Cover illustration

These eyes are hot . . .

A "brain freeze headache" describes the cephalic sensation one has when drinking a supercooled "slurpee" too quickly. This odd sensation represents vascular and neurological compromise with the sudden temperature reduction. Any predatory fish that would negotiate the thermoclines from the relatively warmer epipelagic waters to those of near freezing at ocean depths of 500 metres or more would face a formidable challenge, especially if the fish is ectothermic (cold blooded), since such changes would impede muscular activity as well as neurological and visual mechanisms, including photoreception. The swordfish (*Xiphlius gladius*), a highly visually directed predatory species, as well as other billed fish, such as marlin and sailfish, solves these problems with unique evolutionary adaptations.

Swordfish spend a portion of their day in relatively shallow waters of 50–100 metres, where they may themselves be preyed upon by sport and commercial fishermen. But, they also may spend as much as 12–19 hours at depths of 300–700 metres, and frequently below the 300–400 metre range. At this depth the water temperature will be a "brain freezing" 2–8°C. Neurological, visual, and muscular physiology is impeded by such temperatures and those fish that live at these mesopelagic depths permanently (see *BJO* 2001 March and September cover illustrations and essays) have different physiology. Predators at this depth are generally neither as fast swimming nor as long ranging as swordfish. Swordfish, as the best example of the billed fish, have evolved the most functionally distinct and enlarged extraocular muscles in the animal kingdom (see Figs 1 and 2). These extraocular muscles have at least six different types of muscle fibres, and one very special set of fibres in a mass directly beneath the brain. These fibres, in a dramatic illustration of the plasticity of muscle, have lost the myosin and actin fibrils of neighbouring extraocular muscle cells but have elaborated more enzymatic and mitochondrial engines for energy production per cell than any other skeletal fibre known. The mitochondrial volume as a percentage of cellular volume is two to three times that of most active aerobic muscle cells. Since the energy produced cannot activate muscle activity, heat is created and dissipated to the vascular plexus that permeates these powerful energetic knots. These cells have evolved thermogenic tissue at the expense of contractile ability. The circulation comes directly from the carotid artery through the gills where it is oxygenated and directed to these "heaters." Although the blood is depleted of its oxygen in thermogenic preparation, it is warmed considerably with a countercurrent system and passed directly through the choroid and then through the vascular system of the brain. Even the superior rectus muscle belly coincident with these "heaters" has direct access to the brain since the muscle belly at this point has a very thin overlying bone between it and the meninges. This allows for improved potential energy capture, and for the brain to maintain temperatures 20–30°C higher than the surrounding water temperature, facilitating smooth neurological and visual operation.

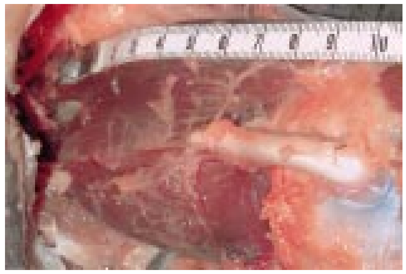

Figure 1 Orbital dissection of swordfish (*Xiphlius gladius*). Note the large extraocular muscles, with the optic nerve and the globe lying to the right in the photograph. The nerve can be seen in the middle right of the photograph and lies along the plane of division of these two extraocular muscles. The extraocular muscle along the upper half of the photograph is a superior rectus; the ruler is in centimetres. (Photograph I R Schwab.)

These extraocular muscle "heaters" are interesting enough to consider, but swordfish are among the finest and most versatile of oceanic predators and would not be among these elite without other interesting features. Sporting eyes the size of tangerines, this visual predator has at least two, and perhaps three, visual pigments with a lower limit of 420 nm, which means that the animal cannot see into the ultraviolet. The asymmetrical distribution of the rods, single cones, and double cones provides some understanding of the evolutionary solutions to the visual problems faced by this deep water predator. There are double cones that predominate in the dorsal retina with almost no single cones to be found. These double cones may have one visual pigment, or perhaps two and probably assist in discrimination and movement detection in depths below the animal. The ventral retina contains more single cones, suggesting that these photoreceptors are vital in determining potential prey, threats, or even depth above the animal. The large circular crystalline lens is piscine in nature, and blocks light below 400 nm, and thus limits any visual perception into the ultraviolet.

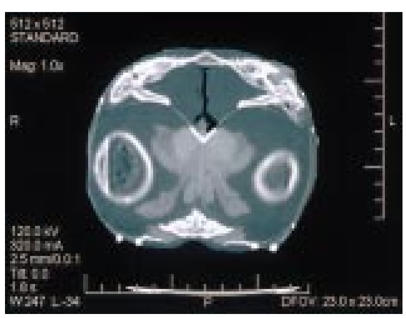

Figure 2 Computed tomography scan of the orbit of swordfish (*Xiphlius gladius*). Note the large mass of extraocular muscle which includes the thermogenic tissue and the thin roof of the orbit overlying this mass and adjacent to the intracranial cavity. (Thanks to John Boone, PhD, and Este Bailey-Geraghty for the CT scan.)

Yet, when excited, and that includes when hunting, the stripes on the flanks of the billed fish (swordfish and their kin), seen clearly on the cover, flash ultraviolet in an optokinetic fashion *which cannot be perceived by any of its kin*. Presumably, this cryptic coloration, created from iodophores in its skin, has no function such as location, threat, courtship, or mating between other swordfish, but must be used for predation. At least two of its favourite prey, the slimy mackerel and the horse mackerel, do see in the ultraviolet. There is evidence to suggest that this flashing ultraviolet pattern created by a rapidly swimming swordfish will create confusion in a school, by breaking up the single bulky form of these magnificent predators.

The swordfish, then, can play hide and seek to improve its hunting skills, becoming one of the most formidable of pelagic predators.

Ivan R Schwab,

University of California, Davis, Department of Ophthalmology, 4860 "Y" St Suite 2400, Sacramento, CA 95817, USA; irschwab@ucdavis.edu

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