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RESEARCH ARTICLE

Vibrissal sensitivity in a harbor seal (*Phoca vitulina*)

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ABSTRACT

Prior efforts to characterize the capabilities of the vibrissal system in seals have yielded conflicting results. Here, we measured the sensitivity of the vibrissal system of a harbor seal (*Phoca vitulina*) to directly coupled sinusoidal stimuli delivered by a vibrating plate. A trained seal was tested in a psychophysical paradigm to determine the smallest velocity that was detectable at nine frequencies ranging from 10 to 1000 Hz. The stimulus plate was driven by a vibration shaker and the velocity of the plate at each frequency–amplitude combination was calibrated with a laser vibrometer. To prevent cueing from other sensory stimuli, the seal was fitted with a blindfold and headphones playing broadband masking noise. The seal was sensitive to vibrations across the range of frequencies tested, with best sensitivity of 0.09 mm s^{-1} at 80 Hz. Velocity thresholds as a function of frequency showed a characteristic U-shaped curve with decreasing sensitivity below 20 Hz and above 250 Hz. To ground-truth the experimental setup, four human subjects were tested in the same paradigm using their thumb to contact the vibrating plate. Threshold measurements for the humans were similar to those of the seal, demonstrating comparable tactile sensitivity for their structurally different mechanoreceptive systems. The thresholds measured for the harbor seal in this study were about 100 times more sensitive than previous in-air measures of vibrissal sensitivity for this species. The results were similar to those reported by others for the detection of waterborne vibrations, but show an extended range of frequency sensitivity.

KEY WORDS: Vibrissae, Whiskers, Seal, Vibrotactile, Mechanoreception, Psychophysics

INTRODUCTION

Most mammals possess specialized tactile hairs, but the vibrissae (whiskers) of some aquatic mammals are notable for their derived structure and function. The vibrotactile sense of pinnipeds relies on sturdy, specialized vibrissae and supporting hypertrophied neural architecture (Ladygina et al., 1985; Marshall et al., 2006; Hyvärinen et al., 2009; Ginter et al., 2012; Mcgovern et al., 2015), and can gather information from both terrestrial and marine environments. Pinnipeds use their vibrissae for the tactile discrimination of surfaces (Dehnhardt, 1994; Dehnhardt and Kaminski, 1995; Grant et al., 2013) and the detection and following of underwater wakes (Dehnhardt et al., 2001; Gläser et al., 2011). Although behavioral and histological evidence suggests that the vibrissal system in pinnipeds is adapted to extract complex tactile information from the environment (Dehnhardt et al., 2014, 1998, 2001; Dehnhardt and Kaminski, 1995; Hanke et al., 2012; Wieskotten et al., 2010, 2011), the sensitivity of this sensory modality is not fully understood. A few studies have utilized different methods to directly measure the tactile sensitivity of seals to a range of stimulus frequencies. However, these studies have yielded conflicting results.

Early electrophysiological studies measured neural responses in anesthetized seals to mechanical stimulation and tuning forks and found that most nerve fibers were sensitive to frequencies below 500 Hz (Dykes, 1975). Primed sensitivity in this region is not surprising for an animal that is adapted to detect hydrodynamic stimuli, the frequency content of which is typically below 200 Hz (Bleckmann et al., 1991; Bleckmann, 1994). Dykes (1975) also reported that very large amplitudes were required to induce the neural firing rate to lock to the frequency of stimulation, leading to the conclusion that the system was not highly sensitive overall. However, those types of measurements are not ideal for assessing the overall sensitivity of the vibrissal system.

Subsequent studies utilized less invasive psychophysical methods to investigate vibrissal sensitivity in seals trained to respond to vibratory stimulation. Renouf (1979) and Mills and Renouf (1986) measured behavioral response thresholds of a harbor seal contacting a vibrating rod with its vibrissae. The response thresholds that they measured indicated that seals were relatively insensitive at low frequencies (<500 Hz), contrasting with the neurophysiological findings of Dykes (1975) and deviating from the expected overlap with biologically relevant stimuli. In addition, the sensitivity thresholds overall were elevated relative to what would be expected from an animal that is highly reliant on this mechanoreceptive system for prey detection. Considering the behavioral abilities of these animals to track wakes and determine hydrodynamic features (Dehnhardt et al., 2001; Wieskotten et al., 2010, 2011), the seal's vibrissal system would need to be highly sensitive. Although there are limited psychophysical data to allow for comparison with other whiskered mammals, it has been demonstrated that the rat (a known vibrissal specialist) can detect stimulus movements as slight as 11 µm at 80 Hz with their vibrissae (Adibi and Arabzadeh, 2011). This value is nearly ten times lower than the thresholds reported by Renouf (1979) for seals at a similar frequency. While the early in-air studies on vibrissal sensitivity in seals laid good groundwork for investigating this sensory system, the technology available has vastly improved since the time those studies were performed and a re-visit to this approach is warranted.

A more recent behavioral study was conducted under water by Dehnhardt and colleagues (1998), who used a psychophysical procedure to measure the sensitivity of a harbor seal to low-frequency (10 to 100 Hz) waterborne vibrations produced by an oscillating sphere. The amplitude of the received stimulus was calculated based on the distance from the sphere to the seal's vibrissae and detection was demonstrated for the seal at the micrometer level of water motion. While there is minimal data from mammalian whiskers to compare this with, the hydrodynamic receptors of fish, cephalopods and

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Received 10 December 2014; Accepted 21 May 2015

List of symbols and abbreviations

a	acceleration
CV	coefficient of variation
d	displacement
f	frequency
FA	false alarm
rms	root mean square
v	velocity

crustaceans can detect water movements of less than a micrometer (Tautz and Sandeman, 1980; Bleckmann and Topp, 1981; Budelmann and Bleckmann, 1988; Bleckmann and Münz, 1990; Wiese and Marschall, 1990; Bleckmann, 1994). Therefore, it is reasonable to conclude that the underwater sensitivity thresholds reported by Dehnhardt et al. (1998) are within a reasonable range for a hydrodynamic specialist. However, the range of frequency sensitivity demonstrated is relatively narrow, implying that detection is limited to hydrodynamic signals of 100 Hz and below. In other phyla, detection has been demonstrated beyond this frequency range (Tautz and Sandeman, 1980; Bleckmann and Topp, 1981; Budelmann and Bleckmann, 1988; Bleckmann and Münz, 1990; Wiese and Marschall, 1990; Bleckmann, 1994) and biogenic hydrodynamic signals as well as those generated by the animal's own movement may have relevant frequency content above 100 Hz.

Our aim in the present investigation was to resolve the discrepancies in the prior data by testing the sensitivity of a harbor seal to directly coupled vibrations delivered in air. To accomplish this, we trained a seal to report detection of the motion of a vibrating plate and utilized a psychophysical procedure to measure the smallest velocity that was detectable as a function of frequency. By physically coupling the stimulus to the vibrissae, we were able to directly measure sensitivity to vibrissal movement, without confounding factors from propagation through a medium. To support direct comparison to prior measures, we utilized test stimuli from 10 to 1000 Hz and report sensitivity in parameters of velocity, displacement and acceleration. Furthermore, we measured the sensitivity of the human thumb in an identical paradigm and compared the vibrotactile thresholds obtained with those for the seal. Comparing our human measures with the extensive body of data available on this haptic system assured confidence in the thresholds reported for this seal, and provided comparative insight into the performance of this tactile system.

RESULTS

An adult male harbor seal subject was successfully trained to report detection of vibratory stimuli received by direct contact with his vibrissae. The seal performed the psychophysical task in the absence of any extraneous visual, auditory or tactile cues. The seal responded to all test frequencies presented (10–1000 Hz), with lowest response thresholds for velocity measured in the range of 20–250 Hz (Table 1). A plot of the velocity thresholds as a function of stimulus frequency was used to establish the seal's vibrotactogram (Fig. 1), which displays a general U-shape, with best sensitivity of 0.09 mm s^{-1} at 80 Hz and decreasing sensitivity (corresponding to increasing thresholds) below 20 Hz and above 250 Hz. There is an irregularity present at 800 Hz, where the measured threshold is higher than that observed at adjacent frequencies.

While the stimuli presented to the seal were directly calibrated in units of velocity (mm s^{-1}) by laser vibrometry, the measured thresholds are also reported in units of displacement (mm) and acceleration (mm s^{-2}). Regardless of which parameter of motion is used to express the thresholds (velocity, displacement or acceleration) the frequency of best sensitivity remains at 80 Hz, but the shapes of the vibrotactogram curves differ (Fig. 1). When expressed in terms of displacement, the thresholds decrease as a function of frequency. When the same thresholds are expressed in terms of acceleration, the thresholds increase with increasing frequency.

To ensure that the measured sensitivity thresholds were not biased by spatial variability across the vibrating surface of the stimulus plate, the reported thresholds for the seal were referenced to the highest velocity measured on the plate's surface. Spatial mapping of the stimuli revealed that variation in signal amplitude was smallest at lower frequencies (between 10 and 80 Hz) and greatest at higher frequencies (800 and 1000 Hz). These frequency-dependent patterns of velocity caused by modes of vibration were quantified by coefficients of variation (CV) (Table 1) and visualized as relative amplitude plots to illustrate areas of higher and lower velocity (Fig. 2). The frequencies for which the seal showed the most sensitive velocity thresholds (10 to 250 Hz) had low spatial variability in stimulus presentation.

When the stimuli were further characterized by mapping the surface vibrations of the stimulus plate with the beam of the laser vibrometer at two angles (45 deg and 90 deg) relative to the surface of

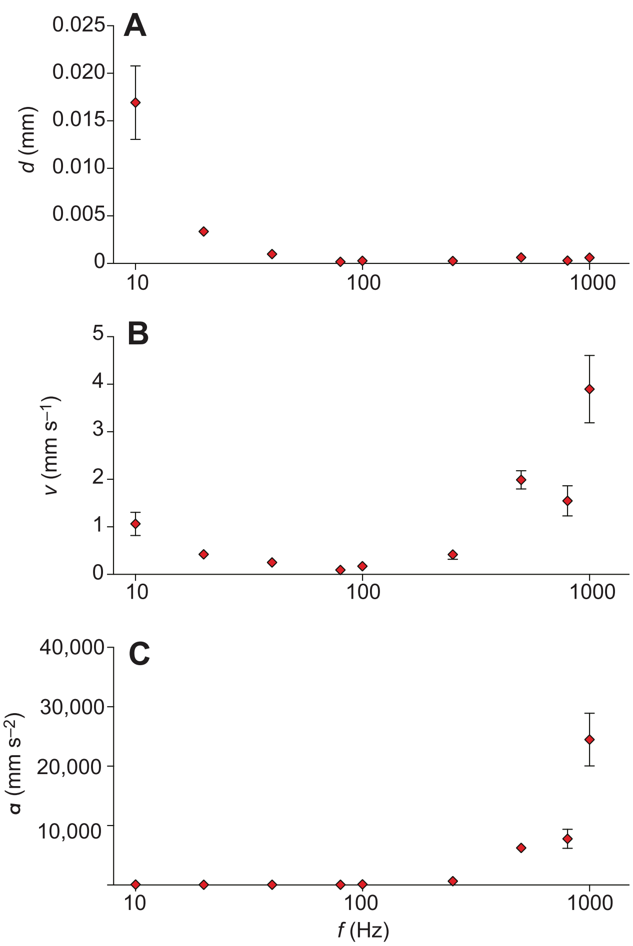

Fig. 1. Response thresholds obtained for the seal at each test frequency. The vibrotactograms are shown in terms of (A) displacement (mm), (B) velocity (mm s^{-1}) and (C) acceleration (mm s^{-2}), although the stimuli were directly measured in units of velocity only. Error bars represent ±s.d. of thresholds from three sessions at each frequency.

Table 1. Summary of measured thresholds by frequency

	Seal (N=1)				Human (N=4)	
f (Hz)	Velocity threshold (mm s^{-1})	CV	FA rate (%)	Test order	Mean velocity threshold (mm s^{-1})	s.d.
10	1.06	0.06	26	7	0.91	0.30
20	0.42	0.02	22	6	1.35	0.29
40	0.25	0.05	25	1	0.52	0.35
80	0.09	0.07	17	2	0.14	0.05
100	0.17	0.45	22	3	0.17	0.07
250	0.42	0.24	26	4	0.09	0.04
500	1.99	0.48	18	5	0.37	0.16
800	1.55	0.69	18	8	1.33	0.55
1000	3.90	0.52	21	9	1.98	1.09

For the seal, velocity thresholds, coefficient of variation (CV) calculated from stimulus variation across the plate at each frequency, false alarm rate (FA) and test order are shown; for humans, the mean velocity thresholds are provided.

the plate, corresponding CV values reveal relatively consistent vibration patterns at frequencies up to 500 Hz. Greater inconsistencies between the two laser orientations appear at frequencies above 500 Hz, reflecting a more elliptical path of plate movement.

The sensitivity measurements obtained for four human subjects that contacted the stimulus plate with their thumb were similar to those of the seal in terms of absolute thresholds and comparable in terms of relative frequency sensitivity (Table 1; Fig. 3). The threshold values for humans were determined from the measured velocity at the center point of the plate, rather than referenced to the highest velocity on the plate's surface, as the thumb only contacted this position during testing. The minimum mean velocity threshold for the human subjects is 0.09 mm s^{-1} at 250 Hz, compared with 0.09 mm s^{-1} at 80 Hz for the seal. Sensitivity at 20 Hz is lower for the human subjects than at surrounding frequencies. The frequency of best sensitivity is 250 Hz when thresholds are expressed in terms of velocity or displacement. When thresholds are expressed in terms of acceleration, the minimum threshold varies between 10 and 80 Hz across subjects.

DISCUSSION

The harbor seal in the present study could detect vibrations received from the vibrissae at all frequencies tested. The range of best sensitivity (20–250 Hz) agrees with the frequency characteristics of biologically relevant hydrodynamic signals. As harbor seals use their vibrissae to detect and follow hydrodynamic wakes (Dehnhardt et al., 2001; Schulte-Pelkum et al., 2007), it would be advantageous for the vibrissal system to be optimized for detection in this frequency range. The sensitivity of the seal also overlaps with the signals produced by the vibrissal structure during flow interactions. Excised seal vibrissae produce a distinct low-frequency vibrational signal (<300 Hz) when exposed to low-velocity (0.5 m s^{-1}) water flow under laboratory conditions (Murphy et al., 2013). The spectral characteristics of these vibrissal signals correspond closely to the frequency sensitivity of the sensory system revealed by psychophysical testing.

The velocity thresholds for the harbor seal produced a U-shaped curve with a low-frequency roll-off below 20 Hz and a steeper high-frequency roll-off above 250 Hz. While we consider these data

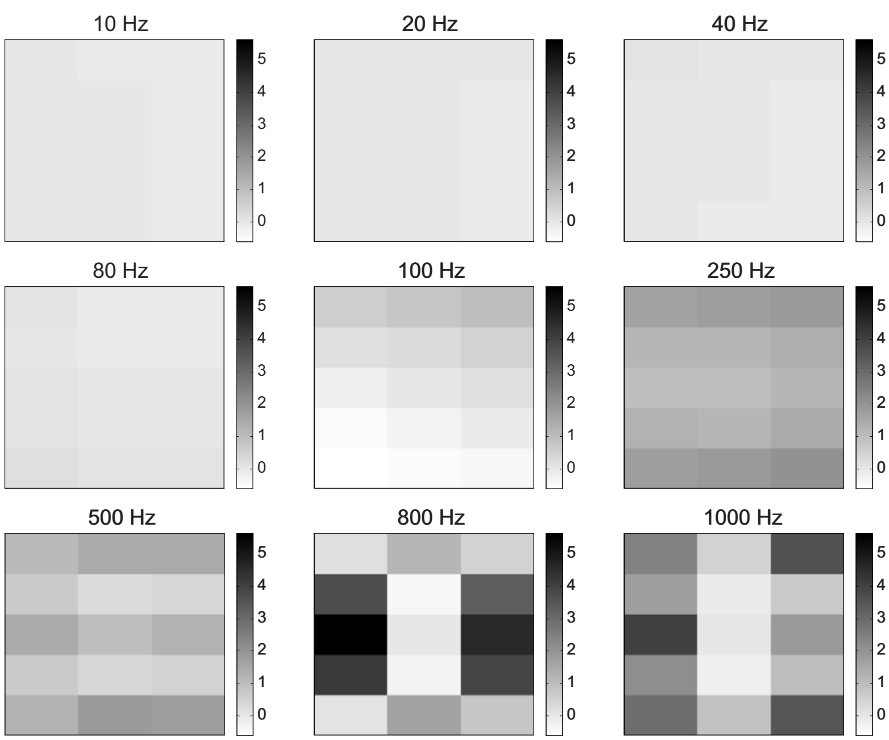

Fig. 2. Relative amplitude plots illustrating spatial variation in signal amplitude for each test frequency. Signal velocity was recorded at 15 discrete points across the surface of the stimulus plate, with the laser oriented at a 45 deg angle to the plate surface (in line with the axis of vibration), as in daily calibration. The shading intensity at each point on the grid indicates the difference in velocity between that point and the center of the plate, divided by the velocity at the center of the plate. The shading scale is expressed in terms of this ratio number and shading intensity reflects higher (darker) and lower (lighter) deviations from the center position. Vibration amplitude is spatially consistent across the plate for frequencies below 500 Hz, while distinct modes of vibrations are visible for 800 and 1000 Hz.

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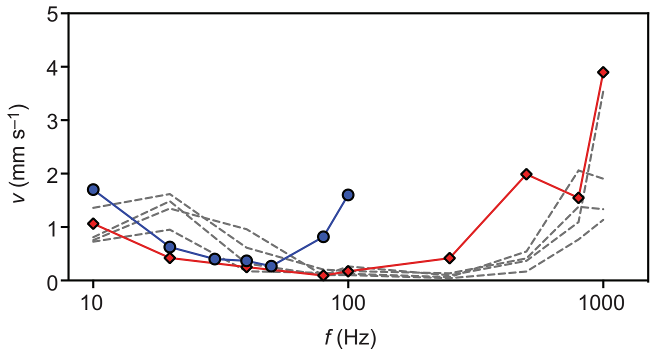

Fig. 3. Comparative vibrotactograms for two harbor seals and four human subjects. The velocity thresholds for the harbor seal tested in the current study (red) are shown with the same measurements obtained for four human subjects (dashed lines). Sensitivity thresholds for the harbor seal tested by Dehnhardt et al., 1998 using underwater stimuli are shown for comparison (blue). The data obtained in air for harbor seals by Renouf (1979) and Mills and Renouf (1986) are not shown here as those aerial thresholds, when converted from displacement to velocity, range from 3.6 to 110 mm s^{-1} and cannot be accommodated by the scale of this figure.

primarily with respect to the directly measured metric of velocity, the component of motion that is most relevant to the seal vibrissal system is not known. It is possible that the system is responsive to more than one metric. It is therefore advantageous to also represent sensitivity thresholds in terms of displacement and acceleration. As there is no standard unit for reporting mechanoreceptive thresholds, considering the thresholds in all three parameters of motion allows comparisons to be made with other studies.

When expressed in units of displacement and acceleration, the minimum threshold for the harbor seal in this study remained at 80 Hz. The displacement curve showed a sharp decrease in threshold levels below 80 Hz. Above this frequency, the displacement thresholds were similarly low, showing a plateau in best sensitivity. Conversely, the acceleration thresholds showed a plateau below 80 Hz and a sharp increase in threshold level above this frequency. The shapes of the displacement, velocity and acceleration sensitivity curves for this harbor seal are in general agreement with those reported for another harbor seal tested under water (Dehnhardt et al., 1998). These trends are also consistent with the shapes of the curves reported for the hydrodynamic receptors of other aquatic animals; these include some species of fish, crayfish, cephalopod and sea snake (Bleckmann, 1994; Dehnhardt and Mauck, 2008).

Although the shapes of the curves allow for inter-species comparisons, they do not confirm which parameter(s) of motion are biologically salient to the receptor system. The component of motion that the vibrissal system is responsive to cannot be determined using absolute threshold data from sinusoidal stimuli. This would require an experimental design sufficient to decouple the different parameters of motion. Such a study has recently been attempted with rats and results suggest that velocity is the relevant parameter for this taxon (see Adibi et al., 2012). While is plausible that velocity may also be the relevant parameter of motion for the seal's vibrissal system, this conclusion cannot be drawn from the available data.

Comparison with previous measures

The present study helps to resolve the conflicting findings from previously reported measures of vibrissal sensitivity in the harbor seal. Despite generally similar methods, the thresholds determined here are on average of 100 times lower than those reported by prior psychophysical measures collected in air (Renouf, 1979; Mills and Renouf, 1986). The frequency range of best sensitivity is also lower in the present study (<250 Hz) compared with the range identified earlier (>500 Hz). The relatively high displacement thresholds previously measured at frequencies below 500 Hz led to the conclusion that seals are insensitive to vibratory motion at lower frequencies. In contrast, here we show good sensitivity overall, with best sensitivity in the low-frequency range. In the time since the previous in-air studies were conducted, the technological resources available for signal generation and processing have vastly improved. Using the current methodology we were able to attain greater experimental control in order to provide a more accurate characterization of the vibrotactile abilities of this species.

In terms of frequency sensitivity of the vibrotactile system, our findings generally support the limited available neurophysiological data (Dykes, 1975). Studies of neural responses to vibrissal stimulation identified best sensitivity below 512 Hz, which is confirmed by the frequency trends identified here. However, the results of neurophysiological studies had suggested that the seal vibrissal system was relatively insensitive overall, based on the stimulus amplitude required to induce phase-locked neural firing. In contrast, here we report good sensitivity across a range of frequencies, with behavioral thresholds that are orders of magnitude lower than the 'tuning points' reported by Dykes. The present study probably provides a better assessment of the capabilities of the vibrissal system, because the neurophysiological measures did not collect absolute threshold data and the methodology used to identify phase locking of fibers does not necessarily indicate minimum detectable stimulus level.

The sensitivity thresholds reported here are most similar to those previously measured in an underwater psychophysical paradigm (Dehnhardt et al., 1998). The absolute stimulus amplitudes fall within a similar range, although different frequencies of best sensitivity are apparent. While we report a frequency of best velocity sensitivity (80 Hz) that is similar to that from the underwater study (50 Hz), the range of frequency sensitivity is wider in the present study, with good detection extending to stimuli above 100 Hz, where the prior underwater data indicate a roll-off. It is difficult to determine whether the upper range of frequency sensitivity reported in the underwater study indicates a limitation of the sensory system or a limitation imposed by hydrodynamic coupling of the stimuli to the sensors. While it is unlikely that the receptor itself functions differently in air and under water, it is probable that the way the stimulus interacts with the vibrissae differs between mediums. Because we directly coupled vibrations to the sensors, the points of contact on the vibrissae were moved at the same rate as the stimulus. In the prior underwater measures, the animal was detecting vibrations that were propagating through the water. It is possible that as frequency increased, the waterborne vibrations did not stimulate movement of the vibrissae adequately to excite the receptors. To determine whether hydrodynamic coupling was responsible for the observed differences in high-frequency sensitivity, direct measurement of vibrissal movement, or else calibration of received hydrodynamic signals, would be required.

Relevance to understanding the sensory system

The expanded frequency sensitivity observed in the present study suggests that biologically relevant signals also span this frequency range. While the seal in this study was able to detect vibrations up to the testing limit of 1000 Hz, hydrodynamic signals are not known to contain frequencies above a few hundred Hz. It is possible, however, that the vibrissae themselves vibrate at these frequencies during swimming and tracking of hydrodynamic disturbances. The speed at which a seal passes through a hydrodynamic disturbance may influence the frequency at which the vibrissae move, with greater swim speeds generating higher-frequency oscillations.

The low absolute detection thresholds measured in the present study demonstrate acute sensitivity of the vibrissal system and highlight the importance of fine-scale vibration detection in seals. Especially sensitive detection capabilities may be of particular importance to seals considering the fact that the morphology (Hanke et al., 2010) and orientation (Murphy et al., 2013) of the vibrissae have been shown to suppress the amplitude of vibration. In the context of this reduced amplitude effect, changes in whisker vibrations caused by encountering a hydrodynamic disturbance while moving through the surrounding fluid present a distinct input signal to the vibrissal system. Sensing these small vibrations and detecting very small variations may be the key to the remarkable hydrodynamic detection and discrimination abilities displayed by seals.

Validity of vibrotactile threshold measurements

We have confidence in the accuracy of the threshold measures reported in this study. In order to ensure that there were no extraneous cues available to other sensory modalities during testing, we thoroughly measured all acoustic artifacts and took precautions to eliminate or mask potential confounding cues. Furthermore, in order to obtain the most accurate estimation of vibrotactile threshold levels, great care was taken to characterize the test signal that was received by the subject at the point of contact by the vibrissae. This was achieved by careful calibration and mapping of the test stimuli at the position of vibrissal contact.

Quantifying the spatial variability of signal amplitude across the surface of the plate yielded a measure of confidence in stimulus calibration. At the frequencies of best sensitivity for the seal, signal quantification is highly reliable because of minimal variation in signal amplitude. The greatest spatial variation occurred at the higher frequencies in the test range, particularly at 800 and 1000 Hz. Although the thresholds for the seal are referenced to the point of highest vibration on the plate, the complex modes of vibration that occurred at these high frequencies resulted in a less-constrained threshold estimate. This spatial variability in signal amplitude may account for the irregularity in the curve shape that occurs between 500 and 800 Hz in the velocity threshold curve for the seal. The irregularity is not likely to indicate an increase in sensitivity from 500 to 800 Hz, rather it suggests that the threshold at one of these frequencies may be under- or over-estimated. Variation over the surface of the stimulus plate would have influenced only the threshold measurements of the seal, because vibrissal contact was spread out across the entire surface of the plate, whereas human subjects contacted only the center point of the plate during testing.

In order to validate the behavioral and technical methods used to test the harbor seal, the procedure was adapted with few modifications for comparison to the better-understood human mechanoreceptive system. Human vibrotactile thresholds display a U-shaped velocity curve with best sensitivity around 250 Hz (Gilmer, 1935; Geldard, 1940; Sherrick, 1953; Verrillo, 1963, 1966). Although threshold amplitude differs slightly depending on the portion of the finger being stimulated and the contact area, the overall shape of the vibrotactile curve is maintained (Gilmer, 1935; Verrillo, 1962). The performance of the four human subjects in the present study agreed with the available data for the human hand, with best sensitivity of 250 Hz. The notch at 20 Hz in the human sensitivity curves is consistent with the data from previous studies and is representative of a shift in the receptors that mediate the sensation of vibration (Johansson et al., 1982; Gescheider et al., 2002; Morioka and Griffin, 2005). The similarities in the performance of the human subjects in the present study to prior measures of tactile sensitivity for humans confirms the accuracy of the experimental methods used and provides further confidence in the measured thresholds for the seal.

Interestingly, the detection thresholds collected for the seal touching a vibrating object with the tips of his vibrissae are generally similar to those of human subjects touching the same object with their thumb. Because the experimental setup was optimized for testing the seal, we are limited in the conclusions that can be drawn from this cross-species comparison. However, the parallels in performance between the seal vibrissae and the human thumb demonstrate acute tactile sensitivity for these structurally different mechanoreceptive systems and present opportunities for future experimentation.

In conclusion, the directly measured and carefully controlled experimental signals used in this study enabled a more complete understanding of the sensitivity of the harbor seal vibrissal system. The detection thresholds obtained for the seal in this study counter previous findings from neurophysiological and in-air psychophysical studies suggesting that the vibrissal system is insensitive to low-frequency input. Our data are consistent with measures of the underwater sensitivity of this vibrotactile system, as well as with what is known of the stimulus characteristics of biologically relevant hydrodynamic stimuli. Because the testing approach enabled the performance of the system to be measured in response to direct stimulation of the vibrissae, it provides an understanding of the perception of a known signal delivered to the sensor's surface. Quantifying the relationship between the sensor surface and signal is valuable, not only to the biological community attempting to understand tactile reception in animals, but also to the growing body of researchers interested in biomimetic modeling of whisker-inspired sensors.

MATERIALS AND METHODS

One harbor seal and four human subjects were tested using a psychophysical procedure to measure velocity thresholds for vibrational stimuli, detected from a calibrated oscillating contact plate (see supplementary material Movie 1). The harbor seal contacted the plate with his vibrissae (Fig. 4) and each human subject contacted the plate with the pad of their thumb. A go/no-go behavioral response paradigm, conducted using a modified method of limits or staircase procedure (Stebbins, 1970), was used to measure absolute sensitivity to sinusoidal stimuli at nine frequencies from 10 to 1000 Hz. Details of the experiment are provided in the following sections.

Subjects

The primary subject was a captive-born, 24-year-old adult male Pacific harbor seal (*Phoca vitulina richardii* Gray 1864) identified as *Sprouts* (NOA0001707). He was housed at the University of California Santa Cruz (UCSC) at Long Marine Laboratory. This seal had extensive prior training relevant to the current experiment, including experience participating in a variety of psychophysical auditory and visual experiments. He had normal hearing capabilities (Reichmuth et al., 2013) but had poor vision due to chronic bilateral cataracts. Prior to the current study, he had been trained to perform behavioral tasks while wearing either headphones or a blindfold, similar to those used in the current procedure. *Sprouts* consumed ∼5 kg of freshly thawed capelin (*Mallotus villosus*) and herring (*Clupea* spp.) each day, a quarter of which was provided during daily training and testing for this study. His diet was not constrained for experimental purposes and he

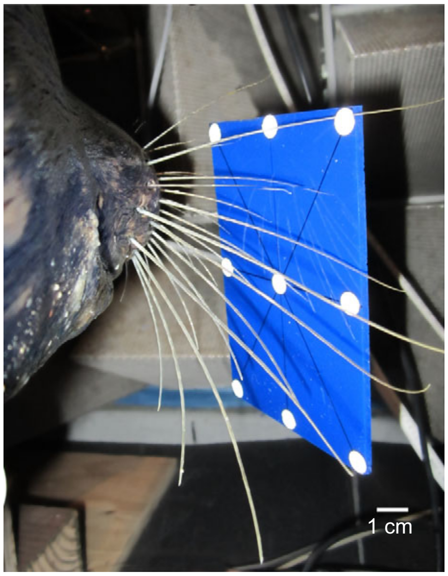

Fig. 4. Contact of the seal vibrissae with the stimulus plate during testing. When positioned at the chin cup station, the vibrissae of the seal's right mystacial bed contacted the stimulus plate. The plate dimensions and orientation maximized the number of vibrissae contacting the surface during testing.

was maintained at a healthy weight throughout the study. Testing was conducted from May to July 2012, prior to the summer molt. The vibrissal array was fully-grown and intact during this period. Animal research was authorized under National Marine Fisheries Service permit 14535 and was conducted with the approval of the Institutional Animal Care and Use Committee at UCSC.

Four humans were tested during the same time period. These were one male and three females, aged 20 to 24 years with no significant sensory deficits. The human subjects were assistants at Long Marine Laboratory who volunteered to participate in the experiment. Research with human subjects was conducted under a Category 2 exemption by the UCSC Internal Review Board.

Testing environment

The experiment was conducted at Long Marine Laboratory in a custom-designed, hemi-anechoic, sound-attenuating chamber (Eckel Industries, Cambridge, MA, USA) that was located near the seal's living enclosure. This chamber, designed for audiometric testing, was subdivided into a testing room suitable for large animals and an adjacent, sound-isolated control room with space for controlling equipment and an experimenter. A detailed description of the testing chamber is provided by Southall et al. (2003) and a schematic of the experimental set-up is provided in Fig. 5.

Stimulus generation

Sinusoidal waveforms were used to drive oscillatory movements of a rigid rectangular contact plate made of acrylic sheet (1140 mm high×760 mm wide×2.8 mm thick). The vibratory stimuli generated had a frequency of 10, 20, 40, 80, 100, 250, 500, 800 or 1000 Hz and a total duration of 1000 ms, including 25 ms linear rise/fall times. Signals above 1000 Hz were not tested because of strong acoustic artifacts above this frequency.

Signals were generated with an RP2 real-time processer (Tucker-Davis Technologies, Alachua, FL, USA) controlled with a custom-written MATLAB script on a PC computer. The signals were attenuated with a PA5 programmable attenuator (Tucker-Davis Technologies Alachua, FL, USA), amplified by a Pyle Pro PPA200 power amplifier (Pyle Audio, Brooklyn, NY, USA), and used to drive a SignalForce GW-V4 shaker system (Data Physics Corp., San Jose, CA, USA). The shaker motor was coupled to an aluminum rod (750 mm long×4 mm diameter) that was attached to the rear of the contact plate by a tee nut glued to a metal, fixed-angle hinge that held the plate at a rigid 45 deg angle to the axis of the rod.

The stimulus generation equipment was located in the control room of the experimental chamber. The shaker motor was vibration isolated from the surrounding substrate using foam and Sorbothane shock absorption padding (IsolateIt, Burlington, NC, USA). The aluminum rod that extended from the shaker passed through the wall of the control room into the test room through the center of a 50-cm-long PVC conduit that was encased on the control room side with sound-isolating foam. To maintain the rod at a parallel angle to the floor as it entered the test room, the rod was suspended with elastic rubber bands where it exited the conduit through a 1.2-cm-diameter hole in the conduit cap. No portion of the vibration-driven components were in direct contact with any portion of the testing room.

Stimulus calibration

A single-point laser vibrometer (CLV1000 controller with CLV700 sensor) (Polytech Inc., Irvine, CA, USA) was used to measure the velocity (v) in mm s^{-1} of the contact plate during stimulation by the sinusoidal test signals. During calibration, the laser vibrometer was positioned at a 45 deg angle to the plate surface, so that the laser beam was in line with the axis of the oscillating rod; consequently, the laser beam was in line with the axis of the movement of the plate. Velocity measurements were obtained before and after every session from the center point of the contact plate. During calibration, signal frequency was held constant while velocity was measured at 12 discrete amplitudes, starting at a supra-threshold level and attenuating in 6 dB steps until the signal was buried in the noise floor. This amplitude range encompassed all stimulus levels used during testing at each frequency. Corresponding displacement (d) values (in mm) and acceleration (a) values (in mm s^{-2}) were calculated from the velocity measurements, with d determined as $v/2\pi f$ and a determined as $v2\pi f$ (where f=frequency in Hz).

Stimulus mapping

In order to map the vibration levels across the surface of the plate, fine-scale spatial mapping was conducted before and after the experimental term. For each of the nine test frequencies, laser vibrometer recordings were obtained

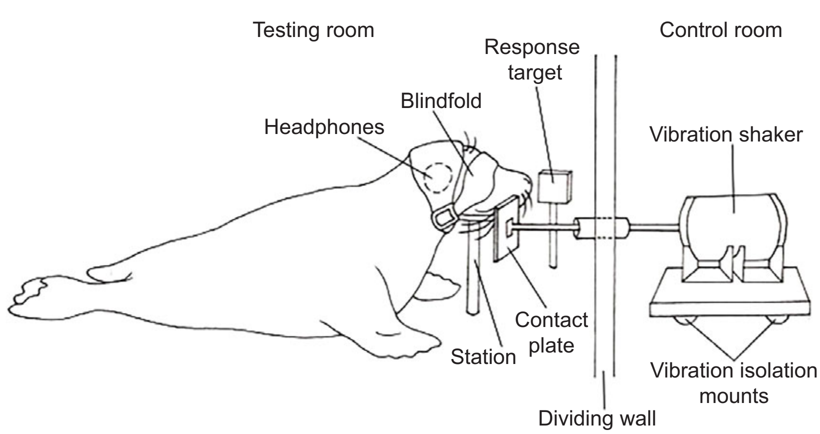

Fig. 5. Schematic of the experimental setup. The experimental chamber is divided into an acoustically isolated testing room, where the stimulus is delivered to the subject, and a control room, where the signal is generated by an experimenter. For simplification purposes, only the central components of experimental setup are illustrated here and the figure is not drawn to scale.

from 15 evenly spaced points across the surface of the plate. At each point, recordings were made at the same 12 signal amplitudes used during daily calibrations. The amplitude of motion of the plate was determined to be linear across all stimulus amplitudes, therefore measurements of motion could be made at one stimulus amplitude. Calculations of spatial variability and determination of vibration modes for each stimulus frequency were based on the starting (highest) amplitude level.

Modes of vibration, or resonance patterns, were visualized by referencing the velocity between each mapping point and the center point of the plate (daily calibration position). To quantify spatial variation of signal amplitude for each test frequency, a coefficient of variation (CV) was determined. The CV was calculated by dividing the standard deviation of velocities across the plate by the average of velocities across the plate. In order to characterize the movement of the plate in multiple planes, mapping was carried out with the laser vibrometer positioned at two orientations. For each of the 15 spatial positions, recordings were made with the laser oriented at a 45 deg angle to the plate surface (in line with the axis of vibration, as in daily calibration) and with the laser oriented at a 90 deg angle to the plate surface (45 deg angle to the axis of vibration).

Experimental controls

Controls were put in place to ensure that subjects responded only to the vibrational test stimuli. These controls included evaluating and eliminating any extraneous vibrotactile, visual and acoustic artifacts associated with stimulus generation as well as preventing the possibility of behavioral cueing from human experimenters. The presence of confounding vibrotactile cues in the testing area was systematically evaluated using laser vibrometer measurements. Recordings were made from all surfaces that the subjects came in contact with while the stimulus was generated at each frequency at supra-threshold levels. These recordings confirmed that the stimulus plate was the only available surface with any detectable movement.

To eliminate any possibility of visual cues during testing, the seal wore a soft, customized blindfold made of opaque neoprene during testing (Fig. 5). Human subjects were oriented in such a way during testing that the contact plate was not visible. Even so, it is notable that at all frequencies, movement of the plate was not visually detectable to humans at the stimulus levels used during testing at all frequencies. Independent human observers, not touching the contact plate but visually observing the plate during stimulus generation, confirmed that the test signals could not be identified on the basis of visual cues.

To mask potential acoustic artifacts associated with vibration of the contact plate, broadband masking noise was played through headphones worn by the subjects. The masking stimulus consisted of a Gaussian noise distribution with the frequency of greatest energy centered at the test frequency. The masking signal was generated by an RP2 real-time processer (Tucker-Davis Technologies, Alachua, FL, USA), amplified by a VP1000 voltage preamplifier (RESON Inc., Goleta, CA, USA), and transmitted through TDH-39 headphones (Telephonics Corporation, Farmingdale, NY, USA) that were seated in rubber ear cushions. The seal wore a custom-made neoprene headband that held the headphones snugly in place over the ears. Prior to testing at each frequency, an ER-7C probe microphone (Etymotic Research, Elk Grove Village, IL, USA) was used to record the spectrum and level of the acoustic signal associated with supra-threshold signal generation in the absence of the masker, from beneath the ear cushion of the headphones while placed on the seal. This information was used to determine the appropriate shape and amplitude of the masking sound for each test frequency based on published critical ratio values for harbor seals (Southall et al., 2003). The characteristics of the masker were then verified by recording the masking noise from beneath the headphones, in the presence and absence of supra-threshold signals, to confirm sufficient masking levels to prevent the detection of acoustic cues. Human subjects were provided with foam earplugs that they wore beneath HDA 200 headphones (Sennheiser Electronic Corporation, Old Lyme, CT, USA) that presented the same masking noise given to the seal. Since humans have similar or higher critical ratios than seals (Hawkins and Stevens, 1950), the seal's maskers were more than adequate to mask potential signal artifacts. Independent human observers, who listened for the signal during trials while wearing headphones but not touching the contact plate, confirmed that the test signals could not be acoustically detected at the stimulus levels used during threshold testing.

For the seal trials, an assistant was present inside the testing chamber with the animal. This assistant was 'blind' to the presentation of the test signal and received instructions from the experimenter via headphones following each trial. For human sessions, the subjects were alone in the testing room.

Psychophysical procedure

The seal was trained using operant conditioning with positive (fish) reinforcement to participate in the experiment. At the start of each session, he was cued by an assistant to move from his living enclosure to voluntarily enter the testing chamber and allow the door to be closed behind him. Once in the chamber, he was fitted with the headphones and the blindfold by the assistant, and then was cued to rest his lower jaw on a contoured chin rest. In this stationing position, the vibrissae on his right muzzle touched the surface of the contact plate, as shown in Fig. 4. He was able to flex his vibrissae forward to obtain firmer contact with the plate but was not permitted to move his jaw from the station or contact the plate with any part of the skin. The animal's head and vibrissae remained still and in position throughout the trial interval. During testing, an average of 14 whiskers contacted the stimulus plate on each trial. This was confirmed by video recording of trials and analysis of still images captured during the trial interval of 136 trials.

During the session, an experimenter controlled the test trials and viewed the session on a closed-circuit video system. A go/no-go response paradigm was used in which the seal reported detection of a vibratory signal by pressing a response target to his left and the absence of a vibratory signal by remaining in position at the chin station. Prior to every trial, the assistant checked the placement of the headphones and blindfold and then cued the seal to position at the station. Once the seal was correctly positioned, the experimenter initiated the acoustic masker for 5 s. The masking noise delineated the trial interval for the subject. Both signal-present and signal-absent trials were used. During a signal-present trial, the vibratory signal was delivered via the plate at a variable point during the trial interval. During a signal-absent, or 'catch' trial, only the acoustic masker was played.

Correct responses included pressing the response paddle after the presentation of a vibratory signal (hit) and remaining motionless in the station for the entire trial interval in the absence of a vibratory signal (correct rejection). Correct responses of either type were marked for the seal by a brief whistle followed by one piece of fish given by the assistant. Incorrect responses included failing to respond during the trial interval to the presentation of a vibratory signal (miss) and touching the response paddle on a signal-absent trial (false alarm). Following incorrect responses of either type, the masker was terminated and the subject was prompted to reposition at the station.

Sessions included approximately 60 trials and were conducted 1–2 times per day. The order of signal and catch trials in a session were counterbalanced using a MATLAB-generated pseudorandom schedule that constrained the maximum run length of a particular trial type to four. A signal was presented during the trial interval on 50–60% of the trials. This trial ratio maintained a consistent false alarm rate throughout the experiment. On signal-present trials, the frequency of the vibratory signal was the same throughout the session and the amplitude of the signal was varied using an adaptive up–down descending method of limits (e.g. a descending staircase procedure) (Cornsweet, 1962). A session began with several easily detectable 'warm-up' trials at supra-threshold level. The velocity of the signal was then attenuated by 4 dB after each successful trial until the subject's first miss. The velocity was then increased by 4 dB after each miss and decreased by 2 dB following each subsequent hit. A session continued until five consecutive hit-to-miss transitions within 6 dB of attenuation were completed. Sessions were conducted at the same frequency until the seal maintained stable performance for at least three consecutive sessions as described below. The nine test frequencies were tested in non-consecutive order. At the conclusion of the experiment, the threshold for the first test frequency was re-measured as a reliability check. The re-measured threshold was within 3% of the original threshold and ensured that no practice effect had occurred during the course of the experiment.

Human subjects were tested in the same experimental chamber as the seal with only a few differences in procedure. Humans received written and verbal instructions regarding the testing procedure prior to the initiation of the experiment. At the start of each session, the human subject was fitted with earplugs and headphones, and then seated at a 90 deg angle to the seal's chin cup. The subject's left hand was placed in the seal's chin cup, with the weight of the hand resting in the cup and the fleshy pad of the thumb touching the center of the contact plate. Because the testing apparatus was optimized for data collection with the seal, the human procedure was designed to accommodate the testing setup. The thumb was selected as the testing digit because it could be easily placed on the center of the plate without tension in the hand. The subjects were instructed not to apply pressure to the plate or move their thumb during the trial interval. A visual marker was present at the center of the plate to ensure that the subjects maintained accurate positioning. Subjects reported detection of a signal on a trial by raising their right hand and the absence of a signal by remaining still. For each correct answer, subjects were presented a flashing white light at the termination of the masker. For incorrect responses, the masker was terminated with no additional feedback. A signal was presented during the trial interval on 70% of the trials. All other aspects of the procedure and signal presentation were identical to those used for the seal.

Threshold calculation

Following each session, the calibration data were used to convert signal attenuation in dB to velocity in mm s^{-1}. A session threshold, defined as the 50% detection probability threshold for rms velocity, was calculated as the mean of the velocities of the last five hit-to-miss transitions on signal-present trials. To calculate an overall threshold for a given frequency, three consecutive sessions with stable performance were required. The last five hit-to-miss transitions within each of these sessions needed to show a plateau (no significant slope) and the thresholds for each session needed to fall within 6 dB of each other. Usable sessions were also constrained on the basis of false alarm rate. For the seal, false alarm rates of greater than 0 and less than 30% were accepted. For humans, false alarm rates of greater than or equal to 0 and less than 30% were accepted. At the end of the experiment, an overall threshold for each test frequency was calculated as the mean of the thresholds from the three sessions meeting these criteria.

The velocity threshold determined for each frequency based on the seal's performance on the task was corrected to account for the spatial variation of the signal across the contact plate at that frequency so that the threshold was based on the point of maximum vibration on the plate. Although only the center point of the plate was used for daily calibration of the velocity threshold, the mapping data (quantified as the CV) revealed frequency-dependent non-linearities across the surface of the plate caused by modes of vibration. Therefore, a threshold correction factor was identified and applied to account for spatial variability in velocities on the contact plate. This factor was calculated as the maximum velocity at any point on the plate divided by the velocity at the daily calibration position. The threshold determined for each test frequency was multiplied by this correction factor, so that the final reported threshold was referenced to the maximum vibration velocity anywhere on the plate. This ensured a conservative estimation of performance and compensated for points of vibrissal contact other than the center point of the plate. Threshold corrections were based on spatial mapping of stimuli with the laser beam oriented at a 45 deg angle to the plate surface, as in daily calibrations. No correction factor was necessary for the human data, as the thumb contacted only the center point of the plate, where the daily calibration was based.

Acknowledgements

We thank Asila Ghoul for her guidance and assistance in animal training. We thank Waylon Olsen and Hotline Wetsuits for designing and donating the custom headgear worn by the seal. We thank Jenn Cossaboon for the illustration in Fig. 5. We thank Brendan Wakefield for videography and video editing. We thank William Martin for guidance and advice. We thank the members of the Pinniped Cognition and Sensory Systems Lab, especially Caroline Casey, Jenna Lofstrom, Sarah McKay Strobel, Andrew Rouse, Roxanne Beltran, Rebecca King and Sonny Knaub for their assistance in this project. Portions of this work were presented at the 20th Biennial Conference on Marine Mammals, in Dunedin, New Zealand on December 12, 2013.

Competing interests

The authors declare no competing or financial interests.

Author contributions

C.T.M. was involved in all aspects of this study and was responsible for experimental design and data collection. D.M. was involved in technical design and data analysis. C.R. was involved in all aspects of this study. All authors contributed to the writing of this manuscript.

Funding

Funding was provided to C.T.M. by the National Science Foundation Graduate Research Fellowship Program. Indirect support was provided by the Office of Naval Research [N00014-06-1-0295 to C.R.].

Supplementary material

Supplementary material available online at
http://jeb.biologists.org/lookup/suppl/doi:10.1242/jeb.118240/-/DC1

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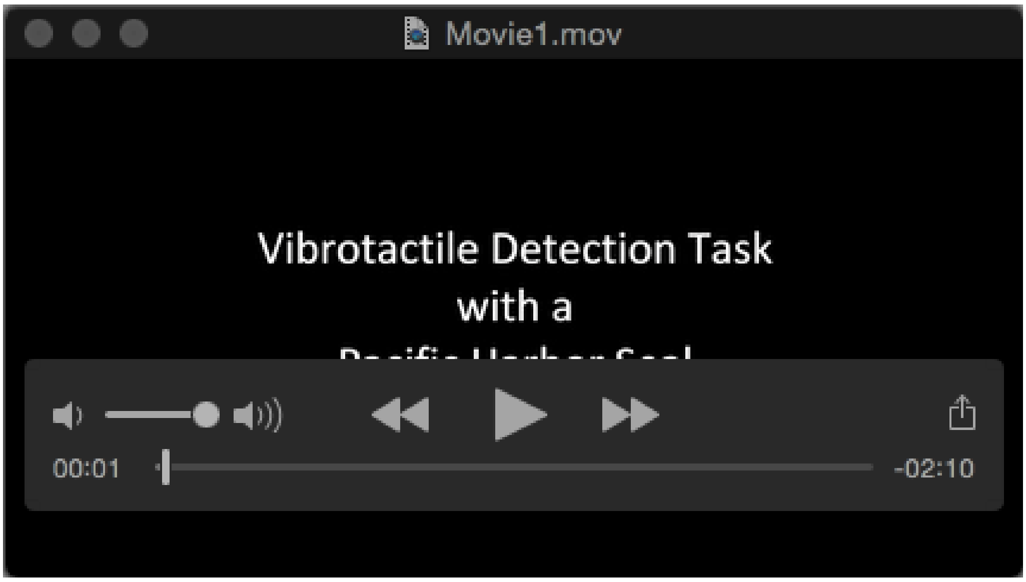

Movie 1. Vibrotactile detection task with a Pacific harbour seal.