenter's own subjective judgements from the determination of FFF.

Calculation of the Q_{10} Value

An exponential curve was fitted to the data for each species, and Q_{10} values were calculated using $Q_{10} = FFF_{temp}/FFF_{temp\ -10°C}$, where FFF_{temp} is the FFF at a particular temperature, and $FFF_{temp\ -10°C}$ is the FFF at a temperature 10°C less than the first.

Correlation of Stimulus Light Intensity and Diving Depth in a Clear Ocean

The radiance spectrum (photons $m^{-2}\ s^{-1}\ sr^{-1}\ nm^{-1}$) of the LED light source for different lamp voltages was calibrated with an Ocean Optics S2000 miniature fiber optic spectrometer and an International Light IL1700 radiometer. The number of lamp photons ($m^{-2}\ s^{-1}\ sr^{-1}$) available for vision in the swordfish retina at different voltages was then determined from the cone's spectral sensitivity (which has an absorption peak wavelength of 488 nm: Fritsches, unpublished results). The optics of the swordfish eye (F-number ≈ 1.25, according to Matthiessen's ratio), had it been present during experiments, would have reduced retinal illumination by about a third. Taking this into account, as well as the known reductions in the intensity and spectrum of daylight with depth in the ocean [13], it was possible to approximately convert experimental light intensities to equivalent light intensities at the eye surface in the ocean, and thereby to equivalent depths. These conversions are based on calculated radiances for dorsally down-welling daylight in a clear ocean. The brightest mean intensity of sinusoidal stimulation used in the experiments corresponded to a depth of approximately 150 m in a clear ocean during the day (down welling radiance ca. 2×10^{18} photons $m^{-2}\ s^{-1}\ sr^{-1}$), and the lowest intensity to approximately 550 m (down-welling radiance ca. 3×10^{12} photons $m^{-2}\ s^{-1}\ sr^{-1}$). It should be stressed that these calculations are approximate; the transmission properties of ocean water vary considerably over the surface of the earth, resulting in an estimated error of up to 75 m in our calculations. Even at one location in the mesopelagic zone of the ocean, the light field is not homogeneous; light intensities directly upwards (as calculated here) are typically 40 times greater than the intensity of light measured horizontally and 300 times greater than light intensities measured directly downward [13]. This means that an intensity measured in the dorsal direction would be measured in the horizontal direction at a depth approximately 100 m shallower [13].

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