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DETERMINATION OF THE VIBRATION SENSITIVITY
OF HARBOUR SEAL (*PHOCA VITULINA*) VIBRISSAE

CENTRE FOR NEWFOUNDLAND STUDIES

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FREDERICK HERBERT J. MILLS



DETERMINATION OF THE VIBRATION SENSITIVITY
OF HARBOUR SEAL (Phoca vitulina) VIBRISSAE

BY

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Master of Science

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ABSTRACT

Psychophysical techniques were employed to measure the sensitivity of the vibrissae of a harbour seal (Phoca vitulina) to sinusoidal vibrations ranging between 100 and 2500 hertz. A control test ensured that the seal was not responding to auditory or other extraneous components of the signal. Vibration detection thresholds were found to decrease with increased frequency up to 1000 hertz and remain relatively constant thereafter. These data were used for evaluation of some previous hypotheses of vibrissae function. Calculations revealed that seals should be able to use their vibrissae to detect objects such as swimming fish vibrating underwater at close range and tactually discriminate between objects (like fish with different scale patterns). Also, vibrissae could theoretically detect underwater sounds produced by fish, but at too close a range to have any practical value.

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CHAPTER ONE: INTRODUCTION

This research project was designed to collect quantitative behavioural data on the vibration detection ability of harbour seal (Phoca vitulina) vibrissae. Information on the working vibrissae system of an intact seal should allow the evaluation of previously proposed functions of vibrissae and provide insight as to the practical value of vibrissae to the seal.

Vibrissae function

Most mammals possess specialized tactile hairs known as vibrissae (also whiskers, sinus hairs, bristles, feelers or sensory hairs [Ling, 1966]). The only mammals that do not have vibrissae are members of the Monotremata and Rhinocerotidae (except possibly Diceros bicornis), the marsupial mole (Notoryctes typhlops), and man (Pocock, 1914; Cave, 1969; van Horn, 1970). Lyne (1959) defined 11 categories of vibrissae according to anatomical location, the hairs in all but the submental (chin) category arranged in bilaterally paired groups. The term "vibrissae" as used in this thesis refers to the mystacial vibrissae of the muzzle and upper lip, although vibrissae are found on other areas of the pinniped face, as well as on the forearms and ankles of some other mammals.

Many possible functions of vibrissae have been proposed. I have identified eight hypotheses which are not necessarily mutually

exclusive.

(1) Vibrissae may act as supplementary sense organs to aid orientation in space. In experiments by Webster and Caccavale (1966), the removal of gerbil vibrissae temporarily disrupted successful maze running. The additional loss of vision seriously upset performance on a previously learned maze. Likewise, rats deprived of vibrissae and rendered anosmic showed a greater deterioration of maze running performance than those deprived of vibrissae only and blinded rats with vibrissae removed were unable to learn a maze (Vincent, 1912). Schmidberger (1932; cited in Nilsson, 1969) observed that blinded vibrissaeless cats failed to avoid objects in their path and had difficulty walking along a narrow passage, but showed no such disturbances when vibrissae were preserved. In visual cliff experiments, intact rats showed no preference for either the deep or shallow side, but vibrissaeless rats preferred the optically shallow side (Shiffman et al., 1970).

Further evidence that vibrissae are used as sensory organs to aid orientation in space comes from studies of a terrestrial mammal in an aquatic environment. Ahl's (1982) results suggest that vibrissae play a role in the successful swimming of yellow-bellied cotton rats (Sigmodon fulviventer), helping to maintain body position and keep the head above water by determining the position of the nostrils relative to the surface. Upon vibrissae amputation (either unilateral or bilateral), 13 of 18 normally strong-swimming rats showed a body tilt and/or nose-dip. With added centrifugal stress, all 18 rats showed body tilting and/or

nose dipping while swimming.

Finally, there is some evidence that vibrissae may play a role in the under-ice navigation of the spotted seal, Phoca largha (Sonnafrank, Elsner, and Wartzog, 1983). The blindfolded subject trying to locate an exit hole in the ice required longer dives when deprived of the use of vibrissae.

(2) Vibrissae may function in detecting air or water currents. Neurophysiological data from cats (Fitzgerald, 1940) and seals (Dykes, 1975) showed whiskers to be directionally sensitive. Trigeminal afferent fibres fired preferentially when whiskers were bent in 1 direction rather than another. This response directionality supports Van Horn's (1970) hypothesis that vibrissae could determine the direction and speed of air currents: he suggested further that the hairs may be able to determine speed. Likewise, Tehsin (1980) hypothesized that leopards use whiskers to detect wind direction. Nakai and Shida (1948) proposed that a current detection ability could allow baleen whales to find their bearings in the open sea. Ling (1977) commented that if this ability existed, the immobility of whale vibrissa follicles, being firmly embedded in the dermis and lacking any musculature, would suggest a passive monitoring role rather than an active probing one for vibrissae in these whales. Yablokov and Klevezal (1962) stated that if the whale is able to perceive water currents, this skill would be more important for accurately locating food than for the general identification of sea currents for the purpose of orientation.

Dykes (1972) contended that all water movement is not monitored by vibrissae. In his neurophysiological comparison of vibrissae sensitivity in an aquatic and a terrestrial mammal, seals were found to be more sensitive to higher frequencies than cats, more of the former's high-frequency rapidly adapting afferent fibres being sensitive to 1028 hertz vibrations, and fewer of their low-frequency fibres sensitive to vibrations of 10-200 hertz. Dykes thought this difference may reflect an evolutionary development to allow seals to filter out low frequency vibrations produced by water turbulence. With the background noise eliminated, a seal could be better able to attend to a specific source vibrating at a higher frequency.

(3) Many researchers have advanced the hypothesis that vibrissae are used during the search for food. Ling (1977) stated that the arrangement, structure and function of the vibrissae are associated with feeding habits in pinnipeds. For example, the mystacial vibrissae of the walrus (Odobenus rosmarus) are compressed frontally as opposed to vibrissae of other pinnipeds and are thus especially suited to locate mollusks and other food items as the walrus "grazes" through the upper centimetres of bottom sediments (Ling, 1977; Fay, 1982). The use of vibrissae in locating food may be especially important for nocturnal feeders or mammals with reduced visual capabilities. The common shrew is known to have poor vision but possesses a well developed vibrissae field useful in tracking tasks (Hyvarinen, 1972). Renouf (1979) hypothesized that marine mammals can use vibrissae to detect the large amplitude water displacements propagated by objects vibrating at low

frequencies (like swimming prey). She noted that visual cues would be of limited use to species inhabiting coastal waters where visibility is often less than 1 metre. Her hypothesis was supported by observations on the feeding behaviour of harbour seals captured as yearlings (Renouf, 1980). The seals' ability to locate fish was not affected by increased water turbidity, but the time required to capture their prey was increased substantially upon the removal of their vibrissae.

(4) Vibrissae may gather information about the static properties of objects by making direct contact. Afferent fibres of the vibrissae have different response characteristics; slowly adapting fibres provide information about shape and position (Mountcastle and Darian-Smith, 1968), and rapidly adapting fibres encode vibrations and movement (Mountcastle, 1968). Thus, since vibrissae are innervated by both types of units, they could assume a role similar to a glabrous skin surface to determine an object's shape (Shiple, 1974) or textural quality (Dykes, 1975). Vibrissae sensitivity to higher sinusoidal frequencies would be important for the exploration of finely textured surfaces (Renouf, 1979). The frequency of whisker vibration would increase with finer surface texture and increased hair speed over the surface. Renouf suggested that with this ability, pinnipeds could distinguish bottom dwelling molluscs and crustaceans from the sea bed.

Walrus may also use vibrissae in this context. The short facial whiskers of the walrus have been observed to sort, select and manipulate food items (Ling, 1977; Fay, 1982), and walrus calves have been seen

brushing their vibrissal "moustaches" over the mother's mammary area while searching for nipples (Fay, 1982).

(5) It has been suggested that aquatic mammals may be able to determine their swimming speed by the correlated degree of bending of their vibrissae (Montagna, 1967). The faster the swimming rate, the more the vibrissae are bent backwards with water resistance. Renouf and Gaborko (1982), however, gathered evidence against this speed sensing function of vibrissae. A harbour seal trained to swim at 6 kilometres per hour did so even after its vibrissae were removed. If vibrissae can perform a speed-sensing function, they are not required for it.

(6) Vibrissae may have a communicative function. Vibrissae touching occurs in sea lions between females and pups, bulls and females, pairs of threatening males, pairs of threatening females and among non-breeders (Peterson and Bartholomew, 1967; cited in Ling, 1977). Display postures involving the erection and spreading of vibrissae in the Pacific walrus (Odobenus rosmarus) and the New Zealand fur seal (Arctocephalus forsteri) have been described (Miller, 1975). Miller believed that vibrissae probably evolved for non-social functions but later assumed importance in social contexts.

(7) Nakai and Shida (1948) suggested that whales might use vibrissae to sense variation in water pressure. Vibrissae able to detect pressure would provide the whale with a functional depth gauge. Yablokov and Klevezal (1962) argued that because blood pressure in the vibrissae

sinus is the same as blood pressure throughout the entire body, there is no formation of a pressure gradient necessary for the estimation of the magnitude of pressure. Ling (1977) also disagreed with this pressure detection function by stating that the location of vibrissae only in the anterior region of cetaceans suggests a more specialized searching role rather than a passive monitoring one.

(8) It has been hypothesized that vibrissae act to receive sonar signals in an echolocation system (Poulter, 1972; Stephens, Beebe and Poulter, 1973). In this capacity, these authors felt that whiskers would function as acoustic sensors. Circumstantial evidence for pinniped echolocation exists (some species produce click vocalizations similar to known sonar signals [Norris, 1969] and harbour seals click more frequently in the dark [Renouf, Galway and Gaborko, 1980]), but experimental evidence from studies on the sea lion, Zalophus californianus (Evans and Haugan, 1963) and the grey seal, Halichoerus grypus (Scronce and Ridgway, 1980) was negative. Renouf and Davis (1982), however, provide recent evidence for echolocation in harbour seals; the seal could locate objects in total darkness and could discriminate between 2 objects that differed only in acoustic impedance, emitting click vocalizations during the performance of the tasks. There is to date no evidence that positively establishes the role of vibrissae, if any, in echolocation.

Psychophysics

These suggested functions have been generated both from observations of mammals using their vibrissae and from speculation arising from anatomical and physiological studies. Studies of these types are usually designed for reasons other than determining the role of vibrissae in behaviour, and therefore, have only indirect bearing on this aspect of vibrissae function.

Direct investigations of the functions of vibrissae are rare. One method of determining the sensory function of a given structure has been to relate its removal to a sensory deficit (Dykes, 1972). However, a criticism of sensory deprivation is that there is no way to ensure that structure removal eliminates only a single channel of sensory input. Inactivating a seal's vibrissae may stress the animal and contribute some psychological upset such that normal behaviour is disrupted for reasons other than the loss of the vibrissae detection sense.

An alternative method of measuring some aspects of sensory function of a particular structure is to define the range of stimuli producing neural activity in the afferent pathways connecting that structure to the brain. Dykes (1972, 1975) delivered mechanical stimulation to a single vibrissae shaft and recorded the amplitude at which a single unit at the infraorbital branch of the trigeminal nerve fired 1 impulse for every cycle of a vibration. By testing single fibres over several frequencies, tuning curves were obtained, plotting the receptors'

frequency response. While Dykes' work gave some indication of the possible limits of the vibration detection ability of whiskers, psychophysical study of the intact seal would carry his conclusions further by considering the sensory capability of the whole vibrissae system rather than the isolated response of a single nerve fibre.

The focus of psychophysical study is the behavioural analysis of sensory function (Stebbins, 1970). Sensory capabilities are discerned through investigations on awake, intact subjects rather than through detailed anatomical or physiological analyses. One type of psychophysical experiment yields an absolute threshold which purports to define the limits of the subject's sensory system (i.e. the minimum detectable energy level of stimulation at a given frequency) and ultimately can be used to establish a functional relationship between environmental stimuli and behaviour.

The threshold is not a single fixed point. Threshold value varies with properties of the stimulus (such as signal amplitude and wavelength) and according to the condition of the subject's nervous system (state of adaptation, level of background activity, motivations, etc.). Since perfect control cannot be maintained over all variables affecting the level of neural activity in the sensory system, even under experimental conditions, a subject's threshold acts as if it were constantly changing. Hence, threshold is defined statistically. The experimenter manipulates stimulus values along one dimension and defines a range between 100 percent signal detection and zero percent signal

detection, within which the subject displays some uncertainty about whether the stimulus has been presented. The average transition value between detection of the signal and failure to detect the signal is the calculated threshold (Stebbins, 1970).

Many methods exist for determining sensory threshold. In this project, the staircase (also tracking or up-down) method of stimulus presentation was used. This method is efficient and typically the one employed in animal psychophysics. A large proportion of the data thus obtained contributes to the calculation of threshold, an important advantage over other methods when the number of experimental trials are limited by the amount of food the subject will ingest. Increments of stimulus signal amplitude are presented in sequential order with the initial signal level for the trial series set by the experimenter and the direction of stimulus change dependent upon the subject's response (i.e. correct signal detection is followed by a decrease in stimulus magnitude, failure to detect by an increase). Ideally, the subject continually tracks the stimulus above and below his threshold.

Why use harbour seals to study vibrissae?

Vibrissae are tactile receptors, sensitive to mechanical stimulation. Thus, aquatic mammals which prey upon moving objects in water might use their vibrissae to detect displacement waves produced by the prey. Since harbour seals prey upon fish at sea and, along with other pinnipeds, have some of the most developed vibrissae of any

mammal, they are good subjects for pursuing this possible function of vibrissae. Vibrissae are stimulated through either sustained or repetitive movement of the shaft (Dykes, 1975). This is due to the presence of 2 types of mechanoreceptors in the follicle: Merkel cells sensitive to pressure and bending (Iggo and Muir, 1963), and Pacinian corpuscles sensitive to vibrations (Scott, 1949; 1951). These mechanoreceptors transduce physical stimulation into electrical activity in afferent fibres of the trigeminal nerve, from which impulses are relayed first to the thalamus and then to the primary somatic sensory cortex where neurons are arranged into discrete "barrels" (Woolsey and Van der Loos, 1970), each the cortical correlate of one mystacial vibrissa. Because of their sensitivity to these types of physical stimuli, vibrissae should be especially useful in a dense fluid medium. Since water is virtually incompressible, any underwater oscillating source propagates a pressure wave and a displacement wave (van Bergeijk, 1964). The vibrissae would be deflected a distance proportional to the displacement wave amplitude. Vibrations travel faster and attenuate less rapidly than they do in air (Renouf, 1979) and could, therefore, pass on information about a source from a greater distance.

The structure, size and high degree of innervation of harbour seal vibrissae supports the hypothesis that vibrissae serve an important function. Pinnipeds have the largest and most highly developed vibrissae of all mammal groups (Ling, 1966; 1977). Unlike many other mammals, even certain other pinnipeds, harbour seal vibrissae are not smooth but have a corrugated pattern that may enhance their usefulness

as tactile receptors. Corrugation increases shaft rigidity, allowing the shaft to reach greater length (Yablokov and Klevezal, 1962) and imparting better stimulus transmission upon the vibrissae, increasing sensitivity especially to higher frequencies (Dykes, 1975). Corrugation may also make the vibrissae more sensitive to water currents (Ling, 1966). The large vibrissae follicle into which the shaft inserts has a thick wall of connective tissue for the attachment of numerous muscle fibres that allow voluntary movement. The follicle also contains an extensive system of 3 blood sinuses instead of 2 sinus regions as in terrestrial mammals (Ling, 1977). This appears to be an adaptation to increase the tactile receptivity of the vibrissae. The engorgement of the sinus with blood produces an increased resistance of the tissue underlying the touch receptors, making the vibrissae touch receptors more sensitive to compression and the vibrissa shaft sensitive to the direction of tactile stimuli (Stephens *et al.*, 1973). Large nerve fibres enter at the base of each follicle and branch throughout. The proportion of afferent fibres associated with vibrissae is greater in the seal than in the cat (85 versus 65 percent) (Dykes, 1975). Dykes also discovered that as opposed to cats, the fibres serving vibrissae in seals had a greater spontaneous rate, more of them were spontaneously active, and more of the rapidly adapting fibres responded to high vibratory frequencies.

Purpose

The purpose of this study was to provide quantitative behavioural

data on the working vibrissae system of an intact animal. Specifically, psychophysical test procedures were designed to determine sensitivity thresholds of harbour seal vibrissae to low frequency vibrations (≤ 2500 hertz). This involved a testing method comparable to that used by Renouf (1979). Extension of Renouf's preliminary work was necessary for several reasons.

(1) Renouf's data indicating that vibrissae sensitivity increases with increased frequency between 50 and 1000 hertz did not ascertain the upper frequency limit. It is not known if harbour seal vibrissae are equally sensitive at still higher frequencies or if vibrissae sensitivity soon reaches a maximum and then decreases.

(2) Studies of other tactile systems have yielded "U-shaped" threshold curves. Unlike the curves of Renouf, sensitivity initially increases with increased frequency to a maximum usually between 250 and 300 hertz, after which threshold values rise (i.e. glabrous skin of the cat hind foot [Jaing, Schmidt and Zimmermann, 1968], monkey hand [Talbot et al., 1968], and human hand [Verillo, 1963]; hairy skin of the human forearm [Merzenich and Harrington, 1969]).

Vibrissae tuning curves of Dykes (1972, 1975) also indicated greatest sensitivity occurs at lower frequencies. One category of rapidly adapting units at the infraorbital nerve responded only below frequencies of 300 hertz, another below 700 hertz, and another showed maximum sensitivity between 60 and 100 hertz. Other data that Dykes

obtained from tuning fork stimulation suggested that most units do not respond above 1000 hertz. Since the threshold curves of Renouf fundamentally differ from those of previous tactile studies over the same frequency range, replication is critical.

(3) The finding that vibrissae sensitivity increased with increasing frequency may be accounted for if the seals were attentive to auditory cues rather than to tactile ones. Although Renouf's calculations demonstrated that the seal should not have been able to hear the auditory component of the vibration exciter signals (the noise levels from the vibration exciter were just below the predicted masked auditory threshold of the seals), it is possible that this signal was, in fact, audible. Research subjects placed in noisy environments have inexplicably been able to hear signals at a level below the predicted masked auditory threshold when the signals contained some special meaning to the individual (i.e. a person at a party hears his name over the loud background conversation). This is the "cocktail party" effect (Pollack and Pickett, 1957). Renouf's experimental method did not include any control testing to determine that the seal was using only tactile cues received through the vibrissae.

(4) Renouf's results may have been subject to response bias. Only 5 catch trials (i.e. control trials presenting no vibration, continued positive responses to which would indicate that the seal was not consistently attending to the sinusoidal signals) were included within the 28 trials per test session. With this small number of catch trials,

the seals likely had a positive bias, that is, a predisposition to indicate that a signal was present when uncertain if the signal was near threshold or absent. Owing to the difficulty of discriminating between very low amplitude signals and no signal, the seal, in trying to receive maximum rewards, might adopt the strategy of reporting stimulus presence unless it was absolutely sure that no signal had been presented. Vibration thresholds would then appear lower than in reality.

By modifying Renouf's (1979) experimental method, I hoped to obtain reliable results to either support her finding that vibrissae sensitivity increases with increased frequency between 50 and 1000 hertz or reject it in favour of the more traditional tactile data. Also, the experiments were designed to extend the frequency range tested (up to 2500 hertz) to determine the upper limit of vibrissae sensitivity. This information should help illustrate the practical usefulness of harbour seal vibrissae and allow specific evaluation of previous hypotheses of vibrissae function associated with vibration detection.

CHAPTER TWO: METHODS

Subject and testing facility

The subject was a male harbour seal (*Phoca vitulina*) maintained in an outdoor holding tank (7.62 metres diameter, 1.37 metres depth) at Memorial University's Marine Sciences Research Laboratory. The animal had been captured as a yearling on Sable Island, Nova Scotia in 1977. Diet consisted of frozen herring supplemented with vitamins (as suggested by Geraci [1975]). Testing was conducted from September 1982 to September 1983 at the Marine Lab's holding tank.

Apparatus

Sinusoids were delivered to the seal's vibrissae from a stainless steel rod fitted into a vibration exciter mounted on a bridge structure 1.0 metre above the seal tank. A 0.70 by 1.45 metre wooden platform was constructed beneath the vibrating rod and 0.10 metre above water level (see Figure 1). The seal lying on the platform had access to the vibrating rod. A plywood yoke fixed to the end of the platform permitted the seal's head to extend just far enough through a hole to contact the vibrating rod with protracted vibrissae but with no other part of its face or body (see Figure 2).

The equipment which vibrated the subject's vibrissae is diagrammed in Figure 3. Sinusoidal signals (from 100-2500 hertz) were produced by

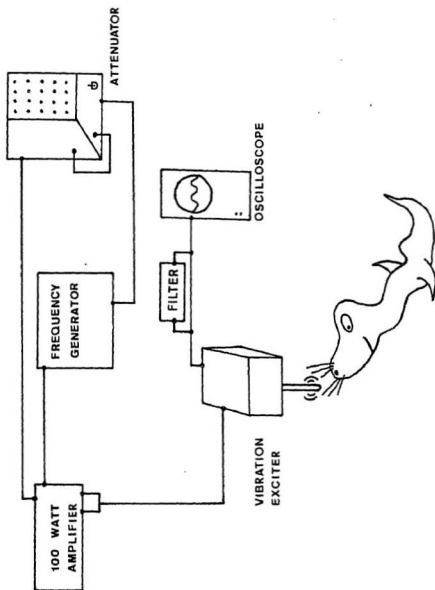
Figure 1: Photograph of wooden platform fixed above the seal holding tank for all training and testing procedures.



Figure 2: Photograph of plywood yoke and vibration exciter rod.



Figure 3: Diagram of equipment that delivered sinusoids to the seal.



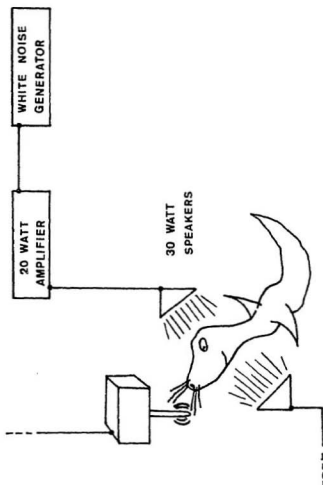
a Hewlett Packard Model 3310A function generator and fed through a 20-position variable stepwise attenuator to allow pre-setting of desired signal intensities. The signal passed through a photogate with an 80 millisecond rise time to a 100-watt Realistic MPA-100 amplifier and was then transduced with a Bruel and Kjaer Type 4809 Vibration Exciter housed in a Plexiglas box. A stainless steel rod (15.36 centimetres length, 0.64 centimetres diameter) fixed to the center of the exciter's surface delivered signals to the vibrissae. A Wilcoxon Model 104 accelerometer was attached to the vibration exciter to measure the signal amplitude. The accelerometer output was monitored with a Hewlett Packard Model 1220A oscilloscope and Krohn Hite Model 3550 band pass filter.

To prevent the seal from hearing the signal, white noise was broadcast from 2 30-watt speakers suspended on either side of the vibrating rod (see Figure 4). White noise was produced by a Grason-Stadler Model 1724 noise generator and amplified by a 20-watt Realistic MPA-20 Amplifier. A General Radio Model 1551-C' sound level meter with built-in octave filter monitored noise and signal level. The sinusoidal signals averaged 13.6 [$\pm$ 6.0] decibels re: 20 micropascal below the seal's masked auditory threshold over all threshold tests (refer to Appendix A).

Procedure

The seal was shaped (using small pieces of herring as a reward) to

Figure 4: Diagram of equipment that delivered white noise to the seal.



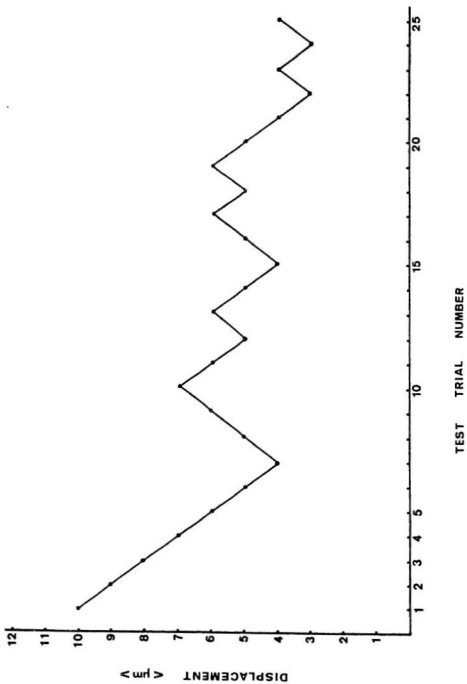
lie upon the platform, place its head through the plywood yoke and contact the vibrating rod with its vibrissae. It was then trained to open 1 of 2 doors of a feeder box fixed to 1 side of the platform (see Figure 5), the lower door if a vibration was detected and the upper door if no vibration was perceived. A single training trial consisted of the seal lying upon the platform, contacting the vibration exciter rod with its vibrissae, then on command, opening 1 door of the feeder. A correct response was rewarded with herring and vocal praise while an incorrect response (or any inappropriate behaviour) was punished by withholding the reward, a loud vocal "No" and a 2 minute timeout period. Correct trials were separated by 30 seconds. In each training session, 50 percent of the trials presented a signal readily detectable by the seal (for example, 500 hertz at 300 micrometers displacement) and 50 percent presented no signal (no vibration). The frequency and amplitude of the signal were varied throughout the training period but were always well within the seal's detectable range as determined by Renouf (1979). One training session of 30 to 80 trials was held per day.

When the seal had correctly distinguished signal presence from absence on at least 90 percent of the trials on 3 consecutive training days, threshold testing began. Each test session consisted of 50 trials, 25 of which were threshold test trials, presenting a vibration in order to calculate a threshold of vibratory displacement at a single frequency. A threshold was obtained by varying signal intensity between trials according to the subject's response (see Figure 6). If the seal indicated it could detect the signal (by opening the lower feeder door),

Figure 5: Photograph of feeder box fixed to the wooden platform.



Figure 6: Seal test trial responses during a single threshold test at 1500 hertz (16 July 1983).



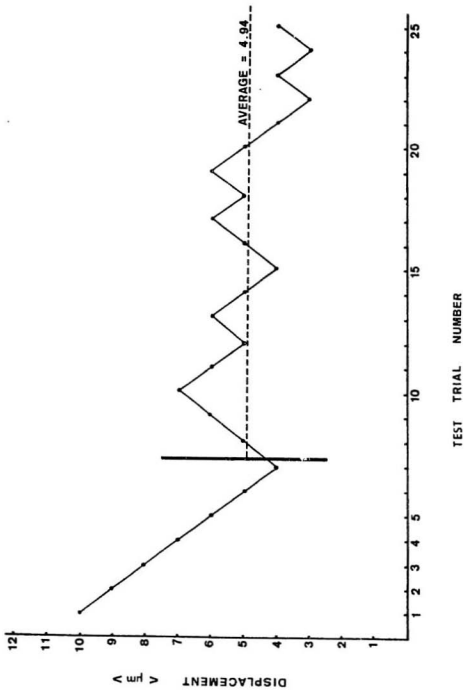
signal amplitude was decreased on the following test trial. If the seal could not detect the signal (it opened the upper feeder door), then signal amplitude was increased on the following test trial. The seal was rewarded for each signal detection response and neither rewarded nor punished for not detecting the signal. The seal's threshold for a particular frequency was calculated by averaging the intensity of all signals presented on the trials following the first reversal of the stimulus intensity (see Figure 7). Two separate threshold estimates were obtained at each frequency.

To monitor the reliability of the seal's performance, 25 catch trials were interspersed randomly among the 25 threshold test trials. Twelve (or 13) of the catch trials were 'signal' trials, presenting a readily detectable vibration (according to Renouf's [1979] thresholds) and 13 (or 12) of the catch trials were 'no-signal' trials, presenting no vibration. Rewards/punishments were administered as in the initial training trials.

After every 3 sessions of threshold testing, a retraining session(s) was conducted to ensure the seal's response remained reliable. Retraining followed the format of the initial training sessions. Threshold testing was resumed when the seal attained the 90 percent correct criterion in a retraining session.

A control test was designed to ensure that the seal based its responses upon vibrations received through the vibration exciter rod

Figure 7: Estimate of the seal's vibrissae threshold from threshold test results at 1500 hertz (16 July 1983).



rather than upon the auditory component of the signal. After all thresholds were acquired, a separate hearing control test was performed at 500, 1000 and 1500 hertz. Before each control test was run, retraining sessions were conducted until the seal responded correctly on 90 percent of the trials. The control test was carried out in the following session at the same frequency as that presented during retraining. Control tests were similar to a regular retraining session of 30 trials except that the stainless steel rod was disconnected from the vibration exciter (i.e. the vibration exciter signal was still audible and the rod was fixed in the usual position but it did not vibrate). White noise was presented during the test. Rewards were given as in regular retraining - the subject's response 'OFF' during signal presence was punished as being incorrect even though the rod was stationary (and therefore an 'OFF' response was really correct) for all trials.

CHAPTER THREE: RESULTS

Figure 8 plots the seal's vibrissae sensitivity to vibrations from 100 to 2500 hertz. The thresholds are mean values from the 2 separate estimates at each frequency (see Table I). Vibrissae were least sensitive at the lower frequencies, 100, 250, and 500 hertz, requiring an average vibration greater than 30 micrometres before stimulus detection was possible. At 750 hertz and above, sensitivity was higher with all threshold values below 12 micrometres and all but 1 below 8 micrometres. The smallest detectable vibration (2.12 micrometres) was at 1000 hertz. Beyond 1000 hertz, thresholds were slightly higher and remained relatively constant, ranging only 4.09 micrometres between 1250 and 2500 hertz. The seal averaged 50.8 [standard deviation: $\pm$ 16.1] percent correct on all 'no-signal' catch trials and 77.2 [$\pm$ 15.7] percent correct on 'signal' catch trials (see Table II).

Results of the hearing control tests were similar at all 3 test frequencies (see Table III). The percent correct values differed considerably between retraining and control sessions. In retraining sessions the seal averaged 90.3 percent correct in discriminating signal presence from absence (92.3 [$\pm$ 7.7] percent correct 'OFF', 88.2 [$\pm$ 5.9] percent correct 'ON'). In the control sessions the seal averaged only a 49.5 percent correct response record (72.0 [$\pm$ 11.4] percent correct 'OFF', 26.9 [$\pm$ 12.9] percent correct 'ON').

Figure 8: Thresholds of the seal's vibrissae to vibrations between 100 and 2500 hertz.

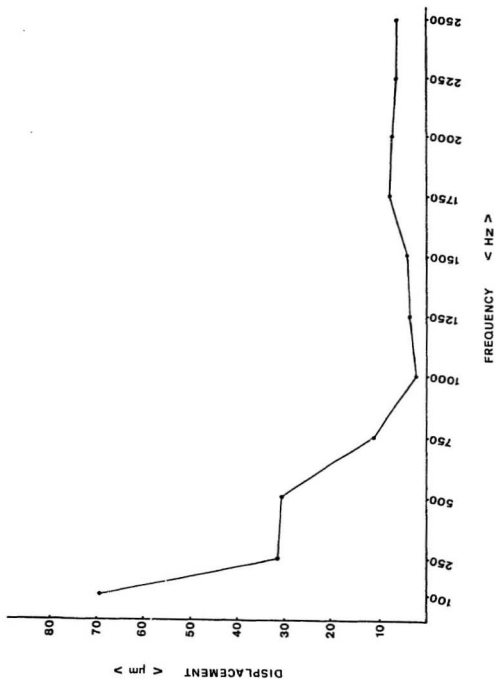


TABLE I: Vibratory thresholds (in micrometers)
measured at each frequency

FREQ	ESTIMATE 1			ESTIMATE 2			MEAN
(hertz)	$\bar{X}$ 1	N	SD	$\bar{X}$ 2	N	SD	$[\bar{X}_1 + \bar{X}_2] / 2$
100	66.50	20	47.93	72.00	15	40.39	69.25
250	38.95	19	6.36	24.21	19	13.36	31.58
500	33.81	21	12.73	26.84	19	4.78	30.33
750	19.91	23	2.79	3.33	9	0.71	11.62
1000	1.73	11	0.65	2.50	8	1.20	2.12
1250	3.90	20	2.40	3.84	19	1.50	3.87
1500	3.80	10	2.62	4.94	18	1.11	4.37
1750	7.70	10	0.95	8.21	19	1.72	7.96
2000	8.57	23	1.12	5.94	18	0.73	7.26
2250	8.50	22	1.01	4.70	20	0.92	6.60
2500	7.52	23	1.44	5.00	20	1.62	6.26

TABLE II: Proportion of correct catch trials
in threshold tests

FREQ (hertz)	ESTIMATE NUMBER	PROPORTION CORRECT		
		NO-SIGNAL CATCH TRIALS	SIGNAL CATCH TRIALS	COMBINED
100	1	.538	.833	.680
	2	.385	1.000	.680
250	1	.750	.846	.800
	2	.615	.917	.760
500	1	.583	.769	.680
	2	.583	.769	.680
750	1	.583	.462	.520
	2	.583	.769	.680
1000	1	.750	.538	.640
	2	.385	.667	.520
1250	1	.385	.750	.560
	2	.462	.667	.560
1500	1	.308	.833	.560
	2	.308	.917	.600
1750	1	.769	.583	.680
	2	.462	.917	.680
2000	1	.769	1.000	.880
	2	.462	.833	.640
2250	1	.538	.583	.560
	2	.231	1.000	.600
2500	1	.417	.583	.480
	2	.308	.750	.520
AVERAGE :		.508	.772	.635
(SD) :		(.161)	(.157)	(.099)

TABLE III: Results of hearing control test

PERCENTAGE OF CORRECT RESPONSES				
	RETRAINING SESSION		CONTROL SESSION	
	signal OFF	signal ON	signal OFF	signal ON
500 Hz:	.846	.941	.588	.308
1000 Hz:	.923	.882	.786	.375
1500 Hz:	1.000	.824	.786	.125
AVERAGE:	.923	.882	.720	.269
(SD) :	(.077)	(.059)	(.114)	(.129)

CHAPTER FOUR: DISCUSSION

Comparison of present results with Renouf (1979)

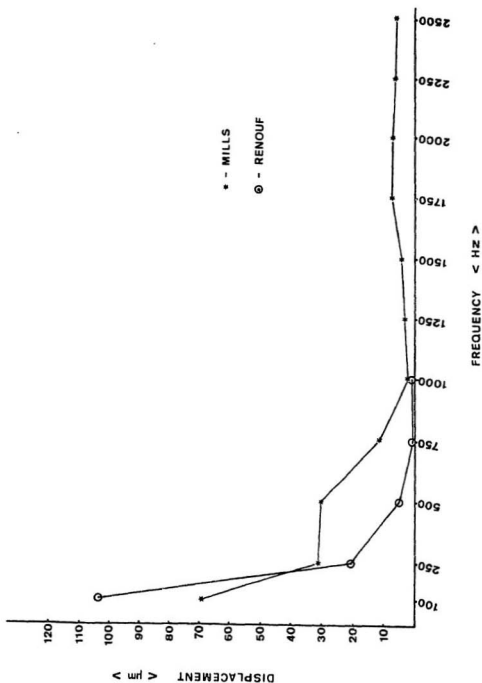
Data from the present study generally support the preliminary work of Renouf (1979). The curve shape (from 100-1000 hertz) was similar to that of the 3 curves obtained by Renouf with sensitivity thresholds decreasing with increasing frequency (see Figure 9). Threshold values, however, differed somewhat from her values. At 100 hertz, the present threshold was lower than those plotted by Renouf (69.25 versus 103.20 micrometres), while at 250 hertz and above, the present values were higher (31.58 versus 20.84 micrometres at 250 hertz, 30.33 versus 5.49 at 500 hertz, 11.62 versus 0.76 at 750 hertz, and 2.12 versus 0.91 at 1000 hertz). The smallest detectable amplitude was also higher (2.12 versus 0.76 micrometres) and appeared at 1000 hertz, instead of at 750 hertz as in the preliminary work. No upper frequency limit was apparent in either set of curves.

Why do present threshold values differ from Renouf's 1979 values?

A number of methodological modifications were initiated in the present study as an improvement on Renouf's original experimental procedure.

(1) The present method was designed to reduce subject stress as much as possible. Problems arose in Renouf's work because the seals were

Figure 9: Comparison of present thresholds with Renouf's (1979) thresholds [average values from 3 seals].



transferred from the regular holding tank to a dry testing room. In the present study, all experimental procedures were performed in the seal holding tank to prevent stressful movement to a separate site. A platform constructed just above the water's surface allowed the subject easy and efficient access to the vibrating rod. A mesh net divided the seal tank when necessary to prevent interference from other seals.

As a consequence of reducing the stress, I was able to train the seal to respond correctly on 0.90 percent of the trials whereas Renouf's seals were able to be trained to only a 0.80 criterion. In my study, threshold testing was not begun until the seal responded correctly on at least 27 of 30 training trials on 3 consecutive days. This 0.90 criterion was also met in the regular retraining sessions held after every 3 threshold tests before testing was resumed.

(2) The signal presented during training/retraining sessions was not of fixed frequency and amplitude but varied between sessions in both frequency and intensity (although always well above threshold). Renouf used a single tone (100 hertz, 82 decibels re: 20 micropascal) for all training trials. It was hoped that varying the signal would prevent the seal from being confused when signal intensities were varied during threshold tests. Also, a variable signal in training sessions prevented the seal from telling the difference between training and threshold testing procedures.

(3) Twenty-five catch trials were interspersed among the 25 trials used

for threshold determination, an increase over the 5 catch trials among 23 test trials used by Renouf (1979). All of Renouf's catch trials were 'no-signal' trials, presenting no vibration. In contrast, my procedure included both 'no-signal' catch trials and 'signal' catch trials (presenting a readily detectable vibration). If all catch trials in the present study presented no signal, the seal might have adopted a "when-in-doubt-say-'No'" strategy since on 50 percent of the trials "No" would have been the correct response. With such a bias, thresholds might have been artificially high (Schusterman, 1974). It was hoped that the inclusion of 'signal' catch trials would offset this.

Although the threshold curve shape is similar to that of Renouf's curves, threshold values at all but 1 frequency are higher than the corresponding thresholds obtained from each of her 3 seals. Renouf's use of only 5 catch trials and resulting subject bias could account for this difference. Confronted with only 5 'no-signal' catch trials per test session, Renouf's seals would have received rewards on the majority of threshold test trials by indicating signal presence whenever they were not certain that the signal was absent. This "when-in-doubt-say-'Yes'" strategy would result in lower signal amplitudes being presented to the seal and consequently a lower vibration threshold. If the seal's responses were not biased, a score on 'no-signal' catch trials of near 50 percent correct would be expected (Schusterman, 1974). In the present study, the seal responded correctly on 50.8 percent of the 'no-signal' catch trials. The 77.2 percent correct response on 'signal' catch trials was understandable since the

signal should have been easily detected and, therefore, not subject to the same response bias constraints.

Hearing control test

The hearing control test addressed the major criticism of Renouf's (1979) study which was that increasing sensitivity could have been a result of the seal being attentive to auditory rather than to tactile cues from the vibration exciter. The present study corroborates Renouf's results in so far as it showed that the seal's lowered thresholds at higher frequencies were not because the seal was hearing the signal. The control sessions were exactly parallel to the retraining sessions in that the seal had to distinguish vibration exciter signal presence from absence just as in the regular training sessions. The only difference was that during the control sessions the vibration exciter rod was fixed and did not vibrate when the vibration exciter signal was either present or absent.

Since the retraining and control sessions should not have appeared outwardly different from each other, the seal should have based all its responses upon the same stimulus. Rod vibration correctly indicated signal presence versus absence only in the retraining sessions as the rod was disconnected in the control session. However, any other stimulus associated with the vibration exciter (i.e. auditory component of the signal, incidental vibrations) were potentially available to the seal in both the retraining and control sessions since the vibration

exciter signal was present even when the rod was disconnected.

The seal was 90.3 percent correct in discriminations in the hearing control test retraining sessions and only 49.5 percent correct in the control sessions. No difference in percent correct scores should have occurred between the retraining and control sessions if the seal were attending to anything other than rod vibration. This hearing control test testifies that increasing vibrissae sensitivity with increasing frequency is not an artifact of the seal detecting the auditory component of the signal.

Evaluation of suggested functions

A major value of the threshold data is their application to evaluating suggested functions of vibrissae. The following examples determine whether several proposed functions are reasonably within the sensory capacity of harbour seal vibrissae. In doing so, they illustrate a practical application of quantitative behavioural data and demonstrate the power of behavioural studies over anatomical and physiological investigations in ascertaining the role of sensory information in an animal's behaviour.

Example 1: Consider the hypothesis that vibrissae may detect water displacements of vibrating objects. Harris and van Bergeijk (1962) provide an equation to approximate the magnitude of the near field displacement wave produced by a dipole sound source, one that vibrates

without changing volume (like the tail beat of a swimming fish). Given a fish's dimensions and tail beat frequency and excursion, and by extrapolating the threshold curve to approximate the seal's sensitivity threshold at the fish's tail beat frequency (representing the minimum displacement the seal can detect), the maximum distance at which the displacement wave can be detected may be calculated. For example, consider a 30 centimetre herring with a flank area of 6 by 6 centimetres and tail excursion of 8 centimetres. A fish of these dimensions swims with a tail beat of 30 hertz (Bainbridge, 1958). Extrapolating the threshold curve to a frequency of 30 hertz, yields a conservative estimate of the seal's minimum detectable displacement of 270 micrometres. According to the equation, the displacement produced by such a herring should be detectable from a distance of 40 centimetres (refer to Figure 10 for calculation). Seemingly, water displacement detection is possible with vibrissae, although useful only within close range.

A seal might use this ability to coordinate actual prey capture since at near distances visual focusing may be difficult and the seal's snout may obstruct its view of the fish (Renouf, 1979). Renouf (1980) showed it is more likely that seals use vibrissae information for prey chase and capture rather than for the location of prey. Recently, Kenble and Lewis (1982) have concluded that the role of vibrissae in predatory behaviour is more important in close proximity to the prey. Upon vibrissae amputation, northern grasshopper mice (Onychomys leucogaster) showed increased kill latencies (from disrupted pounce

Figure 10: Calculation of the distance at which harbour seal vibrissae detect the water displacement of a swimming herring.

Distance at which displacement is detectable:

Using Harris and van Bergeijk's (1962) equation for a dipole source, where:

d = minimum detectable displacement
= 270 micrometres

A = radius of source
= 6 centimetres

r = distance from source
= ?

Δ = displacement of source
= 8 centimetres

θ = angle between direction of source motion and
vector joining source to detection point
= 0 degrees

$$d = (A^3 / r^3) \Delta \cos \theta$$

$$0.27 = (60^3 / r^3) (80) \cos 0$$

$$r = 400 \text{ millimetres}$$

Therefore, a 30 centimetre herring swimming with a tail beat of 30 hertz could likely be detected at a distance of 0.40 metres.

timing when the cricket was 1-3 centimetres away), but exhibited no difference in latency to initiate pursuit or in killing and consumatory behaviour.

Example 2: Threshold data may also be used to evaluate Poulter's (1972) suggestion that vibrissae act as acoustic sensors. For instance, can harbour seals use their whiskers to "hear" common underwater sounds such as those produced by the swim bladders or pharyngeal teeth of fish? Consider the 92 decibels re: 20 micropascal noise emitted by herring at 1000 hertz (Fish, 1954). Using the equation for a monopole sound source (Harris, 1964), at 1000 hertz, where the seal's minimum detectable displacement is 2.1 micrometres, this source could be detected from a distance of 9.6 micrometres (see Figure 11).

Therefore, sound wave detection with whiskers is at least theoretically possible. However, limited to such a close range, this ability would be of questionable value. For sounds of this nature, the ears would obviously be more efficient acoustic detectors than vibrissae.

Example 3: The present threshold curve also supports the hypothesis that pinniped vibrissae could gather information about objects by making direct contact. As vibrissae explore a surface, their frequency of vibration increases with finer surface texture and increased shaft speed. Very small vibratory thresholds at high frequencies mean that vibrissae should be sensitive enough to tell the

Figure 11: Calculation of the distance at which harbour seal vibrissae detect the underwater noise emitted by a herring.

Converting decibels to pressure:

$$\text{decibels} = 20 \log \left(\frac{p}{p_o} \right)$$

$$92 = 20 \log \left(\frac{p}{20} \right)$$

$$p = 7.96 \text{ Dynes/square centimetres}$$

Distance at which displacement is detectable:

Using Harris' (1964) equation for a monopole source, where:

$$\begin{aligned} d &= \text{minimum detectable displacement} \\ &= 2.1 \text{ micrometres} \end{aligned}$$

$$\begin{aligned} p &= \text{pressure} \\ &= 7.96 \text{ Dynes/square centimetres} \end{aligned}$$

$$\begin{aligned} w &= 2\pi f \quad (f = \text{oscillating frequency}) \\ &= 2\pi 1000 \end{aligned}$$

$$\begin{aligned} \rho c &= \text{acoustic impedance of medium} \\ &= 150\,000 \text{ centimetres} \end{aligned}$$

$$\begin{aligned} r &= \text{distance from source} \\ &= ? \end{aligned}$$

$$\begin{aligned} \lambda &= \text{wavelength of oscillating frequency} \\ &= c [\text{velocity of sound in water}] / f \\ &= 150 \text{ centimetres} \end{aligned}$$

$$d = \left(\frac{p}{\rho c} \right) \left(1 + \left[\frac{\lambda}{2\pi r} \right]^2 \right)^{1/2}$$

$$.00021 = \left(\frac{7.96}{2\pi 1000 [150000]} \right) \left(\frac{150}{2\pi r} \right)$$

$$\begin{aligned} r &= .00096 \text{ centimetre} \\ &= 9.6 \text{ micrometres} \end{aligned}$$

Therefore, a 92 decibel re: 20 micropascal noise at 1000 hertz could be detected by the seal from a distance of 9.6 micrometres.

difference between common objects in its natural environment by touch alone (i.e. tactually distinguish herring from capelin, crustaceans from the sea bed, molluscs from bottom mud, etc.).

To evaluate the feasibility of this suggestion, consider the example of seal vibrissae brushing over the scale pattern on a herring's surface at a rate of 100 centimetres per second. I estimated from a herring that there is an average of 2.5 scale overlaps per centimetre, and in this case, the frequency of vibrissae vibration would be 250 hertz. The amplitude of vibration would equal the scale thickness, which I measured at 50 micrometers. Because this amplitude is greater than the seal's threshold of detectable vibration at 250 hertz (31.58 micrometers), the seal should be able to discriminate the texture of this surface (see Figure 12). At different vibrissae speeds, the frequency of vibration and hence, the vibration threshold, would differ, thus giving the seal some control over the limits of its texture discrimination ability.

Problems

Nearly all psychophysical studies with pinnipeds have used only a single test subject (i.e. Mohl 1967, 1968; Terhune and Ronald, 1971, 1972; Terhune, 1974) because of difficulties in maintaining and testing live marine mammals in the laboratory. Even though I was similarly forced to use one seal, since Renouf (1979) used 3 seals, the animal I

Figure 12: Calculation of the frequency and amplitude of vibration of vibrissae in direct contact with a herring's surface scale pattern.

Consider a seal's vibrissae brushing over a herring's scale pattern at a rate of 100 centimetres per second:

typical distance between overlapping scales = 0.4 centimetres
number of overlaps per centimetre = 2.5 overlaps / centimetre

frequency of vibrissae vibration
= (2.5 overlaps/centimetre) (100 centimetres/second)
= 250 overlaps/second
= 250 hertz

At 250 hertz, the seal's vibration threshold is equal to 31.58 micrometres.

typical scale thickness = 50 micrometres
therefore, amplitude of vibrissae vibration = 50 micrometres

50 micrometres > 31.58 micrometres

Thus, at this rate of movement, the seal should be able to discriminate the texture of a herring's surface.

tested in this project was in effect a fourth subject at 1000 hertz and below.

Ideally, a double blind testing procedure was desirable but impossible to implement since the experimenter had to be aware of signal presence and absence to properly reward/punish the seal. Thus, the experimenter was careful to monitor his own behaviour during training and testing sessions. For example, during vocal commands, voice inflection was constant whether the vibration exciter signal was present or absent, movements to switch on the vibration exciter signal were mimicked for trials when the signal was absent, and no motion to administer herring rewards through the feeder box (hand gesture, head movement) was made by the experimenter until the seal's snout had fully entered a feeder box compartment.

A possible criticism of this procedure is that threshold testing was conducted in air only. If sensitivity thresholds differ in air and water, use of these values to evaluate vibrissae performance underwater would not be valid. Renouf (1979), however, reasoned that air and water measurements should be similar because (1) the vibrissae directly contact the vibration exciter rod and (2) tissue of the vibrissa follicle is virtually incompressible.

A drawback of this study was that the frequency range tested was only from 100 to 2500 hertz. Further testing for a definitive upper frequency limit was not possible as equipment limitations prevented

sinusoidal signals of sufficient amplitude from being generated at frequencies outside of this range. Different equipment would be required before vibrissae sensitivity to tones below 100 hertz or above 2500 hertz could be investigated.

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APPENDIX A

Example masked threshold calculation: 500 hertz (Estimate 1)

harbour seal critical ratio (Renouf, 1980) = 25 decibels
 tone frequency = 500 hertz
 band level (from white noise speaker) = 90 decibels

Conversion of noise to spectrum intensity (using octave
 band line in "Band level-Spectrum level Conversion Table"
 [Albers,1965]):

500 hertz corresponds to "conversion in decibels"
 of 26 decibels

Spectrum noise level
 = band level - "conversion in decibels"
 = 90 - 26
 = 64 decibels

Masked threshold = critical ratio + spectrum noise level
 = 25 + 64
 = 89 decibels

At a frequency of 500 hertz, a tone louder
 than 89 decibels will be audible over the white noise.

The loudest signal level recorded from the vibration
 exciter was 74 decibels.

89 decibels > 74 decibels

Therefore, the vibration exciter signal should not have been
 audible over the white noise.

Table IV: Summary of masking calculations

tone freq [hertz]	band level [A]	conversion in decibels [B]	spectrum noise [C=A-B]	masked threshold [C+25]	loudest signal recorded
100 1	90	18	72	97	74
2	90	18	72	97	74
250 1	94	23	71	96	74
2	90	23	67	92	75
500 1	90	26	64	89	74
2	90	26	64	89	74
750 1	90	28	62	87	76
2	90	28	62	87	74
1000 1	90	29	61	86	76
2	90	29	61	86	76
1250 1	96	29	67	92	71
2	96	29	67	92	74
1500 1	90	30	60	85	71
2	96	30	66	91	74
1750 1	96	31	65	90	74
2	96	31	65	90	74
2000 1	96	32	64	89	84
2	96	32	64	89	80
2250 1	98	32	66	91	90
2	96	32	64	89	84
2500 1	90	33	57	82	75
2	99	33	66	91	79

* All table entries are in decibels.

* "Conversion in decibels [B]" estimated from Albers' (1965).

* The subscripts "1" and "2" following the tone frequency denote Estimate Number 1 and Estimate Number 2.



