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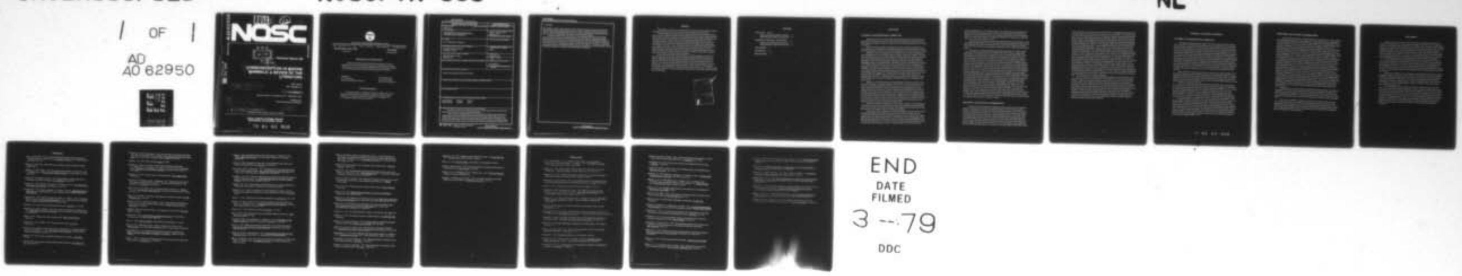

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CHEMORECEPTION IN MARINE MAMMALS: A REVIEW OF THE LITERATURE

WR Lowell
WF Flanigan, Jr

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Biosciences Department

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The presence or absence of a chemoreceptive capacity in marine mammals has drawn relatively little attention from the research community outside the Soviet Union.

Toothed whales are typically labeled anosmic (lacking a sense of smell), since they do not have the peripheral olfactory structures typically associated with terrestrial mammals. Baleen whales are known to possess reduced olfactory tracts; their olfactory bulbs also may be reduced or absent. Although the neural structures that mediate taste in terrestrial mammals have been reported to be present in both groups of whales, cetaceans have been considered to have a poor sense of taste because typical mammalian taste receptors have

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Little work has been done by either Western or Soviet researchers with regard to chemoreception among the other orders of marine mammals (Pinnipedia, Carnivora, and Sirenia). Pinnipedia are typically labeled microsmatic (having a poor sense of smell); research has been restricted to histological examination of the nasal pathways and neural anatomy. Sea otters are credited with a keen sense of smell, but no quantitative work has been reported. The chemosensory abilities of Sirenia remain unknown. The tongues of noncetacean marine mammals have been histologically examined and found to resemble those of terrestrial mammals. No other investigations of gustation in noncetacean marine mammals have been reported.

SUMMARY

The presence or absence of a chemoreceptive capacity in marine mammals has drawn relatively little attention from the research community outside the Soviet Union.

Toothed whales are typically labeled anosmic (lacking a sense of smell), since they do not have the peripheral olfactory structures typically associated with terrestrial mammals. Baleen whales are known to possess reduced olfactory tracts; their olfactory bulbs also may be reduced or absent. Although the neural structures that mediate taste in terrestrial mammals have been reported to be present in both groups of whales, cetaceans have been considered to have a poor sense of taste because typical mammalian taste receptors have been thought to be absent. Soviet researchers, however, recently have reported that gustatory receptors are present on some cetacean tongues and that the tongue of *Tursiops truncatus* appears to be well innervated. They have been conducting investigations which seem to be aimed at describing a specialized gustatory capability in cetaceans. No experimental work has been reported by Western scientists.

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CONTENTS

CETACEANS

ANATOMICAL AND PHYSIOLOGICAL CORRELATES

Although the brains of modern whales show a high degree of cerebral development, particularly in the auditory centers, they have reduced or absent olfactory structures. It is likely that these attributes are part of a complex system of specialized adaptation to a marine environment.

Areas of the telencephalon or forebrain known to have olfactory functions in terrestrial mammals are also present in both toothed and baleen whales. Comprehensive descriptions of the anatomy of these centers are given by Filimonov (1965) and Jacobs et al. (1971).

Migration of the nares during cetacean evolution from the anterior location seen in most mammals (as well as in the extinct cetacean suborder Archaeoceti (Edinger, 1955)) has been accompanied by several functional changes. Generally, olfactory receptors and innervations of the nasal system have been lost or reduced as compared to terrestrial mammals (Breathnach, 1960). Adult toothed whales typically lack the bulb and tract elements of a mammalian olfactory system (Breathnach, 1960; Pilleri and Gihr, 1970; Morgane and Jacobs, 1972). Sinclair (1966) has described both olfactory bulbs and tracts in fetal *Stenella*, but they appear to atrophy at an early stage of development and are not seen in adults (Kamiya and Pirlot, 1974). The olfactory bulbs and tracts of adult baleen whales are reduced, but more closely resemble the olfactory apparatuses seen in terrestrial mammals than do those of toothed whales (Jacobs et al., 1971). Intermediate between the usual toothed cetacean condition and that seen in baleen whales are three types of toothed whales: *Hyperoodon, Delphinapterus*, and *Physeter*. These genera have been reported to show rudiments of both olfactory bulbs and tracts (Jansen and Jansen, 1969; Pilleri and Gihr, 1970; Morgane and Jacobs, 1972).

Maderson's (1968) investigation of the nasal passages of *Tursiops* produced no evidence for the presence of olfactory epithelia. Sinclair (1951), however, describes a possible olfactory nerve plexus embedded in the dura in the area above the cribiform bone of a single *Tursiops* adult. Whether a connection exists between this ganglion and the brain or sensory receptors is not known for adults, but Sinclair reports tracing afferent branches to the region of the muscosa of the blowhole in a fetus. Remnants of the nasopalatine canals of the fin whale (*Balaenoptera physalus*) have been examined, but neither chemoreceptors nor vomeronasal organs have been reported (Quay and Mitchell, 1971). Kellogg (1928) describes the olfactory organs of baleen whales as pouches which hang from the dorsal walls of the narial passages. Innervation of these structures is provided by the distribution of the olfactory nerves to the mucous membranes of the pouches.

The neural anatomy of the gustatory or taste system is relatively unstudied (Kruger, 1966). However, the structure of certain cranial nerves and the highly developed gustatory nuclei of the thalamus in the midbrain (Kruger, 1959) suggest that this system is functional and may play a role similar to that seen in terrestrial mammals.

Anatomical receptors for gustation in terrestrial mammals typically take the form of characteristic papillae on the tongue and taste buds in the pits of its surface. Western researchers have reported that the sense of taste is poor in cetaceans and that typical mammalian receptors are absent (Arvy and Pilleri, 1970; Bradley, 1971; Yamasaki et al., 1976). Some Soviet researchers have reported the absence of typical mammalian papillae and taste buds (Sokolov and Volkova, 1971; Shvyrev, 1976), but there also have been reports that the relatively large surface depressions found on cetacean tongues are lined with a sensory epithelium (Sukhovskaya, 1972; Yablokov et al., 1972). Furthermore, this epithelium has been described as histologically similar to that of terrestrial mammals. Sukhovskaya and Belkovich (1973) have reported finding "taste papillae, similar to those of other mammals" and have noted that these papillae "are situated in small pits in the tongue root." They also report that "typical taste buds were found."

Innervation of the tongue of *Tursiops* is described by Gilevich and Khomenko (1976) and Valiulina and Khomenko (1976) as consisting of two nervous plexuses, one deep and the other superficial. The latter authors describe "vast receptor fields" situated on the superficial plexus. These receptors are described as being both free nerve endings and encapsulated bodies.

The presence of typical mammalian telencephalic organization in toothed whales, coupled with their apparent lack of more peripheral olfactory structures, suggests these speculations: (1) peripheral olfactory structures do exist, but remain undescribed; (2) the telencephalic olfactory centers have assumed a nonchemosensory function; or (3) these centers maintain a chemosensory function, but are innervated by peripheral structures unlike those which are known to serve as olfactory receptors in terrestrial mammals. With regard to the first speculation, it should be noted that the likelihood of omitting peripheral structures when dissecting a large cetacean brain has been recognized by numerous workers (Edinger, 1955; Breathnach, 1960). Tissues are often poorly preserved or partially missing prior to dissection, thereby increasing the probability of misinterpretation. Other anatomists, however, feel that these structures are definitely lacking (Jacobs et al., 1971; S. H. Ridgway, personal communication). The second speculation has been addressed by several authors, who give detailed information regarding nonolfactory functioning of telecephalic formations in toothed whales (Pribram and Kruger, 1954; Filimonov, 1965; and Jacobs et al., 1971). In conjunction with the third speculation, it is known that gustatory impulses are mediated in terrestrial mammals by the trigeminal, facial, glossopharyngeal, and hypoglossal cranial nerves (Breathnach, 1960; Jansen and Jansen, 1969; Morgane and Jacobs, 1972). These tracts are well developed in cetaceans, with the trigeminal being the largest in terms of quantity of fibers for both toothed and baleen whales (Jacobs et al., 1971). Free nerve endings from the trigeminal may provide terrestrial mammals with olfactory information (Moulton, 1967). The possibility that this cranial nerve might play an important chemoreceptive role in marine mammals is addressed in detail by Jacobs et al. (1971). These authors speculate that trigeminal inputs might synapse with the telencephalic chemosensory centers, i.e., that the olfactory tubercles may serve as portals for trigeminal inputs, and thereby impart chemosensory information of a nonolfactory origin .

BEHAVIORAL AND ECOLOGICAL CONSIDERATIONS

Numerous behavioral observations suggesting a chemoreceptive sensory capability in cetaceans are found in both the Western and Soviet literature. Food preferences and the refusal of "undesirable" food items are frequently mentioned (Bowers, 1973; Caldwell and Caldwell, 1972; Sokolov and Kuznetsov, 1971). Recent interviews with feeders and trainers at the NOSC Marine Sciences Laboratory support published accounts. For example, when an unfamiliar fish was placed in their tank, captive porpoises often closely approached the fish before showing a lack of interest in the item as food. Frequent descriptions were also given of animals mouthing food but subsequently rejecting "unfavored" items. While these episodes suggest that chemoreception could play a role in food selection, it is possible that tactile sensation and echolocation also may have been involved. Baleen whales feed in waters which often have a characteristic odor, and some workers have suggested that these animals may use chemosensory capacities to sense the presence of food (Purves, 1967; Yablokov et al., 1972). After observing the behavior of six species of toothed cetaceans (*Delphinapterus leucas, Physeter catodon, Phocaena phocaena, Berardius, Ziphius,* and *Orcina orca*) and six species of baleen whales (*Balaenoptera musculus, B. physalus, B. borealis, B. acutorostrata, Eschrictius gibbosus,* and *Megaptera nodosa*) during whaling operations, Kleynenberg et al. (1964) hypothesized the existence of a "special organ capable of sensing chemical stimulation of the surrounding medium." Evans and Bastian (1969) discussed the possibility that chemosensory information may be used as a cue to detect the previous presence of other cetaceans. Yablokov et al. (1972) reported that belugas "panic" when entering areas of water which contain traces of conspecific blood. These authors also described the following incident. A herd of belugas when approached by hunters appeared to be frightened and fled to the open sea. A subsequent herd approached the same area, and upon reaching the spot where the previous herd turned back, they exhibited the same behavior. Fish, as well as aquatic amphibians and reptiles, have been reported to display a "fright" or "alarm" response when placed in containers which previously held frightened or injured members of their species (Bardach and Villars, 1974; Burghardt, 1970). Perhaps a similar response occurs in belugas. Kuznetsov (1974) described "perianal glands" in male toothed whales, with ducts emptying directly into the water. These ducts may provide a chemical cue for conspecific chemosignaling. A "strange, penetrating smell" has been reported for the Indus river dolphin, *Platanista*, and appeared to be periodic (Pilleri et al., 1976). This scent might conceivably be a cnemical signal. Frequent urination in toothed whales has also been described (Yablovkov et al., 1972) and this may be a means of signaling.

The only reports of controlled behavioral investigations of chemoreception in cetaceans have been a series of Soviet studies. In one experiment, the oral cavities of *Tursiops truncatus*, which were trained to hold their mouths open out of water, were bathed with various solutions. The animals were trained to push a manipuladum if the solution was a chemical or to swim to a feeding station if the solution was saltwater. Results indicated that the animals could discriminate between the control water and the chemical cues and that different response times were elicited by different chemicals (Sokolov and Kuznetsov, 1971; Kuznetsov, 1974). In another experiment, galvanic skin responses were investigated in restrained dolphins (*Delphinus delphis*) and porpoises (*Phocaena phocaena*), while the oral cavities of these animals were perfused with a stream of saltwater into which various concentrations of test chemicals were injected. Results indicated that chemical substances elicited unconditioned galvanic skin responses.

PINNIPEDIA, CARNIVORA, AND SIRENIA

ANATOMICAL AND PHYSIOLOGICAL CORRELATES

The apparent highly specialized nature of the cetacean brain has attracted a great deal of attention, but the relatively unspecialized gross neural anatomy of the remaining orders of marine mammals has elicited only cursory interest. While evolving many adaptations which allow exploitation of marine environments, seals, sea lions, walruses, sea otters, manatees, and dugongs all spend variable amounts of time on land (Nishiwaki, 1972) and retain certain characteristics in common with terrestrial mammals. Pinniped neuroanatomy has been reviewed by Harrison and Kooyman (1968). They conclude that, although basically similar to those of terrestrial carnivores, the brains of pinnipeds are more spherical, the cerebrum more convoluted, and the olfactory areas somewhat reduced. Scheffer (1958) and King (1964) conclude that the sense of smell is poor in pinnipeds. Kuzin and Sobolevsky (1976) have described the olfactory epithelium of the fur seal as typically mammalian. They conclude that olfaction is "well developed in the fur seal" and that "it plays an exceptionally important part in the fur seal's life." Experimental investigation of pinniped olfactory sensitivity (that might or might not support any of the above conclusions) has not been reported.

King (1964) has reported that taste buds are reduced in pinnipeds. Bradley (1971) described the tongues of various otariids and phocids as variably possessing the four typical mammalian papillae. He also noted that the chief gustatory structures are the circumvallate papillae, except in the sea lion. Kubota (1968) has described the tongue of the fur seal as apparently showing typical mammalian characteristics, except that foliate papillae are absent and the number of taste buds is reduced.

Sea otters are less well known anatomically than pinnipeds. Their neuroanatomy, however, has been recently described and compared with the neuroanatomy of what might be considered their terrestrial counterpart, the marten (England and Dillon, 1972). As in all the aquatic mammals discussed here, the cerebral development of the sea otter shows increased fissuring and complexity when compared to its terrestrial relative. Also, the olfactory bulbs are reduced in size. However, Kenyon (1969) has described the olfactory sense in sea otters as being more important than vision as a warning system. The tongue of sea otters has been reported to resemble that of other mustelid carnivores (Bradley, 1971).

Little information is available on the central nervous system or sensory receptors of sirenians (Murie, 1874). Friant (1954) has described the brain of the manatee as being similar to that of terrestrial mammals such as the ox. The telencephalon, however, is much more developed than that of cetaceans, and olfactory bulbs and tracts are present. Hartman (1969) has assumed the sense of smell to be rudimentary, if not altogether absent. The inner surface of the lips contains large papillae. These apparently act as a mechanical aid during feeding (D. Magor, personal communication), but have not been examined with respect to sensory function. Sirenian tongues have been reported to have circumvallate (manatee) or foliate (dugong) papillae (Bradley, 1971).

BEHAVIORAL AND ECOLOGICAL CONSIDERATIONS

Experimental investigations of chemoreception in pinnipedia have not been reported, but numerous incidental observations suggest that chemoreception may be well developed. Evans and Bastian (1969) have reported that many handlers express a "high regard" for the olfactory sensitivity of this group. Trainers recently interviewed at NOSC in San Diego were generally in agreement with the opinions cited by Evans and Bastian. Peterson and Bartholomew (1967) have speculated that mother-pup recognition in *Zalophus californianus* could be mediated by olfaction. Valdimirov (1975) has reached a similar conclusion with respect to the fur seal, as have Ono (1972) for the stellar sea lion and Kaufman et al. (1975) for the Weddell seal. The strong scent of pinniped males has been described (Hamilton, 1956; Peterson and Bartholomew, 1967), and may function as a directional signal for females or in marking territories. There are numerous reports of the necessity of a downwind approach to pinnipeds to avoid alarming them in the field. Peterson and Bartholomew (1967) have described California sea lions avoiding a stagnant pool of water, formerly used by them for wetting on warm days, after the carcass of a dead pup fell into the pool. A succession of adults approached the pool as if to enter, but moved away after apparently sniffing at the carcass. Muzzle-to-muzzle contact and nuzzling have been often described for all families of pinnipeds. Evans and Bastian (1969) and Ross (1972) have stressed the importance of olfactory communication during these encounters. Kaufman et al. (1975) have reported underwater female-pup nose-to-nose contact. Underwater recognition of pups may be aided by this behavior, as mothers can identify pups other than their own and react aggressively to strangers even below the surface. While they offer no evidence to support their claim, Kuzin and Sobolevsky (1976) have concluded that olfaction plays a part in fur seal orientation and navigation to breeding grounds. Kinne (1975) has offered a similar hypothesis. Sergeant (1970) pointed out that young harp seals orient into the wind during their solitary northward migrations. It seems possible that these animals might maintain this orientation by olfactory means.

Observations of sea otters by Kenyon (1969) indicated that animals in the wild must be approached so that the wind-carried presence of man is not signaled. This author also describes how otters when given a variety of food items will lick each item and then return to eat the preferred food. When encountering one another in the water, sea otters have been reported to often sniff genitalia in much the same fashion as terrestrial carnivores (Loughlin, 1977).

The sensory capabilities of sirenians are poorly known. Moore (1956) noted that nose-to-nose contact may involve olfaction and that much nose-to-body contact occurs among these aquatic mammals. It has recently been determined that manatees favor certain food plants over others and that they are able to select their preferred items from an assortment of vegetation (D. Magor, personal communication). It is possible, however, that this selection is mediated by tactile receptors.

CONCLUSIONS

Historically, it is not unusual for the earlier work and conclusions of anatomists, particularly neuroanatomists, to have significant influence on the later work of those interested in the psychophysiology and behavior of an organism. This has been the case for marine mammals. In comparison to terrestrial mammals, cetacean brains are large in relation to body weight. The auditory centers are usually well developed and the olfactory areas greatly reduced. Peripherally, chemosensory receptors that are anatomically similar to those of terrestrial mammals may be reduced or absent. It is not surprising, therefore, to find that most psychophysiological research on cetaceans has been directed toward hearing and sound production. Chemoreception has been virtually ignored, at least by Western investigators.

Early examinations by neuroanatomists of the brains of pinnipeds, sea otters, and sirenians revealed that gross structures (with the exception of the olfactory areas which are reduced) were similar to those in brains of their terrestrial relatives. It would appear that these similarities satisfied the curiosity of many anatomists and psychophysiologists, for most of their work has been on terrestrial mammals. No studies of pinniped chemoreception are known or have published studies appeared dealing with the sensory abilities of sea otters and sirenians.

Functional conclusions, such as assessments of sensory ability based on the study of comparative anatomical structures, can be erroneous. For example, on the basis of anatomical findings it was long thought that birds possessed a relatively poor sense of smell (Bang and Cobb, 1968; Welty, 1975). However, recent behavioral investigations have demonstrated that many birds are highly sensitive to olfactory stimulation (cf., Wenzel and Sieck, 1972). There is also evidence suggesting that olfactory navigation occurs in the homing pigeon (Benvenuti et al., 1977).

It is possible that marine mammals may be able to smell and/or taste. The large amount of circumstantial evidence provided by observers of marine mammal behavior and the experimental results reported by Kuznetsov (1974) suggest that perception of chemical cues from the environment may play a more important role in the behavior of these animals than the anatomical evidence indicates. Soviet investigations suggest that cetacean chemoreception is probably gustatory in nature, i.e., they taste rather than smell. Be that as it may, only Soviet investigators have attempted behavioral studies of chemoreception in marine mammals, and they have confined their attention to cetaceans. Whether any species of marine mammal possesses chemoreception remains to be objectively demonstrated or confirmed.

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