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Some related aspects of platypus electroreception: temporal integration behaviour, electroreceptive thresholds and directionality of the bill acting as an antenna

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This paper focuses on how the electric field from the prey of the platypus is detected with respect to the questions of threshold determination and how the platypus might localize its prey. A new behaviour in response to electrical stimuli below the thresholds previously reported is presented. The platypus shows a voluntary exploratory behaviour that results from a temporal integration of a number of consecutive stimulus pulses. A theoretical analysis is given, which includes the threshold dependence on the number of receptors and temporal integration of consecutive stimuli pulses, the close relationships between electrical field decay across the bill, electroreceptive thresholds and directionality of the platypus bill acting as an antenna. It is shown that a lobe shape, similar to that which has been measured, can be obtained by combining responses in a specific way from receptors sensing the electric field decay across the bill. Two possible methods for such combinations are discussed and analysed with respect to measurements and observed behaviour of the platypus. A number of factors are described which need to be considered when electroreceptive thresholds are to be determined. It is shown that some information about the distance to the source is theoretically available from the pattern of field decay across the platypus's bill. The paper includes a comparative analysis of radar target tracking and platypus prey localization.

Keywords: platypus; electroreception; electroreceptive threshold; behaviour; directionality

1. INTRODUCTION

The platypus has evolved a highly effective means of solving the tasks of detecting and locating prey. It is capable of finding and eating half a kilogram of small, freshwater invertebrates (half its own body mass) in a single night. With its eyes, ears, and nostrils closed under water it appears to make use of its electroreceptive sense, first reported by Scheich *et al.* (1986). The bill contains electroreceptors located in parasagittal stripes within the bill skin (Andres & von During 1988; Gregory *et al.* 1988; Manger & Pettigrew 1996). There are, however, many details about the functioning of the electroreceptive sense that are still unsolved. One question concerns discrepancies in the reported values of thresholds for the detection of electric fields. Other questions are how the platypus bill functions with regard to directionality when acting as an antenna, considering the very low frequencies involved, and how the platypus can localize its prey by means of the directional, but very wide, electroreceptive lobe of the bill, in the manner shown in behavioural studies. In this paper, these questions are addressed and are shown to be closely related.

In the case of the discrepancies in threshold measurements, these result partly from the different techniques used by the different research workers in their studies of the electroreceptive system of the platypus. First, we can differentiate between behavioural studies and measurements of evoked potentials. Second, there is a difference between recordings from peripheral electroreceptor axons and from the cortex. Recordings of the electromyogenic output of a variety of platypus prey items also provide important information regarding the electrical threshold of the platypus. Starting from the prey items and following the electrosensory pathway of the platypus, the following measurements can be mentioned.

One prey item, *Macrobrachium australiense*, recorded by Scheich *et al.* (1986), was seen to produce an electromyogenic potential of approximately $1000\,\mu V\,cm^{-1}$. In a more comprehensive study, Taylor *et al.* (1992) showed that from a variety of platypus prey items, a range of electromyogenic potentials, from $12\,\mu V\,cm^{-1}$ up to $1800\,\mu V\,cm^{-1}$, could be recorded.

Gregory *et al.* (1988) recorded from peripheral electroreceptor axons, and reported that axon depolarization occurred at a lowest threshold of $2000\,\mu V\,cm^{-1}$.

When recording cortical evoked potentials, Scheich *et al.* (1986) reported thresholds of lower than $60\,\mu V\,cm^{-1}$. A second study of the cortical threshold of electroreception

was carried out by Proske *et al.* (1992). Using surface electrodes, this study recorded a lowest threshold of $300\,\mu\mathrm{V\,cm^{-1}}$. Measurements by Krubitzer *et al.* (1995) help to explain some of the differences reported by Proske *et al.* and Scheich *et al.* Using microelectrode recording from layer IV of the cortex of the platypus, it was shown that the electrical threshold across the cortex varied, ranging from a lowest threshold of $20\,\mu\mathrm{V\,cm^{-1}}$ up to a level of $2400\,\mu\mathrm{V\,cm^{-1}}$. This range in electrical thresholds was seen to be closely correlated with a functional map of the decay of electrical fields across the bill of the platypus.

With regard to behavioural thresholds, in the first description on platypus electroreceptivity, Scheich *et al.* (1986) reported a variety of thresholds for different animals, ranging from a low of $50\,\mu\mathrm{V\,cm^{-1}}$, up to $500\,\mu\mathrm{V\,cm^{-1}}$. Further behavioural studies (Manger & Pettigrew 1995) have shown that the platypus is directionally sensitive to electrical stimulation. A preferred axis for stimulation was determined to be around $80°$ from the rostral pole of the bill, and around $20°$ down. This preferred axis is around 60 times more sensitive than non-preferred axes. This directionality can account for the discrepancy in electrical thresholds of the behaving platypus as reported by Scheich *et al.*, as the direction from which the stimulus was presented was not controlled. Also, this study showed a reflexive behaviour of the platypuses to electrical stimuli, with thresholds ranging between 50 and $75\,\mu\mathrm{V\,cm^{-1}}$ for eight different platypuses, in agreement with the lowest behavioural thresholds reported by Scheich *et al.* (1986).

Despite this range in reported electrical thresholds, some consistency can be seen. Platypus prey items emit large enough electromyogenic potentials for the platypus to detect. Both behavioural studies confirm that below $50\,\mu\mathrm{V\,cm^{-1}}$ the platypus appears not to be able to detect electrical stimuli, at least not on a basis of immediate detection after one stimulation. Cortical physiology provides a range of thresholds, all within the reported range of the electromyogenic potentials of the prey items. However, recording from peripheral electroreceptive units give the highest electrical threshold, $2000\,\mu\mathrm{V\,cm^{-1}}$, above the range of electromyogenic potentials recorded from prey items. Similar discrepancies in threshold between behaviour and physiology in electroreceptive fish have been reported as will be discussed later. The common theme is that behavioural thresholds are usually one or more orders of magnitude below the physiological thresholds recorded from the peripheral receptor.

In this paper, we present what we believe is a new behaviour of the platypus in response to electrical stimuli below the thresholds previously reported, and show that, by using temporal integration, the platypus can detect these 'sub-threshold' stimuli. Signal detection theory, correlated with the number of electroreceptors on the platypus bill, predicts that the platypus could detect electrical stimuli below the level at which we have recorded positive behavioural responses. This analysis correlates closely with projected results from behavioural data.

As will be shown in this paper, this new behaviour can also, in combination with previously described reflexive and voluntary behaviour, cast more light on how the platypus might find the direction to the prey. A theoretical analysis will be given showing how a lobe shape, similar to

that which has been measured, can be created by receptors sensing the electrical field decay across the bill. This analysis will furthermore reveal other important factors that need to be considered when the thresholds for detection of electric fields are to be determined. It will also show that some information about the distance to a prey item could theoretically be available from combined responses of electroreceptors on the bill. The apparent similarities between a platypus's prey localization and radar target tracking have induced a comparative analysis of the methods used by radar and platypuses in related tasks.

2. MATERIALS AND METHODS

Five platypuses (*Ornithorhynchus anatinus*), four males and one female, were used in this study. These platypuses form a subset of the platypuses used for previous behavioural (Manger & Pettigrew 1995), physiological (Krubitzer *et al.* 1995; Manger *et al.* 1996) and anatomical studies (Manger & Pettigrew 1996; Manger *et al.* 1995). Platypuses were caught and housed as described by Manger & Pettigrew (1995).

Platypuses were exposed to electrical stimuli while exhibiting a resting behaviour, in which muscle movements were minimal and the heart rate of the animal was around 20 beats $\mathrm{min^{-1}}$ (Manger & Pettigrew 1995), lowering the chance of self-generated electrical potentials interfering with the experiment. Square wave stimuli were generated using a function generator, which passed a continuous signal to an envelope generator, the number of envelopes per second being controlled by a trigger source. The resultant square wave was passed through two $10\,000\,\Omega$, ten-turn potentiometers, then presented to the platypuses via a mobile electrode. This system was powered by a 30 V DC power source, and has been described in more detail previously (Manger & Pettigrew 1995).

Three square waves per second were presented to the resting platypus, and the time it took the platypus to respond was noted. A repetition rate of three square waves per second was chosen because at this rate the sensitivity of the platypus is not diminished, whereas at higher repetition rates the sensitivity is diminished (Manger & Pettigrew 1995). The strength of the electrical field was determined by direct measurement through two stainless steel recording electrodes, placed 10 cm apart. These electrodes were connected to an oscilloscope, with a calibration of $100\,\mu\mathrm{V\,cm^{-1}}$ over the entire screen (of ten divisions). This gave a smallest calibration of $10\,\mu\mathrm{V\,cm^{-1}}$ for every division on the oscilloscope screen.

3. EXPERIMENTAL RESULT. VOLUNTARY EXPLORATORY BEHAVIOUR

As stimuli of small amplitude were presented to the platypuses, to determine the lowest-amplitude square wave that would elicit a reflexive head saccade (Manger & Pettigrew 1995), another electrically driven behaviour was noticed. When voltages around $50\,\mu\mathrm{V\,cm^{-1}}$ were presented to the platypuses, occasionally it took a few repetitions of the stimulus before they responded. The response was a voluntary exploratory movement of the head in the direction of the source of the electrical
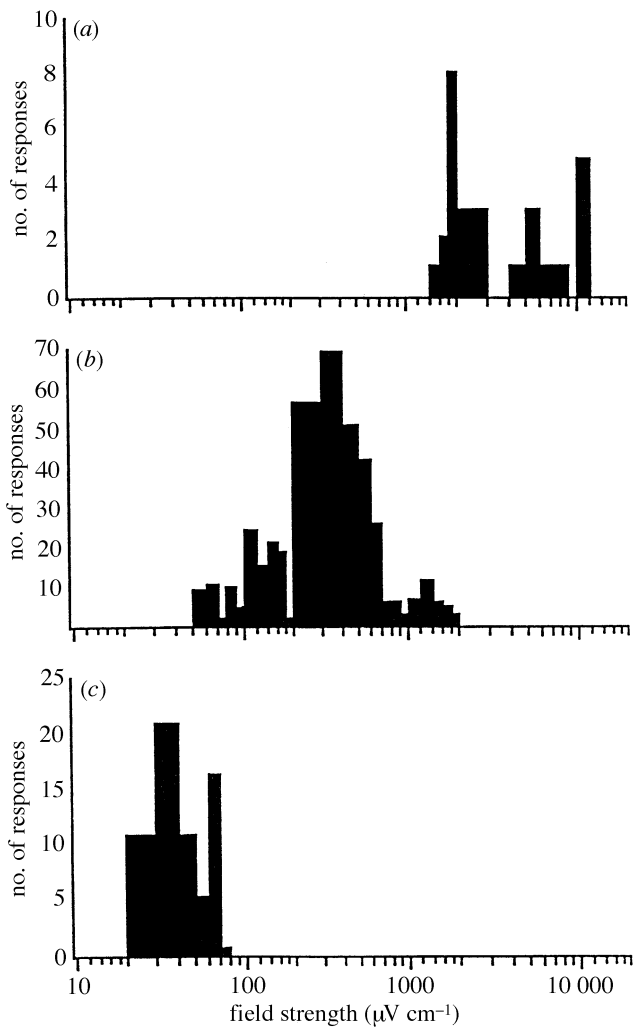
Figure1. Behavioural responses to different electrical field strengths. (*a*) The voltage range tested that elicited an aversive response from the platypus, where the head saccade was in a direction contralateral to the stimulus and/or the platypus swam away from its rest following the stimulus. (*b*) The voltage range over which it was possible to elicit a saccade that was sensitive to the origin of the electrical pulse in the water. (*c*) The voltage range over which many repetitions of the electrical stimuli were needed before eliciting exploratory movements of the bill towards the electrode. (*a*) and (*b*) from Manger & Pettigrew (1995).

stimulus. This response involved a few lateral swings of the head followed by a movement of the rostral half of the body towards the electrode. As lower voltages were presented to the platypuses, more repetitions were needed before this behavioural response was seen. For example, a voltage of $25\,\mu\mathrm{V\,cm^{-1}}$ needed 160 repetitions of the square wave before a response was elicited, whereas around 10 repetitions were needed for a voltage of $35\,\mu\mathrm{V\,cm^{-1}}$, and a voltage of $60\,\mu\mathrm{V\,cm^{-1}}$ was recognized after one or two pulses (see figures 1 and 2; figure 1 also shows behavioural responses with respect to reflexive head saccades). From these results it is evident that the platypuses can perform a temporal integration of a number of 'sub-threshold' electrical stimuli to form a response resulting in active exploration of the stimulus source. As will be discussed later, the described voluntary behaviour, in combination with other observations, can also indicate something
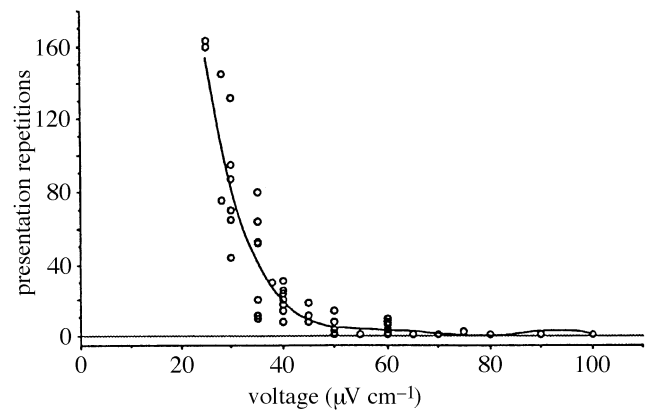

Figure 2. Graph of voltage of presented square waves versus the number of presentations required to elicit a response. Raw data from one behavioural session.

about the way the platypus can find the direction to a source.

4. THEORETICAL ANALYSIS

(a) *Threshold dependence on number of receptors*

As mentioned earlier, there is much confusion about the absolute lowest threshold of electrical sensitivity of the platypus. There are a number of factors determining this threshold and the question of lowest threshold can be better understood by the use of a theoretical analysis. A first factor determining the threshold is the number of receptors.

If we follow signal detection theory (Green & Swets 1974):

$$\text{absolute threshold} = \text{receptor threshold}/\sqrt{\text{number of receptors}}.$$

An estimate of the number of mucous gland electroreceptors is 20 000 per half bill (Manger & Pettigrew 1996). This gives for half of the bill:

$$\text{absolute threshold} = 2000/\sqrt{20\,000} = 14.1\,\mu\mathrm{V\,cm^{-1}},$$

and for the whole of the bill:

$$\text{absolute threshold} = 2000/\sqrt{40\,000} = 10\,\mu\mathrm{V\,cm^{-1}}.$$

However, it is possible that a more effective summation than simple averaging takes place in the cortex of the platypus.

(b) *Threshold dependence on temporal integration*

If we follow the data for the voluntary exploratory response behaviour (figure 2) and apply a power fit to the data (correlation coefficient $= -0.95$) we get:

$$\text{repetitions} = 10^{9.4249} \times (\mu\mathrm{V\,cm^{-1}})^{-5.1793}.$$

A few examples are as follows:

$60\,\mu\mathrm{V\,cm^{-1}} = 1.4$ repetitions (head saccade threshold),

$25\,\mu\mathrm{V\,cm^{-1}} = 160$ repetitions (lowest voltage tested to give a reliable behavioural response),

$12\,\mu\text{V cm}^{-1} = 6800$ repetitions (equal to theoretical 'averaging' threshold using the number of sensory serous glands on half of bill),

$9.8\,\mu\text{V cm}^{-1} = 19\,500$ repetitions (equal to the theoretical 'averaging' threshold using number of mucous gland electroreceptors on half of bill).

The lowest field strength a platypus can sense is yet to be determined. Although we have reliable behavioural data showing responses down to $25\,\mu\text{V cm}^{-1}$, from the two analyses shown above, it is possible that the platypus is sensitive to field strengths as low as $10\,\mu\text{V cm}^{-1}$. However, it would be quite difficult to test this sort of integration (around 20 000 presentations) as the platypus could never hold its breath for long enough, or the experimenter maintain the electrode still enough for that length of time.

(c) *Relationships between field decay across the bill, directionality and electroreceptive threshold*

Directionality of radio and radar antennas can be obtained through phase differences of received or transmitted waves between different points of the antenna. As has been previously pointed out (Manger & Pettigrew 1996), the directionality of the platypus bill, acting as an antenna, cannot result from phase changes between different receptors owing to the very low frequencies involved. The only available means of shaping the lobe of the bill seems to be to make use of the decay of the received electric field across the bill.

A crucial question is in which manner the electrical field decays as a function of distance from the platypus prey. From electromagnetic theory, it follows that the electrostatic field from a point source decays in proportion to $1/d^3$, where d is the distance from the source, whereas from a spherical body with even distribution of charge over the surface and radius R the decay is proportional to $(R/d)^2$, and from a cylindrical body with radius R it is proportional to R/d (Landau & Lifshitz 1975; Reitz *et al.* 1993). In previous behavioural experiments the electrode had a cylindrical shape and the measured field strength in $\mu\text{V cm}^{-1}$ (Manger & Pettigrew 1995, fig. 16) decayed nearly inversely to the distance, in accordance with theory. In a real situation with a live shrimp in the natural habitat of the platypus, the field decay is dependent on so many factors that it is difficult to express the decay in a simple formula. In the theoretical analysis that follows we will assume that the field decays in proportion to $1/d^x$, where $x = 2$, but results will also be given for the case $x = 3$.

The field decay across the bill leads to a difference in response from receptors at different distances from the prey. In the study by Manger & Pettigrew (1995), it was pointed out that, with respect to the head saccade reflex, the latency of approximately 43 ms allows for more than one synapse to be involved in some form of signal processing before a directed movement of the head is elicited. Some cues about what this processing could be, can be obtained from observations of the behaviour of the platypus in combination with measurements of the resulting lobe shape and also in combination with an analysis of how the field decay can be effectively used to
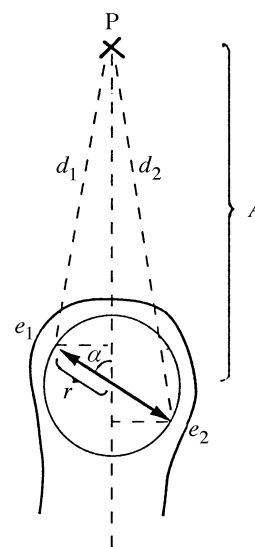

Figure 3. A first theoretical method for obtaining directional information using electric field decay across bill.

achieve directionality with high angular resolution. The sensing of the field decay across the bill must involve a sensing of the differences in response from different receptors. The largest difference will be obtained from receptors furthest away from each other in the direction of the propagation of the electric wave. Two theoretical methods of obtaining information about the direction to the prey are discussed below.

Method 1. Assume that the difference D between two electric field strengths (e_1 and e_2), from two receptors furthest away from each other on a circle with a given radius r, are formed and presented as a function of the angle α with respect to the direction to the prey P. The distance between the prey and the centre of the circle is A (see figure 3). With a given field strength at the prey and the distances to the two receptors being d_1 and d_2, then

$$e_2/e_1 = d_1^2/d_2^2,$$

$$D = e_1 - e_2 = e_1(1 - d_1^2/d_2^2),$$

where, using the rule of Pythagoras for the sizes of the sides of triangles,

$$d_1^2 = (r\sin\alpha)^2 + (A - r\cos\alpha)^2,$$

$$d_2^2 = (r\sin\alpha)^2 + (A + r\cos\alpha)^2.$$

The magnitude of D as a function of α is shown in figure 4, when $r = 2$ cm and the distance A from the origin of the circle to the prey is 10 cm. From figure 4 it can be seen that information about the direction to the prey can be obtained with higher angular resolution from the sharp dip in the curve rather than from the flat maximum. This means that although the difference between receptors positioned in the direction of the prey will give the largest response, the difference between receptors positioned nearly orthogonal to this direction can give better information about the direction to the prey. If the information from figure 4 was available to the platypus, and its brain could translate this information into coordinates with respect to where to swim, it would not have to swing
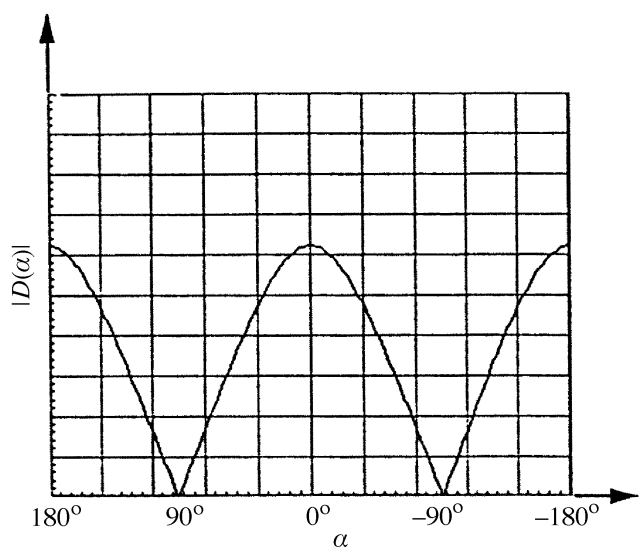
Figure 4. Magnitude of difference signal D as a function of angle α (the shape of the curve is identical when using a cubic field decay, $x = 3$).

its bill sideways and there would be no axis of preference for eliciting a head saccade. This is not in agreement with measurements and observed behaviour. It is, furthermore, not an effective use of the receptors to get high sensitivity and good directionality as only some of the receptors are used to form the maximum of the curve in figure 4, and only some of them are used to create the dip area.

Method 2. This describes a more effective use of available receptors. Assume that all or most of the differences in electric field strengths are obtained as differences between receptors positioned orthogonal to the forward direction of the bill and preferably between receptors furthest away from each other. With the bill pointed in the direction of the prey, all receptors would be engaged in creating the area near the dip of the curve in figure 4, giving information with high angular resolution. When the bill is swung sideways all receptors will be engaged in forming the area near that of highest sensitivity. Assume that β is the angle from the forward direction of the bill to the prey, as shown in figure 5, and that e_1 and e_2 are the field strengths at two receptors positioned orthogonal to the direction of the bill. The distance between the receptors is b, the distances to the prey are d_1 and d_2, and A is the distance between the prey and a centre point between the two receptors. The square of the distances as a function of the angle β can, in this case, be shown to be

$$(d_1)^2 = [(b/2)\sin(90 - \beta)]^2 + [A - (b/2)\cos(90 - \beta)]^2,$$

$$(d_2)^2 = [(b/2)\sin(90 - \beta)]^2 + [A + (b/2)\cos(90 - \beta)]^2.$$

The sum S and difference D between e_1 and e_2 will be

$$S = e_1 + e_2 = e_1(1 + d_1^2/d_2^2),$$

$$D = e_1 - e_2 = e_1(1 - d_1^2/d_2^2).$$

The sum signal and the magnitude of the difference signal as a function of β is shown in figures 6 and 7, when the distances between the receptors is 4 cm and the distance A from the centre point between the receptors to
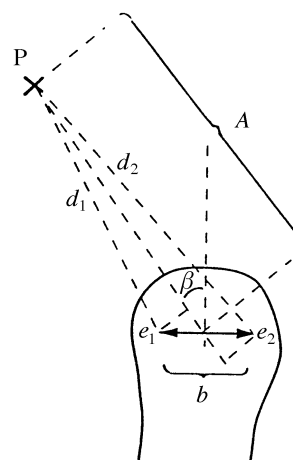
Figure 5. A second theoretical method of obtaining directional information using electric field decay across bill.
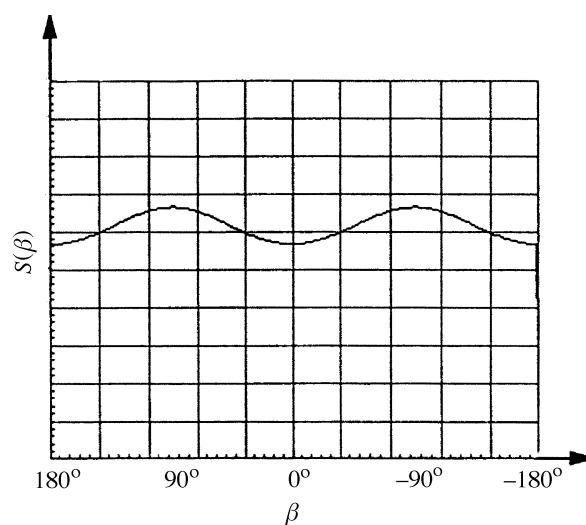
Figure 6. Sum signal S as a function of β.

the prey is 10 cm. It can be seen that the sum lobe is nearly omnidirectional and cannot give much information about the prey. With increasing distance to the prey the sensitivities in all directions will be even more alike. The difference lobe has a sharp dip in the forward direction with close similarity to the lobes shown in fig. 13*f* in Manger & Pettigrew (1995). These lobes result from measurements of the directionality of the electrically elicited head saccade, measured by the threshold distance for eliciting head saccades from a square wave electrical stimulus of constant amplitude. The maxima of the lobes are situated in a plane with highest sensitivity *ca.* 20° down. Apart from the similarities in lobe shape, the following four observations can be made.

1. The electroreceptor organs are arranged mainly in parallel stripes along the bill (Andres & von During 1988; Manger & Pettigrew 1996).
2. It has been shown that the platypus is far more sensitive to fields decaying across the stripes, than along the stripes (Manger & Pettigrew 1995).
3. When the presence of a prey item has been detected, it is necessary for the platypus to swing its bill sideways in order to find the direction to the prey by means of the
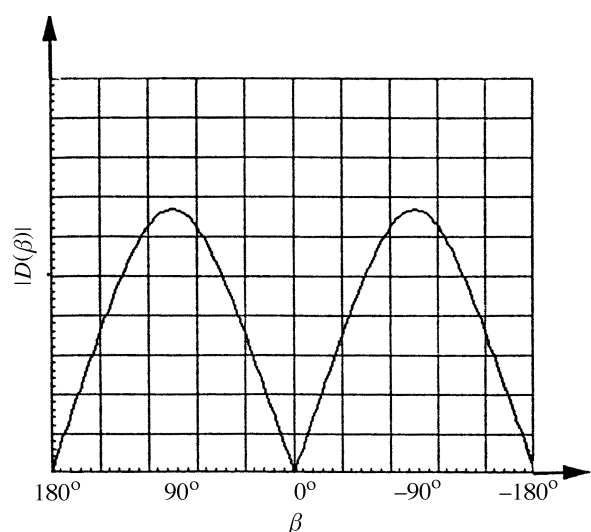
Figure 7. Difference signal D as a function of β (the shape is identical when using a cubic field decay, $x=3$).

Figure 8. Relationship between magnitude of difference signal and the sum signal as a function of relative distance d_1/b at $\beta=90°$.

dip in the lobe. This is in agreement with the observed voluntary exploratory behaviour after presentation with a stimuli of small amplitude. After a few repetitions the response did involve a few slow lateral swings of the head before the movement of the rostral half of the body towards the electrode, as described earlier in this paper. It is also in agreement with the observed patrol behaviour. In fig. 14 in Manger & Pettigrew (1995), the transition from pre-patrol to patrol behaviour, triggered by contact with a prey item, was shown. After interaction with a shrimp, the bill was swept in a very regular pattern with increased number of sweeps per second and increased size of sweeps. The lateral swing of the bill in the direction of the prey in the head saccade reflex will also help to point the dip area closer to the direction of the prey, which can give improved information about the direction to the prey. Whether the bill should be swung to the left or right can be seen from whether the response from the receptors on the left or right half of the bill is strongest (the difference signal being positive or negative).

4. The decay of the electric field, resulting from the muscular activity of the platypus heart and from similar electromyogenic potentials, will be less across the stripes than along the stripes, particularly in the resting position. Electrical background noise will therefore be reduced when differences are sensed across the stripes. This is a form of common mode rejection related to similar noise reduction mechanisms in rays (Montgomery 1984).

Taking the more complex arrangement of electroreceptors in the upper and lower cutaneous, palatal and lingual surfaces of the bill into account (Manger & Pettigrew 1996), it is understandable that lobe shapes can be created in agreement with those observed and shown in fig. 13 in Manger & Pettigrew (1995).

A type of difference signal as discussed above seems to be very useful for the platypus. It seems questionable whether a sum lobe is created as well. A higher sensitivity is of little use if there is no information about the direction to the prey.
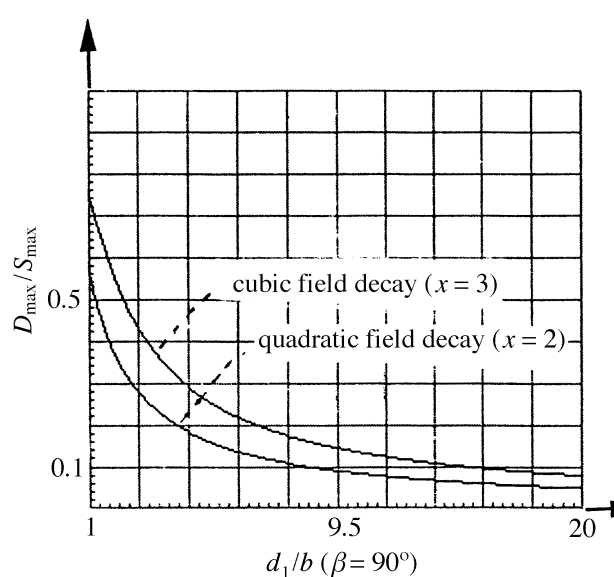
It is important to observe that, because it is the decay of the electrical field across the bill that creates the difference signal, the sensitivity of the difference signal for a given field strength near the bill is dependent on the distance to the prey. That means that different thresholds will be observed depending on whether the given field strength near the bill is created by a strong source at a large distance or by a weaker source closer to the bill. This could be a further reason for the observed discrepancies with respect to measured thresholds. The relationship between the amplitude of the difference signal D from two receptors, and the sum signal S as a function of relative distance d_{rel} (distance from a centre point between the receptors to the prey divided by the distance between the receptors) at the angle for largest amplitude of the difference signal, can be shown to be

$$D_{max}/S_{max} = (2d_{rel} + 1)/(2d_{rel}^2 + 2d_{rel} + 1),$$

where $d_{rel}=d_1/b$ and $\beta=90°$.

This relationship is shown in figure 8. It can be seen that at larger distances (more than about six times the distance between the receptors) this ratio decreases slowly as a function of distance, whereas closer to the bill it varies more rapidly. With the same field strength at the edge of the bill, the sensitivity of the difference signal will be higher for a cubic field decay ($x=3$) than for a quadratic decay ($x=2$).

Relationships of this kind will be important as soon as platypus behaviour or combined responses from several receptors are studied. It should be observed that, through such a mechanism, weak sources closer to the platypus will be favoured in detection, as compared with strong sources at longer distances. The first kind of source is more likely to be prey for the platypus.

It is also interesting to observe that, from knowing the way that the electric field strength decays in a straight direction from the prey, some information about the distance to the source can theoretically be available to the platypus. With two receptors at a distance b from each
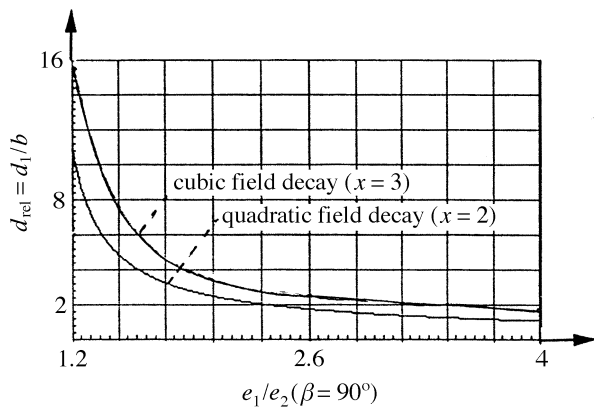
Figure 9. Relative distance to source as a function of e_1/e_2 for receptors situated in the direction of the source.

other in the direction to the prey (for example two receptors on the same stripe when the bill is directed towards the source), and with a distance d_1 from the nearest receptor to the source, then

$$e_1/e_2 = (d_1 + b)^2/d_1^2 = (1 + b/d_1)^2,$$

which gives

$$d_1/b = d_{rel} = 1/(\sqrt{(e_1/e_2)} - 1).$$

This relationship is shown in figure 9 for e_1/e_2 between 1.2 and 4. A theoretical solution to determine the distance to the source is therefore to compute $1/(\sqrt{(e_1/e_2)}-1)$ for two receptors on the same stripe when the difference between receptors orthogonal to the stripes is zero. Because of the described relationships, the pattern in the SI bill map in the cortex (Krubitzer *et al.* 1995) will probably be different with different distances to the source for a given electric field strength at the edge of the bill. In the cortex, modules of neurons exist with the same receptive field on the bill, but with varying thresholds and low dynamic range (Manger 1994; Krubitzer *et al.* 1995; Manger *et al.* 1996). It is, however, an open question if the platypus can or does make any use of changes in such a map with respect to the described distance dependence. It would work best for relatively short distances (less than ten times the distance between sensing receptors). In this situation it would also be most useful as, at shorter distances, the time difference in arrival of mechanical and electrical waves is smaller than for longer distances to the source. As described in Pettigrew *et al.* (this issue), the arrival time will be different to the mechanoreceptors and electroreceptors on the bill, which gives another theoretical way to acquire distance information.

5. A COMPARISON WITH METHODS FOR TARGET DETECTION AND ANGULAR TRACKING IN RADAR SYSTEMS

Some tasks in radar tracking are similar to those of a foraging platypus. A target (prey) must first be detected and then tracked so that the antenna (bill) can be continuously directed towards the target (prey) while the missile or aeroplane (platypus) is approaching it in the right direction. The head scanning behaviour of the platypus, after a prey has been detected, seems at a first glance to
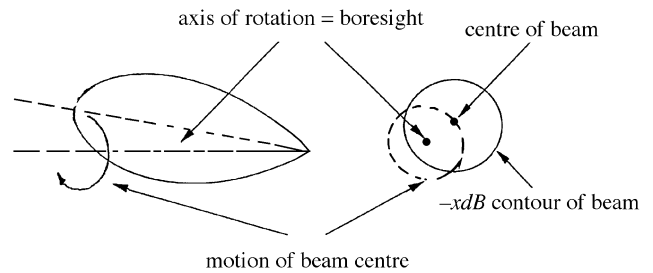
Figure 10. Conical scan antenna lobe.

be similar to certain scanning movements of radar antennas during target tracking. A closer look at, and comparison between, the methods that are used to solve the similar tasks could be of interest.

Temporal integration is used in radar systems to enhance the sensitivity in target detection. This is, for example, accomplished by the radar screen. The screen can remember and add (integrate) the responses to consecutive pulses hitting the same position on the screen and do so also for consecutive sweeps of the antenna past the target. From the discussion earlier in this paper, it is evident that a resting platypus can also integrate a number of consecutive responses from a weak source in order to increase the sensitivity of detection. It is more questionable if it can do so from sweep to sweep when it swings its head, as this imposes the existence of an integrating 'map' (display) of the observed environment in its brain.

In radar tracking systems, the information required to keep the antenna directed toward a target can be obtained in different ways. A classical method is to use a 'conical scan' antenna system (Biernson 1990). A slightly tilted narrow antenna lobe is made to rotate as shown in figure 10. The signal received from a target away from the axis of rotation will be modulated during the rotation. From the modulation it is possible to deduce how the antenna should be directed to get the target on the axis of rotation.

Information with regard to tracking in one plane can be obtained by remembering and comparing the responses when the lobe is positioned successively in two directions. If one of the signals is subtracted from the other, a difference signal with a positive sign will give information to position the antenna in one direction, and a difference signal with a negative sign to position the antenna in the opposite direction. When the difference signal is zero, the target is on the axis of rotation and the antenna can consequently be 'locked' to the target. In the radar case, the speed of rotation is so high, and the relative distance to the target so large, that the magnitude of the received signal from the target has not altered significantly between the two positions. From observed values of the time it takes for the platypus to swing its bill from one direction to the other, in comparison with its swimming speed towards the prey (Manger & Pettigrew 1995) and the temporal variations in the electromyogenic potentials produced by the prey (Taylor *et al.* 1992), it can be deduced that the platypus cannot successfully make use of a similar method.

A second method to automatically keep the antenna directed towards a target is used in so-called 'monopulse' radar tracking systems (Biernson 1990). In these systems

symmetry axis = boresight

contour of
overlapping lobes

overlapping lobes
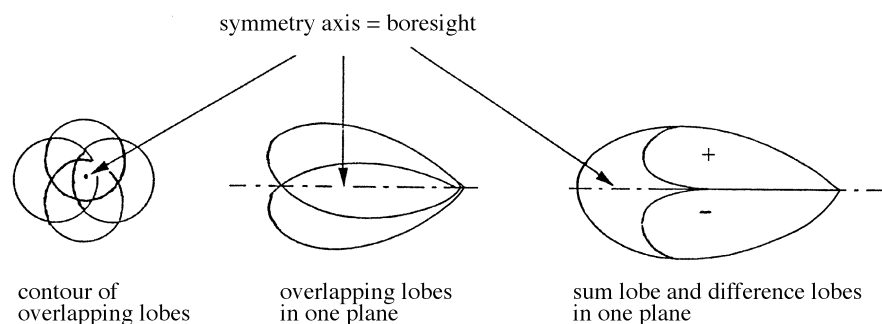in one plane

sum lobe and difference lobes
in one plane

Figure 11. Monopulse antenna lobes.

the scanning lobe is replaced by four, fixed, overlapping lobes slightly tilted in four directions away from a symmetry axis. For signal reception the signals from the lobes are combined into one sum signal, corresponding to a lobe in the direction of the symmetry axis, and two difference signals each corresponding to two difference lobes in orthogonal planes. The lobes are pointing slightly sideways and have a sharp dip to zero in the direction of the symmetry axis (see figure 11). As a result of the difference operation, the two difference lobes in the same plane are connected with signals of opposite polarity. Because of this, the signals from the difference lobes can be used to automatically position the antenna and keep the target in the direction of the symmetry axis. With the antenna in this direction, the amplitude of the difference signals will be zero and the antenna will be 'locked' to the target. The target can at the same time be observed by means of the signal from the sum lobe. The method derives its name from the fact that directional information can be obtained during each single pulse. This contrasts with the 'conical scan' method where a comparison is made between received pulses when the antenna is pointing in different directions during a scanning movement.

Certain similarities are evident when the monopulse radar tracking method is compared with the strategy to make use of electric field decay across the bill of a platypus. By sensing the difference between responses from electroreceptors situated orthogonally with respect to the direction of the bill, difference lobes of the same type as in the radar case can be formed in one plane. As the receptors are distributed symmetrically, a simple arrangement would be to form the difference between the responses from those on the one half of the bill from that of the other half. As mentioned above, a more complex processing involving receptors on all four surfaces of the bill (Manger & Pettigrew 1996), upper and lower cutaneous, palatal and lingual, can account for the creation of observed lobe shapes (Manger & Pettigrew 1995, fig. 13). The bill of the platypus is evidently not being 'locked' in the direction to the prey as the platypus performs scanning movements with large amplitudes (Manger & Pettigrew 1995, fig. 14). It could, however, be able to keep track of the direction to the prey during the scanning movement through the sharp dip between the two difference lobes.

6. DISCUSSION

As can be seen from the above analysis, the question of the threshold for electroreception in the platypus is complex. Starting with the threshold for nerve depolarization, in

Gregory *et al.*'s (1988) physiological studies, $2000\,\mu\mathrm{V\,cm^{-1}}$ was found to be the lowest point at which a one-to-one correlation between stimulation and axon depolarization was seen. This level coincides with that which in the behavioural study of Manger & Pettigrew (1995) was found to be an aversive stimulus to the platypus, presumably depolarizing all 40 000 electroreceptors on the bill (each with 16 nerve terminals (Manger *et al.* 1995)).

A first factor that increases the sensitivity and lowers the threshold is a summation of peripheral inputs from a large number of receptors. A similar summation is also seen in most varieties of electroreceptive fish studied both behaviourally and neurophysiologically. For example, sharks and rays show a modulation in heart rate when presented with field strengths as low as $0.005\,\mu\mathrm{V\,cm^{-1}}$ (Kalmijn 1982), compared with the ampullary unit threshold of $1\,\mu\mathrm{V\,cm^{-1}}$, an increase in sensitivity of around 200 times. With catfish the behavioural threshold of $1\,\mu\mathrm{V\,cm^{-1}}$ is also around one order of magnitude more sensitive than the ampullary receptor unit threshold of $6\,\mu\mathrm{V\,cm^{-1}}$ (Kalmijn 1974). These examples coincide with the enhanced sensitivity of the behaving platypus over the electroreceptor unit threshold of $2000\,\mu\mathrm{V\,cm^{-1}}$. The head saccade threshold of $50\,\mu\mathrm{V\,cm^{-1}}$ (Manger & Pettigrew 1995) corresponds to an enhancement of 40 times. Microelectrode recordings from the cortex similarly give lower thresholds, varying from $20\,\mu\mathrm{V\,cm^{-1}}$ up to $2400\,\mu\mathrm{V\,cm^{-1}}$ (Krubitzer *et al.* 1995). In the cortex a summation of responses from a number of receptors can have occurred. Electroreceptive fish have furthermore the added ability of sensory enhancement using a sensory cell, an option not available to the platypus. However, communication between the 16 nerve terminals in each mucous gland, as described in Manger *et al.* (1995), may improve the sensitivity of the platypus.

A second factor that also increases the sensitivity, as described in this paper, is the temporal integration of a number of repetitions of the stimulus. This extends the electrosensitivity of the platypus down to levels that are not fully testable experimentally, but threshold levels as low as $25\,\mu\mathrm{V\,cm^{-1}}$ were obtained in this behavioural study. In order to observe such enhancement in thresholds, responses after a number of stimulus repetitions must be observed.

Detection of the presence of a prey item is of little use without any directional information. The directionality of the platypus bill as studied by Manger & Pettigrew (1995) indicated a symmetrically situated axis of preference about 60 times more sensitive than non-preferred axes. It is therefore important to note the direction to the stimulus source when electroreceptive thresholds are observed.

The way the directionality from a number of electroreceptors is obtained also affects the way thresholds should be observed. As described in this paper, several observations point to the fact that differences between responses from receptors situated orthogonal to the direction of the bill are being used by the platypus to detect and find the direction to stimulus. In such a situation, it is the value of the decay of the electric field in the direction of the source, rather than the strength of the field at the bill, that determines the behavioural threshold for electroreception. Similarly, it is this decay that determines the thresholds at points in the electroreceptive pathway where difference processing has occurred. The decay of the field can be expressed in $\mu V\,cm^{-1}\,cm^{-1}$ and is a function of the distance to the source as well as of the strength of the field at the bill. When thresholds are given related to the strength of the field at the bill, the distance to the source must also be known in order to determine the value of the field decay at the bill. The field decay across the bill can, furthermore, not be determined unless the manner in which the field decays is known. As was discussed earlier, the field from the cylindrical electrode (Manger & Pettigrew 1995, fig. 16) decayed nearly inversely to the distance. In that example the field at threshold at the edge of the bill was $50\,\mu V\,cm^{-1}$ and the decay across the bill $25\,\mu V\,cm^{-1}$. If the field decay had been proportional to the inverse of the square of the distance, a similar decay of $25\,\mu V\,cm^{-1}$ across the bill would have been obtained with a field strength of only $37\,\mu V\,cm^{-1}$ at the edge of the bill for a source at the same distance. In the case of a cubic field decay, the same figure would have been $31\,\mu V\,cm^{-1}$. It is therefore likely that the measured threshold of $50\,\mu V\,cm^{-1}$ is higher than would have been obtained in a natural situation.

Directional information is essential, but as shown in this paper, directionality is obtained at the expense of some reduced sensitivity compared with that of a theoretical sum lobe, when lobe shaping is performed using field decay. As described above, the method, however, favours detection of weak sources at short distances compared with strong sources at long distances which produce similar field strengths at the bill. This could perhaps aid the suppression of signals from sources not being prey for the platypus.

7. CONCLUSION

The platypus can, as has been demonstrated, lower its electroreceptive threshold using a form of temporal integration of a number of consecutive stimulus pulses. A theoretical analysis has explained a number of factors that must be considered when electroreceptive thresholds of the platypus are to be determined. These factors include the directionality of the bill and the distance to the source for a given field strength at the bill. It has been shown that the type of observed lobe shape of the platypus bill can be obtained by creating differences between responses from receptors situated orthogonally to the direction of the bill. The lobes of the bill with a sharp dip in a forward direction can effectively be used to obtain directional information with high angular resolution

using scanning movements of the head. Some information about the distance to the prey is theoretically available from the information of the electrical field decay across the bill.

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