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Paddlefish and Platypus: Parallel Evolution of Passive Electroreception in a Rostral Bill Organ

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Abstract

A comparison is made between a mammalian, monotreme species and an actinopterygian fish that have each, independently, evolved a similar, spoonbill-shaped rostral bill organ whose array of electroreceptors provides sufficient spatial information for prey capture in a freshwater environment without the need for visual cues. The platypus, *Ornithorhyncus anatinus* (Monotremata, Mammalia), has approximately 40,000 electroreceptors arranged in parasagittal rows on the bill organ. By means of behavioral and electrophysiological recording experiments in platypus, it has been shown that this array of electroreceptors can trigger an accurately directed head saccade to intersect aquatic prey that emit electrical signals. The threshold field strength for prey detection by platypus signals is 50 microvolts/cm, two orders of magnitude more sensitive than individual electroreceptors. The paddlefish, *Polyodon spathula* (Osteichthyes, Actinopterygii), can similarly execute a lateral head saccade to intersect prey, with a threshold field strength around 10 microvolts/cm, considerably more sensitive than the presumed sensitivity of individual electroreceptors. The remarkable anatomical and behavioral similarities between these two independent electroreceptive systems are described and discussed. Major differences between the two bill-organ systems include the mechanism of transduction at the electroreceptors and a prominent cooperative role played by 60,000 mechanoreceptors that are interdigitated among the electroreceptors in the platypus bill but not in the paddlefish.

1. Introduction

This paper grew out of a mutual recognition by the authors of the striking similarities between the rostral bill apparatus of the paddlefish and the platypus. This fish and this mammal each use the unusual sensory abilities of their bills to locate and catch small freshwater prey. Although neither of us has worked on the other's species, our knowledge has grown as we interacted. As a result we decided to try to present a comparison that illustrates the con-

vergent similarities and important differences between these extraordinary animals that have independently evolved the use of passive electroreception by an elaborate rostral bill organ to catch aquatic prey.

We begin with a brief account of the biology of the two species and place them each in evolutionary context. We then give a detailed description of the electroreceptors and their arrangement in the bill organ in each species, with an account of the similarities and differences. We describe the lateral head saccade that is directed toward an electrically active prey in both species and show how this behavior has been used by investigators of both species to define the directionality and the threshold sensitivity of the electrosensory system. Since both species show far greater sensitivity to electrical stimuli at the whole animal level than at the level of individual receptors, we discuss this commonly observed discrepancy assuming that there is signal processing of the combined activity of large numbers of receptors. We show how both species avoid DC fields and finish with a discussion of the role of underwater mechanoreception as an adjunct to electroreception. This emerging bimodal viewpoint that considers waterborne mechanical stimuli arises from the extensive system of interdigitated electroreceptive and mechanoreceptive cortical neurons known in platypus, along with the mechanosensitivity of electrosensory ampullae in paddlefishes. Finally, we discuss the similarities and differences between the underwater prey detection systems of paddlefishes and platypus in the context of conservation issues.

2. Biographical Sketches of the Animals

2.1. Paddlefishes

The paddlefish, *Polyodon spathula*, is among the most primitive of bony-finned fishes (Osteichthyes, Actinopterygii), and together with sturgeon comprises an order of secondarily cartilaginous fishes, the Acipenseriformes. The North American paddlefish is one of only two extant species in the family Polyodontidae

whose origins extend back into the Cretaceous period, over 100 mya; the sister species *Psephurus* is native to China. Paddlefishes once ranged throughout the turbid midwestern rivers of the United States.

By virtue of their elongated rostrum (i.e., bill or paddle), paddlefishes are unique among the approximately 25,000 species of living fishes. Unlike other fishes with long noses and jaws, the paddlefish rostrum is an elongation of its cranium. In platypus, the upper bill is maxillary and is fused to the cranium. The prominent rostrum comprises one-third the length of the fish, even more in small fishes, and is responsible for the common functional misrepresentation indicated by the synonymic names "spoonbill cat" and "shovelnose cat." Paddlefishes also are notable for their large size, once known to reach 75 kg and 2 m, which they achieve by feeding on a rich zooplankton resource at the base of the food chain. As filter feeders, and one of the largest riverine species of fishes, they are the ecological equivalent in freshwater of baleen whales and large filter-feeding marine fishes such as the whale and basking shark.

Only recently (Wilkens et al., 1997) has the evolutionary significance of the paddle been correlated with the fish's planktonic diet and its muddy, nonvisual environment. In feeding experiments, small paddlefishes readily capture tiny plankton (*Daphnia*) without benefit of their visual, chemical, or hydrodynamic senses (Wilkens et al., 2001). This suggests the existence of an alternate sensory mechanism. Like the platypus bill, the paddlefish rostrum is covered by an extensive array of electroreceptors, here the ampullae of Lorenzini (Jørgensen et al., 1972). Thus, the rostrum and its ampullary electroreceptors comprise the functional equivalent of an antenna, a sensory device with sufficient sensitivity to detect the electric fields of their planktonic prey (Wilkens et al., 1997; Russell et al., 1999).

While we have established the role of the electroreception in planktivorous feeding in small juvenile paddlefishes, the sensory mechanisms used by large adult fishes have not been determined. Unlike juveniles that feed selectively by capturing individual plankton, large

fishes feed nonselectively by sieving plankton from the water using comb-like gill rakers not fully developed until fishes reach 22–23 cm in length (Rosen and Hales, 1981). However, large healthy fishes occasionally are found missing their paddle, presumably the result of mutilation by boat propellers. Since juvenile fishes have not been observed in the wild except with their paddles intact, it is presumed that the electrosensory system is an adaptation primarily benefiting young paddlefishes when feeding selectively (i.e., capturing plankton one at a time).

2.2. Platypus

The platypus, *Ornithorhyncus anatinus*, is one of three living species of monotremes (egg-laying mammals with a single opening, the cloaca, for both excretory and reproductive functions) (Griffith, 1978). The only other two extant monotremes (*Tachyglossus aculeatus* and *Zaglossus brujnii*) are land-dwelling, spine-covered echidnas that arose relatively recently (20–30 myr) from an ancient platypus lineage that can be traced back more than 100 myr (Pettigrew, 1999). The first specimen of a platypus to reach the West was believed at first to be a fake, as it was thought that the duck-like bill had been cunningly stitched to the luxuriant fur (Griffith, 1998). Platypus live in a long burrow with an entrance close to, or below, water level. The tunnel can be a tight fit, particularly in the breeding female's burrow, which is much longer than usual. The length and fit ensure that the platypus is dry by the time it reaches the nest area at the end, even when there is a high frequency of hunting sorties to the water that would tend to wet the tunnel, as for the breeding female. Eyes, nostrils, and ears are all closed underwater and prey are located by a combination of electroreception and mechanoreception (see below). Prey are benthic and include crustaceans, insect larvae, worms, and fishes. On an average foraging trip, which is usually at night, a platypus may consume half its weight in prey, in total darkness. Juveniles may hunt in daylight as well, perhaps because they are smaller, with a greater metabolic rate, and/or because they are less skillful at finding prey and

therefore need to spend more time in this activity (J.D. Pettigrew, unpublished). An extensive series of behavioral observations has clarified how platypus use electroreception, perhaps in conjunction with mechanoreception, to locate aquatic prey in three dimensions (Manger and Pettigrew, 1995; Manger et al., 1996; Pettigrew et al., 1998). The 40,000 electroreceptors on the bill form a directional antenna that allows instantaneous determination of the azimuth and elevation of a prey's electrical discharge so that a head saccade can be directed accurately toward it. By combining mechanosensory and electrosensory inputs together in an extraordinary cortical structure resembling the celebrated ocular dominance columns of primates, the platypus may be able to fix the third coordinate of its prey, distance, from the time-of-arrival difference between the electrical signal and its later mechanical wave produced by prey.

Early development after hatching takes place in the burrow, with the female providing milk that is secreted onto her fur rather than from a nipple (Griffiths, 1978). Electroreceptors develop on the bill at this very early stage, before mechanoreceptors, suggesting that electroreceptors may have a functional role, perhaps in suckling, before the juvenile enters the water for the first time (Manger et al., 1999).

3. Arrangement of Electroreceptors on Rostrum and Bill

3.1. Paddlefish Ampullae

The paddlefish skin covering the upper and lower surfaces of the paddle, the head, opercular flaps, and lower jaw is penetrated by numerous pores, 65–140 mm in diameter and just visible to the naked eye. An 80-cm fish was estimated to have 57,365 pores (Kistler, 1906), with numbers as high as 75,000 per fish (Nachtrieb, 1910). Pores occur in clusters of 5–25 that are more numerous near the lateral margins of the paddle, but absent from an 8–10-mm wide strip along the midline of both upper and lower surfaces.

Each pore opens into the pear-shaped lumen of an ampullary organ 100–250 μm deep. The lower half of the ampulla is lined by a sensory epithelium of ciliated receptors and supporting cells (Jørgensen et al., 1972). Tight junctions near the luminar surface join the receptor and supporting cells. The receptor cells form synapses with the nerve endings of primary afferent neurons that converge into anterior lateral line nerves that travel to the brain. Each receptor synapses with several nerve terminals and each primary afferent innervates numerous receptor cells. Although characterized early on as sensory organs (Kistler, 1906), Nachtrieb (1910) argued vigorously that the ampullae were secretory organs owing to the gelatinous secretions inside the pits. Their electrosensory function as ampullae of Lorenzini was established unequivocally by the anatomical study of Jørgensen et al. (1972).

3.2. Platypus Electroreceptors

Electroreceptors are readily recognized in low-power micrographs (even in obliquely lit naked-eye views) because of the pores that penetrate the thick epidermis to enable the necessary flow of current to the nerve endings. There are two kinds of electroreceptor that can be easily recognized in low-power micrographs and SEM views of the bill skin because of differences in the size and shape of the flower-petal-like arrangement of keratin that surrounds the pore and that opens when the bill is immersed (Manger et al., 1996). These two kinds of electroreceptors are associated separately with serous and mucous glands. The role of the serous gland electroreceptors is still obscure and they will not be considered further here, except to note that they have a lower density and completely different distribution on the bill from the mucous gland electroreceptors and have been speculated to be involved in near-field or DC detection (Manger and Pettigrew, 1997). Mucous gland electroreceptors are much more common, with a total of 40,000 distributed over all the epidermal surfaces of the bill, with a marked concentration at the edges and a striking parasagittal stripe arrangement on the dorsum of the bill (Fig. 22.1).
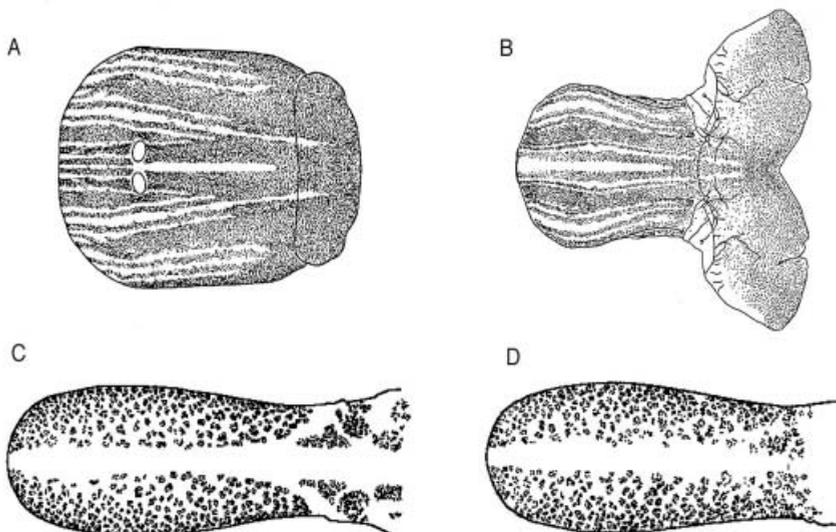

FIGURE 22.1. Electroreceptor arrays in platypus and paddlefishes. Views of upper and lower surfaces of the rostral bill organ of each species (there are also many electroreceptors on the inner surfaces of the upper and lower mandibles, not shown). Approximately 40,000 electroreceptors in platypus (mucous gland type) are arrayed in parasagittal rows, with a prominent raphe lacking in receptors along the midline. About 50,000–60,000 electroreceptors in paddlefishes (ampullae of Lorenzini type) are arranged in clusters with a prominent midline raphe where afferent nerve fibers travel.

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As their name suggests, mucous gland elec-
troreceptors are modified mucous glands. The
base of the gland duct is penetrated radially by
about one dozen free nerve endings, originating
from a daisy-chain-like arrangement of lateral
connections between nerve terminals where
it is suspected that there are gap junctions
that would act to reduce noise (Manger and
Pettigrew, 1998; Pettigrew et al., 1999). The free
nerve endings pass through a barrier that is
inferred to have very high impedance to lie in
electrical contact with the medium at the center
of the gland duct without any associated epithe-
lial cell specialization (Fig. 22.2). This arrange-
ment contrasts strongly with electroreceptors
in the paddlefish where epithelial receptor cells
provide the transducing interface between
the nerve ending and electric current in the
aqueous environment.

The parasagittal stripe arrangement sug-
gested to investigators that there might be
integration between the output of different
electroreceptors that lay with a parasagittal
arrangement to each other. This was tested
electrophysiologically and behaviorally. Recep-
tive fields of electroreceptors recorded at the
level of the neocortex show elongations that
are roughly parallel to the sagittal axis, in
accord with this suggestion (Krubitzer et al.,
1991). Moreover, when the sensitivity of the
whole bill is measured using the head saccade
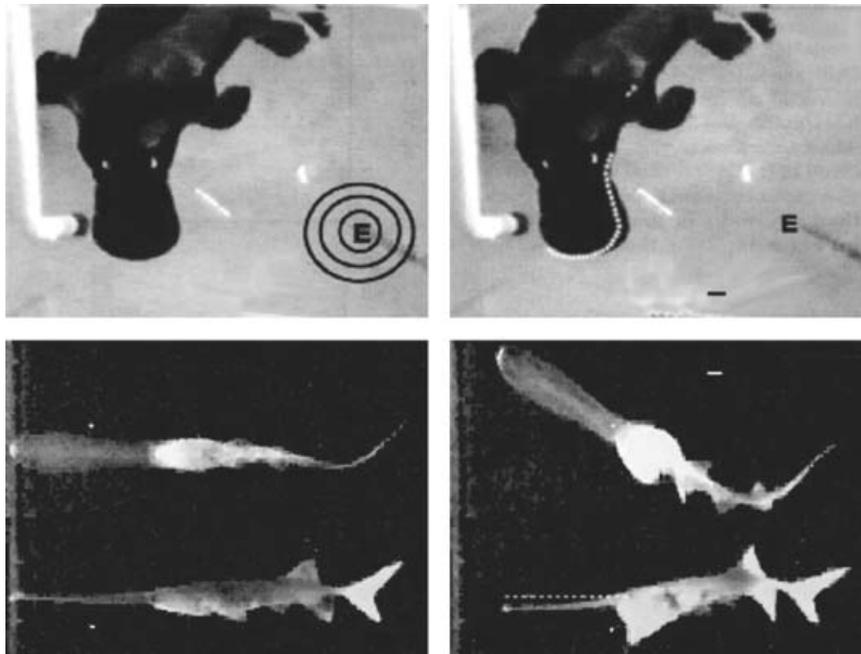paradigm, the axis of maximal sensitivity is

FIGURE 22.2. (A) Arrangement of free nerve endings
in platypus mucous gland electroreceptor. Up to 12
myelinated fibers lose their myelin sheaths on enter-
ing the base of the gland duct. Lateral extensions of
the free nerve endings originate from bulb-shaped
expansions filled with mitochondria. The lateral
extension joins all participating fibers in a daisy chain
around the base of the duct, presumably to facilitate
some form of common-mode rejection of electrical
signals that are not shared in all terminals. A termi-
nal filament pierces the electron-dense zone around
the duct to lie free in the mucous-filled ambient.
Note there there is no associated epithelial cell
involved in electrical transduction at the terminal
in the platypus, as there is in the paddlefish. (B)
Generalized ampullary electroreceptors, as found in
the paddlefish rostrum. Note that the afferent nerve
endings terminate on ciliated sensory epithelial cells
that are responsible for transduction, in contrast to
the free nerve endings seen in the mammalian
electroreceptor.

found lateral, slightly forward and down from an axis at right angle to the lateral edge of the bill (Manger and Pettigrew, 1997). Given the complex, slightly curved shape of the bill, this is what would be expected if there were a general principle of integration that favored electroreceptors along the sagittal axis.

3.3. Comparison

The paddlefish lacks the tell-tale parasagittal stripe arrangement of electroreceptors that may reveal the underlying strategy by which the platypus integrates information from such a large number of receptors in its central nervous system. Yet, a parasagittal axis of integration is suggested in the paddlefish too, by the fact that paddlefish electroreceptors are distributed preferentially along the rostrum edges. A parasagittal organization is also suggested by the preference for lateral strikes that indicates that the paddlefish, like the platypus, is most sensitive to signals that emanate laterally, rather than frontally or from any other direction.

The fine structure of the electroreceptors in the two taxa, as might be expected from their separate phylogenetic derivations, is completely different. The trigeminal nerve endings of the platypus lack any associated epithelial cell specializations, instead showing an elaborate structure where a dozen or more nerve terminals are linked circumferentially around the pore, into which penetrate a dozen or more free nerve endings. This structure is unstudied physiologically and even microscopical information is scanty, but it seems very likely that the terminals are all linked by gap junctions that would form a pool of receptors that could act to reduce electrical noise from one pore, just as coupled pools of photoreceptors use simultaneity to reduce noise in low light levels where the signal-to-noise ratio is low. Under normal circumstances for the electroreceptive systems there is a high noise level, so it is easy to imagine a useful role played by a coupled pool of detectors that were all signaling the field strength in the same pore and performing some kind of common mode rejection operation. The absence of an epithelial cell to provide a recep-

tor potential and to transduce the electrical signal could explain why platypus electrosensitivity is relatively low compared with the paddlefish, whose electroreceptors involve an epithelial receptor cell whose physiology is well-known from extensive studies of other passive electric fishes and which have lower thresholds than the platypus (Wilkens et al., 1997).

4. Lateral Head Saccade

4.1. Paddlefishes

The swimming undulations of the paddlefish trunk impart a lateral oscillating motion to the rostrum, with the cranium acting as the fulcrum. Paddlefishes are ram ventilators (Burggren and Bemis, 1992), so swimming is continuous. This saccade-like motion may serve to enhance prey detection by increasing the width of the electrical scan field. Rapid lateral saccades, a yaw-like motion, also characterize the motion sequences involved in prey capture, as dictated by the broad, flat shape of the rostrum. For example, as plankton drift by lateral to the rostrum the paddlefish makes sudden flexions that jerk the head and rostrum toward the prey as the mouth begins to open (Fig. 22.3). From the moment of detection the strike and gulp sequence takes 150–200 ms. For plankton encountered above or below the rostrum, a more complex motion sequence ensues. The fish initially rolls about its long axis, up to 90° or more, followed by the same lateral saccade, now directed in a vertical or oblique plane. Thus, each rapid strike, regardless of prey location, results in a slicing motion of the rostrum through the water that affords the least resistance. Plankton are captured by these accurate feeding strikes, up to 8–9 cm from the rostrum, some of which involve acrobatic combinations of rolls, lateral saccades, and complete turns if the plankton drifts past the mouth.

4.2 Platypus

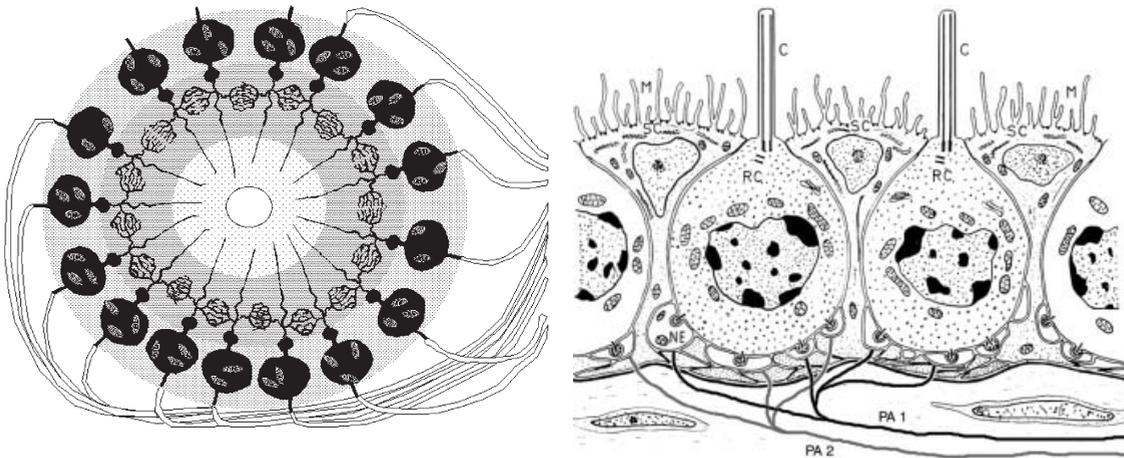The platypus lateral head saccade is elicited reflexly by a brief electrical stimulus. If the

FIGURE 22.3. Head saccades to electrical stimuli by platypus and paddlefishes. *Stationary platypus*: The two video frames are taken 60 msec apart, with the platypus at rest in a tank (see Manger and Pettigrew, 1995 for more details). The electrical stimulus was a square-wave pulse from a unipolar electrode (E) that produced a field at the near side of the bill of around 200 mV/cm. The resulting saccade toward the stimulus had a small amplitude in this habitu-ated platypus (saccades during patrolling and prey capture are larger), but can readily be seen by referring the right bill edge to the angled exhaust pipe on the left side of the figure and by reference to the dotted outline, which shows the position of the bill's left edge at 0 msec. In a swimming platypus, a saccade like this will act to reset the swimming direction behind the head so that the platypus changes direction and swims toward the prey. Saccades to electrical stimuli can follow to 15 Hz.

(A fast sequence of saccades can be viewed at www.uq.eud.au/nuq/jack/platypus.html.) *Swimming paddlefish*: The prey item, *Daphnia*, is shown as a white highlight. The electrical discharge (no other sensory cues are available to the fish in this darkened tank illuminated with infrared) triggers a lateral and slightly downward-directed saccade, along with jaw opening, that will permit the paddlefish to swallow the prey. In both species, the spatial information that guides the accurate directionality of the saccade has been gathered almost instantaneously from the elec-trical field generated by the stimulus, rather than being the result of an algorithm to track the field strength as the animal moves through it (e.g., the Kalmijn algorithm). Instantaneous determination thereby implies sophisticated signal processing by the spatial array of electroreceptors on the bill. Scale = 1 cm in both cases.

platypus is swimming, the head saccade causes resetting of the swimming rhythm of the body behind the head. In this way, the head saccade causes the platypus to swim toward the source of the stimulus (videotape in Manger, 1998). The head saccade is directed accurately toward the direction of the electrical source, whether this is above, below, or lateral to the bill, although it is much more sensitive to sources that emanate laterally, forward, and down, along the axis of the electroreceptive system. In captivity, platypus are intensely curious about gentle electrical stimuli, which are explored and mouthed. This exploratory behavior soon habit-uates, but the head saccade remains, with the

platypus unable to suppress it after thousands of trials. The head saccade behavior can then form a useful basis for the exploration of the parameters of electroreception, such as thresh-old and directionality.

4.3 Comparison

Given the similar orientation of the rostrum and bill, it is perhaps not surprising that both paddlefish and platypus have evolved a short-latency head saccade with the same lateral direction to move through the water toward prey with least resistance (Fig. 22.4). Since both rostrum and bill have similar shapes and have

the greatest concentration of electroreceptors along the edges, both would be expected to have axes of greatest sensitivity to electrical stimuli that originate laterally, rather than frontally or along some other axis, as has been shown for the platypus and as seems very likely for the paddlefish, too. The similarities in prey capture style can thus be attributed to several factors that have combined to ensure that an explosive strike by the bill has shortest latency when the bill orientation, neck muscle arrangement, and greatest sensitivity of the electroreceptor system are all optimal for a laterally directed saccade.

It is worth considering the underlying neural basis for a well-localized strike of this kind.
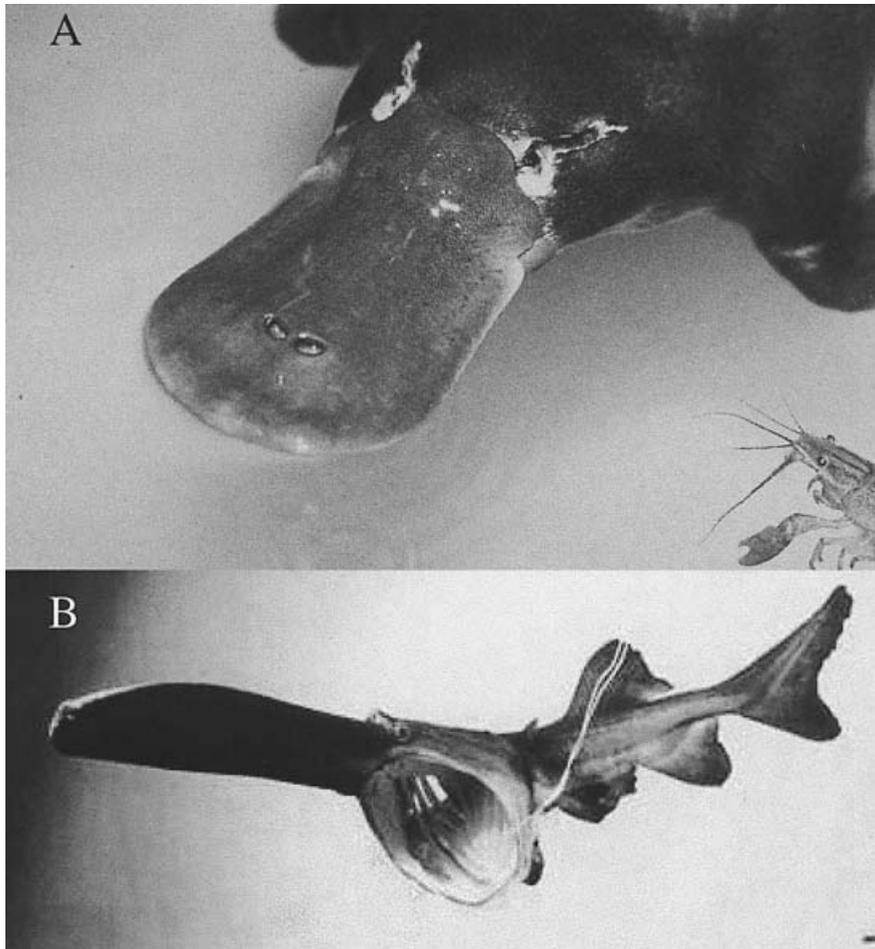

FIGURE 22.4. Comparison of platypus with paddlefish to show the similarity of the paddle-shaped bill organ and rostrum respectively. (A) The bill organ of the platypus (and one of its prey, the yabbie, *Cherax spp.*). About 40,000 electroreceptors and 60,000 mechanoreceptors form a sensory array that enables the capture of small benthic invertebrates, as well as some vertebrates such as fishes, without any assistance from vision, hearing, or olfaction. Note the numerous pits formed by the opening of the mucous gland electroreceptors on the bill; these pits are barely visible where they are in sharper focus on the more proximal region of the bill, near the eye. (B) Young paddlefish attacking the dipole wires as if trying to capture plankton: Its rostrum is innervated by about 60,000 ampullary electroreceptors that enable the capture, using the prey's electrical discharge, of free-swimming invertebrates such as *Daphnia*.

Many passive electric fishes appear to use Kalmijn's "approach algorithm" to localize a dipole, but note that this cannot be true for the lateral head saccades of platypus and paddlefish, which are instantaneously directional and do not require successive approximation toward the target. Both platypus and paddlefish must "know" at very short latency, the shape of the electric field generated by the prey in order to localize it so accurately and quickly. Such a calculation would involve the simultaneous reporting of field strength from a large number of the electroreceptors distributed over the rostrum or bill. This calculation would be aided by the bill shape, whose flattened lateral dimension and high density of electroreceptors would help ensure that changes in field strength would be most detectable along just the axis most relevant to localizing the prey for a strike. The elaborate neural mechanisms that would provide a platypus with a "map" of field strength over the surface of the bill have been well-described (Krubitzer et al., 1996; Calford et al., 1998). We can only assume that there are similar mechanisms that subserve the high density of electroreceptors on the similarly shaped rostrum of the paddlefish.

5. Sensitivity

5.1. Paddlefishes

A lateral head strike, like the platypus's head saccade, can be elicited from a paddlefish by a *Daphnia* at 10 cm. Since *Daphnia* produce field strengths of around 1 mV/cm, the paddlefish's sensitivity is around 10 mV/cm, assuming a cubic fall-off in field strength from this circumscribed, tiny prey. Since a directed response would require the coordinated activity of many electroreceptors, we can assume that not all receptors will be stimulated with strengths as great as 10 mV/cm and that signal detection algorithms will be applied by the paddlefish nervous system to look at activation across the array. Little is known about the details of this process, which is responsible for the much greater sensitivity of the whole animal when compared with sensitivity of individual electroreceptors. The electrical threshold for detecting and avoiding a DC field, such as created by a metallic object underwater, is much smaller, around 0.5 nV/cm in the paddlefish. The difference between these two thresholds is not explained, but could derive from the punctate nature of stimulation with *Daphnia*, where one would expect different receptors in the array to be subject to markedly different stimulus strength according to their position in relation to the *Daphnia*, compared with the more uniform pattern of stimulation that one would expect from a large, submerged metal object.

5.2. Platypus

The most extensive studies of the electrosensory threshold of platypus were conducted using the lateral head saccade to a brief electrical stimulus (Manger and Pettigrew, 1998). If one adopts a one-to-one criterion for a head saccade following an electrical pulse, the threshold field strength is 50 mV/cm. This is 20–50× less than the 1–2-mV/cm threshold established for single nerve fibers emanating from the electroreceptors themselves (Gregory et al., 1987a,b; 1988), the difference being accountable in terms of signal detection in the massively enlarged bill-representation of the platypus brain. Little is known about the signal detection algorithms that are used by the platypus brain, but some idea of their sophistication can be gained by a study of time averaging that showed that a platypus can act as a computer of average transients and lower its threshold if the same electrical stimulus is presented repeatedly! (Farrebrandt et al., 1999). This phenomenon will be familiar to readers who have wondered whether their name may have been called in a noisy environment, only to have their suspicion confirmed when the call is repeated. If the same electrical stimulus is repeated many times, the platypus threshold falls to a low of 10 mV/cm.

The electrical threshold for detecting a DC source in platypus is not known, but from experiments with avoidance of metal objects we can assume that it is equal to, or less than, the threshold for a lateral head saccade.

5.3. Comparison

Both taxa have remarkable similarity in the sensitivity of the strike to electrical stimuli generated by prey, with the paddlefish system having an order of magnitude greater sensitivity than the platypus, at 10 mV/cm. To strike at a *Daphnia*, the platypus would have to be 3 cm away, rather than the 10 cm at which a paddlefish can successfully strike its favorite prey. One would imagine that caddis-fly larvae, a favored platypus prey item with size and field strength in the range of *Daphnia*, would permit the closer approach needed by the platypus to elicit a strike. On the other hand, more mobile platypus prey that would require active pursuit and more distant detection, such as *Macrobrachium* and *Ateya*, have long bodies and strong fields compared with *Daphnia* and would be detectable by the platypus at 10 cm (Pettigrew et al., 1999). Whether these larger crustaceans would also be attractive to the paddlefish, as this comparison suggests, is an unanswered question.

In contrast to the systematic study of paddlefish avoidance of DC fields (Wilkens et al., 2000), there is no detailed study of the threshold for avoidance of DC fields by platypus. The greatly enhanced sensitivity of the paddlefish to DC fields raises the possibility that platypus may also be more sensitive to such fields than they are to AC fields such as those generated by prey, but the available data are agnostic on this point. It has been suggested that the less common serous gland electroreceptors mediate DC detection in platypus. This separation of function certainly echoes the dramatic difference in threshold between the detection of AC and DC in paddlefishes. For these reasons it might be profitable to look for a segregation of both structure and function in paddlefishes and to undertake a more extensive study of DC thresholds in platypus.

6. Role of Mechanoreception

6.1. Paddlefishes

Any mechanical disturbance created by a *Daphnia* at the rostrum of the paddlefish when it is located 10 cm away is presumably very small and unlikely to be detectable compared with the threshold electrical stimulus of 10 mV/cm at this distance. For this reason, the mechanosensory properties of the ampullary receptors are not likely to play as important a role in detection of *Daphnia* as their electrosensory properties. Nevertheless, this aspect may be worthy of further investigation, both because the ampullary receptors do have acute mechanical sensitivity and because the near-field mechanical stimulation produced by *Daphnia* may cause surprises in the same way that the mechanical stimulation provided by platypus prey had unexpected effects on the sensory system for prey detection in the bill.

6.2. Platypus

There are 60,000 mechanoreceptors in the platypus bill, interspersed with the 40,000 electroreceptors. It was generally assumed that these mechanoreceptors were not involved in the electroreceptive detection of aquatic prey, but rather in processing the direct contact with prey that had been captured. That view has been overturned by a number of new observations: (1) When the bill is out of the water, the mechanoreceptors, "pushrods," are tightly enclosed within a pore that opens upon immersion of the bill to free the rod and thereby enable it to respond to small movements in the water. (2) At the neocortical level, there is an elaborate anatomical interdigitation of the mechanoreceptive and electroreceptive representations that enables them to cooperate in a sophisticated way so that individual neurons can signal the time of arrival difference between electrical and mechanical stimuli. (3) Finally, larger prey items, such as shrimp, generate substantial mechanical disturbance at the platypus bill, well above thresholds for the pushrods, when they escape with tail flicks at distances comparable to the threshold distance for electroreception (Pettigrew et al., 1999).

Taking these new observations all together, it seems that electroreception and mechanoreception cooperate intimately in the platypus. A huge cortical area is devoted specifically to this cooperation in the brain (Calford et al., 1998).

Just as the shape of the electrical field produced by a prey item could be deciphered by the bill's electroreceptors, so the distribution of mechanical disturbance over the bill that is produced by prey movements could be deciphered by the distributed array of abundant pushrods and thereby provide information about the location of the prey. Since the arrival of the mechanical information will be delayed in relation to the distance of the prey, in contrast to the electrical information, which travels too close to the speed of light to provide any practical latency information, close coordination between the two sensory systems could lead to precise information about the distance of the prey (Pettigrew et al., 1999).

6.3. Comparison

Since the paddlefish also judges the distance of the prey quite accurately for a strike, one wonders if mechanoreception might play a role in paddlefish prey detection, as it does in platypus. The much greater electrosensitivity of the paddlefish system makes this unlikely. The much closer distances that a platypus must approach in order to detect the electrical activity of prey also mean that there is a greater likelihood that the mechanical stimuli from the same prey will be capable of exceeding the threshold of the pushrods. The fact that the platypus also has two completely separate sets of receptors, each one of which seems to be highly specialized for underwater mechanoreception and electroreception, respectively, argues that both may be significant in a way that is not true for the paddlefish, where any role of mechanoreception would have to be carried out by the same set of receptors that is also involved in electroreception.

7. Conservation Issues and Electroreception

Electrofishing may be having a deleterious impact on platypus in Australia. Forty thousand electroreceptive pores in the platypus bill lower its electrical impedance and make it vulnerable to the intense current generated by the electrofishing devices used to sample fish stocks in the waterways. Direct observations on rescued platypus indicate that they are immobilized in the vicinity of the probe for a number of minutes. Stress, to which platypus are particularly vulnerable, often causing death within a few hours of capture, and drowning would be possible consequences if the affected platypus were not rescued from the water.

There is no information about the impact of electrofishing on paddlefishes, but we predict that this will not be inconsequential because the ampullary electroreceptors provide a large number of parallel paths for the high-intensity current from the high-voltage probe, just as the pores in the platypus bill lower its impedance and increase its vulnerability. Because the ethical concerns over a larval fish are likely to be less constraining than over a mammal, it is possible that the paddlefishes might be able to provide some baseline information about the effects of high voltages on bill electroreceptors.

Paddlefishes have also been impacted by electrofishing. No systematic study has been made to determine whether paddlefishe are more or less susceptible than other fishes to high-voltage electrofishing, or to determine rates of recovery and/or mortality, although fishes have been observed to leap out of the water and break their rostrum in violent swimming collisions in response to current pulses. Other signs of stress, with limited recovery of normal swimming and latent mortality, have been reported (Scarnecchia et al., 1999), with physical damage including ruptured blood vessels and notochord. However, electrofishing has been touted recently as a successful sampling technique for paddlefishes, but with immediate mortality rates of 10% (Lein et al., 1997).

Paddlefish electrosensitivity presents an additional conservation issue with respect to migratory behavior. Fishes migrate upstream to spawn in smaller streams and tributaries (Purkett, 1961), and from river channels to flooded backwaters that provide seasonal planktonic food (Stockard 1907). Tracking studies document that fish migrations of several hundred kilometers are common (Russell,

1986; Pitman and Parks, 1994), in one case with recapture 2,000 km downstream (Rosen et al., 1982). During migration, paddlefishes face unnatural electrical fields produced by metal gates in locks and dams, and are reluctant to pass through partially open gates (Southall and Hubert, 1984). Sensitivity to metallic sources, first noted by Jørgensen et al. (1972), was recently quantified in an avoidance study by Gurgens et al. (2000). Fishes detected a 2.5-cm diameter bar at distances up to 38 cm, swimming away in an excited avoidance response. Field studies may eventually demonstrate the need to insulate these barriers in sensitive habitat areas.

8. Conclusion

Fundamental research on the platypus is strictly limited at present because of its status as a national icon. There are some ironies in this, since it was the neuroethological approach, using a combination of electrophysiological and behavioral investigations, that was responsible for the present knowledge of platypus electroreception and its beneficial application to both display and field contexts.

Display arenas for captive platypus are extremely popular because viewing this extraordinary mammal in the wild is made difficult by its nocturnal, secretive underwater habits. Captive displays had been associated in the past with high mortality from stress. These arenas now incorporate the new information about thresholds for electroreception into their design, with marked improvement of the welfare and longevity of the platypus. Design of screening and grounding for the aquarium to protect it from stray electrical fields caused by switches, SCRs, and electrical pumps, for example, can now be guided by the quantitative information about threshold sensitivity of the electrosensitive system. Such information became available only because of the carefully controlled neuroethological approach in the laboratory that involved capture and investigation of a small number of healthy animals. While purely behavioral observations in the field might now in hindsight be able to provide

some observations on electroreceptive thresholds, the historical facts show that the key elements in these advances were laboratory-based and multidisciplinary, including electron microscopy of bill receptors and electrophysiology from individual nerve fibers and nerve cells. In other words, the very small numbers of platypus taken for these investigations is more than counterbalanced by the beneficial information about this species that was gained. This conclusion is supported also by a consideration of field conditions such as impact of water impedance on electroreception. Another potential area where precise information about platypus electroreception will be vital is the problem of the impact of electrofishing, which raises questions about platypus welfare that are potentially much more serious than the laboratory investigations that gave rise to the only relevant current source of information on the problem.

The quantitative laboratory-based information about electroreception is also relevant to field studies, in relation to the wide variation of salinity and water impedance in eastern Australian waterways. While it is clear that platypus can tolerate very low impedance conditions, such as in small waterways loaded with electrolytes that run off from cow pasture, it is unlikely that they could catch highly mobile prey, such as shrimp, under these conditions. This is because relatively pure, high-impedance water is necessary if the field generated by a mobile prey is sufficiently large to be detected by the platypus at a distance that would permit successful pursuit. In a small polluted stream, low water impedance may still be compatible with capture of prey if they are relatively immobile, like the caddis-fly larvae that are common in such situations. The platypus can then approach closely, inside the very small threshold radius that will obtain in such low-impedance situations. In contrast, rapidly moving prey, or rapidly moving water, or both, will severely impact on the platypus's ability to track prey in conditions of low water impedance. This may explain how platypus are so successful at catching fast-moving shrimp in pure streams, and perhaps illuminate the presently unexplained absence of platypus from increas-

ingly saline streams on the western drainage of the Great Dividing Range.

One of the most extraordinary findings in these studies, the close coordination of electroreception and mechanoreception in a complex central array that is reminiscent of primate ocular dominance columns, was made just as laboratory-based platypus studies were being phased out. In the future, fruitful investigations would involve study of the combined action of mechanoreceptive and electroreceptive waterborne stimuli that originate from the same target. We predict that combined stimuli of this kind will be much more effective in eliciting platypus behavior than electrical or mechanical stimuli alone.

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