

dolphins than in humans (15 μm , cf. 5 μm maximum) and somewhat faster in frequency (13 Hz, cf. 11 Hz). Ridgway and Carder (1990) showed that the dolphins responded to a vibratory stimulus by entraining their spontaneous microvibrations to the frequency of the stimulus and by increasing the normal amplitude of the microvibrations. This level of control of spontaneous microvibrations suggests a possible mechanism for damping turbulence by flexing the body surface away from regions of higher pressure and toward regions of lower pressure in the water flowing over the dolphin. Currently there is no evidence showing that dolphins actually use this mechanism.

Pinnipeds

The most obvious marine mammal tactile sensory structures are the vibrissae of pinnipeds. Not only are they obvious when viewing the animal (Fig. 4-14), they are also highly innervated peripherally and well-represented cortically with large areas devoted to input from the vibrissae. Anatomical and physiological studies have been more successful in demonstrating their importance than have behavioral studies. Dykes (1975) showed that the vibrissae of harp seals and harbor seals were heavily innervated with slowly and rapidly adapting nerve fibers. Both fiber types had a range of thresholds resulting in a sensory system that could provide detailed information about static displacement and vibratory stimuli. The sensitivity of the vibrissae is enhanced by the rich supply of blood vessels in the dermal sheath (Ling 1966), which could provide adaptive changes in the compliance, or flexibility, and by the histologically prominent circular sinuses around the vibrissae (Stephens et al. 1973, Hyvärinen 1989). In ringed seals, Hyvärinen (1989) found that each vibrissal follicle is innervated by 1000 to 1600 fibers.

Ladygina et al. (1992) mapped the body surface of northern fur seals onto the somatosensory cortex. The fur seal has a duplicate somatosensory projection in the cortex. Although a duplicate projection of the entire body has been observed in some monkeys (Merzenich et al. 1978, Nelson et al. 1980, Sur et al. 1982), it usually only occurs for those parts of the body involved in particularly fine tactile discriminations such as the forepaw of the gray squirrel (*Sciurus carolinensis*) (Sur et al. 1978, Nelson et al. 1979, Krubutzer et al. 1986), the hand of prosimian primates (Carlson and Welt 1980, Sur et al. 1980, Carlson and FitzPatrick 1982, FitzPatrick et al. 1982, Carlson et al. 1986), and the vibrissae of the opossum (*Didelphis virginiana*) (Pubols et al. 1976). Ladygina et al. (1992) calculated magnification factors (the relative distance between two cortical recording places to the distance between the two locations on the body that provided maximum stimulation of the cortical sites) and found that the factor varied

from 0.01 to 0.5. On the trunk, the value was 0.01, meaning that a 1-mm shift in recording location in the cortex resulted in a 100-mm shift in the most sensitive body area. For the vibrissae, the factor was as large as 0.5, meaning that a 1-mm shift in recording location in some areas of the cortex corresponded to only a 2-mm shift on the maxillary vibrissal pad. This indicates the extensive cortical space allocated to tactile input from the vibrissae.

Dykes (1975) determined, using electrophysiological recordings from nerves innervating the vibrissae of harbor seals, that the threshold for responses to vibratory stimuli were less than 7 sec of arc. All of the rapidly adapting fibers responded to vibratory stimuli of 256 Hz, but at 1024 Hz only 15% of the fibers followed the vibratory stimulus, and at 1500 Hz, fewer than 1% of the fibers followed the stimulus. In contrast, psychophysical studies by Renouf (1979) and Mills and Renouf (1986) indicated a marked increase in sensitivity to vibratory stimuli as frequencies increased to a peak sensitivity at 1000 Hz, with little decline in sensitivity out to 2500 Hz, the highest frequency tested.

Dykes (1975) postulated that the sensitivity of the slowly adapting nerve fibers to small, but not large, displacements, and the ability of the rapidly adapting nerve fibers to detect very small vibratory stimuli meant that the vibrissae were innervated to provide information about contour and texture. Behavioral results are in line with this prediction.

Kastelein and van Gaalen (1988) showed that a walrus (*Odobenus rosmarus*), fitted with eye cups blocking vision, could use its vibrissae to distinguish between a square and a triangle even when the surface areas of the stimuli were gradually decreased to 0.4 cm^2 . Dehnhardt (1990) demonstrated that a California sea lion, deprived of vision by eye cups, could distinguish among five different three-dimensional objects when allowed to touch them with its vibrissae. In a subsequent experiment (Dehnhardt 1994), this same sea lion detected diameter differences as small as 0.33 cm for discs with a mean diameter of 1.12 cm. This threshold led to a Weber's fraction (minimum detectable diameter difference/mean diameter) of 0.29. The sea lion tactile thresholds followed Weber's law, which states that Weber's fraction should be constant (i.e., ΔD will increase as D increases). Weber's fraction was also 0.29 for discs with a mean size of 8.74 cm. Studies on two harbor seals showed similar values for Weber's fraction at disc sizes of 1.12 cm, but values as low of 0.13 (male) and 0.08 (female) for discs of 5.04 and 8.74 cm (Dehnhardt and Kaminski 1995). Thus, the best tactile size discrimination threshold for the California sea lion was about twice as great as it was for harbor seals. The small number of individuals tested and the individual variability observed preclude definitive species rankings on tactile ability. However, it is interesting to note that the Weber's frac-

tions attained by the harbor seals are similar to those reported for the hands of lower primates such as macaque monkeys (Semmes and Porter 1972, Carlson et al. 1989). Also the Weber fractions for tactile size discrimination by sea lions and harbor seals are similar to those obtained for visual size discriminations by these and other marine mammal species (California sea lion, Schusterman et al. 1965; harbor seal, Feinsein and Rice 1966; spotted seal, Wartzok and Ray 1976; South African fur seal, Busch and Dücker 1987). This similarity between tactile and visual discrimination Weber fractions is an indication of the importance of tactile discrimination for pinnipeds.

All-or-none behavioral experiments, which investigated the transmission of phasic (i.e., not static) information through the vibrissae, showed little difference in the animal's ability to complete the task whether vibrissae were present or not. Renouf (1980) recorded the length of time harbor seals required to capture live fish. Animals with vibrissae clipped off showed no increase in time required in either clear or murky water. Although the vibrissae might not serve a role in fish capture, they could well be important for benthic feeding, particularly at depths where light levels have fallen below threshold. Benthic prey have been observed in fecal samples of harbor seals (Härkönen 1987) and ringed seals (Kelly and Wartzok 1996). Lindt (1956) described Southern sea lions (*Otaria byronia*) swimming near the benthos with their vibrissae erect and touching the sea bottom. Kelly and Wartzok (1996) reported that ringed seals repeatedly dove to the bottom on apparent feeding dives.

As a test of Montagna's (1967) suggestion that one function of the vibrissae might be speed sensing, Renouf and Gaborko (1982) trained a seal to swim through hoops maintaining a constant speed of 6 km/hr. When the animal was able to do this, its vibrissae were cut off. After the removal of the vibrissae, the seal was still able to maintain the same speed. However, this was not a good test of Montagna's hypothesis because the seal was able to see the sequence of hoops even after the vibrissae were removed and thus had other possible speed-sensing cues.

The one all-or-nothing experiment that showed an important role for the vibrissae was a static recognition task. Sonafrank et al. (1983) reported that a blindfolded seal attracted to a hole through the ice using an acoustic cue would ascend directly up through the center of the hole when its vibrissae were unimpeded. However, when the blindfolded seal also had its vibrissae restricted, it still found the hole through the acoustic stimulus just as effectively but bumped into the under side of the ice just lateral to the hole. When finally in the hole, apparently through trial and error, it ascended more slowly to the surface than when the vibrissae

were free. A blindfolded seal with free vibrissae but without an acoustic cue would swim directly under an open hole and not detect it. The vibrissae apparently were unable to provide the seal with usable information on the differences in the reflected pressure wave from the ice and the open hole.

Sirenians

The dugong has the most developed sensory hairs of any marine mammal (Kamiya and Yamasaki 1981). These hairs are present over the entire surface of the body, being most dense on the muzzle. A similar pattern is seen in hair distribution in manatees. Marshall and Reep and coworkers (Marshall et al. 1998, Reep et al. 1998) have recently completed studies of the bristles, hair, and bristlelike hair of the facial region of Florida manatees. The bristles appear to be modified vibrissae. They are used in tactile exploration of the environment and appear quite sensitive to touch (Hartman 1979, Marshall et al. 1998). The bristles are different from vibrissae, however, in that they can be actively everted and used in a grasping fashion during feeding and manipulation of objects. The manatee is unique among marine mammals in its ability to use its vibrissae or bristles in a prehensile manner. There appears to be a one-to-one relationship between the number of perioral bristles and the number of neuronal clusters in the region of the cerebral cortex devoted to tactile sensation from the face (Marshall and Reep 1995, Reep et al. 1998).

Magnetic Detection

Water has almost no effect on magnetic flux density. Thus magnetic sensors should be equally effective underwater as in the air. Interest in animal use of the earth's magnetic field was stimulated by Keeton's (1971) finding that the orientation ability of homing pigeons could be disrupted by attaching magnetic coils to the heads of the birds on days when the sun was not visible. A number of studies stimulated by this finding gradually developed methodological and theoretical criteria that should be kept in mind when evaluating the possibility of biomagnetism in marine mammals. Magnetite is the material that has been consistently implicated in magnetic field reception in species easier to work with than marine mammals. Magnetite can be formed through biochemical processes within the body, but unfortunately ferromagnetic materials are also ubiquitous industrial pollutants, and great care must be exercised in determining the origin of any "magnetite" detected in an animal. One way of distinguishing functional magnetite from contamination is through considerations of the size and characteristics of magnetite needed to function as a magnetic detector.

Kirschvink and Walker (1985) argued that single-domain crystals are the most likely form of magnetite to be used in magnetosensation. A second consideration is the chemical composition of the magnetite. Magnetite with few oxides other than iron oxide is more likely derived from biochemical reactions within the animal, whereas magnetite with oxides of rare earth metals, such as titanium and manganese, is more likely of geologic origin (Walker et al. 1985). A third consideration is the consistency of location of magnetite in the same tissues of each specimen from the same species or higher taxa.

The magnetic material found in cetaceans most fully meets the third criterion. Magnetic material was found in the dura matter in the area of the falx cerebri and the tentorium cerebelli (Bauer et al. 1985) in three odontocete species, bottlenose dolphins, Dall's porpoise, Cuvier's beaked whale (*Ziphius cavirostris*), and one mysticete, the humpback whale. The dura is the tough outer membrane covering the brain. The falx cerebri is the region of the dura separating the cerebral hemispheres, and the tentorium cerebelli is the region of the dura separating the cerebrum and the cerebellum. These are the locations where magnetic material has been found in adult cetaceans. Any conclusions regarding the role of this magnetic material in magnetoreception must be tempered by noting that the amount of magnetic material in the dura appears to increase with age (Bauer et al. 1985). The falx cerebri and tentorium cerebelli are the areas of the dura that show increasing ossification with age (Nojima 1988), and magnetite is known to provide structural support by increasing the hardness of chitin in teeth (Kirschvink and Lowenstam 1979). Thus, magnetite in this region may be more related to the ossification of these tissues than to a magnetic sensory system.

The amount of magnetic material isolated from cetaceans to date has not been sufficient to confirm it as single domain magnetite or even to identify it conclusively as magnetite (Bauer et al. 1985). The magnetic material does not, however, appear to be contamination with the probable exception of the first report in *Tursiops* (Zoeger et al. 1981). It is difficult to dissect animals as large as cetaceans using non-magnetic tools and to carry out the dissection in a clean environment to avoid contamination.

Although the anatomical studies remain equivocal, there is correlational evidence that some cetaceans are using magnetic information to guide their movements. Klinowska (1985, 1986) compared locations in the United Kingdom where dead stranded cetaceans were found and where live strandings took place. She found that all cases of live strandings took place at points where local lows, or valleys, in the magnetic fields intersected the coast or islands. There was no

such correlation between strandings of dead cetaceans, which had presumably been washed ashore by currents, and the magnetic field orientation. Because of reversals of the magnetic field over geological time and the spreading of the ocean sea floor, there are alternating bands of magnetic orientation running north to south parallel to the mid-ocean rift where the sea floor spreading originates (Vine 1966). If whales were able to sense these alternations in the magnetic field, they could use these patterns as north-south highways on their annual north-south migrations. An indicator of magnetic field dip would provide information on position along the north-south axis, and if they could keep track of how many reversals they crossed, they could use this information for east-west positioning (Kirschvink and Walker 1985).

Kirschvink and colleagues (Kirschvink et al. 1986, Kirschvink 1990) have extended and confirmed Klinowska's (1985, 1986) United Kingdom study to the United States. The following species were significantly more likely to strand at sites where geomagnetic lows intersected the coastline: long-finned pilot whale (*Globicephala melana*), short-finned pilot whale (*G. macrorhynchus*), striped dolphin, Atlantic spotted dolphin (*Stenella frontalis*), Atlantic white-sided dolphin (*Lagenorhynchus acutus*), common dolphin, harbor seal, sperm whale, pygmy sperm whale (*Kogia breviceps*), and fin whale.

In contrast to the results of Klinowska and Kirschvink, Brabyn and Frew (1994) found no correlation between magnetic field orientation, minima, or gradients and the locations of live strandings in New Zealand. A possible explanation for the different results is the absence of a consistent orientation of the magnetic contours around New Zealand compared to the sea floor of the North Atlantic off the east coast of the United States and around the United Kingdom.

Attempts to demonstrate sensitivity to magnetic fields in laboratory experiments have been unsuccessful with cetaceans (Bauer et al. 1985). This result is not surprising when compared to studies with more tractable laboratory animals. A key feature of successful experiments is the freedom of the animals to move extensively within the altered magnetic fields. Under these conditions, which are difficult to duplicate for marine mammals, laboratory demonstrations of magnetoreception have been successful in salamanders (Phillips and Adler 1978), honeybees (Walker et al. 1989), and tuna (Walker 1984).

Walker et al. (1992) looked at free-swimming fin whales and found that migrating animals were associated with lows in the geomagnetic gradient or intensity. Because of the great difficulty in obtaining substantial numbers of pure anatomical specimens and in conducting laboratory ex-

periments demonstrating magnetoreception, correlational studies rather than definitive studies will continue to be the norm.

Summary

Marine mammals are acoustically diverse, with wide variations not only in ear anatomy, but also in frequency range and amplitude sensitivity. In general their hearing is as acute as that of land mammals, and they have wider ranges. Although marine mammals exhibit habitat- and size-related hearing trends that parallel those of land mammals in that larger species tend to have lower frequency ranges than smaller species, the majority of species have some ultrasonic capability and there are multiple specialized, auditory adaptations in odontocetes that provide large species exceptional high frequency hearing capabilities. Both mysticetes and odontocetes appear to have soft-tissue channels for sound conduction to the ear. Sirenians may have analogous adaptations. It remains unclear whether pinnipeds use soft-tissue channels in addition to the air-filled external canal for sound reception. Comparisons of the hearing characteristics of otarids and phocids suggest that there are at least two types of pinniped ears, with phocids being better adapted for underwater hearing. Sea otter ears are the most similar to those of land mammals of all marine mammal ears that have been investigated, but they do have some aquatic-related features, and it is not known how well they hear underwater. No data are available on polar bear hearing.

All marine mammals have middle ears that are heavily modified structurally from those in terrestrial mammals in ways that reduce the probability of barotrauma. The end product is an acoustically sensitive ear that is simultaneously adapted to sustain moderately rapid and extreme pressure changes, and which appears capable of accommodating acoustic power relationships several magnitudes greater than in air. It is possible that these special adaptations may coincidentally provide acoustically protective mechanisms that lessen the risk of injury from high intensity noise, but no behavioral or psychometric studies are yet available that directly address this issue.

Visual adaptations parallel the extent to which marine mammals have returned to the marine environment. Although light is extinguished more quickly in water than in air, there is sufficient light that vision is an important sensory modality for marine mammals at almost all depths they inhabit. The lens in the eyes of cetaceans has become more like a fish lens to accommodate for the loss of focusing power of the air-cornea interface. Sirenians, despite of their long history as a fully marine species, have not made as many adaptations to achieve acute underwater vision as have cetaceans.

Just as in audition, pinnipeds have compromised full underwater adaptation to allow for functional vision in air as well. One result of these compromises is that although pinnipeds can see well in air in bright light, acuity decreases with declining light levels. The polar bear has a basically terrestrial eye. The sea otter has developed a unique accommodation mechanism to provide good visual acuity in air and underwater. All marine mammals carefully studied have both rod and cone retinas, but few studies have ascertained if they can detect colors. The most likely reasons for the multiple pigment systems is to be able to maximize sensitivity and detection over a wide range of depths and light levels.

Olfaction has declined as adaptation to a marine environment has increased, and is apparently nonexistent in cetaceans, rudimentary in sirenians, and still an important modality, particularly for behavioral interactions, in pinnipeds. The little work that has been done in taste sensation indicates that most tested species can detect the various categories of tastes defined by humans. Gustatory tests are difficult to conduct and quantify for species living in water. Also, it is difficult to define ecologically relevant gustatory discriminations for marine mammals.

Cetaceans have greatest tactile sensitivity near the blow-hole where detection of the air-water interface is important. Tactile sensitivity over the trunk of the body appears to be sufficient to provide the sensory input needed to actively damp turbulence, but how the afferent and efferent pathways link and are used to achieve this goal remains an open question. The vibrissae of pinnipeds are extensively developed, richly innervated, and as well-represented cortically as are the hands of some primates. They provide the animal with information about contour and texture, but seem to be less adapted for the transmission of phasic information such as speed sensing.

Magnetic sensation has been investigated primarily in cetaceans. There is evidence that the movements of several cetacean species correlate with geomagnetic patterns. Evidence of a mechanism for detection of geomagnetism is very weak. Magnetite has been identified in the brains of several species, in the same regions of the dura matter, but the increase in concentration with age, which parallels the ossification of these structures, raises questions as to the function of magnetite in these areas. It is likely that most progress on working out the exact mechanisms of magnetic sensation will likely take place in species more tractable than marine mammals.

One irony of sensory system research is that the more tools we invent to explore animals and their senses the greater the hints we receive that our reach is still too short. How extensive is our research arm currently? We know marine mammals use frequencies we cannot hear, but techno-

logically we can detect and transduce their frequency range into something we can analyze. Tools that help us probe and visualize how marine mammal sounds are produced and processed, like fast biomedical imaging, are helpful but still comparatively limited. All marine mammals carefully studied are sensitive to about the same range of visual wavelengths as humans. Consequently, vision studies can be conducted more straightforwardly on marine mammals because there is no need to transduce the frequencies they see into ones we see. Chemosensation may be reduced in marine mammals, but we should also consider that we may simply not yet have asked the proper questions or developed adequate tools to measure responses in terms we understand. The anatomical sophistication and the extensive cortical space allotted to vibrissal sensory processing implies a more important role than we have yet determined. Our greatest shortcoming is that we cannot yet measure or observe reliably and frequently in the truly relevant environment for marine mammals: at depth in a free-ranging animal. Until we do, we cannot truly understand what is happening in any marine mammal's ear, eye, or brain, and what transpires in the real world of most marine mammals, the open ocean and the deeps, will remain a mystery.

Notes

1. The conventional unit of frequency, the Hertz, abbreviated Hz, is named after a nineteenth century German physicist and is equal to 1 cycle/sec, or 1 cps. kHz is an abbreviation for kiloHertz, or 1000 cps.
2. All physical constants were obtained from the CRC Handbook of Chemistry and Physics, 66th edition (Weast 1985) unless otherwise noted.
3. Like sonic, the airborne sound reference pressure is based on a human metric. The lowest sound level the normal human ear detects at 2 kHz is a diffuse field pressure of 20 μ Pa, which has an acoustic power density of approximately 1 picowatt/m². Therefore, the common human threshold in air for 2 kHz, which is at or near the most sensitive frequency in a normal human ear, is $20 \log(20 \mu\text{Pa} / 20 \mu\text{Pa}) = 20 \log 1 = 0 \text{ dB re } 20 \mu\text{Pa}$, or 0 dB SPL. In some older literature, dB SPL is used when decibel values reported were based on ambient pressure as reference, which is generally stated in the text.
4. An octave is a doubling of frequency. For any initial frequency (f), the octave range is $2f$, but because the scale is nonlinear, the center frequency is $f \cdot 2^{1/2}$. Because octaves are self-referential, two animals may have radically different hearing ranges in terms of frequency, but equal octave spans (e.g., 30–15,000 Hz vs. 100–50,000 Hz; nine octaves in each case).
5. Typical values for human critical ratios (CR) at speech frequencies are 10 to 18 dB.

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