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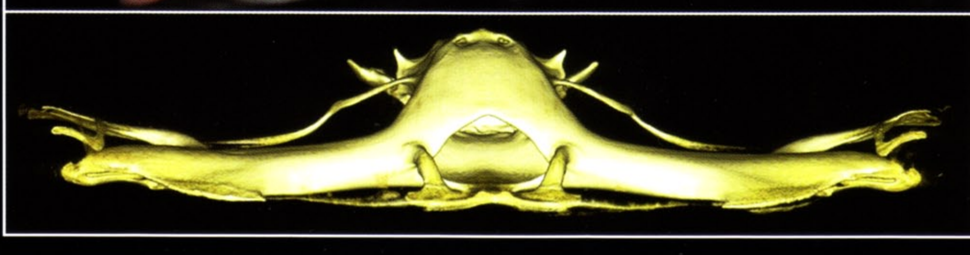

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Cover illustration

Keeping a cool head

Sharks always draw a crowd. We have a macabre fascination with these creatures because of their commanding presence and predatory lifestyle. The hammerhead shark evokes further interest because of the bizarre morphology of its head. What purpose would such a head serve and how does the creature manage its sensory input?

The class Chondrichthyes arose in the Silurian approximately 415 million years ago, and includes all fish having a cartilaginous skeleton. Evolutionarily, these fish followed a different path by separating from teleosts or bony fish. Teleosts eventually led to tetrapods and terrestrial creatures (*BJO* September 2006), but the chondrichthyes evolved in a different direction that now includes the modern elasmobranchs—sharks, skates and rays. The last common ancestor of both cartilaginous and bony fish probably arose approximately 430 million years ago. That ancestor had a primitive piscine-like eye and first showed a superior oblique muscle attaching anteriorly to the globe, a key step in evolution. Extant cartilaginous and bony fish have similar eyes that possess more similarities than differences from each other, providing a window on the sequence of ocular evolution.

Sometime during the Oligocene (34–24 million years ago), the hammerhead family (Sphyrnidae, having eight species) arose within the elasmobranchs as a peculiar evolutionary anomaly. The narrowed, dorsal–ventral flattened head, termed a "cephalofoil", probably evolved for improved sensory perception, but not necessarily vision. The unusual cephalofoil design allows for improved stereo-olfaction and electroreception. Hammerheads have among the largest olfactory bulb to brain ratios of any species and must rely heavily on this sense. The scalloped hammerhead has an olfactory rosette/bulb that occupies 7% of its total brain mass as compared with approximately 3% for sharks in other families (Kajiura, SM *et al J Morp* 2005;**264**:253–63). Hammerheads have special grooves leading to the wide-spaced nares (essentially the nasal passages at the distal tips of the cephalofoil) that lead to enormous olfactory rosettes; thus, these sharks have true stereo-olfaction. This ability is defined as true olfactory tropotaxis, or the ability to compare odour from one side with another, and to orient towards or away from that odour. These olfactory abilities almost certainly lead this cartilaginous fish to its prey as hammerheads can detect one part per 25 million of blood in sea water.

The cephalofoil also houses electroreceptors, called the "ampullae of Lorenzini", unique to elasmobranchs and the chimaera. This unique organ senses low-level electric current in water, with sampling carried out via pores distributed along the dorsal and ventral surfaces of the cephalofoil. The utility of the electrosensory abilities is poorly understood, although prey location and migration have been proposed. While scything its way through water, a hammerhead processes odours, weak electric currents and visual inputs, although it is not clear how these signals are reconciled and integrated.

What role does the morphology of the eye and vision play in the sensory abilities of *Sphyrna lewini*?

Sharks have a surprisingly thin cornea (approximately 160 μm), with epithelium making up to one third of that thickness with no functioning endothelium. Sharks maintain corneal clarity with only a primitive endothelial layer, or none at all, by keeping their corneae compact with perpendicularly oriented collagen fibrils or sutural fibres.

Much like other elasmobranchs, sharks accommodate using a protractor lentis, which pulls the lens away from the retina as compared with teleosts (bony fish) that have a retractor lentis muscle that moves the lens towards the retina (*BJO* April 2006). This suggests that the last common ancestor of sharks and teleosts, mentioned above, probably had rudimentary, if any, accommodation. Accommodation must have evolved, and in different ways, as these classes diverged.

The retina of *S lewini* has not been well studied, but it contains rods and cones in sharks such as the lemon shark, *Negaprion brevirostris*, and the silky shark, *Carcharhinus falciformis*, which have between 5:1 and 12:1 rods to cones. Some investigation into another species of hammerhead, the bonnet head, shows a dorsotemporal visual streak or band of increased ganglion cells, but it is not understood how this is used. Almost nothing is known about the visual field of hammerheads and how they combine the two different monocular visual fields.

An interesting, but as yet unstudied, aspect of the hammerhead eye is the anatomy of the optic nerve. The nerve may course a foot or more from the eye to the brain, as if a stalk, on the dorsal aspect of the "hammer" with no cartilaginous canal or much protection, as can be seen in the computed tomography scan below. The chiasm is completely crossed as in bony fish, suggesting that the last common ancestor in the shallow Ordovician seas had a similar anatomy. The optic nerves lead to the optic tectum, analogous to the visual cortex in mammals. The tectum also receives auditory, mechanoreceptive, electroreceptive, somatosensory and trigeminal nerves. It is not clear how these inputs are integrated, but the high degree of sensory input suggests that these creatures are very much tuned in to their surroundings, with magnificent sensory perception and a very cool head.

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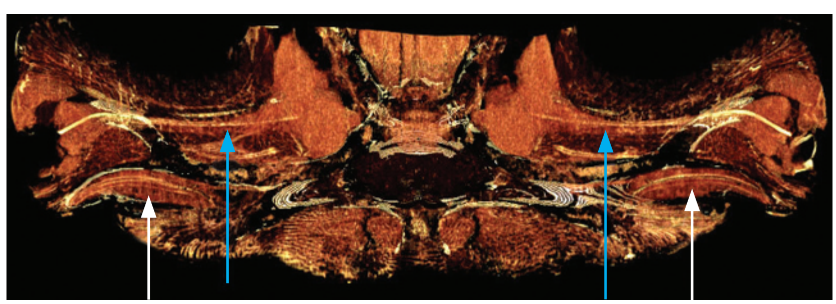

Figure 1 Olfactory organs to absorb scent (olfactory rosettes) in *Sphyrna lewini* as illustrated by white arrows, and optic nerves with blue arrows (computed tomography scan with false colour).