Veterinary Research Communications, 10 (1986) 245—268
Elsevier Science Publishers B.V., Amsterdam — Printed in The Netherlands

Review

THE ROLE OF VIBRISSAE IN BEHAVIOR: A STATUS REVIEW

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(Accepted 25 November 1985)

ABSTRACT

Ahl, A.S., 1986. The role of vibrissae in behavior: a status review. Vet. Res. Commun. 10: 245-268.

Vibrissae or tactile hairs are an important part of the tactile sensory apparatus of many mammals. A wide range of suggested functions found in the literature include food acquisition, prey attack, aggression and attack behavior, facial expression in intraspecies communications, dispersion of pheromones, maintaining head position in swimming, and a wide range of environmental monitoring (e.g., current detection in water, wind direction on land). There is little work done specifically on domestic animals or their feral relatives. Work on the tactile senses in general and vibrissae in particular is an open field of study. A set of general questions for study of vibrissa function in domestic animals is presented.

INTRODUCTION

One of the more striking facial features of mammals is the presence of vibrissae or whiskers or tactile hairs (term preferred by the Nomina Anatomica Veterinaria, 1983). In fact vibrissae (term preferred by most authors) are found in almost all mammals except Homo sapiens; some other mammals may lack external vibrissae as adults but develop them pre-natally only to lose them before birth (Cave, 1969). The term vibrissa comes from the Latin "vibrio," meaning to vibrate, an appropriate name for these facial hairs, for at least in some rodents, they vibrate with exquisite regularity and consistency. The universality of vibrissae and the marvelous variety and array in which they appear suggest that they are important in the life of the animal (Pocock, 1914). Studies on marsupials (Lyne, 1959) and on carpal vibrissae (Beddard, 1902) point to the great variation among species while that within species is low (Dun and Fraser, 1959). There have been numerous suggestions through the years that this variation has adaptive significance; the question is not whether vibrissae are important in animal behavior, but how they function and what behaviors are involved. A study of anatomy and physiology as well as direct observations on vibrissae are important aids in suggesting hypotheses regarding their function. The present review should familiarize the reader with the major aspects of vibrissal biology and their role in behavior.

0165-7380/86/$03.50

DESCRIPTION AND OCCURRENCE

Vibrissae as hairy outgrowths of the skin are a character unique to mammals, and are distinct from pelage hair in several major ways: (1) they are much longer than pelage hairs; (2) they may be localized to the facial region, though in many species they also occur on the forearm and/or the ventral body surface; (3) the follicles from which the vibrissae grow are extremely large and highly innervated compared to follicles of pelage hairs, (4) the vibrissae follicles possess blood-filled sinus tissues; (5) each vibrissae follicle is represented in the sensory cortex of the brain in a very precise way.

The vibrissae have been grouped and named in a variety of ways by different authors so that the terminology in the literature is not standardized. For example, some authors will include the rhinal vibrissae when discussing the mystacial ones while others do not. A persuasive case can be made for distinguishing among mystacial vibrissae on the basis of their embryological deviation and developmental patterns (Yamakado and Yohro, 1979). The nomenclature given in _Nomina Anatomica Veterinaria_ (1983) is not complete enough to describe the variations of vibrissae found in mammals. The classification suggested below is based on the location of vibrissae, either Facial or Body. The tactile hairs of the mystacium (the upper lip) are called primary vibrissae; all others whether on face or body are known as secondary vibrissae (Pocock, 1914; Lyne, 1959; Davidson and Hardy, 1952).

Facial Vibrissae

Mystacial: upper lips, usually arranged in well-defined rows. The top row (most dorsal) is labelled A, the next B, and so on to E as generally there are five rows present.

Rhinal: dorsum of muzzle, caudal to the rhinarium.

Submental: lower lip and chin; symmetry not generally apparent.

Interramal: one or more (may occur in a tuft) caudal to the mandibular symphysis; symmetry not generally apparent.

Superciliary (Supraorbital): tuft over each eye, usually above its medial part.

Subocular (Suborbital): beneath the eye.

Genal: one or two tufts in the area of the cheek. Upper genal are caudal to the eye, lower genal are caudal to the angle of the jaw.

Body Vibrissae

Ulnar-carpal: one or more on the palmar surface of the forearm near the wrist.

Medial antebrachial: forearm, usually halfway between wrist and elbow.
Anconeal: near the elbow.
Calcaneal: on the medial part of the ankle.
Venter: located on the ventral body surface.

Every mammal will not have vibrissae at all these locations but most all mammals except humans show evidence of vibrissae at some time in their life (pre- or post-natal) on some part of the body. Most research has been done on facial vibrissae with special interest in the mystacial ones, at least partly because of their importance as a model for neurophysiological study.

ANATOMY

The long whisker or vibrissa has its origin in a very large and quite specialized follicle which is 5-6 times larger than the follicle of a regular pelage hair (Andres and von During, 1973). Each follicle gives rise to only one protruding hair, never two or more as can be found in some pelage follicles. One or more sebaceous glands is also associated with each vibrissa. Muscles attached to pelage hairs are the arrector pili, smooth muscles under autonomic control. In contrast the follicles of vibrissae are attached to striated muscles under voluntary control, though smooth and striated muscles are associated with sinus follicles of the big-clawed shrew, _Sorex unguiculatus_ (Yohro, 1977). Studies of the attachment of these muscles show that they apparently vary from species to species. The mystacial sinus muscles in the white mouse are of two types: (1) extrinsic in which there is some attachment to the skeleton and (2) intrinsic in which origin and insertion are from sinus to sinus with no bony attachments (Dorfl, 1982). The types of muscle attachments shown in _Mus_ and _Sorex_ are rather different and support the notion that vibrissae may be used in quite different ways.

The structure of the vibrissal follicle is quite complex with an impressive nerve and blood supply. Each follicle is supplied with one or more blood filled sinuses enclosed by connective tissue with a variety of nerve receptor types associated with the sinuses. The nerve receptors associated with these sinuses are of several types, including Merkel receptors, Pacini-like corpuscles, straight lanceolate terminals, branched lanceolate endings, branched circular lanceolate receptors, and endings of unmyelinated nerve fibers (Andres and Van der Loos, 1966; Stephens et al., 1973; Gottschaldt et al., 1973). As the vibrissae is moved externally, the motion is transmitted to the turgid sinuses and thus passed to the receptors. Excellent diagrams of vibrissal follicles can be found in several references (Andres and von

During, 1973; Stephens, Beebe, and Poulter, 1973). The great variety of arrangements of these specific elements of these sinuses suggests specialization and adaptation to specific functions in the animal (Goldschmid-Lange, 1976). The common feature to all vibrissal follicles seems to be their large size, the presence of blood-filled sinuses, numerous nerve fibers, and striated muscles.

The afferent nerve fibers of mystacial vibrissae project through the trigeminal nerve to the contralateral vetrobasal thalamic nuclei in the brain stem (Gottschaldt and Young, 1977) and thence to the somatosensory cortex contralateral to the vibrissae themselves (Jeanmonod et al., 1977). Each mystacial vibrissa is represented by a separate "barreloid" in the brain stem nuclei and a "barrel" in the cortex. These barreloids and barrels are discrete anatomic units in all species studied so far; there is strong evidence that each vibrissae is represented by only one barreloid and one barrel thus giving a precise one to one mapping from the surface through the nervous system to the brain (Weller and Johnson, 1975; Jeanmonod et al., 1977). Though most vibrissal nerve output goes contralateral, there is some evidence that each vibrissae also has some ipsilateral fibers as well. The ipsilateral response shows a 4-5 millisec delay, suggesting that each hemisphere can compare information from the two mystacial pads (Pidoux and Verley, 1979). Much of the work on afferent fibers from the mystacial sinuses to the brain has been carried out in cats, laboratory rats, mice, and hamsters, but the patterns described so far are consistent for the different species. Precise neurophysiological mapping for vibrissae other than from the mystacium has not been done to my knowledge. This lack of knowledge about the secondary vibrissae suggests some interesting questions. Are these secondary vibrissae less important to the animal or is that assumption made because of the nomenclature or becuase those on the rest of the face and body are less dramatically visible?

In the laboratory rat, sensory and motor innervation of mystacial vibrissae seems to be completely separated in different cranial nerves, with the afferents traveling through the infraorbital-trigeminal route and the efferent innervation from the zygomatic branches of the facial nerve (Greene, 1963).

DEVELOPMENT

In the post-natal development of laboratory rats, the ears open 5 days after birth and the eyes 7 days later, but rat pups are born with vibrissae. Those on the mystacium average 1-2 mm. in length at birth and have been present since fetal day 14 (Park, 1970). In mice, all vibrissal follicles and their accompanying hairs all develop faster and earlier than for the general pelage (Davidson and Hardy, 1952). Such early development of a sensory structure suggests their use in tactile location of their food source postnatally and perhaps some prenatal function as well.

Growth studies on vibrissae of laboratory rats and mice show that vibrissae grow a constant amount each day. At the same time, vibrissae show a progressive and consistent increase in their cross-sectional area. Though growth rate is the same in the sexes, males have a slightly longer period of growth, and thus slightly longer vibrissae. Age is not a factor in vibrissal growth until the animal nears death at which time growth slows perceptibly. A plucked vibrissae is followed by the appearance of another from the same follicle 8-11 days later; the new whiskers which emerge following plucking grow at the same rate as before (Ibrahim and Wright, 1975).

There has been some argument about the occurrence of telogen (resting phase) in vibrissae, but work by Young and Oliver (1976) supports the presence of a very short telogen (few days) in vibrissal follicles while pelage follicles may be in telogen for weeks or months. At least in the rat, the blood sinus does not regress in telogen. Vibrissae are retained for a long time and probably are not shed in cycles like the pelage. In the brush-tailed opossum (Trichosurus vulpecula), the same vibrissae are retained for more than a year. All plucked vibrissae (even repeatedly) rapidly regenerate a new hair whether the follicle was in anagen (active growth stage) or telogen (Lyne et al., 1974). Again these observations on early development and rapid replacement of vibrissae suggest the importance of these mechano-transducers to the life of the animal.

The effect of adequate nutrition on pelage is well known, and one would expect to find such effects on vibrissae as well. In laboratory mice (C3H) food was withheld from adults for 3 days while their follicles were in anagen. Growth rate of the vibrissae was reduced after one day of food deprivation, but growth recovered to near normal 3 days after returning the mice to a full diet; however, these whiskers did not grow as long as for the normal controls (Ibrahim and Wright, 1975). Other nutritional studies seem to contradict these conclusions; newborn rats were exposed to a reduced food supply (18 pups per mother rather than the usual control group of 6 pups per mother). All facial vibrissae of the experimental group came in earlier than for the normal group (from 1 day early for the submental to 6 days early for the lower genal) and grew faster while the pelage of these nutritionally deficient pups grew in more slowly (Park, 1970). It was suggested that premature vibrissae development in malnourished newborn rats is the manifestation of an adaptive mechanism which facilitates the location of the food source. These results are most interesting but need to be repeated in rats and other species as well. Should these observations of malnutrition and premature vibrissal development be correct, they suggest that vibrissae are organs somewhat protected from environmental hazard, a fact which would provide strong support for the importance of vibrissae.

If mouse mothers are malnourished, there are specific changes in the cortical barrels of the offspring (Vongdokmai, 1980). A 2-day delay in the development of the barrels can be observed as well as a reduction in the area of the barrelfields and a reduction in the number of neurons. Vongdokmai suggested that poor nutrition has a profound (and implied direct) effect in the developing brain. However, other research suggests that the skin generates the vibrissal pattern and that this pattern is imposed from periphery to cortex in temporal sequence (Andres and Van der Loos, 1982). If this is true, it is hard to interpret what is a primary malnutrition effect on the cortex and one that primarily affects the vibrissae and secondarily the cortex. Nutrition does play an important role in development, but the precise effect of malnutrition on vibrissal development and growth in all stages from fetus to adult have not been studied in enough detail to clearly describe the effects. This presents an open field for research.

Viral infections (Friend, Moloney, Caa-Br-M, C25-M and 1504-A) in mice can lead to a decrease in the number of vibrissae, and a shortening and an irregular shape to those that do appear (Rowe, 1983). In addition, the vibrissal sinus can be a site of extra-medullary hematopoiesis, though this did not appear to be the basis for the deformities in the hair and sinus.

Though the vibrissae are present and visible at birth on most mammals, extensive studies in the laboratory mouse indicate that the entire tactile system from periphery to brain does not mature until at least 4-5 days after birth. The original studies (Woolsey and Van der Loos, 1970) described structures in the somatosensory cortex, given the name barrels because of their shape. These barrels correspond, one to one, to the vibrissal follicles on the contralateral side of the mystacium. If the vibrissal follicles are injured right after birth, these barrels fail to develop in the brain (Van der Loos and Woolsey, 1973). Further studies (Woolsey and Wann, 1976) showed that damage to the vibrissal follicle up to day 6 after birth results in changes from normal in the cortical barrel. In similar studies cortical deficits were found up to day 4 (post-natal), but not in day 5 mice of two different species, Mus musculus and Peromyscus leucopus (Weller and Johnson, 1975). Woolsey and Van der Loos (1970) were using M. musculus in their work as well, but the lack of temporal correspondence can possibly be explained in several ways. First there are strain differences in developmental age of Mus that could account for the differences observed. Second, the vibrissae of the mystacium are derived embryologically from 3 different growth centers of facial primordium and these each differ in timing of their development (Yamakado and Yohro, 1979). The major point is, however, that intact vibrissae for at least four days after birth are necessary for normal somatosensory cortex development in the laboratory mouse. The afferent fibers from the vibrissal follicles synapse in the trigeminal nucleus and again in the ventrobasal thalamic nuclei on the way to the somatosensory cortex of the brain.

Are the observations on laboratory rats and mice universal? That is, are barrels found in the somatosensory cortex of other mammals that possess vibrissae. Recognizing the conservatism of nature in repeating successful patterns, one would expect to find similar structures from periphery to cortex, in primitive mammals as well as the more advanced ones. There is some more direct evidence that such a contention is correct, for barrels have been described in the somatosensory neocortex of the brush-tailed opossum, an active and agile arboreal marsupial with large, well-developed vibrissae (Nowak and Paradiso, 1983). Other work with domestic cats follows afferent impulses from the periphery to the cortex, and the pattern is similar in cats and rodents (Gottschaldt and Young, 1977).

One of the interesting concerns which arose as a result of this work was the question of what mechanisms underlie these brain maps of the periphery. Are they brain induced, skin induced, or some subtle interaction of the two? Since the follicle pattern of vibrissae in mice is laid down 7 days before birth and that of the barrels several days after birth, it seems reasonable to suggest that the pattern develops in the skin first. Other work confirms that the skin alone can generate the vibrissae map from the periphery back to the cortex (Van der Loos and Dorfl, 1978; Andres and Van der Loos, 1982). The pattern appears in temporal sequence just as a nerve impulse would follow from vibrissal stimulation: follicle to trigeminal nucleus to ventrobasal complex to barrels of the somatosensory cortex. No other sensory system of rats or mice is known to exhibit the discreteness of this vibrissa to barrel path (Van der Loos and Dorfl, 1978). Again, the neuro-physiological uniqueness of the vibrissal system suggests its importance in the life of mammals.

PHYSIOLOGY

Virtually all neurophysiological work on vibrissae has been done on the mystacial vibrissae in laboratory rats, or cats. The laboratory rat has especially long vibrissae which spray out from the rostrum in a star-like pattern, and are repeatedly whisked over the surface around the snout in a regular pattern. The classic studies of Vincent (1912) attest to the importance to the rat of this tactile sense, for when adult rats were deprived of their whiskers it was more difficult to learn a maze than when deprived of vision, hearing, or olfaction. The exquisite sensitivity of vibrissae in rats is suggested by the variety of changes in mechanical stimulation which a single vibrissa can encode. Recording from the trigeminal ganglia, the stimulation of a single vibrissa can give information about peripheral location of the stimulus, direction of deflection, time of onset and termination of stimulation, the amplitude, and velocity (Zucker and Welker, 1969). In addition temporal patterns of stimulation can be distinguished including duration and rate of repetition of the stimulus, and can distinguish between stimulus to the entire mystacium as compared to that given a single vibrissa. That the vibrissae can so well discriminate among the array of mechanical stimuli is perhaps less surprising when considering that afferents from the vibrissae are the most represented structure in the trigeminal ganglia (Kruger and Michel, 1962; Nord, 1967). There are a variety of receptor types in the sinus (Andres and von During, 1973), as well as a variety of afferent fiber types. The cat has two slow adapting afferent units as well as high and low velocity threshold rapid adapting units; each mystacial vibrissae is probably endowed with all types (Gottschaldt, Iggo and Young, 1973). These studies have been extended to cats and seals (both the gray and harbor species), finding that differences between the species were minor (Dykes, 1975). An excellent review of neurophysiological studies of mystacial vibrissae in the laboratory rat has been done by Gustafson and Felbain-Keramidas (1977).

GENETICS

Vibrissae in mice have been recognized as very conservative characteristics, that is, there is almost no variation in the numbers of vibrissae in wild populations (Dun and Fraser, 1959; Pennycuik and Rendel, 1977). However, with the introduction of the sex-linked semi-dominant gene Tabby (Ta); the number of secondary vibrissae not only decreases but also becomes more variable (Kindred, 1963). Other mutations are also known to affect mouse vibrissae, including the glabrous mutant, a recessive which results in crooked vibrissae and the suppression of primary hair growth; the nude mutant is similar except that they lack vibrissae at birth (Tsuji and Matsushita, 1972). In the ICR stock of albino mice, a mutant is known which increases the number of mystacial vibrissae; interestingly, the cortical barrelfield in these mice is correspondingly larger (Welker and Van der Loos, 1983). In nude mice, the vibrissae project to atypical regions of the brain. In mottled mice the vibrissal projection to the contralateral cortex is reportedly similar to that of normal mice, but there is no ipsilateral projection of fibers (Verley and Pidoux, 1981).

Mutations in vibrissae number are known in other species as well. A recessive mutant in rats has been induced by X-radiation in which the mutants show either no vibrissae or a few abnormally short ones; the mutation has been called, appropriately, vibrissaeless. In a closed colony of Hartley guinea pigs, a hairless mutant with wrinkled skin and shorter than normal vibrissae was reported (Reed and O'Donoghue, 1979). A gerbil mutant was reported that is born with a bald appearance and abnormally short vibrissae because they are easily broken (Swanson, 1980).

These mutants and others surely to be described in the future are an important resource for research and will undoubtedly reveal more about the role of vibrissae in behavior, interaction of genes and environment in the control of brain development; behavioral studies on these mutants could also be most useful in helping understand the relationships of brain and behavior.

BEHAVIOR

The literature of vibrissae and behavior makes fascinating reading; the greatest concentration of work on vibrissae and behavior has concerned aggression especially in rats, mice, and to a lesser extent, cats. The remaining articles on behavior cover such a broad range that few real conclusions can be drawn except that vibrissae play a role in a great variety of behaviors and that there is much to be learned.

The Behavioral Section is divided into four parts: 1) environmental survival 2) environmental monitoring, 3) social behavior and communication, 4) aggression

Environmental Survival

Environmental survival considers the use of the vibrissae in the animal's mode of life in the environment, acquisition of food, mate acquisition, care of young, locomotion, etc. One of the earliest studies of vibrissae and mode of life (Beddard, 1902) found that ulnar carpal vibrissae were present on mammals which used their forearms in climbing and/or grasping, but were absent on those mammals whose forearms were used for walking only. In a classic work on facial vibrissae, the relationship between a mammal's mode of life and its vibrissal development were stressed, emphasizing the importance of observations on living animals to support conclusions which were drawn from preserved specimens (Pocock, 1914). Facial vibrissae are highly developed in active arboreal, aquatic or semi-aquatic species and are poorly developed in aquatic and terrestrial herbivores (especially the larger ones like cattle). A study of the vibrissae of Apodemus, the Old World field mice, showed that the development of vibrissae is related to the mode of life of each species within a genus: a small vibrissal field is associated with burrowing species and a large one with the more arboreal ones (Kratochvil, 1968).

However consistent the conclusions of researchers working on correlation of vibrissal fields and mode of life, showing how the vibrissae are useful to their possessors is not easy to demonstrate. A direct attempt to test survival value of vibrissae for small rodents in the wild was made by dividing each of two species of mice (Reithrodontomys megalotis and Microtus californicus) into three groups: (1) no vibrissae clipped, (2) vibrissae clipped on one side and (3) vibrissae clipped on both sides (Pearson, 1962). These mice were tagged, released, and retrapped 3-6 weeks later. Clipping the vibrissae did not affect the probability of a mouse's survival. However, Pearson was unwilling to conclude that vibrissae have no survival value: "...it is perhaps safest to follow the course of some others who have sought in vain to gather from nature experimental confirmation of evolutionary theory, and to conclude that vibrissae have survival value...under...circumstances other than those prevailing in the present experiment." The profusion of elegant work on vision, hearing, olfaction, and taste contrasts with the halting work on vibrissae. Since we as a species lack the tactile vibrissae, and indeed seemingly rely less on our tactile sense than other species, might it not be more difficult for us to conceive how such a sense could be useful?

There are several lines of evidence which suggest that vibrissae are important in food getting both in weanling and adult mammals. The early prenatal appearance of vibrissae (Park, 1970; Davidson and Hardy, 1952) suggests a function in successful nursing. To test this hypothesis, Wistar strain rat pups were injected with a local anesthetic (lidocaine) into the vibrissal pad or had their infraorbital nerves cut (Kenyon et al., 1982). This resulted in weanling rats that were unable to attach to the maternal nipple, whereas clipping the vibrissae with scissors did not affect attachment. They interpreted these results to mean that perioral tactile sensation but not vibrissae are important to successful nursing. However, clipping vibrissae with scissors leaves a stub which may be more sensitive than the unaltered one. This research needs to be repeated with special attention to distinguishing between vibrissal and non-vibrissal sensation of the perioral region. Similar, but carefully controlled research in species that are more mature at birth than laboratory rats may shed light on the role of the other senses in nursing behavior.

Some adult mammals use vibrissae in food acquisition. Studies of predation on crickets by northern grasshopper mice (<u>Onychomys leucogaster</u>) that had their vibrissae removed show that this amputation had no effect on the initial pursuit of the cricket nor on the killing and eating of the cricket once caught (Kemble and Lewis, 1982). However, the time required to catch and pin a cricket with the forepaws increased for divibrissated mice. The behavior associated with predation involves integration of several sensory modalities, with vision and hearing important in detecting the prey at a distance, while the tactile sense (intact vibrissae) is more important as the prey comes into close proximity. Captive harbor seals (<u>Phoca vitulina</u>) also use their vibrissae in capturing fish which form a major part of their diet (Renouf, 1980). In observing fish-catching of two yearlings in clear and murky water, vibrissae removal did not affect the time required to search for the fish, however, the time required to catch the prey was greater without vibrissae. In murky water with no vibrissae, the prey escaped 3-4 times as often as when the water was clear and the vibrissae were present. The lack of vibrissae was a much greater disadvantage in catching prey than was murky water alone. As with grasshopper mice preying on crickets and seals on fish, it seems that the search for prey is a function of eyes and ears, but the manipulation of the prey at close quarters is intimately associated with functional vibrissae, particularly among those that must manipulate still-live prey to the mouth for ingestion.

Even in more passive feeding situations vibrissae may play a role in prey detection. Aquatic mammals which feed on bottom-dwelling molluscs may detect appropriate food by tactile monitoring of texture differences of the ocean bottom (Renouf, 1979). Pelagic feeders like baleen whales may use vibrissae to detect food. Whales like Balaenoptera musculus have a uniform distribution of vibrissae on their upper and lower jaws; when seeking food they "travel" slowly at the surface. Vibrissae probably can detect the size and location of plankton at close range and thus direct animal movement toward the food (Yablokov and Klevesal, 1969). Discussion with veterinarians and farmers who work with horses have convinced me that the vibrissae of large terrestrial herbivores are important in locating and identifying textures of grass that are appropriate to eat. Hafez (1975) does not specifically mention vibrissae in cattle, but believes that "...a sense of touch plays a major role in determining which items are rejected and which are preferred."

There is some evidence that vibrissae are important to cats and laboratory rats in mouse killing, a predatory behavior. Mouse killing by cats may be a well-integrated process with the eyes important for target location in large areas but not in small ones (MacDonnell and Flynn, 1966). The tactile cues, particularly associated with vibrissae, are especially important in completion of the attack, i.e., biting the mouse. If the afferent nerves of vibrissae of laboratory rats are destroyed, there is a great decrease in the numbers of mice attacked and killed but an increase in the number of attacks required for each successful kill. Tactile clues seem to excite and direct attack behavior and contribute to biting behavior of the rat (Gregoire and Smith, 1975). Anesthetizing the mystacial pad of laboratory rats suppressed mouse killing on the first trial, but not on subsequent trials. This suggests that lack of vibrissae (or vibrissal sensation) is a hindrance, but that learning and/or accommodation to the altered tactile sense is possible (Thor and Ghiselli, 1975). Mouse killing behavior by laboratory rats may be related to strain differences among the rats studied, age differences, differences in the rats' experience or handling, or other subtle experimental conditions not yet defined. It seems likely that vibrissae are involved in predatory behavior, especially since many predators have such large and well developed vibrissae.

Vibrissae are also important in other survival-related tasks such as maze navigation. The gray seal (Halichoerus grypus) possesses very long vibrissae that are under exquisite motor control; they run mazes with ease. The ability of the gray seal to rapidly change directions in a maze in the dark suggests tactile cues in the close proximity of the face are involved (Oliver, 1977). In contrast to this, a study of maze running in kangaroo rats (Dipodomys merriami) showed that depriving these animals of vibrissae was not sufficient to significantly decrease their maze-running ability, but depriving them of vision was (Webster and Webster, 1975); visual and vibrissal deprivation together had a slightly stronger effect than visual deprivation alone. There is good evidence to suggest that kangaroo rats are more dependent on their eyes than are member of Rattus (Vincent, 1912). That vibrissae seem less important to kangaroo rats than gray seals makes the point then that species' differences are very important in considering the role of vibrissae in behavior. Some species are highly visual (e.g., humans) while others use vision little or not at all. It seems particularly important, then, that in all studies of vibrissae that species as well as strain be carefully indicated.

Almost all mammals are able to swim without being taught, even for those species that are primarily terrestrial; vibrissae may play a role in this behavior. Mice of several species (Peromyscus maniculatus bairdii and Mus musculus) and strains (M. musculus A/J, C57BL/6J and 129/J) showed impaired survival in a water submersion test when deprived of vibrissae, though species and strain differences were apparent (Werboff and Anderson, 1967). Cotton rats with intact vibrissae are excellent swimmers, but removal of the vibrissae resulted in the rats being unable to maintain body position in the water or to keep their head above the water (Ahl, 1982).

The size of vibrissae and their location on the animal is related to the mode of life; a case can be made for the importance of vibrissae in several survival tasks including nursing, food acquisition, navigation through mazes, and swimming.

Environmental Monitoring

In observing vibrissae one noticeable feature is that some species continually move their vibrissae in a repetitive pattern over the surface in front of the snout (laboratory rats, mice, deer mice and some other small rodents), while other rat species (Sigmodon) may only move their vibrissae when their body position shifts. Some species have vibrissae that are practically immobile (whales, pigs, rhesus monkeys) while pinnipeds have extraordinarily well-developed sinus muscles and very mobile vibrissae. These differences undoubtedly are important in considering the function of vibrissae in behavior.

Vincent's (1912) work on vibrissae functioning as monitors or sensors in the environment explored the behavior of laboratory rats in a maze when the rats were deprived of various sensory modalities (eyes, nose, vibrissae), either singly or together. She concluded that vibrissae are tactile organs which function in equilibrium, locomotion, the discrimination of surfaces, and that vision and tactile senses may serve the animal simultaneously or interchangeably, depending on the situation. This work was extended using a visual cliff apparatus; rats with intact vibrissae ignored the visual signals of a "cliff," moving on the basis of tactile information from the vibrissae alone. However, when deprived of vibrissae, rats showed a marked preference for the "shallow side" of the visual cliff. It seems that tactile clues prevail over visual clues when the two senses present conflicting information (Schiffman et al., 1970). This suggests that vibrissae could serve for depth perception in small nocturnal mammals, or perhaps even in diurnal climbers like tree squirrels.

In contrast with laboratory rats, cats have exceptionally good eyesight, as well as sporting an impressive array of vibrissae. Cats have good distance vision with poor accomodation for near vision, thus the vibrissae may serve as a near-the-face substitute for vision. Cat vibrissae probably function to protect the face and eyes from scrapes or scratches, particularly in arboreal habitats (Fitzgerald, 1940). Supporting such a claim, experimental work recorded responses from nerves to the lateral and medial rectus and retractor bulbi muscles while stimulating the mystacial vibrissal pad. Stimulation of the vibrissal pad elicited retraction and then abduction of the ipsilateral eyeball, leading to the conclusion that the tactile information from the upper lip is integrated into oculomotor system of the cat (Gogan et al., 1981). In dogs, the slightest displacement of superciliary vibrissae lead to a reflex eyeblink (Van Horn, 1970). A case can be made for the value of vibrissae in protecting hunting dogs from eye injury by reviewing observations of dog breeders who have worked dogs with and without vibrissae (McGill, 1982). Monitoring the nearby environment for objects damaging to the eyes or face seems to an important function of vibrissae in some species.

Other terrestrial monitoring functions for vibrissae have been less well studied but provide some intriguing hypotheses. Marler and Hamilton (1966) suggested that olfactory and tactile senses could be combined so an animal could determine the strength and age of chemical signals by calibrating the distance between its muzzle and the marked object (a branch or rock). In orienting to the home box area, newborn kittens probably use their olfactory sense first and their tactile (especially vibrissae) second (Hafez, 1975). Michael Fox (as reported in McGill, 1982) has suggested that wild canids detect wind current direction with their vibrissae with the animal turning into the wind to sample for odors. Fox also hypothesized that subtle variation in the earth's geomagnetic field might be detectable by vibrissae. Both hypotheses appear to be testable, and certainly in the case of the latter, should it prove correct, would lead to some fascinating insights into animal navigation.

Functions of vibrissae in water are similar to those on land though the two media are different: water is denser than air; vibrations in water travel faster than in air; when an object vibrates in water, the incompressible water generates a displacement wave. In fact sea lion vibrissae (Zalophus californianus) might serve as an acoustic sensors (Poulter, 1972). This hypothesis was disputed by Renouf (1979); his work with harbor seals (Phoca vitulina) found that audible underwater sources produce water displacement above the vibrissae threshold of harbor seals only at very close range. This work, however, does support the notion that pinnipeds can sense water displacement with their vibrissae and thereby can determine the properties of an object without having to touch it directly. Bottlenose dolphins (Tursiops truncatus) may use their "sensory pits" (sinus follicles lacking external vibrissae) to detect speed and pressure changes in the water (Palmer and Wedell, 1964). Reasoning from anatomical data and limited field observations, it is suggested that aquatic mammals may detect water depth and water current direction (Yablokov and Klevesal, 1969). Much as for terrestrial species marine mammals seem to use vibrissae for close range perception and to use the tactile sense in conjunction with others (e.g., sound for the long range in water). Even for marine mammals with fairly good eyesight, the lateral placement of the eyes and large snout in some species may obstruct visual clues and thus render vibrissae more important at close range (Renouf, 1979).

In observing the Greenland seal (Pagophilus groenlandica), the rhinal or nasal vibrissae always precede the seal's nostrils out of the water and this suggests that the vibrissae reaching the air might notify an animal of when to open the nostrils when surfacing. At first such an interpretation seems farfetched, but the observation is consistent with experimental evidence in cotton rats (S. fulviventer); they cannot keep their noses above water when swimming unless their vibrissae are intact (Ahl, 1982).

Social behavior, communication and learning

A variety of information suggests a role for vibrissae in social behavior and communication, and to a lesser extent learning. In marine mammals the rhinal and mystacial vibrissae are under voluntary control, and at least four muscles of facial expression are involved in moving the vibrissae (Ling, 1977). These muscles (levator nasolabiales, orbicularis oris, levator palpebrae superioris, and buccinator muscles) are well developed in humans and are important in visual communication. Since animals do not have the broad expanse of hairless skin against which to display muscle movement, perhaps these muscles result in changes in vibrissae pattern which could serve for visual communication among members of a species. Work with walruses (_Odobenus rosmarus_) and New Zealand fur seals (_Arctocephalus forsteri_) shows that both species exhibit similar facial expressions in a variety of social and non-social contexts. Characteristic patterns of vibrissae were recognizable in highly submissive animals, with high intensity threat, grooming, yawning, and investigation of objects. The similarity of vibrissal-related facial expressior in these two species of pinnipeds is reminiscent of the similarity of facial threat expressions of canid species or of primate species (Miller, 1975). In the California sea lion (_Z. californianus_), vibrissal touching occurs in almost every close interaction (Peterson and Batholomew, 1967); touching occurs between females and pups, bulls and females pairs of threatening bulls, pairs of threatening females, and among young non-breeders. Even in several encounters between sea lion and human, the vibrissae were gently whisked over the human face while the sea lion repeatedly opened its nostrils. This latter observation implies a joint role of tactile and olfactory senses. In fact, in some aquatic mammals, notably southern elephant seals (_Mirounga leonina_), the vibrissae are exceptionally well supplied with apocrine-like glands (Ling, 1966). Since apocrine glands are often associated with pheromone production, pheromones produced here may be broadcast by the waving action of the vibrissae. Among domestic animals, pigs have apocrine glands associated with very coarse vibrissae in the mental gland (Montagna and Yan, 1964), though there is no work of which I am aware that suggests any particular behavioral or communicative role for these porcine vibrissae.

A number of scientists from Vincent (1912) to the present have suggested an "emotion component" to behavior following vibrissal removal. A decrease in the general activity level of dogs after devibrissation is reported by McGill (1982), while others (Koranyi et al., 1963) report a decrease in motivation in laboratory rats. The role of vibrissae in emotion-related "sudden death" has been a subject of lively discussion following Richter's (1958) paper. Richter placed wild R. norvegicus with trimmed vibrissae in strongly agitated water; all rats died in 2.8 minutes without detectable signs of having drowned. His interpretation was that loss of vibrissae was a major sensory deprivation, and combined with force locomotion (swimming) in an unusual environment (churning water), was sufficiently stressful to lead to psychologically caused (the "emotion factor" of other authors) sudden death. Others (Hughes and Lynch, 1978) suggest that Richter's reported decrease in the survival rate of devibrissated rats was not due to psychological stress but rather to the inability of the rats to determine the position of their nostrils relative to the surface of the water. Experimental work supports this conclusion (Hughes and Lynch, 1978; Ahl, 1982). However, before negating all suggestions that animal emotionality is associated with the tactile senses, it is well to remember that in humans tactile sensation is intimately tied to emotion in touching, hugging, kissing, and sexual foreplay. Certainly in some strains of laboratory mice, intact vibrissae are a sign of high rank in the social hierarchy (Long, 1972). We do not know enough to draw any firm conclusions about vibrissae and emotion in mammals.

Does devibrissation affect an animal's ability to learn, independent of their role as tactile sensors? Some argue that an animal's place in the social hierarchy is associated with ease of learning and the faster the learning, the higher the level. If this is true, then reducing an animal's social position should reduce its learning ability (Long, 1972). Pain can also reduce one's ability to learn, and in one dog obedience school, trainers claim that as vibrissae grow back after plucking, the blunt stubs painfully prick the objects which dogs are attempting to pick up with their mouths. The pain then inhibits the dog's ability to learn the mouth pick-up tasks of obedience training (McGill, 1982). There is a wealth of speculation regarding the role of vibrissae in social behavior, communication, and learning. Hypotheses are many but carefully demonstrated facts are few. This is a broad and open field for research.

Aggression

Aggression is a forceful physical action directed toward another animal; two major types of aggression will be considered here: (1) irritable, due to fear, shock; (2) conspecific, relating to social dominance or territorial delineation.

It has long been known that a mild foot-shock to a laboratory rat causes the rat to assume an upright, boxing stance, and if another rat is present, then the two rats "box" each other in a stereotypical fighting response. Vibrissal removal further decreases shock-induced fighting behavior in rats already deprived of vision (Flory et al., 1965). Neither total removal of olfactory bulbs nor surgical removal of the eyes had an effect on the rate of shock induced fighting, but cutting the vibrissae greatly reduced this aggressive behavior (Bugbee and Eichelman, 1972). Facial anesthesia suppressed aggressive attacks in rats that had no prior aggressive experience. However, facial anesthesia used after an animal had one prior aggressive experience led only to a temporary decrease of fighting once normal sensation to the mystacium returned (Thor et al., 1974). Anesthetizing the mystacium or plucking the vibrissae both decreased fighting; without vibrissae, fighting as vigorous as that shown in pre-experiment levels returned more slowly and less completely than for rats only treated with anesthesia; vibrissae sensation appears necessary for upright posture and boxing in naive rats but not experienced ones (Thor and Ghiselli, 1975). Again this is evidence for vibrissae as part of an integrated behavioral unit, but one for which prior learning can result in behavioral accommodation if the tactile sense is lost. In laboratory rats, this alternative route in this integrated behavior may be vision. The interpretation of this work is made more difficult by the fact that lesions of the ventrobasal thalamus abolished the shock-elicited fighting entirely (Kanki and Adams, 1978). This was not expected in a response thought to be a visually released behavior, for this area of the brain is the main relay for transmission of tactile sensations from head (and body) to the cerebral cortex. The output of seven individual cells in the laboratory rat midbrain (reticular formation) that fired during fighting was recorded; these same cells fired when the contralateral vibrissae were stimulated and furthermore they fired in a similar pattern as for fighting. These cells are likely part of an integrated mechanism for pain-induced fighting rather than for sensory processing or motor organization (Pond et al., 1977).

Fighting between conspecifics, especially among "strangers" is also influenced by vibrissae. Vibrissae removal and mystacial pad anesthesia of adult male Swiss albino mice greatly reduced the number of aggressive social encounters that normally ensue (Katz, 1976). Similar observations were confirmed in laboratory rats (Flannelly et al., 1976). There was no decrease in non-aggressive social interactions among rats with lidocaine treated mystacium; this suggests that aggression against strangers or intruders is initiated by olfactory cues but continues only when the vibrissae are intact. In another experiment vibrissae were removed from intruder rats and were introduced to known dominant males. The predominant behavior of the intruder changed from the boxing posture (when vibrissae were intact) to "freezing;" the devibrissated strangers suffered almost three times as many wounds as the intact strangers. When the stranger had intact vibrissae, the mutual touching of vibrissae led to mutual boxing postures which decreased attacks on the stranger. When two dominant rats faced each other (one with and one without vibrissae), there was little effect on the behavior of either animal (Blanchard et al., 1977). The conclusion that vibrissae are not necessary for an aggressive attack but rather for defense, does not necessarily follow, for there is evidence from other studies that devibrissation will not affect behavior of experienced fighters (Thor and Ghiselli, 1975). Since Blanchard's et al. (1977) strangers appear to have been reared alone (i.e. inexperienced in fighting), this study must be viewed with caution. The gist of the entire body of work on aggression, however, suggests the essential role of the vibrissae in territorial defense.

Conspecific aggression may take several forms, territorial, social dominance, arguments over food, etc. When housed together, some inbred strains of laboratory mice (C57BL and C3H) showed loss of hair on face and body as well as of vibrissae, though there were some intact mice in each cage. When females were put together, one female trimmed the vibrissae of all her cage mates in one day. In males caged together, ferocious fighting went on for about ten days before the losers (identified by their body scars) allowed their whiskers to be trimmed by the winner. The vibrissae trimming occurred after, not during the fighting. In interstrain studies, some strains were dominant over others, and some other strains (e.g. A/J, CBA) did not whisker or hair trim (Long, 1972). These observations were extended using a "tube dominance test" in which pairs of mice from the same cage met each other inside a clear tube, having been introduced from opposite ends of the tube (Strozik and Festing, 1981). Dominance findings from these tests were matched with whisker-trimming data to indicate that the whisker trimmer is indeed the dominant mouse. Further observations showed that whisker trimming was more common among males than females; in an all male cage, there was one trimmer and the rest were trimees, but in all female cages, usually more than one mouse was trimming vibrissae. Whisker trimming also occurred among mated pairs, with a male trimming his partner until she became pregnant, after which no more trimming occurred. These studies suggest other questions: for example, what is the effect of devibrissation on birthing and the willingness to nurse, that is, maternal behavior? Would devibrissated males be able to mate with unaltered females?

SUMMARY

From this review of vibrissae function in behavior, it is obvious that vibrissae play an important role in the behavior of mammals. There is a broad spectrum of functions proposed or demonstrated for vibrissae in environmental survival, environmental monitoring (both aquatic and terrestrial), social behavior and communication, and some kinds of aggression. Research on this specialized tactile sense is scattered in the literature without a major organized focus or approach to the work. Many of the behavioral functions proposed for vibrissae are speculative, that is they are suggested by the anatomy or by limited observation. Adequate experimental testing is yet to be done for most of these proposed functions. Very little information is available on domestic animals. This means that research on vibrissae and behavior is an open field with much promise; perhaps research on vibrissae will help us in understanding the human tactile sense as well. From these journal sources and from unpublished observations made by myself and others, it would seem reasonable to outline directions of study which may be useful in learning more about the role of vibrissae and behavior in our domestic animals or their feral counterparts.

1. In feral caprine, bovine, and equine species, do vibrissae play a role in the detection of wind currents, potentially giving information about weather?
2. In grazing species in which eyes are fixed at the side of the head, is information about "near to the head" events, e.g. height of grass to be grazed, kind of grass, passed on through vibrissae?
3. In feline species, are the eyes used in more distant vision while the vibrissae give clues about nearby objects? Could such well-developed vibrissae be especially useful in arboreal situations?
4. Do vibrissae play a role in maternal behavior in the maternal-newborn interaction?
5. Do vibrissae in some species play a supporting role in relation to pheromone distribution? Finding of apocrine glands intermixed with vibrissae in a variety of species is a clue to such a function.
6. Do the vibrissae play a role in the normal behavior and feeding of mammals (especially aquatic mammals) in captivity, for the normal behavior of felines in zoos?
7. Could problems with mating and/or aggression (or lack thereof) and maternal behavior in zoo animals be related to vibrissae damage?

In summary, research on the tactile senses in general, and vibrissae in particular, is a wide open field with the potential for many important behavioral studies.

Acknowledgement

Thanks to Ms. Martha McAllister and Ms. Marsha Wise for their help in preparing the manuscript and to Dr. Al W. Stinson for an early reading of it.

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