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Sensory receptors in monotremes

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This is a summary of the current knowledge of sensory receptors in skin of the bill of the platypus, *Ornithorhynchus anatinus*, and the snout of the echidna, *Tachyglossus aculeatus*. Brief mention is also made of the third living member of the monotremes, the long-nosed echidna, *Zaglossus bruijnii*. The monotremes are the only group of mammals known to have evolved electroreception. The structures in the skin responsible for the electric sense have been identified as sensory mucous glands with an expanded epidermal portion that is innervated by large-diameter nerve fibres. Afferent recordings have shown that in both platypuses and echidnas the receptors are excited by cathodal (negative) pulses and inhibited by anodal (positive) pulses. Estimates give a total of 40 000 mucous sensory glands in the upper and lower bill of the platypus, whereas there are only about 100 in the tip of the echidna snout. Recordings of electroreceptor-evoked activity from the brain of the platypus have shown that the largest area dedicated to somatosensory input from the bill, S1, shows alternating rows of mechanosensory and bimodal neurons. The bimodal neurons respond to both electrosensory and mechanical inputs. In skin of the platypus bill and echidna snout, apart from the electroreceptors, there are structures called push rods, which consist of a column of compacted cells that is able to move relatively independently of adjacent regions of skin. At the base of the column are Merkel cell complexes, known to be type I slowly adapting mechanoreceptors, and lamellated corpuscles, probably vibration receptors. It has been speculated that the platypus uses its electric sense to detect the electromyographic activity from moving prey in the water and for obstacle avoidance. Mechanoreceptors signal contact with the prey. For the echidna, a role for the electrosensory system has not yet been established during normal foraging behaviour, although it has been shown that it is able to detect the presence of weak electric fields in water. Perhaps the electric sense is used to detect moving prey in moist soil.

Keywords: platypus; echidna; electroreceptors; mechanoreceptors; cutaneous; sensation

1. INTRODUCTION

This is a review-style account of sensory receptors in the bill of the platypus and snout of the echidna. It includes description of aspects of the central processing of their information and speculations about their significance for the behaving animal. The account will, by necessity, be restricted to cutaneous sensory receptors served by branches of the trigeminal nerve. Virtually nothing is known of the properties of receptors in other parts of the body of these animals.

The platypus and echidna belong to a small group of animals, the monotremes, a group characterized by possession of a number of primitive mammalian features including, as their name implies, a cloaca, the reptilian pattern of limb girdles and, of course, the well-known habits of laying eggs and suckling their young. There are three living members of the group, the platypus, *Ornithorhynchus anatinus*, the echidna, *Tachyglossus aculeatus*, and the long-nosed echidna, *Zaglossus bruijnii*. Platypus and echidna remain, today, widespread throughout south-eastern Australia. It is probably fair to say that the echidna is the more common animal, with its range extending to the central deserts and tropical north (Griffiths 1968). Because of its secretive habits, it is easy to be misled about the abundance of the platypus. Certainly, in a number of specific locations it is quite common, although its present-day distribution is rather more restricted than it was 100 years ago (Grant 1992). The long-nosed echidna is found only in New Guinea where it is now extremely rare, being restricted to remote mountain forests. At the present time there have been no detailed studies of sensory receptors in *Zaglossus*, although a recent report described structures resembling the electroreceptors and mechanoreceptors of platypus and echidna (Manger *et al.* 1997). This means that the account presented here will largely be restricted to the platypus and echidna.

In describing sensory receptors in monotremes, a comparative approach will be taken, where possible. The existing evidence suggests that the monotremes as a group left the mainstream of mammalian evolution at least 110 million years ago and that the ancestral animal was platypus-like (Archer *et al.* 1992). Divergence of the monotremes from other mammals probably occurred while Australia was still part of the large land mass, Gondwanaland, which included Antarctica and South America. At present, what are thought to be the oldest remains of monotremes come from South America (Pascual *et al.* 1992).

The early divergence of the monotremes from other mammals means that they have evolved as an independent

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group for a long time. The view taken here is that modern monotremes possess a number of primitive characteristics but are, nevertheless, highly evolved animals. The modern monotreme is therefore not simply a primitive transition form between reptiles and mammals, but possesses many features unique to the group, not least of which is its electric sense.

The electric sense in the platypus and echidna is unique among mammals and it will be described first. Its uniqueness has attracted more interest than other senses, although some information has been obtained on mechanoreceptors as well, receptors with which the platypus bill and echidna snout are richly endowed. The description of responses to mechanical stimuli, and the specialized structures in the skin with which they are associated, will be presented separately, although the electric and tactile senses will be considered together for some of the speculations about their roles in prey location and capture.

2. ELECTRORECEPTION

The ability of animals to be able to detect weak electric fields in their environment was recognized only relatively recently, perhaps because we, ourselves, are unaware of any but the strongest fields. Thus, the ampullae of Lorenzini in elasmobranch fish were first thought to be mechanoreceptors, then thermoreceptors and chemoreceptors. It was not until the late 1950s that convincing behavioural evidence was provided for an electroreceptive role. At about the same time the tuberous receptors of mormyrid and gymnotid fish were recognized as electroreceptors. It was not until the 1980s that electroreceptors were described in urodele amphibians and monotremes.

Electrosensory systems are present in a diverse range of fish, including the primitive lampreys, yet their absence in some bony fish has led to speculation that they evolved and were lost again at least twice (Bullock 1986). Given that no other known mammals have an electric sense, it is safe to assume that the electric sense in monotremes has evolved, *de novo*, for yet a third time. It is a measure of the gap, in evolutionary terms, between the monotremes and other mammals, that within this group of animals an entirely new sensory system has evolved, including the specialized cutaneous receptors, their afferent pathways to the brain and the necessary central processing circuitry. What is especially fascinating is that the design of the system as found in monotremes differs fundamentally from that in fish and amphibians. The simplest way to interpret this fact is to speculate that the precursor structures in the ancestral stock that gave rise to monotremes did not favour the development of a system comparable to that found in fish.

In all fish and in amphibians, the electroreceptors are a secondary cell system, like that in the eye and ear. That is, there is a specialized receptor cell that responds to a stimulus by producing a receptor potential. That, in turn, leads to synaptic transmission and activation of the primary sensory neuron. In monotremes, the evidence suggests that it is the distal terminals of the afferent nerve fibres themselves which are the transduction sites for electric stimuli, so that here the primary event leads to production of a generator potential and the triggering of action potentials without an interposed synapse.

3. ELECTRORECEPTORS IN MONOTREMES

The discovery of electroreception in the platypus was made against a background of speculation about how the platypus catches its prey. It is known that the platypus feeds in the murky water of rivers and streams, often at night, and when it dives to the stream bottom it closes its eyes, ears and nares. Then how was a platypus able to catch half of its body weight in live prey in one night? It must have a sixth sense! (Burrell 1927). In 1986 Scheich and colleagues proposed that the platypus had an electric sense. The idea was originally provoked by some close-up photographs of the bill showing rows of pores reminiscent of the surface appearance of the mouths of electroreceptor organs in certain fish. Scheich *et al.* (1986) made a number of important behavioural and electrophysiological observations in support of their claim of an electric sense.

A platypus swimming in a tank would dive and turn over a brick behind which lay a live battery but would ignore similar bricks concealing flat batteries. In another experiment, the platypus was able to swim around an almost invisible Perspex plate suspended in the water, across which an electric field had been set up. It would bump into the plate when the field was switched off. Switching an electric field on and off across a pair of metal plates produced reflex movements of the head when the platypus swam between them. In an anaesthetized platypus, gross electrical stimulation of the surface of the bill generated evoked potentials from the surface of the brain. Scheich *et al.* (1986) speculated that the electroreceptors were located in the skin of the bill and the platypus used its electric sense for negotiating obstacles underwater and detecting live prey by means of the electromyographic (EMG) activity accompanying their movements.

Our contribution to the story of electroreception in monotremes was that we made the first recordings from the electroreceptors themselves, establishing beyond doubt the existence of an electrosensory system in these animals (Gregory *et al.* 1987). In a subsequent series of experiments we established, based on behavioural and electrophysiological evidence, that the echidna, too, has an electric sense (Gregory *et al.* 1989*b*). Because much of what we know today comes from studies of the platypus, we will describe it first.

4. THE PLATYPUS

The recordings from the receptors provided evidence that the structures responsible for generating activity in response to weak voltage pulses applied to the skin were what Andres & von Düring (1984) had called sensory innervated mucous glands, structures whose presence in the bill had already been noted nearly 100 years earlier (Poulton 1894; Wilson & Martin 1893). Andres & von Düring used modern histological methods to provide the first detailed description of these end organs. Because virtually nothing is known of the functions of the other two glands found in bill skin, the sensory serous gland

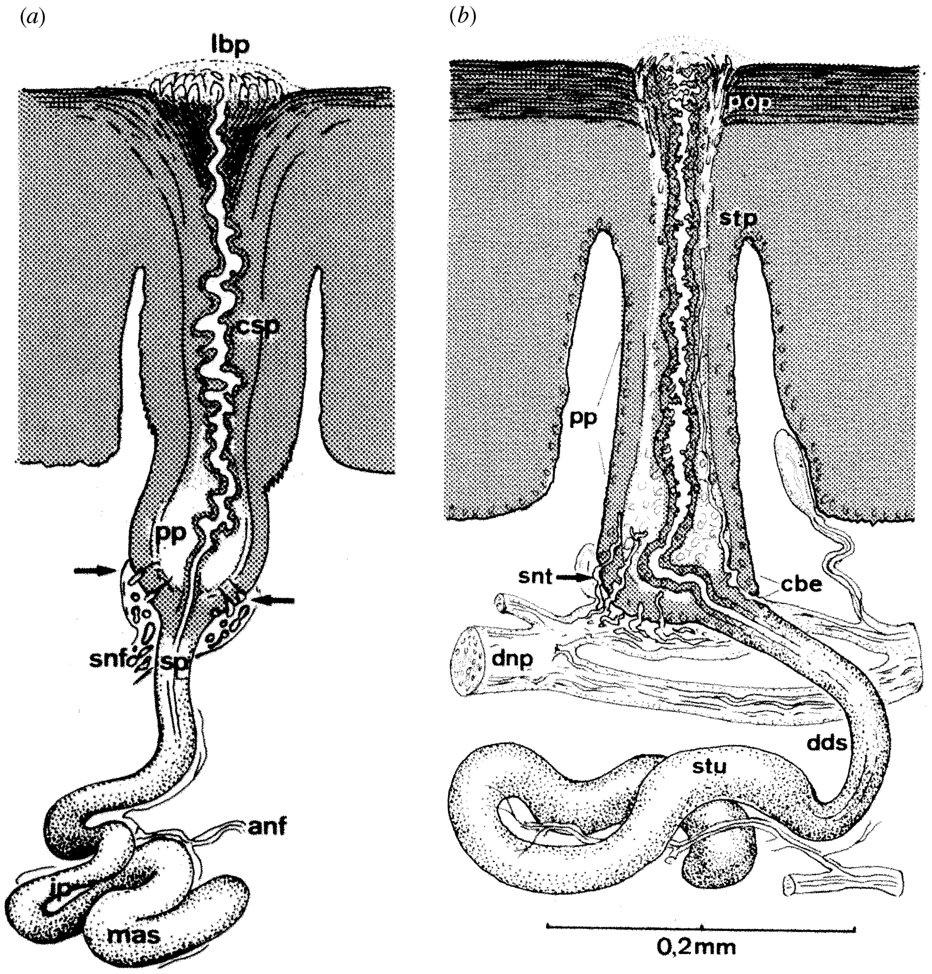

Figure 1. Sensory mucous glands in platypus and echidna. (*a*) Diagram of platypus sensory mucous gland: lbp, large, blossom-like pore; csp, coiled sinus portion; pp, papillary portion; sp, straight portion; ip, isthmic portion; mas, main segment secretory portion. Sensory nerve fibres (snf) supply the papillary portion of the gland (arrows), whereas autonomic nerve fibres (anf) supply the secretory portion. Reproduced, with permission, from Andres & von Düring (1988). (*b*) Diagram of echidna sensory mucous gland: pop, pore portion of gland; stp, straight portion; dds, dermal duct segment; stu, secretory tubule. Sensory nerve terminals (snt) arise from a dermal nerve fibre plexus (dnp). The intra-epidermal segment of the gland shows a club-shaped enlargement (cbe) of the papillary portion (pp). Here the sensory nerve terminals penetrate the epidermal layer. Reproduced, with permission, from Andres *et al.* (1991).

and the non-innervated gland, these will only be mentioned in passing.

(a) ***Structure***

The structure of the mucous sensory gland can be subdivided into a number of regions. That lying deepest below the surface in subdermal tissues is the region of the gland which actively secretes mucus. It consists of a coiled tube, closed at its end, in the walls of which are the secreting cells (figure 1). The gland duct, the dermal segment, ascends towards the skin surface, and reaches the sensory innervated region, the papillary portion. In this region there is an invagination of the epidermis, which expands into a bulb-like structure about 500 μm below the skin surface. The gland duct, coming from below, passes through the centre of the bulb and continues on up to the surface. The lumen of the duct is lined with keratinocytes that are arranged at the mouth of the gland in a 'blossom-like arrangement'. Within the papillary portion there are two distinct layers of cells between the epidermis and the gland duct. Closest to the duct is a layer of loosely packed cells with large intercellular spaces. Below it and directly overlying the germinal epithelium of the epidermal layer is a layer of flattened cells that are tightly packed and have numerous tight junctions between them (Andres & von Düring 1984). Large, myelinated sensory axons terminate at a paranode in the region adjacent to the germinal layer. The terminal region of the axon is characterized by being filled with intracellular organelles, mitochondria and neurofilaments, as well as exhibiting elaborate myelin figures (Iggo *et al.* 1988). This is presumably an area of intense metabolic activity and perhaps the region in which the resting activity, characteristic of the electroreceptors, is generated. From the paranode, a small axonal bulb projects into the packed cell layer. Distally, the bulb tapers to a fine axonal spine or filament which projects beyond the packed cell layer to terminate among the loosely packed cells, but without actually reaching the gland duct itself. From the base of each axonal spine, a lateral filament projects in the direction of adjacent axon terminals, forming a circle of branches between the ring of nerve endings surrounding the gland duct (Manger *et al.* 1995). Whether lateral filaments from adjacent axons actually make contact with one another remains uncertain. It has been speculated that the mucus in the gland duct represents a low-resistance pathway from the skin surface down to the nerve endings in the papillary portion of the gland.

The sensory mucous glands are distributed over the inner and outer surfaces of the bill of both the upper and lower jaws, and on the front surface of the shield. Each gland is supplied with up to 30 myelinated sensory axons. A total of 30 000–40 000 mucous sensory glands has been counted in the platypus bill, innervated by an estimated 380 000–640 000 stem axons. Taking the average number of 16 axons per mucous sensory papilla (Manger *et al.*

1995), it suggests that any one stem axon, on average, does not supply more than one or two terminals, implying a very fine grain for the innervation of the gland duct system. The mucous sensory glands are not scattered randomly across the bill but are arranged in rows to make a series of parasagittal stripes (Andres & von Düring 1984; Manger *et al.* 1995).

Sensory serous glands have essentially the same structural components as the sensory mucous glands but are smaller, have fewer axon terminals and are uniformly scattered across the surface of the bill. Their function remains to be elucidated. The similarity of their structure to that of the sensory mucous glands strongly favours the interpretation that they are part of the electrosensory system. We may, of course, have recorded from sensory serous glands unknowingly, but whenever we were able to associate a receptor structure with electroreceptor activity it was a sensory mucous gland.

(b) *Afferent responses*

When we made our first recordings from receptors in the skin of the upper bill of the anaesthetized platypus (Gregory *et al.* 1988), the very first impression was of a large volume of ongoing afferent traffic as recorded in a fragment of the infraorbital nerve. Recordings from functionally single afferents revealed that the ongoing irregular discharge, typically maintaining a rate of 30–40 Hz, could be modulated upwards or downwards by bipolar electrical stimulation of the moist surface of the bill. A cathodal pulse, i.e. a voltage pulse at the negative electrode, increased the discharge, whereas an anodal pulse reduced it. Moving a roving cathode across the bill surface while applying voltage pulses revealed a single spot of maximum sensitivity, less than 1 mm in diameter. When the spot was marked with fine insect pins and the piece of skin subsequently processed for histology, the pins were seen to straddle the mouth of a mucous sensory gland. This result was achieved on three separate occasions.

In two series of experiments, recordings were made from a total of 25 electroreceptor afferents (Gregory *et al.* 1988, 1989*a*). For each afferent there was only one receptive spot, making it unlikely that extensive branching of the axons takes place, other than perhaps some terminal branching within a gland. This result matches the anatomical estimate of a 1:1 or 1:2 ratio for axons to terminals. Because each gland is served by an average of 16 myelinated axons it poses the question of their role. A potential gradient between the inside of a gland and a remote source somewhere on the skin surface would be expected to be distributed approximately uniformly across the papillary epithelium of the gland so that rather similar signals would be generated at each afferent ending. Perhaps such a large number of parallel inputs from the one gland serves to improve signal-to-noise ratios and allows for signal amplification.

Receptor thresholds were measured to uniform field stimulation, achieved by placing the bill in a Perspex chamber filled with tap water and using a pair of large aluminium plate electrodes on either side of the bill (Gregory *et al.* 1989*a*). Multi-unit recordings from a coarse strand of infraorbital nerve produced a just-detectable response with a field strength of 4 mV cm^{-1}. This compares with thresholds for cerebral cortical evoked activity and behavioural responses in the microvolt range. One possible explanation for the lower behavioural threshold is that the multiple innervation of each mucous gland allows integration and averaging by the central nervous system of the activity in the population of axons coming from each gland. A simple, alternative explanation is that we somehow missed making recordings from the most sensitive receptors. Perhaps they are the sensory serous glands? Anatomical measurements and estimates from conduction velocity measurements (Gregory *et al.* 1989*a*) suggest that the diameters of afferents in the mucous sensory glands are about 8 μm, whereas those supplying the serous gland are somewhat smaller (Andres & von Düring 1988).

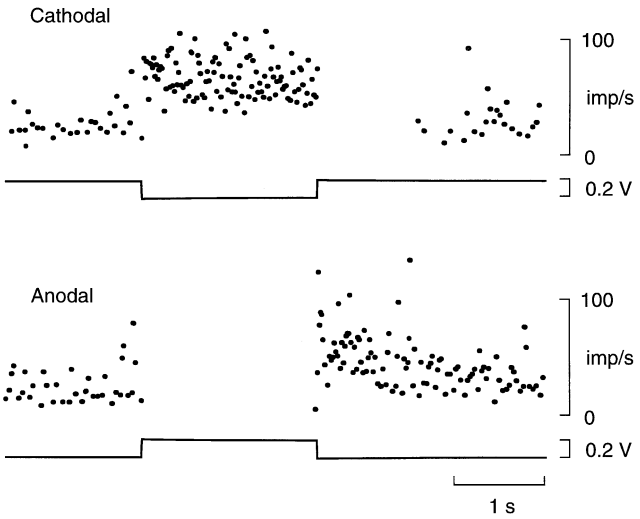

Figure 2. Responses of a platypus electroreceptor in skin of the upper bill to bipolar stimulation of the moist skin surface. The upper trace in each pair of records shows an instantaneous frequency display of action potential discharge, while the voltage pulse applied to the receptive field of a single electroreceptor is shown below. Each dot represents an action potential, and its height above zero (calibration on the right) is proportional to its instantaneous frequency. Upper records, cathode at centre of receptive field; lower records, anode at centre of field. A cathodal pulse (2 s) raises firing above the background level, followed by a brief period of silence at the end of the pulse, before firing resumes again. The anodal pulse silences the discharge, followed by a post-anodal rebound discharge.

The electroreceptors were examples of slowly adapting receptors with pronounced dynamic sensitivity. In response to a step-function cathodal pulse, receptors showed an initial peak in their discharge, which then adapted to a lower maintained rate. At the end of the pulse there was a brief period of silence before the receptor resumed its background activity (figure 2). In response to an anodal pulse the receptor was silenced for the duration of the stimulus. At the end of the pulse there was a post-anodal rebound discharge. For pulses of 2 s, the rebound discharge could last for 4 or 5 s, depending on the strength of the stimulus. While very long stimulus pulses were not tried, a cathodal pulse of 2 s produced a maintained response well above the resting level. The recordings suggested that the receptors were capable of sensing DC as well as AC signals. This point is mentioned because it has been suggested that receptors associated with the mucous sensory glands respond to AC signals, whereas a DC signal such as that associated with the 'galvanotactic response' might be signalled by sensory serous glands (Manger & Pettigrew 1995). A galvanotactic response is exhibited by a free-swimming platypus when it orientates towards a metal rod introduced into the water at a distance of 15–20 cm. Our own recordings all indicate both a DC and AC sensitivity which, we assume, is coming from receptors within the mucous sensory glands.

The large transients observed in the responses at the beginning and end of a voltage step led us to try stimulating with sinusoidal voltages (Gregory *et al.* 1989*a*). Thresholds in the range 50–100 Hz were lower by half compared with low-frequency signals, emphasizing the dynamic sensitivity of the receptors. In their original account, Scheich *et al.* (1986) suggested that the platypus could detect the EMG generated by the tail flick of a swimming shrimp at a distance of 5 cm. The tail flick had a fundamental frequency of about 140 Hz, putting it into the optimum sensitivity range of the receptors. Our current view about receptor responsiveness is that the platypus uses the dynamic sensitivity to detect high-frequency signals generated by moving prey, whereas the sensitivity to steady voltages is used for underwater navigation and obstacle avoidance.

The latency of a response to a step-function voltage pulse depended on the stimulus strength. For recordings from the infraorbital nerve at the base of the bill, it was 1.1–1.8 ms. When the conduction distance was taken into account, for 11 electroreceptors the mean delay in initiation of a response to suprathreshold stimuli was 0.8 ms. This is rather longer than the 0.1 ms required to set up an action potential by electrical stimulation of a nerve fibre (utilization time). Furthermore, rheobase for exciting electroreceptors (stimulus width for lowest threshold) was 20 ms compared with 1–2 ms for peripheral nerve fibres. Both the latency and rheobase measurements suggest that the primary event in electroreceptor excitation involves more than just the opening of voltage-gated cation channels.

Presumably, an adequate stimulus leads to modulation of the resting current responsible for the background activity in the afferent. Our measurements suggest that the stimulus–response relation is approximately symmetrical in the depolarizing and hyperpolarizing directions for stimulus pulses in the range from 0 to 20 mV cm^{-1} (Gregory *et al.* 1988). An important objective of future experiments will be to obtain information about the transduction process itself. For that it will be necessary to make direct recordings from the axonal spines and their lateral processes.

(c) *Central processing*

The electroreceptor afferents project to the cerebral cortex of the brain, and so are likely to evoke in the animal a conscious sensation. Nothing is known of the afferent pathway taken by trigeminal afferents in the platypus, or whether there is any processing of the information at the relays, as seems likely. By analogy with other mammals, the cell bodies of the electroreceptor afferents are likely to lie in the Gasserian ganglion, and the first synaptic interruptions would be in the principal trigeminal nucleus. The second-order neurons would project to the contralateral ventral posterior nucleus of the thalamus via the trigeminal lemniscus, and the third-order neurons would transmit the information to sensory cortex. Lesion experiments indicate the cortical activity in response to stimulation of bill skin arises at a depth of 1–3 mm, suggesting that the cells are in the pyramidal and ganglion cell layers (Iggo *et al.* 1992).

Evoked activity was recorded from the surface of the cerebral cortex in response to either local bipolar stimulation of the moist surface of bill skin, or to a uniform field generated between two aluminium plates located on either side of the bill in a bath filled with tap water. It was found that the projection was strictly crossed. Using both local and field stimulation there was no evidence of any uncrossed projection. Nor was there any evidence of any inhibitory projections, crossed or uncrossed.

Threshold for a response from the cortex was a field strength of 300 μV cm^{-1}. This is approximately 13 times lower than the 4 mV cm^{-1} measured for single receptors. Our preferred explanation for this discrepancy is that the multiple innervation of each gland allows integration and averaging of incoming information, perhaps also amplification along the projection pathway. The value of 300 μV cm^{-1} compares with 50–200 μV cm^{-1} obtained for a single cortical neuron by stimulating the bill with pairs of needle electrodes, 10 mm apart, held 1 mm above the surface of the bill skin (Manger *et al.* 1996).

Recordings of unitary activity showed that, unlike the receptors, none of the cortical neurons showed maintained responses to voltage pulses. Typically, there were only two or three impulses at stimulus onset, even with strong stimuli. Latency of a cortical-evoked response using field stimulation was about 10 ms, and for unitary responses it was 14–18 ms (Iggo *et al.* 1992). With needle stimulation, latencies were 26 ms for mechanically responsive units and 33 ms for multimodal units (Manger *et al.* 1996). The origin of this difference remains unclear, but an obvious possibility is the anaesthetic. In our experiments we used chloralose, whereas ketamine was used by Manger *et al.* Assuming (i) an axonal conduction velocity of 56 m s^{-1} (Gregory *et al.* 1989*a*), (ii) an impulse initiation time of 0.8 ms, (iii) a conduction path to cortex of about 120 mm, and (iv) a 2 ms delay at each of the two synapses, gives a central latency of 8.9 ms, not far short of the minimum value of 9.4 ms that we recorded (Iggo *et al.* 1992).

The region of the contralateral cortex from which activity could be evoked lay entirely within the boundary of the bill's somatosensory area plotted previously by Bohringer & Rowe (1977). It meant that there was no separate area dedicated specifically to the processing of electrosensory information. It was possible to plot an outline of the bill on the surface of the cortex by moving a concentric stimulating electrode across the bill and mapping the evoked potentials. The map showed the outline of the half-bill oriented dorsolaterally, its base towards the midline, the tip pointing slightly forwards, directed towards the lateral border. It was found that the cortical area assigned to the edge of the bill was represented many times more strongly than the upper surface. Although the density of mucous glands was greater on the edge than on top of the bill, this difference was insufficient to account for the difference in strength of the projection.

It was concluded that information coming from the edge of the bill is particularly important to the animal.

In a brief report, Langner & Scheich (1986), using the activity marker 2-deoxyglucose, showed that after electrical stimulation of the bill, the labelled areas of cortex were a series of rostrocaudally orientated rows reminiscent of the strip distribution of the sensory mucous glands across the upper surface of the bill reported by Andres & von Düring (1984). The cortical rows had a periodicity of 700–900 μm. Our own recordings did not reveal evidence of such rows. In fact, we had difficulty in getting sizeable recordings at all in response to stimulating the top of the bill. However, most of our measurements were made using surface recordings, so we may well have missed this organization.

Stimulating the bill electrically with needle electrodes, and mechanically with brushes, fine glass probes and pointed sticks, while recording activity extracellularly from single cells, revealed a total of four cortical fields (Krubitzer *et al*. 1995; Manger *et al*. 1996). The distinctness of each field was argued, based on the similarity of responses obtained within it, the preferred stimulus that evoked a response and the completeness of the representation of the body periphery within the field. The main projection area, SI, which is probably the area from which we had made our recordings, was characterized by the small receptive fields of the cortical neurons and the presence of cells that responded both to electrical and mechanical stimulation. Regions where cells responded only to mechanical stimulation were interdigitated with regions containing the bimodal cells. No examples were seen of cells that responded only to electrical stimulation of the bill.

The question of convergence of two stimulus modalities onto single cortical neurons had been raised earlier (Iggo *et al*. 1992). In those experiments a concentric needle electrode had been constructed which, when placed immediately over a region of skin, stimulated the electroreceptors. The electrode was attached to a mechanical stimulator so that it could also be used to apply controlled mechanical stimuli to the same site on the skin. Extracellular recordings of unitary activity in the cortex revealed cells that responded to both stimulus modalities. When electrical and mechanical stimuli were applied at short intervals, there was some evidence of occlusion of the discharge, suggesting that both stimuli were accessing the same cells.

The observations of Krubitzer *et al*. (1995) confirmed the existence of bimodal cells and showed that they had larger receptive fields than units responsive to only mechanical stimuli. Bimodal cells were associated with parts of the cortex staining less intensely for cytochrome oxidase, an activity marker, than mechanical units. This was related to the fact that mechanical units showed background activity, whereas bimodal units remained silent in the absence of a stimulus.

Threshold of cortical bimodal neurons to electrical stimulation of the bill was found to vary over a wide range, from 20 μV cm^{-1} to 2400 μV cm^{-1}. Response latency was about 25 ms, which became a little shorter during combined electrical and mechanical stimulation. The range of stimulus strengths between threshold and maximum was quite narrow, suggesting cells were either silent or fully activated. A series of modules was identified across the cortical surface. These were areas 500–800 μm wide in which the same area of bill skin was repeatedly represented. It was suggested that modules were so arranged across the cortical surface that, based on differences in cell thresholds, the direction of the source of a stimulus in relation to the bill could be encoded. Here the striped arrangement of the receptors across the bill's surface would provide additional directional information (Krubitzer *et al*. 1995).

(d) *Behaviour*

The experiments of Scheich *et al*. (1986) had established two important aspects of the electrosensory behaviour of the platypus. The animals appeared to be able to respond both to rapidly changing voltages and to steady voltages. That, in turn, led to the suggestion that its electric sense allowed the animal to detect moving prey as well as stationary objects with a potential gradient across them, such as underwater obstacles.

More recent experiments have shown that when a swimming platypus was presented with square wave pulses from a bipolar electrode, this produced reflex head movements towards the electrode and snapping at the electrode (Manger & Pettigrew 1995). After repeated presentations, the platypus no longer mouthed the electrode but still produced reflex head movements, called saccades by the authors. Pulse frequencies between 1 Hz and 16 Hz gave stimulus-entrained head movements. Threshold for a response was 50–60 μV cm^{-1}, producing a movement of 1 mm amplitude. Movement amplitude increased to 3 mm with a field strength of 1 mV cm^{-1}. The direction of the stimulating electrode from the bill, at which stimulus entrainment could be evoked at its greatest distances, was a position 80° lateral from the rostral pole and 20° ventral to it. This preferential axis was symmetrical for the two sides of the bill and was at right angles to the parasagittal strips of mucous sensory glands across the bill. Sensitivity of the animal to the stimulus varied over two orders of magnitude from the preferred orientation to the least sensitive direction. It was speculated that head saccades help the platypus locate the direction of a stimulus using reorientation of the head to present the most sensitive part of the bill to the stimulus.

(e) *Mechanoreceptors*

Although interest has centred on the electroreceptors in the platypus, given their unique place in the sensory biology of mammals, some new information has also become available about mechanoreceptors in monotremes. Indeed, during the experiments in which we made our first recordings of electroreceptors in skin of the platypus bill, we made a number of observations, in passing, of the properties of mechanoreceptors. Given that there is now evidence for bimodal cells in platypus cortex—cells that respond to both electroreceptor and mechanical inputs—the properties of mechanoreceptors have acquired new significance for the story of electroreception in monotremes.

The single most prominent structure in skin of the platypus bill to which a mechanoreceptive function has been assigned is the push rod. Push rods were first referred to by Poulton (1885). He described them as hair-like rods, projecting with a convex tip from the skin surface, surrounded by a slightly raised margin. At their base the push rods were seen associated with a number of lamellated corpuscles resembling Pacinian corpuscles. It led Poulton to speculate that, 'The obvious use of the rods is to supply special movable areas (of skin), yielding to surface pressure which is thus communicated to the terminal organs below'.

A more recent description of push rods was provided by Andres & von Düring (1984). The rod consists of a column of flattened spinous cells filled with tonofibrils and with many tight junctions between neighbouring cells, giving compactness and mechanical rigidity to the rod. Each rod is separated from the surrounding epidermis by a dermal papilla of much more loosely packed cells. This means that the rod is able to move relatively independently of adjacent tissue. The push rod is associated with four types of nerve endings, all of which are supplied by myelinated stem axons. There are two kinds of vesicle chain receptors, the central and the peripheral vesicle chain. As their name implies, these consist of a series of bead-like enlargements of the axon as it ascends towards the skin surface in the core of the push rod or near its edge. There are close attachments between the epidermal cells and the vesicular enlargements of the axon. There are between 7 and 13 of these central chains of beads supplied by 5–8 axons. It has been noted that the terminal portion of the central vesicle chain terminates only a few layers of cells from the skin surface (Manger & Pettigrew 1996). An average of 40 axonal branches from 20 stem axons supply the peripheral vesicle chain receptors, which lie at a depth of three cell layers from the edge of the rod. The peripheral vesicle chain receptors form a concentric circle of endings around the cluster of central vesicle chain receptors, separated from them by a distance of about 6 μm.

The base of the push rod is associated with two specialized receptors supplied by large myelinated nerve fibres, Merkel cell complexes and lamellated corpuscles. Among the cells comprising the base of the rod lie the Merkel cells, about 12 in number, and their associated nerve terminals, all supplied by just one or two axons. Between three and six lamellated corpuscles lie, in various orientations, immediately below the push rod. They are smaller than Pacinian corpuscles, being 60 μm long, compared with 1 mm in the cat and kangaroo, and have fewer lamellations, 13 compared with 30 in the kangaroo and over 100 in the cat (Quilliam 1963; Gregory *et al.* 1986).

Push rods are scattered uniformly across the surface of the bill, with the edge of the bill having the highest density. It has been estimated that the inner and outer surfaces of both the upper and lower jaws have a total of 46 500 push rods (Manger & Pettigrew 1996).

Despite the prominence of its structure and its relative abundance in skin of the bill, so far no recordings have been made of afferent activity that can unequivocally be associated with the push rod. A difficulty encountered with recordings made at the level of the infraorbital nerve in the platypus was that it was not possible to study mechanoreceptor responses until all electroreceptor afferents had been removed from the filament of nerve on the recording electrode. This was because the high level of background activity in the electroreceptors obscured all other responses.

Mechanoreceptor responses fell into three classes: rapidly adapting, slowly adapting, and receptors with intermediate properties (Gregory *et al.* 1988). It may be that the slowly adapting and intermediate units represented response variation within the same population, but the size of our sample was too small to establish this. However, both kinds showed some irregularity of their discharge and in that respect they resembled type I slowly adapting receptors, which are the Merkel receptors (Iggo & Muir 1969). Skin indentations of 20 μm amplitude were sufficient to evoke a response and strong stimulation produced rates of firing of up to 500 impulses s^{-1}. The rapidly adapting receptors were sensitive to vibration showing a 1:1 stimulus–response relation over the range 150–600 Hz. Threshold was lowest at 150–250 Hz. Above 600 Hz, responses became 1:2, and above 800 Hz the receptors no longer responded. It was assumed that the vibration receptors were the lamellated corpuscles.

Although a comparison with known receptor types in other mammals made it relatively easy to assign a function to the Merkel cell complexes and lamellated corpuscles, it remains unclear what role is played by the vesicle chain receptors. In future experiments, more attention should be paid to responses mediated by afferents at the smaller end of the Aα range and in the Aδ range, given that vesicle chain receptors are served by smaller axons than the other receptor types.

Pettigrew *et al.* (this issue) have measured water displacement and EMG activity produced by the tail flick of a freshwater shrimp, a common prey species of the platypus. They proposed that the displacement they measured was able to stimulate push rods at distances as great as 50 cm. Based on the measured differences in the time of arrival at the bill of the electrical and mechanical signals, and the presence in sensory cortex of neurons with different preferred intervals for facilitation of responses to bimodal inputs, it was proposed that distance was coded for by these neurons. Directional information was provided by the directionality of responses in the electroreceptor array in the bill stripes, as well as perhaps the push rods presenting with different angles towards the source of the signal.

In a more parsimonious interpretation, the electroreceptors act as short-distance teloreceptors, allowing the animal to detect nearby obstacles and swimming prey. The platypus will pursue the prey by following the potential gradient back to its source. The final attack phase is reinforced by feedback from mechanoreceptors as the tip of the bill actually makes contact with the prey. Perhaps, therefore, the electric sense in the platypus could be considered a 'distance touch sense' (Proske 1992).

5. THE ECHIDNA

When the story of electroreception in the platypus broke, an immediate, obvious question was whether all three representatives of the group possessed the sense or whether it was unique to the platypus. Certainly it was easier to imagine the need for an electric sense in an animal that spent most of its time in water, such as the platypus, than in a fully terrestrial animal like the echidna. Up to that time, in fact, there was no other known example of a fully terrestrial animal equipped with electroreception.

We had carried out a study of cutaneous receptors in the snout of the echidna some years previously (Iggo *et al.* 1985), but the thought of searching for electroreceptors had not entered our minds. In fact, with hindsight, some of the responses probably were from electroreceptors (see below). Once it was known that the platypus possessed an electric sense, we decided to search for evidence for a similar sense in the echidna. In the event we obtained behavioural and electrophysiological evidence for electroreception in the echidna.

(a) *Structure*

Our electrical recordings, followed by histological analysis of marked skin structures, established that, like in the platypus, the electroreceptors were the mucous sensory glands. There have been two recent reports of the structure and innervation of these glands (Andres *et al.* 1991; Manger & Hughes 1992).

About one-quarter of the mucous glands found in the skin of the snout of an echidna contain a sensory innervation. Interestingly, the sensory mucous glands are all crowded into the tip of the snout. In the lip region of the upper and lower jaw there are seven mucous sensory glands per square millimetre of skin. Each gland is surrounded by several non-innervated glands in a regular arrangement, suggesting some functional relationship. The general structure of the sensory mucous gland is similar to that in the platypus, although in a number of respects it is less specialized (figure 1). There is a coiled secretory portion in the subdermal region with a gland duct that ascends to the skin's surface. The mouth of the gland is separated from adjacent epidermal tissue by a sheath of flattened, keratinized cells. The elaborate floral array of keratinocytes of the platypus receptors is absent. The intra-epidermal portion of the gland exhibits a club-shaped enlargement, which is formed by an invagination of the epidermis. Between the epidermis and the gland duct there is a layer of densely packed cells, 2–3 cells thick and overlying it a layer of loosely packed cells. The wall of the duct itself is lined with cells that have microvilli on their luminal surfaces. Two kinds of nerve terminals have been identified in association with mucous sensory glands in the echidna (Andres *et al.* 1991). The type I ending resembles in a number of respects the terminals seen in the platypus receptors. A large myelinated axon terminates at a paranode in the germinal epithelium of the epidermal layer and an axonal spine projects from there towards the gland lumen. The paranode is filled with intracellular organelles and myelin figures. The terminal itself is about 5 μm in diameter and 30 μm long. It contains clusters of mitochondria and a receptor matrix comprising a tubular network but no cytoskeletal structures such as neurofilaments and microtubules. The type II terminals arise from small-diameter (2.5 μm) myelinated axons. These are filamentous terminals up to 200 μm long, which contain neurofilaments. Receptor matrix is present at restricted sites along the terminal and at the tip. Both type I and type II terminals end in the spinous cell layer without penetrating the layer of cells lining the lumen of the gland.

(b) *Afferent responses*

We recorded from receptors in snout skin of the anaesthetized echidna by subdividing fragments of the infraorbital nerve. During the first recordings that we made one important difference emerged between the receptors in the echidna and the platypus. Receptors in the echidna typically did not exhibit any background activity. The presence of electroreceptors only became apparent when voltage pulses were applied to the skin surface. Here it was important to distinguish between responses of electroreceptors and mechanoreceptors. In practice, this was not difficult as voltages required for maintained responses from electroreceptors were typically an order of magnitude lower than for excitation of mechanoreceptors.

Although receptors typically had no background activity, a number developed a resting discharge during the course of the experiment. The cause for this change remained unclear, but it was noted that wiping the skin with physiological saline acted as a powerful stimulus for the receptors, presumably as a result of the electrochemical gradient set up by the salt solution. When background activity was present, the rate was somewhat lower than that in the platypus, with a mean value of 18 impulses s^{-1} for the three units studied. Mean threshold for a response was 22 mV cm^{-1} (range 1.8–73 mV cm^{-1}) using field stimulation with the snout immersed in tap water. Bipolar stimulation showed that each receptor had a single punctate receptive field. Cathodal stimulation was excitatory and anodal stimulation inhibitory. When the unit showed no background activity the only sign of a response to anodal stimulation was a post-anodal rebound discharge. Peak firing rates were 100 impulses s^{-1}. Sinusoidal voltages produced responses over the range 0.2–300 Hz. Optimal stimulus frequency was 25–50 Hz. Threshold measured with sinusoidal voltages was typically lower than with step-shaped pulses, the lowest value obtained for a unit being 11 mV cm^{-1}. Estimates of conduction velocity of afferent axons using stimulus–response latencies and conduction distances gave values of 10–18 m s^{-1}, which is almost three times slower than for the platypus electroreceptor afferents.

Electroreceptors in both the echidna and platypus responded to rapid warming or cooling of the skin. Sustained cooling eventually silenced the unit (Gregory *et al.* 1989*b*). With hindsight, receptors that had been identified in a previous study of echidna snout skin as thermoreceptors were probably electroreceptors (Iggo *et al.* 1985). This raises the question of whether the skin is supplied with true thermoreceptors. Future studies should consider testing each presumed thermoreceptor for electroreceptor properties.

Consideration of the number and distribution of electroreceptors in the two monotreme species so far studied leads to the conclusion that this sense is of much less importance in the echidna than in the platypus. In the platypus, nearly half of the nerve fibres in the trigeminal nerve are associated with the electroreceptors, which are distributed across the entire surface of the bill. In the echidna, the receptors are found only in the tip of the snout, and they make up a much smaller fraction of the population of axons in the trigeminal nerve. Electroreceptors in the echidna appear to be supplied by smaller axons than in the platypus, have lower peak firing rates, and rarely show background activity. Interestingly, receptors in both species had generally similar response properties, cathodal stimulation being excitatory, anodal inhibitory. Curiously, the lowest receptor thresholds measured in the two species were also similar, 4 mV cm^{-1} for the platypus and 1.8 mV cm^{-1} for the echidna. Receptor threshold in the echidna corresponds closely to the measured behavioural threshold (see below), whereas in the platypus the behavioural threshold appears to be lower by at least two orders of magnitude.

(c) *Central projection*

The echidna has a highly folded cerebral cortex compared with the smooth cortex of the platypus. Somatosensory cortical fields in the echidna have been described by Abbie (1938), Lende (1964) and Ulinski (1984). The most detailed account comes from Krubitzer *et al.* (1995). These authors described four fields in somatosensory cortex, the field Sl corresponding to the primary receiving area. Here, neurons responding to cutaneous mechanical stimuli had the smallest receptive fields. Not unexpectedly, the snout representation took up a disproportionately large area of the cortex. Some neurons in field PV (parietal ventral) also responded to cutaneous stimuli. No attempt was made to record from neurons responsive to electrosensory inputs, although by comparison with the platypus, these should be sought in Sl. However, the task of finding such neurons is likely to be much more difficult in the echidna if only about one-quarter of the 400 eccrine glands in the snout tip are electroreceptors (Andres *et al.* 1991). That will mean a total of about 2000 axons subserving electroreception compared with about 500 000 axons in the platypus. Nevertheless, it will be important, in the future, to establish a cortical representation for electrosensory inputs in the echidna, to determine whether cortical neurons are arranged in any identifiable pattern and whether they include bimodal neurons, as in the platypus.

(d) *Behaviour*

Given the very much smaller electrosensory system in the echidna, the question might be asked, is this system nothing more than an evolutionary vestige, a remnant from the ancestral, platypus-like monotreme stock that gave rise to the modern echidna? We addressed this question by designing a forced-choice behavioural experiment with one animal (Gregory *et al.* 1989*b*). The animal was trained to press a lever in a tap water-filled trough to receive its food reward. Once this task was learned, which took several weeks of training, the animal was presented with two troughs one of which had a weak electric field across it. Whenever the animal chose the trough with the electric field, it received a food reward. This, too, the animal learned to do; in fact, it learned to do it rather quickly. It was then possible to systematically lower the strength of the field and observe the animal's behaviour. Between trials the field was switched at random between the two troughs. It was found that the animal could correctly pick the trough with the electric field across it, down to a field strength of 1.8 mV cm^{-1}, which corresponded to the lowest threshold obtained in recordings from electroreceptors.

That leaves the question, what role, if any, does the electrosensory system play during normal foraging behaviour? This remains another challenge for the future. One recent attempt has been made by Augee & Gooden (1992). Free-ranging echidnas fitted with radio-tracking transmitters had batteries, charged or flat, buried in their path. The animals dug up and investigated charged batteries significantly more often than non-charged objects. It is also interesting to note that it has been remarked on that echidnas have an uncanny ability to detect live prey when it is buried in moist soil (Smith *et al.* 1989). Echidnas become particularly active after rain and, when observed feeding, they appear to probe the soil in an exploratory fashion with their nose. Suddenly, they will begin to dig furiously to expose a moving beetle or caterpillar. It is conceivable that the movements of the prey generate short-range electric signals that the electroreceptors in the snout tip are able to pick up. Perhaps the reason why the echidna always has a runny nose is to maintain a low resistance pathway between sources of electric current in the soil and the electroreceptors.

(e) *Mechanoreceptors*

Here, discussion will be restricted to the structure unique to the echidna and platypus, the push rod and its associated nerve endings. Recent descriptions of push rods in echidna snout skin have been provided by Andres *et al.* (1991) and Manger & Hughes (1992).

In their general appearance the push rods, which are distributed uniformly across the entire surface of the snout, appear to be a less specialized, less differentiated structure than the platypus push rod (figure 3). The rod itself is composed of a column of flattened, spinous cells, which are cross-linked by tight junctions. The tip of the rod emerges at the skin surface with a dome-like projection. The rod is typically 300 µm long with a diameter of 50 µm. Along part of its length the push rod remains separated from adjacent regions by connective tissue papillae which gives it a degree of independent mobility.

An average of ten myelinated axons and their terminations are associated with each push rod. There are four kinds of endings, the central vesicle chain receptors, peripheral vesicle chain receptors, Merkel cell complexes and lamellated corpuscles. In the basal, expanded portion of the push rod there are 18–26 Merkel cells supplied by about four axons, and between five and eight lamellated corpuscles, supplied by 2–3 axons, lie immediately below the push rod. The close association of Merkel cell complexes and lamellated corpuscles with the push rod strongly suggest that it has a mechanosensory function, providing a means of selectively transmitting surface stimuli down to the end organs lying in the deeper layers.

We have attempted, in two separate sets of experiments, to associate push rods with responses of mechanoreceptors (Iggo *et al.* 1985, 1996). In the more recent study, attempts were made to systematically sample the infraorbital nerve, making recordings from larger, multi-unit strands of nerve. The hypothesis was that mechanical stimulation of a discrete region of skin would selectively evoke activity in all of the mechanoreceptors associated with the push rods located in that area. However, it was found that adjacent afferents in the nerve often had widely separated receptive fields, suggesting that at the level of the recordings,

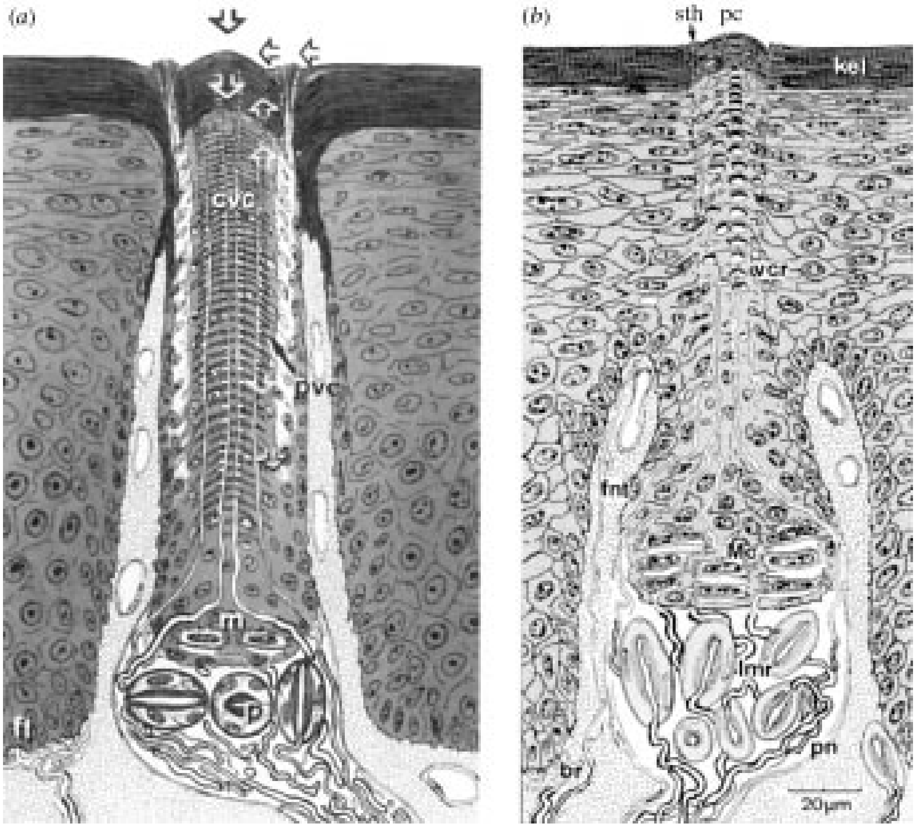

Figure 3. Push rods in skin of the platypus bill and echidna snout. (*a*) Platypus push rod: cvc, central vesicle chain receptors; pvc, peripheral vesicle chain receptors; m, Merkel cell receptor; p, paciniform corpuscle; ft, free nerve terminal. The arrows indicate the postulated directions in which the push rod is able to move. The width of the push rod in the region of the Merkel cells is approximately 80 µm. Reproduced, with permission, from Andres & von Düring (1984). (*b*) Diagram of echidna push rod. The nerve supply includes the central and peripheral vesicle chain receptors (vcr), the Merkel complexes (Mc) and lamellated corpuscles (lmr). The perineural sheath (pn), enclosing the nerve fibre bundle, extends to surround the lamellated corpuscles. A borderline receptor (br) is located with its free nerve terminal (fnt) in the papilla of connective tissue alongside the push rod. The push rod cone (pc) is enclosed by a layer of vertically orientated, keratinized cells (sth) within the outer keratinized layer (kel). Reproduced, with permission, from Andres *et al.* (1991).

afferents coming from different regions of snout skin were already thoroughly intermixed. That is, the population of afferents associated with a particular push rod did not travel together in the nerve.

An interesting observation made in both of the above-cited works was that most responses observed were from slowly adapting receptors. Some of these had a regular discharge in response to skin indentation, typical of type II slowly adapting mechanoreceptors, the Ruffini endings (Chambers *et al.* 1972). Others had a more irregular discharge typical of type I receptors, the Merkel cell complexes (Iggo & Muir 1969). One small group of units was rapidly adapting and showed responses to vibrations over the range 50–800 Hz, presumably representing responses coming from the lamellated corpuscles.

Careful mapping of receptive areas for type I receptors showed that the region of maximum sensitivity was well below 100 µm in diameter. On two occasions the centre of the receptive field of a slowly adapting receptor was marked with insect pins and the outer layers of skin in the centre of the field penetrated with a needle coated with the dye fast green. At the end of the experiment the marked region of skin was excised and processed for histological examination. In sections in which fast green was present, two push rods could be identified within 100 µm of the marked site. Although the discreteness of the receptive fields of the receptors and the close proximity of push rods to the marked area is suggestive of an association between the two, some uncertainty remains. It will require direct recordings from identified receptors to finally establish the role of push rods as structures transmitting mechanical stimuli. Furthermore, an attempt should be made to record as close to the skin as possible, where the mixing of afferents from different areas remains at a minimum.

Additional evidence in support of a mechanosensory role for push rods comes from consideration of sensory receptors in other animals. A structure resembling the push rod is Eimer's organ in skin of the mole. It consists of a column of epidermal cells with a single nerve fibre at its centre. Below the column are Merkel cell complexes and lamellated corpuscles (Quilliam 1966; Catania 1995*a*,*b*). Recordings from the cerebral cortex of the star-nosed mole revealed multi-unit discharges with both phasic and tonic components in response to mechanical stimulation of the star (Catania & Kaas 1995). Given that Eimer's organs resemble push rods and that the star of the star-nosed mole is not supplied with any other large receptor structure, this is the best evidence yet that push rods are mechanoreceptors.

Finally, it is interesting that both in the echidna snout and platypus bill there is an extensive venous cavernous system in dermal and subdermal layers. The echidna snout could therefore be considered as containing erectile tissue which, when engorged with blood, would lead to an outward bulging of the skin surface and thus allow for better mechanical contact to be made with the surroundings. That, in turn, would be expected to sensitize its push rod system. Is it possible that, during its nose probes, as the echidna closes in on a prey item, it is able to raise the sensory acuity of its mechanosensory system and so facilitate the final attack phase?

6. THE LONG-NOSED ECHIDNA (*ZAGLOSSUS*)

Relatively little is known about sensory receptors in the beak of the long-nosed echidna. This is probably due to its extreme rarity. The first person to comment on the rich array of 'touch organs' in nose skin of *Zaglossus* was Kolmer (1925). He observed both sensory innervated 'sweat' glands as well as a regular array of papillae containing Merkel cells. More recently, Manger *et al.* (1997) have described both sensory innervated mucous glands and push rods in skin of the nose of *Zaglossus*. The mucous glands resemble in a number of respects the mucous sensory glands of the platypus but are supplied by fewer axons. The distribution of sensory innervated glands appears to be restricted to skin of the front third of the nose. There were about 12 such glands per square millimetre of the skin. Interestingly, there appeared to be many more of these gland receptors in *Zaglossus* than in the short-nosed echidna. Estimates give 40 000 gland receptors for the platypus, 3000 for *Zaglossus* and 100 for *Tachyglossus*. All of the mucous glands seen in *Zaglossus* appeared to be innervated. There were no non-innervated glands as are found in *Tachyglossus* and *Ornythorhynchus*.

Push rods, resembling those found in *Tachyglossus*, were found in skin of the front of the beak. They often lay adjacent to sensory mucous glands. The details of their structure remain to be resolved. Based on the relative numbers of innervated mucous glands in *Zaglossus* and *Tachyglossus*, Manger *et al.* (1997) concluded that *Tachyglossus* had virtually completely lost the use of its electroreceptive system, whereas *Zaglossus* had been forced to become more limited in its range, being restricted to the wet mountain forests of New Guinea. *Zaglossus* locates earthworms and insects in the damp leaf litter on the forest floor, which it probes with its beak and scratches with its claws (Griffiths 1978). It is conceivable that electrical activity associated with moving prey items helps *Zaglossus* find its food.

7. CONCLUSIONS

Inevitably, when a relatively small group of investigators studies an entirely new sensory system in animals which are rather rare and have to be caught in the wild, it is not surprising that a lot of the information remains fragmentary. An issue of particular importance for resolution by future investigators is the relationship between the electrosensory and mechanosensory systems and what this means for sensory perception in the platypus. Another important matter that needs to be resolved is the difference in response properties of mucous sensory and serous sensory glands, given that both are likely to be part of the electrosensory system. Why does each gland receive such a dense polyneuronal innervation? What are the main events in the stimulus transduction process? What are the properties of the afferent pathways to the brain and what is the significance of the multiple representation of different bill areas across the surface of the cerebral cortex? Why is the bill edge so strongly represented?

For the echidna, the outstanding unanswered question must remain the role, if any, of its electrosensory system in normal foraging behaviour. Is it safe to conclude that the echidna has virtually completely lost its electroreceptive system (Manger *et al.* 1997)? Is this sense relegated to being nothing more than an evolutionary vestige? Certainly, the evidence suggests that when necessary the echidna can make use of its electric sense to locate food (Gregory *et al.* 1989*b*). Other matters for future investigations are the central projection of electrosensory information in the echidna and the function of the push rods. If push rods represent an efficient means of transmitting mechanical stimuli from the skin surface to the receptors in the deeper layers, why did such a system only evolve in moles and monotremes? Is an important consideration the venous cavernous system found in the noses of these two groups of animals?

The importance of this kind of research involving unusual sensory systems in diverse groups of animals is that it provides us with a broader perspective of the design and operation of such systems. The new knowledge acquired will not only extend our understanding of animals, but it will help to give us better insight into our own sensory experiences.

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