Box jellyfish

Like other jellyfish, the box jellyfish have neither a head nor a central brain; but unlike other jellyfish, they have well-developed eyes and display visually guided behavior. Recent findings on their optics indicate that they are at an early phase of eye evolution, where excellent visual performance does not have the same meaning as it does in other animals.

Nasty stingers

The box jellyfish, or Cubozoa, have a box-shaped body, with stinging tentacles attached at the four lower corners of the animal (Fig. 1). Across the world there are some 20 described species, and at least the same number probably remain to be described. Most are warm-water animals from tropical and subtropical seas. Although some species of box jellyfish are harmless, others are among the most venomous animals known. At the tropical beaches along the coast of northern Australia, public swimming is banned in the warmer half of the year because of the presence of a large (maximum width 30 cm or 12 in.) species of box jellyfish, *Chironex fleckeri*, which fishes for prey close to the shoreline. Humans that get extensive stings of this species suffer cardiac arrest and die within minutes after exposure. The 68 recorded deaths of *Chironex* stings in Australia probably are only a small percentage of the actual number, as *Chironex fleckeri* or equally lethal species exist throughout southeastern Asia. In addition, there is a smaller species (1 cm or 0.4 in.) of box jellyfish, *Carukia barnesi*, that gives a hardly noticeable sting that induces severe systemic effects starting some 20 minutes later. In Australia this is known as the Irukandji syndrome, and the victims may suffer for days or weeks from severe general body pain, deep anxiety, and extremely elevated blood pressure. Yet another species of box jellyfish (*Carybdea alata*) occurs in large numbers once every 4 weeks on Hawaiian beaches, keeping swimmers out of the water for a few days on each lunar cycle.

Fig. 1 Box jellyfish *Tripedalia cystophora* with all four sensory clubs visible. (© *Dan-E. Nilsson*)

Behavior and vision

The behavior of box jellyfish is strikingly fishlike. They display rapid directional swimming and skillfully avoid colliding with obstacles. All known species are strictly coastal, and many inhabit the shallow area next to the shoreline on sandy beaches, rocky shores, estuaries, or mangrove swamps. Box jellyfish are distinguished by a high metabolic rate, and they need to find and remain in places where food is abundant. Crustaceans and fish aggregating close to the shore are the typical diet for most species. Other types of jellyfish are open ocean drifters, and when currents carry them close to the shore they run a high risk of getting washed up or damaged in the surf. Box jellyfish are specialized to navigate and survive in the dangerous zone close to the shore.

This lifestyle is the probably why they have well-developed eyes, whereas other jellyfish at best have ocelli (simple invertebrate eyes composed of photoreceptor and pigment cells). The eyes of box jellyfish are impressive in design and number. On each of the four sides of a box jellyfish, there is a sensory club, termed a rhopalium, carrying one large-lens and one small-lens eye, and two pairs of pit eyes (Fig. 2). This makes a total of 24 eyes of four types in each individual. However, the eyes are not huge: sensory clubs range in length from 0.3 to 1.2 mm (0.012 to 0.05 in.) depending on species, and the large-lens eyes vary between 0.15 and 0.8 mm (0.006 and 0.03 in.). Despite the small size, the lens eyes are fully equipped with a retina, vitreous, lens, cornea, and a mobile iris. The sensory clubs are attached and suspended by a thin flexible stalk, and a crystalline weight allows the clubs to retain a vertical orientation irrespective of the orientation of the animal. There are indications that the sensory clubs also have an olfactory patch opposite the eyes, and there are mechanoreceptors in the stalk. The sensory clubs are thus multisensory structures serving vision, smell, and balance. The interior of the sensory club contains a small brain, which communicates with its neighboring sensory clubs via a ring nerve. Branches from the ring nerve form a diffuse nerve net innervating the muscles.

Fig. 2 Sensory club, 1 mm or 0.04 in. tall, of *Chiropsalmus* sp., with the typical set of six eyes. (© *Dan-E. Nilsson*)

These are the main components of the sensory and nervous system that endows box jellyfish with an almost fishlike behavior. There is no central brain, but all information processing and muscle coordination must result from the joint action of the identical brains in the four sensory clubs, and the ring nerve that joins them. This is an unusual and amazingly simple system for an animal capable of navigation, precise positioning, and even courtship behavior in some species. Even though the different species of box jellyfish inhabit very different coastal locations, the eyes and nervous systems hardly vary at all. All have the same set of 24 eyes of four types arranged in a stereotyped way on the sensory club. Evidently, inconspicuous variations on the common theme account for the differing behavior and choice of environment in different species.

Visual physiology

Recent investigations of the lens eyes of the best model species of box jellyfish, *Tripedalia cystophora*, have revealed that they rely on graded index optics, where the center of the lens has a much higher refractive index than the periphery. It produces high-power lenses that are free of spherical aberration and are much superior to homogeneous lenses. This type of advanced biological lens has long been known to exist in the eyes of fish and invertebrates such as octopus and squid, but it was a surprise to find the principle in an animal as primitive as a jellyfish. It was even more surprising to find that the good lenses are not used for acute vision in box jellyfish. The retina is too close to the lens to pick up a sharp image, and the consequence is blurred vision. At first glance this may seem like a poorly designed eye, but careful mapping of receptive fields of individual photoreceptor cells in the retina revealed that the blurring generates receptive fields similar to those of large field motion detector neurons in the brain of other animals. Findings that box jellyfish eyes are colorblind add to the similarities with large field motion detector neurons. The obvious explanation is that the lens eyes of box jellyfish are devoted to large field motion detection and are tuned to extract information about self-motion and the presence of large nearby objects.

More eye than brain

All evidence now suggests that the optical apparatus of box jellyfish eyes is specialized for single visual tasks, and that this allows them to remove redundant visual information before it reaches the retina. Eyes of most other animals serve a multitude of visual tasks and need to pick up as much visual information as possible even though each task uses only limited subsets of the information. Having a general-purpose eye requires the neural capacity to separate and extract the information used for each visual task. The jellyfish way of having one eye type for each visual task lifts a burden from the nervous system, and it suddenly becomes understandable how these animals can generate complex behavior with their simple nervous system. Evidence is accumulating that the largest of the two lens eyes serves large field motion detection used in monitoring self-motion and warning for collisions. It is not yet clear which visual tasks are served by the remaining three types of eye.

Evolutionary relationships

Box jellyfish belong to the phylum Cnidaria, which is a sister group to all bilaterally symmetric animals (Bilateria). Complex visual systems are common among Bilateria, but among cnidarians they exist only in box jellyfish. As to whether the common ancestor to Cnidaria and Bilateria had eyes and vision, the probable answer is both yes and no. The biochemistry of photoreceptor cells seems to date back to a common ancestor, although we have yet to learn whether jellyfish photoreceptors are in all respects equivalent to those of Bilateria. In contrast, advanced eyes and visual processing have clearly formed independently in the two groups. The visual system of box jellyfish is of unique interest not only because of its largely independent evolution but also because it offers our only insight into how visually guided behavior can be realized in a radially symmetric creature.

See also: Eye (invertebrate); Nervous system (invertebrate); Photoreception; Vision

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For Further Study

Topic Page: Biological & Biomedical Science: Zoology:Cnidaria

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