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# RESPONSES OF ELECTRORECEPTORS IN THE PLATYPUS BILL TO STEADY AND ALTERNATING POTENTIALS

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SUMMARY

1. This is a report of further observations on the response characteristics of electroreceptors in the bill of the platypus, *Ornithorhynchus anatinus*, first described by Gregory, Iggo, McIntyre & Proske (1987).

2. The main finding is that, with the bill immersed in water, applying a potential difference between large plate electrodes on either side of the bill, produced detectable responses in a population of electroreceptors to field strengths as low as 4 mV $cm^{-1}$. Threshold for individual receptors lay between 4 and 25 mV $cm^{-1}$.

3. An electric dipole placed in the water close to the receptive field could also elicit responses, threshold being lowest when the cathode was near the centre of the field. On several occasions the most sensitive spot was seen, under the microscope, to correspond to the mouth of a mucous sensory gland (Andres & Von Düring, 1984). Response intensity fell when the dipole was moved further away, the drop being less steep in a direction over the top of the bill towards the mid-line.

4. For individual receptors the latency of the first impulse initiated by supramaximal voltage pulses was 1·1–1·8 ms. Latencies tended to be shorter when the site of the receptor lay closer to the recording electrodes. Plotting each latency against conduction path length for eleven receptors gave an approximately linear relation from which was calculated an average axonal conduction velocity of 56 m $s^{-1}$. The plot yielded an estimate of impulse initiation time of 0·8 ms. It is argued that this is too short to include a synaptic delay. A peripheral synapse is found in all non-mammalian electroreceptors.

5. Electroreceptors responded to both steady and rapidly changing potential gradients. For ramp-shaped gradients of 1–50 V $s^{-1}$ peak firing rate was approximately proportional to log stimulus velocity. In response to sinusoidal potential changes a 1:1 relation between each afferent impulse and the peak of the stimulating waveform could be obtained over the range 12–300 Hz. Threshold was at its lowest at 50–100 Hz. Tuning curves measured with the bill immersed in water were little different from those obtained by focal stimulation with the bill in air.

6. It is concluded that platypus electroreceptors, supplied by the trigeminal nerve, and which are therefore not part of the acoustico-lateralis system as in non-

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mammalian electroreceptors, are also unique in not having a peripheral synapse. Furthermore, they are able to respond to both steady and rapidly changing voltage gradients. Receptor threshold measured with the bill under water is significantly higher than recent estimates of the behavioural threshold reported by Scheich, Langner, Tidemann, Coles & Guppy (1986).

## INTRODUCTION

In a recent study we reported the presence of electroreceptors in the bill of the platypus *Ornithorhynchus anatinus* (Gregory, Iggo, McIntyre & Proske, 1987, 1988; Iggo, Proske, McIntyre & Gregory, 1988). Responses were recorded in the trigeminal nerve to weak cathodal pulses applied with platinum electrodes across the moist surface of the bill. For each receptor a discrete spot of maximum sensitivity could be localized with a roving cathode. Anodal stimulation suppressed on-going activity. Since the platypus normally feeds under water, presumably using electrolocation to detect moving prey (Scheich, Langner, Tidemann, Coles & Guppy, 1986), an important question which remained unanswered was what was the sensitivity of the receptors to electric fields in an aquatic environment.

Here we report further observations on the responses of electroreceptors in the platypus, their sensitivity to alternating potentials at different frequencies and the latency to square-wave pulses. In particular, activity has been recorded during application of electric fields with the bill underwater. Using field stimulation, we confirm our earlier findings that these receptors are responsive both to steady and to rapidly changing potential gradients.

## METHODS

The two animals used in these experiments were caught in nets in the wild. To minimize the effects of stress on capture, both received an intramuscular injection of 1 mg of dexamethazone immediately after removal from the net. One animal, a 2·4 kg male, was immediately taken to the laboratory and the experiment commenced straightaway. The other animal, a 1·1 kg female, was kept for 2 days in a glass tank partly filled with water. Bricks were placed in the tank so that it could climb out of the water and sit in air or remain in the water, as it chose. This animal fed freely on small fish put into the tank and remained in excellent condition for the holding period.

Anaesthesia was induced with an intraperitoneal injection of chloralose at a dosage of 60 mg (kg body weight)$^{-1}$. A tracheal cannula was inserted. Respiration soon became shallow and irregular and both animals were artificially respired for the duration of the experiment, using an open-circuit pump, at a rate of 14 breaths min$^{-1}$. The respiratory volume was adjusted to maintain expired $CO_2$ concentration close to 5%, measured with a Datex monitor. Heating was provided by an electric blanket with feed-back control from a cloacal probe. The normal body temperature of 32 °C was maintained within 1 or 2 degrees throughout the experiment.

The head was held between two pins driven lightly into the skull. The infraorbital branch of the trigeminal nerve was exposed on the left side after collapsing the eye and removing part of the temporal bone. Because large blood vessels run within the nerve, it was not transected. Instead, strands were dissected from the exposed, lateral surface of the nerve and cut centrally. These strands were subdivided further on a glass dissecting plate to obtain filaments containing only one, or a few functional afferent fibres. Afferent activity was recorded with bipolar platinum electrodes, displayed on a digital oscilloscope and stored on flexible disc, either as action potentials or as an instantaneous frequency display, after passage through a time–amplitude window discriminator (BAK). The multiunit activity in some nerve filaments was rectified and integrated before being recorded, using a circuit which had a time constant of 0·02 s.

Electrical stimulation of receptors in the bill was carried out in a number of ways. Receptors were located, with the bill in air, by exploring the surface with a fine wire cathode, the fixed anode being elsewhere on the bill. The most sensitive spot having been located, focal stimuli of various shapes, amplitudes and durations were delivered through this electrode.

In one experiment, approximately uniform potential gradients and potential fields set up by a roving dipole were used as stimuli with the bill immersed in tap water (resistivity about 30 kΩ cm; since local tap water is untreated, resistivity values are likely to be similar to those in the animal's normal habitat). To achieve this, the bill was placed in an open, water-filled tank about 10 cm wide, 10 cm long and 6 cm deep, made of acrylic sheet. The bill projected into the tank through a hole at one end. A piece of thin latex rubber sheet attached with cyanoacrylate adhesive to the 'shield' at the proximal end of the bill and to the tank formed a watertight seal. Aluminium plate electrodes measuring 10 × 6 cm were placed at either side of the tank to establish an approximately uniform electric field when a potential difference existed between them. The potential gradient was thus at right angles to the antero-posterior axis and, since the left side of the bill was tilted up for access to the orbit, was at about 45 deg to the animal's normal horizontal plane, from upper right to lower left. A 1 cm dipole at various distances from the bill and at a number of different orientations was also used as a stimulus while it and the bill were in water. Rectangular and triangular stimuli were derived from an isolated stimulator (Grass SIU5) supplied with appropriate waveforms. Sinusoids were derived from a function generator, AC-coupled to remove any DC component of the generator's output. Stimulus amplitude was monitored as the voltage between the electrodes.

To estimate afferent conduction velocity, latencies were measured to strong rectangular cathodal stimuli delivered through an electrode at the site where sensitivity was greatest. The length of the conduction path was taken to be the straight-line distance between the stimulating cathode and the nearest recording electrode.

## RESULTS

### *Mechanoreceptors*

Responses were recorded from a total of eight receptors identified as mechanoreceptors and from nine identified as electroreceptors. There was no difficulty in distinguishing between the two classes of receptor. Stimulating pulses of 10 V or more were required to elicit intermittent activity from mechanoreceptors while stimuli in the millivolt range were adequate for electroreceptor excitation. Electroreceptors were insensitive to all but the most gross mechanical stimuli (Gregory *et al.* 1988). The mechanoreceptors included four units which were rapidly adapting in their response to a sustained stimulus. Vibration applied to the skin surface elicited maintained, frequency-locked, 1:1 responses over the stimulus range, 10–500 Hz. A fifth receptor was slowly adapting, maintaining a discharge for the duration of an applied mechanical pulse. The remaining three units were not studied in any detail. Conduction velocity measured for one unit with rapidly adapting responses was 32 m $s^{-1}$. This receptor appeared to be excited by pressure applied to a surface structure which was probably a push rod (Andres & Von Düring, 1984). When the animal's bill was fully immersed in water there were no obvious changes in the responses of mechanoreceptors to maintained or intermittent stimuli. No further observations were made on mechanoreceptors.

### *Electroreceptors*

Each of the nine electroreceptors could be localized to a discrete spot by using a roving cathode to explore the moist bill surface. Inspection of the area under the microscope revealed, for four of the receptors, in confirmation of a previous report (Gregory *et al.* 1988), that the spot corresponded to the mouth of a large mucous

sensory gland (Andres & Von Düring, 1984). For the remaining five units the site of maximal sensitivity was not accessible to inspection under the microscope since it lay on the inside of the upper lip or on the edge of the shield.

*Field stimulation*

An important issue and one which had not been resolved in our prevous study was the sensitivity of electroreceptors to electric fields underwater. Therefore during part of one experiment the bill was immersed in tap water and responses recorded to both steady and alternating fields. In this way it was hoped to obtain measurements of receptor threshold under conditions similar to those used to determine behavioural thresholds (Scheich *et al.* 1986).

We first tried to obtain some indication of the population response of electroreceptors to uniform field stimulation. To achieve this a rather coarse filament of nerve containing many afferents was dissected free and the on-going activity integrated. Here it should be remembered that almost all electroreceptors show resting activity while none of the mechanoreceptors studied so far do, so that the integrated signal derives mainly from electroreceptors. With the bill under water, a potential gradient of 4 mV $cm^{-1}$ applied across the plate electrodes and with the cathode closer to the receptors produced a just-detectable increase in integrated signal. Reversal of electrode polarity produced a reduction in signal. In practice it was found that small decreases in activity were more readily detected than small increases.

An attempt was made to measure the stimulus–response relation for the population of receptors in the filament. Step function pulses, 200 ms in duration, were applied across the stimulating plates while recording the integrated signal. Activity increased in proportion to the size of cathodal pulses and with anodal pulses quickly reached a minimum value (Fig. 1). The cathodal pulse was increased up to a point where it began to elicit visible reflex movements of the bill.

The records of integrated activity include electrical artifacts associated with the onset and termination of the stimulating pulse. The response was therefore measured 170 ms after the onset of the pulse, at a time when the artifact was negligible, and is plotted against stimulus strength in the lower part of Fig. 1. The level of activity in the absence of any stimulus has been designated 0. A cathodal stimulus of 4 mV $cm^{-1}$ gave a measurable response ($T$). An anodal stimulus of $-104$ mV $cm^{-1}$ produced the signal minimum ($-1{\cdot}7$), representing therefore complete suppression of activity. Cathodal pulses of increasing amplitude produced larger responses in an S-shaped relation. It is of interest that there is no sign of response saturation with strong cathodal pulses, in contrast to the behaviour of single units (Gregory *et al.* 1988). Perhaps at higher stimulus strengths receptors are recruited which have high thresholds to the field with this particular orientation.

Some measurements were made of changes in the level of integrated activity in response to fields set up by a 1 cm dipole placed in the water at various distances from the centre of the receptive field. Exploration of the bill surface had shown that electroreceptors with afferents in the filament used for recording came from an area bounded by the dashed line in the left-hand drawing of Fig. 2. When the dipole was placed underneath the bill even strong stimuli did not elicit a detectable response.

With strong shocks it was always important to make sure that they produced no reflex movements, as these excited particularly mechanoreceptors. With the dipole 1 cm from the edge of the bill, in line with it, and the cathode closer to the bill, a

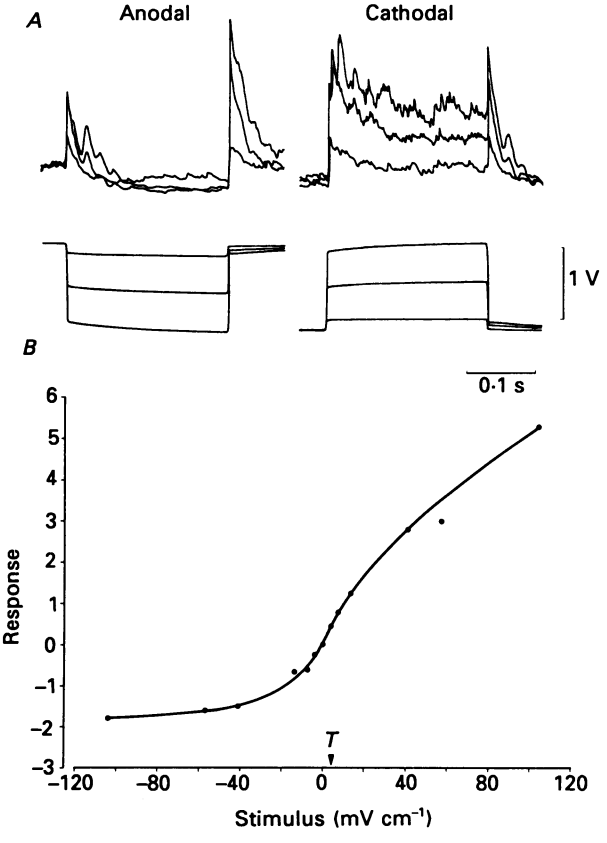


Fig. 1. Uniform field stimulation. *A*, integrated activity recorded in a strand of trigeminal nerve containing afferents from a number of electroreceptors located in the bill. The bill was immersed in tap water. Upper traces, integrated activity; lower traces, three superimposed 200 ms step-function stimuli applied between plate electrodes 10·5 cm apart on either side of the bill. When the electrode nearer to the receptors was made the cathode, receptor discharge increased, while with reversed polarity the discharge decreased, followed by rebound excitation at the end of the stimulus. Electrical artifacts associated with the onset and termination of each stimulus were included in the integrated signal. *B*, level of integrated activity recorded 170 ms after onset of the stimulus plotted against stimulus amplitude. Response = amplitude of integrated activity, scaled in arbitrary units relative to the resting discharge = 0. Cathodal stimuli shown as positive, anodal as negative.

stimulus of 3·9 V produced a level of integrated signal of +2·7 (Fig. 2). Threshold in this position was 1·2 V. If the cathode was brought very close to the bill edge threshold fell to 220 mV. If the electrode was now rotated, keeping the position of the cathode constant but bringing the anode close to the edge of the bill, the recorded signal was −1·5, representing virtually complete suppression of activity. Still keeping

the position of the cathode the same, when the anode was made to lie parallel to the bill but in a direction towards the back of the head, the signal was −0·2 indicating virtually no effect. With both poles parallel to the bill but the anode facing towards the front the signal was +1·4 (Fig. 2).

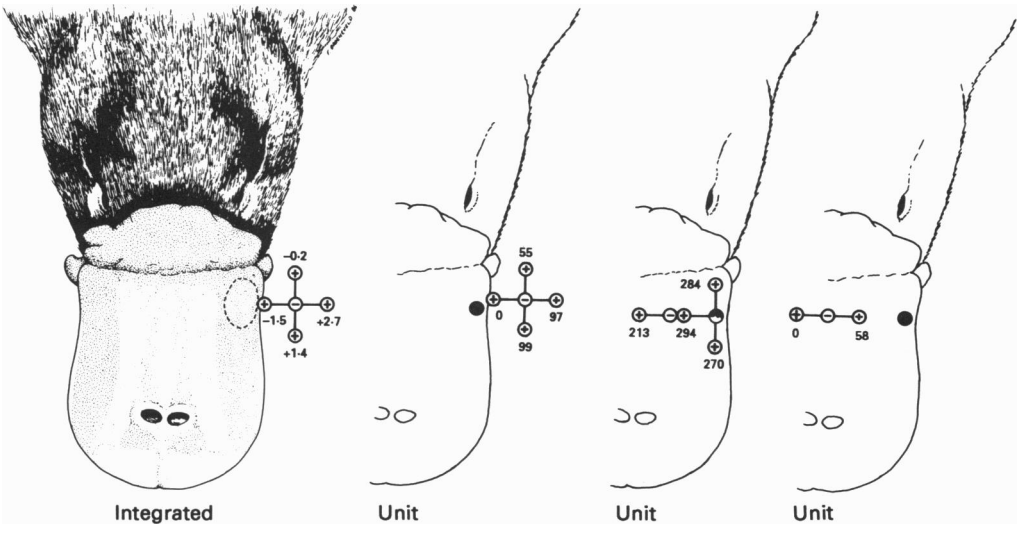


Fig. 2. Stimulation of electroreceptors with an electric dipole while the bill is immersed in tap water. The full outline of the head on the left indicates the border of the receptive field on the bill (dashed line) for a number of receptors whose afferents all ran in the same strand of nerve. The numbers indicate the level of integrated activity recorded in the nerve in response to a 200 ms step stimulus of 3·9 V applied across the dipole, for four different orientations of the electrode, each time keeping the position of the cathode constant at 1 cm from the edge of the bill while rotating the anode. The three partial outlines on the right give the response intensity, in impulses per second, of a single identified receptor with receptive field shown by the filled circle. The second figure from the left shows unitary responses for the same positions from which the integrated activity had been elicited. The two right-hand figures give responses when the dipole was progressively moved across the bill.

This experiment was carried further by dissecting from the strand of nerve from which the population responses had been recorded, a piece containing a functionally single electroreceptor afferent. The receptive field for the unit is shown in Fig. 2. Several electrode positions have been drawn in on the outlines of the bill, and the numbers represent the mean rates of firing recorded during a 5 V stimulating pulse, 200 ms in duration. The second figure from the left gives the same electrode positions as were used for recording the population response and the third and fourth show additional positions. Notice that the highest firing rates were elicited with the cathode over the receptive spot, while the orientation of the anode made little difference. As the dipole was moved to the left, across the bill, or to the right, away from it, responses became weaker although the fall-off in response was more gradual across the bill. With the dipole at about the mid-line, 3 cm from the receptive spot,

some response could still be detected (58 impulses $s^{-1}$, figure on the right). The conclusion from this experiment is that both integrated activity and single units show strong directional sensitivities to voltage gradients.

Thresholds for uniform field stimulation measured on three single electroreceptors were 4, 6 and 25 mV $cm^{-1}$.

*Latency*

The latency of the response to a supramaximal voltage step with the cathode over the most sensitive spot varied between 1·1 and 1·8 ms, being longer when the distance

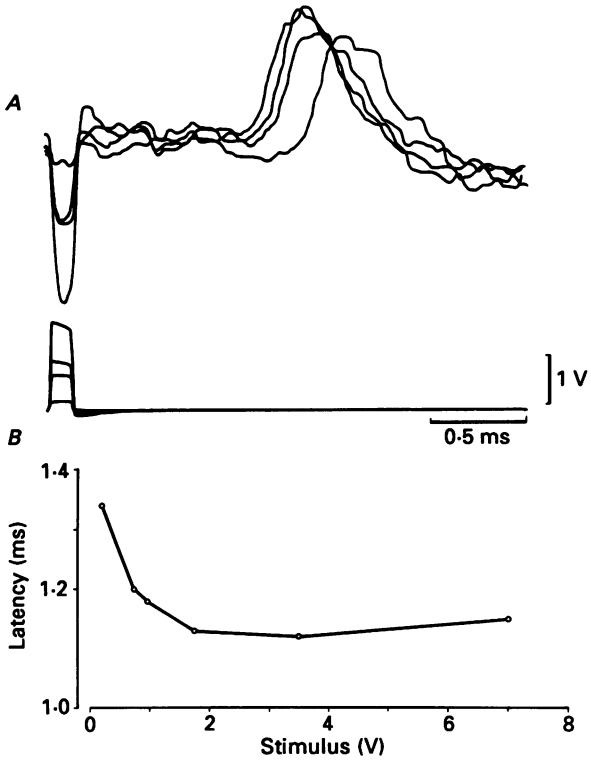


Fig. 3. Latency of impulse elicited in an electroreceptor by 0·1 ms voltage pulses. *A*, as stimulus strength is increased (lower trace) there is a progressive reduction in latency of the recorded action potential (upper trace). *B*, plot of latency *versus* stimulus strength shows that 2 V or more are required to achieve the minimum latency for this receptor (1·1 ms).

between the receptive spot and the recording electrodes was greater. Therefore, some of the delay can be accounted for by axonal conduction time. There was measureable latency variation when using stimuli close to threshold and a progressive reduction in latency at stronger stimulus strengths (Fig. 3). For the receptor in Fig. 3 the distance between the identified gland pore, beneath which the receptor presumably lay, and the first recording lead was 20 mm. The minimum latency was 1·1 ms, giving a calculated conduction velocity of 18 m $s^{-1}$. Values for eleven receptors (three values

are included from a previous series of experiments) ranged between 15 and 30 m $s^{-1}$ (mean 24 m $s^{-1}$). These must obviously be underestimates as at least some of the latency will include the impulse initiation time. Estimates from electronmicrographs give approximate axonal diameters of 8 $\mu$m for axons innervating gland duct receptors (K. Andres, personal communication). If the relation between axonal conduction velocity and fibre diameter is about 6 (Hursh, 1939), a diameter of 8 $\mu$m would give an estimated conduction velocity of 48 m $s^{-1}$. For the receptor in Fig. 3 the estimate of axonal conduction time is therefore about 0·5 ms, leaving an impulse initiation time of 0·7 ms.

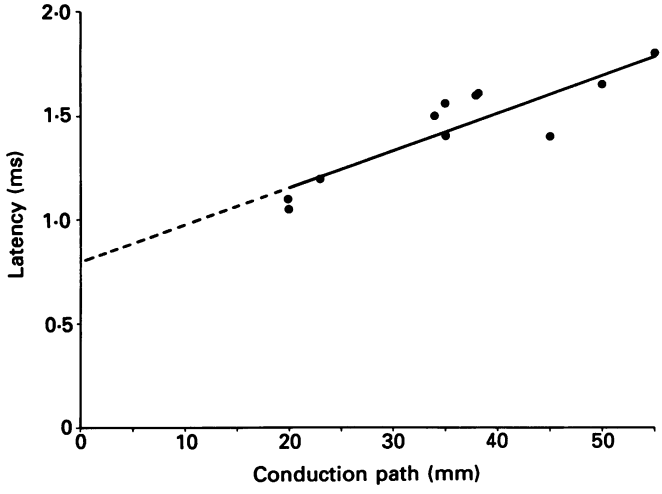


Fig. 4. A plot of latency of the first impulse elicited in response to a voltage step against conduction path for eleven identified electroreceptors. Data for three of the receptors came from a previous series of experiments. The path length was determined by measuring the distance between the point of maximum sensitivity on the bill surface for that receptor and the position of the first recording lead. Reciprocal of slope of regression line indicates average conduction velocity of 56 m $s^{-1}$. Intercept gives an impulse initiation time of 0·8 ms.

The proportionality between the measured value of latency and the length of the conduction path suggested that the principal determinant of latency was axonal conduction time and that impulse initiation time did not differ very much between receptors. A plot of latency against conduction distance for the eleven units is shown in Fig. 4. The regression line gives a conduction velocity of 56 m $s^{-1}$. The intercept on the ordinate was 0·8 ms. The data from this sample of units therefore suggest that, on average, axons serving electroreceptors conduct at 56 m $s^{-1}$ and the overall latency includes an impulse initiation time of 0·8 ms.

*Responses to dynamic stimuli*

In our original observations of platypus electroreceptors it had been noted that they responded both to steady potential gradients and to rapidly changing potentials. The sensitivity to alternating potentials was thought to provide the basis for the

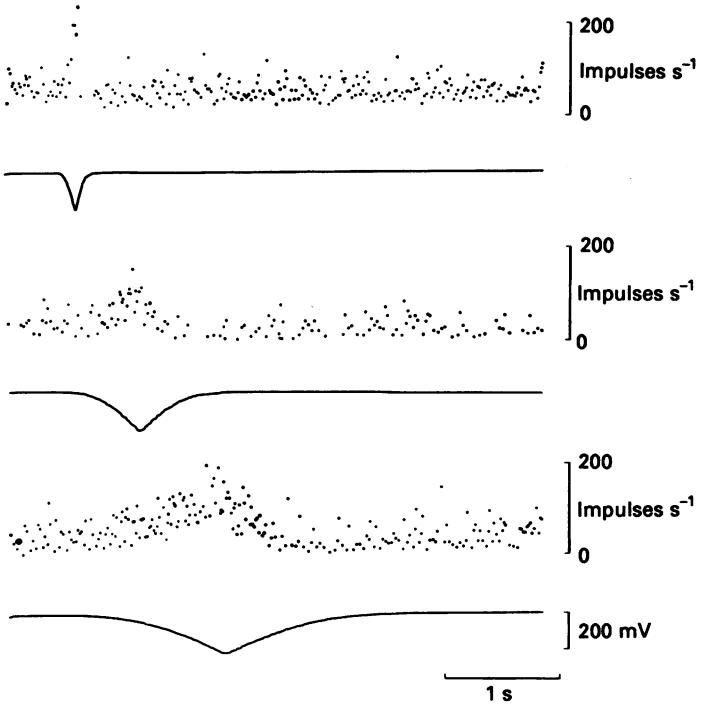


Fig. 5. Response of electroreceptor to focal stimulation of the moist bill surface with a pair of platinum electrodes with the cathode over the point of maximum sensitivity. In each of the three pairs of records the upper trace is an instantaneous frequency display of receptor discharge in response to a triangular voltage pulse (lower traces). The more rapidly rising voltages elicit higher peak firing rates from the receptor.

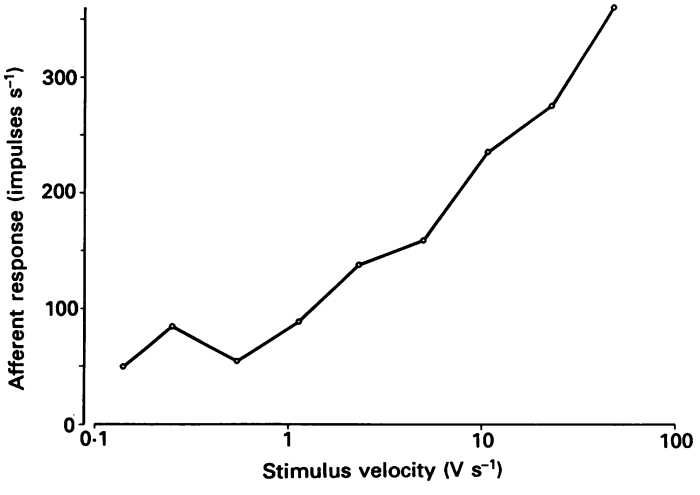


Fig. 6. Relation between afferent response (peak rate minus resting rate) and stimulus velocity over the range 0·1–50 V s$^{-1}$.

platypus' ability to detect moving prey. Behavioural evidence indicates that the platypus is able to respond to potentials generated by muscular contraction associated with the tail flick of a fresh-water shrimp (Scheich *et al.* 1986; Gregory *et al.* 1987).

Here we have examined further the dynamic sensitivity of electroreceptors. All of the measurements were made with the bill out of water, the stimulating electrodes being in contact with the moist surface of the skin and the cathode over the point of

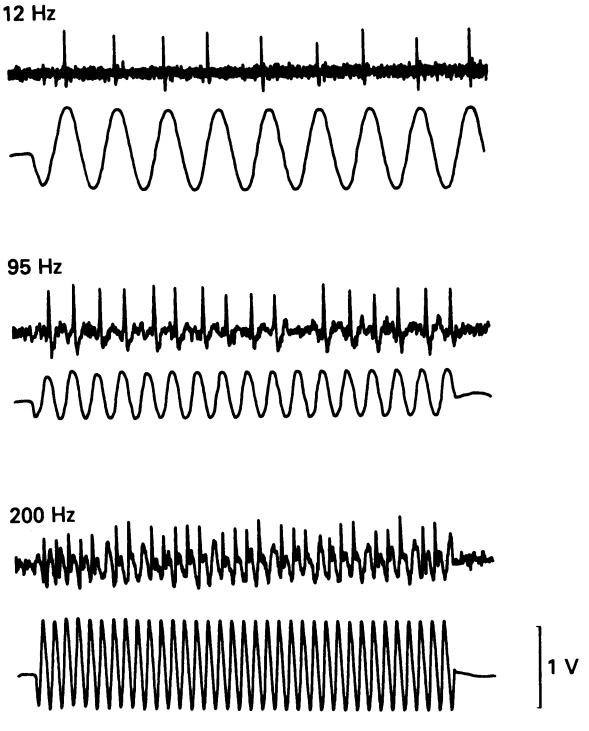


Fig. 7. Responses of an electroreceptor to focal stimulation with sinusoidal waveforms of different frequencies. In each of the three panels the upper trace is the afferent response, the lower trace the monitored voltage.

maximum sensitivity. Ramp-shaped potentials with progressively steeper slopes produced proportionately higher firing rates. An example using velocities of 1·7, 1·4 and 0·2 V $s^{-1}$ is shown in Fig. 5. The relation between firing rate (peak rate minus resting rate) and log rate of voltage change can be approximated by a straight line over the range 1–50 V $s^{-1}$, indicating a logarithmic dependence of firing rate on stimulus velocity (Fig. 6).

The dynamic sensitivity of electroreceptors was examined further by measuring responses to sinusoidal potential changes (Fig. 7). At low frequencies and large amplitudes a receptor would give multiple bursts of impulses during each stimulus cycle. As the voltage was reduced the response fell, becoming entrained in a 1:1 relation with each cycle of the waveform. If voltage was dropped further the response became intermittent. The frequency range over which thresholds were lowest was

50–100 Hz. Measurements of entrainment threshold relative to its minimum value are shown for two units in Fig. 8. There was a small but distinct increase in threshold at frequencies below 50 Hz, down to 12 Hz, the lowest frequency used. Above 100 Hz there was a steep increase in threshold, shown by both units. Above 300 Hz

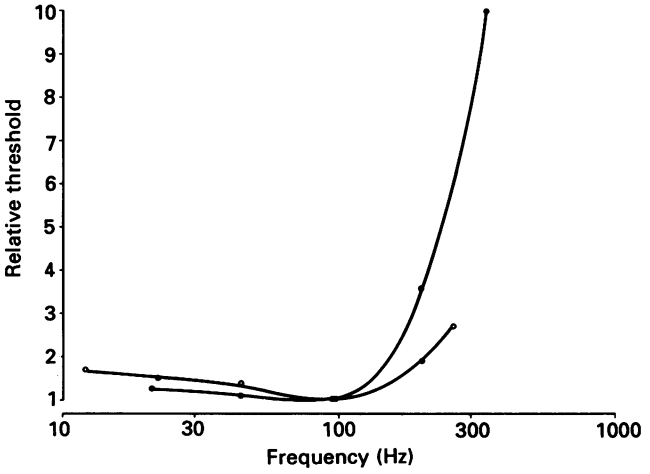


Fig. 8. Plot, for two electroreceptors, of threshold for an entrained response to sinusoidal stimulation at different frequencies expressed relative to threshold minimum. Thresholds are lowest between 50 and 100 Hz, and rise steeply at higher frequencies and more gradually at low frequencies.

stimulus artifacts became too large to determine whether the receptor was still responding or not. However the progressive increase in threshold suggests that receptors were not likely to respond at much higher frequencies. On several occasions sinusoidal fields were also applied with the bill immersed in water. Here the shape of the threshold–frequency relation remained essentially the same.

## DISCUSSION

### *Field stimulation*

The important new observations provided by these experiments are the measurements made on electroreceptors with the bill immersed in water. Threshold for integrated activity from multiunit recordings was 4 mV $cm^{-1}$. This corresponds well with measurements made under the same conditions on single units (4–25 mV $cm^{-1}$). These values are, however, higher than behavioural thresholds measured by Scheich *et al.* (1986). Field strengths required to reliably change an animal's behaviour from 'patrol' to 'search' phase were about 1 mV $cm^{-1}$. Animals could avoid underwater obstacles which carried DC currents, at a distance corresponding to a gradient of $< 200\ \mu V\ cm^{-1}$. Finally, animals could be made to investigate a hollow brick when a field was switched on behind the brick giving a transient with a gradient of 330 $\mu V\ cm^{-1}$, measured in front of the brick. Clearly, therefore, there remains a discrepancy between threshold measurements made using the whole

animal and from single units. One obvious possibility is that we simply didn't record from the most sensitive receptors. Perhaps these are not even found in the bill. It is probable too, that central processing of afferent information from the very large population of receptors allows greater sensitivities to be achieved than those estimated by visual inspection of single-unit recordings. Furthermore, had we resorted to averaging techniques in assessing responses of single receptors the measured thresholds would have been lower.

*Latency*

In previous experiments we were able to show that structures in the skin of the bill which gave rise to the electroreceptor responses were the innervated mucous gland receptors (Gregory *et al.* 1988). Histological examination of nerve terminals at the base of each mucous gland reveals no signs of any synaptic structures (Andres & Von Düring, 1984; Iggo *et al.* 1988). The main purpose of the latency measurements was to try to confirm by electrophysiological means that there was no peripheral synapse in these receptors. All non-mammalian electroreceptors have a peripheral synapse.

In response to brief step-shaped voltage pulses, increasing stimulus strength over a wide range, while initially producing progressive reductions in latency of the evoked impulse, did not lead at higher stimulus strengths to a sudden further drop, suggestive of a stimulus which had bypassed a peripheral synapse. Our estimate of the peripheral delay between application of the stimulus and the initiation of a nerve impulse is 0·8 ms. This is very much shorter than latencies measured for other electroreceptors where it is known that there is a peripheral synapse. Murray (1974) measured a latency of 10–50 ms for elasmobranch ampullary receptors where only 'a few milliseconds' were accounted for by nerve conduction time. Münz, Claas & Fritsch (1984) measured a latency of 5–7 ms for ampullary electroreceptors in the lateral line of the axolotl. Here nerve recordings were made close to the receptors, certainly closer than in our own experiments so that rather little of the delay represented nerve conduction time. We conclude that for electroreceptors where there is known to be a peripheral synapse the measured latency is much longer than we recorded here, supporting our contention that in the platypus receptor there is no peripheral synapse.

However, 0·8 ms is a surprisingly long delay time for a stimulus acting directly on the axonal membrane. The utilization time for impulse initiation in most mammalian peripheral nerve is only about 0·1 ms. This raises the possibility that the process of impulse initiation in platypus electroreceptors involves more than just simple depolarization of an axonal membrane. The only additional piece of evidence we have on this point comes from an observation made in passing and to which no particular significance was assigned at the time. A simple strength–duration curve was constructed using step-function cathodal pulses of different durations. It was found that rheobase was reached only for pulses of 20 ms duration, or longer. This is much longer than for most peripheral myelinated nerve where rheobase is reached with stimulus widths of only 1–2 ms. We conclude that while stimulus transduction in platypus electroreceptors does not involve transmission across a synapse, events at the nerve terminal are more complex than a simple depolarization of the axonal membrane, be it the membrane of the axonal spines which project into the lumen of the gland or the first node of Ranvier (Iggo *et al.* 1988).

*Dynamic sensitivity*

The data presented in this report provide a more complete description of the dynamic sensitivity of electroreceptors in the platypus first reported by us (Gregory *et al.* 1987). Over a large part of the dynamic range, between velocities of 0·5 and 50 V $s^{-1}$ there is a linear relation between the size of the response and the logarithm of the rate of voltage change. A logarithmic relation allows sensitivity to be maintained down to low gradients (Fig. 6). The tuning curves measured using sinusoidal voltage changes gave a region of maximum sensitivity between 50 and 100 Hz (Fig. 8). This finding is of some interest as it demonstrates that while platypus electroreceptors respond to both steady and alternating potentials their maximum sensitivity is to alternating potentials, a fact likely to have some bearing on the functional role of the receptors. While it has been speculated that the DC sensitivity might allow the platypus to detect contact potentials between the water and river bank or obstacles on the stream bottom it appears the receptors are optimally tuned for higher-frequency signals, perhaps those generated by moving prey. Observations of a freely swimming platypus while it is searching for food on the bottom of an aquarium show the animal continuously moving its bill rapidly from side to side at a rate of about seventy-five movements per minute. Perhaps these movements ensure that, for detection of low-frequency signals, receptor sensitivity remains within its optimal range.

An important consideration for dynamic sensitivity is the length of canal between the outside of the gland and the nerve endings. Long canals have a high wall capacitance and therefore attenuate high frequencies (Murray, 1974). Estimates from micrographs give a path length of about 0·5 mm in the platypus. This is similar to the canal length for electroreceptors in fresh-water fishes. Here 'the electroreceptors have short canals and the effective stimulus is exclusively formed by the voltage drop across the skin' (Kalmijn, 1974). One aspect of this kind of arrangement is that a radiating system of canals is needed to provide all-round sensitivity. Yet, in the platypus, as far as we know, electroreceptors are found only in the bill. The platypus has few natural predators under water. The electroreceptors are therefore likely to be used principally for the detection of prey. It seems that they provide the animal with a kind of antenna with which to search for food in its dark and often murky world.

In conclusion, we have measured the thresholds of platypus electroreceptors to electric fields with the bill immersed in water, and their responses to rapidly changing potential gradients. Maximum receptor sensitivity appears to be to changing rather than steady gradients. Measurements of latency lead to the conclusion that there is no peripheral synapse. What the events are that lead up to impulse initiation will be the subject of future experiments.

The animals were obtained while one of us (U.P.) held a current permit from The Victorian Department of Conservation, Forests and Lands (permit No 87/16). The participation of Ainsley Iggo in the experiments was made possible by a travel grant from the William Ramsey Henderson Trust while on leave from the University of Edinburgh.

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