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Electroreception and the feeding behaviour of platypus (*Ornithorhynchus anatinus*: Monotremata: Mammalia)

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SUMMARY

It has previously been shown that platypus are sensitive to small electrical fields. It was predicted that platypus use their electrosensitivity to locate the source of foodstuffs on the bottom of the freshwater river systems in which they live, because the platypus are nocturnal, and close their eyes, ears and nostrils while underwater.

In this paper we demonstrate for the first time that platypus are indeed sensitive to electrical waveforms that imitate the electromyogenic potential's of fleeing prey, and following stimulation show interest in area surrounding the electrodes. We also show that platypus respond with a reflex after stimulation with a square wave, and show that this reflex is directionally tuned to the origin of the electrical pulse, with a preferential sensitivity axis 40 times more sensitive than non-preferred axes. The strong directional sensitivity explains previous discrepancies in the lowest threshold for platypus electroreception, which we find to be 50 μV cm^{-1}. Platypus are also sensitive to galvanic fields.

We present the data in the light of standardized feeding strategies of the platypus, and discuss the integration of the findings into these feeding strategies. We surrounded our platypus enclosure with a Faraday cage, thereby eliminating excess electrical noise, a suggested new addition to the husbandry regime of platypus.

1. INTRODUCTION

The dietary preferences of the platypus and the manner in which it forages for food have been known for many years (Burrell 1927; Faragher *et al.* 1979; Grant 1989). That the bill is the main sensory organ of the platypus was also suggested by the enormous trigeminal nerve, and the expanded neocortical representation of the bill (Home 1802; Bohringer & Rowe 1977). Yet mystery surrounded the fact that the platypus could gather half its own body mass in food each night with its eyes, ears and nostrils closed and underwater. Tactile perception alone, although highly developed in the bill of the platypus (Bohringer 1981; Bohringer & Rowe 1977), could not account for this extraordinary success in finding around a half kilogram of small, freshwater invertebrates in a single night. Burrell (1927), after an extensive series of observations, speculated on the possibility of a 'sixth sense' that assured the platypus of the direction in which its prey was located.

An ultrastructural analysis (Andres & von During 1984) revealed receptors in the platypus bill with an unusual morphology that suggested the possibility of electroreceptive capabilities. This possibility was later confirmed by behavioural and physiological studies (Scheich *et al.* 1986). The electroreceptors of the platypus are modified mucous glands (Gregory *et al.* 1988), and are located in parasagittal stripes within the bill skin (Andres & von During 1984). A presumptive type of electroreceptor, a modified serous gland, is also found in the bill skin of the platypus. These presumptive serous gland electroreceptors are most dense around the rostro-lateral poles of the upper and lower bill (Andres & von During 1988).

Since these discoveries on the electroreceptive features of the platypus, another monotreme, the short-beaked echidna, *Tachyglossus aculeatus*, has also been described as possessing electrosensory capabilities (Gregory *et al.* 1989). However, the limited numbers of electroreceptors in the beak of the echidna suggest that electroreception is not as well developed in this species (Andres & von During 1991; Manger & Hughes 1992). It is still unknown if the New Guinea Echidna, *Zaglossus bruijni*, has electroreceptors.

There remain a number of unsolved problems connected with platypus electroreception. Controversy still exists over the lowest possible electrical field strength to which the platypus will respond. Behavioural experimentation revealed thresholds ranging from 50 μV cm^{-1} to 300 μV cm^{-1} (Scheich *et al.* 1986). Peripheral nerve recording from peripheral electroreceptor units set the lowest threshold at 2 mV cm^{-1} (Gregory *et al.* 1988). Cortical recording with surface electrodes gave a threshold of 300 μV cm^{-1} (Proske *et al.* 1992), whereas cortical recording with a microelectrode showed a threshold of 20 μV cm^{-1} (Manger *et al.* 1993). Recordings of the electrical output of a variety of platypus prey items showed a range of 12 μV cm^{-1} to 1800 μV cm^{-1} at close quarters (< 2 cm) (Taylor *et al.* 1992). If one accepts the lower

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threshold values the platypus appears capable of detecting all of its normal prey by electrical signals alone. However, it remains to be determined why the threshold varies so much from study to study.

Many species of fish have been reported to possess electroreceptive capabilities far more sensitive than that described for the platypus (for review, see Bullock & Szabo 1986). Sharks and rays have been shown to be the most sensitive fish with a lowest behavioural threshold field strength of 0.005 μV cm^{-1} (Kalmijn 1982). However, the ampullary electroreceptors in these fish respond to higher field strengths, with a lowest threshold value of 1 μV cm^{-1}. Other fish also respond to weaker electrical fields than the platypus, these include members of the Chondrostei (afferent threshold: 10–100 μV cm^{-1}) (Zakon 1986), Ictalurus (afferent threshold: 6 μV cm^{-1}; behavioural threshold: 1 μV cm^{-1}) (Kalmijn 1974) and Teleostei (afferent threshold: 50–100 μV cm^{-1}) (Zakon 1986). Some amphibia have also been shown to be electroreceptive with afferent ampullary electroreceptor units having a threshold of 5 μV cm^{-1} (Zakon 1986). Behavioural studies of axolotl electrosensitivity found responses to stimuli as low as 25 μV cm^{-1}, however the axolotls would respond to electrical field strengths of 100 μV cm^{-1}, 47% of the time (Himstedt *et al.* 1982). The platypus has one feature in common with all of the electroreceptive fish (and the amphibia): the behavioural thresholds are generally one or two orders of magnitude below the receptor unit threshold, indicating some sort of summation of electrosensory inputs.

In this paper we present a detailed analysis of the feeding behaviour of the platypus and how electroreception is used to facilitate prey capture. The results were obtained from around 10000 presentations of varying electrical stimuli to platypus, plus over 100 h of video recording the platypus while they were feeding. The electrically screened arena in which we have kept platypus is described, as it has not previously been used for platypus husbandry, and takes into account the electroreceptive capabilities of the platypus. We give a brief description of initial attempts to guide the behaviour of freely swimming platypus with electrical stimuli. We then show how we took advantage of a previously described, underwater, resting behaviour (Burrell 1927) to facilitate the presentation of electrical stimuli to the platypus. The use of this resting behaviour allowed us to discover an electrically driven behaviour mediated reflexively. Using this reflex, electrical behaviour, and the resting behaviour, we investigated the three dimensional properties of the platypus bill with respect to its electroreceptive capabilities, finding that the bill has a preferential sensitivity axis. This preferential axis is analysed with respect to the head scanning behaviour exhibited by hungry, ‘patrolling’ platypus (Scheich *et al.* 1986).

The general pattern of feeding behaviour of the platypus has only been described as sidelines of studies describing other aspects of platypus behaviour (Hawkins & Fanning 1992; Scheich *et al.* 1986), with the interest focused on what and how much the platypus ate and weighed (Grant *et al.* 1977; Carrick *et*

Table 1. *Summary of the number of platypus used in this study, the sex, capture location and time, and length of time spent in captivity*

(This table also shows what behavioural findings were discovered with which animals, and provides some indication of the chronological order of the findings presented in this paper.)

platypus number	sex	capture location	capture date and time	captive period/ days	ipsiversive head saccade threshold/ (μV cm^{-1})	swimming behavioural threshold/ (μV cm^{-1})	modified resting behaviour	directionality of bill	discomfort threshold/ (μV cm^{-1})	galvanotaxis	ECG monitoring	head saccade latency/ (ms)
1	male	Kobble Ck	16/1/91; 4.55 a.m.	14		100						
2	female	North Pine R.	12/8/91; 6.40 p.m.	32		120	x					
3	male	Brisbane R.	4/1/92; 8.15 p.m.	40	55	120	x	x				
4	male	North Pine R.	10/3/92; 10.50 p.m.	12	50	110	x	x				
5	male	North Pine R.	10/3/92; 11.30 p.m.	40	60		x	x	2000			
6	male	Little Yabba Ck.	30/7/92; 3.30 a.m.	40	75		x	x	1800			
7	female	Brisbane R.	20/10/92; 6.45 p.m.	14	50		x	x	2100		x	42.3
8	male	Brisbane R.	20/10/92; 8.00 p.m.	35	50		x	x	1850	x	x	44.5
9	male	Widgee Ck.	7/3/93; 11.20 p.m.	40	65		x		2000	x		43
10	male	Mary R.	11/3/93; 9.30 p.m.	40	60		x			x		

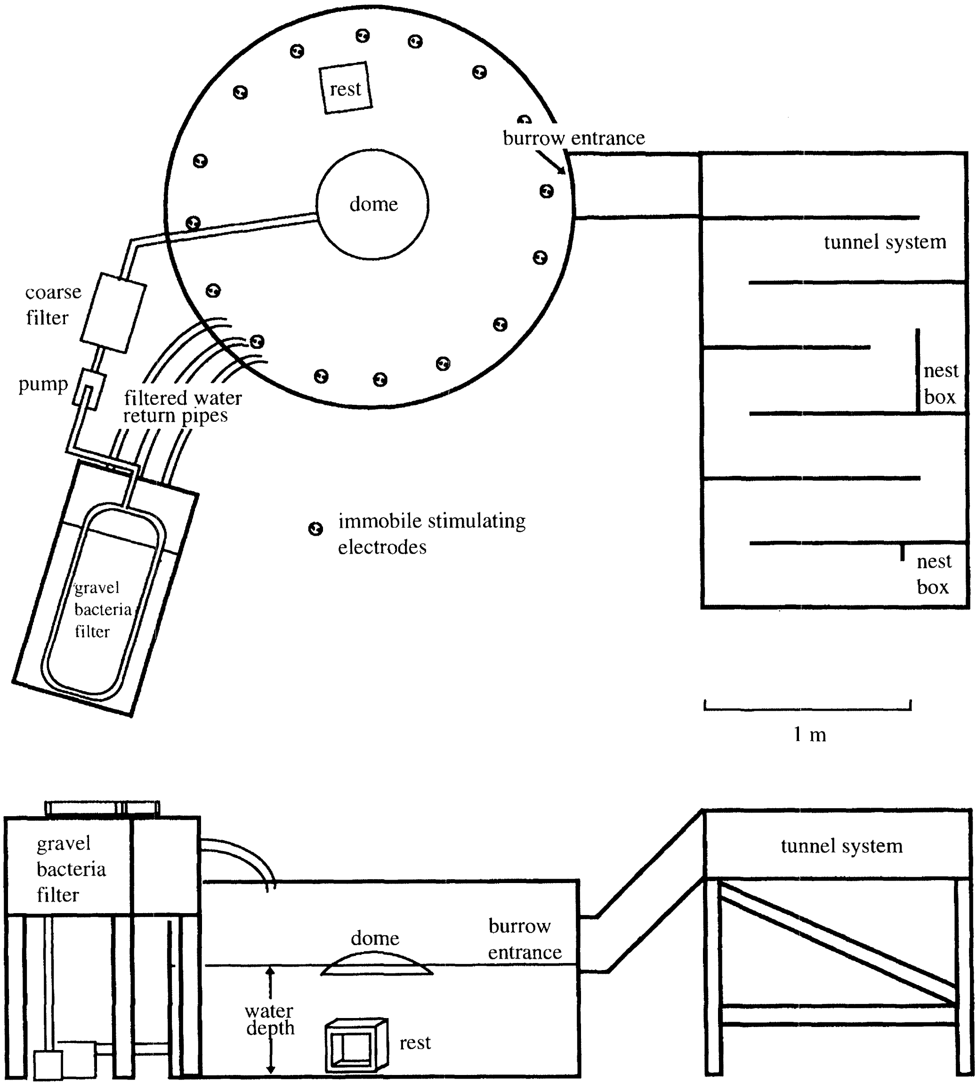

Figure 1. Diagram of the platypussary as viewed from above and from the side. The tank, filled with water to a depth of 40 cm, is connected to a tunnel system which is 40 cm above the water level. The length of the tunnel is designed to: (i) imitate the length of tunnels dug by platypus in the wild; and (ii) to ensure ample time for the excess water on the fur of the platypus to be preened off. In the tunnel system are two nest boxes in which fresh hay and leaf litter was provided. The Faraday cage, constructed from wire mesh, surrounded the tank and the tunnel system and was ground to the mains. The water in the tank was turned over 10 times per hour through the bacteria driven filter system.

al. 1979), but no detailed descriptions of the various aspects of feeding of the platypus have been reported. To this end we provide an in-depth analysis of the feeding behaviour of the captive platypus as observed by video taping the feeding platypus under infra-red illumination or dim red darkroom lighting.

The results of this study are discussed from a variety of aspects. We discuss the integration of the electrosensory capacities into the observed foraging strategies, particularly in the context of the acquisition of its normal prey. We detail the similarities and differences seen in responses to electrical stimuli between platypus, electroreceptive amphibia and electroreceptive fish, and discuss the biological significance of generalized behavioural characteristics of electroreceptive sensory systems. Finally, we discuss platypus husbandry in the light of the electrical sensitivity of the platypus and the additions we made to the enclosure in which platypus were kept.

2. MATERIALS AND METHODS

A total of ten platypus, eight males and two females, were used in this study. The animals were kept for an average of four weeks, some up to six weeks, in a platypus arena, or platypussary (Burrell 1927). These platypus were netted at various sites from the following watercourses in South East Queensland; Brisbane River, North Pine River, Mary River, Little Yabba Creek, Amamoor Creek, Widgee Creek and Kobble Creek. Capture times ranged from 6 p.m. in the evening through to 5 a.m. in the morning, with all but two captures occurring before midnight (see table 1).

The platypussary consisted of a tank connected to a tunnel system (see figure 1). The tank was two metres in diameter, one metre high and constructed of fibreglass. The average water depth was forty centimetres. A Perspex dome (depth of 50 mm, diameter of 500 mm), placed in the centre of the tank at water

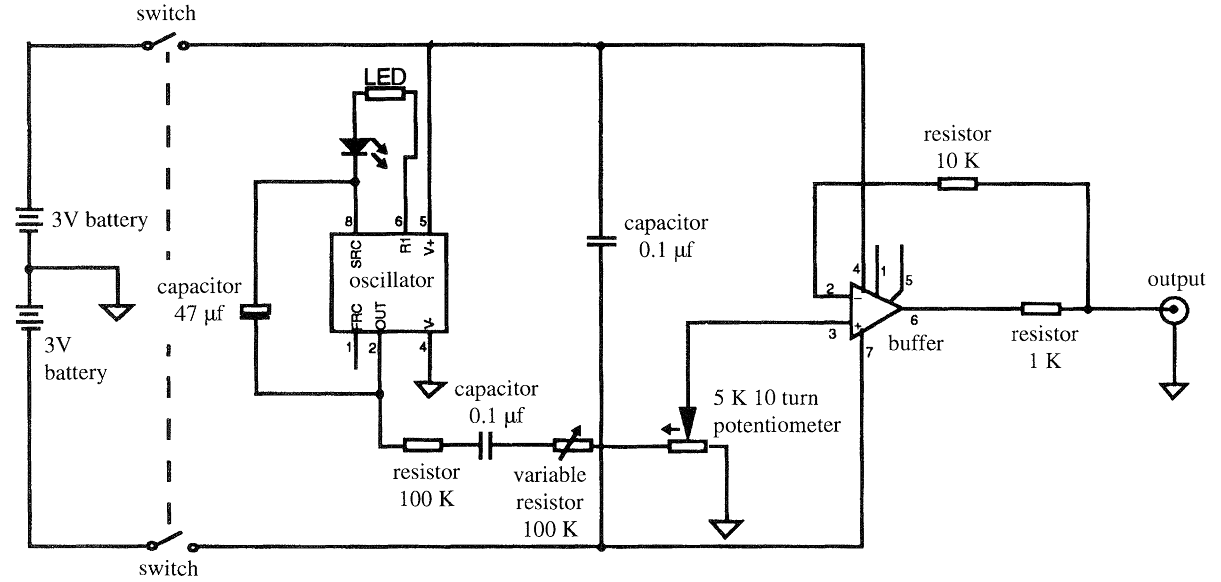

Figure 2. Circuit diagram of an electrical lure ('artificial shrimp' mark II) used in behavioural experiments on platypus electroreception. This circuit was connected via shielded cable to a mobile electrode (see text for details), and was used to present 10 ms square waves to the platypus.

level, allowed the platypus to sit, out of the water, and preen, or to lodge themselves underwater beneath the dome to rest. Two other underwater rests were provided for the platypus. The first was a hollow cement cube (side 200 mm) with two sides removed, allowing a short tunnel with the dimensions of 170 mm × 170 mm × 170 mm. The other rest was the filter system inlet pipe (25 mm PVC piping). The filter inlet pipe entered 150 mm from the bottom of the tank, protruded 200 mm, then turned ninety degrees and extended to the bottom of the tank to take in water. In all cases the inlet pipe appeared to be the favourite rest. A bacteria gravel filter with activated charcoal, river gravel and coral rubble was used to keep the water clean, as the platypus were both fed and presented with electrical stimuli in this water. The water was changed fortnightly. The average conductivity of this water was 630 $\mu S\ cm^{-1}$.

A thirteen metre tunnel was attached to the tank at water level and was freely available to the platypus at all times. This length of tunnel approximates the natural burrow length of the platypus (Burrell 1927). This continuous wooden tunnel had a width of 300 mm and a height of 250 mm, and was lined with brown, waterproof, outdoor carpet. Two nesting boxes (250 mm high × 300 mm wide × 400 mm long) were built in as part of the tunnel. Fresh hay and leaf litter was provided in both nesting boxes. The first nesting box was eight metres from the tunnel entrance, the second, and more favoured nesting box, was located at the end of the tunnel. This length of tunnel ensured that in average conditions a platypus would be only damp upon reaching the termination nest box, in which it would preen, after leaving the tank. We found that the nest box became unduly wet on one occasion, when it was housing two platypus at the same time. This was during mid-winter when the evaporation rate was reduced, and when greater than average disturbance for behavioural experiments increased the number of daily excursions to and from the tank.

Generally, only one platypus at a time was kept. However, occasions where two platypus were kept at the same time created no difficulties, apart from the aforementioned problem with dampness in winter. Two platypus would either share, or use separate, nesting boxes with no apparent animosity, often being found asleep in the same nesting box. The only space for which the animals vied was the rest under the filter inlet. Most often the larger animal would dislodge the smaller by pushing it with its bill, who then would be content with one of the other two rests. Platypus were fed live 50 g red claw yabbies, *Cherax quadricarinatus*, each animal eating between 9–13 of these per night, with one platypus eating 22 yabbies in one night (this adult male platypus, caught in the North Pine river, was 58 cm long, tip of tail to tip of bill) .

This whole system, tank and tunnel, was shielded from external electrical fields by a Faraday cage which was grounded via the earth pin of the mains power circuits. The Faraday cage allowed major reductions in background electrical noise created by 240 V equipment and lighting in the room and in other parts of the building. Within the water the background electrical noise was reduced from around 1000 $\mu V\ cm^{-1}$ down to an average of 20 $\mu V\ cm^{-1}$. In the air within the cage, background electrical noise was reduced from 150–500 $\mu V\ cm^{-1}$ down to 6 $\mu V\ cm^{-1}$.

(*a*) *Initial stimulation paradigm*

Initial behavioural trials involved stimulating the platypus as it was freely swimming. Sixteen pairs of electrodes were placed around the bottom of the tank, 15 cm from the edge and evenly spaced. Electrical pulses resembling electromyogenic potentials of platypus prey items (Taylor *et al.* 1992) were passed through these electrodes (5 mm diameter stainless steel screw heads). These imitation bioelectric potentials were generated by a microprocessor and controlled by a software package. Limitations to this system were the range of imitation bioelectric potentials available (four: large and small Atyid shrimps; Palaemonid shrimps; and Leptophleblid larvae), discontinuous amplitude control, and no repetition rate control. The fixed electrode, mobile platypus system also made it difficult to discern real electrically driven platypus behaviour from general swimming movements. The final problem with this stimulation system was the use of 240 V, 50 Hz electronics. The electronics used here increased the 50 Hz background noise to unacceptable levels.

(*b*) *Second stimulation paradigm*: '*artificial shrimp*'

After the relatively unsuccessful attempts at stimulating the free swimming platypus in the above manner, the use of the resting behaviour (described fully later) allowed us to stimulate the platypus with a mobile electrode. An oscillator which produced a square wave (repetition rate of two per second) which was powered by a single 1.5 V battery was used to create electrical pulses. The amplitude of the electrical pulse was controlled by by a 5000 Ω, one turn potentiometer. The created electrical pulse was presented to the platypus via two brass rings (2 cm diameter, 1 cm wide, 2 mm thick, 10 cm apart). The circuit described here (see figure 2) was placed inside a small plastic tube, the brass rings at either end. This piece of stimulating apparatus became known as the 'artificial shrimp', due to the resemblance in its size to the shrimp which the platypus were fed. However, there were some limitations with the artificial shrimp: no repetition rate control, a clumsy amplitude control, and a limitation in the waveforms which could be presented to the platypus.

(*c*) *Stimulation Paradigm III*

A system driven by a 30 V DC power supply was used to create waveforms presented to the platypus. This system consisted of a function generator which passed a continuous signal type to an envelope generator, the generation rate of which was controlled by a trigger source. The resultant electrical waveform was passed through two 10000 Ω, 10 turn, potentiometers, then presented to the platypus via a mobile electrode. A mobile electrode consisting of two brass rings, as described for the artificial shrimp, were attached to a 10 cm rod of Perspex. The Perspex rod was joined at right angles to a 50 cm handle for easy manipulation. The right angle permitted easy control over the orientation of the dipole that was presented to the platypus. The function generator allowed the presentation of either square, sawtooth, or sine waves (0.1–10 000 Hz). The envelope generator gave a variable rise time (0–10 ms), a variable sustain time (1 ms–1 s) and a variable fall time (0–10 ms). When presenting square waves through the envelope generator an override of the rise and fall time was employed to give rise and fall times of around 7 ns. The trigger source allowed 0.1 to 1000 presentations of the waveform per second. The potentiometers allowed precise control of the amplitude of the electrical signal presented to the platypus. The amplitude of each stimulus was checked via a pair of stainless steel recording electrodes in the water which were connected to an oscilloscope. These recording electrodes were 10 cm apart, and the oscilloscope had a capacity of 1 mV cm^{-1}, which could be multiplied by ten, allowing us to easily check amplitudes of the stimuli, the range on the oscilloscope screen being 10 μV cm^{-1} for every division. During presentation of the waveforms

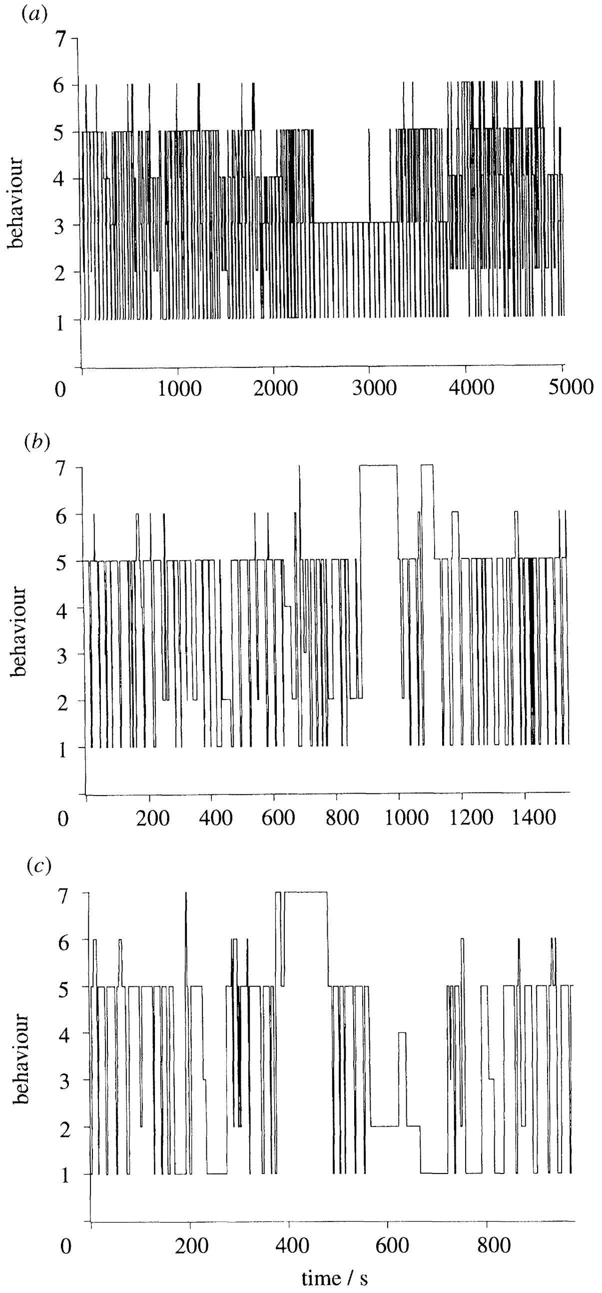

Figure 3. These figures summarize three different bouts of feeding activity observed during overnight video recording of the platypus. Feeding activity has been divided into six different behaviours: 1, on the surface of the water, presumably breathing; 2, on the surface of the water with food in the bill, presumably breathing; 3, wedged beneath a rest; 4, wedged beneath a rest eating food; 5, 'patrolling' for food; 6, swimming with food in its bill. A seventh behaviour – preening – was also seen occasionally. These diagrams are useful in that if followed carefully, the changes from one behaviour to another can be seen, and so providing a description that is difficult to write. (*a*) *ca.* 80 min of feeding; (*b*) *ca.* 27 min; (*c*) *ca.* 15 min.

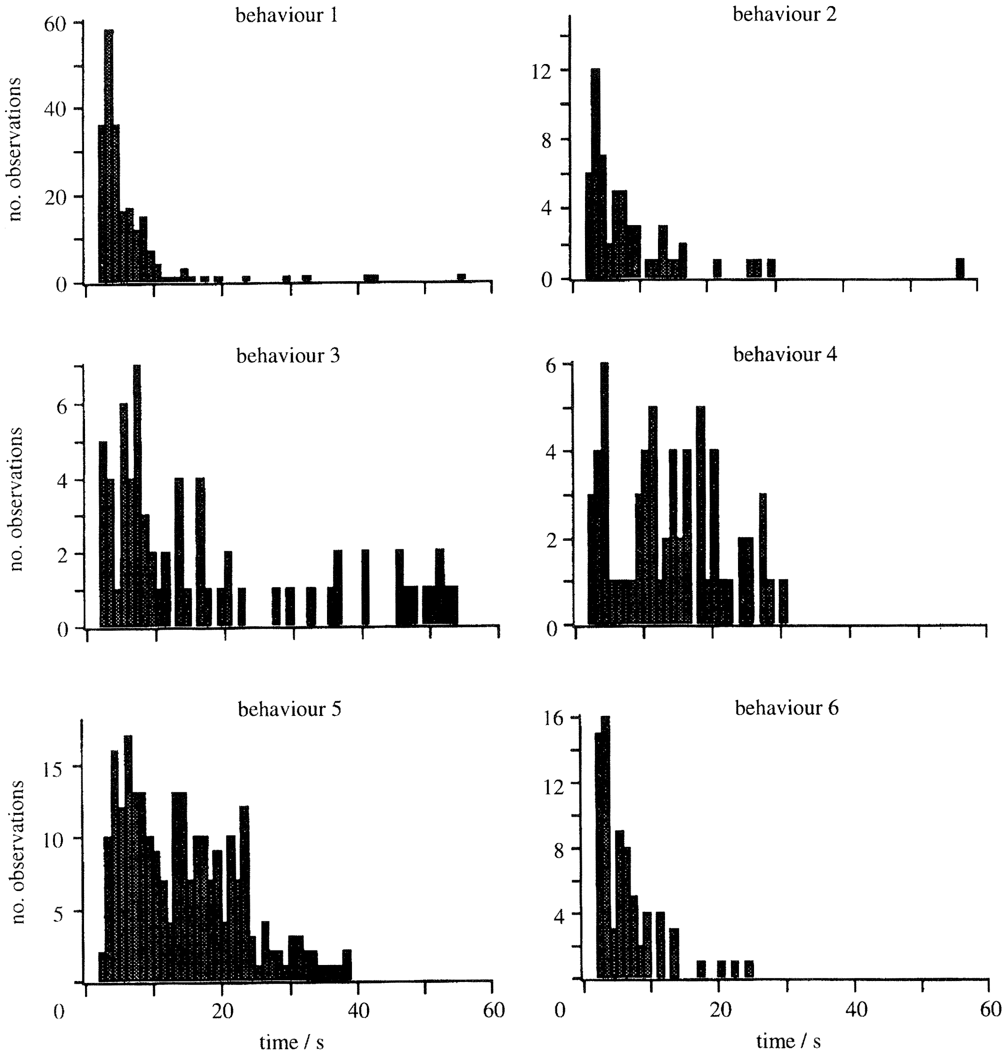

Figure 4. Durations of the six feeding behaviours. This series of histograms, frequency of observations versus time (s), demonstrate the normal range of time over which a behaviour is observed. These histograms are plots of the graphs shown in figure 3. For example behaviour 1 is seen to occur many times below 10 s, as opposed to behaviour 5, which is seen equally frequently between 3 and 25 s. Note the long bouts observed for behaviours 3 (resting underwater) and 4 (resting underwater with food).

generated with this system the platypus exhibited the resting behaviour. This paradigm made for simple and repeatable stimulation of the platypus, and as the platypus was resting the elicited behavioural responses were easy to discern.

(*d*) *Galvanotaxis stimulation*

A metal rod of sufficient surface area to elicit a galvanotaxic response was introduced to the water. The distance at which the rod elicited any behaviours was noted and the corresponding electrical field strength determined.

(*e*) *Video recording*

All behavioural experiments and recording of normal feeding behaviours were done under infra-red illumination or red darkroom light, minimizing visual cues, and monitored using a charge-coupled diode (CCD) video camera with the infra-red filter removed (Howland *et al.* 1991) connected to a video recorder and monitor. Video recording of the behavioural responses allowed frame by frame (50 Hz, or 20 ms sampling) analysis of the observed behaviours. Each of the behaviours described required particular adaptations for presenting the electrical stimuli. For each new behaviour, the method of presentation is described.

(*f*) *Electrocardiogram telemetry*

Platypus were lightly anaesthetized with an intramuscular injection of 0.4 ml of Ketamine, and a one channel amplitude-modulated (AM) radiotelemeter (Sirtrack, New Zealand), triggered by the electrocardiogram (EKG) was glued to the back of the platypus. Two platinum coated electrodes were pierced through the skin on the lateral aspect of each thoracic wall. Wires from the electrodes to the backpack were glued to the fur to prevent the platypus removing both the wires and the electrodes. Within two days of attachment of the telemeter, the platypus had preened the device into its fur. A radio receiver was tuned to the telemeter frequency of 151 mHz, the output of this radio receiver was entered into the audio input channel of a video recorder, along with the video of the behaviour the platypus was exhibiting at the time. This allowed precise correlation of behaviour and heart rate. It should be noted that the platypus was swimming freely during these recordings, this being different to the traditional studies of heart rate and diving, where forced submersions are used (Johansen *et al.* 1966; Jones *et al.* 1987). Heart rate was visualized with a MacLab data acquisition system, and analysed by using the commercially available program Igor. Behaviours corresponding to different heart rates were correlated with the video images.

3. RESULTS

(*a*) *General features of the feeding behaviour of the platypus*

Overnight video recording of the tank in which the platypus would feed allows us to present an in-depth analysis of its behaviour. Seven behaviours, six associated with feeding, plus preening, were consistently seen (see figure 3). The most consistent, and most obvious, was the platypus breaking the surface of the water and breathing (behaviour 1) (see figures 3 and 4). The platypus would spend an average of 6.36 s (normal range 2–15 s) on the surface breathing, with this behaviour entailing 16.95% of the total time the platypus was in the water. Alternatively, the platypus would surface with some food in its bill. As we were feeding the platypus live 50 g shrimp, it was easy to discern if the platypus had food in its bill (behaviour 2). The length of stay on the surface was increased to an average of 9.2 s (range 2–17 s) when the platypus surfaced with food in its mouth. It is presumed that the platypus can also breath as well as hold food in its mouth. This behaviour accounted for 6.44% of total time in the water. Described fully later in this paper, is a behaviour we call resting (behaviour 3). The platypus is seen to wedge itself beneath solid objects below the level of the water for periods that average 15.3 s, however, the wide range of times over which this behaviour is exhibited, from 2–63 s, shows this average not to be very significant (behaviour 3). This behaviour was the third most frequent behaviour seen, totalling 15.3% of the time the platypus spent in the water. As described later, when there are people present, the length of stay under the rest increases dramatically. While the platypus is exhibiting this resting behaviour it may also use the time to kill, shell, and eat the shrimps it has caught (behaviour 4). The average time the platypus spent on this behaviour was 15.2 s (range 2–31 s), totalling 11.64% of total tank time. The platypus exhibits two behaviours while swimming, the first is a behaviour, previously termed 'patrolling' (Scheich *et al.* 1986), where the platypus swings its head from side to side, presumably searching for food (behaviour 5). The platypus in this study devoted 41.3% of the time to patrolling for food, with these bouts lasting an average of 14.1 s (range 2–38 s). This patrolling behaviour is also described in more detail later, due its relevance to the findings of behaviours exhibited by the platypus when presented with electrical stimuli. The second behaviour seen while the platypus is swimming, is the platypus swimming with a shrimp in its bill (behaviour 6). Usually when this behaviour is seen the platypus is heading for somewhere, either the rest, or to the surface, this behaviour

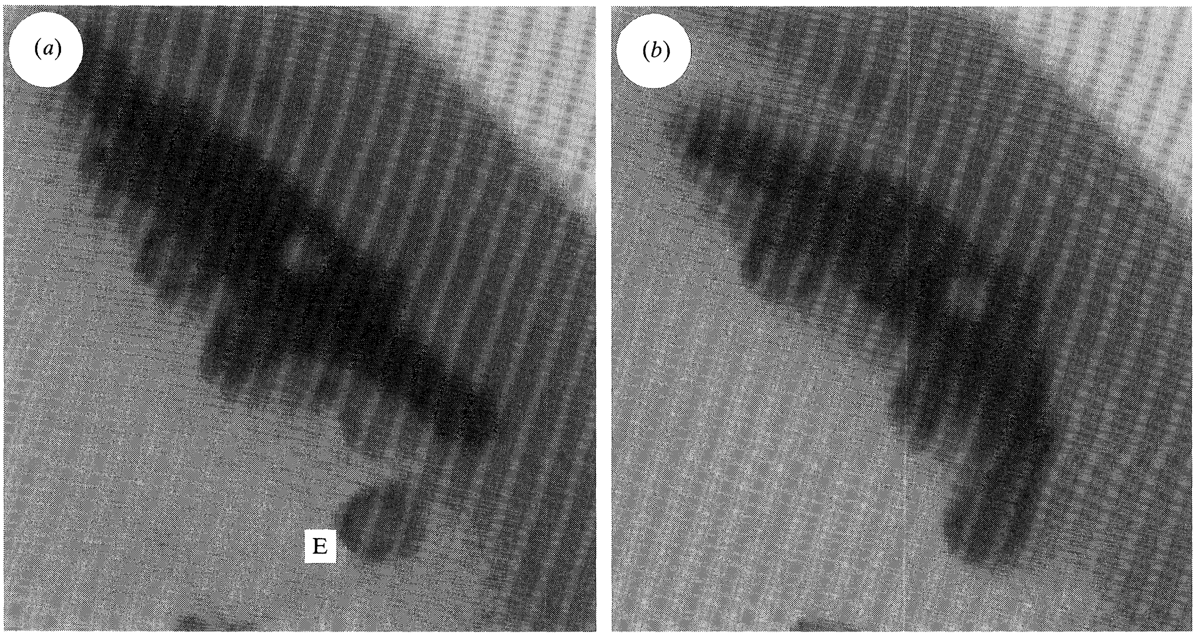

Figure 5. Initial attempts to stimulate the platypus through fixed electrodes, as the platypus was swimming around showed a variety of behaviours. Of these the easiest to discern was the head turning behaviour. As a platypus approached an electrode (E), electrical waveforms were passed through the electrodes at a rate of two every second. The platypus would approach these electrodes from random directions (*a*), and upon sensing an electrical pulse, turn its head so as to place the bill over the area of the electrode (*b*). The field strength in the illustrated case was approximately 0.8 mV cm^{-1} at the point where the bill first starts to turn in (*a*). The threshold field strengths for eliciting this behaviour varied widely, perhaps because of the head swinging behaviour and the marked directionality of the bill described later.

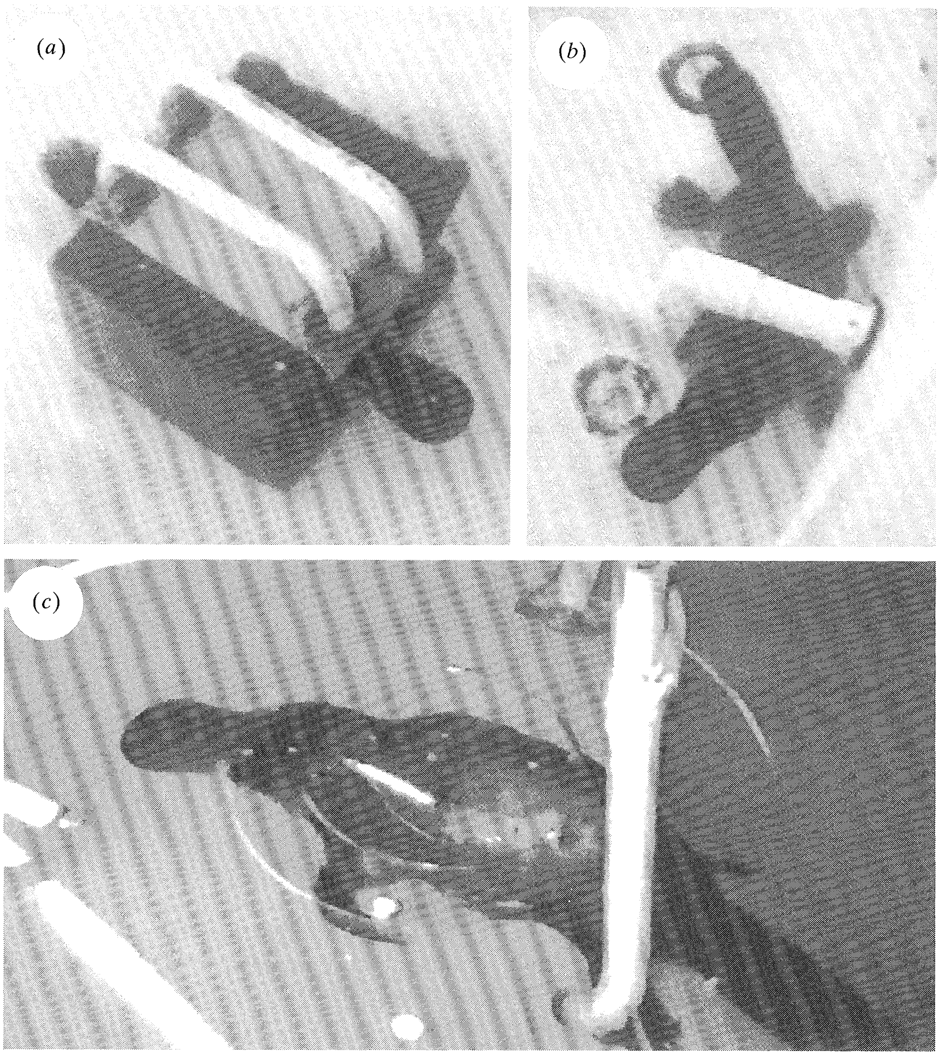

Figure 6. Three different rests were provided for the platypus. (*a*) Platypus inside the concrete tunnel; (*b*) platypus beneath the filter inlet pipe; (*c*) platypus beneath the transparent Perspex dome. The filter inlet pipe was the favoured site for resting underwater.

lasting an average of 6.63 s (range 2–26 s), and comprising 5.82 % of the total time the platypus spends in the water. Another behaviour seen during these overnight video recordings was preening (behaviour 7). The platypus would preen in one of two ways, either it would float on the surface of the water, preening with its hindlimb, or it would climb onto the dome in the middle of the tank, out of the water, and then preen itself. The preening bouts lasted between 11 and 88 s, being 2 % of the time the platypus spent in the tank.

(*b*) *Initial tials*

As mentioned earlier, a series of behavioural trials were undertaken with a freely swimming platypus. A swimming platypus would circle the edge of the tank at the bottom, probably searching for food. The platypus would move its head from left to right in a scanning motion. The swimming velocity and scanning angle of the freely swimming platypus changed dramatically under certain circumstances, this being the 'patrol' behaviour described by Scheich *et al.* (1986) (see §3*f*). The changes in these parameters and their causes are described more fully later, and discussed with respect to the directional ability of the platypus bill. The changes in swimming behaviours caused problems with repeatability and reliability of the experiments. However, the observed electrically driven behaviours do add to the results. Four readily observed behaviours were seen in association with electrical stimuli presented to a freely swimming platypus.

1. Head turning behaviour. The high speed of the swimming behaviour combined with the head swinging behaviour tended to mask orientation to an electrical stimulus; however, orientation of the head to the electrode was repeatedly observed (see figure 5). The thresholds for eliciting the head turn varied widely, probably because of the variable orientation of the bill with respect to the stimulus (see §3*e*).

2. As the platypus passed over the electrode, the platypus was seen to suddenly turn its whole body 180° to come back to investigate the area surrounding the active electrode.

3. As the platypus swam near the active electrode, the head was swung towards, over and around the active electrode, with the animal seeming to linger in passing by this area.

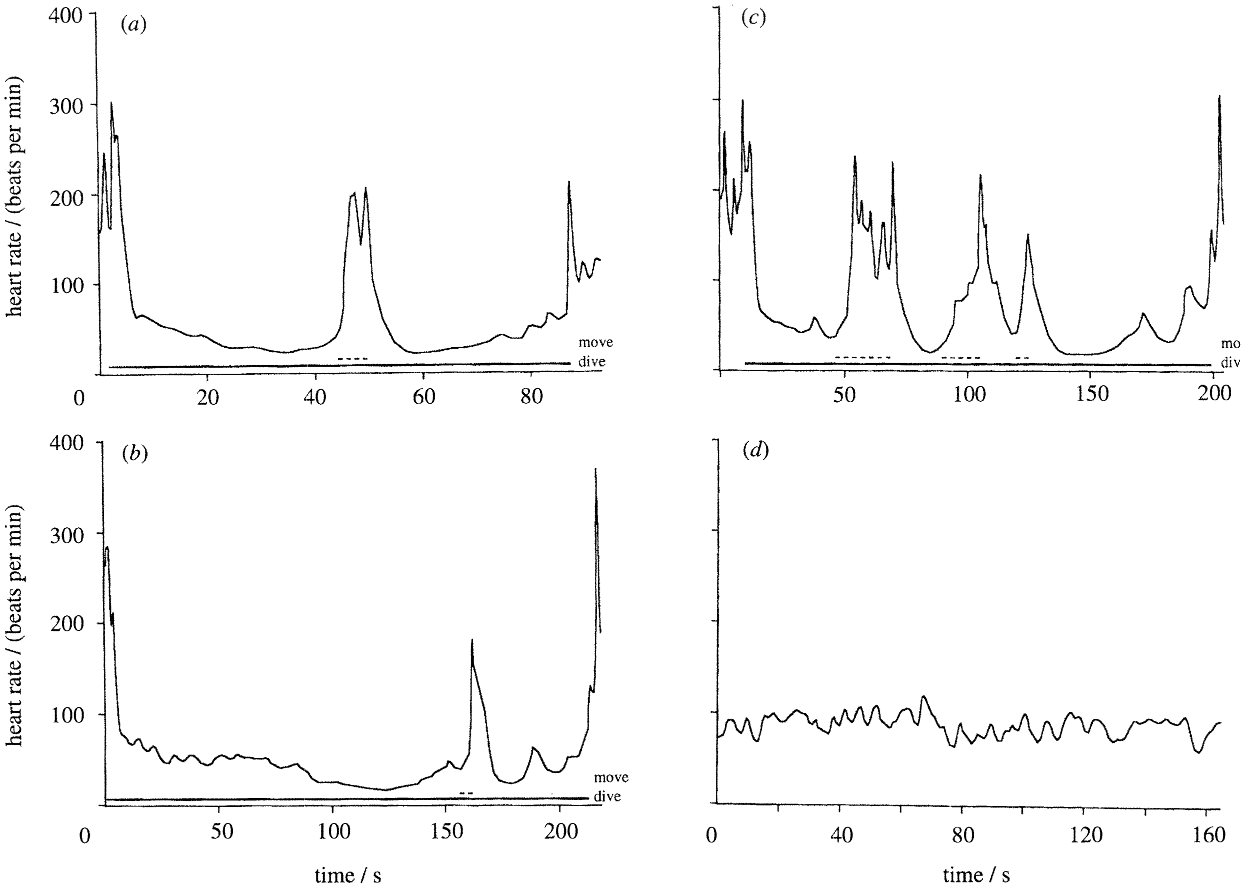

Figure 7. Plots of the instantaneous heart rate (reciprocal interbeat interval) of the platypus during three different dives (*a*, *b*, *c*), and during a quiescent period in the burrow (*d*). Note the bradycardia associated with the first few seconds a platypus is wedged beneath a rest. This is followed by a steady decline in the heart rate, down to the slowest rate. This steady, slow decline may be interrupted by occasional tachycardias that are a result of a disturbance to the platypus which cause movement around or away from the rest. Towards the end of the dive there is a steady rise in heart rate, perhaps associated with an anticipated end point for the dive. The post-dive tachycardia is associated with the platypus surfacing.

4. An avoidance type response, in that when the amplitude was increased the platypus would maintain its circular path around the tank. However, the platypus would swim up and over the active electrode, not quite breaking the surface, but definitely to avoid the active electrode.

The lowest reliable threshold that could be obtained with this style of stimulation was 100 $\mu V\ cm^{-1}$, with the aversive response being seen at 10 $mV\ cm^{-1}$.

(*c*) *Resting behaviour*

Previously in this paper we have described three pieces of equipment that were in the water of the platypussary: a Perspex dome, a concrete tunnel, and the filter inlet pipe (see figure 6). These were described as underwater rests. When the platypus is searching for food the length of the stays under the rest were an average of 15.3 s. However, when people were present in the room, the average time spent under the rest increased to 3 min, the longest stay observed being 8 min. While the platypus was wedged below one of these rests a distinct bradycardia was recorded. This bradycardia appeared within 3 s of the platypus wedging itself under one of the rests (see figure 7). While floating on the surface of the water, or while diving and swimming, the platypus had a heart rate between 150 and 200 beats per minute. A quite marked pre-dive tachycardia was observed in the last few seconds before a dive. The heart rate would reach levels of around 300 beats per minute. Within 3–4 s of the platypus wedging itself under the rest, the heart rate would have slowed down to around 70 beats per minute, or 23 % of the pre-dive tachycardia. For the next 60–120 s of the dive the heart would slowly decrease to levels as low as 20 beats per minute, or 6.6 % of the pre-dive tachycardia. These periods of extensive bradycardia were associated with minimal movement of the platypus. Platypus would move whilst remaining wedged under the rest when they were disturbed, for example by the 50 g shrimps they were eating. During these periods of movement the heart rate would show a rapid tachycardia, up to around 200 beats per minute, before showing an equally rapid bradycardia to return to slower heart rates. It was interesting to observe that in all dives recorded there appeared to be an anticipatory rise in the heart rate before the platypus surfaced for another breath. For a period ranging between 10 and 50 s (depending on dive length), the heart rate would slowly rise from the

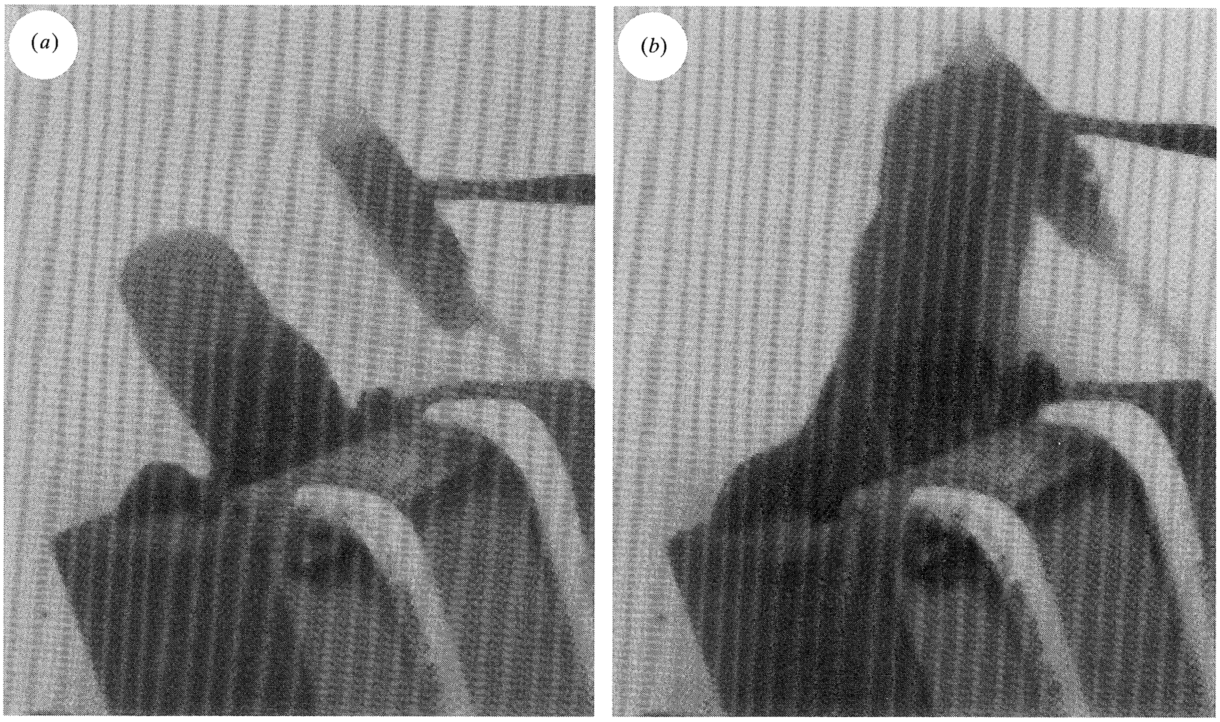

Figure 8. Initial attempts to mouth the electrical stimulus: To respond to an electrical pulse with a saccadic movement of the head the platypus must first undergo habituation to the electrical transient. Pulses are presented to the platypus (*a*), which initially the platypus finds attractive, and so mouths the electrode (*b*), however, after about one hundred such episodes, with no reward, the platypus no longer attempts to mouth the electrode.

lowest levels up to a rate of around 70 beats per minute. As soon as this rate was reached, coinciding with the platypus emerging from under the rest, a dramatic increase in heart rate was seen. This increase in heart rate took around 2–6 s, and was associated with a post-dive tachycardia, where heart rates were seen to range between 200 and 400 beats per minute (also dependent on dive length). When in the burrow, presumably sleeping, the heart rate of the platypus did not demonstrate the wide variability shown while the platypus was in the water. The heart rate slowly oscillated between 75 and 120 beats per minute, with an average of 99 beats per minute. A full description of the diving physiology of the platypus has been recently provided by Evans *et al.* (1994).

Burrell (1927) first documented this resting behaviour with a series of experiments aimed at testing the sense of smell of the platypus. The most convenient aspect of this behaviour was the manner in which the platypus held its head. The bill was held a few centimetres from the bottom of the tank, generally along the axis of the spine. The head was also held very still (for periods of up to 2 min). The bradycardia associated with the resting behaviour, as well as the lack of muscular movement, lowered the self-generated electrical fields of the platypus to an insignificant level. For the aforementioned reasons, this voluntary and reliable behaviour of the platypus turned out to be quite useful for presentation of electrical stimuli, and except for where it is mentioned, the rest of the results presented here were found while the platypus were exhibiting this resting behaviour.

(*d*) *Electrically driven head saccades*

(i) *General features*

Following the relatively unsuccessful attempts at investigating the electroreceptive behaviour of the platypus as it was freely swimming we changed our method of stimulation (second paradigm), and found a new and far more reliable behaviour associated with the presentation of electrical fields to the platypus, the head saccade. When initially presented with transient electrical signals the platypus would appear to rapidly re-orient (or saccade) its head towards the electrode and mouth it (see figure 8). After around one hundred trials without reward the platypus would cease mouthing the stimulus. It was noticed then that when presented with an electrical transient the platypus would initially saccade towards the stimulus, but then the head would return to its resting position (see figure 9). The platypus appeared to be doing its best to ignore the stimulus. The third set of stimulus generation equipment was then designed and used for the remainder of the behavioural trials reported here. This laterally directed head saccade proved to be the most reliable assay for testing platypus electroreception, especially as the trials were undertaken while the platypus was 'resting' underwater. The head saccade also allowed us to present over 10 stimuli per second to the platypus. In one remarkable session of behavioural testing, a platypus responded with a lateral head saccade 136 times in 40 s, with 100% reliability to stimuli with a constantly changing repetition rate (from 1 Hz up to 10 Hz). The efficiency and reliability of this head saccade is quite evident, and so was used for the majority of behavioural trials reported here.

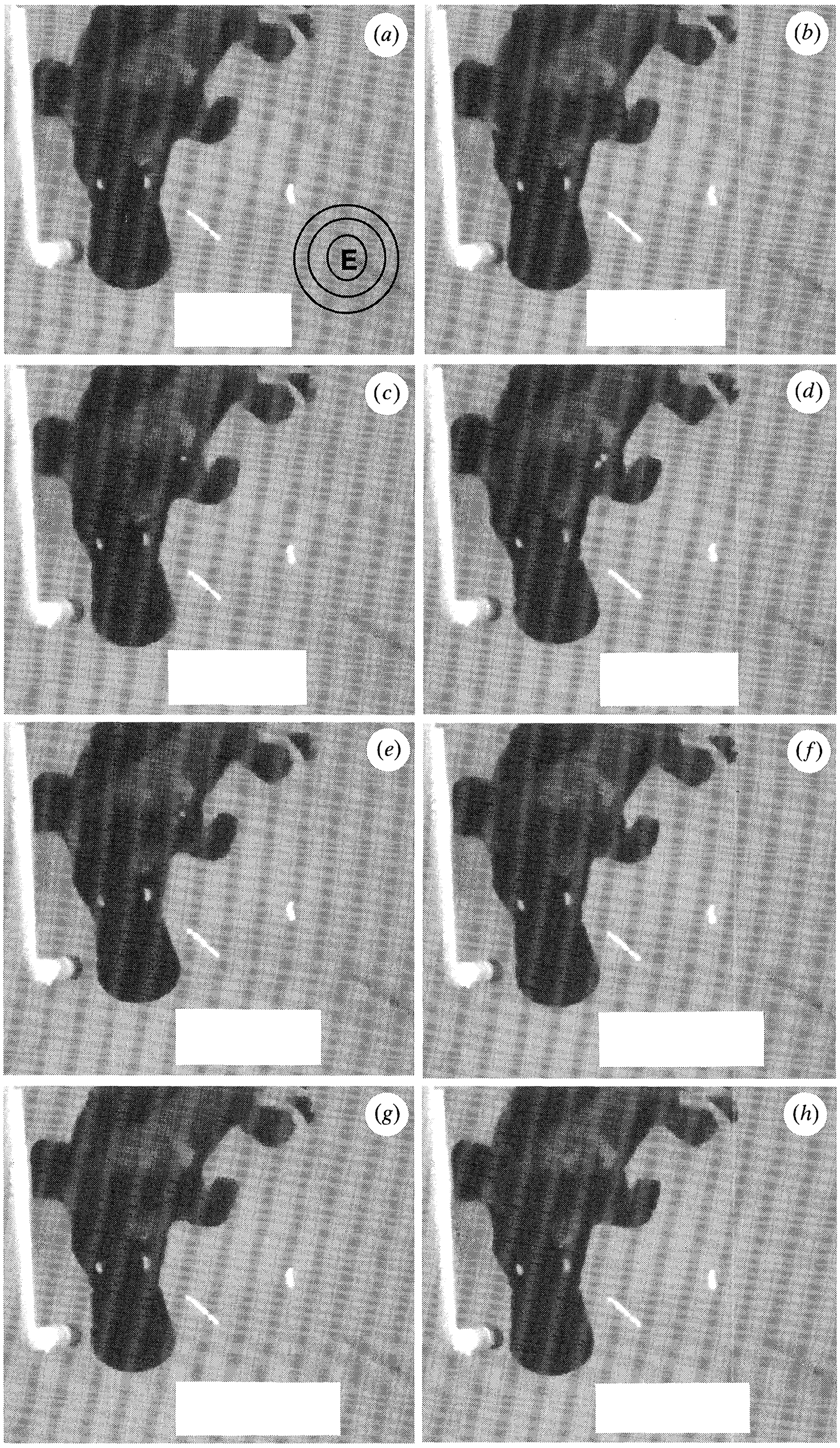

Figure 9. Head saccades to an electrical stimulus. After habituation to the electrical transients the platypus was unable to ignore the electrical signal, and every time an electrical transient was presented to the platypus a saccadic movement of the head and bill was observed. The eight consecutive video frames shown here demonstrate the latency of the head saccade (43 ms) and the duration of the saccade. E represents the position of the electrode, the rings representing the electrical pulse at time = 0.

(ii) *Latency*

The latency of this head saccade was measured using a photosensitive linear detector. The detector was waterproofed and placed under the bill of the resting platypus. A punctate light source (10 cm diameter field) was aimed at the bill and a series of head saccades induced. The electrical pulses and amplified DC level output of the photodetector were recorded onto separate channels on a Racal reel to reel tape recorder. Latency periods were measured using the program Scope on a Mac Lab system. It was found that 43.4 ms (s.d. = 4.9) after presentation of an electrical stimulus

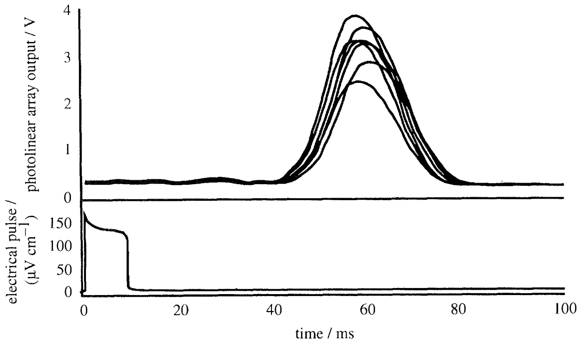

Figure 10. Head saccades recorded using a linear array of photodetectors immersed just under the platypus bill: Seven superimposed traces of DC level output from the photolinear detector used to determine latency and time frame of the direction sensitive head saccades (electrocephalokinetic reflex). Note that at around 43 ms the saccade begins, takes around 15 ms to reach its maximum amplitude, and takes another 20 ms for the head to return to the original resting position. The lower portion of the graph shows the electrical pulse (150 μV cm^{-1} in this instance) associated with the head saccades as recorded from electrodes in the tank; note the capacitance effect of the water distorting the square wave.

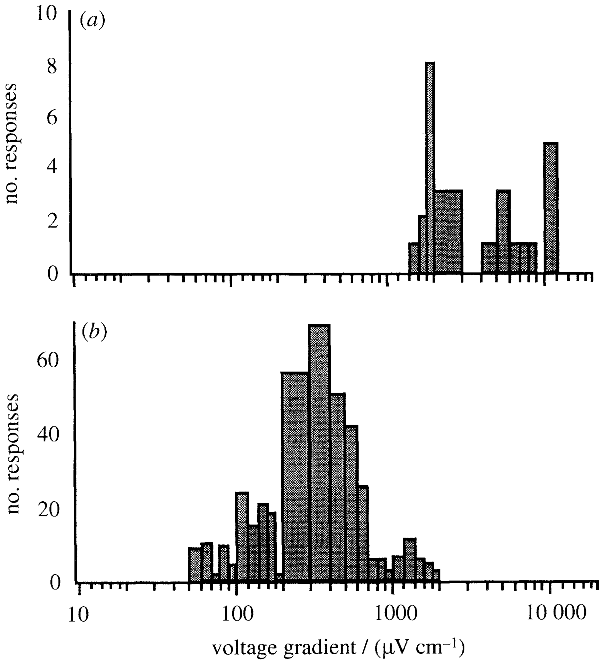

Figure 11. Behavioural responses to different voltage gradients. (*a*) Voltage range tested that elicited an aversive response from the platypus, where the head saccade was in a direction contralateral to the stimulus and/or the platypus swam away from its rest following the stimulus. (*b*) Voltage range over which it was possible to elicit a saccade that was sensitive to the origin of the electrical pulse in the water. The size of these head saccades depended on the field strength of the electrical stimulus. Avoidance behaviour was seen at voltages above 1.5 mV cm^{-1}, a value in the range that activates peripheral electroreceptors and that might be associated with synchronous activation of all electroreceptors. The threshold field strengths for the head saccade behaviour is seen at 50 μV cm^{-1}. Note that there is some overlap in field strength ranges between the two behaviours.

the platypus would initiate movement of the head towards the source of the electrical stimulus (see figure 10). This result was confirmed with high speed film (400 frames per second). It would take approximately 15 ms for the outflick of the head of the platypus to be completed. As the platypus would recognize that no reward of food was associated with 10 ms square waves, the head would return to its original resting position. This return phase of the head saccade took approximately 20 ms, the entire saccade, including latency, lasting around 80 ms.

(iii) *Threshold*

The lower threshold range for reliably eliciting the head saccade response was between 50 and 60 μV cm^{-1} for all platypus studied (see figure 11). The physical size, i.e. the lateral distance the edge of the bill moved during a saccade, also changed with voltage level. At voltage levels around the threshold, the saccade was nearly imperceptible, with movements as small as 1 mm. However, these movements were directly correlated to the square wave stimulus. At higher voltages, approximately 1 mV cm^{-1}, the saccade was up to 3 cm. The angular velocity of the movement averaged 506° s^{-1} and ranged between 400° s^{-1} and 700° s^{-1}.

(iv) *Repetition rate*

This head saccade is precisely time-locked to each presentation of a square wave. As the repetition rate of the square wave is increased, the head saccades phase lock to the square waves, the platypus showing a remarkable ability to stay exactly in time with the square waves. The maximum number of repetitions per second that the platypus could phase lock ranged between 11 and 16 repititions per second. This range depended on the individual animal and how it appeared on that day (i.e. lethargic or active). Another important finding is the increased sensitivity at the lower repetition rates. Various repetition rates of square waves with the same amplitude and duration were presented to the platypus. The distance from the bill that the head saccade phased locked with the square waves was noted. It was seen that at repetition rates of 0.1 per second, the platypus was far more sensitive, and that at repetition rates over 10 per second, the mobile electrode had to be very close to the edge of the bill to induce phase locking (see figure 12).

To test the upper limit of repetition rates that the platypus could follow, the duration of the square wave was modified. As the platypus were exhibiting the resting behaviour, and responding with head saccades to presentation of square waves, the duration of the square waves was slowly increased. As the duration of the square wave reached around 80 ms, two head saccades were seen in response to every square wave (the on and off phases of the square wave) presented to the platypus. This indicates that the upper repetition rate that the head saccades can work with is 12.5 repetitions per second. This falls into the range previously tested. It is also interesting to note that this test shows that the platypus is responding in the same manner to both positive and negative DC shifts.

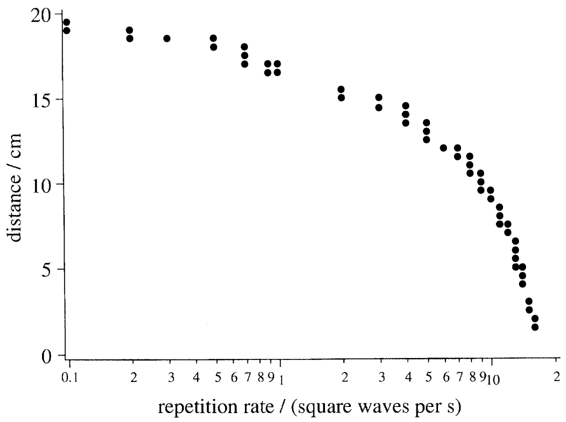

Figure 12. Dependence of head saccades on the repetition rate of the electrical stimulus. A fixed amplitude (100 μV cm^{-1}), variable repetition rate stimulus was presented to the platypus. Note that the head saccades follow repetition rates in excess of 10 Hz, but that higher field strengths (closer approach of the fixed amplitude stimulus) are required at higher repetition rates. There is a high correlation between the variables.

(*e*) *Directionality of the bill*

The striped array of electroreceptors along the bill of the platypus (Andres & von During 1984), and the ability of the platypus to accurately locate electrical stimuli (Scheich *et al.* 1986), made it of interest to determine if the platypus was differentially sensitive to electrical stimuli. To do this we again made use of the resting and head saccade behaviours. The mobile electrode was presented to the bill from a variety of different directions. A square wave with a fixed amplitude and frequency was used. The mobile electrode was advanced towards the bill, in the axis of the chosen direction, until a phase locked head saccade was seen. At this point the distance away from the electrode was noted. Plotting of the field decay allowed us to accurately ascertain the voltage that the platypus was sensing. The head saccade altered in its outflick direction according to the direction from which the electrical pulse was originating. With the electrode positioned above the bill, in the medial sagittal plane, an upwards flicking of the bill was seen. From below the bill in this same plane, downwards flicking was seen, and so forth for all directions tested.

The most sensitive direction, termed the preferential axis, occurred eighty degrees lateral from the rostral pole of the bill and twenty degrees ventral. This preferential axis was symmetrical. Comparisons of the threshold for stimulation along the preferential axis compared to non-preferred axes shows that the preferential axis is around 100 times more sensitive than the non-preferred axes. It is very interesting to note that the preferential axis found here is orthogonal to the mucous gland electroreceptor stripes on the bill, and where the axis approximately crosses the bill is where the presumptive serous gland electroreceptors are most dense (Andres & von During 1988) (see figure 13 and table 2).

(*f*) *Patrol behaviour*

Scheich *et al.* (1986), previously described three behaviours in the location of food by the platypus.

Table 2. *One of the data sets recorded for the directionality testing*

(The data is in the form of spherical coordinates, the 0,0,0 coordinates indicating the zero position, which was between the nostrils on the bill of the platypus, and the 0,0,15 coordinates representing a line that is continuous with the body axis. This data was used to draw the iso-threshold surface represented in figure 13*d–f*. The data is easiest to interpret if one imagines the 0,0,0 coordinates as the centre of a modified sphere, 0,0,15 as the 'north' pole, and other coordinates as representing latitude (co-latitude) and longitude (co-longitude), with the radial distance representing the distance from the centre of the sphere. As one progresses away from the 0,0,0 coordinate the radial distance increases. As one progresses away from the pole in a single direction, the co-latitude increases, and as one circumscribes the pole, the co-longitude changes relative to the upper mid-sagittal plane of the platypus, which is shown as the 0° plane. Therefore, the lower mid-sagittal plane is represented by 180°.)

co-latitude/deg	co-longitude/deg	radial distance/cm
0	0	0
0	0	15
30	0	7
30	30	8
30	60	10.5
30	90	19.5
30	120	19
30	150	22.5
30	180	20.5
30	210	22.5
30	240	19
30	270	19.5
30	300	10.5
30	330	8
60	0	5
60	30	9.5
60	60	12
60	90	27.5
60	120	26
60	150	25
60	180	19
60	210	25
60	240	26
60	270	27.5
60	300	12
60	330	9.5
90	0	4
90	30	6.5
90	60	9.5
90	90	23.5
90	120	27
90	150	25.5
90	180	12.5
90	210	25.5
90	240	27
90	270	23.5
90	300	9.5
90	330	6.5
120	0	3
120	30	4
120	60	7
120	90	21.5
120	120	22
120	150	17.5
120	180	11
120	210	17.5
120	240	22
120	270	21.5
120	300	7
120	330	4

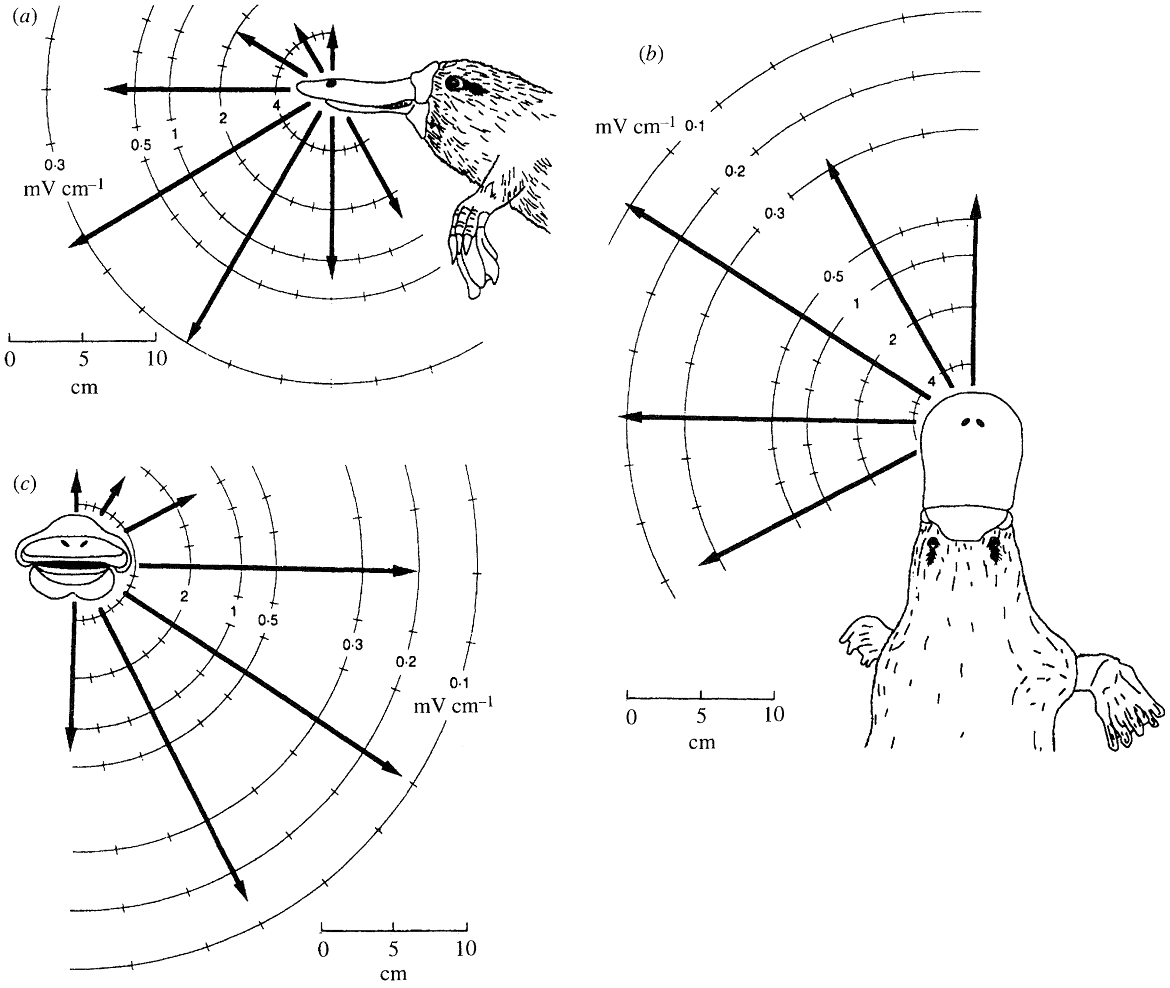

Figure 13 (*a–c*). For description see opposite.

These were: a patrol behaviour, where '2–3 undulatory sweeps' of the head were made every second; a search behaviour, with erratic head movements over a specific area of interest to the platypus; and an attack behaviour, where the object of interest was mouthed.

With respect to the preferential sensory axis of the bill, described above, the patrol behaviour is of most interest. It is during the patrol behaviour that the platypus appears to be most interested in locating food items. Before the patrol behaviour is seen a platypus will just slowly swim around the circumference of the tank, with the occasional non-direction preference head sweep, and does not appear to put any effort into finding food. However, after the platypus senses something of interest with its bill, be it a live shrimp, or an electrical stimulus, a dramatic shift into patrol behaviour is seen. The swimming velocity of the platypus increases from an average of 0.1 m s^{-1} up to 0.3 m s^{-1}, i.e. swimming close to its own body length every second. Secondly, the head sweeps become very regular. The platypus sweeps from left to right every time (see figure 14). During these sweeps the axis of the bill was compared to the axis of the spine, and we see that pre-patrol behaviour had an average sweep angle of 30.3°, and patrol behaviour an average of 52.6°. The frequency of the sweeps during patrol behaviour was an average of 2 sweeps per second (pre-patrol = 0.3 sweeps per second), confirming the observation of 2–3 per second by Scheich *et al.* (1986).

It is interesting to analyse this sweep behaviour with respect to the preferential axes of electroreception. As described above there is a pre-patrol behaviour associated with slow swimming, and smaller and more infrequent sweeps of the bill across the bottom of the tank. This was analysed with respect to the preferential sensitivity axis of the bill. The preferential sensitivity axis was seen to cover 0.042 $m^2\ s^{-1}$ during these phases of pre-patrol swimming (see figure 15). Upon changing the behaviour to patrolling, with a higher swimming velocity, and larger and regular sweeps of the bill, the area which the preferential sensitivity axis covered increased to almost three times that of the pre-patrol, reaching an average of 0.114 $m^2\ s^{-1}$.

(*g*) ***Reversal of head saccade***

The amplitude of electrical pulses presented to the platypus that is required to elicit an aversive response was tested under the resting behaviour conditions, and using the head saccade reflex. The amplitude of the initial square wave presented to the platypus was around 100 μV cm^{-1}. Time-locked head saccades were initiated and slowly the amplitude of the square wave was increased. As the amplitude of the square wave reached around 1.8 mV cm^{-1}, a change in the head saccade was seen (see figure 11). Instead of a saccade towards the source of the electrical stimulus, the platypus would saccade away from the source of the

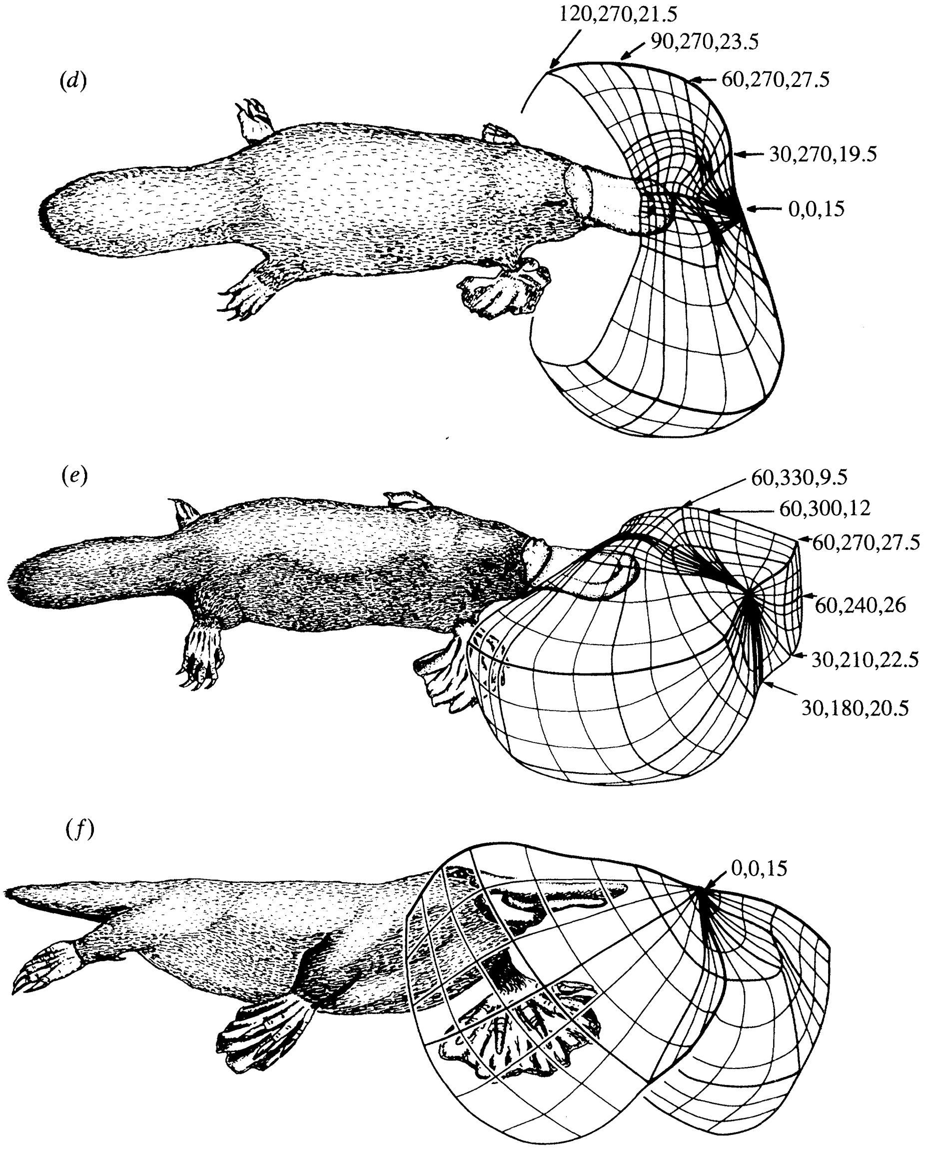

Figure 13. Directionality of the electrically elicited head saccade: measured by the threshold distance for eliciting head saccades from a square wave electrical stimulus of constant amplitude. The length of each arrow gives the distance at which the stimulus first elicited saccades which were time-locked to the stimulus (2 Hz); circles give the electrical field strengths (in mV cm^{-1}) that would be experienced at the bill if the stimulus were presented at that distance. Note that the stimulus elicits head saccades at much greater distances, corresponding to much lower electrical field strengths at the bill, if presentation of the stimulator dipole occurs from some, preferred directions. (*a*) Side elevation: sampled directions in the mid-sagittal plane; (*b*) plan view: sampled directions in the horizontal plane through the bill; (*c*) front elevation: sampled directions in the coronal plane through the bill. Figures (*d–f*) show a compilation of the directional testing behavioural data in the form of an iso-threshold surface (see table 2). Note the symmetrical lobes that form the surface, indicating that the areas of greatest sensitivity are around 80° from directly in front and down approximately 20°. (*d*) View from above and behind; (*e*) view from above and in front; (*f*) view from below and in front. The figures on the surface represent coordinates from table 2.

stimulus. After three to five consecutive presentations of this aversive stimulus, the platypus would appear to be annoyed, and swim away from the rest it had wedged itself under.

(*h*) *Gradient of fields across the bill*

Of major interest, especially considering the striped array of electroreceptors on the bill of the platypus, is the gradient of the electrical fields across the bill. Electrical fields decay in an inverse square manner as they pass through water. The manner in which the square waves were decaying in water was checked, and is shown in figure 16. So to check the gradient of fields across the bill, stimuli of various amplitude were presented to the bill originating along the preferential axis. The distance away at which the platypus would respond with a head saccade was noted. The various decay rates were then measured with the oscilloscope. The width of the platypus bill (5–7 cm) was then marked on the plot of the decay at the distance where the platypus first gave a response (see figure 16). When a head saccade was elicited the field strength dropped from around 50 $\mu\mathrm{V\ cm}^{-1}$ at the edge of the bill closest to the electrode to around 25 $\mu\mathrm{V\ cm}^{-1}$ at the edge of the bill furthest from the electrode. It is interesting to

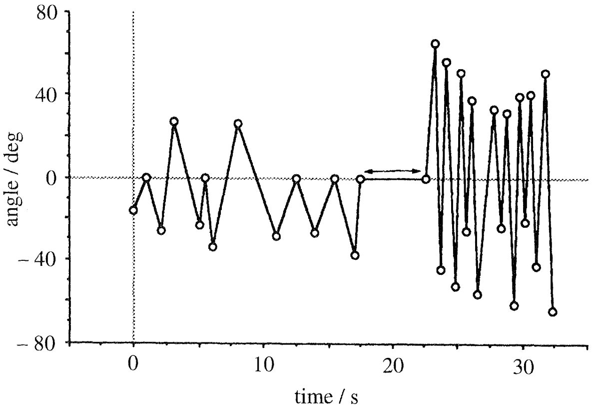

Figure 14. Transition from pre-patrol to patrol behaviour, triggered by contact with live prey. The points represent the maximum angle that the bill axis deviates from the body axis during the head sweeps, to the left and right. During pre-patrol it is obvious that the number of sweeps per second and the size of the sweeps is much smaller and irregular when compared to patrolling. Interaction with a shrimp (arrow) caused the transition from pre-patrol to patrol.

note that when we superimpose a figure of the electroreceptor stripes of the bill onto the field gradient at distances relevant to thresholds experience for the head saccade behaviour, we see that the drop in field strength between and across the stripes is quite small, in the range of 1–5 μV cm^{-1}, depending on the width of the stripe, the distance between stripes, and the proximity of the stripe relative to the origin of the electrical dipole (see figure 16).

(*i*) *Galvanotaxis and associated behaviours*

Testing of the platypus for galvanic sensitivity proved positive. When a metal rod was introduced to the water the platypus showed three types of responses. The 'first reaction' (Kalmijn 1974), was observed. This involved a visible twitch of the body as the metal rod was introduced to the water in which the platypus was exhibiting the resting behaviour. The metal rod was then brought closer to the platypus and, at a distance of 15–20 cm, corresponding to a voltage gradient of 500 μV cm^{-1}, the platypus would orient towards the metal rod. Following this initial orientation, the platypus would make three or four exaggerated sweeps of the bill, usually followed by tactile investigation of the rod. On the first few introductions of the metal rod to the platypus, the platypus would orient towards the rod, and follow this orientation with mouthing of the rod (see figure 17). These behaviours are described as 'galvanotaxis' by Kalmijn (1974). The final behaviour seen was an aversive response to the galvanic fields. If the metal rod was brought within 5 cm of the platypus, corresponding to a voltage gradient of 5 mV cm^{-1}, a series of rapid small head oscillations occurred, this was followed by the platypus swimming away from the rest it had wedged itself under. Kalmijn (1974) describes a third response to galvanic fields in fish, where strong galvanic fields caused immobilization, he termed this 'galvanonarcosis'. The aversive response of the platypus to strong galvanic fields, even though not causing immobilization, can also be described as galvanonarcotic (see figure 17).

4. DISCUSSION

(*a*) *The direction-sensitive head saccades*

Previous reports (Burrell 1927; Faragher *et al.* 1979) and the present investigation have found that the platypus requires a substantial amount of food each night, sometimes eating half its own body mass in the one night (*ca.* 0.5 kg). To obtain this amount of food in one night, in a freshwater stream where there is no certainty of the position of food would require something quite extraordinary. The most comprehensive of the early platypus naturalists, Burrell, hypothesized a sixth sense that would assure the platypus of the direction in which its prey is located. These musings were confirmed by a recent report (Scheich *et al.* 1986) detailing an electrical sense in the platypus. We have shown in this paper that the platypus does indeed have the ability to detect the direction from which an electrical dipole originated, and we have also shown that this directional detection is mediated in around 43 ms. Is this directional response a reflex? Two observations lend support for this directional detection response being a reflex.

1. The reliability of the response. As stated earlier, in one behavioural session we obtained 136 responses in 40 s with 100% reliability. This is typical of many behavioural sessions. The head saccade response is a derived response from a real behaviour shown by the platypus. When an electrical transient was presented to an uninitiated platypus, the platypus would saccade towards the stimulus and follow on until it could touch the electrode with the bill. If a stimulus of sufficient size was presented, the platypus would move its head around and not find anything to touch, as the electrode could be a greater distance from the bill. After repeated trials such as this the platypus would stop following through with the bill, and all that was seen was a saccadic movement of the head. The fact that a saccadic head movement was seen every time an electrical stimulus of sufficient strength was presented furthers the notion that this electrically driven response is mediated by a reflex.

2. The second observation lending support to this being a reflex driven response is the short latency from initial electrical stimulation to initiation of movement of the head in the direction of the stimulus origin, approximately 43 ms. However, this is a comparatively long latency for a monosynaptic reflex, for example the human knee jerk response has a latency of approximately 22 ms. It seems then, that more than one synapse is involved in this behaviour, and some processing may occur before eliciting a directed movement of the head. If we theorize on at least 50 cm of axon length for passage of action potentials, and assume a sensory conduction velocity of 250 cm s^{-1} (Gregory *et al.* 1988) (from the rostral pole of the bill to the back of the skull would be 12 cm maximum), we

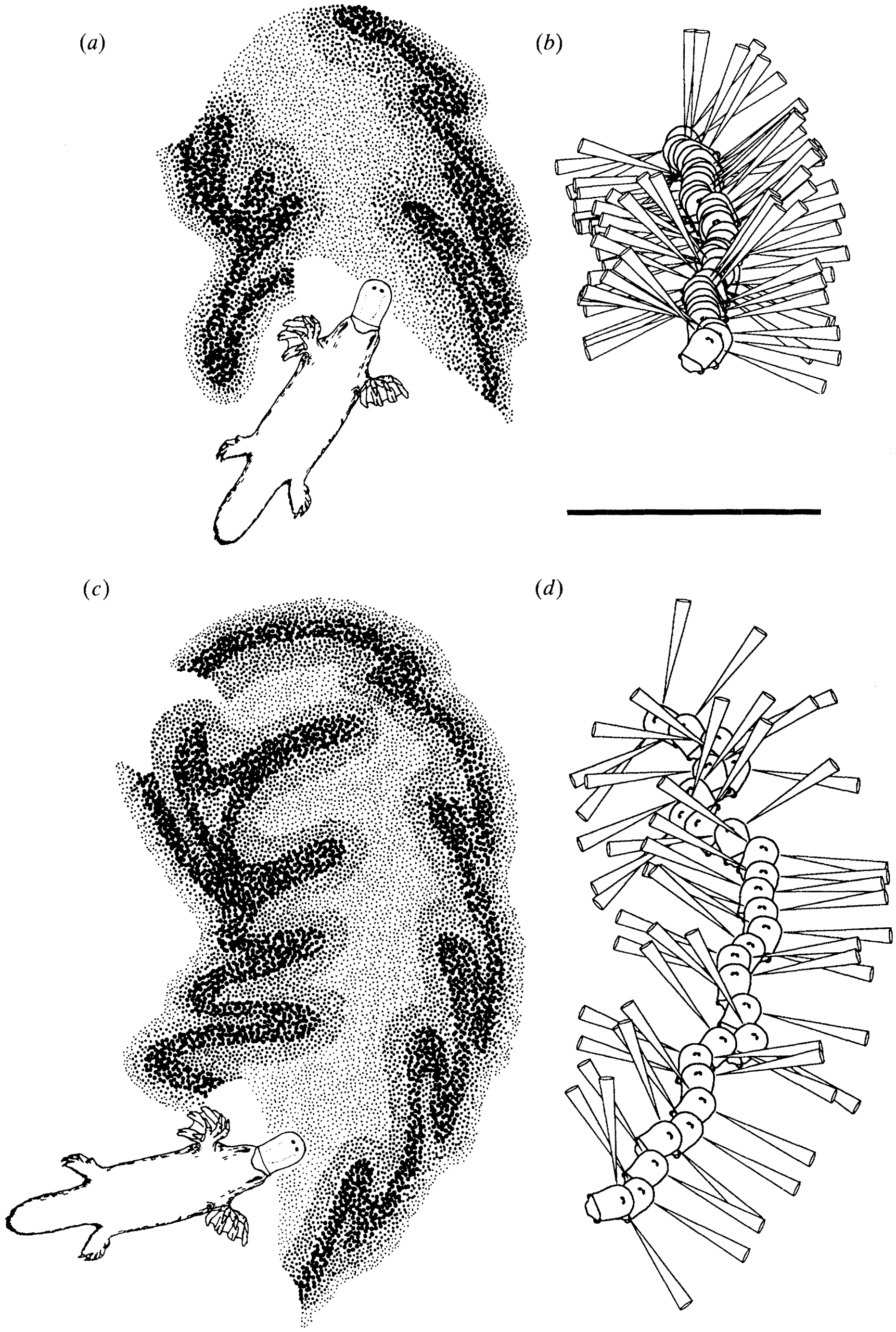

Figure 15. Representation of the sweep of the bill's preferred axis across the bottom both before (*a*,*b*) and during (*c*,*d*) the patrolling phase. Diagrams (*a*) and (*c*) represent the intersection with the ground of three areas of sensitivity when the platypus is swimming approximately five centimetres above the ground. It is best to imagine the iso-threshold surface (figure 13) when looking at this figure. The darkest region represents the 10° surrounding the preferential sensitivity axis, the medium area represents 20° surrounding the preferential sensitivity axis, and the light area the rest of the isothreshold surface that intersects the ground. Diagrams (*b*) and (*d*) show kinesographs of the head swinging motion with the preferential sensitivity axis approximated, demonstrating the position of this axis at intervals of 100 ms. Note the almost threefold coverage of area per unit of time when the platypus is patrolling (*d*).

still have around 16 ms remaining (assuming 2 msec neuromuscular junction delay). In 16 ms more than 8 synapses in the central nervous system could be crossed, allowing much processing to occur. It is therefore reasonable to assume that higher centres play an important role in mediating the direction in which the head moves. Does the probable involvement of higher centres eliminate this directional detection response being a reflex?

As described earlier these head saccades are a conditioned response. An unconditioned platypus will saccade towards the origin of an electrical dipole and then follow the saccade with exploratory movements of the head in the area from which the electrical dipole originated. What role does this sort of response have in the normal feeding pattern of the platypus? This type of response may reset the swimming rhythm of the platypus, directing the animal towards a food source,

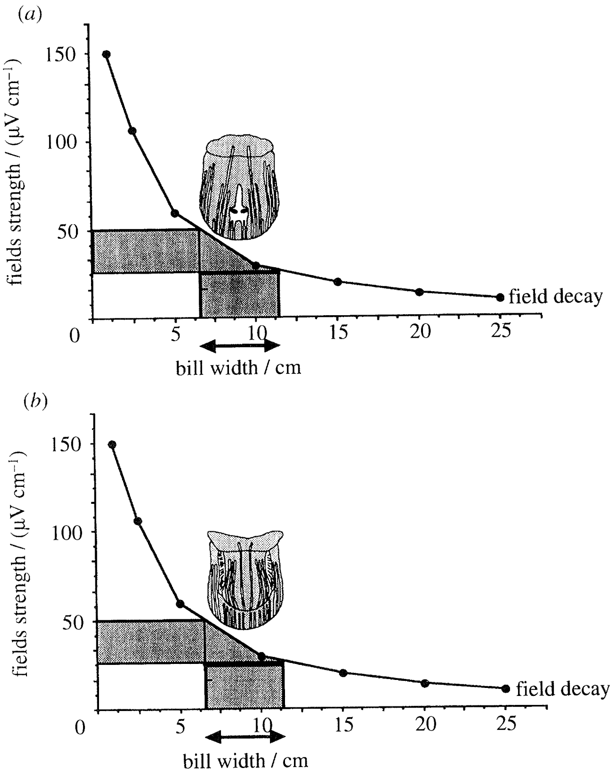

Figure 16. Change in field strength across the platypus bill for a typical field used in the present experiments. It is interesting to examine the decay of the field strength across the platypus bill in relation to the stripes of mucous gland electroreceptors. In these two diagrams we see the decay across the bill from above (*a*), and below (*b*), corresponding to voltages which produced the head saccade behaviour. The behavioural records presented here were obtained from the same animal as that which the distribution of electroreceptors in the bill skin was discerned. The decay of the field between stripes is around 5 µV cm^{-1} for the stripes nearest the origin of the electrical pulse, decreasing to around a 1 µV cm^{-1} difference between the stripes farthest from the origin of the electrical pulse.

quickly and accurately. We have observed a variety of behaviours of the freely swimming platypus (see §3*b*) that support the suggestion that the swimming rhythm is altered dramatically following exposure to electrical stimuli. This reflexive response may also work on a smaller scale. Rather than reorienting the whole body while swimming there are other feeding strategies of the platypus in which a directed saccade may be useful. Platypus often turn over rocks and disturb the substrate of a pool quite dramatically, using both bill and forepaws to stir up the substrate. During these bouts, the platypus swims with its whole body oriented at a steep angle to the bottom of the pool. The platypus has no time for body reorientation in this case, however, a rapid movement of the head in the direction of fleeing prey will enable the platypus to capture the prey.

This type of short latency, direction sensitive movement has a strong resemblance to a behaviour previously described for the barn owl (Knudsen *et al.* 1979). Results from behavioural and neuronal studies of the barn owl have shown saccadic movements of the barn owl head when orienting to an acoustic stimulus. The latency between sound stimulation and initiation of head movement by the barn owl averaged 100 ms, however, the shortest response time latency was 55 ms, comparable to the 43.4 ms of the platypus. The fastest angular head velocity recorded for the barn owl was 779° s^{-1}, comparable to the range we found for the platypus (400–700° s^{-1}). Knudsen *et al.* (1979) also report that the barn owl 'displayed little natural tendency to fixate on sounds from above regardless of sound level...One owl never responded well to high targets even after hundreds of trials'. This is similar to platypus in that the threshold required to elicit an upwards directed head saccade was at least two orders of magnitude above the more sensitive, downward, laterally directed head saccades. It appears likely that this reflects the positions of prey relative to both animals when hunting.

Both the electrically driven head saccade of the platypus and the acoustically driven head saccade of the barn owl are analogous to that of eye saccades studied in animals with moveable eyes, such as cats (Distler & Hoffman 1992), monkeys (Hoffmann *et al.* 1992) and frogs (Masino & Grobstein 1990). These eye saccades have been commonly termed the optokinetic reflex. Physiological studies of the neuronal structures subserving the optokinetic reflex have identified the

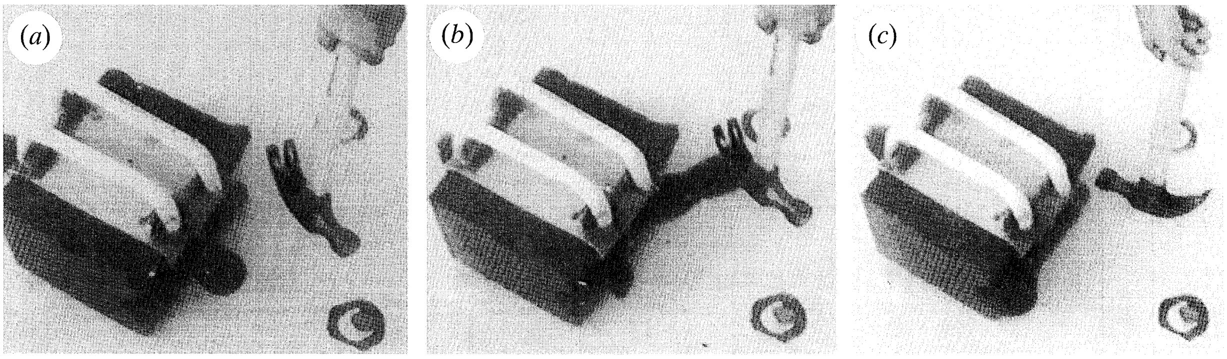

Figure 17. Reaction of the platypus to the presentation of galvanic fields. To dramatize the presentation an ordinary claw hammer has been used. Initially the platypus is at rest in the concrete tunnel (*a*). The hammer head is slowly brought towards the platypus, and corresponding to a voltage gradient of around 500 µV cm^{-1} the platypus swings its head towards the hammer head, thoroughly investigating the galvanic field, and also the hammer head with touch (*b*). After full examination of the hammer head the platypus swings its head away from the hammer head (*c*), appearing somewhat annoyed with its presence.

lateral geniculate nucleus, primary visual cortex, visual areas in the superior temporal sulcus, dorsal terminal nucleus of the accessory optic tract, and the nucleus of the optic tract to be the major components of information flow (Distler & Hoffman 1992; Hoffman *et al.* 1992). What the optokinetic reflex and the platypus and Owl head saccades have in common is that they all function to locate a stimulus accurately, using the reorientation to expose the most sensitive part of the sensory epithelium to the stimulus. With the optokinetic reflex this is the fovea of the eye, with barn owl head saccades it is the facial disk maximizing the auditory and visual resolution, and with the platypus head saccades it is the array of tactile push-rod receptors in the skin of the bill. We term the short latency directional detection and re-orientation response of the platypus to an electrical dipole the 'electrocephalokinetic' reflex.

Further studies on the barn owl head saccades have isolated neural circuitry specific to coding horizontal and vertical head movements (Masino & Knudsen 1990). It is probable that the platypus, after receiving an electrical stimulus, encodes centrally, the origin of the dipole as a point in its own extrinsic or abstract electrical coordinates and passing this abstract code to an area of the brain which translates the abstract coordinates into specific horizontal and vertical movements of the neck musculature, similar to the barn owl. However, further research into the neuronal circuitry of the motor system of the platypus is required to see if this is really the case.

The electrocephalokinetic reflex has obvious benefits for the platypus. If the platypus was chasing a mobile prey item, such as the Atyidae shrimp, short latency head movements towards the shrimp would greatly increase the probability of the shrimp being touched by the bill and providing more accurate clues to the location of the shrimp for the platypus, eventually allowing the shrimp to be caught.

(*b*) *Electroreceptive threshold*

As mentioned earlier, there is much confusion about the absolute lowest threshold of electrical sensitivity of the platypus. Neurophysiological recording from electroreceptor axons showed a threshold of 3–4 mV cm^{-1} (Gregory *et al.* 1988), however, no averaging techniques were employed to test these receptors at voltage gradients below this synchronous firing threshold. Behavioural experiments (Scheich *et al.* 1986) gave a threshold of 50–300 μV cm^{-1}, whereas cortical recordings with surface electrodes gave a threshold of 300 μV cm^{-1} (Proske *et al.* 1992) and with microelectrodes a threshold of 20 μV cm^{-1} (Manger *et al.* 1993). The lowest field strength a platypus can sense is yet to be determined, although we have presented reliable behavioural data showing several platypus to be responsive to electrical stimuli with field strengths as low as 50 μV cm^{-1}. Our observations confirm the lowest behavioural threshold found by Scheich *et al.* (1986). Presently, it seems sensible to assume that the working threshold for a foraging platypus would be the equivalent to the threshold for the head saccade response. Anything in its immediate environment that produces a brief electrical transient with a voltage gradient above 50 μV cm^{-1} is probably considered to be food by the platypus.

The strong directionality of the bill that we have described is relevant to any study involving a freely swimming platypus. Since the sensitivity varies over two orders of magnitude from the most sensitive axis to the least preferred directions, failure to control for head orientation could result in variations of this magnitude. The directionality explains the range of behavioural thresholds described by Scheich *et al.* (1986).

Summation of peripheral inputs to increase sensitivity is 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 5 nV cm^{-1} (Kalmijn 1982) compared with the ampullary receptor unit threshold of 1 μV cm^{-1}, an increase in sensitivity of around 200 times. With catfish the behavioural threshold of 1 μV cm^{-1} is also around one order of magnitude more sensitive than the ampullary receptor unit threshold of 6 μV cm^{-1} (Kalmijn 1974). These examples coincide with the enhanced sensitivity of the behaving platypus over the electroreceptor unit threshold. The reliability of the head saccade reflex has enabled us to set a behavioural sensitivity threshold at about 60 times lower than the receptor threshold. This is consistent with averaging from around 2000 receptors. Since the total number of electroreceptors on half of the bill is around 20000 (Manger *et al.* 1993), the true threshold could be lower still. The threshold we have found is close to the noise level in the tank, and we would not be surprised to find a lower threshold.

Summation of peripheral inputs to enhance sensory perception appears to be a common feature across electroreceptive systems. It is possible that with further studies of behaviour, neurophysiology and anatomy of electroreception in fish, amphibia and platypus, the factors influencing this enhancement will be understood more fully.

(*c*) *Saccades to stronger electrical fields*

We have shown that the electrocephalokinetic reflex of the platypus has a lower threshold of 50 μV cm^{-1}. At a field strength between 1.5–2 mV cm^{-1} it was noticed that the movement of the head was reversed, this being interpreted as the platypus displaying an aversive response. After two to five aversive saccades at these field strengths (around 2 mV cm^{-1}) the platypus would cease its resting behaviour and swim away. It is very interesting that this aversive electrocephalokinetic reflex is at a field strength similar to that reported for threshold levels for individual mucous gland electroreceptors (Gregory *et al.* 1988). The fact that an electrical dipole of around 2 mV cm^{-1} elicits an aversive response by the platypus supports the argument for summation of inputs across the entire electroreceptor array. Does this mean that at voltage gradients of 2 mV cm^{-1} every mucous gland electroreceptor is simultaneously sending a series of nerve impulses to the brain? If this is the case, and we suspect it is, then it is not surprising that the platypus shows an aversive response to voltage gradients this high. This can be likened to the startle response of most animals upon hearing a loud noise, or after being subjected to bright flash of light.

(*d*) ***Galvanotaxis and other responses***

Various aquatic animals have been shown to respond to galvanic fields in the water. These include unicellular organisms, higher invertebrates, fish, and even amphibians (Bary 1956; Koehler 1926; Scheminsky *et al.* 1941; Parker & van Heusen 1917). When a metal rod was presented to the platypus, the platypus would approach and attempt to mouth the metal rod. This behaviour has been described as galvanotaxis (Kalmijn 1974).

Three reactions to galvanic fields by the platypus were noted in this study, these being the first reaction, galvanotaxis, and galvanonarcosis. Kalmijn (1974) previously described similar responses in both electroreceptive fish (Siluridae, Ictaluridae, Claridae, Plotosidae, Gymnarchidae, Gymnotidae, Apteronotidae, Polyodontidae, Scyliorhinidae and Rajidae) and fish not known to be particularly electrosensitive (Cyprinidae, Cottidae, Mugilidae, Sparidae, Gadidae and Serranidae). No proposal has been put forward concerning the physiological basis of reactions to galvanic fields. However, it does confirm that the platypus, and a variety of fish, are responsive to pure DC fields (bearing in mind that the DC field becomes AC when the animal moves relative to the source of the DC field). Scheich *et al.* (1986) showed that the platypus was responsive to a DC field created by a 1.5 V battery. However, the field strength required to elicit a galvanotaxic response, 500 μV cm^{-1}, is far lower than this previous report. When recording from a peripheral axon from an electroreceptor, Gregory *et al.* (1988) found a frequency tuning curve that showed the platypus' mucous gland electroreceptors to be preferentially responsive to stimuli from 12 Hz to 100 Hz. Frequencies below 12 Hz were not tested so it is uncertain whether the mucous gland electroreceptors are responsible for the galvanotaxic responses. Serous gland electroreceptors in the bill of the platypus have not undergone peripheral nerve unit recording studies so this DC sensibility can not be ascribed to a particular electroreceptor type. The biological relevance of galvanic sensitivity to fish is still a matter of conjecture, as it is in the platypus. However, the fact that the platypus has this sensibility indicates that the electroreceptors, in both fish and platypus, are responsible for detecting any galvanic stimulation. It is interesting to note that the voltage gradient required for galvanotaxis in the platypus is: (i) far higher than the voltage gradient required when detecting square waves; but (ii) corresponds to voltage gradients measured in freshwater habitats (Peters & Bretschnieder 1972).

(*e*) ***Electronavigation***

Scheich *et al.* (1986) demonstrated that the platypus will avoid clear objects that are charged with a weak electrical current. They termed this behaviour electronavigation. However, whether the platypus can actually use its electrosensory capacities to electronavigate is still a matter of conjecture. Kalmijn (1982) has shown that sharks and rays can use their electrosense as an active compass to navigate within the earth's magnetic field. It has also been shown that Ictalurus (Finger 1986; Kalmijn *et al.* 1976*a*,*b*; Peters *et al.* 1974) uses its electrosense to navigate around the freshwater ponds which it inhabits. Peters & Bretschnieder (1972) have shown that there are DC voltage gradient differences of up to 300 μV cm^{-1} in these freshwater pools, well within the sensory capacities of catfish (Ictalurus), and the platypus. It is possible that the platypus can use its electrosense to navigate around its habitat. Further experiments, in the mode of Kalmijn *et al.* (1976*a*,*b*) are needed to see if the platypus has this ability, but were beyond the scope of the present study.

How do the two electroreceptors in platypus bill skin relate to electrosensation?

Is has been shown previously that there are two types of glands in the bill skin of the platypus that have been modified to function as sensory receptors (Andres & von During 1988). These are a modified mucous gland, and a modified serous gland. There are around 40000 modified mucous glands, compared with around 14000 modified serous glands (Manger *et al.* 1993). The distribution of the mucous sensory glands is a striking series of parasagittal stripes, while the serous sensory glands show greatest density at the rostrolateral pole of the bill, with a rapid decrease in density towards the middle and caudal portions of the bill. Gregory *et al.* (1988) have recorded action potentials from peripheral nerves that innervate the mucous sensory glands. These sensory glands gave rise to action potentials when stimulated by square waves in the range of 3–4 mV cm^{-1}, with modulations of the resting discharge rate seen with triangular waves with frequencies in the range of 140 Hz. No peripheral nerve recordings have been made from the serous sensory glands. The sensory mucous gland is the only structure identified in the platypus bill skin to be sensitive to electricity, however, due to the morphology of the serous sensory gland it is concluded that these will also be sensitive to electrical gradients (Andres & von During 1988). So, are the behaviours described here mediated by the mucous gland electroreceptors, the serous sensory glands, or a combination of both ? The preferential axis for directionality of the bill, reported here, may argue for either receptor type or a combination of both. The preferential axis is roughly orthogonal to the parasagittal stripes of mucous gland electroreceptors. It may be inferred from this that the mucous gland electroreceptors are acting as branches of a directional antenna, both above and below the bill, as they form a rough continuum around the bill, despite the interruption of the mouth. The curvature of the lower bill, and hence the stripes, also accounts for the downward aspect of the preferential axis. It can be speculated that the basal firing rate of each stripe of mucous gland electroreceptors is either up or down modulated when presented with electrical gradients below electroreceptor unit threshold. It is interesting to note here that our results show that the change in field strength between stripes is quite small, in the range of 1–5 $\mu V\ cm^{-1}$ per stripe. It is possible that the stripes closest to the origin of the electrical dipole, therefore receiving the greatest amount of current, will be modulated the most. This modulation in basal firing rate may then be processed centrally, allowing the platypus to determine the origin of an electrical dipole.

If the axis of preferential sensitivity of electroreception was extrapolated through the bill it would be seen to cross the bill at the point where serous sensory glands are most abundant. It may be that the directionality of the bill seen in the behavioural tests reported here is related to the distribution of the serous sensory glands. However, due to the striking array of mucous gland electroreceptors, and their demonstrated sensitivity to brief electrical stimuli (Gregory *et al.* 1988), we believe it is the mucous gland electroreceptors that are responsible for the electrocephalokinetic reflex. It is possible that the serous gland electroreceptors are responsible for the galvanic sensibility described in this paper. If this is the case, then the serous sensory glands are sensitive to modulations in DC field strength. A sensitivity such as this could be used for two behaviours. First, a DC level detector could allow the platypus to navigate in freshwater ponds, as suggested earlier. Second, a DC level detector could allow the platypus to be sensitive to the DC fields that surround living organisms. Accurate localization of immobile prey (Taylor *et al.* 1992) that emit no rapid transient electromyogenic potentials could be made in this way. These prey items, such as fly larvae grow in large numbers in cracks and grooves in the rocks at the bottom of the pools the platypus inhabit, and do make up a significant proportion of the diet of the platypus. Platypus turn rocks over while feeding, as described earlier, and investigate the surface thoroughly with their bill. A DC level sensitivity combined with the very sensitive tactile sensibility of the bill would allow accurate localization of these immobile prey items.

(*f*) *Similarities to electroreception behaviour in the fish*

The major similarity between platypus electroreception and passive electroreception in various fish is that all species use this ability to locate the source of food. Kalmijn (1966) first demonstrated this showing that the ray could detect the heartbeat of a food item when covered in an agar container, eliminating the possibility of any other sensory stimulation. We have also shown, for the first time, that the platypus uses its electroreceptive capabilities to find food. When the platypus is stimulated with a square wave it is guided to the source of the electrical dipole by a reflex of the head and after touching the electrodes begins to mouth them. These results provide compelling evidence that electroreception is used for prey detection and localization. We have also shown that the platypus investigates the area around electrodes that are emitting electrical waveforms that resemble the electromyogenic potentials (Taylor *et al.* 1992) that are propagated in the water following the escape response of various food items. This is further evidence of the use of electroreception in the food search behaviour of the platypus.

(*g*) *Feeding patterns and electroreception*

In this study we have shown a detailed analysis of the feeding pattern of what we believe to be normally feeding platypus (see §3*a*, figures 3, 4 and 15). We described six behaviours associated with feeding. Of these six behaviours the one of most significance, where electroreception is concerned, is behaviour 5, or patrolling. It is when the platypus is exhibiting this behaviour that the electroreceptive system would be of most use in guiding the platypus to food sources. It is significant that the platypus spends some 40 % of its time in the water exhibiting this patrolling behaviour, indicating that the platypus may be actively using its electroreceptive system for these periods. It is also significant that the patrolling behaviour increases the area coverage by threefold when compared with pre-patrol behaviour. This reduces coverage of the bottom of the tank, in our arena, from a period of 64 s for pre-patrol behaviour, down to 24 s for patrol behaviour. The increased probability of detecting food with the patrolling behaviour is obvious. Our figures differ sharply from those reported for platypus in display arenas (Hawkins & Fanning 1992 (Taronga Zoo); Krueger *et al.* 1992 (Healesville Sanctuary)). Our data shows that approximately 40 % of the platypus' time is spent foraging, however, the platypus on display at Taronga Zoo and Healesville Sanctuary showed significantly less time foraging: 20–25 %, and 6.6 % respectively. During feeding bouts our platypus spent 15.3 % of its time wedged beneath a rest, remaining stationary, this compares with up to 80 % of the time with display animals at Taronga Zoo and 15 % with animals at Healesville Sanctuary. Obviously there will be variations in the observations depending on the individual platypus observed. However, it is clear that many more detailed observations, such as those presented here, are needed to find a 'normal' pattern for platypus. Such a normal pattern may be useful in determining if a platypus is adapting to its captive environment.

(*h*) *Faraday cage*

The Faraday cage surrounding the platypus enclosure provided an effective reduction of the ambient electricity, and allowed accurate measurements of the electrical dipoles presented to the platypus to be made. In light of the findings presented here, that 2 $mV\ cm^{-1}$ is a large enough field strength to produce an aversive response, it seems reasonable that Faraday cages should be employed as a general feature of platypus enclosures, thus eliminating electrical fluctuations of 50 Hz signals in the range of 1 $mV\ cm^{-1}$ from the captive platypus' environment. Stress appears to be the only significant factor in the high mortality rate of captive platypus (Whittington 1991). Use of a Faraday cage may be useful in reducing stress of the captive platypus by reducing exposure to excess electrical noise. Gregory *et al.* (1988) have shown mucous gland electroreceptors to be sensitive to 50 Hz electrical fields, further validating the need to implement Faraday cages as a standard part of platypus enclosures. Often, the platypus we caught would feed on the night of capture, especially if caught early in the evening. The platypus would then continue eating at a rate of approximately half a kilogram per night, depending on the size of the platypus. This is in contrast to the reported 'initial mass loss', and 'steady declines' in body mass of other platypus used for laboratory studies (Carrick *et al.* 1979).

5. CONCLUSION

The demonstrated electrical sensitivity of the platypus explains how, with its eyes, ears and nostrils closed, at night, and underwater, the platypus manages to locate food. Electroreception in the platypus is dependent on various structural and functional aspects. These include distinctive distributions of peripheral electroreceptors and neurological specializations for processing electrosensory information. In this paper we have demonstrated that electrosensory information is processed by a complex reflex which we term the electrocephalokinetic reflex. This reflex determines the origin of an electrical dipole and initiates movement of the bill and head towards this origin in 43.4 ms. This reflex explains how it is possible for the platypus, every night, to gather half its own body mass in shrimps and fly larvae from the detritus of the freshwater streams it inhabits.

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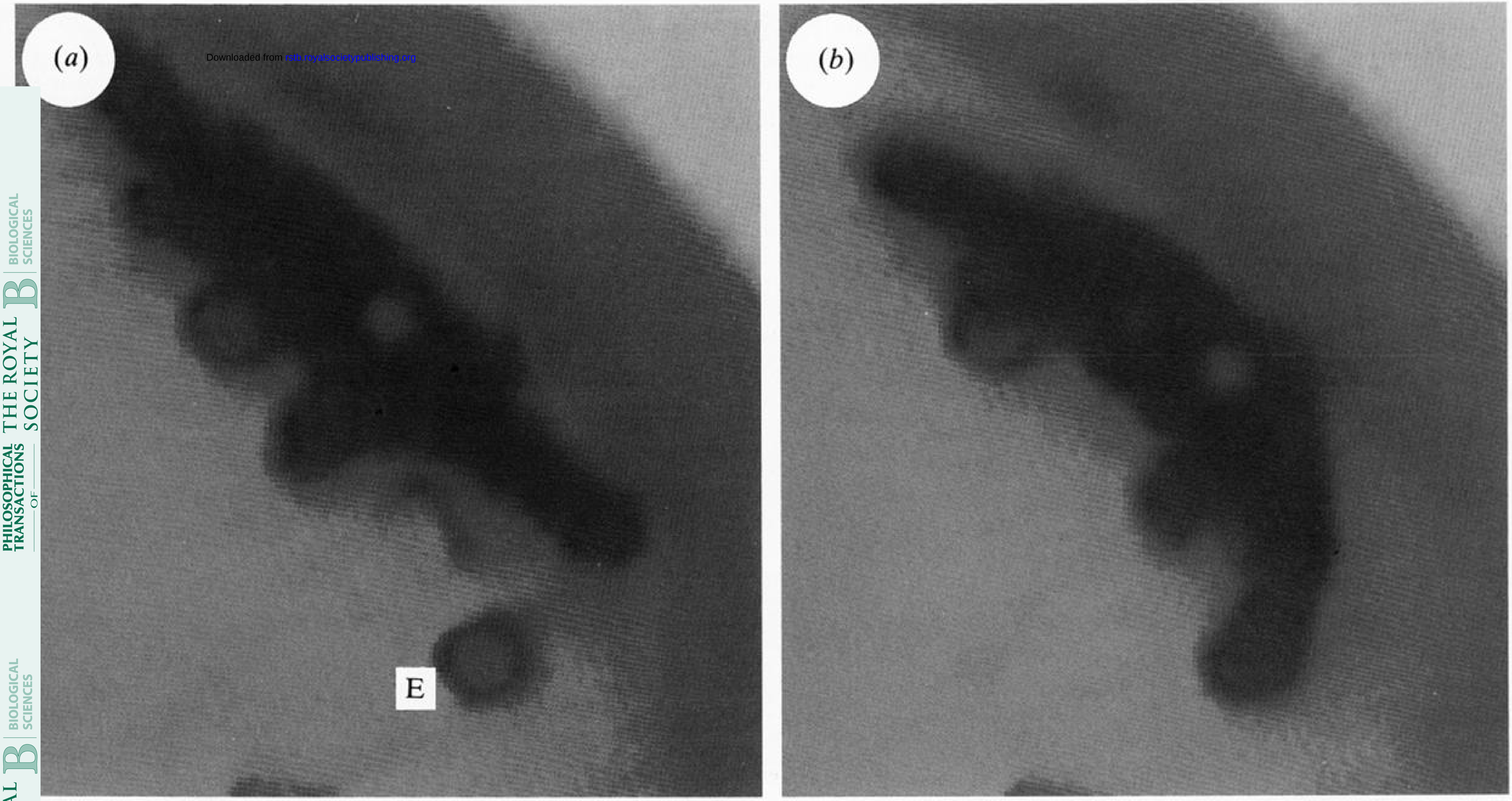
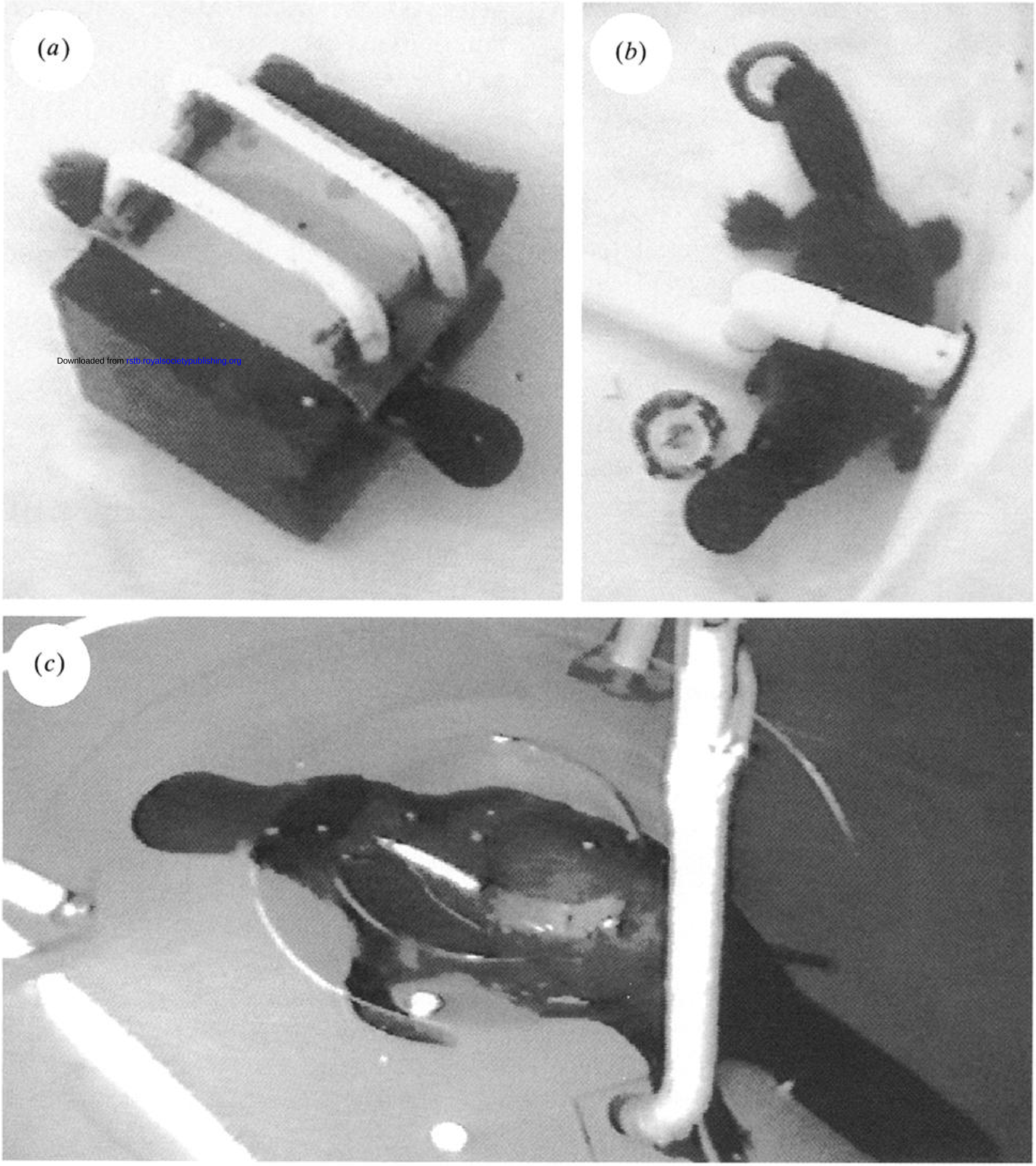


Figure 5. Initial attempts to stimulate the platypus through fixed electrodes, as the platypus was swimming around showed a variety of behaviours. Of these the easiest to discern was the head turning behaviour. As a platypus approached an electrode (E), electrical waveforms were passed through the electrodes at a rate of two every second. The platypus would approach these electrodes from random directions (*a*), and upon sensing an electrical pulse, turn its head so as to place the bill over the area of the electrode (*b*). The field strength in the illustrated case was approximately 0.8 mV cm^{-1} at the point where the bill first starts to turn in (*a*). The threshold field strengths for eliciting this behaviour varied widely, perhaps because of the head swinging behaviour and the marked directionality of the bill described later.



gure 6. Three different rests were provided for the platypus. (*a*) Platypus inside the concrete tunnel; (*b*) platypus neath the filter inlet pipe; (*c*) platypus beneath the transparent Perspex dome. The filter inlet pipe was the favoured e for resting underwater.

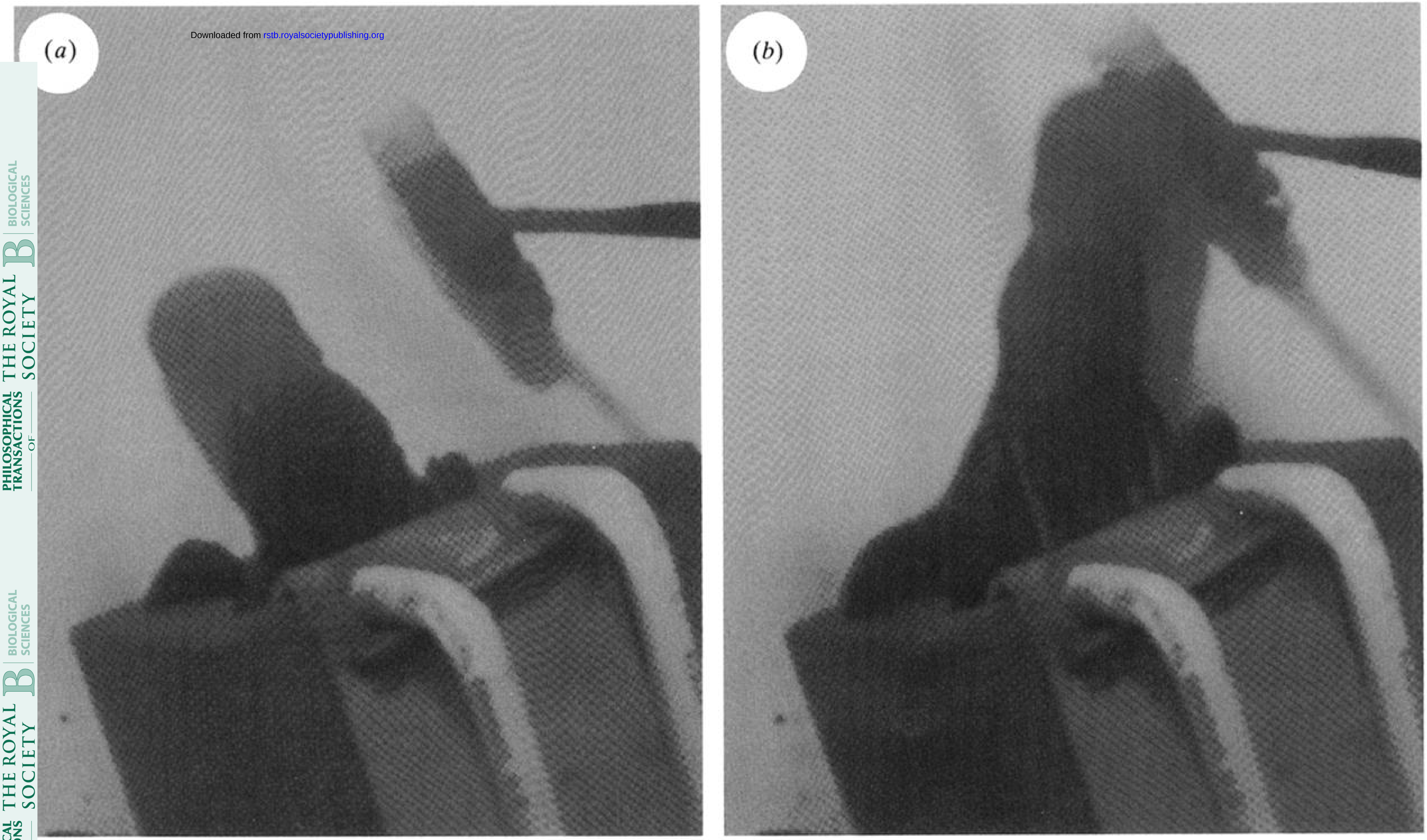
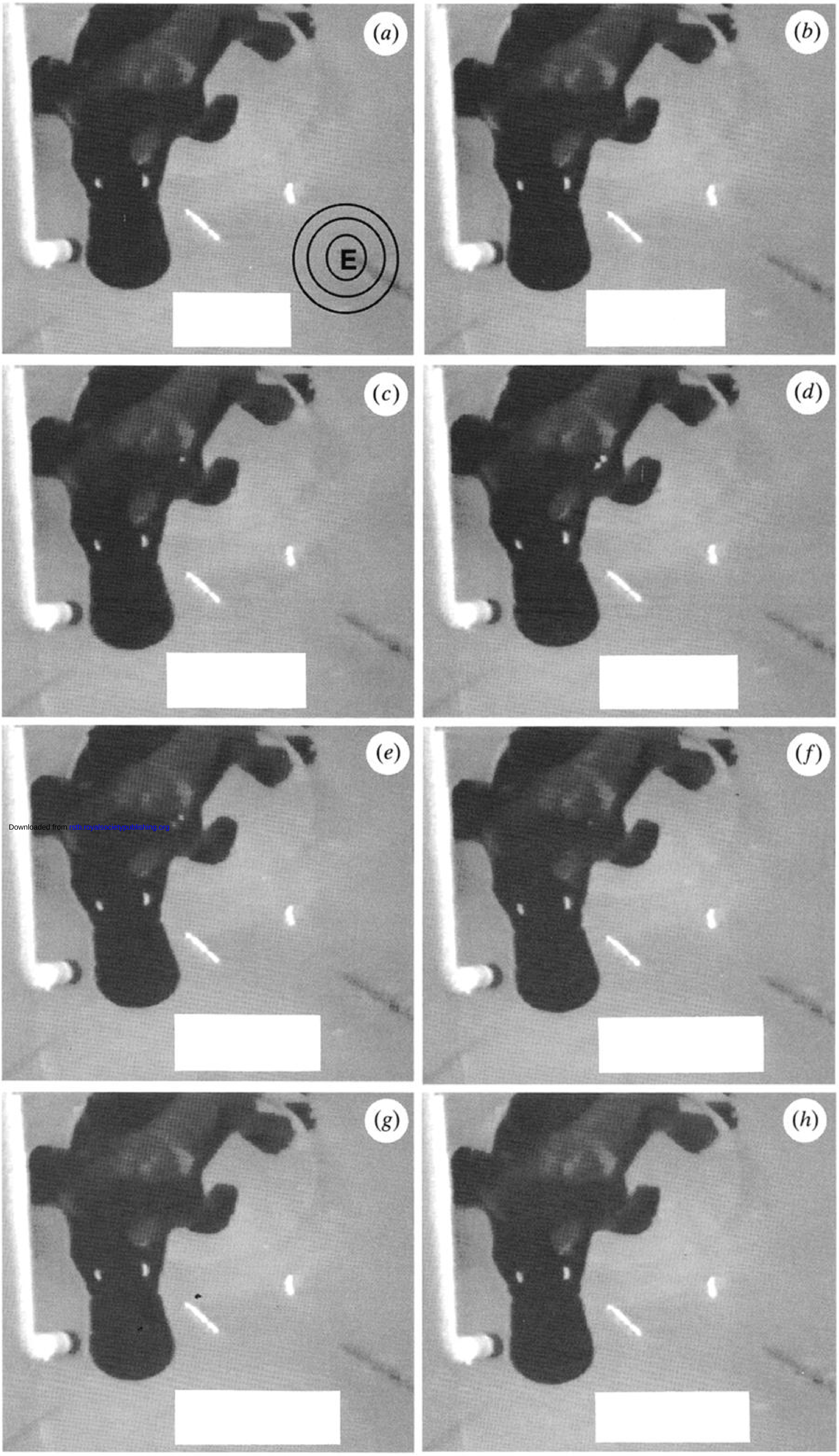


Figure 8. Initial attempts to mouth the electrical stimulus: To respond to an electrical pulse with a saccadic movement of the head the platypus must first undergo habituation to the electrical transient. Pulses are presented to the platypus (*a*), which initially the platypus finds attractive, and so mouths the electrode (*b*), however, after about one hundred such episodes, with no reward, the platypus no longer attempts to mouth the electrode.



igure 9. Head saccades to an electrical stimulus. After habituation to the electrical transients the platypus was unable ignore the electrical signal, and every time an electrical transient was presented to the platypus a saccadic ovement of the head and bill was observed. The eight consecutive video frames shown here demonstrate the latency f the head saccade (43 ms) and the duration of the saccade. E represents the position of the electrode, the rings epresenting the electrical pulse at time = 0.

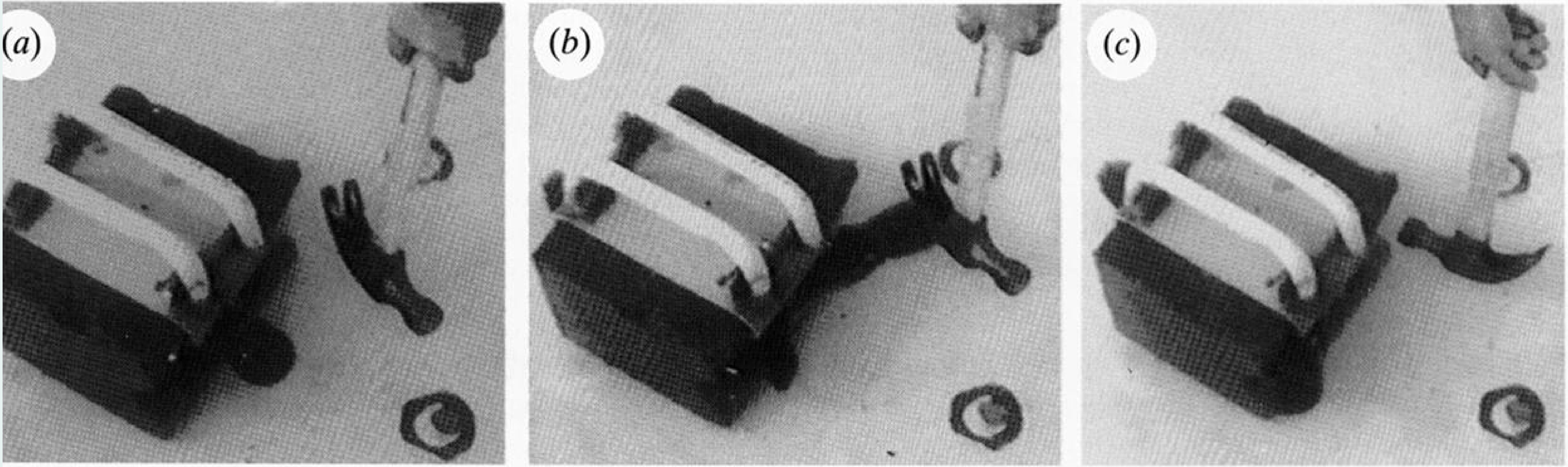


Figure 17. Reaction of the platypus to the presentation of galvanic fields. To dramatize the presentation an ordinary claw hammer has been used. Initially the platypus is at rest in the concrete tunnel (*a*). The hammer head is slowly brought towards the platypus, and corresponding to a voltage gradient of around 500 μV cm^{-1} the platypus swings its head towards the hammer head, thoroughly investigating the galvanic field, and also the hammer head with touch (*b*). After full examination of the hammer head the platypus swings its head away from the hammer head (*c*), appearing somewhat annoyed with its presence.