PROCEEDINGS OF THE ROYAL SOCIETY B

FirstCite® e-publishing

Proc. R. Soc. B
doi:10.1098/rspb.2011.1127
Published online

Electroreception in the Guiana dolphin (*Sotalia guianensis*)

Nicole U. Czech-Damal[1], Alexander Liebschner[2], Lars Miersch[3], Gertrud Klauer[4], Frederike D. Hanke[3], Christopher Marshall[5], Guido Dehnhardt[3] and Wolf Hanke[3,*]

[1]*Biocenter Grindel and Zoological Museum, University of Hamburg, Martin-Luther-King-Platz 3, 20146 Hamburg, Germany*
[2]*German Federal Agency for Nature Conservation, Marine and Coastal Nature Conservation Unit, Isle of Vilm–Branch Office, 18581 Putbus, Rügen, Germany*
[3]*Institute for Biosciences, University of Rostock, Albert-Einstein-Strasse 3, 18059 Rostock, Germany*
[4]*Department of Cellular and Molecular Anatomy (Anatomy III), J.W. Goethe-University, Theodor-Stern-Kai 7, 60590 Frankfurt, Germany*
[5]*Department of Marine Biology, Texas A&M University, 5007 Avenue U, Galveston, TX 77551-5923, USA*

Passive electroreception is a widespread sense in fishes and amphibians, but in mammals this sensory ability has previously only been shown in monotremes. While the electroreceptors in fish and amphibians evolved from mechanosensory lateral line organs, those of monotremes are based on cutaneous glands innervated by trigeminal nerves. Electroreceptors evolved from other structures or in other taxa were unknown to date. Here we show that the hairless vibrissal crypts on the rostrum of the Guiana dolphin (*Sotalia guianensis*), structures originally associated with the mammalian whiskers, serve as electroreceptors. Histological investigations revealed that the vibrissal crypts possess a well-innervated ampullary structure reminiscent of ampullary electroreceptors in other species. Psychophysical experiments with a male Guiana dolphin determined a sensory detection threshold for weak electric fields of 4.6 $\mu V\ cm^{-1}$, which is comparable to the sensitivity of electroreceptors in platypuses. Our results show that electroreceptors can evolve from a mechanosensory organ that nearly all mammals possess and suggest the discovery of this kind of electroreception in more species, especially those with an aquatic or semi-aquatic lifestyle.

Keywords: electroreception; vibrissal system; vibrissal crypt; whiskers; dolphin; sensory system

1. INTRODUCTION

Aquatic and semi-aquatic mammals often differ significantly from their terrestrial ancestors in their anatomy, physiology, and not least in the functionality of their sensory systems and the role that they play in orientation, communication and feeding [1,2]. Although the various aquatic environments of the world are by no means uniform, the operating range of the visual system under water is quite often reduced by low light levels or turbidity, while mechanical senses, such as hearing, echolocation, active touch and the perception of water movements, gain in importance. Electroreception—the ability to sense electric fields—is operative only in aquatic (or at least moist) environments. Electroreception can be both active and passive. In active electroreception, the animal generates an electric field and senses the distortions of this electric field from objects of varying conductivity and capacity in its habitat. It is found in the weakly electric fishes (Mormyriformes and Gymnotiformes) [3,4]. In passive electroreception, electric fields generated by an item in the vicinity, often a prey animal, are perceived. Passive electroreception is known in many fishes (including elasmobranches, lampreys, paddlefish and catfish [5]), in some amphibians [6,7] and in proterian mammals (i.e. platypuses and echidnas [8–10]).

Toothed whales inhabit many ecological niches in the aquatic environment and forage on various types of pelagic and benthic prey. In general, detection of prey in these marine mammals is ascribed to echolocation, but it is more likely a multimodal process of various senses including vision and passive listening. Other aquatic mammals, such as harbour seals, lack a biosonar system and use their prominent mystacial vibrissae to detect and track hydrodynamic trails of prey [11,12]. The structures in the skin that bear the vibrissae are referred to as vibrissal follicle-sinus complexes (F-SCs) [13,14], as the highly innervated hair follicle is surrounded by an ample blood sinus complex and a dense tissue capsule. In contrast to seals, most toothed whales atrophy or lose their vibrissal hairs postnatally and only empty crypts, which we term vibrissal crypts, remain visible in an array of 2–10 on each side of the upper jaw [15] (figure 1). These vibrissal crypts are often described as vestigial structures lacking innervation and the characteristic blood sinuses [15,16], which are probably reduced in favour of the sonar system. By contrast, our thermographic studies of vibrissal crypts in an adult Guiana

*Author for correspondence (wolf.hanke@uni-rostock.de).

Electronic supplementary material is available at http://dx.doi.org/10.1098/rspb.2011.1127 or via http://rspb.royalsocietypublishing.org.

Received 31 May 2011
Accepted 5 July 2011

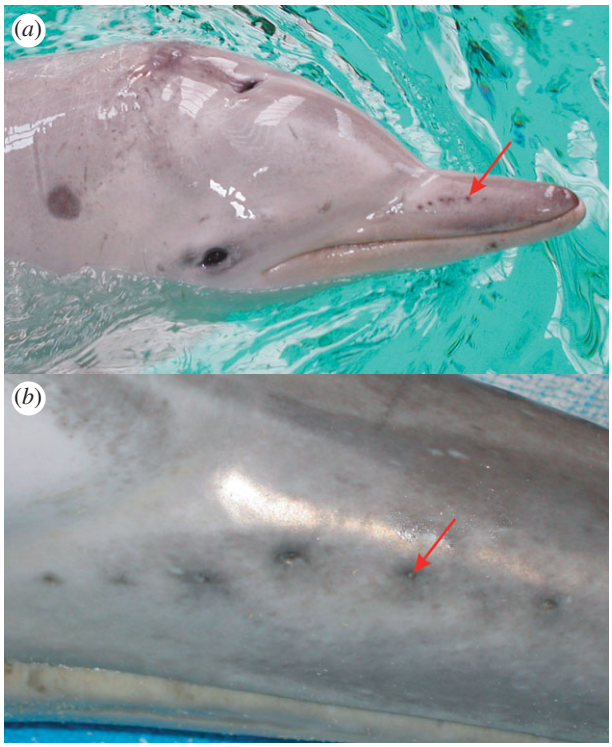

Figure 1. Vibrissal crypts of the Guiana dolphin. (*a*) Location on the rostrum. (*b*) Close-up view. Arrows indicate a single vibrissal crypt.

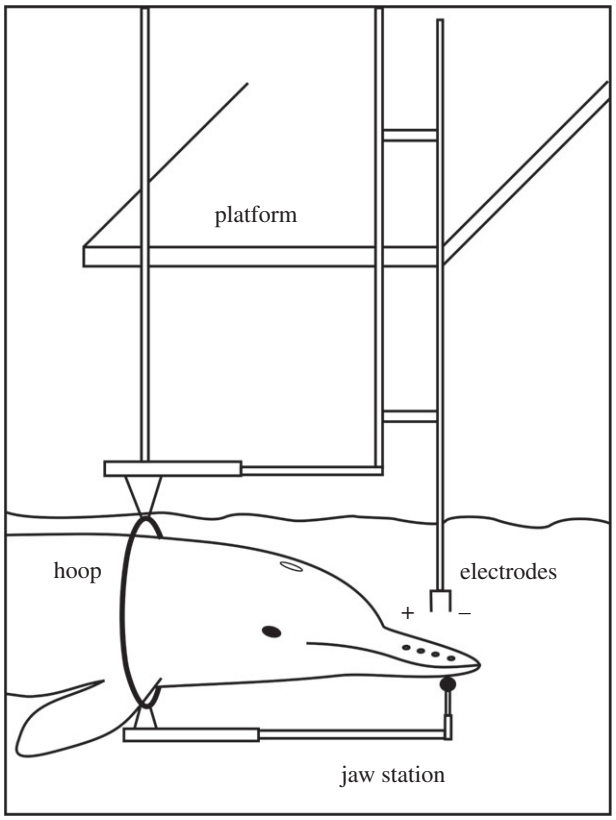

Figure 2. Experimental setup for the psychophysical experiments on the electrosensitivity in the Guiana dolphin. The dolphin was trained to position itself in a hoop and rest its rostrum on a jaw station. This way, the position of the rostrum was reproducible from trial to trial. Electrical signals were delivered by two electrodes at a distance of 10 cm from the rostrum in half of the trials. The dolphin received a food reward for leaving the station when a signal was present and for remaining in station when no signal was present.

dolphin (*Sotalia guianensis*) suggested that they are functional sensory units [17]. Similar to the F-SCs in harbour seals, spots of intense thermal radiation were found to be associated with each single vibrissal crypt [17]. To determine whether vibrissal crypts in the Guiana dolphin are truly vestigial structures or if they are functional sensory units, we investigated them histologically. Based on the morphological results and on the feeding ecology of the Guiana dolphin, we developed the hypothesis that the vibrissal crypts function as electroreceptors. We tested this hypothesis in a psychophysical experiment.

2. MATERIAL AND METHODS

(a) *Histology*

Vibrissal crypts were obtained from a 29-year-old male Guiana dolphin (*S. guianensis*) that had been kept at the Dolphinarium Münster, Germany, for 15 years and died of natural causes. Tissue samples of the rostrum were fixed in 7–10 per cent paraformaldehyde and stored in 4 per cent paraformaldehyde. Vibrissal crypts were dissected macroscopically and embedded in Paraplast Plus (Sherwood Medical, St Louis, MO, USA). Samples were sectioned into cross, sagittal and transversal 7 µm slices on a Leica RM 2135 rotary microtome. For general histology, sections were stained with standard Masson–Goldner trichrome staining technique [18]. Innervation was investigated immunohistochemically with nerve-fibre-specific polyclonal rabbit anti-PGP9.5 (1 : 4000; UltraClone Ltd., Cambridge, UK). After deparaffinization, sections were pretreated for 40 min in methanol containing 0.5 per cent hydrogen peroxide to block endogenous peroxidase. After several rinses in 0.01 M phosphate-buffered saline (PBS), pH 7.4, they were incubated for 48 h at 4°C with the primary antibody diluted in PBS containing 0.5 per cent Triton X-100, 0.01 per cent sodium azide and 1 per cent bovine serum albumin. Sections were rinsed in PBS, incubated for 30 min with the secondary antibody Histofine Simple Stain MAX PO (R) (Nichirei Corporation, Tokyo, Japan) and rinsed again. For visualization, AEC Simple Stain Solution (Nichirei Corporation, Tokyo, Japan) was applied for 15–20 min. After a final wash in tap water and in de-ionized water, sections were mounted in Aquatex (Merck, Darmstadt, Germany). Owing to autolysis of the tissue, staining was inconsistent across the sections. Therefore, intraepithelial innervation was investigated additionally with a modified silver impregnation technique [19]. Histological sections were examined and photographed using an Axiophot light microscope (Carl Zeiss, Oberkochen, Germany) equipped with a SemiCam digital camera (PCO, Kelheim, Germany).

(b) *Behavioural detection threshold*

A 28-year-old male Guiana dolphin kept at the Dolphinarium Münster, Germany, served as the experimental subject. The dolphin was trained to respond to electrical stimuli in the order of magnitude of those generated by small to medium-sized fish, its natural prey [20,21]. Using a go/no-go paradigm, we determined the dolphin's detection thresholds for short square wave stimuli in a custom-made set-up (figure 2). Electric field stimuli were generated at a distance of 10 cm from the dolphin's vibrissal crypts by a

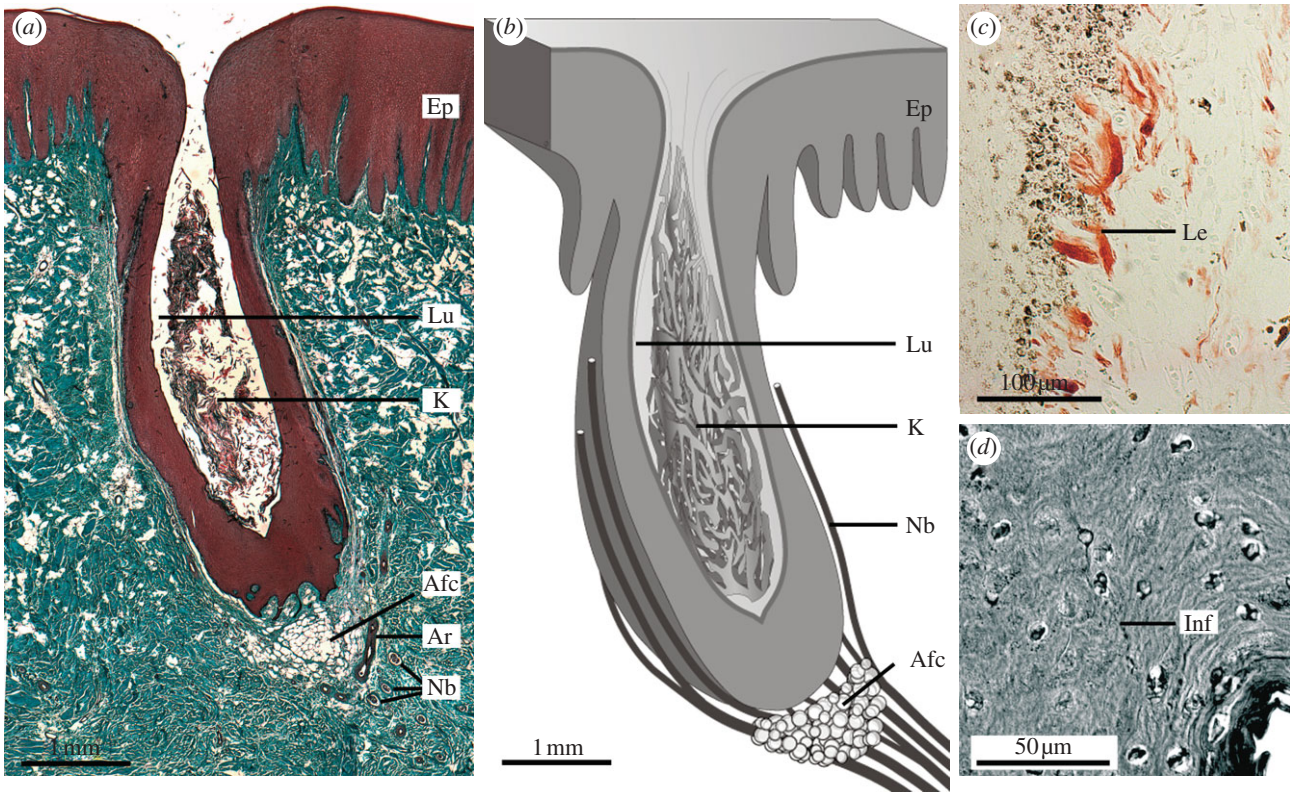

Figure 3. Histology of the vibrissal crypts in the Guiana dolphin. (*a*) Longitudinal section through a representative vibrissal crypt stained with Masson–Goldner trichrome. (*b*) Schematic drawing. The vibrissal crypt consists of an ampulla-shaped invagination of the epidermal integument lacking most characteristic morphological features of mammalian follicle-sinus complexes (F-SCs). (*c*) Vibrissal crypt innervation with lanceolate endings. (*d*) Intraepithelial nerve fibre reaches close to the lumen. Ep, epidermis; Lu, Lumen; K, meshwork of corneocytes and keratinous fibres; Afc, agglomeration of fat cells (probably the former hair papilla); Ar, artery; Nb, nerve bundles of the deep vibrissal nerve; Le, lanceolate endings; Inf, intraepithelial nerve fibre.

battery-powered circuit that passed electric currents between two copper wire electrodes. The copper wire electrodes were 2 mm long, 1 mm thick and 1.5 cm apart. Electric currents were varied from 1 to 3.5 mA and were applied for a stimulus duration of 3 s. The battery-powered stimulus generator ensured that the stimulus circuit was floating (i.e. there was no electrical connection of either of the two stimulus electrodes with the ground of the facility or with any other item in the experimental set-up). The stimulus circuit was powered by a 9 V battery. Upon triggering, a timer based on a NE555 timer chip generated a square wave pulse of adjustable length (3 s was used). The electric field at the location of the nearest vibrissal crypt was measured using non-polarizable Ag/AgCl electrodes (1 cm long, 0.1 mm thick, 1 cm apart) with an AD620 amplifier (Analogue Devices, Norwood, MA, USA) and an analogue–digital converter card (Daq-Card 6026-E, National Instruments, Austin, TX, USA) in a battery-operated laptop computer. Measurements showed fluctuations of signal strength of less than 10 per cent during stimulus application. We trained the dolphin to station itself in the experimental set-up by placing its head in a hoop and touching a small target with the tip of its rostrum. This way the electrodes were located exactly above the dolphin's most anterior pair of vibrissal crypts (figure 2). The dolphin was trained to leave its station in trials where a stimulus was presented (go response), and to remain in station for at least 12 s in trials where no stimulus was presented (no-go response). Tests were conducted double-blind by one trainer and one experimenter. The trainer handled the experimental animal and informed the experimenter as soon as it was in station and ready for a trial. The experimenter, who was not visible to the trainer nor to the animal, did or did not apply an electric stimulus, following a pseudorandom order. After the trainer had indicated the response of the dolphin, the experimenter informed him about the presence or absence of an electrical stimulus. The trainer then rewarded the animal with food if its decision to stay or to leave the station had been correct.

The dolphin's sensory threshold was determined using a combination of the staircase method and the method of constant stimuli [22]. For each of six stimulus strengths, 31 trials were performed during the final data collection (186 trials total). For control, the experiment was repeated with the vibrissal crypts covered by a plastic shell. The plastic shell consisted of a hard plastic hood that was fixed to the upper side of the dolphin's rostrum by suction cups and a rubber foam half-tube that covered the vibrissal crypts (electronic supplementary material, figure S1). Forty trials were performed at a stimulus strength clearly above threshold. Additional control tests with a plastic shell that was identical in construction, but allowed seawater to contact the vibrissal crypts, verified that the subject was willing to cooperate while wearing the shell.

3. RESULTS

(a) *Histology*

Staining with Masson–Goldner trichrome showed that the vibrissal crypts consisted of an ampulla-shaped invagination of the epidermal integument lacking most of the characteristic morphological features of mammalian F-SCs (such as a hair shaft, a hair papilla, pronounced root sheaths, a blood sinus system and a capsule; figure 3), justifying the

usage of the term 'vibrissal crypt' instead of F-SC. The crypts varied from 4.1–7.1 mm in length and 1.2–4.3 mm in width. Their expanded lumen was filled with a meshwork of keratinous fibres and corneocytes. Instead of a blood sinus system, the crypts were encircled by a capillary network derived from large muscle-bound blood vessels, which appear to be responsible for the increased temperature seen in the previous thermograms [17]. Immunohistochemical labelling with anti-PGP9.5 revealed a dense innervation by infraorbital branches of the trigeminal nerve of 300 axons per crypt. Most nerve endings were free nerve endings and lanceolate endings (figure 3*c*) that were concentrated in the lower two-thirds of the crypt. Merkel cells were also present and were evenly scattered along the epidermal basal layer. In addition, silver staining [19] revealed intraepithelial nerve fibres frequently distributed throughout the crypts (figure 3*d*), which have not been described in F-SCs of other mammals so far.

(b) *Behavioural detection threshold*

The Guiana dolphin responded very well to stimuli below 10 $\mu V\ cm^{-1}$. The dolphin responded calmly, and generally with a delay of approximately 2 s after stimulus onset; involuntary head saccades, as described in the platypus [23], were not found. The dolphin's sensory threshold was determined at 4.6 $\mu V\ cm^{-1}$ by interpolating the percentage of correct go responses to stimuli (or hit rate) at the last stimulus intensity above threshold and the hit rate at the first stimulus intensity below threshold (figure 4). In control tests with the plastic shell covering the vibrissal crypts, the dolphin did not react to high-intensity electric field stimuli (40 trials performed). However, the dolphin's response behaviour was not impaired by a half-shell cover that was identical in construction, but allowed seawater to contact the vibrissal crypts. Hence, we conclude that the dolphin's responses were owing to electroreception.

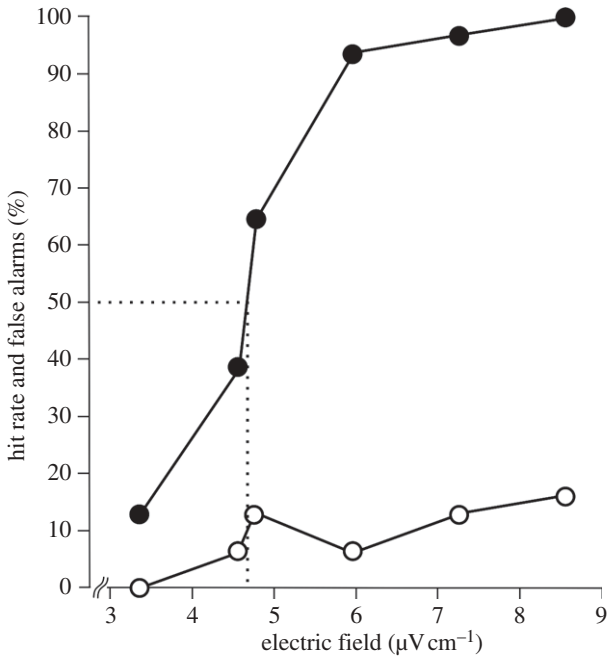

Figure 4. Experimental results from the psychophysical study on the electrosensitivity in the Guiana dolphin. Abscissa: the electric field strength at the location of the nearest vibrissal crypt, calculated from the current through the stimulus electrodes. Ordinate: percentage of correct choice during stimulus-present trials (hit rate) or, respectively, percentage of go responses during stimulus-absent trials (false alarm rate). Black circles: hit rate (i.e. the animal left the station correctly in response to an electric stimulus). White circles: false alarms (i.e. the animal left the station erroneously when no signal was present). At 50 per cent hit rate, the dolphin's absolute detection threshold for the electrical signals is defined (4.6 $\mu V\ cm^{-1}$).

4. DISCUSSION

The data presented here show that the vibrissal crypts in the Guiana dolphin are not vestigial structures. Based on the psychophysical results and on the similarities in the morphology with electroreceptors in the platypus and the echidnas, we conclude that during evolution, the vibrissal system has functionally transformed from an originally mechanoreceptive system into an electroreceptive system.

The histological investigation demonstrated that in addition to their 'simple structure' (when compared with F-SCs), vibrissal crypts in the Guiana dolphin possess a dense innervation and blood supply, supporting our hypothesis that they are functional structures. The number of axons innervating the vibrissal crypts is less than that in pinnipeds [24–26], but exceeds the number of 80–200 axons found in F-SCs of terrestrial mammals [13,14,27–29]. The ampullary shape of the crypts was reminiscent of ampullary electroreceptors of other aquatic predators, such as the ampullae of Lorenzini in elasmobranch fishes and the mucous gland electroreceptors in platypuses (*Ornithorhynchus anatinus*), which also display an elongated epithelial canal [30,31]. These types of sensory organs are known as passive electroreceptors and have evolved independently multiple times [30–35]. The data presented in this study represent a second incidence of electroceptors and electroreception ability in mammals.

The morphological organization of the vibrissal crypts in the Guiana dolphin differs from that of electroreceptors in the platypus (for example, the 'daisy chain' of interlinked sensory fibres that might play a role in noise reduction in platypus is not present in the Guiana dolphin), but there are also many similarities. Both are innervated by the trigeminal nerve and do not possess any secondary cells or specialized nerve terminals that project into the lumen, as found in fish [30]. In platypuses, the specific arrangement of free nerve endings [30,31] is assumed to play a crucial role in the transduction process. Similarly, in the Guiana dolphin, intraepithelial nerve fibres are located near the lumen of the crypt and may be involved in the perception of the electrical stimuli. It is striking that both the electroreceptors in the monotremes as well as the vibrissal crypts in the Guiana dolphin contain intraepithelial nerve endings. This feature is not known in any F-SC-derived structures other than the vibrissal crypts of the Guiana dolphin, but is believed to be the basis of electroreception in the platypus and the echidna [8]. In addition, an important component of ampullary canals related to the process of electroreception appears to be a glycoprotein-based gel in fish [36] and mucus in the platypus [37]. In our live Guiana dolphin, a gel-like substance was permanently emitted from the vibrissal crypts. The histologically investigated vibrissal crypts were extensively filled with a meshwork of shedded corneocytes and keratinous fibres. The continuous epidermal renewal of the skin in

toothed whales suggests that desquamated corneocytes of the stratum corneum were trapped in the lumen of the vibrissal crypt. Further studies are needed to analyse the chemical and electrical characteristics of the substance emitted from the Guiana dolphin's vibrissal crypts. We propose that it could play a role equivalent to the glycoprotein-based gel in fish and the mucus in the platypus. Baum *et al.* [38,39] demonstrated that the skin of pilot whales (*Globicephala melas*) exhibits a kind of biogel embedded in the nanoridges of epidermal cells, which is suggested to function as a cutaneous antifouling system. Like the gel in ampullary electroreceptors of fish, it is rich in glycoproteins and thus could function as an electrically conductive gel that enhances the sensitivity of the system to voltage gradients. We therefore suggest that the intraepithelial nerve endings in the vibrissal crypts of the Guiana dolphin in combination with the biogel might play a role in the transduction process within the electrosensory system.

The sensitivity of the Guiana dolphin to the electrical stimuli was approximately one order of magnitude higher than that of platypuses, which has been estimated to be about 40–50 $\mu V\,cm^{-1}$ using behavioural methods [9,23,40,41]. Both the Guiana dolphin and the platypuses exhibit lower sensitivity than elasmobranch fishes, where sensory thresholds lie in the nanovolt range [41]. However, their sensitivity is well suited to the bioelectric fields caused by prey items. Taylor *et al.* [42] measured the electrical fields generated by aquatic animals using two electrodes 5.73 cm apart and found that goldfish of 5–6 cm body length produced electric fields of 90 $\mu V\,cm^{-1}$, with an energy peak at 3 Hz. In flounders, bioelectric fields of 1000 $\mu V\,cm^{-1}$ have been reported [43].

In platypuses, as in other electroreceptive species, the passive electrosensory system is used for the detection of bioelectric fields of benthic prey [44]. Observations on the Guiana dolphin suggest benthic feeding behaviour as well, indicated by mud-plumes at the water surface after feeding, as well as mud adhering to the dolphin's body [45]. This is consistent with the finding that bottom-dwelling fish species are common prey items of the Guiana dolphin [20,46–49]. Benthic feeding behaviour is a common feeding mode in many toothed whales. A most peculiar benthic feeding strategy called 'crater-feeding' has been described in bottlenose dolphins (*Tursiops truncatus*) of the northwestern Bahamas [50]. Applying this strategy, the animals dive and bury themselves into the sand up to the pectoral fins to capture hiding fish, and leave the craters after which this feeding behaviour was named. Bottlenose dolphins and several other cetacean species possess vibrissal crypts as well, suggesting that electroreception may be present. Further studies are being conducted on this subject.

The Guiana dolphin inhabits coastal regions and is generally associated with shallow and protected estuarine waters, bays, mouths of rivers and turbid waters [51]. Suspended particles should often greatly reduce visibility in these habitats, specifically when the sediment is disturbed. We therefore suggest that the electroreceptors on the dolphin's rostrum maximize the likelihood of close distance prey detection in turbid water or while digging in the substrate, and function at least as a supplementary sense to echolocation during benthic feeding.

The experiments were carried out under the guidelines established by the European Communities Council Directive of 24 November 1986 (86/609/EEC).

This work was supported by grants from the Deutsche Forschungsgemeinschaft and Volkswagen-Stiftung to Guido Dehnhardt. We thank the Dolphinarium Münster, Germany for providing the experimental animal.

REFERENCES

1 Thewissen, J. G. M. & Nummela, S. 2008 *Sensory evolution on the threshold: adaptations in secondarily aquatic vertebrates*. Berkeley, CA: University of California Press.
2 Collin, S. P. & Marshall, N. J. 2003 *Sensory processing in aquatic environments*. New York, NY: Springer.
3 Lissmann, H. W. 1951 Continuous electrical signals from the tail of a fish, *Gymnarchus niloticus*. *Nature* **167**, 201–202. (doi:10.1038/167201a0)
4 von der Emde, G. 2006 Non-visual environmental imaging and object detection through active electrolocation in weakly electric fish. *J. Comp. Physiol. A* **192**, 601–612. (doi:10.1007/s00359-006-0096-7)
5 Collin, S. P. & Whitehead, D. 2004 The functional roles of passive electroreception in non-electric fishes. *Anim. Biol.* **54**, 1–25. (doi:10.1163/157075604323010024)
6 Fritzsch, B., Wahnschaffe, U., Decaprona, M. D. C. & Himstedt, W. 1985 Anatomical evidence for electroreception in larval *Ichthyophis kohtaoensis*. *Naturwissenschaften* **72**, 102–104. (doi:10.1007/BF00508148)
7 Münz, H., Claas, B. & Fritzsch, B. 1982 Electrophysiological evidence of electroreception in the axolotl *Siredon mexicanum*. *Neurosci. Lett.* **28**, 107–111. (doi:10.1016/0304-3940(82)90216-6)
8 Proske, U., Gregory, J. E. & Iggo, A. 1998 Sensory receptors in monotremes. *Phil. Trans. R. Soc. Lond. B* **353**, 1187–1198. (doi:10.1098/rstb.1998.0275)
9 Scheich, H., Langner, G., Tidemann, C., Coles, R. B. & Guppy, A. 1986 Electroreception and electrolocation in platypus. *Nature* **319**, 401–402. (doi:10.1038/319401a0)
10 Gregory, J. E., Iggo, A., McIntyre, A. K. & Proske, U. 1989 Responses of electroreceptors in the snout of the echidna. *J. Physiol. Lond.* **414**, 521–538.
11 Dehnhardt, G., Mauck, B. & Bleckmann, H. 1998 Seal whiskers detect water movements. *Nature* **394**, 235–236. (doi:10.1038/28303)
12 Dehnhardt, G., Mauck, B., Hanke, W. & Bleckmann, H. 2001 Hydrodynamic trail following in harbor seals (*Phoca vitulina*). *Science* **293**, 102–104. (doi:10.1126/science.1060514)
13 Rice, F. L., Mance, A. & Munger, B. L. 1986 A comparative light microscopical analysis of the sensory innervation of the mysticial pad. 1. Innervation of vibrissal follicle-sinus complexes. *J. Comp. Neurol.* **252**, 154–174. (doi:10.1002/cne.902520203)
14 Hyvärinen, H., Palviainen, A., Strandberg, U. & Holopainen, I. J. 2009 Aquatic environment and differentiation of vibrissae: comparison of sinus hair systems of ringed seal, otter and pole cat. *Brain Behav. Evol.* **74**, 268–279. (doi:10.1159/000264662)
15 Ling, J. K. 1977 Vibrissae of marine mammals. In *Functional anatomy of marine mammals* (ed. R. J. Harrison), pp. 387–415. London, UK: Academic Press.
16 Yablokov, A. V. & Klezeval, G. A. 1969 Whiskers of whales and seals and their distribution, structure and significance. In *Morphological characteristics of aquatic mammals* (ed. S. E. Kleinenberg), pp. 48–81. Moscow, Russia: Izdatel'stvo Nauka.
17 Mauck, B., Eysel, U. & Dehnhardt, G. 2000 Selective heating of vibrissal follicles in seals (*Phoca vitulina*) and dolphins (*Sotalia fluviatilis guianensis*). *J. Exp. Biol.* **203**, 2125–2131.
18 Goldner, J. 1938 A modification of the Masson trichrome technique for routine laboratory purpose. *Am. J. Pathol.* **14**, 237–243.

19 Spaethe, A. 1984 Eine Modifikation der Silbermethode nach Richardson für die Axonfärbung von Paraffinschnitten. *Verhandlungen der Anatomischen Gesellschaft* **78**, 101–102.

20 Borobia, M. & Barros, N. B. 1989 Notes on the diet of marine *Sotalia fluviatilis*. *Mar. Mamm. Sci.* **5**, 395–399. (doi:10.1111/j.1748-7692.1989.tb00353.x)

21 Araujo Pansard, K. C., de Castro Bezerra Gurgel, H., de Araujo Andrade, L. C. & Yamamoto, M. E. In press. Feeding ecology of the estuarine dolphin (*Sotalia guianensis*) on the coast of Rio Grande do Norte, Brazil. *Mar. Mamm. Sci.* (doi:10.1111/j.1748-7692.2010.00436.x)

22 Gescheider, G. A. 1976 *Psychophysics: method and theory.* Hillsdale, NJ: Lawrence Erlbaum Associates.

23 Manger, P. R. & Pettigrew, J. D. 1995 Electroreception and the feeding behavior of platypus (*Ornithorhynchus anatinus*, Monotremata, Mammalia). *Phil. Trans. R. Soc. Lond. B* **347**, 359–381. (doi:10.1098/rstb.1995.0030)

24 Hyvärinen, H. & Katajisto, H. 1984 Functional structure of the vibrissae of the ringed seal (*Phoca hispida*). *Acta Zool. Fennica* **171**, 27–30.

25 Hyvärinen, H. 1995 Structure and function of the vibrissae of the ringed seal (*Phoca hispida*). In *Sensory systems of aquatic mammals* (eds R. A. Kastelein, J. A. Thomas & P. E. Nachtigall), pp. 429–445. Woerden, The Netherlands: De Spil Publishers.

26 Marshall, C. D., Amin, H., Kovacs, K. M. & Lydersen, C. 2006 Microstructure and innervation of the mystacial vibrissal follicle-sinus complex in bearded seals, *Erignathus barbatus* (Pinnipedia: Phocidae). *Anat. Rec. A* **288A**, 13–25. (doi:10.1002/ar.a.20273)

27 Halata, Z. & Munger, B. L. 1980 Sensory nerve-endings in rhesus-monkey sinus hairs. *J. Comp. Neurol.* **192**, 645–663. (doi:10.1002/cne.901920403)

28 Halata, Z. 1975 The mechanoreceptors of the mammalian skin: ultrastructure and morphological classification. *Adv. Anat. Embryol. Cell Biol.* **50**, 3–77.

29 Rice, F. L., Fundin, B. T., Arvidsson, J., Aldskogius, H. & Johansson, O. 1997 Comprehensive immunofluorescence and lectin binding analysis of vibrissal follicle sinus complex innervation in the mystacial pad of the rat. *J. Comp. Neurol.* **385**, 149–184. (doi:10.1002/(SICI)1096-9861(19970825)385:2<149::AID-CNE1>3.0.CO;2-1)

30 Andres, K. H. & von Düring, M. 1988 Comparative anatomy of vertebrate electroreceptors. *Prog. Brain Res.* **74**, 113–131. (doi:10.1016/S0079-6123(08)63006-X)

31 Andres, K. H. & von Düring, M. 1984 The platypus bill. A structural and functional model of a pattern-like arrangement of different cutaneous sensory receptors. In *Sensory receptor mechanisms* (eds W. Hamann & A. Iggo), pp. 81–89. Singapore: World Scientific Publishing Co.

32 New, J. G. 1997 The evolution of vertebrate electrosensory systems. *Brain Behav. Evol.* **50**, 244–252. (doi:10.1159/000113338)

33 von der Emde, G. 1998 Electroreception. In *The physiology of fishes* (ed. D. H. Evans), pp. 313–343. Boca Raton, FL: CRC Press.

34 Bullock, T. H. 1999 The future of research on electroreception and electrocommunication. *J. Exp. Biol.* **202**, 1455–1458.

35 Alves-Gomes, J. A. 2001 The evolution of electroreception and bioelectrogenesis in teleost fish: a phylogenetic perspective. *J. Fish. Biol.* **58**, 1489–1511. (doi:10.1006/jfbi.2001.1625)

36 Brown, B. R., Hutchison, J. C., Hughes, M. E., Kellogg, D. R. & Murray, R. W. 2002 Electrical characterization of gel collected from shark electrosensors. *Phys. Rev. E* **65**, 061903. (doi:10.1103/PhysRevE.65.061903)

37 Manger, P. R., Pettigrew, J. D., Keast, J. R. & Bauer, A. 1995 Nerve terminals of mucous gland electroreceptors in the platypus. *Proc. R. Soc. Lond. B* **260**, 13–19. (doi:10.1098/rspb.1995.0053)

38 Baum, C., Meyer, W., Roessner, D., Siebers, D. & Fleischer, L.-G. 2001 A zymogel enhances the self-cleaning abilities of the skin of the pilot whale (*Globicephala melas*). *Comp. Biochem. Physiol. A-Mol. Integr. Physiol.* **130**, 835–847. (doi:10.1016/S1095-6433(01)00445-7)

39 Baum, C., Stelzer, R., Meyer, W., Siebers, D. & Fleischer, L.-G. 2000 A cryo-scanning microscopy study of the skin surface of the pilot whale *Globicephala melas*. *Aquat. Mamm.* **26**, 7–16.

40 Gregory, J. E., Iggo, A., McIntyre, A. K. & Proske, U. 1987 Electroreceptors in the platypus. *Nature* **326**, 386–387. (doi:10.1038/326386a0)

41 Peters, R. C., Eeuwes, L. B. M. & Bretschneider, F. 2007 On the electrodetection threshold of aquatic vertebrates with ampullary or mucous gland electroreceptor organs. *Biol. Rev.* **82**, 361–373. (doi:10.1111/j.1469-185X.2007.00015.x)

42 Taylor, N. G., Manger, P. R., Pettigrew, J. D. & Hall, L. S. 1992 Electromyogenic potentials of a variety of platypus prey items: an amplitude and frequency analysis. In *Platypus and echidnas* (ed. M. L. Augee), pp. 216–224. Mosman, Australia: The Royal Zoological Society of New South Wales.

43 Kalmijn, A. J. 1966 Electro-perception in sharks and rays. *Nature* **212**, 1232–1234. (doi:10.1038/2121232b0)

44 Manger, P. R. & Pettigrew, J. D. 1996 Ultrastructure, number, distribution and innervation of electroreceptors and mechanoreceptors in the bill skin of the platypus, *Ornithorhynchus anatinus*. *Brain Behav. Evol.* **48**, 27–54. (doi:10.1159/000113185)

45 Rossi-Santos, M. R. & Wedekin, L. L. 2006 Evidence of bottom contact behavior by estuarine dolphins (*Sotalia guianensis*) on the eastern coast of Brazil. *Aquat. Mamm.* **32**, 140–144. (doi:10.1578/AM.32.2.2006.140)

46 de Gurjao, L. M., de Antrade Furtado Neto, M. A., dos Santos, R. A. & Cascon, P. Feeding habits of marine tucuxi, *Sotalia fluviatilis*, at Ceara State, northeastern Brasil. *Lat. Am. J. Aquat. Mamm.* **2**, 117–122.

47 Di Beneditto, A. P. M. & Ramos, R. M. A. 2004 Biology of the marine tucuxi dolphin (*Sotalia fluviatilis*) in southeastern Brazil. *J. Mar. Biol. Assoc. UK* **84**, 1245–1250. (doi:10.1017/S0025315404010744h)

48 Di Beneditto, A. P. M. & Siciliano, S. 2007 Stomach contents of the marine tucuxi dolphin (*Sotalia guianensis*) from Rio de Janeiro, south-eastern Brazil. *J. Mar. Biol. Assoc. UK* **87**, 253–254. (doi:10.1017/S00253154070 53647)

49 Silva, F. J. D., Porpino, K. D., Firmino, A. S. L., de Oliveira, I. T. G. & Simoes-Lopes, P. C. 2010 Bone alterations caused by a sting ray spine in the vertebra of *Sotalia guianensis* (*Cetacea*, *Delphinidae*). *Mar. Mamm. Sci.* **26**, 234–238. (doi:10.1111/j.1748-7692.2009.00312.x)

50 Rossbach, K. A. & Herzing, D. L. 1997 Underwater observations of benthic-feeding bottlenose dolphins (*Tursiops truncatus*) near Grand Bahama Island, Bahamas. *Mar. Mamm. Sci.* **13**, 498–504. (doi:10.1111/j.1748-7692.1997.tb00658.x)

51 de Moura, J. F., Sholl, T. G. C., da Silva Rodrigues, E., Hacon, S. & Siciliano, S. 2009 Marine tucuxi dolphin (*Sotalia guianensis*) and its interaction with passive gillnet fisheries along the northern coast of the Rio de Janeiro State, Brazil. *Mar. Biodivers. Rec.* **2**, 1–4. (doi:10.1017/S1755267208000018)