

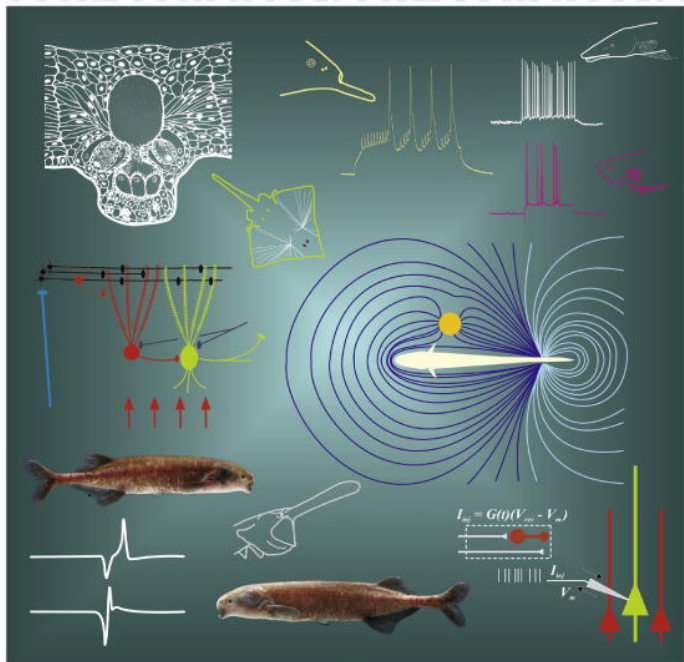


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Introductory Note

Commentary: Ampullary systems

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Ampullary electroreceptors occur in several living vertebrate groups that include the lampreys, chondrichthyans (sharks, rays and ratfish), some cartilaginous bony fish (e.g. sturgeon, bichirs and paddlefish), teleosts (e.g. mormyrids, catfish and gymnotiformes), the coelacanth, lungfish and some aquatic amphibians. This form of electroreceptor has evolved multiple times yet continues to retain morphological and physiological features that indicate functional convergences. Among the most notable are the tight clustering of sensory ampullae and long canals in marine species (e.g. sharks and some marine catfish) and the short transcutaneous microampullae found in exclusively freshwater species (e.g. freshwater stingrays and catfish). In addition, physiological studies on ampullary systems reveal that they are all low pass receptors and likely respond best to electric field stimuli that originate from external sources. Thus ampullae are implicated primarily in the passive mode of electroreception.

Despite these important evolutionary and functional features of ampullary receptor systems, electroreception research on bony and non-bony fishes is largely divergent in focus. Tuberous electroreceptors occur only in teleost fishes that possess electric organs and are highly specialized for detection of self-generated EODs. These stimulus-receptor systems present a high frequency sensory channel used in the active mode for electrolocation of submerged objects and intraspecific communication, and have provided a wealth of neuroethological studies. Yet the electrogenic mormyrids, *Gymnarchus*, and gymnotiformes also possess a separate ampullary system that shows great morphological diversity and operates in the low frequency range. Thus, unlike the ampullary systems of elasmobranchs, chondrosteans and catfish, the functions of the ampullary system of electrogenic teleosts are poorly understood, especially in reference to the natural habits of bony fish. In one of the few studies on the ampullary system of *Gnathonemus*, Gertz et al. (2008) report that ampullary primary afferents appear as unique encoding channels, have an irregular spontaneously discharge activity and stimulus thresholds between 10–100 $\mu\text{V}/\text{cm}$. Stimulus response was low pass at frequencies of 1–60 Hz. These ampullary electroreceptors faithfully encode stimuli in the low pass range, and central convergence of a few receptors would provide a faithful temporal analysis of stimuli. Further work is needed to understand how the ampullary system of electrogenic fishes is integrated with tuberous receptor EOD stimuli in specific behavioral contexts such as prey localiza-

tion. For example, does the ampullary system of *Gnathonemus* interact with the tuberous receptor system during probing for prey with the Schnauzenorgan as described by Nöbel et al. (2008)?

Brown et al. (2008) presented work from his lab on the electric features of the hydrogel found in the long ampullary canals of the great white and reef white tip sharks. In the past, the canal gel has often been characterized as a core conductor in which the electric potential at the pore is represented within the associated ampulla. Brown's work indicates that the shark hydrogel has a lower admittance than seawater (or synthetic hydrogels) and promotes a charge induced voltage gradient along the interior length of the canal. A computational model for primary afferent encoding was presented that incorporates these gel characteristics and the spatial projections of ampullary canals in the swimming ray. Tricas et al. (2008) presented an analysis of the ampullary canal arrays in three elasmobranch species: the sandbar shark, hammerhead shark and stingray. The three dimensional projection vector for each ampullary canal was calculated by dissection of the head (and body of the stingray) and vectors grouped by ampullary cluster. Spherical projection analysis revealed that the buccal and ventral superficial ophthalmic clusters in the sandbar shark, which has a quasi-conical head, approached elevations of $\pm 90^\circ$. In comparison, the expanded cephalophoil of hammerhead shark showed reduced elevation projections at $\pm 60^\circ$ and the dorsoventrally flattened stingray at only about $\pm 40^\circ$. The longest canals and most sensitive associated ampullae projected near the horizontal plane in all species. From this analysis it was proposed that specific behaviors such as location of prey dipoles and encoding of vertical fields from geomagnetic induction may be mediated by different ampullary cluster groups, and is consistent with the functional subunit hypothesis. This work is being extended to neural computational models to help understand the functional role of the complex geometry of elasmobranch electrosensory canal systems, and whether cluster subunit information is retained and integrated centrally.

The paddlefish, *Polyodon spathula*, is a remarkable chondrosteian species that inhabits freshwaters of the Mississippi Valley of North America and is endowed with an elongated dorsoventrally flattened rostrum which is covered with up to 75,000 ampullary receptors. This receptor system is used for the detection and capture of small individual plankton in the water column. No less than one talk, three posters and one manuscript on the ampullary electrosense of the paddlefish were contributed to this conference. Hofmann and Wilkens (2008) summarized their recent work that

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shows the poor directional sensitivity of peripheral paddlefish electroreceptors, and that midbrain units process by two derivative filters the electrosensory information of a moving target across the skin. Midbrain cells perform a temporal analysis of information from one receptor that is equivalent to a spatial analysis of an array parallel to the movement direction of the object as it moves across the snout. The temporal filtering leads to a set of neurons with response properties similar to retinal ganglion cells (center surround) after spatial information processing in the retina. Jung et al. (2008) summarized work on the response properties of midbrain tectal units relative to those in the dorsal octavolateralis nucleus (DON) to global sinusoidal electric stimuli. At 5 Hz both tectal and DON units showed strong phase locked spikes but the units in the former region maintained the response at much lower stimulus intensities. In addition, only tectal units sustained the response at lower frequencies. This strong low frequency, intensity independent phase locking in the tectum is consistent with the behavioral responses reported for this fish. Chagnaud et al. (2008a) report the comparative response of DON principal cells and electrosensory neurons in the midbrain tegmentum to sinusoidal stimuli. Tegmental units showed distinct response differences compared to DON cells including a biphasic response, an increased rather than modulated discharge rate, and lack of frequency tuning. This non-directional information retained in the tegmentum may be important for the detection rather than localization of a nearby prey. The central processing links between prey detection, localization and capture were presented at the conference by Hofmann et al. (2008) with further detail in the contributed manuscript by Chagnaud et al. (2008b). Unlike that found in the sharks and rays, the principal cells in the paddlefish brainstem show no evidence of somatotopic mapping of ampullary receptive fields or enhanced neural sensitivity, a common result of central convergence. Well-defined receptive fields were identified in the tectum mesencephali but only to a moving DC stimulus. Receptive fields on the

anterior portion of the rostrum appeared in the lateral mesencephalic nucleus, whereas fields near the rostral base and head were represented within the tectum. Analysis of prey capture behavior indicates that initial orientation behavior occurs when the prey is adjacent to the anterior rostrum (thus mediated by the lateral mesencephalic nucleus) and captured when near the mouth and head (thus mediated by the tectal units). This study is the first to demonstrate a detailed separation of the likely circuits involved in processing of prey orientation and capture behaviors for the ampullary electroreceptors. In summary, this large body of growing work has now positioned the paddlefish as the 'pièce de résistance' model for study of the single cell processing of ampullary electric cues in the fish brain. This should continue to stimulate great interest and afford comparative opportunities for scientists working with other ampullary fish systems.

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