Features of Dolphin Skin With Potential Hydrodynamic Importance

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The widespread belief that dolphins are capable of extraordinary swimming speed was noted 2,500 years ago by Aristotle, who wrote, "It [the dolphin] appears to be the fleetest of all animals, marine and terrestrial ..." (*Historia Animalium*). In the first of more recent considerations of dolphin hydrodynamic efficiency, Sir John Gray in 1936 cited observations of a fellow scientist who clocked a dolphin passing from stern to bow of a ship making 8.5 knots, from which he calculated a swimming speed of 20 knots [1]. Gray, assuming that the dolphin could have maintained this speed for a considerably longer time, concluded that, with turbulent flow, the animal would have to have muscles seven times stronger than those of other mammals. More inclined to believe that dolphins have a means of achieving laminar flow, he experimented with rubber models in an attempt to determine whether flexions of the body could prevent turbulence; his results were inconclusive [1,2].

Kramer suggested that dolphins have a compliant skin that enhances their hydrodynamic performance by damping incipient turbulence [3,4]. Kramer also was the first to develop a synthetic vessel coating based upon dolphin skin. However, his coating contained no mechanism for active vibration or for other adjustments to changing boundary layer conditions. Lang, in addition to his own studies of dolphin hydrodynamics, reviewed the earlier work and evaluated the various theories [5]. Concerning the idea that dolphins might actively change their skin surface to reduce hydrodynamic drag, he stated, "An alternate explanation for low drag with regard to cetaceans is that they actively adjust the flexibility and movement of their skin to damp out the microscopic disturbances in the laminar boundary layer. Betchov showed that the laminar flow might be extended indefinitely by this means."

Several other authors have suggested that the skin of living dolphins makes adjustments that improve boundary layer conditions to reduce drag during underwater swimming [6, 7, 8, 9, 10]. Their evidence was based on skin anatomy, nerve structures in the skin, electrical potentials from the skin, or from microvibrations. These ideas can best be summarized by a quotation from Khomenko and Khadzhinskiy [9], "One of the reasons that dolphins are so hydrodynamically perfect is that they actively control (by reflexes) their skin, which contains specific receptors connected to the central nervous system."

Innervation of dolphin skin has been described by Palmer and Weddell [7] and by Harrison and Thurley [11,12]. The first authors were especially impressed, saying:

"The presence of longitudinally disposed dermal ridges, the patterned arrangement of the collagen and elastic fibers related to them, together with the passage of preterminal nerves through tunnels in the base of the epidermal ridges to serve large complex terminals attached to papillary walls, all suggest that the skin is a specialized pressure-transducing mechanism. The number and complex arrangement of other nerve terminals in the skin further suggest that the

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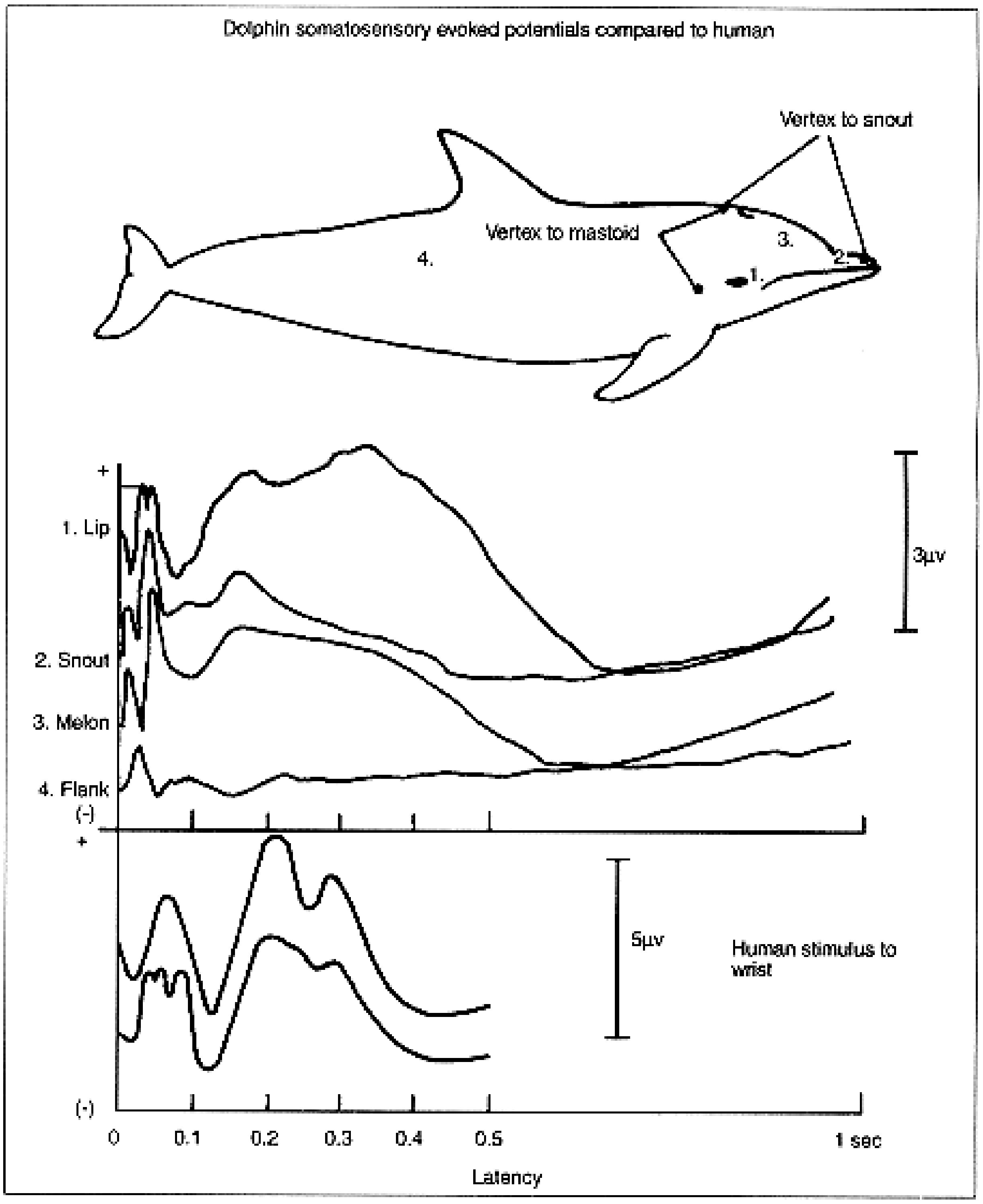
skin is instrumental in enabling the dolphin to become aware of its body image in relation to the water around it; in other words, that the skin has both tactile and proprioceptive functions ... a good case can be made out for regarding the specialized innervation of the skin in *Tursiops truncatus* as part of a complicated sensory-motor mechanism which permits the maintenance of laminar flow ... " [7].

Lende and Welker first studied dolphin skin sensitivity in 1972 [13]. They recorded electrical potentials from an area of the contralateral cerebral cortex to study the representation of this area of somatosensory cortex on the skin surface. Using stimuli such as tapping, or lightly touching or stroking the skin, or by allowing water droplets to fall on the skin, the investigators produced a map of skin sensitivity based upon recordings from this area of cortex. The greatest sensitivity was found in "a broad zone extending below both eyes and ventrally around the neck ..."

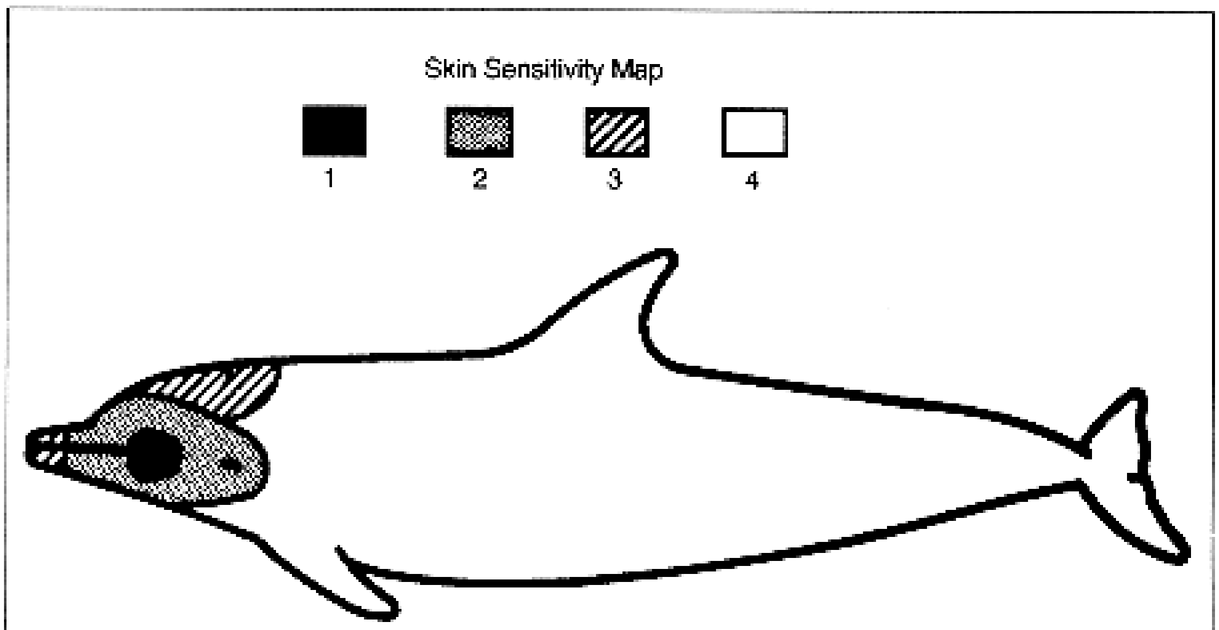
Kolchin and Bel'kovich [14] used the galvanic skin response (GSR) produced by a 0.3 mm weighted wire to make a partial map of body skin sensitivity in the common dolphin, *Delphinus delphis*. Of the body portions studied, they found the dolphin to be most sensitive (10 mg/mm^2) in separate circular areas of about five cm diameter around the blowhole and eyes. The snout, lower jaw, and melon were found to be somewhat less sensitive (10 to 20 mg/mm^2), while still less sensitivity (20 to 40 mg/mm^2) was observed along the back in broad areas both anterior and posterior to the dorsal fin. The authors state that, "from an ecological point of view the results we obtained are not unusual. The values for the threshold of sensitivity to touch in dolphins are 10 to 40 mg/mm^2; this is close to the values for a human being in the most sensitive skin areas, the tactile surfaces of the fingers, the skin of the eyelids, and the lips" [14].

Microvibrations, minute tremor-like vibrations that occur in warm-blooded animals at all times over the entire body, have an amplitude of about one to five μm at frequencies of seven to 13 Hz in relaxed humans. This "minor tremor" is thought to be important in maintaining body temperature [15]. Shivering is believed to be a natural amplification of this continuously present tremor. Microvibrations in dolphin skin were studied by Haider and Lindsley, who observed that the dolphin skin exhibited microvibrations three or four times the amplitude found in human skin [6].

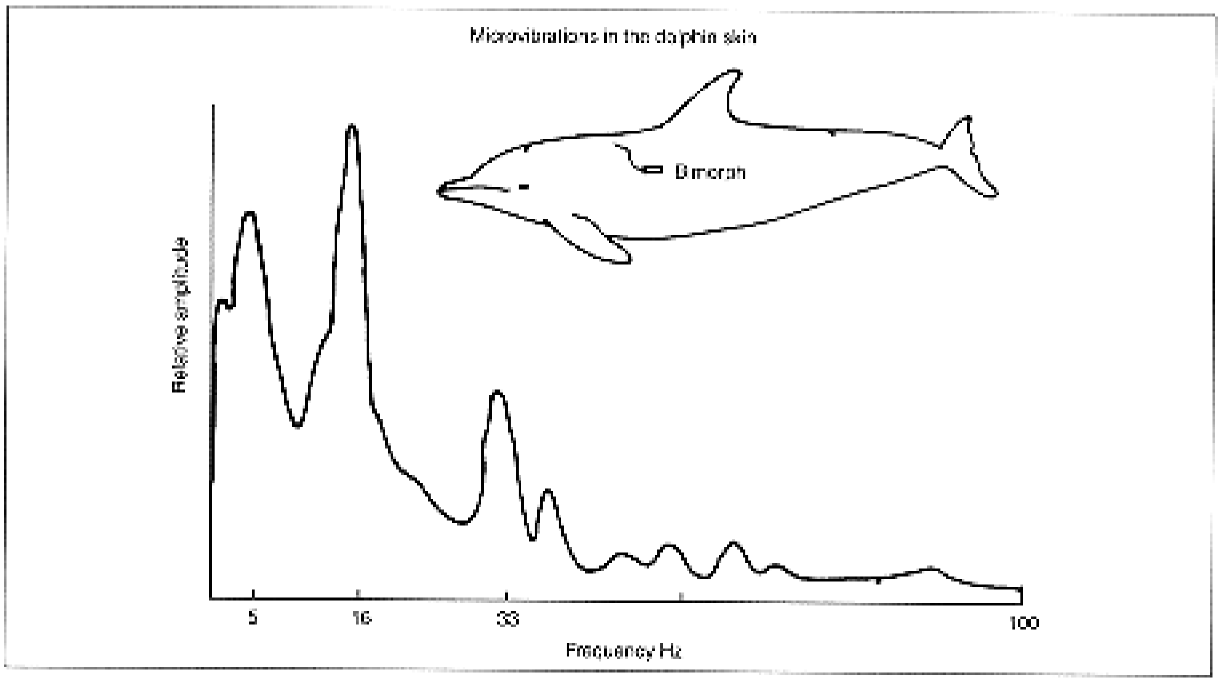
Gross movements of the body surface can be produced by contraction of subcutaneous muscle. The *musculus cutaneous* (formerly known as *panniculus carnosus*)



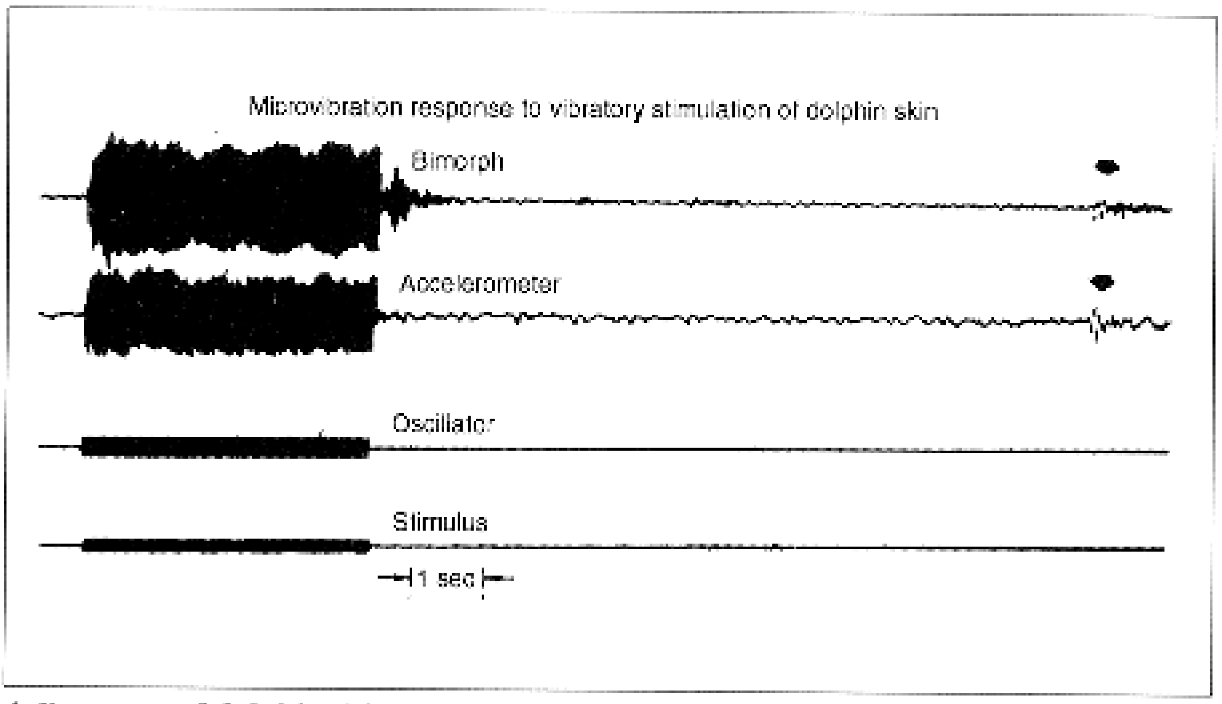
1. Somatosensory evoked potentials from a dolphin compared to those from a human evoked by a stimulus to the wrist. Human evoked potentials redrawn from Allison [25]. Numbers indicate areas where stimuli were delivered to evoke the responses shown. Recording leads were on the dolphin's right side and stimulus sites



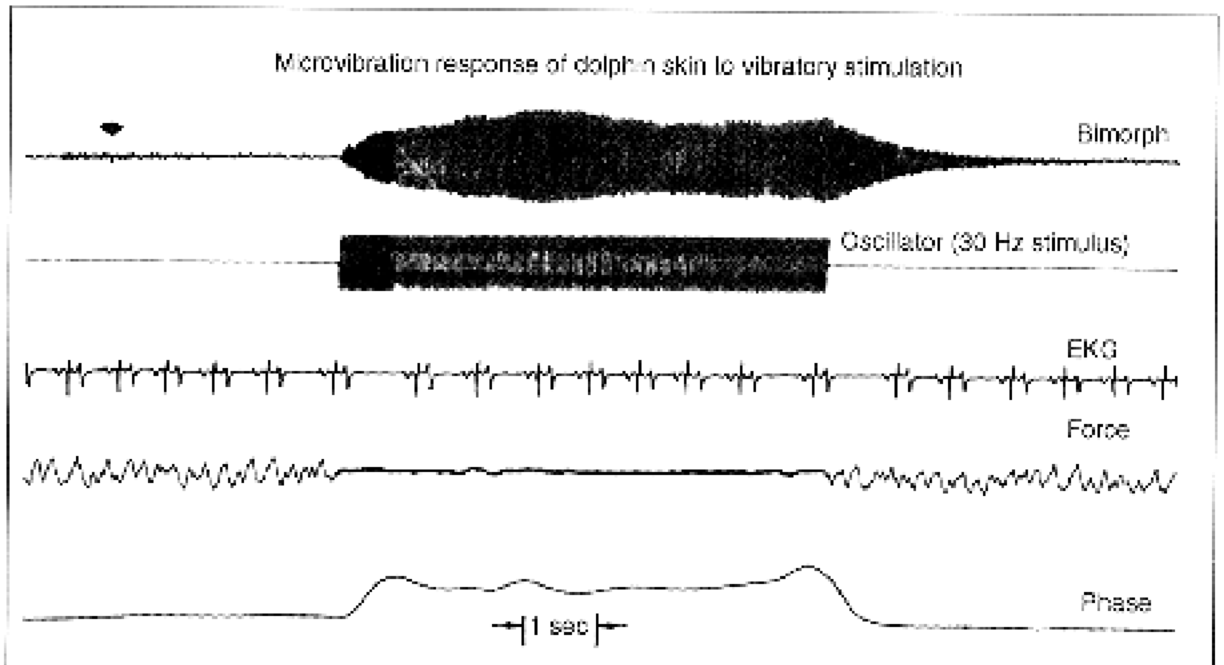
2. Map of dolphin skin sensitivity based on somatosensory evoked potentials. The belly and genital area were not tested. 1, most sensitive, followed by 2, 3 and 4 in descending order.



3. Frequency analysis of microvibrations from the dolphin's skin. A 60-s epoch of signal from a biomorph, positioned as shown in the drawing, was averaged on the SD-350 spectrum analyzer to produce this plot. Major peaks in this period were at 5, 16, and 33 Hz. Significant peaks above 40 Hz were very rarely observed.



4. Response of dolphin skin as recorded from an accelerometer and a biomorph affixed to the skin on the side near the dorsal fin. Activity from both of these sensors continues after the stimulus. Arrows indicate activity before the following stimulus in the series.



5. Response to vibratory stimulation at 30 Hz. Arrow shows activity prior to the stimulus—just one of a series. Activity recorded by the biomorph continues for more than one s after the stimulus is terminated.

is a sheet of muscle that lies beneath the skin in many mammals and is capable of moving the skin. (In horses, a major component of the muscle is called "flyshaker" [16].) The *musculus cutaneous* is especially well-developed in dolphins and other small whales [17, 18]. This thin sheet of muscle covers most of the dolphin's body except for the tailstock, appendages, snout, melon, and mid-back. It lies between the outer blubber layer (hypodermis) and inner blubber layer of subcutaneous fat, and in the bottlenose dolphin, *Tursiops truncatus*, is two to four cm below the skin surface.

We replicated the experiments of Haider and Lindsley [6] and extended the investigations begun by Lende and Welker [13] to find out more about the sensitivity and responsiveness of the dolphin skin. We sought answers to the following questions: Is the dolphin epidermis sensitive to small vibrations? Does the skin respond to low-amplitude vibratory stimulation? Does the dolphin *musculus cutaneous* muscle that underlies much of the skin make rapid contractions in response to stimulation analogous to the rapid "flyshaker" movements of similar muscles in the horse?

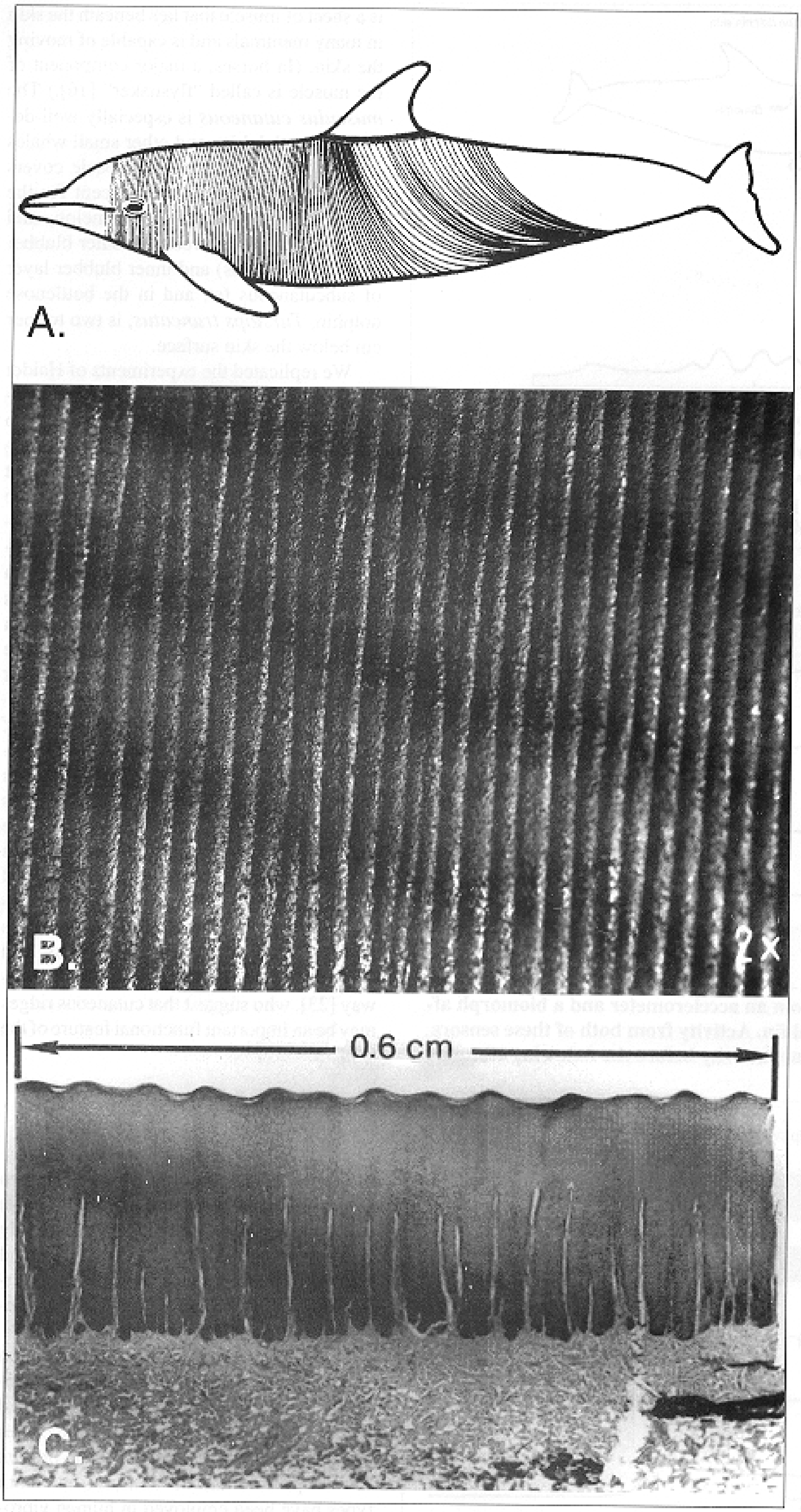
Although the intracutaneous structure of dolphin skin has received considerable attention [7, 12, 19, 20, 21], the cutaneous surface has not been studied in nearly as much detail. Geraci, et al. [20] mention the existence of the ridges, but other writers generally refer to the skin of dolphins and other small whales as "smooth." The appearance and orientation of cutaneous ridges have been documented by Ridgway and Carder [22], and by Shoemaker and Ridgway [23], who suggest that cutaneous ridges may be an important functional feature of the skin.

Materials and Methods

Physiological Studies

For each test, the dolphin subject (two adult females and one adult male bottlenose) was placed in a padded tank in a relatively fixed position with its dorsal surface and blowhole above water. Exposed skin surfaces were kept wet throughout the test period by sponging or misting with water.

The two types of mechanical stimulation used were a moving coil shaker and a piezoceramic bimorph [24]. The former presented stimuli with a great variety of frequencies and amplitudes, the later was used to present low-amplitude tactile stimulation. Both types have been employed in human vibrotactile studies. A function generator controlled stimulus rate and triggered the signal averaging computer; stimulus rates and intervals were varied. Finger-tap and water-



6. a) Sketch showing orientation of cutaneous ridges on a bottlenose dolphin. b) 2× photograph of the skin about 25 cm posterior to the blowhole and about 10 cm lateral to the dorsal midline where ridges run perpendicular to long axis of body. c) A low-power photomicrograph of a section of skin taken parallel to the long axis.

drop stimuli also were presented at low asynchronous rates and few repetitions per set. A polygraph and instrumentation tape recorder were used to monitor electroencephalograms (EEG), microvibrations, electrocardiograms, and electromyograms (EMG) along with stimulus triggering pulses, shaker force, velocity and phase, time code, dolphin phonations, and respiration (see Ref. [22] for details).

Documentation of Skin Surface Ridges

We observed the size and orientation of the cutaneous ridges of the dolphin skin. We photographed the ridges, noted their orientation, and made histological sections. Photographs were made with a special 2x close-up lens. Rough drawings were made of the orientation of the cutaneous ridges. Histological sections oriented with the long axis of the body were made for skin sections taken from one dolphin. The sections were taken 25 cm posterior to the blowhole and 10 cm to the left of the dorsal midline. During processing for histology (mounting in paraffin, sectioning on a microtome, and mounting on microscope slides), we took care that the sections were registered so that shrinkage or stretching could not distort the ridges which were visible readily when seen from the surface or from the lateral margins of the skin section (see also [22, 23]).

Results

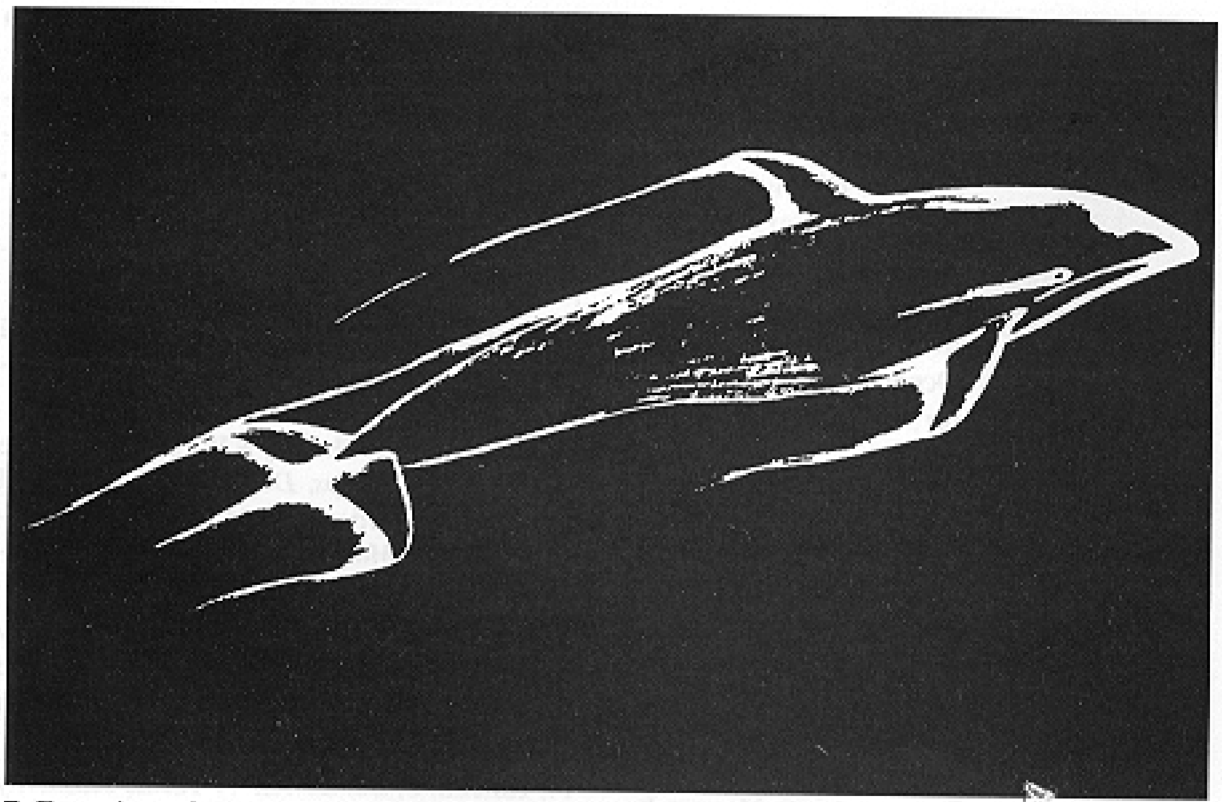
Dolphin Skin Sensitivity

We used the somatosensory evoked potential (SEP) to obtain a gross map of dolphin skin sensitivity. Figure 1 shows averaged potentials evoked by vibrating the dolphin skin compared to evoked potentials from the human wrist [25]. Figure 2 shows a rough map of dolphin skin sensitivity based on the SEP.

Microvibrations in Absence of Stimulation

In our dolphin subjects, microvibration amplitude peaks usually were evident in one or more frequency bands of four to nine Hz, 13 to 20 Hz, 27 to 39 Hz, 45 to 64 Hz, and 75 to 85 Hz. The highest amplitude peak was never above the 45 to 64 Hz range. Microvibrations in the 75-85 Hz range were always less than one or more other peaks and absent when peak activity was in the 27-39 Hz range.

If we accept the reasonable conclusion that activity peaks recorded in the four to eight Hz range were mainly due to breaths (blows), body movements, and large skeletal muscle contractions, then the major microvibration activity in our experiments was in the



7. Drawing of a dolphin swimming through Pacific Ocean waters containing bioluminescent organisms. Turbulence excites the organisms causing them to luminesce. The trunk between the eye and dorsal fin, where the cutaneous ridges run circumferentially, forming lines perpendicular to the direction of water flow, is free of turbulence. Drawn by L.E. McKinley from an underwater bubble on the R/V See Sea off Southern California in the 1960s. (See also Ref. [2].)

13 to 20 Hz range (Fig. 3). Haider and Lindsley mentioned peak activity of 13 Hz in their dolphin subject [6].

Microvibrations during Vibratory Stimulation of the Skin

Figure 4 shows the results of vibrating the dolphin's right side near the dorsal fin. The accelerometer was located on the skin about 10 cm posterior to the vibrating stimulus, and the bimorph 10 cm farther on. The stimuli were presented in a series about 10 s apart. In this instance, activity from both sensors continued (CA) after the stimulus was terminated. Low-level activity also was registered (arrows) just before the succeeding stimulus.

Occasionally, continuing activity (CA) was more pronounced, lasting over one s after a 30 Hz stimulus (Fig. 5). Low-level activity (arrow) is evident just before the stimulus as if the animal anticipated the vibration. This is quite possible since the stimuli were given in regular intervals of five to 20 s. In this case (Fig. 5), the EKG shows prolonged heartbeat intervals around the beginning and ending of the vibration.

A stimulus of 50 Hz given five s after the termination of a 30 Hz stimulus resulted in no CA; however, CA, from the prior 30 Hz stimulus, continued to within two s of the following 50 Hz vibration. CA was seen only after vibrations in the 20 to 45 Hz range.

Because the CA was at roughly the same frequency as the stimulus, we assumed that such activity was an artifact produced by the sensors; however, when we repeated the same stimuli with the same bimorphs and accelerometers using sorbathane or neoprene rubber rather than the living dolphin's skin, this ongoing activity was never found.

Since the CA was found only when we vibrated the skin with frequencies of 20 to 45 Hz, we next reasoned that CA may have been the result of a resonance phenomenon in the dolphin's elastic skin. However, since the CA was present less than 10 percent of the time, a purely physical phenomenon seemed unlikely. If the CA is indeed a resonance in the dolphin skin, the resonance must be effected by internal properties of the skin, e.g., muscle tension or blood pressure in dermal arterioles.

Electromyogram

In all of our experiments, we attempted to insert fine wire electrodes into subcutaneous muscle; however, we were not successful in recording EMG signals that correlated with the stimuli we presented or with the dolphin's responses (SEPs, CAs, or microvibrations). Thus, we were not able to prove whether or not the *musculus cutaneous* is involved in the tiny movements that we observed as microvibrations or as CA.

It is possible that the subcutaneous muscle is responsible for some skin movement, but that discrete areas of the muscle or bundle groupings move specific areas of skin. Perhaps our electrodes were never in the right place at the right time. However, we have never seen dolphin's skin make the characteristic rapid gross movements that can be observed from the horse's "fly-shaker."

Cutaneous Ridges

All dolphins we observed had small, regular cutaneous ridges over much of the surface of their bodies (Fig. 6). These ridges usually were faint at the surface of the skin and could not be seen from a distance; however, they were nearly always visible upon close inspection of the skin of the living animal. The ridges were especially easy to observe at an appropriate oblique angle or with a low-power magnifying lens [22, 23].

Cutaneous ridges were not prominent on the snout, melon, or lower jaw. They became prominent at the level of the blowhole and eyes. From about the blowhole back to the dorsal fin, their orientation was perpendicular to the long axis of the body. The ridges ran circumferentially around the occipital, cervical, and thoracic regions, forming lines perpendicular to the long axis of the body and at right angles to the direction of waterflow past the swimming dolphin. They ran circumferentially around the base of the dorsal fin, but were not prominent on the upper part of the dorsal fin. They were not observed on the flippers except near their insertion to the body. On a level with or posterior to the dorsal fin, the ridges usually were oriented obliquely or, in some cases, almost parallel to the body axis as shown in Fig. 6a, which is a sketch of the approximate arrangement observed in three dolphins.

Discussion

Our studies indicate that dolphin skin is sensitive to vibrations or small pressure changes on its surface. We have shown that the most sensitive areas are located at the angle of gape, and around the eyes, snout, melon, and blowhole (Fig. 2). The exact magnitude of this sensitivity cannot be determined from our data, but we find no reason to disagree with Kolchin and Bel'kovich who suggested that the most sensitive areas of the dolphin skin are about as sensitive as the skin of the human lips and fingers [14]. Since the whisker pits along the dolphin's snout are well innervated, we expected to find them to be more sensitive than the surrounding skin of the snout and adjacent areas of the head. The stimuli we employed did not produce greater responses from the area of the snout containing the whisker pits. Perhaps the pits are sensitive to some specialized stimulus that we did not present.

On a dolphin's spindle-shaped body, transition from laminar to turbulent flow might be expected in the area below the dorsal fin. Supporting evidence for this has been obtained by L. E. McKinley who observed Pacific white-sided dolphins, *Lagenorhynchus obliqudens*, swimming through bioluminescent waters at night [2]. Subsequently, he was able to draw what he had observed (Fig. 7). We had expected that perhaps the skin of this transition area might be extrasensitive; however, our results did not show this.

The dolphin's nervous system detects changes in pressure on its skin surface; however, our results only suggest that the dolphin's skin may reduce drag by moving synchronously with small vibrations impinging on its surface.

Our observations of CA and of occasional amplifications of microvibrations suggest that the dolphin skin may be able to adjust to pressure changes by amplifying normal microvibrations, or by producing vibrations with muscular contractions. Our studies suggest a mechanism by which the dolphin skin might move or vibrate to improve hydrodynamic performance as has been proposed [6, 7, 9, 10, 26]. Dolphin skin is probably sensitive enough to detect turbulent-flow. Drag may be decreased by decreasing the pressure gradient in the adjacent water layer. The skin may actively flex away from higher pressure and toward lower pressure.

We cannot assume that all changes would be aimed at reducing drag. In some cases, i.e., changing directions, stopping, or when a mother "carries" an infant on her pressure wave, it might be advantageous for the animal to increase drag. In such cases, skin movement might simply be reversed in phase to achieve the desired result.

The cutaneous ridges may play an important role in sensory function and in hydrodynamics. When the ridges are preserved in histological sections, their spacing appears to be roughly the same as that of the underlying dermal papillae; however, union of the cutaneous ridges with the deeper epidermal and dermal structures needs better definition, as does their relationship to types and patterns of nerve endings on the surface.

Acknowledgements

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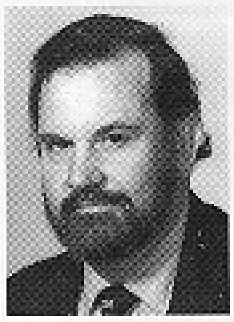

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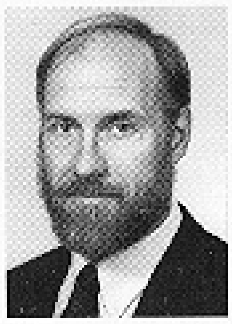

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