

WHY CEPHALOPODS ARE PROBABLY NOT "DEAF"

Moynihan (1985) proposed hypothetical arguments about why cephalopods are deaf. "Hearing" in cephalopods has been a subject of discussion for 75 years, but surprisingly, Moynihan (1985) did not consider the available morphological and physiological data. We would like to summarize these data briefly and add some behavioral information that, in contrast to Moynihan's hypothesis, indicates that cephalopods can perceive underwater vibrations.

Hearing is nearly impossible to define for aquatic animals (Schuijf and Hawkins 1976) because sound and vibrational stimuli are essentially equivalent in an aquatic medium. For vertebrates, sound has been defined operationally (e.g., those stimuli registered by the eighth cranial nerve). A separation can also be made on the basis of an arbitrary spectral factor; in air, for example, it is usual to consider mechanical waves of a frequency range between 0.1 and 100 Hz as vibrations and frequencies above 100 Hz as sounds (Prosser and Brown 1961). In water, such divisions are not meaningful, and thus, operationally, we consider *hearing* as the ability of an animal to sense vibrations (either pressure oscillations or particle displacement) covering a wide frequency range and to integrate this information in order to produce an appropriate behavioral response (Offutt 1970; Maniwa 1976; Hawkins and Myrberg 1983; Stebbins 1983). In vertebrates, the receptors of the relevant sense organ (whether situated externally as in the lateral line system or internally as in the sacculus-lagena-cochlea system) are cells with cilia (hair cells).

BEHAVIORAL EVIDENCE

As early as 1910, Baglioni noted that octopuses responded to disturbances of the water and to sound waves (Baglioni 1910). Wells and Wells (1956) reported that fully recovered, blinded octopuses could locate, from a distance of about 0.5 m, the approximate direction of the source of a vibration caused by tapping the sides of the tank. Young (1960) reported that octopuses are certainly sensitive to vibrations and that they respond to a tap on the laboratory tank by drawing in the head and changing color; he also noted that this response persisted after removal of the statocysts. Hubbard (1960) then performed some preliminary behavioral experiments to test Young's (1960) observations, but the results were equivocal, probably (by the author's admission) because of an inappropriate training paradigm. Dijkgraaf (1963) reported a clear behavioral response by the cuttlefish *Sepia officinalis* to a sound stimulus of 180 Hz. The animals showed distinct color changes even though Dijkgraaf's experimental design ensured that visual input

was eliminated. Maniwa (1976) demonstrated clearly that the squid *Todarodes pacificus* was attracted to a pure tone of 600 Hz; subsequent catch rates were substantially (and statistically) greater, and the technique is now in common use on commercial squid boats in Japan. Furthermore, many squid jigs are made with distinctly placed holes to produce sounds that presumably attract squids.

From our own observations of several loliginid squid species kept in laboratory tanks (see Hanlon et al. 1983), we know that a knock on the side of the tank (with the experimenter hidden) causes squids to jet backward instantly, change color, and sometimes ink. This alarm reaction is typical for cephalopods, and in the laboratory they habituate to this irrelevant stimulus after only a few trials. Field observations support predator sensing by means other than vision. In 1984, one of us (R.T.H.) spent approximately 30 h scuba diving and observing the reef squid *Sepioteuthis sepioidea* in shallow, clear water in the Dry Tortugas, Florida. On three different occasions, all the members of a large school of *Sepioteuthis* (the same species Moynihan works with) were observed showing great alarm (i.e., color pattern and postural changes) for no apparent reason. Despite intense searching, it was not possible to see any fish predators at the limits of human vision (about 25 to 30 m on this reef) until 3 to 4 s later, when fast-swimming predatory fishes (of the family Carangidae) were seen coming toward the squid school. Given the fast speed of the fishes and the keenness of human vision (as well as the observer's considerable experience with the coral-reef fauna), it seems likely that the squids used a sense other than vision to perceive the fishes. Carangid fishes are known to produce a thumping noise as they swim rapidly, and small labrid fishes are known to detect these acoustic signals before they see the carangids and to hide in coral (Steinberg et al. 1965). Corner and Moore (1980) also reported that the cuttlefish *Sepia latimanus* showed alarm reactions to predatory fishes beyond human vision in clear water.

MORPHOLOGICAL AND PHYSIOLOGICAL EVIDENCE

Sundermann-Meister (1978, 1983) was the first to describe a type of ciliated cell in the skin of hatchlings of the squid *Loligo vulgaris* and the cuttlefish *Sepia officinalis*. These cells form lines that are placed distinctly on the head in an anterior-posterior direction. She pointed out that Naef (1928) described these lines in five genera of embryonic cephalopods, although Naef did not know they were ciliated cells. *Loligo vulgaris* has five pairs of lines on the head: two dorsally, two laterally above and below the eye, and one ventrally. *Sepia* has four pairs of lines placed dorsally and laterally like those of *Loligo* but lacks the ventral pair. The hair cells have kinocilia with the "9 × 2 + 2" tubuli arrangement and are probably sensory cells since they have an axon projecting from their base. The cilia project approximately 12 µm from the skin. Arnold and Williams-Arnold (1980) described four types of ciliated cells in the epidermis of embryonic *L. pealei*; their fourth type of cell was aligned in longitudinal rows on the head and arms and appears similar to the ciliated cells mentioned above (Sundermann-Meister 1978, 1983). Furthermore, they described "non-moving bundles of cilia" (Arnold and Williams-Arnold 1980, p. 114) on the mantle and the aboral surface of

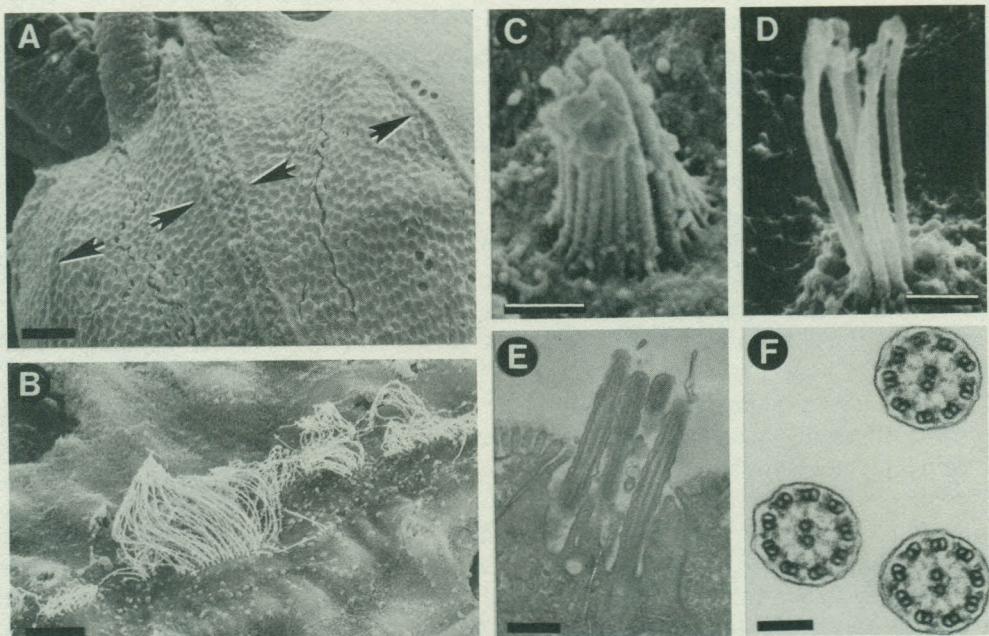


FIG. 1.—Ciliated cells in the skin of young and adult squids. *A*, A scanning electron micrograph (SEM) of the dorsal head of the squid *Loligo forbesi* 3 days after hatching. Arrows indicate longitudinal lines of ciliated cells. *B*, A side view of the cilia of one of the lines of ciliated cells (as in *A*) from a 45-day-old *L. forbesi*. *C*, An SEM of a bundle of cilia of a ciliated cell on the lateral mantle of an adult *L. plei*. *D*, An SEM of the cilia of a ciliated cell on the edge of the fin of a newly hatched *L. pealei*. *E*, A transmission electron micrograph (TEM) of the cilia of a ciliated cell similar to *C* in the lateral mantle of an adult *L. plei*. *F*, A TEM cross section of the cilia of a ciliated cell similar to *D* in a hatchling *L. pealei*. Scale for *A* is 200 μm ; *B*, 20 μm ; *C* and *D*, 1 μm ; *E*, 0.5 μm ; and *F*, 0.1 μm .

the arms. More recently, Hulet (1982) published two micrographs of discrete bundles of kinocilia that are found not only in hatchlings of *Loligo* but also in adults.

All of the aforementioned authors speculated that these ciliated cells may be mechanoreceptors. Furthermore, in the statocyst organs of *Octopus*, *Loligo*, and the deep-sea squid *Vampyroteuthis*, Young (1960) and Stephens and Young (1976, 1982) described ciliated cells of unknown function scattered in the epithelium of the posterior sac. We include in figure 1 some electron micrographs of ciliated cells in the skin of hatchling and adult squids. Figures 1A and 1B show lines similar to the lines of ciliated cells illustrated by Arnold and Williams-Arnold (1980) and Sundermann-Meister (1983). Figures 1C–1F illustrate bundles of cilia on the fins of hatchlings and the lateral mantles of adults; their morphology suggests the possibility of mechanoreception.

Electrophysiological evidence for mechanical wave perception was first presented by Maturana and Sperling (1963), who showed that statocyst crista hair cells are sensitive to low-frequency vibration. Later, Wolff and Budelmann (un-

publ. MS; see also Budelmann 1976), when applying vibrational stimuli of various frequencies to statocyst preparations, found that the hair cells of the crista responded in synchrony with vibrations in the range of 20 to 100 Hz (at 60 dB).

CAN CEPHALOPODS HEAR?

Within our definition of "hearing" (i.e., sensitivity to vibrational stimuli), the available morphological, physiological, and behavioral evidence indicates a good possibility that cephalopods have a sensory system to detect appropriate mechanical disturbances in the marine environment. The structure and distribution of the ciliated cells in the skin resemble a system not unlike the lateral line system of fish (Schuijf and Hawkins 1976) or the vibration-sensitive hair cells in the skin of marine chaetognaths (Feigenbaum 1978). Such externally situated, ciliated cells might be expected to complement vision in schooling behavior of squids; such a role has been demonstrated in fishes (Partridge and Pitcher 1980). Furthermore, cephalopod statocysts are one of nature's most well-developed organs for the detection of gravity and angular acceleration—similar to the vertebrate vestibular apparatus of the inner ear (Budelmann 1976, 1980)—and it is possible that they may also function like the hearing organs of fish (Schuijf and Hawkins 1976).

Moynihan's (1985) speculations about deafness in cephalopods are based on the hypothetical suggestion of Norris and Møhl (1983) that some odontocete cetaceans, the "toothed" whales and dolphins, may be able to stun prey with loud sounds. Moynihan (1985) argued that cephalopods without an acoustic-receptor system might be better able to survive such direct or indirect acoustic attacks by cetaceans and that vision alone might be adequate to detect approaching cetaceans.

We favor a different view. Much predation by cephalopods and vertebrates occurs at night or in mesopelagic or bathypelagic zones, where light is greatly limited or lacking (see Packard 1972; Boyle 1983). Many cephalopods also live in murky water. Vision, therefore, is a restricted resource that may not allow detection of a fast-moving predator until it is too late. Hearing is a far better distance receptor and it does not depend greatly on time of day, depth (i.e., light intensity), or water clarity. It seems more likely from an evolutionary standpoint that, rather than being deaf, cephalopods have developed a sensory system for underwater wave perception that is not only capable of detecting the approach of prey items or predators at such a distance that appropriate behavioral responses can be implemented (e.g., attack prey, escape predators) but also insensitive to frequencies and decibel levels that might be used in acoustic attacks by cetaceans. However, the latter suggestion seems inappropriate because, as Norris and Møhl (1983) and Moynihan (1985) pointed out, the full, focused force of such an acoustic attack would kill the target prey. This would imply damaging all sensory and motor systems in the prey, not just delicate sensory systems like those used for detecting vibrational stimuli.

In summary, we believe that the available evidence (albeit scanty) indicates that some cephalopods are sensitive to vibrational stimuli (perhaps only low frequencies), and in the underwater world that means they are not deaf and have a

sensory system for some form of hearing. Until modern techniques in morphology, physiology, and behavioral analysis are used to test for such a sensory system in cephalopods, it is premature to develop ecological hypotheses about why the system is not there. As Wells pointed out, "the list (of known sense organs of cephalopods) is by no means complete. It shows only where people have bothered to look." (1978, p. 177.)

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