

SELECTIVE HEATING OF VIBRISAL FOLLICLES IN SEALS (*PHOCA VITULINA*) AND DOLPHINS (*SOTALIA FLUVIATILIS GUIANENSIS*)

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Summary

The thermal characteristics of the mystacial vibrissae of harbour seals (*Phoca vitulina*) and of the follicle crypts on the rostrum of the dolphin *Sotalia fluviatilis guianensis* were measured using an infrared imaging system. Thermograms demonstrate that, in both species, single vibrissal follicles are clearly defined units of high thermal radiation, indicating a separate blood supply to these cutaneous structures. It is suggested that the high surface temperatures measured in the area of the mouth of the follicles is a function of the sinus system. In seals and dolphins, surface temperature gradually decreased with increasing distance from the centre of a follicle, indicating heat conduction from the sinus system *via* the follicle

capsule to adjacent tissues. It is suggested that the follicular sinus system is a thermoregulatory structure responsible for the maintenance of high tactile sensitivity at the extremely low ambient temperatures demonstrated for the vibrissal system of seals. The vibrissal follicles of odontocetes have been described as vestigial structures, but the thermograms obtained in the present study provide the first evidence that, in *Sotalia fluviatilis*, the follicles possess a well-developed sinus system, suggesting that they are part of a functional mechanosensory system.

Key words: vibrissa, thermoregulation, infrared thermography, harbour seal, *Phoca vitulina*, dolphin, *Sotalia fluviatilis*.

Introduction

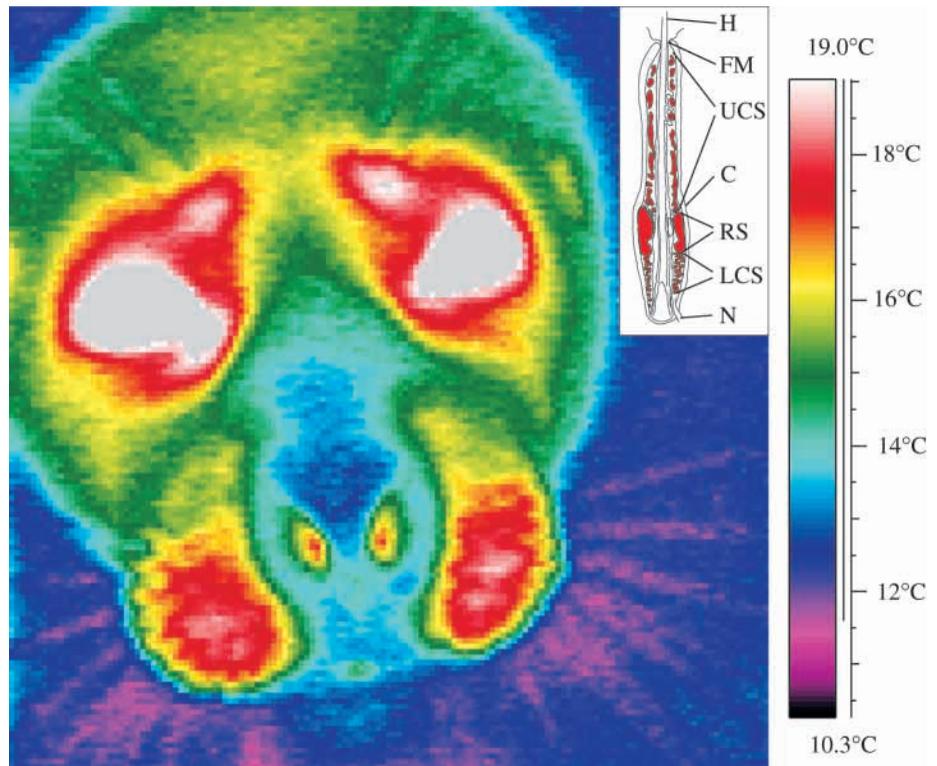
Because of their aquatic lifestyle, thermoregulation is a major problem for marine mammals. Even tropical waters could lead to metabolically expensive heat loss in small cetaceans, pinnipeds and sirenians because of its high heat capacity. Although thermoregulatory specializations seem to be diverse in marine mammals, they have generally adapted to their thermally hostile environment by having small surface-to-body mass ratios, effective thermal insulation provided by a blubber layer encasing almost the whole trunk, and vasoconstriction in the periphery (Innes et al., 1990; Kvadsheim et al., 1997; Scholander and Schevill, 1955; Tarasoff and Fisher, 1970; Worthy and Edwards, 1990).

Vasoconstriction in the periphery results in a reduced skin blood flow and skin temperatures close to ambient temperature. Although a reduction in superficial blood circulation and low skin temperatures are advantageous with respect to thermoregulation, these effects of vasoconstriction would be expected to be physiologically unfavourable for sensory systems located in the periphery. In this respect, not only the potential loss of an adequate temperature level for receptor function and tissue pliability, but also a reduced supply of oxygen and metabolites to the sensory units are significant (Green et al., 1979). As an adaptation to low water temperatures, heterothermic oceanic fishes, for example,

possess heat generators modified from eye muscles that raise the temperature of the eyes and brain above that of the surrounding environment (Block, 1994; Block et al., 1993; Block and Franzini-Armstrong, 1988). Similarly, it has been suggested that the high volume and surface area of the ophthalmic rete found in some cetacean eyes serve to stabilize the temperature of the retina and the optic nerve (Dawson, 1980; Mobley and Helweg, 1990).

Impairment of sensory function by cooling is best documented for the human sense of touch (Bolanowski and Verrillo, 1982; Gescheider et al., 1997; Green, 1977; Green et al., 1979; Stevens and Hooper, 1982; Verrillo and Bolanowski, 1986). The results can be summarized by stating that, in humans, a substantial decrease in skin temperature leads to severe deterioration of tactile sensitivity. In contrast, the tactile sensitivity of the mystacial vibrissae of harbour seals for the detection and discrimination of hydrodynamic stimuli (Dehnhardt et al., 1998a; B. Mauck and G. Dehnhardt, in preparation) and of the texture differences of actively touched surfaces (Dehnhardt et al., 1998b) is not affected by low ambient water temperatures. Infrared thermographic examinations (Dehnhardt et al., 1998b) revealed that the surface temperatures of the mystacial and supraorbital vibrissal pads are maintained as much as 25 °C above ambient air

Fig. 1. Portrait infrared thermogram showing the typical distribution of temperatures measured on the surface of a harbour seal's face. This thermogram was not taken in winter, so the difference between the skin temperatures and the seal's surroundings is not as great as that described by Dehnhardt et al. (1998b). In addition to the eyeballs, the supraorbital and mystacial vibrissal pads (red areas) are clearly defined regions of higher thermal emission than adjacent skin areas. The inset shows a schematic view of a longitudinal section of a vibrissal follicle of *Phoca hispida*. Red areas belong to the tripartite blood-filled sinus system. FM, mouth of the follicle at the skin surface; H, vibrissal hair shaft; UCS, upper cavernous sinus; RS, ring sinus; LCS, lower cavernous sinus; N, nerve bundle penetrating the capsule (C) of the follicle (adapted from Dehnhardt et al., 1998b).



temperature, while thermal radiation from other areas of the face is rather low (Fig. 1). Although these results indicate that the excellent tactile performance of seals at temperatures close to 0°C is based on a selective heating mechanism in the vibrissal pads, the vascular architecture underlying this mechanism remained obscure. Dehnhardt et al. (1998b, 1999) suggested that the high temperatures measured at the surface of the vibrissal pads is a function of the sinus system characterizing each vibrissal follicle (Fig. 1 inset). In particular, the upper cavernous sinus, which is, according to current information, unique to the vibrissal follicles of pinnipeds, may serve as a thermal insulator for the receptors located in the area of the ring sinus. In the present study, we provide evidence to support to this hypothesis by using infrared-thermography to show that the temperature distribution in vibrissal pads is by no means homogeneous, but that each single vibrissal follicle appears as a thermally clearly defined spot of high heat radiation.

In contrast to what is known about mechanoreception in pinnipeds, there is still little information about the significance of this sensory channel in cetaceans. Although good morphological data on vibrissal follicles in cetaceans are still unavailable, it has been suggested that they are well developed and highly innervated in baleen whales, whereas those of adult toothed whales are assumed to be rudimentary, lacking vibrissal hair shafts, blood sinuses and innervation (for reviews, see Ling, 1977; Yablokov and Klezeval, 1969). However, in most odontocetes, an array of two (*Phocoena phocoena*) to ten (*Delphinus delphis*) follicles is situated on each side of the upper jaw. These are conspicuous in the Tucuxi (*Sotalia*

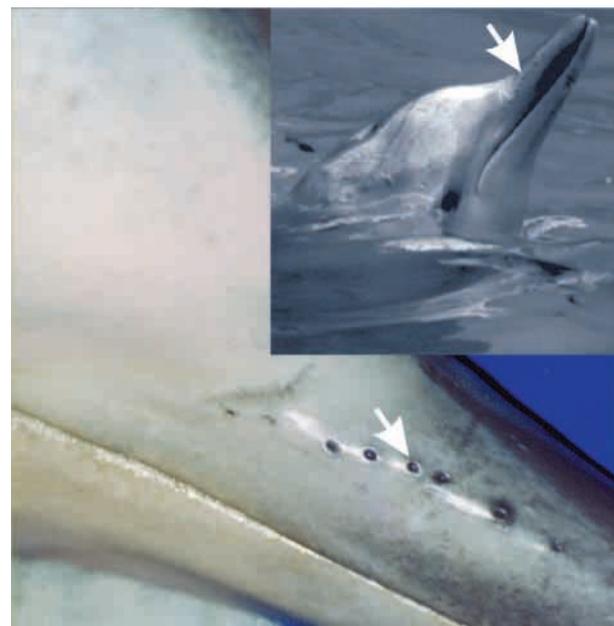


Fig. 2. The dorsal part of the rostrum of a Tucuxi (the dolphin *Sotalia fluviatilis guianensis*) showing the crypts of the right-hand array of vibrissal follicles, which are visible even from a distance (see inset).

fluviatilis guianensis, see Fig. 2). Here, we demonstrate using infrared-thermography that, similar to the situation in seals, the follicle crypts in this tropical dolphin show a substantially higher degree of thermal emission than do the adjacent skin areas, indicating the presence of a well-developed sinus system and suggesting that these follicles are functional sensory units.

Materials and methods

Animals

Thermograms of two harbour seals (*Phoca vitulina*) and two Tucuxi (*Sotalia fluviatilis guianensis*) were obtained. The seals were kept at the Tierpark Rheine, the dolphins at the Delphinarium Münster, Germany. The water temperature of the holding pool at Tierpark Rheine was subject to the seasonal ambient temperature, while the water temperature at the Delphinarium Münster was held $\geq 20^\circ\text{C}$.

Thermographic examinations

The animals were trained to bring the upper part of their body out of the water and immediately to press their lower jaw onto a target held by a trainer. To avoid an impairment of thermographic measurements by cooling due to evaporation from the skin surface, the snout of the animal was quickly dabbed dry. This way, only a few seconds passed between an animal leaving the water and the onset of a thermographic recording.

All infrared images were recorded using an AGEMA 870 Thermocamera (temperature resolution 0.1 K, internal calibration), stored on hard disk as CATS images and analysed using AGEMA IRwin5.1 software. The distance between the skin surface and the camera lens (infrared-lens 20° SW) was 80 cm for portrait images of the animal's head, 20 cm for close-up images of an entire vibrissal pad (see Fig. 3A), and 7–2 cm for close-up images of single follicles. For close-up thermograms, extension tubes ranging from 13 to 31 mm in length were employed. The measurement range was chosen individually for each image to ensure high colour resolution and to cover the large range of temperatures found in the region under examination. The mean surface temperatures of the respective regions were determined using spot, area and isotherm tools from the IRwin5.1 software. A profile tool was used to examine the temperature differences along a line intersecting single follicles and the surrounding regions. A rainbow colour scheme was chosen for all thermograms.

Results

Thermograms obtained from individual seals or dolphins showed, in principle, no difference. The thermograms did not change over time and were reproducible in later sessions. Hence, thermograms are not presented for each of the subjects used, but representative results of the infrared measurements are shown for the two species.

Harbour seals

Thermograms were taken on different days so that the absolute skin temperatures of the seals differed depending on the ambient temperature. However, the overall temperature distribution on the faces of the animals and on vibrissal pads was found to be quite constant.

Fig. 3B demonstrates that the surface temperature distribution in a mystacial vibrissal pad of a seal is not

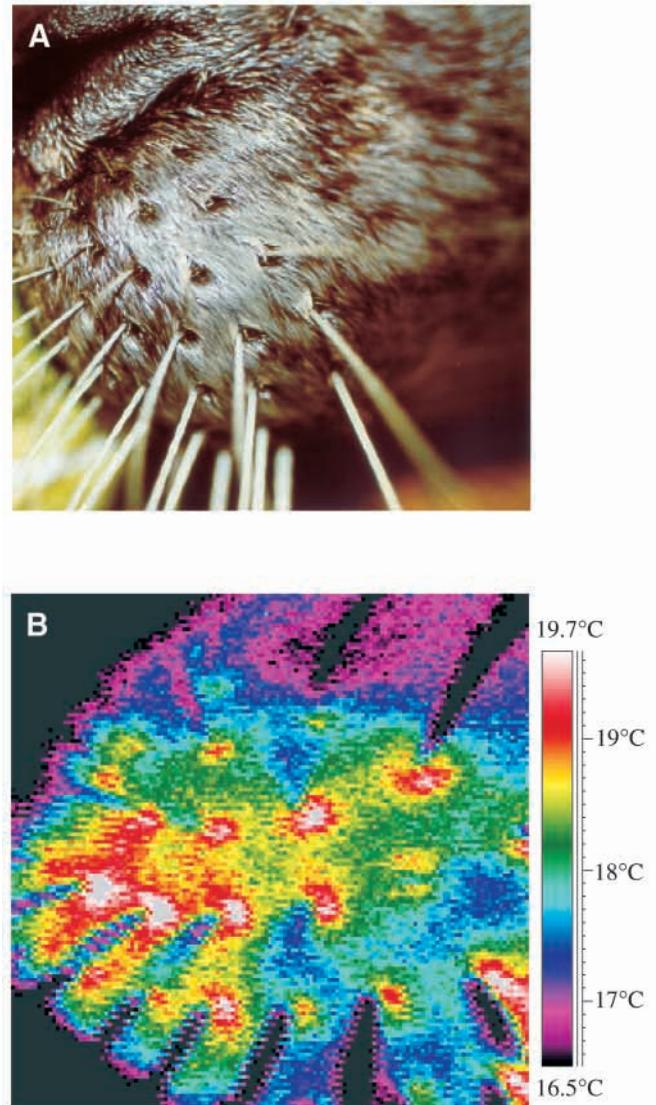


Fig. 3. (A) A close-up photograph of the mystacial vibrissal pad of a harbour seal (*Phoca vitulina*). (B) A close-up thermogram of the left mystacial vibrissal pad of a harbour seal. The vibrissal follicles are the well-defined dot-shaped regions of high thermal radiation (red and pink) compared with the cooler adjacent skin surfaces. The hair shafts have the lowest temperatures (black).

homogeneous: only those small surface areas where single follicles are located showed elevated temperatures of more than 19°C (red and pink areas). Thermal radiation from the surface regions between follicles is clearly reduced (17 – 19°C ; blue, green and yellow areas). Vibrissal hair shafts (black stripes) show the lowest temperatures on the muzzle ($<16.5^\circ\text{C}$, out of the measuring range).

A close-up thermogram (ventro-rostral camera position) of three neighbouring follicles on the left mystacial pad confirms that the regions of highest thermal radiation correlate with the locations of the follicles (Fig. 4A). Most heat is emitted by a semicircular region at the rostro-ventral side of the mouth of the follicle (red areas, spot 1, 21.1°C , and spot 2, 21.2°C), while the corresponding caudo-dorsal part appears to be colder

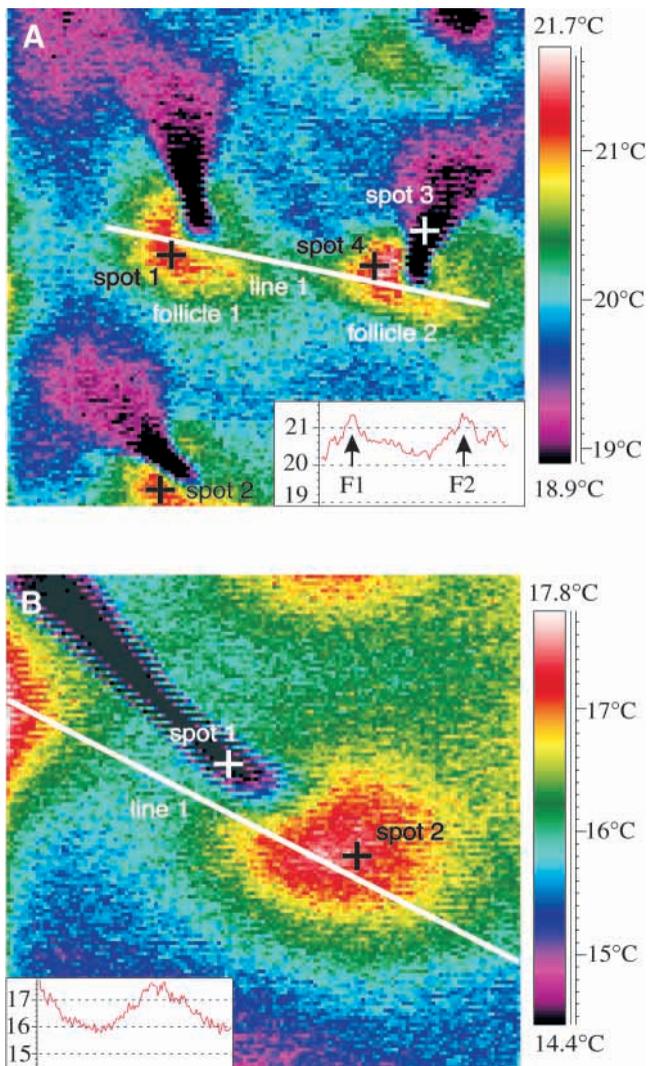


Fig. 4. (A) A close-up thermogram of three neighbouring harbour seal follicles. (A) The temperature graph produced by a profile line intersecting two follicles shows their surface temperatures (red area) to be higher by up to 1.3 °C than that of adjacent skin regions. The vibrissal hair shafts (black) are the regions of lowest thermal radiation. F1, F2, follicles 1 and 2. (B) A close-up thermogram of a single harbour seal follicle. The mouth and the hair shaft (black, spot 1) are inclined to the focal plane of the thermocamera, while the lateral side of the follicle represents the area of highest thermal radiation (red area, spot 2). The temperature graph produced by a profile line intersecting the follicle and its adjacent regions shows that the surface temperatures vary from 15.7 to 17.7 °C, with maximum values at the follicle's lateral side (see profile line, inset). For further details, see text.

(green and light blue areas, 20–20.7 °C). A small layer that immediately encircles the emerging hair shaft (light blue area) is also comparatively cold. An analysis of the temperature distribution using a profile line tool illustrates the temperature gradient along a line through two of the follicles and the area between them (Fig. 4A, line 1). Thermal radiation increases at both follicles, while temperatures decrease in the region between them (Fig. 4A inset). Temperature peaks are as high

as 21.4 °C, and the lowest temperature of the profile line is 20.1 °C. Again, the lowest temperatures are found at the vibrissal hair shafts (black stripes, spot 3, <18.9 °C). Because of the natural vibration of the hair shafts (caused, for example, by wind), their distal parts appear blurred because thermal radiation from the underlying skin areas is partly concealed (violet regions next to black stripes).

A close-up image of a single follicle (caudo-ventral camera position) clarifies the skin temperature distribution in the vicinity of the mouth of the follicle, where the hair shaft emerges (Fig. 4B). The follicle and its mouth are inclined to the focal plane of the infrared-thermocamera so that the hair shaft runs obliquely upwards. The region of highest thermal radiation is the caudo-ventral side of the follicle, where surface temperatures are at least 17 °C (red area, spot 2, 17.7 °C). Outside this area, temperatures decrease in concentric circles (yellow, green and light blue areas) down to 15.7 °C. Along a profile line (Fig. 4B, line 1) starting from a neighbouring follicle in the upper left corner of the thermogram, the temperature drops from over 17.8 °C to 15.8 °C at the area between the follicles (Fig. 4B inset). Along the line intersecting the follicle at the centre of the thermogram, the temperature gradually increases again, reaches a maximum value (17.7 °C) at the caudo-ventral side of the follicle (red area), and then gradually decreases again to below 16 °C. The lowest thermal radiation is found at the vibrissal hair shaft, where surface temperatures are below 14.4 °C (e.g. spot 1, <14.4 °C).

Tucuxi

Fig. 5A shows a thermogram of two vibrissal follicles of a Tucuxi (*Sotalia fluviatilis guianensis*). Although the absolute temperatures are considerably higher than those obtained in thermograms of harbour seals, the follicular areas of the dolphin show a very similar temperature distribution. The areas of highest skin temperature are the almost circular centres of both follicles (area 1, maximum temperature 34.4 °C, spot 1, 34.3 °C, grey isotherm, 34.4 °C, isotherm width 0.1 °C). From these areas, thermal radiation gradually decreases in concentric circles (yellow and green regions). Along a profile line intersecting the two follicles, the temperature reaches maximum values at the two follicles (34.3 °C and 34.4 °C), while the minimum temperature occurs in the region in between the two follicles (33.4 °C, Fig. 5A inset). On both sides of the line connecting the follicles, temperatures decrease below 33 °C (light blue, blue and violet areas, e.g. spot 2, 32.4 °C; spot 3, 33.1 °C; spot 4, 32.7 °C).

A close-up thermogram of a single follicle shows the temperature distribution in more detail (Fig. 5B). The highest thermal radiation is emitted from the follicle crypt (see spot 1, 34.2 °C), with a maximum temperature of 34.5 °C. Outside this area, temperature gradually decreases in almost concentric circles down to below 33 °C (yellow, green, light blue, dark blue and violet regions). Along a profile line intersecting the follicle, temperature gradually increases to a maximum value of 34.4 °C at the follicle crypt (see cursor on profile line) and

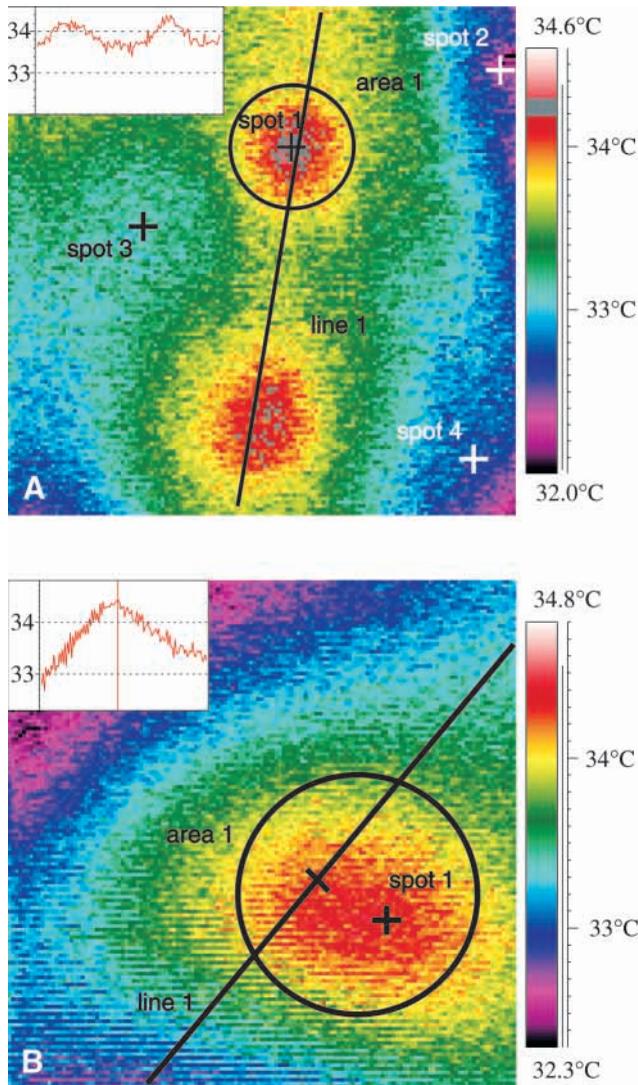


Fig. 5. (A) A close-up thermogram of two neighbouring follicles on the rostrum of a Tucuxi (*Sotalia fluviatilis*). The highest surface temperatures revealed by the profile line tool (see inset, maximum temperature gradient approximately 1 °C) are at the follicle crypts (red areas, e.g. spot 1). This has been confirmed in control thermograms (not shown here) by a tiny metal pointer. The temperature of the skin areas surrounding the follicle crypt gradually decreases (yellow, green, blue areas). (B) A close-up thermogram of a Tucuxi follicle. Although the vibrissal hair shafts are missing, the temperature distribution is very similar to that of harbour seals. The temperature graph produced by a profile line intersecting the follicle showed the highest thermal radiation to be emitted from the follicle itself (red area), where surface temperatures are up to 1.7 °C higher than at adjacent skin areas (see inset, profile line). For details, see text.

gradually decreases again towards the periphery of the follicle. Adjacent skin regions are as cold as 32.7 °C (Fig. 5B, inset).

Discussion

The close-up thermograms presented in this study clearly identified single vibrissal follicles to be selectively heated units

within the mystacial vibrissal pads of seals and on the rostrum of dolphins. Although in thermograms of seals the areas of highest thermal radiation appear as small semicircular zones on only one side of a vibrissal hair shaft (Fig. 4A,B), they should be considered as complete thermal belts surrounding the mouth of a follicle. The seals always protracted their vibrissae to the most forward position when pressing their lower jaw onto the target (Fig. 3A), so the whole vibrissal pad as well as the mouth of each single follicle became dome-shaped. Thus, the camera was always slightly inclined from the vertical towards the mouth of a follicle. Consequently, direct radiation from the rear side of a follicle was missed so that these areas appear to be colder than the side facing the camera (see red rostro-ventral and caudo-ventral aspects of follicles in Fig. 4A,B). This effect is enhanced by the cold hair shaft that partly conceals adjacent skin areas and neighbouring follicles. In contrast, the hairless and immobile follicle crypts of dolphins are arranged in a more-or-less horizontal plane, and the camera lens could be placed almost vertically above the follicle mouth so that these areas appear as compact circular spots in the thermograms.

The thermographic data presented here strongly suggest that the high thermal radiation from the mouth of the follicles is a function of the vibrissal sinus system. The sinus system is considered to play a role in the process of mechanical transduction (Lichtenstein et al., 1990; Melaragno and Motagna, 1953; Rice et al., 1986; Woolsey et al., 1981), and its function as an accessory thermoregulatory structure has not yet been investigated. Although the two functions are not mutually exclusive, the latter is in accordance with the maintenance of high tactile sensitivity by the mystacial vibrissae of harbour seals at extremely low ambient temperatures (Dehnhardt et al., 1998b). In particular, the extensive upper cavernous sinus developed in pinnipeds (Hyvärinen, 1989; Hyvärinen and Katajisto, 1984; Stephens et al., 1973; see Fig. 1 inset), which covers up to 60% of the total length of the follicle and is not supplied with sensory elements, may serve as an active thermal insulator for the receptor area below it. The fact that, within a vibrissal pad, single follicles are thermally clearly defined suggests a separate vibrissal blood circulation that provides the sinus system permanently with warm blood while blood flow is reduced to adjacent skin areas. However, the vascular architecture underlying this mechanism is still to be demonstrated.

All close-up thermograms revealed that the high surface temperature in the area of the follicle mouth gradually decreased with increasing distance from the centre of the follicle. This indicates that the increased temperature of the entire vibrissal pad, compared with the rest of the muzzle, is a function of heat conduction from the sinus system *via* the follicle capsule to adjacent tissues. Since sufficient heat is important not only for the function of mechanoreceptors but also for the mechanical properties of the surrounding tissue, elevated temperatures in the entire vibrissal pad of seals may be important for the mobility of vibrissae and, consequently, for the process of mechanical transduction. In this respect, the

separated vibrissal blood flow may act in combination with the special fatty acid composition of the adipose tissue around the mystacial and supraorbital vibrissal follicles of phocids. This differs from that of trunk blubber in containing an excess of low-melting-point monoenoic fatty acids which, it has been suggested, maintain sufficient fat fluidity and thus the mobility of the vibrissae (Käkelä and Hyvärinen, 1993, 1996).

From behavioural studies, it is increasingly evident that the vibrissal system of pinnipeds is of major biological significance in these marine mammals (Dehnhardt, 1994; Dehnhardt and Dücker, 1996; Dehnhardt and Kaminski, 1995; Dehnhardt et al., 1998a,b; Oliver, 1978). Although operating a sensory system is subject to energetic costs, the selective provision of vibrissae with warm blood in species that otherwise show extensive adaptations to counteract heat loss may be considered as an additional thermal investment allowing the permanent and effective use of this mechanosensory system in a thermally hostile environment. In this respect, vibrissal heating is comparable with the evolution of cranial endothermy in several oceanic fish (e.g. tuna and billfish), which possess local heat generators, modified from eye muscles, that warm their brain and eyes (Block, 1994; Block et al., 1993; Block and Franzini-Armstrong, 1988).

Although detailed morphological studies are still unavailable, the vibrissal follicles of odontocetes have been described as vestigial structures of the integument, having no blood sinuses, blood vessels or nerve fibres (Ling, 1977; Yablokov and Klezeval, 1969). Contrary to this view, the results of our thermographic examination of the vibrissal follicles on the rostrum of *Sotalia fluviatilis* indicate the presence of a well-developed sinus system. Considering the explanations applied for vibrissal follicles of harbour seals, these findings suggest that the follicles of *Sotalia fluviatilis* are functional sensory units. If this is so, it remains speculative what kind of information the animals receive by means of these mechanosensory structures and how physical stimulation is transmitted in the absence of vibrissal hair shafts to the follicle receptors. As has recently been demonstrated for the vibrissal system of harbour seals (Dehnhardt et al., 1998a), it is reasonable to suppose that the vibrissal follicles of dolphins are a hydrodynamic receptor system providing the animals with information about local water disturbances caused by fishes and other organisms (for a review of hydrodynamic reception, see Bleckmann, 1994). By applying vibrations and recording somatosensory evoked potentials, Ridgway and Carder (1990) demonstrated that the dolphin skin is indeed sensitive to vibrations or small pressure changes on its surface. The areas of highest sensitivity were located at the head, i.e. at the angle of the gape, at the rostrum, the melon, around the eyes and at the blowhole. Although Ridgway and Carder (1990) suggest that the dolphin skin is sensitive enough to detect turbulent flow, the stimuli that were employed did not produce greater responses from the skin area containing the follicle crypts than from the surrounding skin of the snout. However, a potential hydrodynamic receptor function for the follicles may not be evident in response to

mechanical vibration applied directly to the skin but only to medium flow.

Visualizing the flow field around a swimming dolphin using flow-induced bioluminescence of plankton, Rohr et al. (1998) found the boundary layer to be extraordinarily thin on the melon and rostrum of dolphins. Any water disturbance or turbulence caused and left by moving objects may travel through this thin boundary layer and act as a hydrodynamic stimulus on a sensitive skin area located there. It is tempting to speculate that hydrodynamic stimuli reaching the follicles by travelling through this thin boundary layer on the rostrum of dolphins might provide information to these marine mammals that has so far been disregarded. An anecdotal report tells of a blindfolded bottlenose dolphin following a live fish that had been introduced to its pool after an echolocation experiment. Although the animal emitted no detectable sonar signal, it positioned itself adjacent to the fish and was able to follow and catch it. It was suggested that the dolphin made use of its hearing to track and capture the fish (Wood and Evans, 1980; cited in Au, 1993). Although this interpretation may be correct, another possibility is that the dolphin tracked the local water movements left by the fish. However, much work has still to be done on the morphology of the follicles and using behavioural experiments to test these hypotheses.

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