ELECTRORECEPTION IN MONOTREMES

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Summary

I will briefly review the history of the bill sense of the platypus, a sophisticated combination of electroreception and mechanoreception that coordinates information about aquatic prey provided from the bill skin mechanoreceptors and electroreceptors, and provide an evolutionary account of electroreception in the three extant species of monotreme (and what can be inferred of their ancestors). Electroreception in monotremes is compared and contrasted with the extensive body of work on electric fish, and an account of the central processing of mechanoreceptive and electroreceptive input in the somatosensory neocortex of the platypus, where sophisticated calculations seem to enable a complete three-dimensional fix on prey, is given.

Key words: electroreception, monotreme, platypus, mechanoreception, evolution.

Introduction

The monotremes, or egg-laying mammals, have been a subject of special fascination ever since their first description was greeted by Western scientists with great scepticism (Home, 1802). Many thought that the platypus was a clever hoax perpetrated by careful attachment of a duck-bill and webbed feet to the skin of a mammal (Griffiths, 1998). Perhaps a greater mystery concerned the ability of a platypus to catch half its body mass of benthic invertebrates under water on the darkest night with all of its obvious sensory channels (eyes, ears and nostrils) tightly closed. The 'sixth sense' suggested to explain this puzzling ability (Burrell, 1927) has finally proved to be the bill sense, a sophisticated combination of electroreception and mechanoreception that coordinates the information about aquatic prey provided from the bill skin by 100 000 separately innervated mechanoreceptors and electroreceptors.

A brief history of monotreme electroreception

Rumours about the possibility of electroreception in monotremes circulated around the International Physiological Congress in Sydney in 1983. The source of these rumours may have been the morphological observations of platypus bill skin showing innervated pores that were reminiscent of ampullary electroreceptors in fish (Andres and von During, 1984). The first clear demonstration of electroreception in the platypus was carried out in Canberra by a joint German–Australian team, who showed that platypus would seek out and attack batteries that were immersed and otherwise invisible (Scheich et al., 1986). This team

established threshold field strengths for detection of approximately $300 \, \mu V \, cm^{-1}$, by using both behaviour and field potential recordings from the somatosensory cortex. Platypus brains from the same study labelled with 2-deoxyglucose showed a specific, stripe-like pattern of activation of the somatosensory cortex in response to electrical stimulation (Langner and Scheich, 1986). Ainslie Iggo, Archie McIntyre, Uwe Proske and John Gregory (Edinburgh and Monash Universities) first accomplished direct recording of electroreceptive afferents of the trigeminal nerve (cranial nerve V) from the bill skin of the platypus (note the contrast with electric fish, where the relevant cranial nerve is the octavo-lateralis; cranial nerve VIII) (Gregory et al., 1988). The afferents showed high spontaneous activity and were activated by cathodal current (Fig. 1), like those in electric fish. The threshold field strengths were, however, surprisingly high, at approximately $2 \, mV \, cm^{-1}$ compared with microvolt sensitivity in freshwater electric teleosts and nanovolt sensitivity in elasmobranchs. Such high electrical thresholds in monotremes were perhaps attributable to the fact that there is no sensory epithelial cell interposed between the electroreceptive nerve terminal and the aqueous environment, as there is in electric fish. In later experiments, the same team showed that electroreceptive afferents were present in the bill/beak of echidnas, and that echidnas could be trained to detect small direct current electrical fields in water (Gregory et al., 1989).

Morphology of electroreceptors

Detailed anatomical studies have established the number and
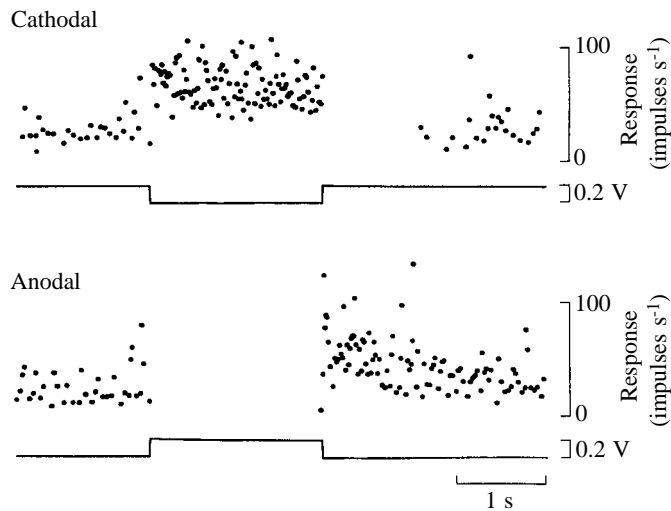
Cathodal

Anodal

Fig. 1. Response of a platypus electroreceptor (bill skin) to bipolar stimulation of the moist skin surface (taken from Proske et al., 1998, with permission).

distribution of electroreceptors and mechanoreceptors in the bill of both the platypus and the short-billed echidna. The platypus is known better from such morphological studies than from physiology, both because of its small size and fragility in

physiological recording experiments, and because its status as a national icon has restricted access to it.

Three different kinds of receptor have been identified in the bill skin of monotremes, all of which have an easily distinguishable surface morphology that makes it possible to determine their density distribution using only a dissecting microscope (Fig. 2A,B). One type is a mechanoreceptor called a push-rod because it is composed of a rod-like pillar of epithelium that crosses the whole epithelial thickness (see Fig. 7). It has an array of sensory neurons at its base that would function to signal displacements of the rod produced by impulses delivered to the free end. Two types of electroreceptor appear as pits formed from secretory ducts of serous and mucous glands, respectively, each surrounded by a petal-like arrangement of epithelium that opens when the bill is immersed in water (Manger et al., 1998). Serous electroreceptors have a smaller pit and are found more densely at the anterolateral edges of the bill; mucous electroreceptors, which are larger, are found in stripe-like parasagittal arrays over the bill surface (Manger and Pettigrew, 1996). The innervation of the electroreceptors is complex, with as many as 16 different afferent nerve fibres forming specialised endings. These are loaded with mitochondria and linked circumferentially by fine, branching processes into a ring or 'daisy-chain' around the pore (Fig. 3).
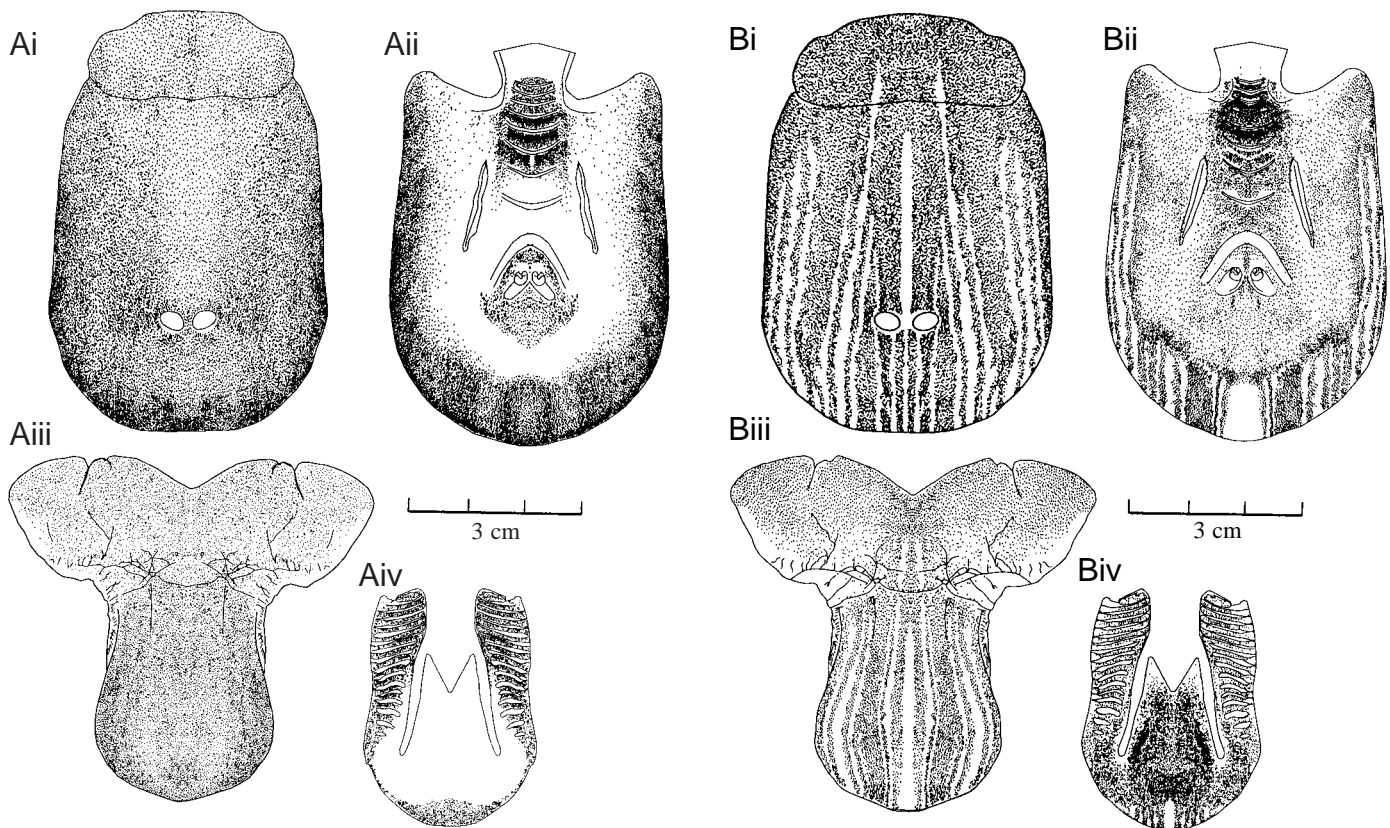

Fig. 2. Distribution of push-rod mechanoreceptors (A) (visible as a touch dome in the dissecting microscope) and (B) mucous electroreceptors (visible as a large pit) in platypus. Note the parasagittal arrays of electroreceptors. The total number of electroreceptors, counting both the outside (i,iii) and the inside (ii,iv) surfaces of both the upper (i,ii) and lower (iii,iv) bills, is approximately 40 000. There are approximately 60 000 mechanoreceptors. (Taken from Manger and Pettigrew, 1996, with permission.)
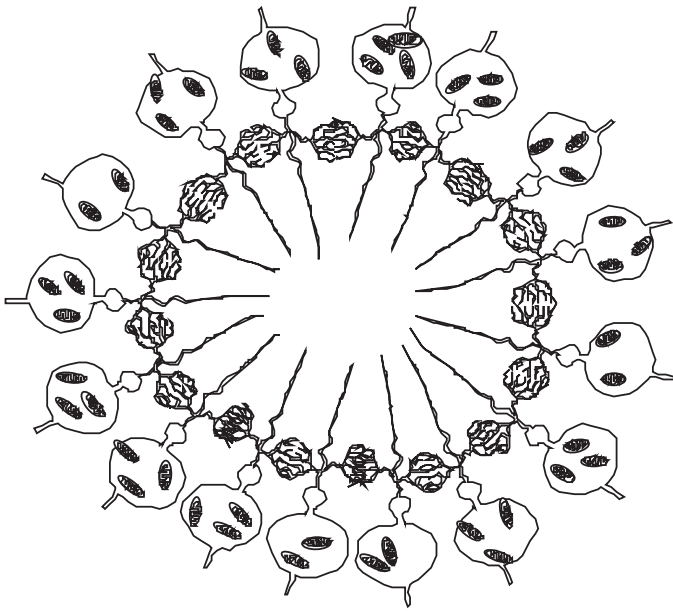
Fig. 3. Diagrammatic representation of a mucous gland electroreceptor showing the tangential arrangement of afferent nerve endings around the pore. The bulbous expansions of each nerve fibre are packed with mitochondria. The terminal naked filaments pierce a high-resistance layer in the epidermis and extend towards the mucous-filled duct. The lateral branches of each fibre extend towards each other. It is not known whether they are electrically coupled.
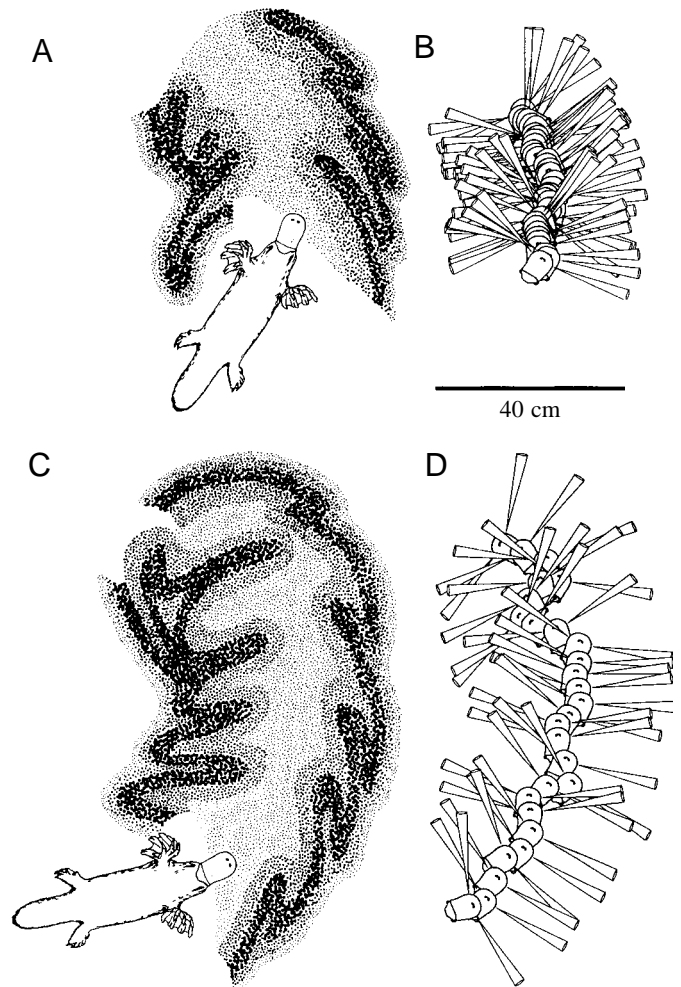

Fig. 4. Scanning head movements of a hunting platypus and the path taken by the axis of greatest sensitivity of the electrosensory system. The preferred axis was defined from thresholds for eliciting head saccades in response to a square-wave electrical stimulus. (A,B) Quiet swimming. (A) The area, extrapolated to benthos, that would be swept out by the axis of greatest sensitivity (light stipple, $10\,^\circ$; dark stipple, $20\,^\circ$). (B) The axis of each bill (narrow cone shape) at 100 ms intervals. (C,D) As in A,B, but after contact with the prey. Note the threefold increase in area covered in the same time in the active phase triggered by contact with the prey ($0.114\,m^2\,s^{-1}$ compared with $0.042\,m^2\,s^{-1}$). (Taken from Manger and Pettigrew, 1995, with permission.)

Behaviour

A striking reflex, in the form of a head saccade elicited by a square-wave electrical stimulus, can be used to investigate both directionality and threshold. Platypus can detect stimuli that generate field strengths as low as $20\,\mu V\,cm^{-1}$ (Manger and Pettigrew, 1996). These behavioural studies therefore demonstrated a much lower threshold for electroreception in the whole platypus than had been found in studies of afferents from the receptors themselves (Manger and Pettigrew, 1996). The signal-processing issues involved in this discrepancy between electroreceptor responses and whole-animal behaviour have been discussed elsewhere (Pettigrew et al., 1998). The same techniques revealed a pronounced directionality of the electroreceptive system of the platypus, with an axis of greatest sensitivity pointing outwards and downwards. This corresponds to a scan of the substratum as the platypus swings its head backwards and forwards in a roughly sinusoidal fashion while swimming (Fig. 4). The new values for platypus thresholds derived from these behavioural studies are now being used to guide the construction of electrical shielding and grounding in public displays of captive platypus, with increased well-being and longevity compared with the previous poor record (Whittington, 1991).

Neural pathways subserving electroreception

Perhaps the most surprising discovery about platypus electroreception was the elaborate neocortical structure involved. This had tangential stripes of mechanoreceptive neurons interdigitated with stripes of electroreceptive neurons (Manger et al., 1996; Elston et al., 1999). This complex arrangement is reminiscent, in both pattern and size of the repeating units, of the ocular dominance columns of primate striate cortex. Its complexity belies the common misconception that monotremes are in some way primitive. The close apposition of mechanoreception and electroreception systems in platypus cortex raises new questions about their relationship. This apposition appears to be a special feature of the platypus and forms another contrast with electroreceptive systems in fish (Table 1).

Table 1. *Comparison of electroreception in electric fish and in monotremes*

Similarities

1. Multiple evolution of similar strategies with different hardware. Monotreme electroreception clearly evolved independently of the same system in fish, just as mormyrids (in the Palaeotropics) have evolved electroreception independently of gymnotiforms (in the neotropics). This is apparent in the different sensory placodes involved, the different sensory transduction mechanisms and the different supporting roles played by mechanoreception (see below).

2. The threshold in the whole animal is much lower than in individual receptors as a result of signal processing of many electroreceptive afferents.

3. The electroreceptor is excited by cathodal current and responds to very low stimulus frequencies.

4. The receptor is protected at the base of the epithelial pore (gland duct in monotremes; ampulla in fish).

Differences

	Platypus	Electric fish
Neural placode	Trigeminal (cranial nerve V)	Octavo-lateralis (cranial nerve VIII)
Major processing site in neuraxis	Forebrain dominates	Hindbrain prominent in processing
Directionality	Dipole source direction is direct	Indirect inference about dipole source 'approach algorithm'
Primary nerve ending	Naked; no epithelial receptor cell; 'daisy chain' of 16 afferents	Epithelial cell transduction
Mechanoreception	Intimate association	Association not prominent
Common-mode rejection	Electroreceptors on bill; muscles disjunctional; high skin impedance	Electroreceptors disjunctional from electric organ; mirror-like plasticity (anti-Hebbian)

Phylogeny

Three living monotremes

All three extant monotreme species have electroreception, judged by the presence of mucous gland electroreceptors in the bill skin. The platypus *Ornithorhynchus anatinus*, from East Coast Australian waterways, has 40 000 electroreceptors; the long-billed echidna *Zaglossus bruijnii*, from wet tropical montane forest, has 2000, while the short-billed echidna *Tachyglossus aculeatus*, widely distributed from alpine areas to desert, has only 400 (Fig. 5). The evidence indicates that there has been a reduction in electroreceptive abilities in the echidnas, with the short-billed echidna having no more than a remnant of this sensory system. In the dry habitat of the short-billed echidna, opportunities for the use of electroreception in prey capture would be unusual (e.g. during rain). It had been shown behaviourally that echidnas can identify small electric fields (see Proske et al., 1998), but it seems reasonable to conclude that, phylogenetically speaking, this ability is 'on the way out' in the echidna.

A simplistic phylogenetic interpretation of these data might be that electroreception is primitively retained in all three taxa and that the echidna represents the plesiomorphic monotreme. Some support for this view could perhaps be
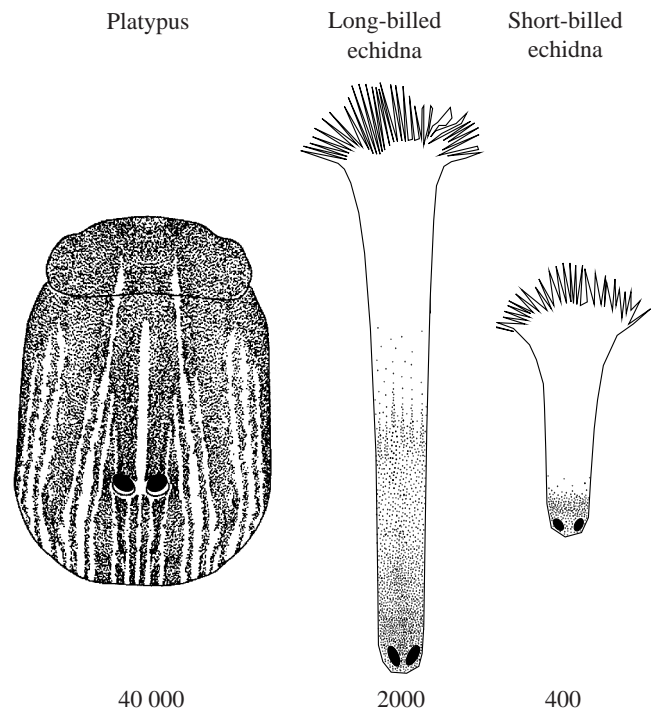
Fig. 5. Electroreception as revealed by bill sensory organs of the three extant monotremes: the platypus *Ornithorhyncus anatinus*, from East Coast Australian waterways, has 40 000 electroreceptors; the long-billed echidna *Zaglossus brujnii*, from wet tropical montane forest, has 2000; the short-billed echidna *Tachyglossus aculeatus*, widely distributed from alpine areas to desert, has only 400. Interpretation of this polarity is problematical from the living forms (which some have used to argue that the echidna is plesiomorphic and the platypus highly derived). Fossil and molecular data show that echidnas diverged only recently and that, therefore, they must have lost the high degree of electroreception found in platypus. (Platypus bill taken from Fig. 2, Manger and Pettigrew, 1996, with permission.)

Platypus — Long-billed echidna — Short-billed echidna
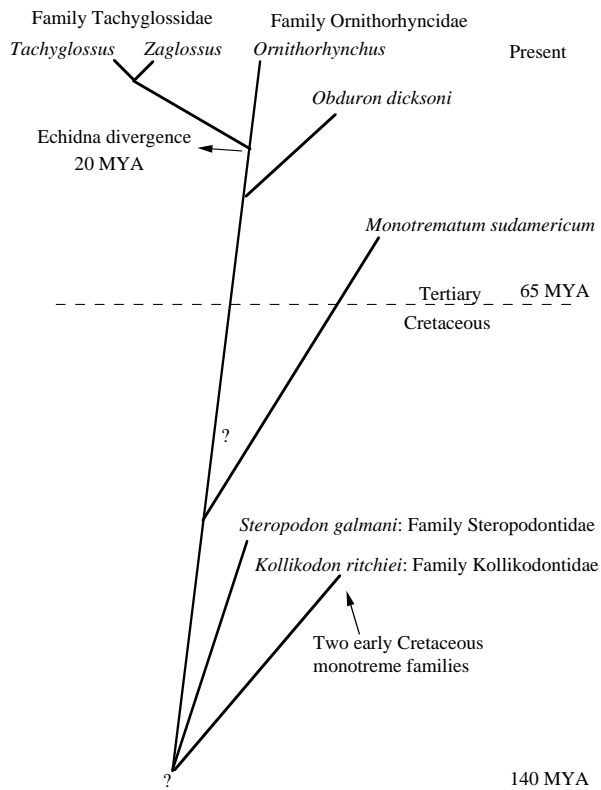
40 000 — 2000 — 400

Fig. 6. Phylogeny of monotremes. Echidna/platypus divergence was very recent (approximately 20 million years ago, MYA, according to DNA evidence). There are no echidna fossils that are older than the Pleistocene. In contrast, platypus fossils have been found all the way back to the Cretaceous. The platypus lineage was clearly diverse (three different families recognised) and successful as well as ancient.

obtained from the highly derived brain and behaviour of the platypus. Fossil and molecular evidence, however, suggests the opposite conclusion, indicating that echidnas are highly modifed, recent offshoots from the main monotreme line, which seems to have been a variant of the platypus plan (Fig. 6). A beautiful, linking series of fossils enables this inference to be drawn, even when the fossil evidence consists only of teeth, which are absent in living platypus. Perfect preservation of the toothed Miocene platypus *Obduron dicksoni,* for example, links Cretaceous platypus teeth unequivocally to the living platypus (Musser and Archer, 1998). Similarly, molecular phylogeny shows that echidnas branched off the monotreme line very recently, with estimates of the divergence varying from 20 to 30 million years ago (see Westerman and Edwards, 1992).

The view that echidnas are highly derived offshoots of the platypus line, rather than the other way around, is important for the interpretation of a number of neurological features, other than electroreception, in which these two monotremes differ. For example, it is now clear that rapid eye movement (REM) sleep is present in both platypus and echidna (Siegel et al., 1996) and that the initial reports of an absence of REM sleep in echidnas were misinterpretations of their highly derived form of REM sleep (Siegel et al., 1998).

Common-mode rejection

Platypus swim vigorously as they forage, swinging the head widely from side to side (see Fig. 4) (Manger and Pettigrew, 1995). We can therefore assume that the electroreceptive system will have interference problems stemming from the fluctuating fields generated by the platypus' own muscles and changes in its body orientation. It is worthwhile speculating how this might be compensated, particularly in comparison with the beautiful systems of reafference used by elasmobrachs (Montgomery and Bodznick, 1999) and the anti-Hebbian plasticity used by mormyrids (Bell et al., 1999). There are a number of factors that might be involved in such compensation.

First, the electroreceptive nerve endings are naked at their exposed tips where they project into the pore and are arranged in a 'daisy chain' that may couple the 16 afferents together (Fig. 3). This is in contrast to fish, where the nerve ending is capped by a sensory cell. This may not help specifically with the problem of self-generated noise, but it seems likely that it could be helpful in the general problem of achieving sensitivity while reducing noise.

Second, the body surface has a very high impedance, with platypus fur rivalling sea-otter fur for the density of hairs (Pettigrew et al., 1998), except on the bill, thereby reducing the contribution of the platypus' own activity to the ambient field in the electroreceptive region of its bill. In fish, by contrast, the electroreceptors are distributed over the body surface in a way that partially separates them from the electric organ, but would still make them susceptible to self-generated electrical noise from active muscles under the more conductive skin.

Third, coupling the mechanoreceptive and electroreceptive systems together should enable the brain to identify those patterns of electrical activity that are caused by mechanical disturbances produced by prey. The brain should also be able to separate those signals caused by electrical disturbances in the environment from electrical disturbances generated by the animal's own movements. It might therefore be appropriate to compare the stripe-like mechanoreceptive/electroreceptive array in platypus S1 cortex, where Hebbian plasticity is thought to be a characteristic feature, with the anti-Hebbian array in the electrosensory pathway of mormyrids. Both systems might then use neural plasticity to separate the prey signals from the background noise. Unfortunately, there is not much physiological evidence available on this point from platypus compared with the beautiful work available from electric fish (Bell et al., 1999).

Directionality of platypus electroreception

Platypus make short-latency head saccades that are highly directional to electrical sources (Manger and Pettigrew, 1995). This behaviour seems to contrast starkly with the best abilities of electric fish, whose passive electroreceptive directional

abilities involve moving along isopotential lines to find the dipole: the 'approach algorithm' (Kalmijn, 1997; Hopkins, 1999). The platypus seems to be able to detect the field non-uniformity directly. This difference may owe something to the complex curved shape of the platypus bill and the enormous representation in the neocortex of the 100 000 electroreceptors and mechanoreceptors distributed over the bill. Time-of-arrival differences in electroreception, from one side of the bill to the other, would be three orders of magnitude too small to be detectable, even if the platypus had the incredible 100 ns time resolution of *Gymnarchus* sp. (Kawasaki, 1997). As for passive electroreception in elasmobranchs (Kalmijn, 1997), the determination of directionality would, therefore, require a complete spatial reconstruction of the shape of the electric field at the array of electroreceptors, so that the system could 'place an arrow' orthogonal to the field lines, pointing to the source 'up' the field gradient.

Such a reconstruction could be achieved by the S1 cortical representation, where there is a detailed topographic representation of the bill surface combined with a representation of different field strengths at each location on the bill. This point-by-point map of the electroreceptors on the bill, combined with different neurons at each point with differing preferred field sensitivity, would enable a reconstruction of the shape of the field lines over the bill. This would provide an output that moved the head in a direction orthogonal to the field lines and, therefore, towards the electrical source. The parasagittal arrays of electroreceptors (Fig. 2B) might explain why the platypus is most sensitive to electrical fields that produce field lines parallel to the long axis of the bill and that decay across the bill. This pattern of sensitivity would also be less subject to the field induced by the platypus' own neuromuscular activity (Fjällbrant et al., 1998).

Hyperacuity

The whole platypus does much better at detecting small electrical signals than individual receptors. For a criterion of a one-to-one relationship between stimulus phase and a single spike discharge, platypus electroreceptors have thresholds of approximately $1–2\,mV\,cm^{-1}$ (Gregory et al., 1988). The whole platypus can, however, detect stimuli with fields as low as $20\,\mu V\,cm^{-1}$, given the appropriate conditions (Fjällbrant et al., 1998). The highly directional response of the platypus head saccades suggests that it must be performing very sophisticated signal processing of the electrical image over large numbers of electroreceptors, some of which must be responding to even lower fields than the $20\,\mu V\,cm^{-1}$ threshold (Pettigrew et al., 1998).

This large improvement by the whole animal over the performance of its individual electroreceptors is also seen in elasmobranchs (in which the whole-animal threshold reaches a record low of less than $5\,nV\,cm^{-1}$; Montgomery and Bodznick, 1999), in mormyrids, in gymnotids (in which the whole-animal threshold varies widely around the microvolt range) and in paddlefish (Wilkens et al., 1997).

Distance judgement

Electric fish can judge distance by comparing the amplitude and gradient of the voltage distribution (von der Emde, 1999). Platypus also appear to be able to judge prey distance, although no behavioural data are available, but only by comparing mechanoreception and electroreception.

The unique specialisation of the S1 cortical representation of the bill has focused attention on the role of mechanoreception. If the mechanoreceptors are used for the direct tactile encounter of the bill with prey, why is there such intimate cross-talk with the electrosensory system whose role might be expected to be over once contact had been made with the prey?

A clue was provided by recent observations of the active opening of receptor pores when the bill of the platypus is immersed. It is eminently reasonable that the pore of the
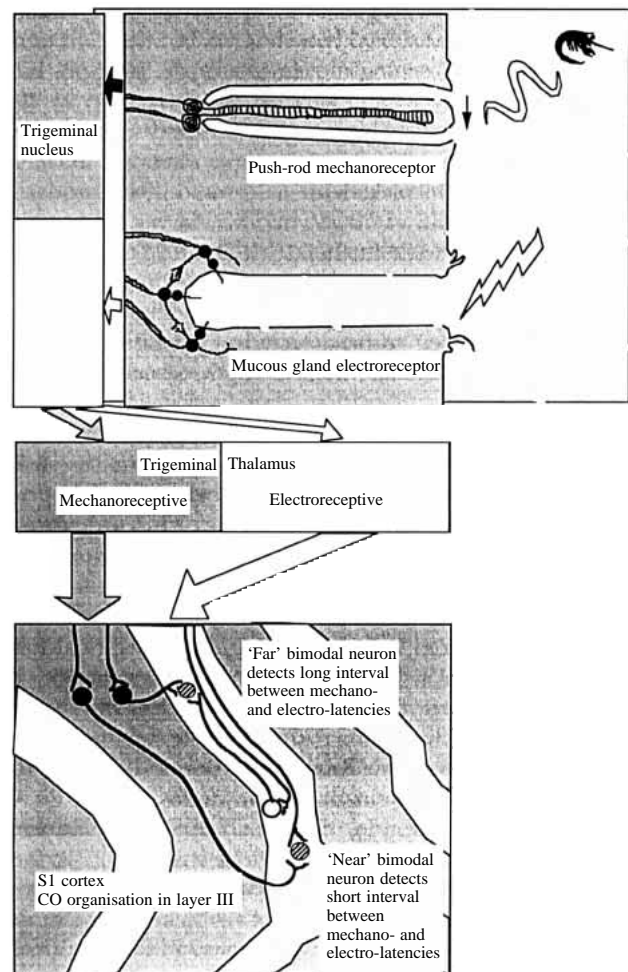
Fig. 7. Integrative processing of mechanoreceptive and electroreceptive information in the stripe-like array that represents the bill skin in platypus S1 neocortex. Bimodal neurons respond both to electrical stimuli and to mechanical stimuli in the water, with some tuning for the delay between inputs. Along with the directionality already demonstrated for platypus electroreception, this array could provide direct information about prey distance (taken from Pettigrew et al., 1998, with permission). CO, cytochrome oxidase.

mucous gland electroreceptors should close when the bill is out of water and open once again, to secrete mucous, when the bill is immersed (Manger et al., 1998). Such a mechanism would avoid deleterious drying and reduced sensitivity of the electroreceptors when the platypus leaves the water. But what can be made of the fact that the push-rod mechanoreceptors also open upon immersion (Manger et al., 1998)? This observation made us wonder whether the mechanoreceptors are primarily designed for the detection of water-borne disturbance rather than direct contact with prey. This idea is further supported by the fact that push-rods in platypus are free to rotate about their base, in contrast to the same structures in the terrestrial echidnas and star-nosed mole, where they are tethered distally to the walls of the pore in a way that would reduce their sensitivity and increase their impedance for lateral displacements. These hints that mechanoreceptors are specialised for the detection of water disturbances led us to test whether both mechanoreception and electroreception cooperate in the long-distance detection of prey (Pettigrew et al., 1998).

Although the final demonstration may not be forthcoming soon, the evidence collected so far supports an arrangement in the S1 cortex in which distant prey produce a mechanical disturbance that arrives some time after the electrical signal from the same prey's movement (Fig. 6) (Pettigrew et al., 1998). Bimodal neurons in the S1 cortex are sensitive to the time-of-arrival differences, so the stripe-like array would provide a direct read-out of prey distance. An alciopid polychaete worm has two retinas with different spectral sensitivities that it uses in a similar bimodal trick to judge depth below the surface (Wald and Rayport, 1977), and scorpions use the difference between near-field and far-field ground-borne vibration to judge distance (Babu and Jacobdoss, 1994). These examples from invertebrates illustrate the principle of using two sensory systems with different characteristics to obtain a 'fix' in depth. The unusual combined array of electroreceptive and mechanorecepive neurons in platypus S1 neocortex may provide the most direct read-out of distance using two different sensory inputs so far seen in a vertebrate.

References

Andres, K. H. and von During, M. (1984). The platypus bill. A structural and functional model of a pattern-like arrangement of cutaneous sensory receptors. In *Sensory Receptor Mechanisms* (ed. W. Hamann and A. Iggo), pp. 81–89. Singapore: World Scientific Publishing Company.

Babu, K. S. and Jacobdoss, P. (1994). Central afferent pathways of long hair sensilla in the ventral nerve cord of the Indian black scorpion, *Heterometrus fulvipes* Koch. *J. Comp. Physiol.* A **174**, 495–505.

Bell, C. C., Han, V. Z., Sugawara, Y. and Grant, K. (1999). Synaptic plasticity in the mormyrid electrosensory lobe. *J. Exp. Biol.* **202**, 1339–1347.

Burrell, H. (1927). *The Platypus*. Sydney: Angus & Robertson.

Elston, G. N., Manger, P. R. and Pettigrew, J. D. (1999). Morphology of pyramidal neurones in cytochrome oxidase modules of the S-1 bill representation of the platypus. *Brain Behav. Evol.* **53**, 87–101.

Fjällbrant, T. T., Manger, P. R. and Pettigrew, J. D. (1998). Some related aspects of platypus electroreception: temporal integration behaviour, electroreceptive thresholds and directionality of the bill acting as an antenna. *Phil. Trans. R. Soc. Lond. B* **353**, 1211–1219.

Gregory, J. E., Iggo, A., McIntyre, A. K. and Proske, U. (1988). Receptors in the bill of the platypus. *J. Physiol., Lond.* **400**, 349–366.

Gregory, J. E., Iggo, A., McIntyre, A. K. and Proske, U. (1989). Responses of electroreceptors in the snout of the echidna. *J. Physiol., Lond.* **414**, 521–538.

Griffiths, M. (1998). Platypus research 1798–1998. (Preface). *Phil. Trans. R. Soc. Lond. B* **353**, 1059–1061.

Home, E. (1802). A description of the anatomy of *Ornithorhynchus paradoxus*. *Phil. Trans. R. Soc. Lond.* **92**, 67–84.

Hopkins, C. D. (1999). Design features for electric communication. *J. Exp. Biol.* **202**, 1217–1228.

Kalmijn, A. J. (1997). Electric and near-field acoustic detection, a comparative study. *Acta Physiol. Scand.* **161** (Suppl. 638), 25–38.

Kawasaki, M. (1997). Sensory hyperacuity in the jamming avoidance response of weakly electric fish. *Curr. Opin. Neurobiol.* **7**, 473–479.

Langner, G. and Scheich, H. (1986). Electroreceptive cortex of platypus marked by 2-deoxyglucose. *First International Congress on Neuroethology.* p 63.

Manger, P. R., Calford, M. B. and Pettigrew, J. D. (1996). Properties of electrosensory neurons in the cortex of the platypus (*Ornithorhyncus anatinus*): implications for processing of electrosensory stimuli. *Proc. R. Soc. Lond. B* **263**, 611–617.

Manger, P. R., Keast, J. R., Pettigrew, J. D. and Troutt, L. (1998). Distribution and putative function of the autonomic nerve fibres in the bill skin of the platypus (*Ornithorhynchus anatinus*). *Phil. Trans. R. Soc. Lond. B* **353**, 1159–1170.

Manger, P. R. and Pettigrew, J. D. (1995). Electroreception and the feeding behaviour of the platypus (*Ornithorhyncus anatinus*: Monotremata: Mammalia). *Phil. Trans. R. Soc. Lond. B* **347**, 359–381.

Manger, P. R. and Pettigrew, J. D. (1996). Ultrastructure, number, distribution and innervation of electroreceptors and mechanoreceptor organs in the bill skin of the platypus, *Ornithorhynchus anatinus*. *Brain Behav. Evol.* **48**, 27–54.

Montgomery, J. C. and Bodznick, D. (1999). Signals and noise in the elasmobranch electrosensory system. *J. Exp. Biol.* **202**, 1349–1355.

Musser, A. M. and Archer, M. (1998). New information about the skull and dentary of the Miocene platypus *Obduron dicksoni* and a discusion of ornithorhynchid relationships. *Phil. Trans. R. Soc. Lond. B* **353**, 1063–1079.

Pettigrew, J. D., Manger, P. R. and Fine, S. L. B. (1998). The sensory world of the platypus. *Phil. Trans. R. Soc. Lond. B* **353**, 1199–1210.

Proske, U., Gregory, J. E. and Iggo, A. (1998). Sensory receptors in monotremes. *Phil. Trans. R. Soc. Lond. B* **353**, 1187–1198.

Scheich, H., Langner, G., Tidemann, C., Coles, R. B. and Guppy, A. (1986). Electroreception and electrolocation in platypus. *Nature* **319**, 401–402.

Siegel, J. M., Manger, P. R., Nienhuis, R., Fahringer, H. M. and Pettigrew, J. D. (1996). The echidna *Tachyglossus aculeatus*

combines REM and nonREM aspects in a single sleep state: implications for the evolution of sleep. *J. Neurosci.* **15**, 3500–3506.

Siegel, J. M., Manger, P. R., Nienhuis, R., Fahringer, H. M. and Pettigrew, J. D. (1998). Monotremes and the evolution of rapid eye movement sleep. *Phil. Trans. R. Soc. Lond. B* **353**, 1147–1157.

von der Emde, G. (1999). Active electrolocation of objects in weakly electric fish. *J. Exp. Biol.* **202**, 1205–1215.

Wald, G. and Rayport, S. (1977). Vision in annelid worms. *Science* **196**, 1434–1439.

Westerman, M. and Edwards, D. (1992). DNA hybridisation and the phylogeny of the monotremes. In *Platypus and Echidnas* (ed. M. L. Augee), pp. 28–34. Sydney: Royal Zoological Society of New South Wales.

Whittington, R. J. (1991). The survival of platypuses in captivity. *Aust. Vet. J.* **68**, 32–35.

Wilkens, L. A., Russell, D. F., Pei, X. and Gurgens, C. (1997). The paddlefish rostrum functions as an electrosensory antenna in plankton feeding. *Proc. R. Soc. Lond. B* **264**, 1724–1729.