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Source: BioScience, 57(5) : 399-407

Published By: American Institute of Biological Sciences

URL: https://doi.org/10.1641/B570505

The Paddlefish Rostrum as an Electrosensory Organ: A Novel Adaptation for Plankton Feeding

LON A. WILKENS AND MICHAEL H. HOFMANN

The ancient Mississippi River paddlefish, Polyodon spathula, *has long been thought to use its oversized rostrum for excavation. Recent studies provide an entirely new interpretation for the function of the paddle, that of an electrical antenna for detecting the electric fields of plankton,* P. spathula*'s primary food. Feeding experiments with juvenile fish demonstrate that paddlefish detect and capture individual daphnia when all sensory modalities except the electrosense have been blocked. The paddle provides space for an extravagant array of ampullary electroreceptors that are found in common with elasmobranchs and primitive bony fish. This exquisite electrosensory organ may also influence the migration of paddlefish in an environment replete with dams and other steel structures, sources of unnatural electric signals (corrosion potentials). In the laboratory, paddlefish are sensitive to and avoid metallic obstacles, even in the dark. Electrosensory processing in the brain involves physiological mechanisms for spatial imaging equivalent to planktivory based on passive electrosensitivity.*

Keywords: paddlefish, rostrum, planktivory, electrosense, ampullae of Lorenzini

Reporting on a paddlefish poaching operation in central Missouri in the early 1990s, a *St. Louis Post-Dispatch* article noted that scientists still did not know the function of the paddlefish's paddle. These large fish, once reaching 75 to 80 kilograms in weight and 2 meters in length, are prized as a source of caviar. A few years earlier, Russell (1986) concluded that "the function of the rostrum is not precisely known." Given a similar statement by Stockard in 1907 that "the function of the peculiar rostrum or snout has not been definitely determined," the mystery of the paddle had persisted for most of the 20th century. This mystery invited investigation and has provided experimental grist for our laboratory for more than a dozen years.

Novelty is a lure for any comparative biologist. The paddlefish, also referred to as the spoonbill or spoonbill cat, qualifies as novel in several respects, not least on account of its elongated rostrum. This extension of the cranium comprises as much as one-third the total length of the fish (figure 1). Unlike other fishes' long snouts, the paddlefish rostrum is not an extension of the upper and lower jaws or of the olfactory system. Furthermore, the paddlefish is a suspension feeder, filtering zooplankton in large quantities from the water. Because of their large size, feeding mechanism, and food resource near the bottom of the food chain, paddlefish are often compared to the marine Mysticeti and characterized as "freshwater whales." Of foremost interest here, our studies have shown that the paddlefish has a robust, rostral-based electrosensory system, a functional antenna positioned at the front of the fish. Our experiments have established not only that the paddle is an electrosensory organ but that the electrosense serves as the primary sensory modality for detecting planktonic prey, a unique and novel function among fish with passive electrosensory systems. The electrosense may also underlie other behaviors, an understanding of which could guide conservation measures for this charismatic fish.

Paddlefish phylogeny and the function of the rostrum

The paddlefish *Polyodon spathula,* native to the entire Mississippi River drainage basin, is one of only two extant species ("living fossils") in the family Polyodontidae, whose extinct representatives date back to the Upper Cretaceous. The highly endangered Chinese paddlefish from the upper Yangtze River drainage area, *Psephurus gladius,* is the only other surviving family member. With the exception of *Psephurus,* the polyodontids are exclusively North American (Grande and Bemis 1991). Paddlefishes, along with sturgeons (Acipenseridae), are the only surviving chondrosteans, a phylogenetically important group of primitive, ray-finned bony fishes and the

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Figure 1. A paddlefish striking at an artificial dipole electrical field applied via a pair of silver wires. Photograph: Lon A. Wilkens.

evolutionary end point for the primitive ampullary-based electrosense more familiar among elasmobranchs. Although the elongated snout is a characteristic of the Polyodontidae, features of the cranium, gill arches, and jaws are distinctly adapted for filter feeding only in the genus *Polyodon* (*P. spathula* and the extinct *P. tuberculata*). No other polyodontid, living or extinct, or sturgeon is known to be a filter feeder. Accordingly, *P. spathula,* hereafter the paddlefish of reference, is considered to be a highly derived fish, unrepresentative of the other members of the family Polyodontidae (Grande and Bemis 1991).

Historically, rostral function in the paddlefish has been associated with digging, as implied by a variety of common names for the species, including spadefish and shovelnose sturgeon in addition to spoonbill. Although skeptical of this function, early authors nevertheless noted that the paddlefish "is described as stirring up with its spatulate nose the mud at the bottom of the waters" (Imms 1904), that it "uses its snout as an organ of excavation in its search for food" (Norris 1923), and more recently that "fishermen generally believe it [the paddle] is used to dig in the bottom for food" (Russell 1986). Scientific skepticism about the use of the paddle in excavation was warranted, however, since digging would be incompatible with the delicate nature of the skin and the shallow ampullary pits spread prominently over the surface of the paddle (figure 2) and adjacent regions of the head and opercular flaps. These pits, or "primitive pores," which were suggestive of sensory structures (Kistler 1906), were predicted to function as tactile (Stockard 1907) or pressure (Norris 1923) receptors, although Nachtrieb (1910) concluded that, to the contrary, the mucus-filled pores served as excretory organs. Since electroreception was not established as a true sensory modality until the early 1960s (Bullock 1974), it was not an option for early 20th-century interpretations of paddle function.

Jørgensen and colleagues (1972) subsequently identified these sensory pits as ampullae of Lorenzini, the electroreceptive organs of elasmobranchs. This anatomical and ultrastructural study provided the first evidence for electrosensitivity in the paddlefish, showing the ciliary receptors at the base of the ampulla with synaptic connections onto the ascending medullated fibers of the anterior lateral line nerve. By inference, paddlefish electrosensitivity was also predicted from a study of the ampullae of Lorenzini in the closely related sturgeon (Teeter et al. 1980). New and Bodznick published preliminary electrophysiological recordings of paddlefish electroreceptors in 1985. Still, despite mounting evidence identifying the "primitive pores" as electrosensors, with which the rostrum is richly endowed (pores in adult fish number as many as 57,365 [Kistler 1906] to 75,000 [Nachtrieb 1910]), the function of the paddle remained unclear. Even though an unspecified sensory function was assumed more recently (Russell 1986, Grande and Bemis 1991), hypotheses for the function of the paddle included its acting as a stabilizer to compensate for drag during ram filter feeding when the mouth is opened wide, or to counteract lift by the heterocercal tail. The primary function of the paddlefish rostrum as an electrosensory antenna will be described in the following sections.

Electrosensory plankton feeding by the paddlefish

Electric fishes have long been known to generate strong discharge voltages, as does the South American eel, whose electric organ was described as early as the 18th century. However, evidence that fish are sensitive to electric signals was reported much later, when blindfolded catfish were shown to vigorously avoid metal rods or wires but did not react to glass or to insulated metal rods (Parker and van Heusen 1917). Jørgensen and colleagues (1972) reported an equivalent passive avoidance behavior in paddlefish in an anecdote supporting their identification of the ampullae of Lorenzini as electroreceptors. We use the avoidance response as a dramatic demonstration of electrosensitivity in our laboratory tanks. Any type of metal rod triggers startle-response escape swimming, whereas paddlefish ignore and frequently bump into glass rods or wooden dowels even under lighted conditions.

The physiological characterization of electrosensory organs began in the 1960s. Their acceptance as electroreceptors required that they meet specific low-threshold electrosensory criteria, since early experiments reported that ampullae were sensitive to changes in temperature and osmotic conditions (reviewed in Bullock 1974). Moreover, general acceptance for the electrosensory modality required a demonstration that it serves a biologically relevant role in fish behavior. For ampullary systems, this was provided in classic experiments showing that sharks could successfully locate and attack flatfish that were hidden beneath the sand and otherwise screened to prevent them from emitting hydrodynamic or chemical signals. That sharks were detecting their prey electrically was confirmed when they attacked dipole electrodes buried in the sand through which current was passed to simulate the prey's electric field (Kalmijn 1971). These and related experiments were unequivocal demonstrations that the electrosense was used in feeding and that it provided information not obtainable by other sensory modalities. Navigation, orientation, mate detection, and predator avoidance have since been shown to rely on the passive electrosense in sharks and rays.

In our study of paddle function, we predicted at the outset that the oversized rostrum and its rich supply of ampullae were features uniquely adapted to detect planktonic prey

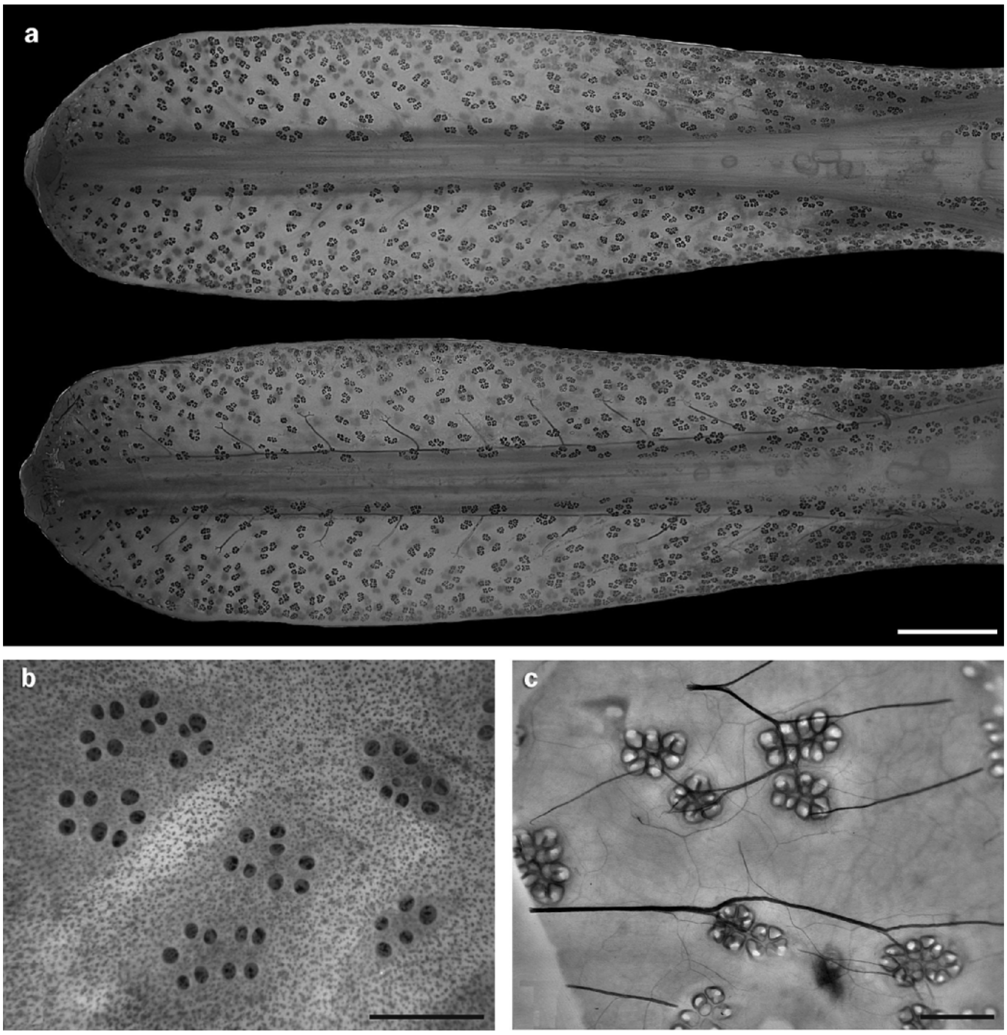

Figure 2. Ampullae of Lorenzini on the rostrum of the paddlefish. (a) Electroreceptive pores stained on the rostrum as viewed dorsally (top) and ventrally (bottom). The whole rostrum is covered with pores except along the midline. Scale bar 10 millimeters (mm). (b) Close-up of pore clusters on the rostrum. Scale bar 1 mm. (c) Skin sample from the operculum, cleared and stained for myelin with Sudan black, showing dense innervation of the electrosensory pores. Scale bar 1 mm. Photographs: Michael H. Hofmann.

(i.e., a sensory system with sufficient sensitivity and spatial resolution for detecting and capturing tiny objects in the turbid, vision-limiting environment of the Mississippi River and its muddy backwaters; Wilkens et al. 1997). To test this hypothesis, we placed juvenile paddlefish (12 to 17 centimeters [cm] long) in a recirculating flume and added plankton that drifted past the fish as the latter swam in place against the current. Paddlefish adapt well to swimming and feeding in an artificial stream environment, in part because they are ram ventilators and swim continuously throughout life. Small paddlefish, available from nearby state fish hatcheries in Missouri and well suited for the small-scale laboratory stream, lack the comblike gill rakers that develop in larger fish as they switch to straining plankton in large quantities from the water. Accordingly, small paddlefish feed by selective prey capture, sensing individual plankton and adjusting their swimming direction to gulp in the small prey, a ram-feeding motion that frequently involves acrobatic maneuvers of yaw and roll. These movements are necessary to keep the paddle from interfering with the path of the mouth toward the prey, and to minimize the resistance that would otherwise be encountered by the large surface of the paddle in rapid vertical movements. For example, paddlefish often feed at the water surface, for which it is necessary to roll nearly 180° in bringing the mouth to a position lateral to or above the rostrum. A fish approaching a plankter above and lateral to the rostrum will yaw to the side, followed by a partial roll and vertical yaw (figure 3a). Prey capture is no doubt facilitated by the wide gaping of the mouth, which is similar to the enormous mouth gape employed by large fish when filter feeding.

We videotaped paddlefish feeding, using cameras focused from the side and bottom of the viewing chamber (14 × 14 × 40 cm), to which the fish were restricted by flow laminators at the front and back. Fish movements were analyzed offline

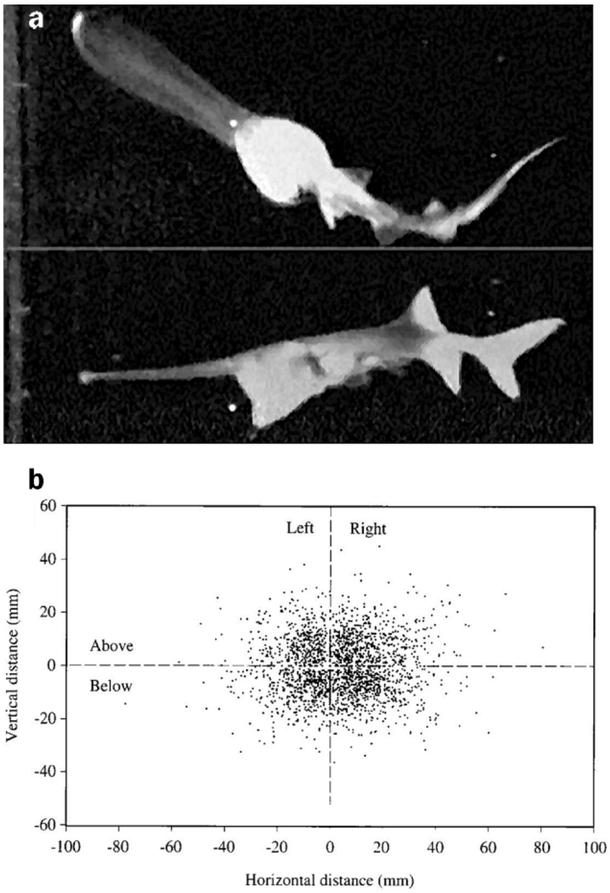

Figure 3. Results from feeding experiments in a flow tank. (a) A video frame with a split image showing lateral (top) and ventral (bottom, via a 45° angled mirror below the chamber) views of the paddlefish. A 90° clockwise roll and yaw response was performed to capture a plankton (view enhanced by a white dot) approaching from above and to the left of the rostrum. The image in the ventral view is reversed by the mirror. (b) For every successful prey capture, the position of the daphnia at the time of first reaction was plotted relative to the midline of the rostrum. Most daphnia were detected at a distance of up to 20 millimeters (mm), but some were as far as 80 mm from the rostrum. Photographs and data: Lon A. Wilkens.

in three dimensions, forward, vertical, and lateral, as they maneuvered to capture approaching plankton, a motion in the flume equivalent to a free-swimming fish approaching relatively stationary plankton. The primary prey organism for paddlefish is the water flea (*Daphnia* spp.), a relatively slow-swimming plankton that is easily cultivated in the laboratory for use in feeding experiments. To quantify feeding behavior, the location of each captured daphnia relative to the midline axis of the rostrum was registered in a vertical reference plane at the rostral tip prior to capture (figure 3b). The distribution of captured daphnia was then represented as a histogram of capture frequency at different radial distances from the rostral midline. The majority of the plankton were captured within 2 cm of the rostrum, with decreasing capture frequency at greater distances. Maximum capture distance from the rostrum was 9 to 10 cm.

The electrosensory role of the rostrum in plankton feeding was then established by eliminating one or more of the sensory modalities of the fish during stream-feeding experiments. After control feeding under lighted conditions, all remaining feeding experiments were conducted in the dark, using infrared (IR) illumination and IR-sensitive cameras. Paddlefish captured plankton in the dark with no discernible limitations, and the distributions of plankton in the reference plane were statistically no different than in the light (Wilkens et al. 2001). Feeding was then tested with a concentrated plankton extract, added to the water in an amount that would overwhelm any potential chemical signal detectable from the live plankton. Again, feeding was not significantly impaired. Similar results were obtained in experiments with the nares of the fish plugged and under turbulent water flow, the latter condition introduced to disrupt the potentially detectable wake trailing a swimming plankton. In a final feeding experiment, paddlefish were offered equal numbers of live daphnia encapsulated in agarose and of empty agarose particles of similar size. Paddlefish fed aggressively, but overwhelmingly selected encapsulated plankton by a ratio of nearly 20:1.

Thus, by a process of elimination, these experiments demonstrate decisively that paddlefish use the electric sense to detect their planktonic prey. Elimination of visual, chemical, and hydrodynamic means of detection, or combinations of those signals, had no effect on paddlefish prey capture. As we describe below, plankton emit weak electrical signals (not unlike those of macroscopic prey) to which an agar coating is electrically transparent. Paddlefish detect this signal in an approaching daphnia or brine shrimp with a mean reaction distance equivalent to approximately one-third the length of the paddle once the plankton passes the rostral tip.

As a final test of the electrosensory feeding hypothesis, one modeled after the shark experiments of Kalmijn (1971), we introduced simulated planktonic electric fields into holding tanks as sinusoidal waveforms using dipole leads with a 5-millimeter (mm) tip separation. Paddlefish readily struck at the electrode tips in the dark at low stimulus intensities, as observed under IR illumination (see figure 1). Stimulus frequencies at 5 to 10 hertz (Hz) elicited significantly higher strike rates (Wojtenek et al. 2001), a close match to the peak frequency sensitivity recorded from paddlefish ampullary receptors. At high intensities, paddlefish actively avoided the electrodes.

An electrosensory mechanism for prey detection gives the paddlefish a strategic niche advantage for feeding in an environment where vision is limited, especially when prey are small. Planktivorous fishes that rely on vision are primarily inhabitants of lakes or ponds, environmental conditions where the water is less turbid (Gerking 1994). This ability to target zooplankton, along with a filter-feeding mechanism that provides high-volume capacity, gives the paddlefish access to a rich source of food low in the food chain. Feeding en masse on suspended prey is a foraging strategy that favors large biomass, either individually (e.g., baleen whales, paddlefish) or as standing stock (e.g., herring) (Sanderson and Wassersug 1993).

The paddlefish rostrum, which would be an awkward appendage for a fish using a structured habitat to hide in or to launch feeding strikes from, nevertheless provides an ideal platform for an extensive, spatially distributed population of electroreceptors. Its function as a feeding antenna is consistent with its position forward of the mouth, and, of equal importance, with the paddlefish's continuous swimming, which facilitates ram ventilation. As a result, early prey detection during continuous forward swimming allows for efficient feeding that would not be possible if the electroreceptors were distributed caudal to the mouth along the trunk, as they are in weakly electric fish. The latter fish, such as the gymnotiforms that live in murky tropical streams, employ a reverse-motion strategy in detecting plankton, in this case by means of an active electrosense. These fish swim backward while scanning plankton, thereby bringing prey into the proximity of their mouths (Lanoo and Lanoo 1993). For paddlefish, the rostral antenna is an evolutionary adaptation ideally tailored to the fish's environment, feeding strategy, and ram-ventilatory swimming. Although untested, electrosensory detection is believed to be more important for particulate-feeding juveniles than for filter-feeding adults.

Planktonic electric fields

After his experiments demonstrating electrosensory detection of flatfish by a shark, Kalmijn (1972) conducted a survey of electric field potentials generated by a variety of marine fishes and macroscopic invertebrates. Teleost fish and crustaceans exhibited "skin" potentials of 0.5 to 1 millivolt, respectively, within a few millimeters of the integument, with direct current (DC) potentials greatest around the mouth and gill openings. Elasmobranchs and other invertebrates had lesser potentials, in the range of 10 to 100 microvolts.

Clearly, the potentials associated with teleosts and crustaceans were within the sensitivity range of sharks, as demonstrated in the aforementioned feeding attacks, and both groups are featured in the diets of sharks. These organisms, however, differ from the paddlefish's prey in that they are macroscopic. The question immediately arose as to whether the relatively tiny planktonic prey of the paddlefish produced detectable field potentials, a likely possibility considering the results of our feeding experiments. To address this question, we measured daphnia potentials by fixing them to a fine glass filament that was swept by a mechanoelectric device past the tip of a silver–silver chloride electrode. We measured DC potentials of up to 1 millivolt as the plankton passed close to the electrode, values equivalent to the potentials recorded from crustaceans in seawater by Kalmijn (1972). Daphnia field potentials are characteristically dipolar, with a positive polarity ventrally at the gape of the carapace, negative dorsally, and modulated by smaller alternating potentials associated with appendage movements. The dipole field of daphnia is well within the sensitivity range of paddlefish, as demonstrated electrophysiologically by passing plankton over the receptive fields of electroreceptors on the rostrum. Indeed, spike train recordings indicate that the paddlefish's sensitivity is sufficient to discriminate the dipole characteristics of the plankton that vary as a function of the orientation of daphnia relative to the rostrum (Wilkens et al. 2002).

The ampullary electrosense of the paddlefish

The presence of ampullary electroreceptive organs is a primitive characteristic shared by the paddlefish and all remaining nonneopterygian fishes, beginning with lampreys (Wilkens and Hofmann 2005). This group includes the chondrichthyians (sharks, rays, and chimeras), sarcopterygians (coelacanths and lungfish), and primitive actinopterygians (bichirs, reed fish, sturgeon, and paddlefish), whose electrosense functions passively (i.e., without active production of electric discharges such as those of the weakly electric teleosts, the Gymnotiformes and Mormyriformes). Ampullary receptors are also found in weakly electric fish and in siluriforms (catfishes), but in these species the receptors are newly evolved and nonhomologous with those of more primitive groups. Ampullae of Lorenzini are most familiar in sharks and rays, in which the pores on the skin of the head open into long gel-filled canals, leading to capsules near the midline and lined with a ciliated receptor epithelium (Murray 1974). In paddlefish and sturgeons, the ampullary canals are short (1 to 2 mm), with the result that their sensory capsules and nerve supply are spread widely over the rostrum and head (figure 2).

In paddlefish, the ampullae exist as prominent clusters ranging from 3 to more than 20 pores in larger individuals. Pore clusters on both the upper and the lower surface of the rostrum are located in patches of skin surrounded by a stellate skeletal lattice and extend laterally to the margin of the rostrum, where they multiply during growth and development. There is an electrosensory "dead space" along the midline axis of the rostrum (figure 2a), where pores are absent. Pore clusters are also found in fields on the dorsal and lateral sides of the head, the lower jaw, and the fleshy opercular flaps (figure 2c).

The ampullae of Lorenzini in paddlefish share many of the physiological properties of the well-studied ampullary receptors in elasmobranchs and other nonteleost fish. The receptor cells that amplify the weak electrical fields are located at the base of the ampulla capsule. The result is a change in the receptor membrane potential that modulates transmitter release at synapses onto primary afferent nerve fibers leading to the brain. The transmitter, in turn, modulates the firing rate of the afferent nerve fibers, an effect superimposed on the spontaneous firing of action potentials in the primary afferent initiated by an internal oscillator in the spike initiation zone. Without stimulation, afferent firing rates are very regular, at a frequency between 30 and 70 Hz. However, power spectra of afferent spike trains show an ad-

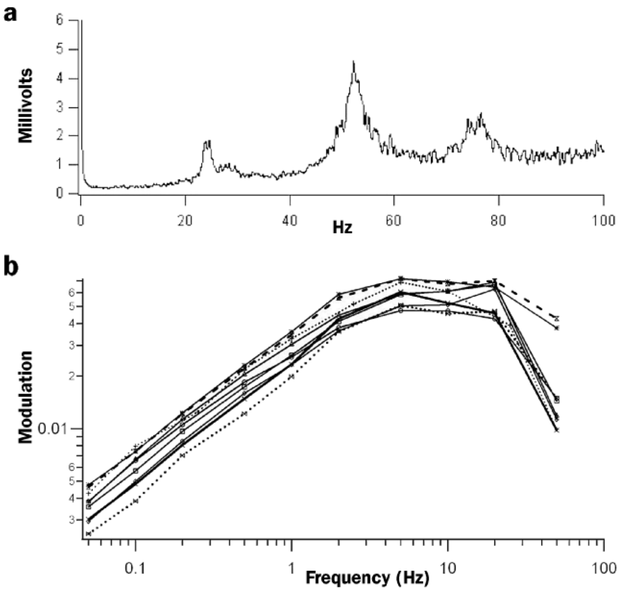

Figure 4. (a) Fourier analysis of ongoing spike trains in primary afferent fibers innervating the electroreceptive ampullae. The prominent peak at 53 hertz (Hz) reflects the spontaneous rate of the afferent spike generator. An additional peak at 23 Hz is assumed to be the result of an epithelial oscillation with unknown function. A third sideband peak at approximately 76 Hz reflects both oscillator frequencies. (b) Responses of primary afferent fibers to sinusoidal stimulation at different frequencies. The linear relationship between frequency and response magnitude resembles a derivative filter. Data: Michael H. Hofmann.

ditional frequency component around 20 Hz (figure 4a). This frequency peak reflects a second epithelial oscillator (EO) assumed to originate from the receptor cells themselves (Neiman and Russell 2001). The function of the EO is unknown, since its oscillation frequency is unresponsive to electrical stimuli and appears to depend only on temperature. Nevertheless, the EO influences activity in the primary afferent fibers with or without electrical stimulation.

It is unknown whether EOs are present in other electrosensory animals. Preliminary data from our studies of sturgeons, the sister group of the paddlefishes, have shown no evidence of EOs and suggest that these oscillations may be unique to paddlefish. However, epithelial oscillations can be detected only by analyzing spike train activity using Fourier transformations or serial correlations. The current literature from studies of other animals has not included such investigations.

As in other electrosensory animals, external electric fields are detected only if they change in time. After the onset of a stationary, nonvarying DC field, the firing rate of the afferent fibers quickly adapts and returns to its spontaneous rate. When testing with sinusoidal fields of different frequency, the best responses are observed around 10 Hz, and sensitivity declines sharply at higher frequencies (figure 4b; Hofmann et al. 2004). At lower frequencies, responses decrease gradually in proportion to stimulus frequency. This and other observations suggest that the firing rate of primary afferents follows the first derivative of the stimulus (i.e., the firing rate is proportional to the rate of change of an external field at any point in time; Hofmann et al. 2005).

In nature, DC fields apparently have no meaning for the animal. However, for an animal in constant motion, such as the ram-ventilating paddlefish, all DC fields effectively change in time. Local dipole fields of the paddlefish's prey will increase or decrease as the fish approaches and passes by. Even large-scale geoelectric fields will vary as a result of motion by the fish, especially for turns or swerving of the head during swimming. Thus, the insensitivity of the receptors to pure DC fields does not mean that DC fields are not detectable, since the movement dynamics of the fish transform any DC field into a time-varying signal.

Electrosensory afferent nerve fibers enter the paddlefish brain at the level of the hindbrain via a dorsal branch of the lateral line nerve. This nerve is by far the largest cranial nerve of the brain, and owes its size in large part to the anterior branch that innervates the ampullary and lateral line receptors of the rostrum. Electrosensory and mechanosensory afferents are segregated into dorsal and ventral branches, respectively (New and Bodznick 1985). To understand electrosensory processing in the brain, we have traced the neuronal circuitry (Hofmann et al. 2002) by injecting dyes that are picked up and transported both anterogradely and retrogradely (i.e., by neuronal dendrites to their axon terminals and from axon terminals back to their dendritic origins). The sole target for electrosensory fibers is the dorsal octavolateral nucleus (DON; figure 5), the first stage of electrosensory processing in the central nervous system. Here, large secondary electrosensory neurons receive input from primary afferent fibers in dendrites that extend into the dorsal part of the DON. These neurons also have extensive dendrites that extend ventrally into the crista cerebellaris, where they receive input from the parallel fibers of granular cells descending from the eminentia granularis of the cerebellum. The function of cerebellar input has been partly investigated in elasmobranchs, where it is involved in filtering out self-induced noise and common mode signals (Bodznick and Montgomery 1992). The role of the DON in adaptive filtering has not been investigated in paddlefish, but anatomical evidence suggests that filtering is probably a major function of the descending cerebellar pathways here as well.

A major source of input to the granular cells of the eminentia is a distinct nucleus, the nucleus preeminentialis (NPE; figure 6a), located medial to the entrance of the trigeminal nerve (Hofmann et al. 2002). The NPE receives input from the midbrain tectum (figure 6c), and NPE neurons are probably premotor (presynaptic) to the large trigeminal motor neurons that innervate the jaw muscles. Dye injections into the trigeminal nerve retrogradely stain the jaw motor neurons and their dendrites in the NPE (figure 6a). Therefore, the NPE appears to drive the motor neurons responsible for jaw movements, while at the same time sending efference copies of motor activity to the DON via the cerebellum. This pathway could be used to filter out self-generated electric signals such as those from jaw movements or opercular pumping. Interestingly, the NPE is absent in sturgeons. Most sturgeons swim with the mouth closed, so the gills are supplied by water that both enters (dorsally) and exits (ventrally) through opercular slits (Vecsei and Peterson 2004). For ram ventilation, the paddlefish mouth is constantly open to various degrees and therefore serves as a source of electrical potential that modulates the fish's own electric field.

Apart from this proposed role in noise reduction, the physiological properties of secondary neurons in the DON do not differ much from those of primary afferent fibers. Sensitivity and receptive field size are similar. DON units are also spontaneously active, but at a somewhat lower rate, and their firing pattern roughly follows the first derivative of the stimulus (Hofmann et al. 2005). The DON is the first brain area where the information from neighboring receptive fields could be spatially analyzed, yet there is no sign of any spatial interaction such as lateral inhibition or movement detection. We also found no evidence for somatotopic organization of rostral receptive fields within the DON, although each DON unit has a well-defined receptive field and thus retains spatial information for source location (Hofmann et al. 2005). Apparently, the signal is analyzed in the time domain with a gain that is proportional to the frequency (i.e., a derivative function).

But why compute the derivative of the stimulus signal? The location of a prey item relative to the body surface can be determined from the spatial pattern of activity in the receptor array in the skin. The distance of an object, however, is not so easy to determine. Without knowing the amplitude or intensity of the source, only the shape of the electrical image on the skin can give information about distance. In a realistic prey-catching scenario, however, the fish is moving relative to the mostly stationary prey. This movement creates an electric field signature in each receptor over time. In a simulation, we have studied the electric field signature of a dipole field moving along the rostrum of the paddlefish and converted this signal to its first derivative, as the DON cells would do (Hofmann et al. 2005). Then we looked at the frequency domain of this derivative and found that there is a characteristic peak frequency that is proportional to the distance of the object, but independent of the amplitude, orientation, and size of the dipole field. Thus, the distance of an object passing alongside the fish can be determined by computing the dominant frequency of the derivative of the electric field signature (Hofmann and Wilkens 2005). A neuronal representation of distance would then require neurons that receive input from the DON and respond selectively to frequencies that in turn represent different distances.

Ascending fibers of the secondary neurons in the DON target three different regions in the midbrain: the tectum, torus semicircularis, and lateral mesencephalic nucleus (figure 5a, 5b). These projections primarily cross to the contralateral side of the brain, but prominent ipsilateral projections are also present. As in other vertebrates, the tectum is probably involved in organizing orienting responses and feeding behavior. Besides electrosensory input, the tectum also receives visual and probably acoustic and somatosensory information. The physiology of tectal units is currently being investigated. Most units are not spontaneously active, or they fire at a slow, irregular rate. Upon stimulation, they produce spikes that are phase locked to a sinusoidal electric field. These experiments indicate that the responses of tectal units are much more heterogeneous than those of DON units. Although broadly tuned, each tectal unit responds to an optimum stimulus frequency that ranges from 0.1 to 10 Hz. Since object distance is proportional to the peak frequency of DON spike trains, as a result of their derivative response function, the population of neurons in the tectum is predicted to represent object distance. We are currently testing this hypothesis by stimulating the paddlefish with a more realistic moving dipole field swept past the rostrum at varying distances and speeds.

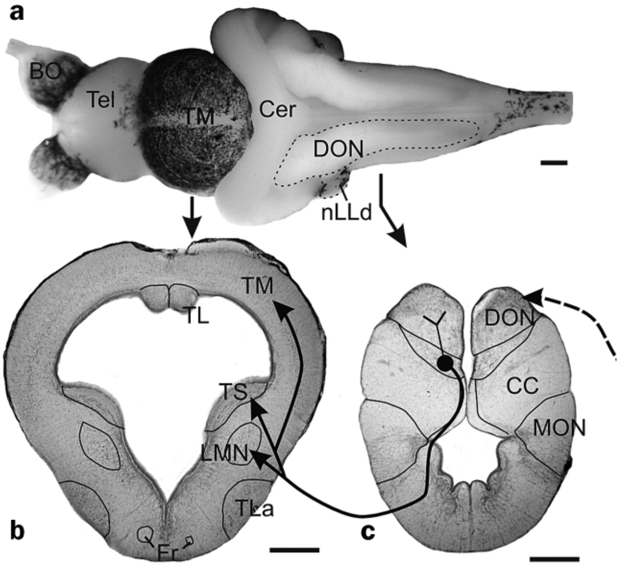

Figure 5. Major ascending electrosensory pathways in the paddlefish brain. (a) The dorsal octavolateral nucleus (DON; dotted outline) is located in the medulla of the hindbrain. It receives all electrosensory fibers from the periphery via the dorsal root of the lateral line nerve (nLLd; dashed arrow in [c]). Secondary neurons in the medulla (arrows; [b], [c]) have dendrites in the DON and project to three midbrain targets, the lateral mesencephalic nucleus (LMN), the torus semicircularis (TS), and the mesencephalic tectum (TM). Abbreviations: BO, bulbus olfactorius; CC, crista cerebellaris; Cer, cerebellum; Fr, fasciculus retroflexus; MON, medial octavolateral nucleus; Tel, telencephalon; TL, torus longitudinalis; TLa, torus lateralis. Scale bar 1 millimeter. Photographs: Michael H. Hofmann.

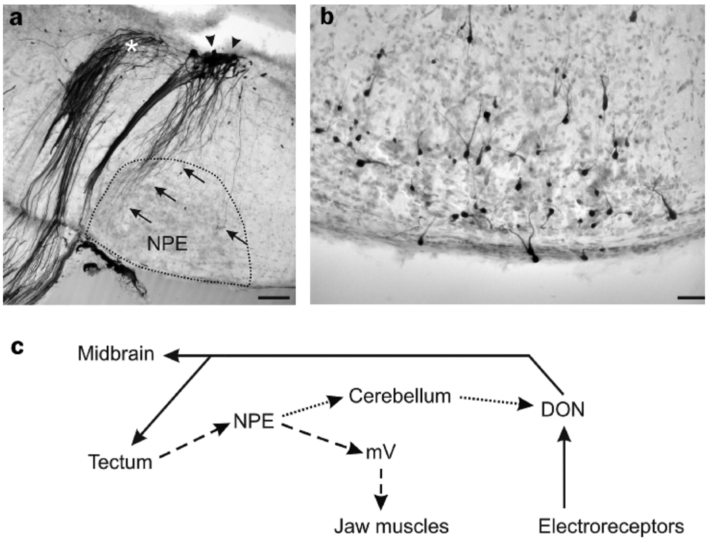

Figure 6. Pathways involved in the jaw movements associated with respiration and feeding. (a) Tracer injections into the trigeminal nerve show the sensory (asterisk) and motor components (arrowheads) of the trigeminal nerve. Large dendrites of the trigeminal motor neurons extend into the nucleus preeminentialis (arrows). Scale bar 200 micrometers (μm). (b) Neurons in the nucleus preeminentialis retrogradely labeled by tracer injections into the cerebellum. Scale bar 50 μm. (c) Schematic drawing of the ascending electrosensory pathways (arrows, solid), the descending motor pathways responsible for jaw movements (arrows, dashed), and the feedback pathway from the nucleus preeminentialis to the electrosensory area that is responsible for filtering out movement artifacts (arrows, dotted). Abbreviations: DON, dorsal octavolateral nucleus; mV, motor neurons of the trigeminal nerve; NPE, nucleus preeminentialis. Photographs and diagram: Michael H. Hofmann.

Environmental considerations for the electrosense

The metal-rod avoidance response of the paddlefish, readily demonstrated in holding tanks, raises the question of whether these fish are influenced by metal structures (such as dams and locks) placed in their natural environment. A metal surface in water is accompanied by an electrochemical corrosion potential that is typically greater in both its intensity and its physical dimensions than the field potentials associated with animate objects. For example, at the surface of an aluminum rod 1 cm in diameter, we have measured potentials of 2 to 3 millivolts that decline exponentially with distance (Gurgens et al. 2000). We then used the same aluminum rod to characterize the paddlefish avoidance response by lowering the rod by remote control into the path of a paddlefish that had established a consistent swim path near the walls of a 95-cm circular pool (Gurgens et al. 2000). Swimming paths were recorded in the dark under IR illumination using computerized tracking software. Paddlefish turned abruptly away from the rod at an average distance of 22 cm, with a maximum avoidance distance of 38 cm. In hundreds of approaches, the paddlefish never bumped into the rod, the closest approach being 10 cm. When a plastic rod or plastic-coated aluminum rod of equal size was lowered, fish either passed close to the obstacle without response or frequently bumped into the rods, an encounter followed by erratic, agitated swimming.

The stimulus that an aluminum rod, or any other larger metal structure in the freshwater habitat, evokes relative to the array of electroreceptors on the rostrum and head of the paddlefish is undoubtedly quite different from that of a small dipole source, such as a planktonic organism. Instead of a small field potential that passes over successive receptive fields, a large-scale corrosion potential is more equivalent to a uniform field potential, a sensory overload that stimulates the entire population of receptors simultaneously. Paddlefish respond to such an “unnatural” stimulus with a distinctive avoidance response. How this translates into behavior in rivers and streams will require additional study. However, paddlefish eventually habituate to the presence of a metal rod in holding tanks if it is presented frequently, so it is possible that they also learn to ignore metal objects in the wild.

Nevertheless, there are indications that fish behavior is influenced by metal structures. Paddlefish migrate over long distances in major rivers and travel upstream in annual spawning migrations, often congregating below hydroelectric dams that block access to spawning sites (Russell 1986). Where dams are constructed to regulate pool levels, Southall and Hubert (1984) report that paddlefish are reluctant to cross the dam until the metal gates are fully open and raised out of the water. The current velocity of a partially opened gate, especially for small fish, also would influence passage upstream, but it remains possible that fish are reluctant to approach these large metal obstacles.

Knowledge of paddlefish electrosensitivity is now being incorporated in considerations for managing aquatic resources and mitigating environmental impacts. For example, we have been consulted concerning the possible impact on paddlefish migrations of metal devices (and their attendant corrosion potential) used to control seasonal water flow into backwaters. High waters in spring typically flood the backwaters and lakes of large rivers, triggering plankton blooms and creating rich, calm-water feeding sites favored by paddlefish; these conditions are typical of Swan Lake, a 1000-hectare backwater of the Illinois River, close to its juncture with the Mississippi River. Consideration has also been given to using the paddlefish electrosense as a physiological mechanism to prevent fish from being swept into the power generators of large dams, that is, by creating an electrical field barrier.

A final, somewhat speculative consequence of the function of the paddlefish electrosense concerns the possibility that it may play a role in sensitivity and orientation to the Earth’s magnetic field. It has been proposed that ampullary electrosensitivity in sharks and rays is associated with electrical signals induced by movement relative to geomagnetic forces (Kalmijn 1974), and sharks have been shown to make homing migrations to feeding locations that track known geomagnetic fields in the Earth's crust (Klimley 1993). Water flow in a stream and river, or the movements of a fish itself, including long-distance paddlefish migrations, are possible sources of magnetically induced electrical signals that are theoretically within the sensitivity range of the paddlefish electrosense. In preliminary experiments, we have demonstrated that paddlefish detect electric fields in the environment created by electrodes placed at opposite ends of a rearing pond. Fish frequently reversed direction when approaching this electrical boundary. There are also unconfirmed reports that paddlefish avoid locations where overhead power lines cross a river. However, additional research will be required to determine whether the paddlefish electrosense is used for migratory behavior.

Acknowledgments

This article was written with support from the National Science Foundation. The authors also acknowledge previous contributions from Frank Moss and colleagues at the Center for Neurodynamics, University of Missouri–St. Louis, and support from the Office of Naval Research. The Missouri Department of Conservation has generously supplied paddlefish from hatcheries in the state.

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doi:10.1641/B570505
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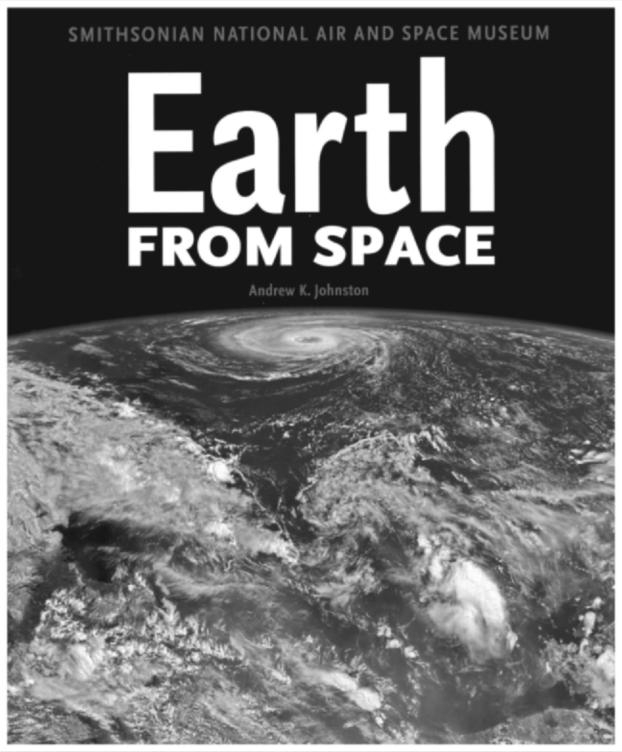
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