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The sensory world of the platypus

J. D. Pettigrew[1]*, **P. R. Manger**[2] **and S. L. B. Fine**[1]

[1]*Vision, Touch and Hearing Research Centre, Department of Physiology and Pharmacology, University of Queensland, Brisbane, Queensland 4072, Australia*

[2]*Neurobiology Research 151A3, Sepulveda VAMC, 16111 Plummer St, North Hills, CA 91343, USA*

Vision, audition and somatic sensation in the platypus are reviewed. Recent work on the eye and retinal ganglion cell layer of the platypus is presented that provides an estimate of visual acuity and suggests that platypus ancestors may have used vision, as well as the bill organ, for underwater predation. The combined electroreceptor and mechanoreceptor array in the bill is considered in detail, with special reference to the elaborate cortical structure, where inputs from these two sensory arrays are integrated in a manner that is astonishingly similar to the stripe-like ocular dominance array in primate visual cortex, that integrates input from the two eyes. A new hypothesis, along with supporting data, is presented for this combined mechanoreceptive–electroreceptive complex in platypus cortex. Bill mechanoreceptors are shown to be capable of detecting mechanical waves travelling through the water from moving prey. These mechanical waves arrive after the electrical activity from the same prey, as a function of distance. Bimodal cortical neurones, sensitive to combined mechanical and electrical stimulation, with a delay, can thus signal directly the absolute distance of the prey. Combined with the directional information provided by signal processing of the thousands of receptors on the bill surface, the stripe-like cortical array enables the platypus to use two different sensory systems in its bill to achieve a complete, three-dimensional 'fix' on its underwater prey.

Keywords: platypus; depth perception; vision; mechanoreception; electroreception

1. INTRODUCTION: NEUROETHOLOGY AND MANAGEMENT

One key to the understanding and management of a wild animal species is its psyche. If one has a detailed understanding of the psychic makeup of an animal, then one also understands the subtleties of the relationship between that animal and its perceived environment. Although an animal's psyche may be inferred through a long series of careful observations of behaviour, more direct, laboratory-based routes are also possible, such as neuroethology. In the neuroethological approach, observations of behaviour are tested and buttressed by direct examination of the nervous system. Neuroethological studies can be very efficient, taking up only a small fraction of the time that would be required by the exclusively behavioural work needed to provide comparable data. Such studies are also very efficient from the point of view of use of a rare species. An example of the latter is the plains wanderer, *Pedionomus torquatus*, whose unusual, low-frequency hearing abilities were characterized electrophysiologically from a couple of specimens when behavioural testing would have required many more specimens and unrealistic amounts of time, given the laconic nature of this rare bird (Pettigrew & Larsen 1990). Laboratory-based brain investigations can also have a degree of precision and flexibility in delivering and measuring stimuli that is difficult to achieve in the field, at least in the early stages of an investigation. A particularly good example of the unexpected results of the increased scope provided by laboratory-initiated investigations is the current transformation of our knowledge about the world of colour in which animals live. The change is partly a result of the use of extended-spectrum equipment that has revealed ultraviolet-based colours, which are not apparent to human eyes, in the displays of birds and fish, but is also the result of increasing understanding of the differences between the visual system of humans and other animals, which drove the investigation of extended-spectrum display colours (Marshall & Messenger 1996).

The platypus is listed as vulnerable, not endangered (Grant 1992). There is nevertheless intense interest in its management. There is direct competition between humans and platypus for use of the fresh waterways on the eastern side of the arid Australian continent. Maximizing our knowledge of the platypus psyche could help minimize this conflict, as well as promoting better general understanding of the way in which this creature carries out its lifestyle, a continuing source of puzzlement and wonder to all those who are acquainted with it. In particular, how does the platypus use its bill to locate and catch distant prey when eyes and ears and nostrils are closed under water?

In this paper we will consider what is known about the sensory systems of the platypus, with special reference to the combined electrosensory and mechanosensory organs of the bill. We put forward a new synthesis of the way in which electrosensory information could be combined with mechanosensory information from water displacement caused by prey movement to enable the platypus to

*Author for correspondence (`j.pettigrew@vthrc.uq.edu.au`).

achieve the prey's precise three-dimensional location in space that would be required for capture. We also suggest some environmental limits for the electrosensory system, calculated from three-way interactions between the electrosensory threshold of the platypus, the impedance of the aqueous environment between platypus and prey, and the size of the electrical signal emitted by different prey. These calculations suggest that platypus will have increasing difficulty catching moving prey as water impedance falls. The effect of lowered water impedance could help explain the puzzling relative absence of platypuses from the lower reaches of the western drainage of NSW and Victorian streams (Grant 1992; Grant & Temple-Smith, this issue).

2. HEARING

Platypuses only rarely make vocalizations. These are emitted quietly in air in the burrow (or nestbox in captivity) (Bennett 1835). A 'tremulous growling' has been observed when platypuses are first woken from sleep and a 'low-pitched squeak' has been noticed when they are injected percutaneously with anaesthetic (P. R. Manger, unpublished observations). No good recordings or sonagrams of these vocalizations have been published. Such vocalizations serve to confirm the view that platypus hearing has evolved for use in air, and not to aid the difficult task of locating prey under water without visual cues. This viewpoint is further supported by the very small fraction of the neocortical surface area devoted to hearing (Krubitzer, this issue), by the fact that there does not appear to be any obvious mechanism to conduct waterborne sound stimuli to the inner ear, nor any suggestion that normal prey might be producing waterborne sound stimuli that could be used by the platypus. It is also possible that hearing in monotremes plays an important role in the detection of ground-based vibrations, although this would be much more important for the echidna than for a platypus safely in its burrow (Gates *et al.* 1974)

The cochlea is well organized, with both eutherian and avian features. There are separated rows of inner and outer hair cells, as in eutherians, although there is more than one row of inner hair cells compared with the single row typical of eutherians (Ladhams & Pickles 1996). Outer hair cells of eutherians have a highly specialized function, with a contractile, calcium-independent, outer protein coat that can follow to very high frequencies to mediate the cochlea's electromechanical feedback response (Gale & Ashmore 1997). The presence in monotremes of outer hair cells with the classical morphology of eutherian outer hair cells suggests that this unique mammalian invention predates the divergence of monotremes and eutherians more than 100 Ma BP (Musser & Archer, this issue). This very early origin of outer hair cell high-frequency specialization is also in line with the suggested early origin of the microbats in the Cretaceous (Pettigrew *et al.* 1989; Pierson 1986; Pettigrew & Kirsch 1995). Of all eutherians, microbats achieve the highest degree of specialization for high-frequency function in outer hair cells (Vater & Lenoir 1992).

There are two studies that determined the audiogram of monotremes electrophysiologically (Gates *et al.* 1974; Krubitzer, this issue). Both found that the most sensitive frequency was around 4 kHz, as in humans, and that the upper level of hearing was around 15 kHz. This relatively high frequency provides further support for the view just expressed that outer hair cells in monotremes have the eutherian electromotor specialization. (In contrast, birds achieve only modest high-frequency cuts. There are unusual cases, in some passerines and owls, where 10–11 kHz is reached, whereas most avian orders cut off around 5–6 kHz.)

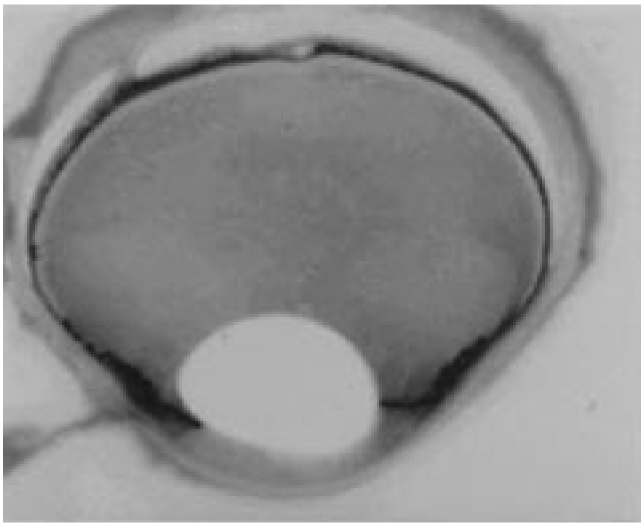

Figure 1. Horizontal cross-section of a flash-frozen platypus eye. Note the flattened cornea, which is matched by a relatively flattened curvature of the anterior surface of the lens. In contrast, the posterior surface of the lens is steeply curved. This arrangement of curvatures is closer to the arrangement found in aquatic, rather than exclusively terrestrial, vertebrates. These visual optics suggest that platypus ancestors may have used their eyes under water much more than the present-day platypus, which keeps its furred lids closed under water.

3. VISION

Although the platypus eye is very small and platypuses are reputed never to open their eyes under water (Burrell 1927), there are a number of features of the eye which suggest that, if vision no longer plays an important role for the platypus under water, it may well have done so in its ancestors.

(a) ***Cornea and lens***

The corneal curvature is relatively flat. The lens is steeply curved on the posterior surface with a relatively flatter anterior surface (figure 1). These are both features that are found in the eyes of aquatic mammals such as otters, sea-lions, etc. (Sivak 1980).

(b) ***Retinal ganglion cell map***

Retinal whole mounts reveal a distribution of ganglion cells with a temporal area centralis where large ganglion cells are concentrated (see figure 2). Both the location, in temporal retina that looks forward into binocular visual space, and the fact that the large ganglion cells are concentrated there, suggest a role in predation. The acuity underlying this specialization (2 cycles deg^{-1}, comparable to a rat) is too low for predation of a high

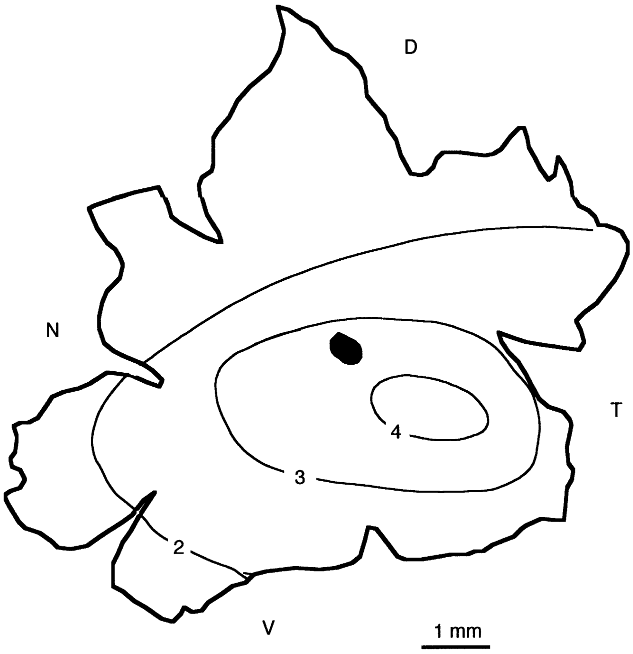

Figure 2. Retinal whole mount from the left eye of a platypus, showing isodensity contours of retinal ganglion cells. There is an area centralis located in temporal-inferior retina with a peak density of 4000 ganglion cells per square millimetre and the centroperipheral gradient is 3.5:1. There is also a weakly accentuated horizontal retinal streak passing inferiorly to the optic nerve (shown in black). The total ganglion cell count is approximately 40 000.

Table 1. *Cortical magnification factors at different recording sites on cortex*

recording sites	separation of recording sites on cortex (mm)	receptive field separation (deg)	cortical magnification factor (mm deg^{-1})
Vr			
1–2	0.50	*ca.* 20	0.025
2–3	0.50	*ca.* 40	0.013
3–4	0.37	*ca.* 12	0.031
4–5	0.80	*ca.* 35	0.023
Vc			
A–B	0.46	*ca.* 25	0.018
B–C	0.40	*ca.* 35	0.011
C–D	0.40	*ca.* 35	0.011
D–E	0.51	*ca.* 15	0.034
E–F	0.51	*ca.* 20	0.026

order and would only be useful at very close quarters (e.g. a shrimp of average prey size would be first detectable at around 1 m using this visual system).

(c) *Correlation of retinal estimate of visual acuity with estimate from visual cortex*

Mapping of the visual cortex in platypus (see Krubitzer, this issue; figure 3), although confirming the relative lack of importance of vision, also raises a further puzzle. One estimate of visual ability can be obtained from the cortical magnification factor, which gives the area of visual cortex devoted to a given angular subtense in the visual field. We calculated this from the data of figure 3, by measuring the receptive field separation (deg arc) as a function of the separation of recording sites in cortex (mm). The values obtained are shown in table 1. In platypuses, the magnification factor is only 0.03 mm deg^{-1}, an order of magnitude or more lower than the values one finds in many mammals with comparable acuity (see table 2). In other words, the predicted retinal acuity is not matched by the visual cortex.

One solution to the puzzle might be provided by a consideration of those mammals that send most retinal ganglion cells to the visual midbrain rather than to the lateral geniculate nucleus that relays to visual cortex. In murid rodents for example, all retinal ganglion cells project to the midbrain, whereas one-third or less project to the lateral geniculate nucleus and visual cortex. In these rodents, visual cortical magnification factors are very low, reflecting the smaller contribution made to the cortical pathway by the retina. According to this line of reasoning, the low visual cortical magnification factor in platypuses would be a reflection of the greater importance of the visual midbrain for its vision, a view that is supported by the small size of the lateral geniculate nucleus and its retinal inputs compared with the much larger optic tectum and its retinal inputs (Krubitzer, this issue).

(d) *Possible platypus ancestors with well-developed vision*

The features of the platypuses' visual optics, suggesting an aquatic adaptation, were a surprise when first seen. We have spent some time carefully watching underwater platypuses to see if they open their eyes, contra Burrell (1927). We have seen a few cases where the platypus opens its eyes just before surfacing, indicating that it is at least not averse to allowing water to flow over its bare cornea. Nevertheless, after six years working with submerged platypuses in a tank with windows, we never saw any reason to doubt Burrell's confident assertion that the eyes are always kept closed under water.

How can one explain these features of the visual system in a mammal that appears to make such little use of vision, particularly under water? We believe that they may represent a puzzling remnant of a former major system, like the short-beaked echidna's electrosensory system (Manger *et al.* 1997). The small number of electroreceptors may not be of much use to the short-beaked echidna in its dry present environment, but nevertheless may provide an indication of past sensory glories in the aquatic, platypus-like monotremes from which it appears to have descended. This view is supported by the presence of a larger number of electroreceptors (intermediate in number between echidnas and platypuses) in the bill of the *Zaglossus*, the long billed echidna, which operates in a moist rainforest environment.

Among the variety of ancient platypus species, some may have had well-developed aquatic vision for underwater prey capture. In this case, the present-day platypus may represent only a narrow part of the original range, most of which did not manage to survive through an evolutionary bottleneck, such as the Cretaceous–Tertiary boundary event. Because this event is widely believed to have favoured those taxa that were preadapted for nocturnal living, the living platypus as well as its Tertiary

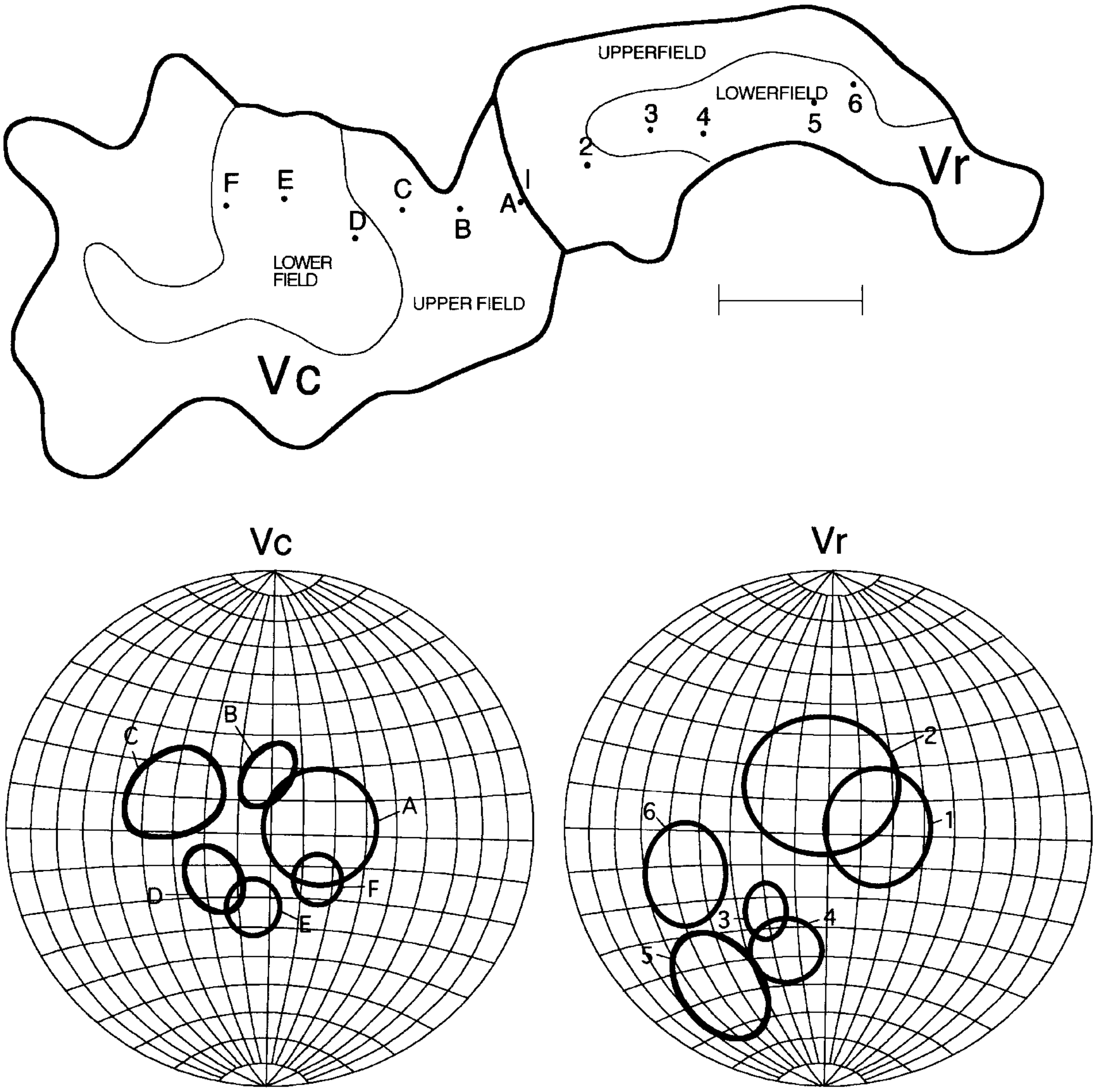

Figure 3. Electrophysiological mapping of platypus visual cortex. There are two areas with a joining border that represents the ipsilateral edge of the visual field. There is a tendency for more cortex to be devoted to the upper visual field, in keeping with the accentuation of the lower retina in the ganglion cell density map (figure 2). The cortical magnification factor, averaged over all the recording sites illustrated, is around 0.013 mm deg^{-1} (table 1). This is lower than predicted from the retinal density map, but is in line with the values found in insectivores, murid rodents and other mammals where only a small fraction of retinal ganglion cells project into the lateral geniculate nucleus, the source of input for the visual cortex mapped here. In these species, all retinal ganglion cells project to the midbrain optic tectum, so it is to be expected that the platypus would also have visual pathways dominated by the retinotectal system. The small relative size and innervation of the platypus lateral geniculate, compared with the optic tectum, is in keeping with this interpretation.

forms (Musser & Archer, this issue) may be present only by virtue of extreme specialization in its prey-capture system that enabled prey detection, location and capture by the bill sensory organs alone without the need for vision. If this is correct, there might be stigmata in the fossil remains of Cretaceous monotremes, such as bigger orbits, smaller septomaxilla and trigeminal nerves, that might reveal less dependence on the bill organ and more reliance on vision than the present-day platypus. Such evidence cannot be garnered from existing Cretaceous material, which is largely confined to teeth, but it is perhaps relevant that all Tertiary platypus fossils have even more trigeminal and bill development than living forms (Musser & Archer, this issue).

4. SOMATIC SENSATION

(a) *Hairy skin*

Most of the body of the platypus is covered by a thick coat of hair, the exceptions being the bill, the webbed portions of the feet and the underside of the tail. Griffiths (1978) provides a brief account of the fur, which was first described by Home (1802) (also see Poulton 1894). In the present study, skin from the ventral body, where the fur has been qualitatively judged to be densest (Griffiths 1978), was sectioned parallel to the epidermal surface and stained with toluidine blue. The fur is arranged into semicircular bundles consisting of one large principal hair (average diameter 45 μm) found at the centre of the semicircle, surrounded by three to five clusters of 10–16

Table 2. *Visual cortical magnification and retinal acuity in some mammals*

species	linear magnification factor (mm cortex deg^{-1})	acuity from ganglion cell density (cycles deg^{-1})	ratio (cycles mm^{-1})
species with well-developed retinogeniculate pathway			
human	15	60	4
marmoset	2	12	6
aotus	1.2	9	7.5
agouti	0.8	9	11
cat	*ca.* 1	12	12
Tammar wallaby	0.4	6	15
ferret	0.2	4	20
flying fox	0.2	5	25
species with dominant retinotectal pathway			
guinea pig	0.06	1.8	30
hedgehog	0.03	1	33
mouse	0.03	1	33
rabbit	0.15	6	40
platypus	0.03	1.8	60

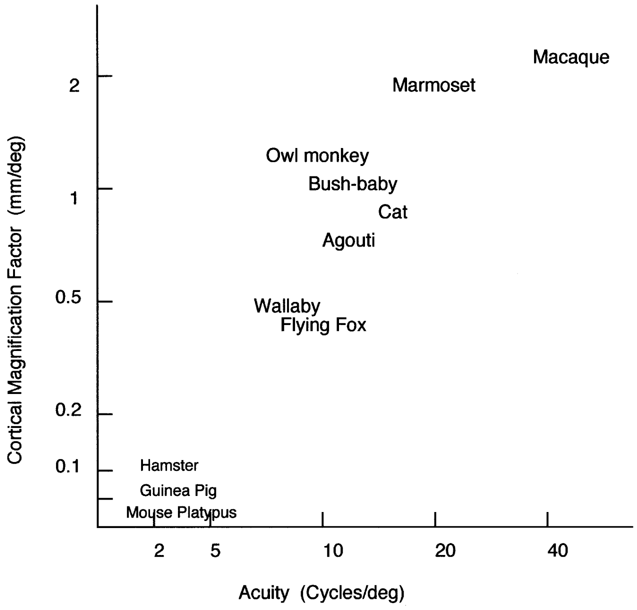

Figure 4. Plot of visual cortical magnification factor as a function of the visual acuity predicted from retinal ganglion cell density. Species that have a lower cortical magnification factor than predicted from their retinal ganglion cell density maps are also species that have a dominant population of retinotectal ganglion cells. For example, in murid rodents (rat and mouse) and hamster, all retinal ganglion cells project to the optic tectum, compared with primates and carnivores, where the majority of ganglion cells are retinogeniculate. The lower than expected cortical magnification factor in the platypus is in line with an emphasis on the retinotectal visual pathway rather than the geniculocortical pathway.

(average 13) fine hairs (average diameter 6.8 μm). Each bundle has one or two apocrine sweat glands associated with the principal hair (see Montagna & Ellis 1960), and our observations showed that only the principal hair had significant innervation. On the ventral surface of the body there were approximately 675.5 hairs mm^{-2} (or 436 000 per square inch). Of these, there were 12.5 principal hairs mm^{-2} (or 8064 per square inch) and 663 fine hairs mm^{-2} (or 427 736 per square inch). The principal hairs are much longer than the fine hairs and flatten out towards the end, and, as described by Home (1802), lie flat on the fine hairs beneath. Grant & Dawson (1978) have studied the insulative qualities of platypus fur and have found that while it is an efficient insulator against heat loss, there is evidence of a counter-current heat exchange system.

(b) *Platypus hair density is second only to sea otter*

The results of the present investigation are in agreement with previously published results of platypus fur. Carter (1965) estimated that there were between 600 and 900 hairs mm^{-2}, whereas the study of Grant & Dawson (1978) gave a mean value of 837 hairs mm^{-2}. The slightly lower value found in the present study may reflect two factors not controlled for: first, the geographic difference in the platypus sampled, those of Grant & Dawson (1978) coming from a temperate New South Wales, whereas those of the present study are from a sub-tropical southeast Queensland, and second, season. Specimens used in the present study were taken during the middle of summer, where air temperature ranged from 30–38 °C (it has been previously described that platypuses moult (Griffiths 1978)). Both the studies of Carter (1965) and Grant & Dawson (1978) compare the density of platypus fur to other mammals. Although the platypus is not the most densely furred mammal, it is a conspicuous second to the sea otter (*Enhydra lutris*), which has a fur density of approximately 1250 hairs mm^{-2} (Grant & Dawson 1978). In most other respects the fur of the platypus is similar to that of other densely furred mammals, for example (in hairs per square millimetre): *Sorex* sp., 300–400; *Talpa* sp., 300–500; *Callorhinus* sp., 400–600; and *Lutra* sp., 350–600 (values from Carter (1965) and Grant & Dawson (1978)). The high density of hair over the body of the platypus is reflected in the organization of the somatosensory cortex, where, in comparison to other mammals of a similar body size, the representation of the body in cortical areas is large (Krubitzer *et al.* 1995). The gracile nucleus of the brainstem, and the ventral posterior lateral nucleus of the thalamus, are also much larger compared with mammals of similar body size (Hines 1929; J. D. Pettigrew, personal observations).

5. THE BILL SENSORY ORGAN

The platypus bill has a high density of both mechanosensory and electrosensory receptors over its surface. Since the first demonstration of electrosensory abilities of the platypus (Scheich *et al.* 1986), much has been learned about its threshold sensitivity, its directionality and the way that electrosensory information is integrated with mechanosensory information. There are still a number of unsolved problems relating to the apparently poor quantitative fit between the electrosensory thresholds of the platypus and the size of the signals produced by prey at the distances at which capture commonly takes place. These problems can be overcome by proposing that the platypus undertakes some sophisticated signal processing that would result in a sensitivity greater than indicated by the crude measured values. Although the quantitative details of this signal processing still cannot be set out, their operation is left in no doubt by a number of features of platypus electroreception that will be detailed below. These include the following: (i) the fact that the system is highly directional, a property that would require that some electroreceptors in the array signal field intensities much lower than the threshold intensity measured for the response; and (ii) the fact that repeated stimuli increase sensitivity.

It is now possible to sketch the way in which the bill organ might achieve a complete three-dimensional 'fix' on the prey by processing both electrical and mechanical signals. Whereas it has usually been thought that electroreception merely extends the range of mechanoreception so that prey can be detected from its electrical signals before it actually makes contact with mechanoreceptors in the bill, it now seems likely that mechanoreceptors can also be used at a distance. This new insight provides a way for prey to be accurately localized in three dimensions when both kinds of input are considered simultaneously, as detailed below.

(a) *Mechanoreceptors and the push-rod complex*

Mechanoreceptor complexes cover the bill (Manger & Pettigrew 1996). In a live platypus, these complexes are visible through the dissecting microscope as small, bright domes. When the bill skin is wet, the domes become more exposed by retraction of the circumference of the edge of the pit in which they reside (Manger, Keast, Pettigrew & Troutt, this issue). This observation suggests that these bill mechanoreceptors are specifically adapted for operation in water and are not designed solely for the transduction of tactile stimuli that make direct contact with the bill skin. This suggestion is further supported by studies of cross-sections of the mechanoreceptor complex that have led to the name 'push rod' being used to describe it. The visible surface dome is the terminal surface of an epidermal rod that is free along its length but which is attached to the base. A number of sensory organs are clustered at the base. These resemble the Merkel cells and Pacinian corpuscles of eutherians. In addition, a neural specialization inside the epidermal rod (like a chain or ladder) extends along its length. In view of the push rod's length, one would expect that it would be free to rotate somewhat around its basal attachment. This is particularly evident when one considers that the platypus push rod is not attached anywhere along its length, in contrast to similar organs in the echidna and the star-nosed mole, which are tethered to the surrounding epithelium near the terminal end (Manger & Hughes 1992; Catania 1995). The platypus push rod would therefore present a greater compliance to approaching water movement than the surrounding epithelium as a whole, because of this possibility for relatively easy relative motion of a rotatory kind between the epithelium of the push rod and surrounding epithelium. An appropriate analogy would be with the vertebrate mechanoreceptive hair cell whose stiffened stereocilia present a surface that is free to rotate at its base in response to motion of water. Combined with the tip links stretched between adjacent stereocilia, this mechanical arrangement of stereocilia increases the sensitivity of the hair cell to small amplitude water movements.

Physiological study has shown that afferent nerve fibres from the push rod are activated by displacements of the tip and that the threshold displacement is around 20 μm (Gregory *et al.* 1987). As it is possible to measure much larger water displacements than this at distances of 20 cm from the tail flicks of platypus prey (see figure 5), it is clear that push rods can detect water displacement *per se*, without the need for direct physical contact with the prey. There is not yet detailed experimental verification of this in the platypus because of the widespread difficulty of working with these animals. Some workers have pointed out the difficulty of finding any obvious difference between afferents from the echidna's push rod and those from non-specialized parts of the skin (Iggo *et al.* 1996). This lack of difference may not be so surprising, given the more tethered nature of the echidna's push rod compared with the platypus and the fact that the experiments in question were carried out with the bill in air. One expects the opening to be clamped tightly over the tip of the push rod in air and any postulated aquatic specialization of the push rod would be most difficult to demonstrate.

(b) *Problems with thresholds*

(i) *Discrepancy between individual electroreceptor thresholds and whole platypus thresholds*

Using a human criterion of one spike per stimulus, Gregory *et al.* (1987*b*) found that individual electroreceptive afferents had thresholds at field strengths around 1–2 mV cm^{-1}. In contrast, the whole platypus can make directional, coordinated responses to artificial electrical stimuli that produce fields with strengths as low as 50 μV cm^{-1}. There is a discrepancy of a factor of 20–40 between these two thresholds. It is generally accepted that the difference can be readily accounted for by some kind of processing of the signals from the thousands of electroreceptors that are immersed and that would all be exposed in various degrees to the electrical field generated by the prey. Even with a crude form of signal averaging, the outputs from only 400 electroreceptors need to be averaged to account for the increased ability of the whole platypus over its individual receptors.

A larger discrepancy arises when one considers the size of the fields emitted by platypus prey and the measured electroreceptive threshold of the platypus.

(ii) *Discrepancy between whole platypus electroreceptive thresholds and field intensities of prey*

The largest field strengths generated by platypus prey were around 1 mV cm^{-1}, in the case of decapod crustaceans such as an ateiid shrimp (Taylor *et al.* (1992). This field would be maintained at the same level for distances comparable to the size of the shrimp (*ca.* 5–10 cm) but would then decay: first in a way that would be related to the orientation of the shrimp's body axis and the three-dimensional shape of the electrical field generated at the shrimp (a cylindrical body, for example, will generate a field decay according to a square-root law) and then according to a cube-root law (at distances that are large compared with the shrimp's size, so that the shrimp looks like a point source). Given the complex shape of the shrimp, the field decay may also have other complications that would need detailed empirical study, of the kind carried out on the field generated by electric fish (Rasnow & Bower 1996).

To guide the sweeping movements of the platypus bill, the shrimp's field would have to be picked up at 10–20 cm. This is a plausible range of distances, depending on the size of the shrimp, as a large shrimp's full-field strength would be picked up at around 10 cm and the platypus's threshold of 50 $\mu V cm^{-1}$ would not be reached until the shrimp were further than about 13 cm away. To be effective at correcting swimming pursuit, as has been observed (Manger & Pettigrew 1995), the field of the shrimp would need to be detected at 20–30 cm or even further. At this distance, field strengths generated at the platypus would be more than three orders of magnitude smaller than at the shrimp, or around 1 $\mu V cm^{-1}$, values at least one order of magnitude smaller than the threshold values that have been measured in behavioural experiments with artificial electrical fields. This calculation makes one wonder how the platypus might carry out prey detection at such distances using electroreception.

The discrepancy can be approached in two ways. First, it has to be realized that the subject of the electrical field generated around a living organism is very complex. In the case of electric fish, it took a great deal of work to define the three-dimensional shape of the field generated by the electric organs (Rasnow & Bower 1996). If the field generated by the shrimp is non-uniform, with directional arms for example, then our crude measurements and calculations on the overall field strength generated by the shrimp might be inappropriate if the platypus is deriving information from parts of the field that were not measured by us. Second, measurements of the overall field strength of an artificially generated electrical stimulus at threshold may bear only a distant relationship to those that might be carried out on the natural field of a shrimp by the complex signal-processing system of the platypus. If we recall that the platypus has 40 000 electroreceptors, all of which are immersed and therefore exposed to the shrimp's electrical field, it is easy to see that signal processing could enormously improve performance. For example, simple, crude averaging of all electroreceptors could achieve a 250-fold improvement over the performance of a single electroreceptor (or a threshold field strength of 4 $\mu V cm^{-1}$). More sophisticated processing could improve this threshold even further.

There are a number of indications that the platypus carries out complex signal processing on the electrical field, from studies of the directionality of the electroreceptive system and from studies of time-averaging of the electrical signals. These all point to an advanced signal-processing capacity that could easily perform better than our simple-minded measurements suggest.

(c) *Directionality*

Platypus make a brief, involuntary, short-latency (40 ms) head saccade to an electrical pulse. The head saccade will follow to high repetition rates (12 Hz) once the platypus has become habituated to artificial electrical stimuli, so that these no longer elicit pursuit (Manger & Pettigrew 1995). The striking feature of the head saccades elicited by electrical pulses is that they are directional. A stimulus dipole in the water above the animal will elicit an upward saccade; an electrical stimulus originating to the animal's right will evoke a lateral saccade toward the right; and so on for stimuli from below and to the opposite side. This behaviour contrasts with electric fish, who can move up iso-potential lines to find an electrical source, but cannot localize the source from a single stimulus presentation in the way that the platypus does (Hopkins 1997).

Details of the electrical threshold for the head saccade help to explain the basis of the directionality (Manger & Pettigrew 1995). Thresholds were lowest for stimuli originating in the downwards and forwards direction. This direction is also the direction orthogonal to the 'stripes' of electroreceptors that run in a parasagittal direction along the bill (Manger 1994). Taken together, the observations suggest that the platypus is reconstructing the pattern of field strengths across the bill. In this way it could determine the origin of the field by associating locations on the bill that signal the same field strength and thereby use the isofield strength lines to estimate the direction along which the field was decaying.

The parasagittal 'stripes' of electroreceptors may reflect an in-built tendency for more neural associations to be carried out along this parasagittal axis. Recording from the cortex tends to confirm this idea in the following three ways: (i) elongated receptive fields encompass more than one electroreceptor; (ii) electroreceptive fields show a bias for parasagittal orientations; and (iii) the cortical map represents a variety of different field strengths (Krubitzer *et al.* 1995; Manger *et al.* 1996). Taking all this together, directionality could be achieved by reconstructing the field lines over the bill and then triggering a saccade orthogonal to the isoelectric field lines. The lower threshold for field lines that run parallel to the edge of the bill and the 'stripes' would then be explained by the preferential bias of the signal-processing system for associations along that axis. Another way to imagine this involves one parasagittal strip of electroreceptors that are linked at some level in the brain so that there is a recognition that all are signalling the same field strength. This would correspond to an electrical stimulus, in a very lateral position, which was generating field lines parallel to the long axis of the bill.

Regardless of the mechanism, directionality of the electroreceptive system provides a clear example of the sophistication of the signal processing to which the platypus has access. To achieve this fine analysis of the spatio-temporal pattern of activation of electroreceptors across the bill, it seems likely that the platypus would be able to interpret much smaller signals at some electroreceptors than the overall signal measured at 'threshold' in our experiments.

One can reach a similar conclusion about the potential for greater sensitivity on the part of the whole system of electroreceptors if one recalls that the single electroreceptor threshold of 1–2 $mV cm^{-1}$ was determined with a criterion of one-to-one following between spike and stimulus. If a signal processor were able to look at all 40 000 electroreceptors simultaneously, a response as weak as only one time-locked spike in many thousands could be detected, with the corresponding 1000-fold improvement in threshold. We do not know how far toward this theoretical limit the platypus may be able to go.

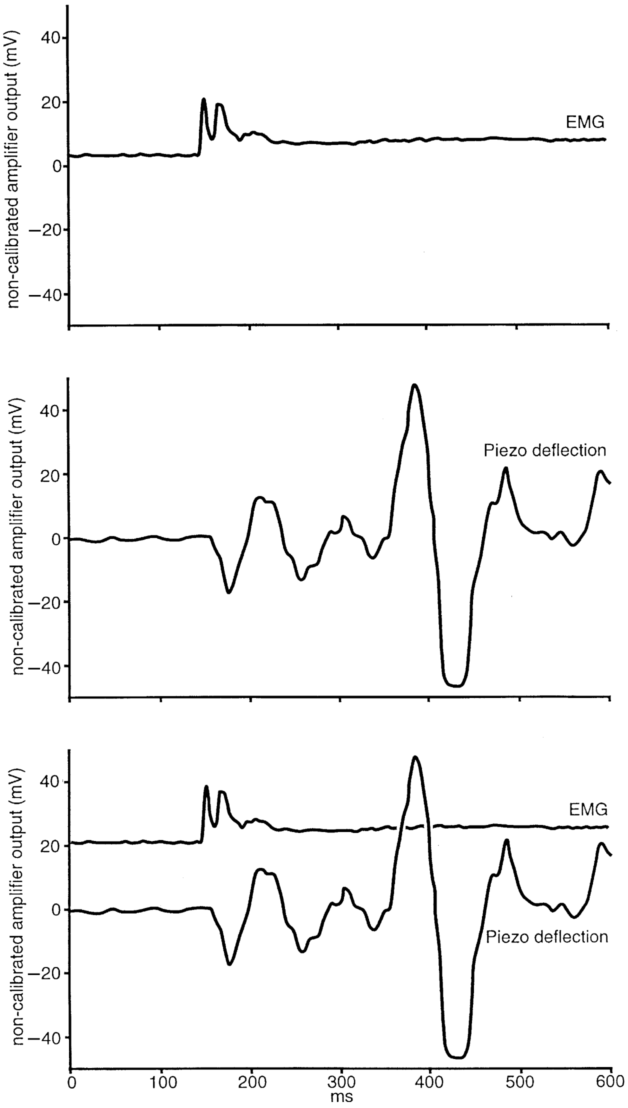

Figure 5. Electrical and mechanical activity recorded at a distance from a tail flick of a crustacean about 5 cm long (*Cherax quadricarinatus*). The mechanical sensor was a bimorph piezo-electric device that was clamped at one end and attached at the other to a light wooden paddle immersed vertically so as to pick up any mechanical disturbance or displacement of the water transmitted from the crustacean 15 cm away. Note that the water displacement occurs about 10 ms after the electrical activity.

6. COMBINED ELECTRORECEPTION AND MECHANORECEPTION

All electroreceptive neurons in the SI cortex of the platypus also receive mechanoreceptive input (Krubitzer *et al.* 1995; Manger *et al.* 1996). Moreover, there is a highly organized array of mechanoreceptive and electroreceptive inputs, as revealed by cytochrome oxidase (CO) staining (Krubitzer *et al.* 1995). There is a marked facilitation of the these two inputs on bimodal electroreceptive–mechanoreceptive neurons, with changes in the temporal properties of the response when both kinds of stimuli are presented simultaneously (Manger *et al.* 1996). Although the direct experiment has not yet been done because of the lack of availability of experimental animals, it seems very likely that this time dependence would result in temporal facilitation at a particular time interval. To speculate further, given the diversity of cortical neurons and the lay-out of the patterned electroreceptive–mechanoreceptive array in SI cortex, it is highly probable that different bimodal neurons would facilitate optimally at a variety of different time intervals. This speculation is supported by the changes in timing observed when the responses of bimodal neurons to combined stimulation are compared with those to stimulation of one modality alone. These changes involve timing in the range 5–20 ms, according to the neuron studied (Manger *et al.* 1996).

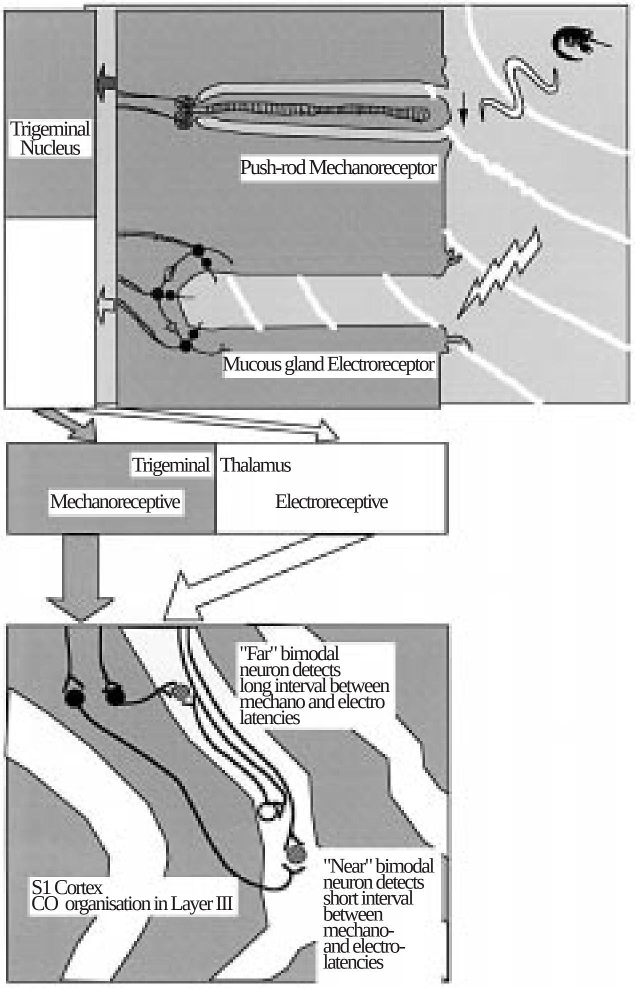

Figure 6. Push-rod mechanoreceptor and electroreceptor input to the stripe-like, highly specialized region of SI neocortex. Bimodal neurons responsive to combined mechanical and electrical stimulation of the bill are sensitive to the time delay between successive stimulation of these two submodalities. Because a natural stimulus, like a shrimp's tail flick, will produce both electrical signals and a mechanical disturbance, we propose that this elaborate system acts to measure the distance of the prey from the time interval between the arrival of the neuromuscular electrical impulse and the later arrival of the mechanical disturbance propagated through the water. The stripe-like arrangement for establishing prey distance from small time differences between two sensory arrays in platypus SI is formally similar to the ocular dominance stripe arrangement for measuring stereoscopic depth from small differences between two sensory arrays (i.e. the two eyes) in the striate cortex of carnivores and primates.

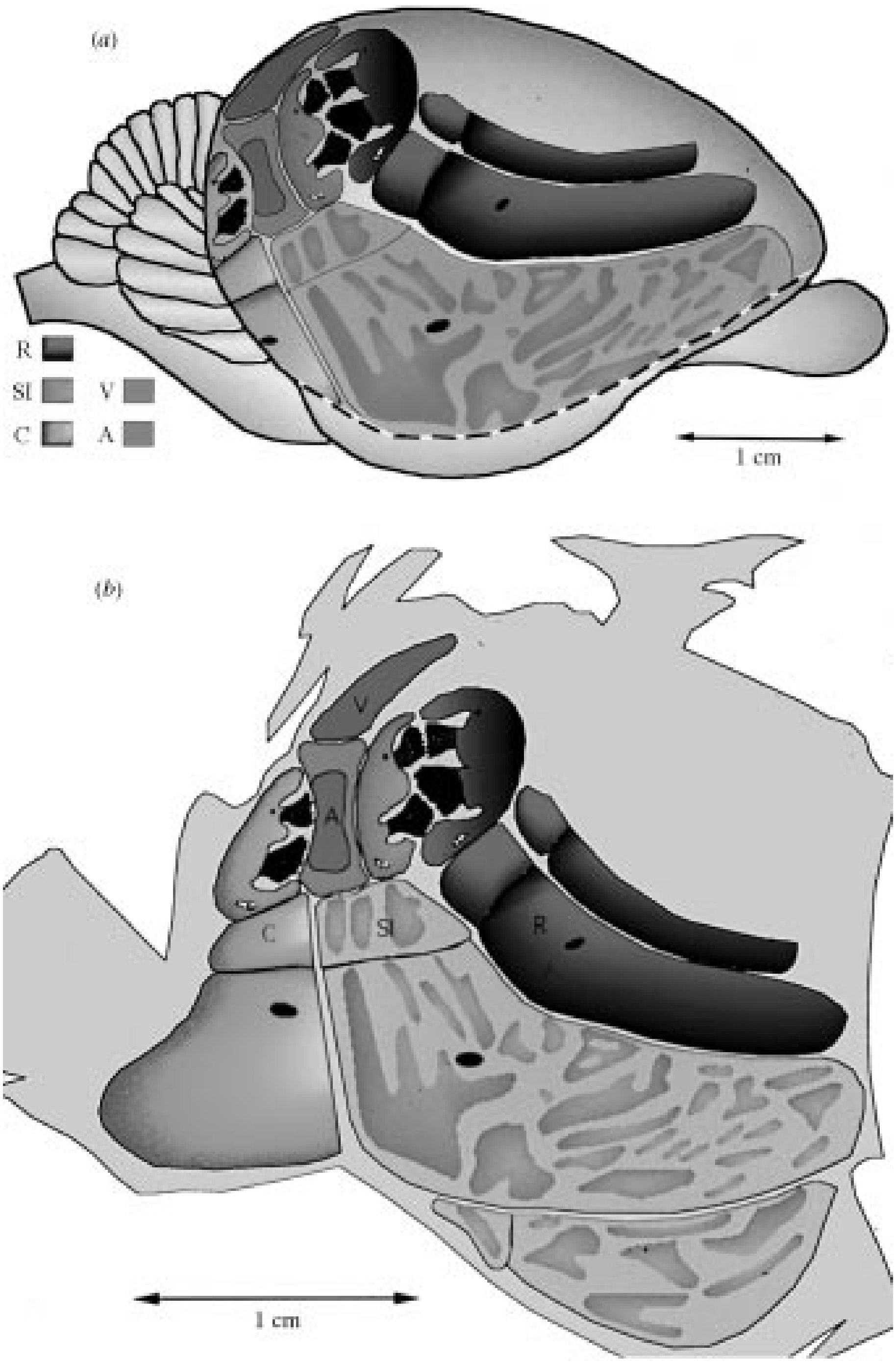

Figure 7. Summary diagram of sensory world of the platypus, as predicted from the various representations of sensory systems within the neocortex. Note that there are three separate somatotopic representations so that somatosensory process dominates. Note further that the bill representation dominates within somatotopic cortex. Within area SI, the somatotopic representation of the bill is further differentiated into subregions of different myelin and CO staining that separate mechanoreceptive processing from electroreceptive processing. Note the small size of visual cortex (green) and note that auditory cortex (yellow) is almost completely surrounded by somatosensory cortex.

What role could be served by bimodal electroreceptive–mechanoreceptive neurons that show facilitation for different time intervals between electroreceptive and mechanoreceptive inputs? To answer this question, we performed a small experiment to test the controversial questions of the adequate mechanical stimulus in water and the time taken for mechanical disturbances to propagate. Given a detectable time lag between arrival of the electrical stimulus and the later arrival of a mechanical stimulus propagated through the water from the tail flick of a prey, such neurons could provide information about prey distance. Such a system would require that the facilitatory times of bimodal neurons (5–20 ms) correspond to the intervals that occur naturally. This proposition is hard to test theoretically because of the differences of opinion about the adequate mechanical stimulus and its speed of propagation in water. We therefore tested this proposition directly using the tail flick of a crustacean known to be a platypus prey item, under conditions that were designed to mimic, as closely as possible, those occurring naturally.

(a) *Propagation of water displacement waves*

We used a live crustacean (*Cherax quadricarinatus*) as the source of mechanical and electrical stimuli. We elicited tail flicks by prodding or squeezing the body of the shrimp. The chamber was 60 cm × 40 cm × 20 cm and filled with tap water (40 nS cm^{-1}). In some experiments, there was a platypus bill immersed near the sensors, but the presence of this potential current sink (*ca*. 20 nS) appeared to have no effect on the results.

(i) *Sensors*

The electrical probe was composed of two insulated wires, bare at the tips (1 mm; impedance *ca*. 100 kΩ). The mechanical probe was a bimorph piezo-electric sensor (RS 285 784) that was clamped at one end and glued at the other to a light wooden rod, 10 cm long (applicator stick, *ca*. 2 mm in diameter). This rod acted as a paddle, when immersed, to maximize the mechanical disturbance in the water, which was then transmitted to the sensor. By increasing the compliance of the mechanotransducing apparatus in this way, we aimed to mimic the push-rod mechanoreceptive apparatus. The push rod has a similar increased compliance to displacements that would have a product moment because they occur at an angle to the long axis of the structure, tending to bend or rotate it about its basal attachment to the dermis.

(ii) *Results*

Shrimp tail flicks caused mechanical displacement waves that could be picked up by the piezo-electric sensor from the other side of the chamber, more than 40 cm away. These mechanical disturbances far exceeded the 20 µm displacement threshold that has been described for the push rod (see figure 5). After a tail flick at a fixed distance, the latency of the mechanical effect on the transducer varied considerably. Latency seemed to increase if the tail flick disturbance broke the surface of the liquid or if the shrimp were closer to one edge of the container. Although there was a clear decrease in latency when the shrimp was brought closer to the transducer, the distance–latency relationship was noisy because of the scatter introduced by the variable effects of the position of the shrimp in depth, or in relation to the walls, when the tail flick occurred. Despite the variability of the latencies we observed in our small chamber, there was a clear delay between the arrival of the electrical signal at the sensors and the later arrival of the mechanical stimulus. The latencies varied over a range of 5–50 ms for the distances studied between 5 and 60 cm.

(iii) *Conclusion*

Latencies between the electrical signal and the later arrival of a mechanical signal generated by natural prey movements are in the range that could be detected by bimodal cortical neurons. Although these latencies are longer than predicted on the basis of some theoretical calculations, they do reflect the more complicated situations that would apply in the field, when the precise nature of the water displacement produced by a tail flick would vary according to the proximity of damping interfaces such as the bottom or the surface or nearby banks. These observations also bear on the controversy over the adequate mechanical stimulus for aqueous mechanoreceptors. Pressure and acceleration have each been put forward as the adequate stimulus in this situation (e.g. Hartline *et al*. 1996; Mogdans *et al*. 1997), but the best explanation for the mechanosensory role of the push rods, at least, appears to be one that involves the detection of water displacement.

We had always assumed that the numerous mechanoreceptors in the platypus bill were involved in transduction of tactile stimuli that made direct contact with the bill. The new observations, all taken together, indicate instead that this structure has a teloreceptive function, just like electroreception, and perhaps operating over a similar range of distances, depending on the size of the prey and the magnitude of the displacement produced. It is a pity that this new insight and the new observations came after the time when platypuses were available for electrophysiological investigation. Nevertheless, the following three considerations argue strongly for a cooperative role between mechanoreception and electroreception of stimuli generated by a distant moving prey: (i) the opening of the push-rod pore upon immersion; (ii) water displacement above the threshold of push-rod activation produced by prey as much as 50 cm from the bill; and (iii) the complex coordinated pattern of neurons in S1 that are bimodal and have properties consistent with the detection and measurement of behaviourally relevant time-lags between the latency of electrical and mechanical stimuli arriving from moving prey at a distance.

(b) *A structure for fixing prey position*

Knowledge about the distance of prey is crucial for a predator. Yet this information is perhaps the hardest to obtain. In primates, the stereoscopic visual system of the geniculostriate pathway has evolved to detect minute differences between the retinal images of the same outside objects (retinal disparities) that have arisen because of the slight differences in viewpoints of the two eyes. One striking structure in this system is the stripe-like pattern of ocular dominance columns that splits the cortical images of each eye into two interlocking sets of bands within the input layer IV (LeVay *et al*. 1980). Although the function of these bands is not completely agreed upon, it is self-evident that they would facilitate the measurement of small retinal disparities by the immediately adjoining disparity-specific binocular neurons of layer III, even if there is little agreement on how this is done. In turn, the measurement of these retinal disparities enables the judgement of distance, so it is appropriate to think of the ocular dominance bands as being part of the system for depth judgements (LeVay & Voigt 1988)

The comparison between ocular dominance bands and the bands observed in platypus S1 cortex now becomes of considerable interest. We are proposing that the S1 bands provide an array of neurons that measure a variety of mechanoreceptive and electroreceptive stimulus parameters, such as the strength of the field at different points on the bill and the difference in time of arrival between electrical and mechanical stimuli from the same prey. The latter parameter leads directly, with no need for further processing, to a measure of absolute prey distance. So both systems of bands, the primate ocular dominance system and the platypus S1 electroreceptive–mechanoreceptive array, could be functioning in the detection of small differences between two input arrays so that distance can be judged.

Directionality of electroreception (and perhaps, also, some directionality of mechanoreception, if we consider the different angles, and therefore sensitivity, that push rods would present to the water from different positions on the curving bill surface) enables the platypus to estimate the approximate direction of the prey. We think that this ability must involve some form of reconstruction of the field decay across the bill, a task that could be performed by the array of electroreceptive cortical neurons with varying receptive field locations and preferred field strengths. In addition to direction, the absolute distance of the prey could be given by the bimodal neurons with varying preferences for time lag between the modalities. Putting both of these abilities together, one can see that the extremely specialized Sl array is well suited to the task of putting a complete three-dimensional 'fix' on the prey: azimuth and elevation in head-centred coordinates, from directionality of the bill, and absolute distance. Seen in this way, the functional outcome solves a number of puzzles. First, why is there such an elaborate structure as the Sl system of bands, and why does this structure involve such an intimate relationship between mechanoreceptive and electroreceptive functions? Second, how does the platypus really catch actively swimming prey, such as shrimp, using only the bill sensory organ? It is clearly much easier to answer this question if the system allows the platypus to know not only the direction to which it must swim or move its head, but also how far away is the prey.

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