The paddlefish rostrum functions as an electrosensory antenna in plankton feeding

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SUMMARY

A novel electrosensory function is presented for the large, plankton-feeding, freshwater paddlefish, *Polyodon spathula*, along with a hypothesis which accounts for the distinctive, elongated rostrum of this unusual fish. Behavioural experiments conducted in the 'dark' (under infrared illumination), to eliminate vision, show that paddlefish efficiently capture planktonic prey to distances up to 80–90 mm. They make feeding strikes at dipole electrodes in response to weak low-frequency electrical currents. Fish also avoid metal obstacles placed in the water, again in the dark. Electrophysiological experiments confirm that the Lorenzian ampullae of paddlefish are sensitive to weak, low-frequency electrical signals, and demonstrate unequivocally that they respond to the very small electrical signals generated by their natural zooplankton prey (*Daphnia* sp.). We propose that the rostrum constitutes the biological equivalent of an electrical antenna, enabling the fish to accurately detect and capture its planktonic food in turbid river environments where vision is severely limited. The electrical sensitivity of paddlefish to metallic substrates may interfere with their migrations through locks and dams.

1. INTRODUCTION

The paddlefish, *Polyodon spathula*, grows to be one of the largest freshwater fish (up to 2 m and 75 kg). Adults filter feed almost entirely on zooplankton such as cladocerans (e.g. the water flea, *Daphnia* sp.) and copepods, sweeping up shoals of the tiny prey from rivers and flood basins. In contrast, small paddlefish which lack functional gill rakers (fish <225 mm in length; Rosen & Hales 1981) are particulate feeders, selecting and capturing zooplankton *individually*. These two modes of plankton feeding have been termed 'microphagy' and 'planktivory', respectively (Sanderson & Wassersug 1993). The plankton are sufficiently small (1–3 mm) that they are unlikely to be detected visually in the natural habitat of the paddlefish, the muddy waters of the Mississippi River drainage (Russell 1986). Further, the visual system of the paddlefish is poorly developed (Hussakof 1910). How, then, do paddlefish detect zooplankton and feed with such great efficiency, as indicated by the large body size of these fish? We propose that the paddlefish rostrum, a long dorsoventrally flattened extension of the head, one-third the length of the fish, is uniquely adapted for sensing small prey electrically in a dark, turbid environment, thereby functioning as an electrical antenna.

That the paddlefish rostrum functions as an electrosensory organ is suggested by the presence of tens of thousands of ampullae of Lorenzini (Jørgensen *et al.* 1972), well-known in elasmobranchs to be electroreceptors (Murray 1962; Szamier & Bennett 1980; Fields *et al.* 1993; Bullock 1974; Kalmijn 1988; Montgomery 1984). The ampullae also extend onto the head and opercular flaps. Indeed, electrosensory responses have been recorded in the paddlefish hind-brain (New & Bodznick 1985). Nevertheless, the function and evolutionary significance of the paddlefish rostrum remain anomalous. In the present study we characterize physiologically the electrosensitivity of paddlefish ampullary receptors on the rostrum, and present behavioural evidence that vision and other sensory modalities are not needed for the detection and capture of planktonic prey. Further, we show that paddlefish exhibit feeding behaviours directed at weak electrical fields generated by dipole electrodes placed in the water, and that paddlefish are able to avoid metallic obstacles. All these lines of evidence indicate that paddlefish possess an electric sense and use it in planktivory and obstacle avoidance.

2. MATERIALS AND METHODS

(a) Plankton feeding

Planktivorous feeding by juvenile paddlefish was examined under near-infrared (880 nm) (NIR) illumination by video analysis of small paddlefish (12–17 cm long, 1.4–2.0 cm

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rostrum width) swimming in a recirculating flow tank (Vogel & LaBarbera 1978). The fish were viewed by two video cameras, one from the left side and one from the bottom (via a mirror). The video signals were combined and recorded on magnetic tape. Fish were restricted by grilles and flow collimators to a 40 cm length of the 14 × 14 cm trough. We used conditioned water from holding tanks adjusted to a conductivity of *ca.* 760 $\mu\text{S cm}^{-1}$ and flowing at *ca.* 10 cm s^{-1} to match average swimming speeds. Fish not fed for 12–24 h readily consumed live adult brineshrimp (*Artemia*), rinsed in fresh water and introduced remotely into the stream at low density via a plastic tube. During data analysis, a captured brineshrimp was aligned with the tip of the rostrum by reversing the video tape. This frame was digitized and the distance of the brineshrimp from the centre of the rostrum was measured using SigmaScanTM software (Jandel Scientific, San Rafael, CA). The analysis of feeding included more than 5000 captures from over 100 h of taped feeding sequences.

(b) Avoidance behaviour

Paddlefish, acclimated for 1 h in a circular tank (95 cm diameter, 30 cm deep) filled with dechlorinated tap water at 800 $\mu\text{S cm}^{-1}$, were monitored videographically under infrared light. Fish circled the tank perimeter, frequently touching the wall with their rostrum. A remote-controlled manipulator lowered obstacles into the water 4 cm from the tank wall as the fish entered a recording zone extending 30 cm from either side of the obstacle. All obstacles (round posts of aluminum, plastic, or plastic-coated aluminum) were 2.5 cm in diameter, 18 cm long, and suspended by string from the manipulator. The video signals were fed to a computerized tracking system (Chromotrack 402, San Diego Instruments) to record the swim paths and measure the minimum approach distances.

(c) Electrophysiology

Paddlefish 35–40 cm in length were anaesthetized in tricane methanesulphonate (0.1 g ml^{-1}), artificially respired by irrigation of the gills, and 'decerebrated' by crushing the juncture between the diencephalon and optic tectum in accordance with an experimental protocol approved by the University's Animal Welfare Committee. Anaesthetic was then discontinued. D-tubocurarine (0.1 ml, 3 mg ml^{-1} ; Lilly, Indianapolis, IN) was injected intramuscularly to eliminate body movements. Afferent nerves (anterior lateral line nerve, ALLn) from the rostrum were exposed near their entrance into the medulla, and unit activity was recorded with metal microelectrodes in the sensory ganglia. In several experiments activity was recorded *en passant* with fine suction pipettes applied to ALLn branches in the rostrum. Spikes were amplified, windowed, and passed to oscilloscope, oscillograph, and computer (CED, Spike II software, Cambridge Electronic Design, Cambridge, MA) for display and analysis. Weak cathodal and anodal stimulus pulses were delivered from a stimulus isolation unit by two Ag–AgCl electrodes, one located near the rostrum, the other near the tail. For determining frequency sensitivity, sinusoidal stimulus waveforms were delivered from a function generator with the stimulating electrode placed near the receptive field relative to a distant bath electrode. Sensitivity was computed as the difference between maximum and minimum instantaneous spike frequencies averaged over 11–300+ stimulus cycles. Electrophysiological responses also were recorded using natural zooplankton prey as the stimulus. Tethered *Daphnia* or *Artemia* were glued with cyanoacrylate to the tips of thin (*ca.* 50 μm diameter) glass probes and positioned along the

rostrum with a calibrated micromanipulator. The electric field potentials from *Daphnia* were monitored using two Ag–AgCl electrodes, one located near the receptive field, the other *ca.* 1 cm away, connected to a differential AC amplifier with bandpass filter settings at 0.1 Hz and 1.4 kHz.

3. RESULTS

(a) Feeding behaviour

First, we demonstrate that juvenile paddlefish detect and efficiently capture individual brineshrimp (*Artemia*) in 'darkness', i.e. without the aid of visual cues. Fish swimming in the experimental flow tank sensed brineshrimp as they passed alongside the rostrum, then turned to engulf the plankters as they neared the head (see figure 1*a,b*). Feeding varied from simply opening the mouth when brineshrimp were close, to acrobatic manoeuvres when brineshrimp passed above or to the side of the rostrum, the latter involving turns and rolls, often bringing the mouth uppermost (see figure 1*b*). The location of brineshrimp relative to the midline of the rostrum was measured in a vertical plane at the rostral tip (as in figure 1*a*). The combined data from six fish including 3078 captures, illustrate the distribution of captured brineshrimp as 'seen' by the fish looking forward (see figure 1*c*). Most of the brineshrimp were captured within 25 mm of the upper and lower surfaces and ± 50 mm lateral to the midline of the rostrum, with an ovoid distribution corresponding to the flattened profile of the rostrum. Some brineshrimp were captured at distances of up to 80–90 mm. Subsequent experiments (to be reported elsewhere) using the natural prey *Daphnia*, show somewhat shorter feeding distances (50–60 mm). We conclude that vision is not required for capturing individual plankton.

Control observations of paddlefish feeding behaviour (under NIR) showed that the hydrodynamic and chemical sensory modalities are not required for planktivorous feeding. Possible hydrodynamic detection of zooplankton by lateral line receptors was tested as follows. First, feeding was analysed in turbulent flow conditions, for comparison with the laminar flow conditions represented in the previous data shown in figure 1, by removing the collimators and vigorously bubbling air and stirring the water upstream of the viewing chamber with a motor-driven propeller. Under these conditions, paddlefish fed readily on brineshrimp tumbling over distances of several centimetres. Second, paddlefish fed readily on brineshrimp individually coated twice with agarose (2% w/v in aquarium water, Sigma type I-A, gel temperature 40°) to eliminate appendage movements and body flexion. Agarose-coated brineshrimp remain viable for 2–3 h, as noted by visible contractions of the intestine and dorsal blood vessels and rhythmic AC field potentials (not illustrated). Agarose particles of similar size and identical composition, but not containing brineshrimp, were seldom captured. Third, the distribution of the vertical coordinates of captured brineshrimp (from data in figure 1) showed that the mean vertical position for all captured plankton was nearly equivalent to the horizontal midplane of the rostrum, slightly above or below the midplane in different fish, departing from it

Figure 1. Capture of brineshrimp without visual cues. A small paddlefish swam in a recirculating fresh water flow tank under near-infrared illumination. (a) Sample video field showing a swimming paddlefish in side view (upper half of the video field) and from the bottom (lower half). One brineshrimp (arrows) has just emerged from the flow collimator (grille) and is aligned with a vertical plane at the anterior tip of the rostrum. The location of the rostrum (R), mouth (M), nares (N) and eyes (E) is indicated. (b) Capture of the same brineshrimp < 1 s later, showing the brineshrimp in the mouth (arrow in side view). Video images are digitally retouched. (c) The locations of 3078 brineshrimp captured by six paddlefish, as measured in (a) and grouped. The origin (0,0) corresponds to the centre of a cross-section of the rostrum, and the location vertical +10, horizontal -10, would indicate 10 mm above and to the left of the rostrum axis.

by <2% of one standard deviation on average. This is of interest because the paddlefish lateral line extends along the length of the rostrum, but only on the ventral surface (Nachtrieb 1910). If hydrodynamic signals were instrumental in detecting plankton, we would predict that the mean vertical coordinate of captures would be underneath the rostrum.

The possibility of chemical sensing of the plankton was also addressed in the experiments with brineshrimp twice-coated with agarose. That coated brineshrimp were readily captured and eaten, as noted above, suggests that chemical signals are not necessary since molecular diffusion is expected to be

greatly reduced by the agarose. Feeding on brineshrimp continued when the nares were blocked (by local application of cyanoacrylic gel). Particulate feeding also continued in the presence of concentrated extracts of brineshrimp (homogenized in a blender, then centrifuged to remove particulate matter) added to the flow chamber; this treatment was expected to present a high chemical background to mask possible olfactory and gustatory cues from passing plankton. All of these experiments designed to exclude vibratory or chemical sensory modalities were conducted under NIR illumination like the previous experiments.

Figure 2. Minimum approach distances to obstacles. Paddlefish 20–25 cm in length, swimming in a circular tank, responded differently to metal and nonmetallic posts lowered into the water. Swim paths were recorded under near-infrared illumination for 15 trials per fish using a computerized tracking system, with $n = 20$ fish tested for each type of post. The mean avoidance distance represents the nearest point in the swim path between the tip of the rostrum and the edge of the obstacle. The control value represents the mean distance for fish swimming past the location of the obstacle, but without the post lowered into the water. The small increases in approach distance relative to control paths resulted from more variable swim paths following collisions with non-conducting posts.

(b) Avoidance behaviour

Previously it was noted that paddlefish avoid metal objects, but not wood (Jørgensen *et al.* 1972). This was confirmed by inserting bars of various metals (1.2 cm in diameter) into the fish tanks. Each triggered a strong startle response. Fish immediately scattered within a 1–2 m radius of the bar and swam excitedly for 5–10 s. There was no response to wood or plastic. Such avoidance behaviour was quantified by lowering obstacles into the path of fish swimming in a circular tank, under NIR. Paddlefish veered sharply away or reversed direction at a mean approach distance of 22.5 cm from an aluminum rod (see figure 2), successfully avoiding it in all instances. In contrast, fish seldom altered their swim path for plastic posts or plastic-coated aluminum posts, approaching both within approximately 2.5 cm (see figure 2), and bumping into each in nearly half the trials. Thus, obstacles with a nonmetallic (nonconductive) surface appeared not to be detected.

(c) Electrophysiology

In electrophysiological experiments, we have demonstrated the sensitivity of paddlefish ampullary receptors to weak electric fields. Action potentials recorded *en passant* from nerve fibres in the rostrum showed that electrosensory afferents are spontaneously active, with spike rates of 50–60 s⁻¹, and are excited by cathodal stimulus currents (i.e. the bath electrode near the rostrum was made negative). This is the same stimulus polarity which excites ampullary receptors in elasmobranchs (Murray 1962; Szamier & Bennett 1980; Fields *et al.* 1993; Bullock

Figure 3. Electrosensitivity of anterior lateral line afferent fibers. (a) Polarity of electroreceptors. Cathodal stimuli (upper traces), in which the electrode near the rostrum was made negative, excited nearby electroreceptors. Anodal stimuli (lower traces) were inhibitory. (b) Frequency sensitivity of an electroreceptor primary afferent, whose site of maximal sensitivity was on the left ventral surface of the rostrum *ca.* 5 cm anterior to the mouth. (c) Spike rate modulation by natural prey. Action potentials from an electroreceptor primary afferent (middle trace), and their instantaneous rate (top trace), were computed while holding a tethered *Daphnia* near the receptive field. A bath recording pipette placed adjacent to the *Daphnia*, just outside the sweep of the antennae (<1 mm), monitored AC voltage transients generated by the rhythmical motions of the thoracic appendages (bottom trace; the DC component of the *Daphnia* electrical signal is not shown).

1974; Kalmijn 1988; Montgomery 1984) and sturgeon (Teeter *et al.* 1980), and is opposite to that for teleost fish. An excitatory response is illustrated in figure 3a (upper panel), in which a high-frequency, rapidly adapting burst at stimulus onset is followed by a brief cessation of

Figure 4. Feeding strikes elicited by electrical signals. Four paddlefish (ca. 30 cm long) swimming in a large tank were monitored remotely under near-infrared illumination by video camera, and their strikes (attempts to ingest dipole electrodes placed near the surface of the water) were recorded with a time-lapse video tape recorder (at 6 $\times$) for the 12 h dark cycle of the aquarium room lighting schedule. The mean strikes per minute for various computer-generated stimulus protocols (frequency–intensity combinations) are plotted. Results were combined from five experiments totaling 60 h of videotaped ‘electrical feeding’ behaviour.

activity at stimulus offset. Anodal stimulation was inhibitory, followed by an excitatory off-response (see figure 3a, lower panel). The responses shown corresponded to voltage gradients of ca. 0.21 mV cm⁻¹ over the length of the 47 cm experimental chamber; however, the sensitivity of these electroreceptors will be characterized elsewhere. Paddlefish electroreceptors were most sensitive to low frequencies, with constant-amplitude sinusoidal stimuli producing maximal responses between 1 and 10 Hz; sensitivity declines rapidly above 20 Hz (see figure 3b). These results are consistent with the low-frequency sensitivity of other ampullary electroreceptors (Bullock 1974; Kalmijn 1988; Montgomery 1984).

Zooplankton in freshwater generate electrical signals in the range of 0.1–1 mV amplitude, consisting of a DC offset potential along with AC transients arising from movements of the body and appendages (E. Wagner, D. F. Russell, X. Pei and L. A. Wilkens, unpublished data). To establish unequivocally that paddlefish electroreceptors are sensitive to zooplankton, the spike activity of electroreceptor primary afferent nerve fibres was recorded with a water flea (*Daphnia*, the natural prey of paddlefish) positioned near the receptive field, 1 mm above the surface of the rostrum (see figure 3c). Electrical transients from the water flea which correspond to its rhythmical appendage movements are monitored in the lower trace. The spike rate of the electroreceptor afferent (top and middle traces) illustrates exquisite sensitivity to the electrical signals generated by *Daphnia*, effectively monitoring the small AC signal components. In other tests using brineshrimp, which generate somewhat larger electric field potentials,

discharge patterns of afferents were modulated at distances of up to 6 cm. A more detailed description of the AC and DC field potentials arising from *Daphnia* and *Artemia*, and the fall-off of amplitude with distance, will be presented elsewhere. When live plankton were swept across the receptive field, at rates approximating the swimming speed of the fish, distinct burst–pause signatures in the spike rate of electroreceptor afferents were produced.

(d) Electrical feeding

In a final demonstration of electrosensory function, feeding behaviour was elicited with a small electrical dipole (0.25 mm teflon-coated silver wires, with exposed tips 1 cm apart), placed just below the water surface. Feeding behaviour was evaluated for sinusoidal signals of varying frequency and intensity, generated by computer in a random sequence of 2 min test epochs separated by 5 s intervals. Paddlefish were readily attracted to the dipole, slowing to ‘investigate’ the signal and often circling the dipole repeatedly while attempting to ingest the wire leads. Average strikes per minute were determined for each frequency–intensity combination of the electrical stimulus (see figure 4). These ‘electrical feeding’ responses were triggered primarily at low frequencies, with peak sensitivity at 10 Hz, a value matching the low-frequency characteristics of the receptors (see figure 3b) and the oscillating signals of planktonic prey (see figure 3c). The feeding response was uniform for test currents at or above 0.25 μ A, with threshold behaviour elicited between 0.005 and 0.05 μ A. The experimental design did not permit accurate determination of the distance at which the stimulus was detected.

4. DISCUSSION

We have presented evidence for a novel use of electrosense, reported here for the first time in the detection and capture of individual zooplankton in particulate (planktivorous) feeding, as seen in juvenile paddlefish. We also provide the initial characterization of ampullary electrosensitivity in the paddlefish rostrum. To date, plankton-feeding fish are known to rely primarily on the visual sense (Gerking 1994), but the turbid paddlefish environment is ill-suited for detecting near-microscopic prey visually. In demonstrating that paddlefish successfully capture plankton, attempt to feed when detecting weak electrical signals, and avoid conducting objects in the environment, *all in the absence of visible light*, we conclude that vision is not required for these behaviours and that its role is secondary to the electrosensory system. These results are analogous to the classic experiments of Kalmijn (1971) showing that sharks recognize and attack electric fields which simulate those of macroscopic (flatfish) prey.

However, the involvement of chemical and hydrodynamic stimuli also must be considered. Planktonic communities are patchy, and dense concentrations of plankton condition the water chemically, e.g. the red tides of dinoflagellates. While such chemical signals

also may exist in the freshwater environment of paddlefish, they do not seem relevant for the capture of individual zooplankton by juveniles, since we have carried out experiments to block or mask possible olfactory or gustatory detection, with little discernible effect on the capture of brineshrimp. The lateral line system of mechanoreceptors is another candidate sensory modality underlying planktivory, and has been proposed to mediate plankton capture in other fish (Saunders & Montgomery 1985). In our experiments demonstrating the capture of agarose-immobilized brineshrimp, the plankton remained alive, but the metachronal motion of leg movements or body flexion were completely eliminated, as verified by visual inspection. Nonetheless, the immobilized brineshrimp were detected and eaten voraciously. To control for a possible hydrodynamic signature from tumbling motions of the coated brineshrimp, comparison was made to feeding on agarose particles, which were rarely consumed. This is analogous to Kalmijn's (1971) use of an agar partition to separate flatfish prey from sharks, except that each brineshrimp carried its own individual agarose partition, so they could still be captured. Further, it is unlikely that plankton generate mechanical signals sufficient to indicate their presence to paddlefish, since recent studies have demonstrated that the long 'hydrodynamic trails' of marine copepods are thin, with dimensions approximating the size of the plankton (Fields & Yen 1993; Yen & Strickler 1996), and are rapidly smoothed by viscosity (Lazier & Mann 1989). Thus, for most brineshrimp captures analysed here, i.e. at distances > 5 mm from the rostral surface, the hydrodynamic signatures may be negligible. In addition, we have shown that planktivorous feeding continues under highly turbulent flow conditions, which would be expected to mask hydrodynamic cues. Turbulence is probably a characteristic feature of the natural habitat. While we have shown that the visual, vibratory, olfactory and gustatory senses are not needed for seemingly normal prey capture, nevertheless prey capture may be quantitatively somewhat different when these other sensory modalities are functional.

The function of the paddlefish rostrum, a unique structure among fish, has long been subject to speculation. It is a common misconception that the paddlefish uses its rostrum to stir prey from the substrate (hence its alternate names 'shovelnose cat' and 'spoonbill catfish'), yet such behaviour has never been documented. The evidence presented here postulates that the paddle has evolved primarily as an antenna used in foraging for planktonic prey. In that individual prey are detected and captured by small fish, it seems reasonable to predict that large fish, although filtering prey nonselectively, are capable of assessing plankton density. This would permit even greater efficiency in the suspension-feeding strategy of paddlefish, enabling them to detect the patch boundaries of plankton and initiate turns.

As an electrosensory organ, the paddlefish rostrum is functionally analogous with the platypus bill (Scheich *et al.* 1986; Manger & Pettigrew 1995), which the platypus uses to aggressively search for substrate-dwelling prey such as crayfish (Gregory 1991). As in the platypus, the flattened rostrum provides maximal surface area

(relative to volume) for the extensive population of electroreceptors presumed necessary for electrical acuity. Also, its elongate shape allows for dynamic spatial registration of the electrical signals of approaching planktonic prey. For this ram-ventilating fish (which must swim continuously), especially during its particulate-feeding stage, it is significant that the rostrum extends in front of the head, thereby acting as an antenna for detecting oncoming prey before they drift past the mouth. A 'reverse' analogy has been proposed for the foraging behaviour of gymnotids (Lannoo & Lannoo 1993), weakly electric fish which swim backwards as well as forwards. In this case, backward swimming, during which fish electrically scan potential prey, brings the mouth into position for the feeding strike.

Suspension feeding by the paddlefish provides for the efficient utilization of energy-rich planktonic resources at a low level in the food chain, a foraging strategy that facilitates either large body size or large standing stocks (Sanderson & Wassersug 1993). This strategy is of limited availability for fish living in turbid environments which rely solely on vision. The evolution of the rostrum as an electrosensory antenna provides access to this foraging niche and may explain why paddlefish are the largest freshwater fish to filter feed.

Other functions, e.g. navigation, also may be served by the paddle. Tracking studies have demonstrated that paddlefish commonly return to the same site after traveling long distances up or down river (Southall & Hubert 1984). That paddlefish, threatened or endangered in certain parts of their range, avoid electrically conducting objects may have implications for their management by wildlife agencies. These fish are reluctant to approach and migrate through the partially opened metal gates of the dams and locks common throughout the upper Mississippi and Missouri Rivers (Southall & Hubert 1984). Coating the gates with an electrical insulator might mitigate such barriers to paddlefish migration.

This research was conducted in accordance with an experimental protocol approved by the Institutional Animal Care and Use Committee of the University. Paddlefish were graciously supplied by Mr. Jerry Hamilton, Blind Pony Fish Hatchery, Missouri Department of Conservation, by Dr Steven Mims and Dr Julia Clark, Aquaculture Research Center, Kentucky State University, and by Ozark Catfisheries, Osage Beach, Missouri. The assistance of Alex Field in maintaining the fish, and of Jeffrey Allison, Mark Cox, Dale Greenberg, Jason Polk, Ann Scharnhorst, Eva Wagner, and Barbara Wettring in experimentation and/or videotape analysis was appreciated. This project was supported in part by grants from the Department of Defense (URISP-ONR), the University of Missouri Research Board, and the Whitehall Foundation.

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