

SENSITIVITY OF THE MYSTACIAL VIBRISSAE OF HARBOUR SEALS (*PHOCA VITULINA*) FOR SIZE DIFFERENCES OF ACTIVELY TOUCHED OBJECTS

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Summary

We studied the capability of one male and one female harbour seal *Phoca vitulina* to discriminate diameter differences of circular discs by means of active touch with their mystacial vibrissae. To prevent the animals from perceiving visual information, they were blindfolded during trials. In a two-alternative forced-choice procedure, the seals were required to choose the larger of two Perspex discs. Weber fractions c (the ratio of the lowest diameter difference detected by the seals on 75% of occasions to the starting disc diameter D , $\Delta D/D=c$) were determined for three standard discs (diameters 1.12 cm, 5.04 cm and 8.74 cm) by the psychophysical method of limits. While the seals achieved Weber fractions of 0.29 (male) and 0.26 (female) at the smallest standard disc, their performance

improved with increasing disc size, resulting in an approximately constant Weber fraction of 0.13 (male) and 0.08 (female) for the two larger standard discs. The difference in performance between the two seals did not reflect a real difference in sensitivity, but may best be explained by a difference in choice behaviour. As a measure of tactile acuity, the Weber fractions obtained for the larger standard discs indicate that harbour seals can use their mystacial vibrissae as efficiently for active touch as monkeys use their hands.

Key words: vibrissae, difference thresholds, active touch, harbour seals, *Phoca vitulina*.

Introduction

Pinnipeds, whose extremities are reduced and adapted to the aquatic environment, rely principally on their vibrissal system for receiving tactile information. The vibrissal follicles of the two pinniped species studied so far (*Zalophus californianus*, Stephens *et al.* 1973; *Phoca hispida*, Hyvärinen, 1989) are richly endowed with mechanoreceptors. According to Hyvärinen (1989), each peripheral vibrissal unit is innervated by 1000–1600 thick nerve fibres, which is about 10 times greater than those known from other mammals. Along with a prominent representation in the somatosensory cortex (Ladygina *et al.* 1985), this strong innervation characterizes the vibrissae of pinnipeds as a powerful tactile system.

Although typically considered as vibrotactile sensors, Dykes (1975) concluded from single unit recordings at the infraorbital branch of the trigeminal nerve of two phocid species (*Phoca vitulina* and *Halichoerus grypus*) that the mystacial vibrissae are principally equipped for active touch performances, such as the discrimination of shape, size and texture of objects in the environment. Recent behavioural experiments have supported this hypothesis and have demonstrated that the tactual capabilities of the tested animals come close to those achieved by mammals with prehensile tactile organs. Kastelein and van Gaalen (1988) have shown that a walrus (*Odobenus*

rosmarus) can distinguish a circular disc from an equilateral triangle by active touch with its mystacial vibrissae, even when the surface area of both shapes was as little as 0.4 cm². Excellent shape discrimination capabilities by means of mystacial vibrissae have been demonstrated for a California sea lion (*Zalophus californianus*, Dehnhardt, 1990). The animal was able to discriminate between five shapes by active touch with the same accuracy as previously achieved by vision. Presented with two shapes decreasing in size, the same sea lion could identify them down to an outer dimension of both shapes of 1.7 cm (G. Dehnhardt and G. Dücker, unpublished data). A psychophysical study by Dehnhardt (1994), also conducted with a California sea lion, described for the first time the resolving power of a vibrissal system for active touch. Required to choose the larger of two simultaneously presented circular discs, the blindfolded sea lion achieved a mean Weber fraction of 0.26.

Since the number, arrangement, size, stiffness and structure of the hair shafts of mystacial vibrissae of pinnipeds show considerable interspecific variation (Ling, 1977; Watkins and Wartzok, 1985), the results obtained for active touch achievements of *Odobenus* and *Zalophus* may not hold for other pinnipeds, especially phocids. In harbour seals *Phoca*

vitulina, for example, the species tested in the present study, there are 44 vibrissae ($\pm 1-2$) on each side of the snout (Fig. 1) and, when not actively raised, their angle of protrusion from the snout is always larger than in sea lions (Fig. 2). While the vibrissal hair shafts of all otariids as well as those of the phocids *Erignathus barbatus* and *Monachus* species are smooth in outline, those of the harbour seal and all other phocid species have waved surfaces (Fig. 3). Although we have no information about the significance of these characteristics of vibrissae in different species, differences in hair structure may be especially associated with a quantitatively and/or qualitatively different response to tactile stimulation. In the present study, we therefore tested the ability of harbour seals to detect diameter differences of circular discs by active touch with their mystacial vibrissae, using the same psychophysical method applied by Dehnhardt (1994) for testing a California sea lion.

Materials and methods

Subjects

The study was conducted at 'Tierpark Rheine', Germany, using two experimentally naive harbour seals (*Phoca vitulina*, L.) as subjects: a 2-year-old female (Rosi) and a male (Robbi), 15 years of age. The holding pool for the seals, a 9.0 m \times 5.0 m \times 1.5 m concrete tank with an adjacent dry platform, did not allow separation of animals during testing. Therefore, the seals were trained to station at a hoop (male) or tennis ball (female) attached to the pool-side across the dry platform while the other seal was tested at the platform with its hind flippers still in water. In this way, the respective test animal was not disturbed during trials. To prevent the seals from perceiving any visual information during trials they were blindfolded with eye caps, usually used for human medical purposes.

Stimuli and test apparatus

A graded set of 22 circular discs (1.12, 1.20, 1.26, 1.59, 1.78, 1.95, 2.25, 2.52, 3.56, 5.04, 5.30, 5.50, 5.80, 6.00, 6.18, 6.40, 6.65, 7.13, 7.57, 7.97, 8.36 and 8.74 cm diameter, made of 2 cm

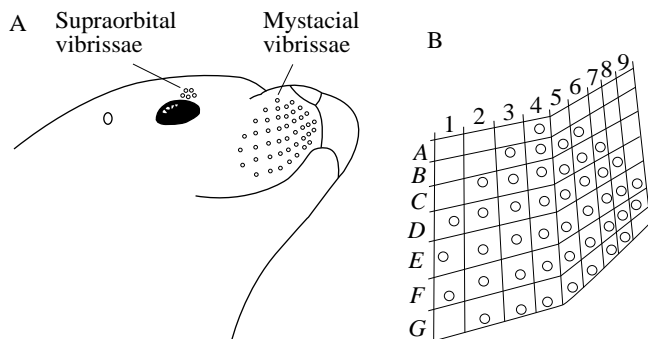


Fig. 1. Distribution of follicles of the mystacial vibrissae within a vibrissal pad of harbour seals. (A) Overview. (B) Exact distribution of vibrissal follicles.

thick Perspex, machined to a tolerance of 0.025 mm) was used for threshold determinations. Two disc-carriers were manufactured, each consisting of a crossbar and an iron rod bent into an asymmetrical U-shape, which was welded to the centre of the crossbar (Fig. 4). The discs were mounted onto the end of the longer shank of the U-shaped rod.

In principle, the same test apparatus was used as described in detail by Dehnhardt (1994), although the height of the stimulus presentation areas (Fig. 4) was reduced so that the discs could be presented 35 cm above the ground. In this way the seals, which are not capable of bending their hind flippers forwards in order to sit in an upright position, could easily reach the discs. In brief, the apparatus consisted of a black wooden wall in which two windows were cut out beside each other. Behind each window there was a U-shaped frame which was capable of being folded back from its vertical position. When the frames were pushed against the windows, the elastic pressure of metal bolts held them in a vertical position. For a trial, the disc carriers were fixed to the hollow ends of the U-shaped frames (Fig. 4), which could then be pushed out of their vertical position by a seal applying a slight amount of pressure with its snout against a disc. At the front of the apparatus, there was a rubber disc between the two windows, serving as a stationing point for the test animal. From this position, a blindfolded seal could easily reach the discs hanging to both sides of its head.

Procedure

A trial started when the subject placed its snout on the stationing point. After the animal had been blindfolded, both



Fig. 2. The female harbour seal 'Rosi' showing the comparatively large angle of protrusion of mystacial vibrissae when not actively raised by the animal (see Fig. 5 in Dehnhardt, 1994, for comparison with *Zalophus californianus*).



Fig. 3. The characteristic surface pattern of vibrissal hair shafts of a California sea lion (top) and a harbour seal (lower). Both hairs were taken from position *E1* (see Fig. 1B) of the respective vibrissal pad of each species. Measured 2 cm above the skin surface, the hair of *Zalophus californianus* is 1.34 mm wide and that of *Phoca vitulina*, measured at a thickening, 0.97 mm.

disc carriers were placed in the U-shaped frames, which were then brought into a vertical position. When the experimenter gave a short blast of a whistle, the seal immediately left the stationing position and began to examine both discs by touching them alternately. The animal was required to indicate its decision by pushing the respective disc out of its vertical position. Upon choosing the correct disc (the larger in diameter), the experimenter again blew a whistle to provide the seal with immediate feedback (secondary reinforcement). For each correct response, the animal was rewarded with a piece of cut herring. Following a choice, both stimuli were removed from the apparatus before the experimenter pushed back the eye caps from the animal's eyes. In order to rule out olfactory cues, the stimuli were cleaned with alcohol before each trial. Each day, two sessions consisting of 16 trials were carried out. During a session, the two stimuli were presented at both positions of the apparatus according to pseudorandom schedules (Gellerman, 1933).

Using a modified method of limits, size difference thresholds were determined for three standard disc diameters: (A) 1.12 cm, (B) 5.04 cm and (C) 8.74 cm. Each test series (A–C) was started with a task in which the test animal showed a reliable discrimination between the standard and a comparison disc (first comparison disc diameters: series A, 5.04 cm; series B, 8.74 cm; series C, 2.52 cm). The size difference between discs was reduced from task to task until a seal failed to make the discrimination. In this way, the upper difference threshold was obtained for standard discs A and B (comparison discs in descending order), and the lower difference threshold for standard disc C (comparison discs in ascending order). The absolute difference threshold ΔD (the difference in disc diameter required to produce a just noticeable difference in sensation) was defined as the difference in diameter between standard and comparison disc at which the test animal performed 75% correct choices. The exact value of ΔD (75% correct choices) was interpolated from an animal's performance at the last diameter difference above threshold and the first diameter difference below threshold. The relative threshold or Weber fraction (c) was calculated as the ratio of the diameter difference at threshold (ΔD) to the

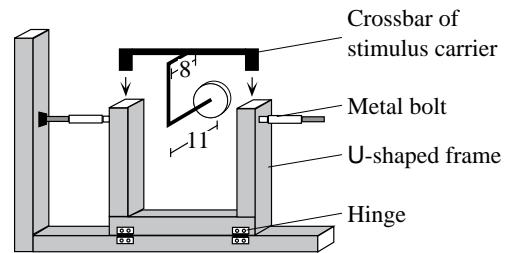


Fig. 4. Schematic drawing of one of the stimulus presentation areas (measurements in cm).

diameter of the starting disc (D). In test series A and B, the starting disc size was the diameter of the standard disc, whereas in test series C it was the diameter of a fictitious comparison disc obtained by subtracting the interpolated value of ΔD from the standard disc. In this way, ΔD was determined as an increase of the starting disc size in all three test series. The criterion for the introduction of a new task was determined by the animal making at least 75% correct choices in three consecutive sessions (36 correct choices at 48 trials; binomial test, $P < 0.001$). When a seal showed an increase or decrease in performance of $\geq 10\%$ correct choices between two sessions as well as when it did not achieve 75% correct choices in three consecutive sessions, it was given the opportunity to improve or stabilize its performance by means of additional sessions.

The behaviour of the test animals in making choices was recorded from behind the apparatus using a video camera. It was focused so that both discs inside the window frames were recorded. From these recordings, the number of times a seal compared both discs in succession during the course of one trial was counted and the way in which the animals touched the discs was described qualitatively.

Results

When presented with the initial discrimination task of test series A (1.12 cm: 5.04 cm diameters) both seals showed a strong preference for the larger disc (100% of the choices). In obtaining size difference thresholds, we took advantage of this unconditioned discrimination by rewarding the seals for their choice of the larger disc throughout the experiments.

Fig. 5A shows the results of the first threshold determination for the standard disc 1.12 cm diameter. Up to a difference in diameter of 1.40 cm, both seals were able to differentiate between the discs without error. A further decrease in diameter difference between standard and comparison disc was accompanied by a decrease in performance until both seals failed to detect a difference in diameter of 0.14 cm (comparison disc diameter 1.26 cm: male 58.3%, female 64.6% correct choices). The interpolated size of the absolute difference threshold ΔD at 75% correct choices was 0.33 cm diameter difference for the male and 0.29 cm diameter difference for the female. These values of ΔD correspond to relative difference thresholds or Weber fractions ($\Delta D/D$) of 0.29 for the male and 0.26 for the female.

When presented with the first task of test series B, where the standard disc 5.04 cm diameter was matched with the largest comparison disc 8.74 cm diameter, the seals were confused by the new disc sizes, resulting in reduced performance during the first session. However, from the second session onwards, both seals showed perfect discrimination by exclusively choosing the larger disc. The results of this test series are illustrated in Fig. 5B. The size of ΔD at 75 % correct choices was 0.63 cm diameter difference for the male and 0.44 cm diameter difference for the female seal. Accordingly, the Weber fraction of the male seal was 0.13 and that of the female 0.09.

During the third threshold determination (Fig. 5C), the final comparison disc diameter that the seals perceived as being smaller than the standard disc of 8.74 cm was 7.56 cm for the male (interpolated value of $D=7.66$ cm diameter, $\Delta D=1.08$ cm diameter difference, Weber fraction=0.14) and 7.97 cm for the female (interpolated value of $D=8.09$ cm diameter, $\Delta D=0.65$ cm diameter difference, Weber fraction=0.08).

The relationship between the Weber fraction and the corresponding starting disc size is shown by the Weber functions in Fig. 5D. The results for both seals indicate that the Weber fraction ($\Delta D/D$) was nearly constant for the two larger disc sizes, but increased greatly for the small starting disc diameter of 1.12 cm by a factor of two for the male and a factor

of three for the female seal. Owing to the low number of threshold values obtained for each animal, the non-linear regression curves are merely of descriptive significance. Since the comparatively high threshold for the small standard disc diameter 1.12 cm had been determined first during the course of the experiment, the lower Weber fractions obtained for the larger discs may have been achieved as a result of the seals' increased experience in making tactile discriminations. For this reason, we determined the size difference threshold for the smallest standard disc once again after completion of test series C. Both seals achieved approximately the same Weber fraction as determined previously (male 0.27; female 0.25).

The number of times that the seals compared both discs in succession during the course of one trial is illustrated in Fig. 6 for each of the three test series A–C. It is obvious that the two test animals differ considerably with regard to their behaviour in making choices. The female seal reacted to decreasing diameter differences, i.e. to the increased difficulty of discrimination tasks, with a steady increase in frequency of successive comparisons in all three test series. In contrast, the male seal only showed a very slight increase in the number of successive comparisons during test series A, when diameter differences approached threshold values. In test series B and C, it kept the number of successive comparisons constant at a

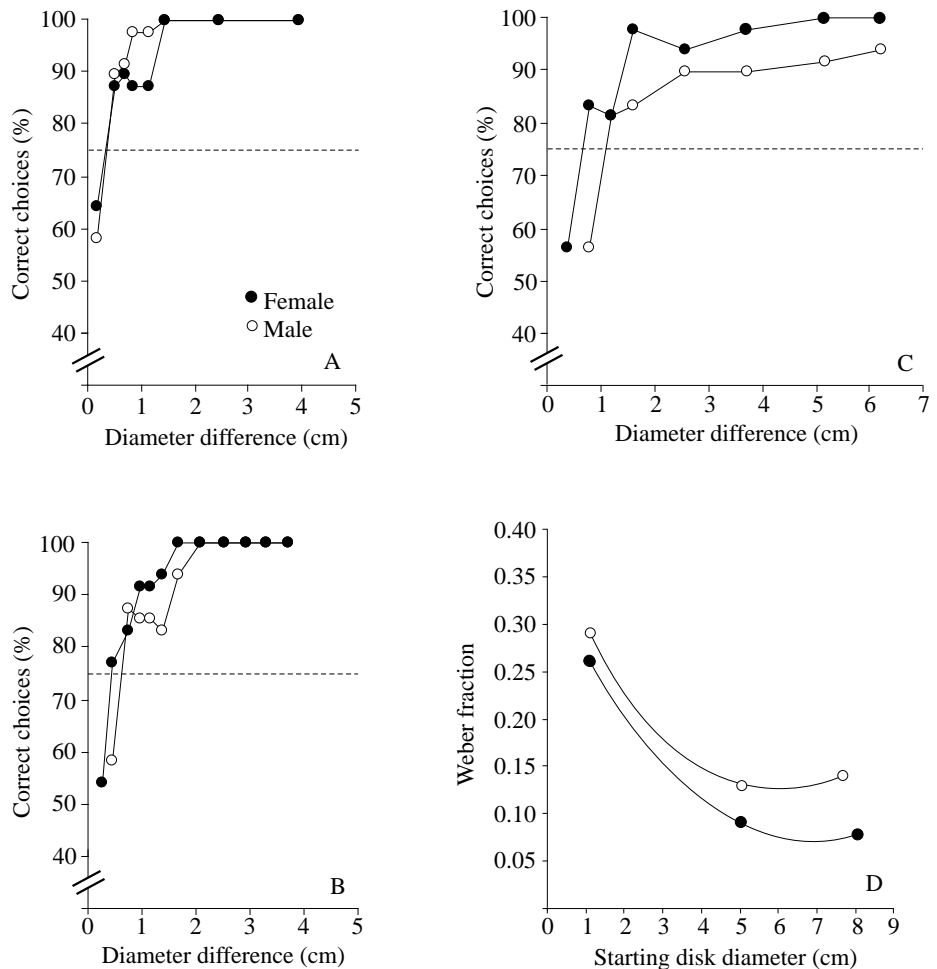


Fig. 5. Psychometric functions of performance on discrimination of diameter differences of circular discs. (A–C) Percentage of correct choices versus difference in diameter between standard and comparison discs. The seals were required to choose the larger disc in each stimulus combination. The horizontal dashed lines at 75 % correct choices mark difference thresholds. Each data point represents the result of 48 trials. (A) Determination of the upper difference threshold for the standard disc diameter 1.12 cm. (B) Determination of the upper difference threshold for the standard disc diameter 5.04 cm. (C) Determination of the lower difference threshold for the standard disc diameter 8.74 cm. (D) Weber functions showing the relationship between Weber fractions (the ratio of the diameter difference at threshold ΔD to the diameter of the starting disc D) and starting disc diameters (D) in both seals.

mean of 1.5 comparisons, irrespective of the difference in diameter between the standard and comparison discs.

Their behaviour in touching the discs was quite similar for both seals and was similar to that described by Dehnhardt (1994) for a California sea lion. As soon as they heard the start signal, the animals left the stationing point and brought their vibrissae into their most extreme forward position. After the localization of a disc, the seal centred its head in relation to the disc, so that the edges of the disc were covered by the vibrissae of both sides of the snout. When touching small discs (up to 3.56 cm in diameter), the seals carried out short lateral head movements, which led to alternating deflections of the vibrissae of both sides of the snout. However, almost no head movements were detectable from the video recordings when the seals touched larger discs (≥ 5.04 cm diameter). Instead, they kept their heads stationary for a fraction of a second while a disc hung centrally between the vibrissae of both sides of the snout. In this way, the vibrissae involved in the tactile process were deflected exclusively by the resistance of the disc. While touching a disc, the vibrissae were not actively moved by the animals.

Discussion

As in species belonging to the other two pinnipeds families, Odobenidae (Pacific walrus; Kastelein and van Gaalen, 1988) and Otariidae (California sea lion; Dehnhardt, 1990, 1994), harbour seals (Phocidae) can use their mystacial vibrissae very efficiently for active touch discriminations. Although the psychometric functions (percentage of correct choices plotted against differences in diameter between standard and comparison discs, Fig. 5A–C) were similar in shape for both animals, the size difference thresholds of the female seal were lower in all test series. This difference in performance may not reflect a real difference in sensitivity, but can be explained by the animals' different behaviour in making choices. While the female always increased the number of comparisons between discs when discrimination became more difficult, the male seal did not compare discs with diameter differences close to threshold more frequently than in tasks where discrimination was easy (Fig. 6). For tactile texture discrimination of humans and monkeys, Sinclair and Burton (1991) have shown that performance is degraded if the number of successive

comparisons is restricted. They argue that a higher number of successive comparisons provides additional information about touched objects and improves performance.

Dehnhardt (1994) determined Weber fractions for a California sea lion ranging from 0.29 for a standard disc of 1.12 cm in diameter to 0.22 for a standard disc of 8.74 cm in diameter, indicating a linear correlation (as predicted by Weber's law, $\Delta D/D=c$) between the starting disc size (D) and the absolute difference threshold (ΔD). In the present study, the Weber fraction of both harbour seals at the small standard disc diameter of 1.12 cm almost perfectly matched that achieved by the sea lion at the same disc size. However, since the Weber fractions of both seals decreased considerably at larger disc sizes (male 0.13; female 0.08) and remained almost constant for the standard discs 5.04 and 8.74 cm in diameter, the Weber functions of our test animals illustrated in Fig. 5D correspond to a modification of Weber's law: $\Delta D/(D+\alpha)=c$, where α is a constant (not determined here; for theoretical considerations concerning the constant α , see Gescheider, 1985; Laming, 1986). To confirm the applicability of this modified psychophysical law to our data, more threshold measurements over a wider range of disc sizes are required.

The lowest threshold obtained for tactile size discriminations of a California sea lion ($c=0.22$; Dehnhardt, 1994) is about twice as high as the lowest thresholds determined for the harbour seals in the present study ($c=0.08$ and 0.13). Since sensory capacity often shows considerable individual variation (Dietze, 1961), and to date only a few individual animals have been tested, it cannot be determined whether these results represent a true difference in differential tactile sensitivity of the vibrissal systems of these species. What can be concluded from this study, however, is that some individual harbour seals can achieve a Weber fraction as low as 0.08. The tactile acuity of other members of this population may be weaker, or possibly better, than this. Whether the Weber fractions obtained for the vibrissae of harbour seals represent good or moderate acuity of this tactile system can best be decided by comparing them with those determined for other species carrying out similar tactile size discriminations. Human subjects measuring the diameter or length of objects using the thumb and index finger achieve a mean Weber fraction of 0.03 (Gaydos, 1958; Stevens and Stone, 1959; Dietze, 1961). Weber fractions determined for the hands of

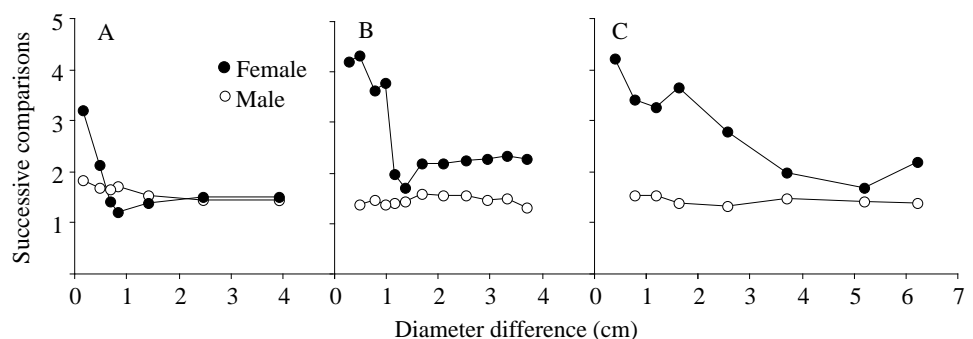


Fig. 6. The number of successive comparisons carried out by the seals as a function of the difference in diameter between standard and comparison discs for each of the three test series A–C. Each point represents the mean value of 48 trials.

lower primates (*Macaca mulatta*, Semmes and Mishkin, 1965; Semmes and Porter, 1972; *Macaca arctoides*, Carlson *et al.* 1989) average 0.10. Compared with this value for the monkey, it becomes clear that the resolving power of the vibrissal system of the harbour seals tested is by no means weaker than that of a prehensile tactile organ. The superiority of the human hand can be attributed to the higher precision of the kinaesthetic sense controlling finger position.

Size discrimination tasks have also been used to determine visual difference thresholds of pinnipeds. For the visual discrimination of circular discs, Weber fractions of California sea lions (Schusterman *et al.* 1965) and harbour seals (Feinstein and Rice, 1966) were estimated to be 0.06. This threshold is similar to those obtained for visual discriminations of other pinniped species (*Phoca largha*, Wartzok and Ray, 1976; *Arctocephalus pusillus*, Busch and Dücker, 1987). While in discrimination tasks involving the perception of size (as well as other spatial stimuli) vision appears to be more accurate than touch (Lederman, 1982), the lowest tactile difference thresholds determined in the present study come close that found for the visual modality of harbour seals, which may give some idea as to the biological importance of the vibrissal system for these animals.

For the tactile size discrimination of the California sea lion, Dehnhardt (1994) suggested a model describing the respective roles of the two sensory subsystems, mechanoreception and kinaesthesia, both contributing to active touch achievements (Gibson, 1962; Loomis and Lederman, 1986). Unlike humans sensing the angles of the finger joints when measuring size differences with the thumb and index finger (kinaesthetic discrimination, John *et al.* 1989), the sea lion carried out identical tactile movements with the entire head. Identical tactile movements for discs differing in size must have resulted in quantitatively different mechanical stimulations of follicle receptors, so that, in this case, the discrimination relies on mechanoreception, whereas its accuracy was co-determined by the kinaesthetic control of tactile movements. When touching small discs, the tactile behaviour of our harbour seals resembled that of the sea lion, suggesting that the same sensory processes underlie their abilities. However, since the seals tended not to move their heads when touching larger discs, so that the degree of vibrissal deflection was merely determined by the size of a disc, kinaesthesia should have been of minor importance for these size measurements.

In which context are these active touch capabilities of importance for seals in the wild? Beside their social function described by Miller (1975), vibrissae may be an indispensable sensory system in prey detection. While it is hard to imagine how a seal could detect pelagic fish by active touch with its vibrissae, this function is conceivable for benthic prey. Observations in the wild lend support to the hypothesis that pinnipeds use their vibrissae when foraging at the sea bottom. Lindt (1956) observed Southern sea lions (*Otaria byronia*) swimming under water with the vibrissae erect while touching the sea bottom '...as if in search of something' (p. 288). A recent study on diving behaviour of lactating female Southern

sea lions also concluded that these animals are bottom-feeders (R. Werner, personal communication). On the basis of otoliths found in faecal samples of harbour seals from Danish and Swedish waters, Härkönen (1987, 1988) demonstrated that benthic prey, especially flatfish, are of supreme importance for these pinnipeds.

The finding that blind seals do not have problems in orientation and are well-nourished throughout the year (Poulter, 1963; Newby *et al.* 1970) also suggests the potential significance of vibrissae for the detection and identification of prey, especially since several experiments have failed to find evidence of a sonar system in pinnipeds (Schusterman, 1968). We do not assume that prey detection in pinnipeds relies exclusively on information received by vibrissae, but hold the view that, when vision is excluded during foraging, good tactual capabilities may be of great importance for these opportunistic feeders. Whether vibrissae are only sensitive to tactile stimulation obtained by active touch or also permit a seal to perceive vibrotactile information will be investigated in a subsequent study.

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References

- BUSCH, H. AND DÜCKER, G. (1987). Das visuelle Leistungsvermögen der Seebären (*Arctocephalus pusillus* und *Arctocephalus australis*). *Zool. Anzeiger* **219**, 197–224.
- CARLSON, S., TANILA, H., LINNANKOSKI, I., PERTOVAARA, A. AND KEHR, A. (1989). Comparison of tactile discrimination ability of visually deprived and normal monkeys. *Acta physiol. scand.* **135**, 405–410.
- DEHNHARDT, G. (1990). Preliminary results from psychophysical studies on the tactile sensitivity in marine mammals. In *Sensory Abilities of Cetaceans* (ed. J. A. Thomas and R. A. Kastelein), pp. 435–446. New York: Plenum Press.
- DEHNHARDT, G. (1994). Tactile size discrimination by a California sea lion (*Zalophus californianus*) using its mystacial vibrissae. *J. comp. Physiol. A* **175**, 791–800.
- DIETZE, A. G. (1961). Kinaesthetic discrimination: the difference limen for finger span. *J. Psychol.* **51**, 165–168.
- DYKES, R. W. (1975). Afferent fibres from mystacial vibrissae of cats and seals. *J. Neurophysiol.* **38**, 650–662.
- FEINSTEIN, S. H. AND RICE, C. E. (1966). Discrimination of area differences by the Harbour seal. *Psychon. Sci.* **4**, 379–380.
- GAYDOS, H. F. (1958). Sensitivity in the judgement of size by finger-span. *Am. J. Psychol.* **71**, 557–562.
- GELLERMAN, L. W. (1933). Chance orders of alternating stimuli in visual discrimination experiments. *J. genet. Psychol.* **42**, 206–208.
- GESCHIEDER, G. A. (1985). *Psychophysics: Method, Theory and Application*. Hillsdale, NJ: Lawrence Erlbaum.

- GIBSON, J. J. (1962). Observations on active touch. *Psychol. Rev.* **69**, 477–491.
- HÄRKÖNEN, T. J. (1987). Seasonal and regional variations in the feeding habits of the harbour seal, *Phoca vitulina*, in the Skagerrak and Kattegat. *J. Zool., Lond.* **213**, 535–543.
- HÄRKÖNEN, T. J. (1988). Food–habitat relationship of harbour seals and black cormorants in Skagerrak and Kattegat. *J. Zool., Lond.* **214**, 673–681.
- HYVÄRINEN, H. (1989). Diving in darkness: Whiskers as sense organs of the Ringed seal (*Phoca hispida*). *J. Zool., Lond.* **218**, 663–678.
- JOHN, K. T., GOODWIN, A. W. AND DARIAN-SMITH, I. (1989). Tactile discrimination of thickness. *Expl Brain Res.* **78**, 62–68.
- KASTELEIN, R. A. AND VAN GAALEN, M. A. (1988). The sensitivity of the vibrissae of a Pacific walrus (*Odobenus rosmarus divergens*). *Aquatic Mamm.* **14**, 123–133.
- LADYGINA, T. F., POPOV, V. V. AND SUPIN, A. YA. (1985). Somatotopic projections in the cerebral cortex of the fur seal (*Callorhinus ursinus*). *Acad. Sci. Moscow* **17**, 344–351.
- LAMING, D. (1986). *Sensory Analysis*. London: Academic Press.
- LEDERMAN, S. J. (1982). The perception of texture by touch. In *Tactual Perception: A Sourcebook* (ed. W. Schiff and E. Foulke), pp. 130–167. Cambridge: Cambridge University Press.
- LINDT, C. C. (1956). Underwater behaviour of the southern sea lion, *Otaria jubata*. *J. Mammal.* **37**, 287–288.
- LING, J. K. (1977). Vibrissae of marine mammals. In *Functional Anatomy of Marine Mammals*, vol. 3 (ed. R. J. Harrison), pp. 387–415. London: Academic Press.
- LOOMIS, J. M. AND LEDERMAN, S. J. (1986). Tactual perception. In *Handbook of Perception and Human Performance*, vol. 2 (ed. K. R. Boff, L. Kaufman and J. R. Thomas), pp. 1–41. New York: Wiley.
- MILLER, E. H. (1975). A comparative study of facial expressions of two species of pinnipeds. *Behaviour* **53**, 268–284.
- NEWBY, T. C., HART, F. M. AND ARNOLD, R. A. (1970). Weight and blindness of harbor seals. *J. Mammal.* **51**, 152.
- POULTER, T. C. (1963). Sonar signals of the sea lion. *Science* **139**, 753–754.
- SCHUSTERMAN, R. J. (1968). Experimental laboratory studies of pinniped behavior. In *The Behavior and Physiology of Pinnipeds* (ed. R. J. Harrison, R. C. Hubbard, R. S. Peterson, R. C. Rice and R. J. Schusterman), pp. 87–171. New York: Appleton-Century-Crofts.
- SCHUSTERMAN, R. J., KELLOGG, W. N. AND RICE, C. E. (1965). Underwater visual discrimination by the California sea lion. *Science* **147**, 1594–1596.
- SEMMES, J. AND MISHKIN, M. (1965). Somatosensory loss in monkeys after ipsilateral cortical ablation. *J. Neurophysiol.* **28**, 473–486.
- SEMMES, J. AND PORTER, L. (1972). A comparison of precentral and postcentral cortical lesions on somatosensory discrimination in the monkey. *Cortex* **10**, 55–68.
- SINCLAIR, R. J. AND BURTON, H. (1991). Tactile discrimination of gratings: psychophysical and neural correlates in human and monkey. *Somatosens. Motor Res.* **8**, 241–248.
- STEPHENS, R. J., BEEBE, I. J. AND POULTER, T. C. (1973). Innervation of the vibrissae of the California sea lion *Zalophus californianus*. *Anat. Rec.* **176**, 421–442.
- STEVENS, S. S. AND STONE, G. (1959). Finger span: ratio scale, category scale and jnd scale. *J. exp. Psychol.* **57**, 91–95.
- WARTZOK, D. AND RAY, G. C. (1976). A verification of Weber's law for visual discrimination of disc sizes in the Bering sea spotted seal, *Phoca largha*. *Vision Res.* **16**, 819–822.
- WATKINS, W. A. AND WARTZOK, D. (1985). Sensory biophysics of marine mammals. *Mar. Mammal Sci.* **1**, 219–260.