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Tactile size discrimination by a California sea lion (*Zalophus californianus*) using its mystacial vibrissae

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Abstract The capability of a blindfolded California sea lion (*Zalophus californianus*) to discriminate diameter differences of circular discs by means of active touch with its mystacial vibrissae was studied. Using a forced choice paradigm the sea lion was required to choose the larger of two simultaneously presented perspex discs. Absolute difference thresholds (ΔD) were determined for 3 standard discs (1.12 cm ∅, 2.52 cm ∅, 8.74 cm ∅) by the psychophysical method of constants. Increasing disc size resulted in an increase in the absolute difference threshold from 0.33 cm for the smallest disc size to 1.55 cm for the largest disc size. The relative difference threshold (Weber fraction) remained approximately constant at a mean value of 0.26. According to a video analysis the sea lion did not move its vibrissae when touching the discs. Instead, it performed precisely controlled lateral head movements, with the touched disc located centrally between the vibrissae of both sides of the muzzle. Since the extent of these head movements was identical at discs to be compared, discs of different size must have led to different degrees of deflection of vibrissae involved in the tactile process, resulting in quantitatively different mechanical stimulations of mechanoreceptors in the follicles. This suggests that the accuracy of the sea lion's size discrimination was determined by the efficiency of two sensory systems: the mechanosensitivity of follicle receptors as well as kinaesthesis.

Key words Vibrissae · Active tactile discrimination Difference thresholds · Kinaesthesis · California sea lion

Abbreviations D starting stimulus size
D_i size of the interpolated comparison disc at 75% correct choices
ΔD absolute difference threshold
c relative difference threshold (Weber fraction)
∅ diameter

Introduction

A characteristic feature of pinnipeds are the conspicuously well developed mystacial vibrissae, also called sinus hairs or tactile hairs, which are arranged symmetrically on both sides of the muzzle in varying horizontal rows (Ling 1977). The lengths of the hairs within a vibrissal pad vary considerably. Those on the side of the muzzle which are more posteriorly positioned are significantly longer than those located on the muzzle tip.

Apart from the particular length and strength of the hair shafts, the vibrissal system of pinnipeds differs from that of terrestrial mammals above all in the stronger innervation of the follicles. In the Ringed seal (*Phoca hispida*) Hyvärinen (1989) could verify that each of the 100 vibrissal follicles is served by 1000–1600 nerve fibres. In the Northern fur seal (*Callorhinus ursinus*) this impressive innervation of the follicles is accompanied by a strong central representation of the vibrissae in the somatosensory cortex (Ladygina et al. 1985), which may give some idea as to the biological importance of this sensory system for these animals.

Stephens et al. (1973) identified different corpuscular mechanoreceptors in the follicles of California sea lions (*Zalophus californianus*), as did Hyvärinen (1989) when examining the follicles of Ringed seals (*Phoca hispida*). Along with free nerve endings, there are Merkel cells (MC), lancet shaped terminations (LST) and Pacinian corpuscles (PC). Because of the existence of slowly adapting (MC) and also rapidly adapting (LST and PC) receptors, sensitivity to static as well as to vibratory stimuli can be assumed (Stephens et al. 1973).

Renouf (1979) and Mills and Renouf (1986) determined behavioral detection thresholds for vibrations for the Harbor seal (*Phoca vitulina*) at 50–2500 Hz. In both studies the animals reached their maximum sensitivity level at a frequency of >750 Hz. In contrast to these re-

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sults, single unit recordings at the infraorbital branch of the trigeminal nerve of Harbor seals and Grey seals (*Halichoerus grypus*) revealed that only very few of the rapidly adapting afferent fibres responded to vibrations of >500 Hz (Dykes 1972, 1975). Additionally, these fibres required a large stimulus amplitude. Due to the functional characteristic of the rapidly and slowly adapting afferent fibres, Dykes assumed that the vibrissal system is primarily equipped for the perception of tactile information which the animals receive through physical contact of the vibrissae to objects in the environment. He postulated active tactile achievements such as the recognition of surface structures as well as the discrimination of both the shape and size of objects.

Active tactile discriminations by means of the mystacial vibrissae have been shown for a Walrus (*Odobenus rosmarus*, Kastelein and van Gaalen 1988) and for a California sea lion (*Zalophus californianus*, Dehnhardt 1990). Both studies indicate that the tactile capability of these pinniped species to differentiate between geometric forms is comparable to that of mammals using prehensile tactile organs for this purpose (Rensch and Dücker 1963).

The present study was conducted to determine the tactile capability of a California sea lion to discriminate diameter differences of circular discs by means of its mystacial vibrissae. Absolute (ΔD) and relative difference thresholds (Weber fractions=c) were determined and compared to the tactile resolving power of the tactile organs of other mammals. Determined difference thresholds for three different standard disc sizes were used to examine whether the tactile achievement of the sea lion was in accordance with Weber's law. This basic psychophysical law predicts that the change in stimulus size that can just be discriminated (absolute difference threshold ΔD) is a constant fraction (Weber fraction or relative difference threshold c) of the starting stimulus size (D) (Gescheider 1985). It is described by the equation $\Delta D{:}D=c$.

Finally, video recordings of the tactile process were used to analyze the function of the vibrissal system during active touch.

Materials and methods

Subject

The investigation was carried out using a 10 years old female California sea lion (*Zalophus californianus*) named Fleur in the Delphinarium Münster, Germany. This was also the subject used in the experiment of Dehnhardt (1990) who demonstrated that sea lions are capable of differentiating between shapes with their mystacial vibrissae.

The sea lion was trained to wear eye caps in order to prevent it from examining stimuli visually during trials. The same eye caps were employed as are used for human medical purposes. They were covered with waterproof adhesive tape and a 4 mm thick rubber lining was fitted on the inside rim. Additionally, each cap was fitted with a rubber band which was used to securely attach the cap to the sea lion's head.

Stimuli

A graded set of stimuli, consisting of 17 circular discs which were made of perspex 2 cm thick, was used. Three of the stimuli served as standard discs (1.12, 2.52 and 8.74 cm ∅) and the remaining 14 stimuli (1.20, 1.26, 1.59, 1.78, 1.95, 2.25, 2.87, 3.19, 3.56, 5.04, 6.18, 7.13, 7.57, 7.97 cm ∅) were used as comparison discs. All discs were machined with a permissable deviation in diameter of 0.025 mm. An 1 cm deep, 6 mm wide screw thread was cut into the centre of one of the flat sides of each disc. Two disc carriers made of 8 mm thick stainless steel were manufactured (Fig. 1B). Each of these consisted of a transverse rod, on whose ends 3 cm long vertical metal supports (at right angles) were to be found. The shorter shank of an iron rod bent into an asymmetrical U shape was welded to the centre of the crossbar in such a way as to be at a 90° angle to it. It was possible to screw a disc onto the end of the longer shank of the U-shaped rod.

Test apparatus

The test apparatus (Fig. 1A,B) consisted of a white Poly Vinyl Chloride (PVC) wall attached to a steel frame. To stabilize the apparatus two supporting bars were affixed to the exterior sides of the equipment.

Two windows were cut out beside each other in the PVC wall. The bottom edge of each window was 53 cm above the ground. A slightly convex shaped rubber disc (10 cm ∅) was affixed to the front of the apparatus between the two windows. This disc served as a stationing point for the sea lion. There was a U-shaped frame behind each of the windows, which was capable of being folded back from its vertical position. A stop block secured between both frames ensured that these could only fall back to an angle of 40°. When the frames were pushed against the windows, the elastic pressure of spring-cushioned spheres incorporated at the free end of metal bolts held them in a vertical position (Fig. 1B).

The disc carriers could be affixed to the hollow ends of the vertical legs of the U-shaped frames. When the frames were in a vertical position the attached discs hung 2 cm in front of the PVC wall, each in the centre of one of the windows. The area around each disc was free of distracting tactile stimuli. The centre of each disc was 22 cm from the stationing point ensuring that it could be reached without straining by the sea lion. A U-shaped frame could be pushed out of its vertical position by the sea lion applying a slight amount of pressure with its muzzle against the corresponding disc.

Experimental procedure

All tests were carried out on a dry platform adjacent to the sea lion's pool. At the beginning of a trial the sea lion positioned itself in front of the apparatus by pressing its nose against the stationing point. Only after the sea lion was in this position were its eyes covered by the eye caps. As soon as the animal was blindfolded both disc carriers with differing sized discs were placed in the U-shaped frames. Both frames were then brought simultaneously into a vertical position so that the discs were placed in the middle of the windows to each side of the sea lion.

After distancing himself 2.5 m from the apparatus, the experimenter gave a short blast of a whistle (approximately 0.5 s) as a signal for the trial to start. Upon hearing the whistle the sea lion immediately left its stationing position and began to examine both discs by touching them alternately. The sea lion was required to respond by pressing its nose against one of the two discs and deflect the disc and the U-shaped frame against the stop block.

If the sea lion chose correctly the experimenter blew a whistle for 2 s and rewarded the sea lion with two fish. If the sea lion chose incorrectly no whistle sounded and no fish were given. Following a choice both discs were removed from the apparatus. After this, the sea lion stationed at the experimenter's hand, who then pushed back the eye caps from its eyes. In order to rule out olfactory cues the discs were cleaned thoroughly with alcohol before

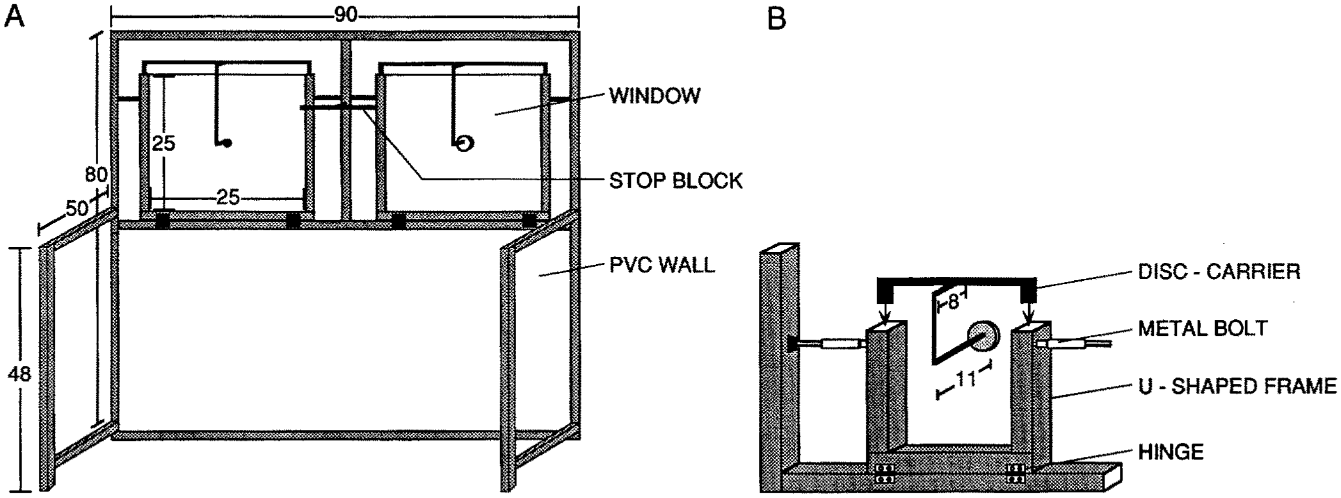


Fig. 1A,B Schematic drawing of the test apparatus (all measurements in cm). **A** Overview of the back of the apparatus. **B** Detail of one of the stimulus presentation areas

each trial. Each day one session consisting of 16 trials was carried out. During a session a standard disc was always combined with the same comparison disc (see below). The discs were presented at both positions of the apparatus according to pseudorandom schedules (Gellerman 1933).

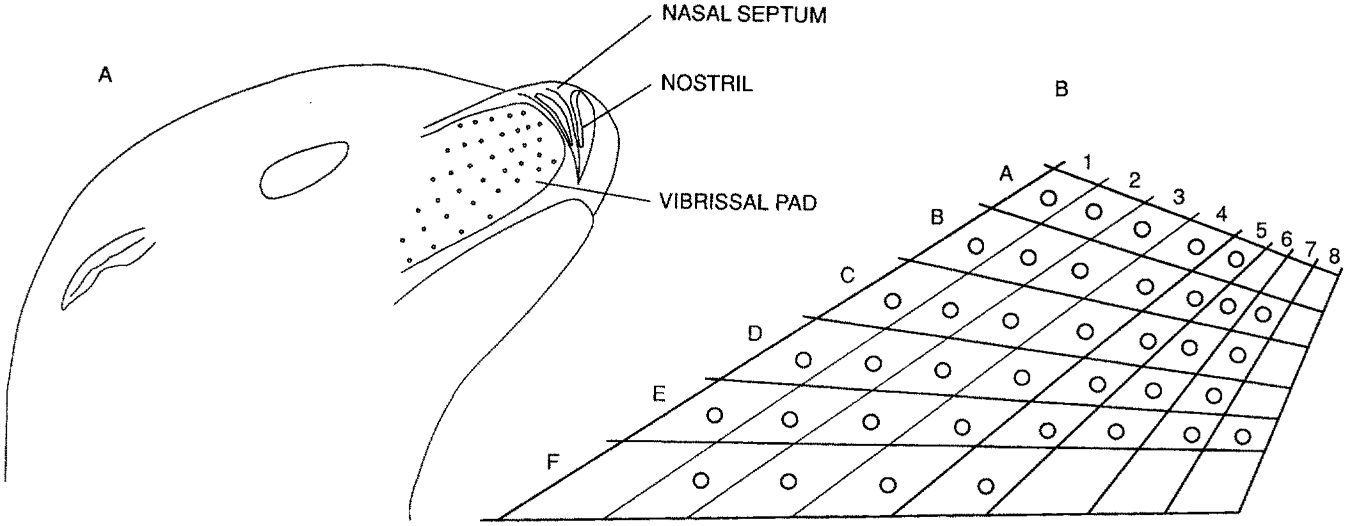
Difference thresholds were determined by a modified method of constant stimuli in a range of three differing standard disc sizes: (A) 1.12 cm ∅, (B) 2.52 cm ∅, and (C) 8.74 cm ∅. In each case, the animal was first confronted with a task where the size difference between the standard and the comparison disc could be regarded as being above threshold. After a successful discrimination the size of the comparison disc was slightly adjusted to the size of the standard disc. In this way the size difference between both stimuli was reduced from task to task until the sea lion was no longer able to differentiate between both discs. In this way the upper difference threshold was obtained for the standard disc A and the lower difference threshold for the standard disc C. For the medium standard disc size B the lower as well as the upper difference threshold were obtained by an ascending series of comparison discs.

The absolute difference threshold was defined as the size difference between the standard disc and the comparison disc at which the sea lion reached 75% correct choices. The exact value of the threshold was calculated by means of linear interpolation from the sea lion's performance at the last size difference above threshold and the first size difference below threshold. The criterion for the introduction of a new task was determined by the sea lion making 75% correct choices in three consecutive sessions. According to the binomial distribution 75% correct choices at n=48 trials is highly significant (P=0.00025). When the sea lion did not achieve 75% correct choices, it was given the opportunity to improve its performance by means of additional sessions. The duration of these learning periods was determined by the sea lion's general willingness to make choices.

Video analysis

During each first session with a new discrimination task a video camera (SABA CVC 76 SI) was placed behind the test apparatus. It was focussed in such a way that only the disc inside the right-hand window frame (from the sea lion's viewpoint) was recorded. Because the discs were made of perspex, each trial could be evaluated in detail afterwards. For each of these sessions the reaction time was measured with a digital clock integrated into the video camera (1/10 s accuracy). The reaction time was defined as the time which passed between the starting signal and the moment the U-shaped

Fig. 2A,B Distribution of follicles of the mystacial vibrissae within a vibrissal pad of California sea lions (n=4). **A** Overview. **B** Exact distribution of vibrissal follicles



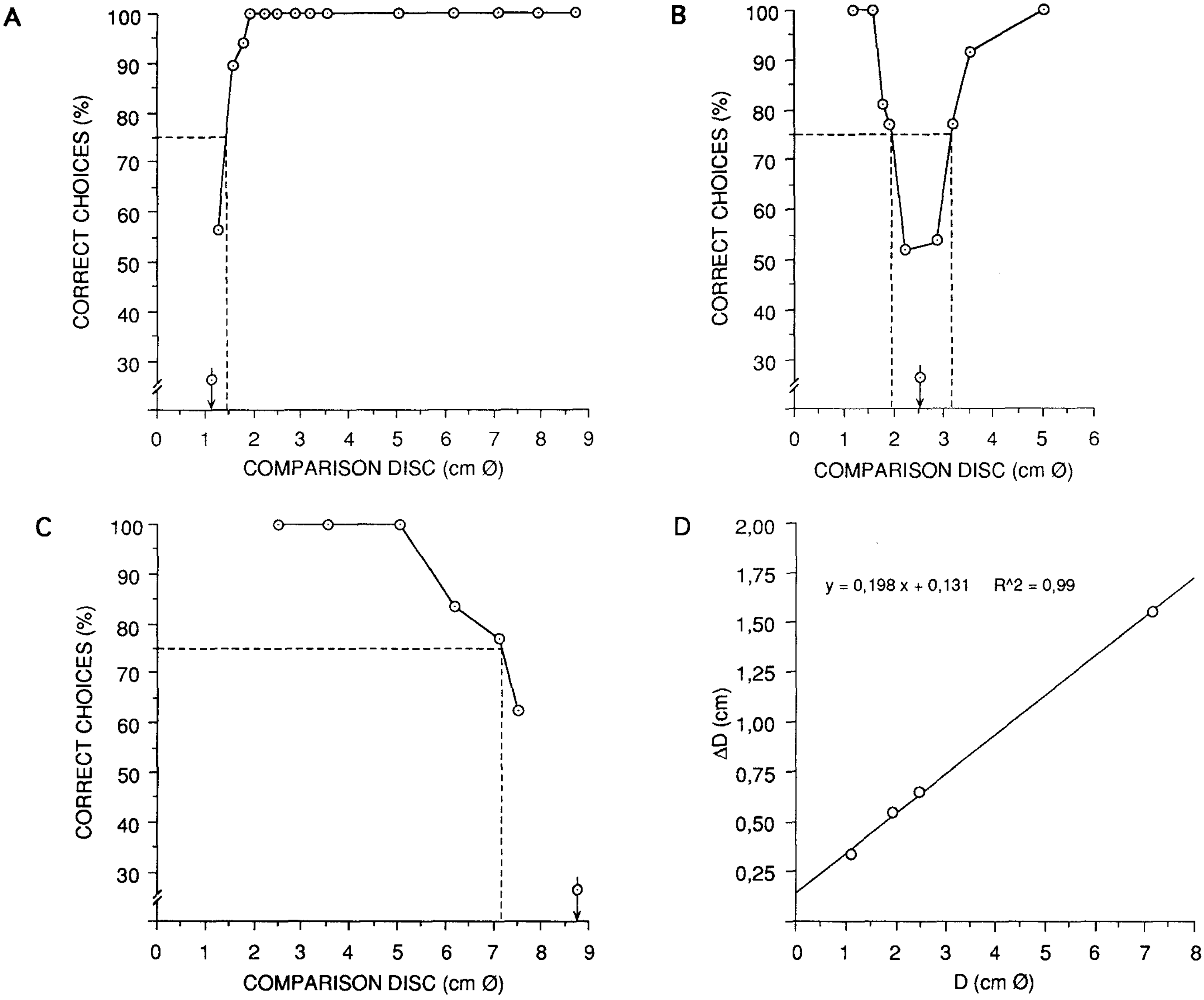


Fig. 3A–D Psychometric functions of performance on discriminating diameter differences of circular discs (**A–C**). Percent correct choices plotted versus the diameter of comparison discs. The sea lion was required to choose the larger disc in each stimulus combination. The *vertical arrows* on the *abscissa* indicate the size of the respective standard disc. The *horizontal dashed lines* at 75% correct choices mark difference thresholds; the *vertical dashed lines* indicate the size of the interpolated comparison disc at threshold. Each data point represents the result of 48 trials. **A** Determination of the upper difference threshold for the standard disc size 1.12 cm Ø. **B** Determination of the upper and lower difference threshold for the standard disc size 2.52 cm Ø. The sea lion had to choose the standard disc during determination of the lower threshold and the respective comparison disc during determination of the upper threshold. **C** Determination of the lower difference threshold for the standard disc size 8.74 cm Ø. **D** Linear regression of the absolute difference thresholds (ΔD) with regard to the corresponding starting stimulus sizes (D)

frame of the chosen disc fell against the stop block. For the same session the number of times the sea lion compared both discs in succession during the course of one trial was also evaluated.

With a video recorder (JVC-HR D 725 EG) a frame by frame analysis of the tactile process was done. By covering the TV monitor screen with a transparent thin sheet foil, on which a millimetre scale was imprinted, the extent of tactile movements could be calculated by measuring the position changes of the sea lion's head in relation to the touched disc. The vertical nasal septum of the sea lion and the drill-hole in the discs'centre served as reference points. During the final session of each discrimination task the video camera was positioned to the right of the sea lion. The recordings made from this perspective made it possible to determine the minimal distance between the muzzle surface and the disc touched.

Before the experiment started, the mystacial vibrissae of the subject as well as those of three other California sea lions (2,1) have been counted and their distribution plotted in detail (Fig. 2). In this way it was possible to identify single vibrissae involved in the tactile process from the video recordings. The vibrissal pads of all 4 measured animals had 38 vibrissae in each pad arranged in 6 more or less horizontal rows parallel to the mouth line (see Fig. 2).

Results

Threshold determination

Initially the ability of the sea lion to differentiate between the largest (8.74 cm Ø) and the smallest disc

(1.12 cm ∅) of the stimulus set was tested. The sea lion spontaneously touched both of the discs in sequence and chose exclusively that with a diameter of 8.74 cm. Because of this strong preference for the larger disc, the sea lion was always rewarded for its choice of the larger disc in each discrimination task during the entire experiment.

The psychometric function in Fig. 3A shows the result of the first threshold determination using the standard disc 1.12 cm ∅. Up to a difference in diameter of 0.83 cm the sea lion was able to differentiate between the discs without error. Performance accuracy was still almost 90% correct choices at a diameter difference of 0.47 cm. With the next smaller comparison disc (1.26 cm ∅) the sea lion's performance accuracy fell to chance level. The interpolated size of the comparison disc D_i at 75% correct choices was 1.45 cm ∅ resulting in an absolute difference threshold ΔD of 1.45 cm–1.12 cm=0.33 cm, and a corresponding relative difference threshold c (Weber fraction) of 0.33:1.12=0.29.

The results of the second test series, in which the lower and the upper difference thresholds for the standard disc 2.52 cm ∅ were determined, are illustrated in Fig. 3B. When the comparison discs were smaller than the standard disc the size of D_i at 75% correct choices was 1.98 cm ∅, which results in an absolute lower difference threshold ΔD of 0.54 cm (c=0.27). The upper difference threshold was determined by further enlarging the comparison discs over and above the standard disc. Here the size of D_i at 75% correct choices was 3.16 cm ∅ (ΔD=0.64 cm, c=0.25).

For the standard disc of 8.74 cm ∅ a threshold value far in excess of those stimulus diameters determined up to this point was obtained (Fig. 3C). By gradually reducing the diameter difference down to 1.17 cm the sea lion's performance fell to 77.1% correct choices. Smaller differences in diameter were no longer identified. The size of D_i at 75% correct choices was 7.19 cm ∅. The absolute difference threshold ΔD was 1.55 cm (c=0.22).

In tasks involving size differences below threshold the sea lion did not improve its performance by means of a learning period (more than three sessions) in any of the three test series. Instead, the animal generally showed an increasing preference for the left-hand side position. In addition, the animal increasingly exhibited non-test oriented behavior. This initially consisted of the animal returning to the stationing position after a short comparison of the discs and only making a choice after being urged to do so many times. On being further confronted with such tasks the sea lion even refused the attempt to put on the eye caps, and moved in a circle while barking loudly. Once the animal behaved in this way no further tests were carried out.

A comparison of the absolute difference thresholds determined for the different standard discs shows that the larger the starting stimulus size (D=1.12 cm ∅; D_i=1.98 cm ∅; D=2.52 cm ∅; D_i=7.19 cm ∅) the higher the corresponding value of the absolute difference threshold ΔD. In contrast, the relative difference threshold c (mean value=0.26 cm) remained approximately constant. This linear correlation between the starting stimulus size and the size of the absolute difference threshold ΔD is illustrated by the linear regression in Fig. 3D.

Choice behavior

In Fig. 4 the sea lion's behavior in making choices is illustrated by the parameters "reaction time" and "number of successive comparisons" itemized for each of the three test series. The parallel course of the curves obtained for the two parameters shows that the length of

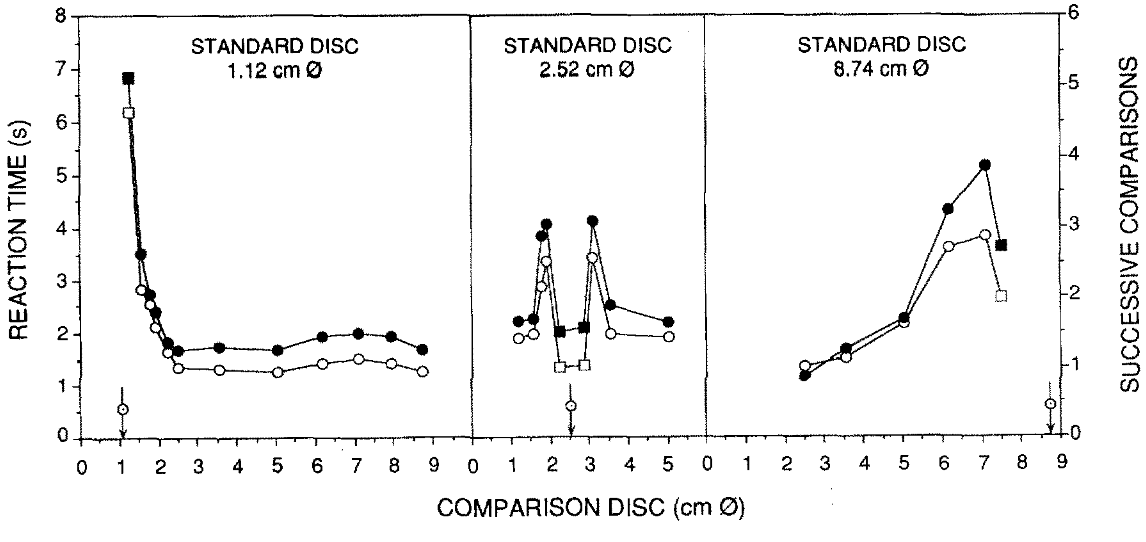


Fig. 4 The relation between the sea lion's 'reaction time' (*open circles*) and the number of 'successive comparisons' (*filled circles*) carried out by the sea lion itemized for each of the three test series. *Open* and *filled squares* indicate 'reaction time' and 'number of successive comparisons' for discrimination tasks, where the size difference was below threshold. The *vertical arrows* on the *abscissa* mark the size of the standard discs. Each point represents the mean value of 16 trials. Both parameters are plotted versus the size of comparison discs, indicating the degree of difficulty of the respective discrimination

the reaction time was determined by the number of successive comparisons. As long as the sea lion was able to perceive a size difference it reacted to the decreasing diameter differences, not by a longer period spent touching the individual disc, but rather by an increased frequency in successive comparisons. This was also the case during the last task of the first test series (standard disc 1.12 cm ∅, comparison disc 1.26 cm ∅), in which the size difference was clearly below threshold. During the test series 2 and 3, the sea lion did not increase the number of successive comparisons when the size difference was below threshold. Instead it developed a position preference, so that in these tasks the values of both parameters were considerably lower than in tasks with size differences above threshold.

Tactile behavior

During the time the sea lion remained at the stationing point at the beginning of a trial, its vibrissae laid back close to the muzzle (Fig. 5, left hand side). As soon as it heard the starting signal the sea lion left the stationing point, and it brought its vibrissae into the most extreme forward position (Fig. 5, right hand side). With the erected vibrissae, the sea lion oriented itself always to the disc in the right hand position first. Once the long vibrissae D/E 1–4 (see Fig. 2) had made first contact with the disc, the sea lion, in a fraction of a second, positioned its head in such a way that the vertical nasal septum was placed in front of the disc. In this way the edges of the disc were covered by the vibrissae of both sides of the muzzle. Once in this position, the sea lion carried out multiple short lateral head movements whose extent to both sides (right/left) of the disc were identical (Fig. 6A). As a result of these head movements the vibrissae of both sides of the muzzle which were involved in the tactile process were deflected alternately. The vibrissae themselves remained in an upright position during the tactile process and were not actively moved by the animal. The extent of the sea lion's lateral head movements are illustrated in Fig. 6A for the three standard discs, for the corresponding final comparison discs still differentiated from the respective standard disc and for the first comparison discs no longer differentiated from the respective standard disc. In the case of the smaller disc sizes (1.12–3.19 cm ∅) the extent of the animal's lateral head movements was a relatively constant 1.16 cm. Upon touching the larger discs measuring 7.13 cm ∅, 7.56 cm ∅ and 8.74 cm ∅, the extent of the lateral head movements did in fact increase (~2.3 cm), however, it also remained relatively constant for these three disc sizes. This indicates that the sea lion carried out virtually identical tactile movements on stimuli to be compared at threshold. The angle of vibrissal deflection caused by these tactile movements could not be measured due to the curvature of the hairs.

The animal took great care not to touch the discs with the muzzle surface during the tactile process. Where this did in fact take place, for example, when orienting itself between the two discs, the sea lion pulled its head back immediately so that only the vibrissae had contact with the disc. Depending on the size of the disc the distance kept between the muzzle surface and the surface of the disc was relatively constant. For the disc sizes 1.12–3.19 cm ∅, the distance averaged 0.9 cm, as compared with 2.4 cm involving the larger discs (Fig. 6B).

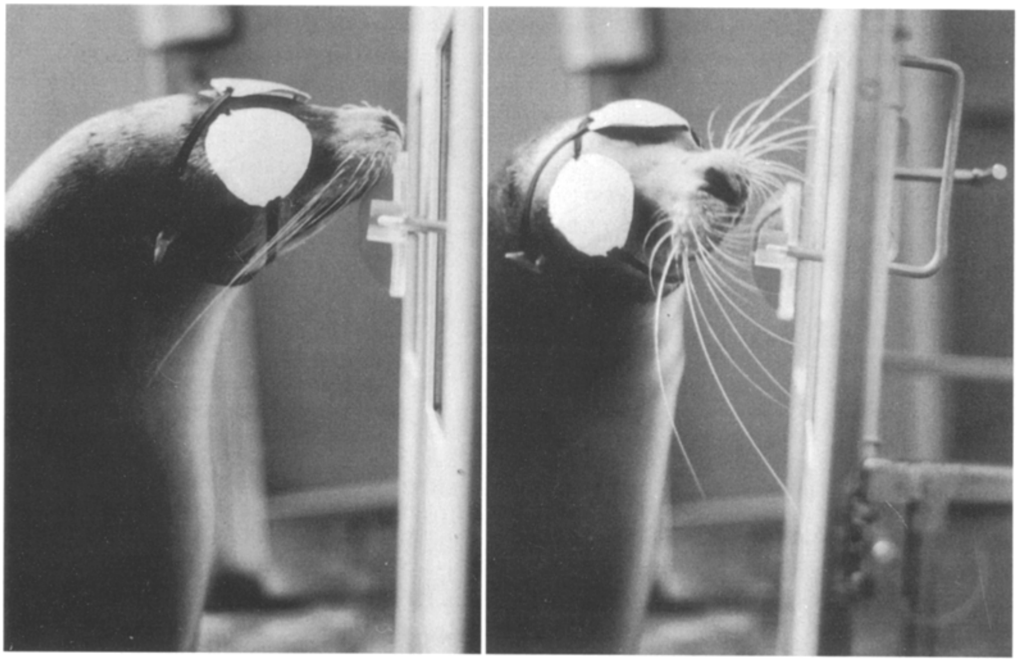


Fig. 5 The sea lion in the stationing position at the beginning of a trial (*left hand side*) and immediately after the starting signal with its vibrissae in the most extreme forward position (*right hand side*)

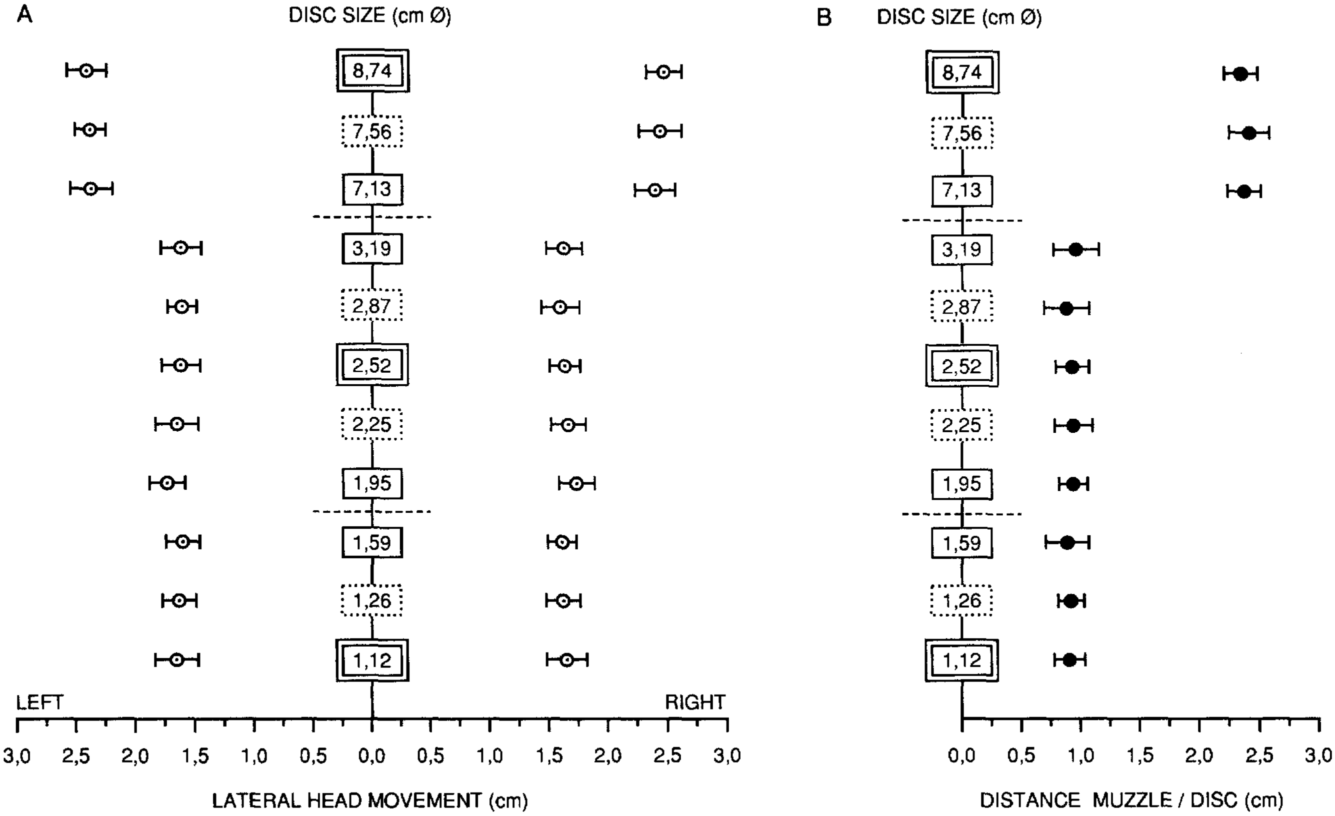


Fig. 6 **A** The extent of the sea lion's lateral head movements while touching a disc illustrated for the three standard discs (*double frames*), the corresponding final comparison disc the animal still distinguished from the respective standard disc (*single frames*) and the first comparison disc the sea lion no longer differentiated from the respective standard disc (*dashed frames*). **B** The distance the sea lion kept between the muzzle surface and the surface of a disc. *Horizontal dashed lines* at ordinates indicate disc sizes belonging to the same test series

Only certain vibrissae in the vibrissal pads of both sides of the muzzle were involved in the size measuring process depending on the distance from the disc and on its size. Up to a disc size of 2.52 cm Ø only one single vibrissa (C7 or D7) on each side of the muzzle was deflected by the lateral head movements. With increasing disc size more vibrissae were naturally involved in the tactile process, which are positioned further posterior in the horizontal rows.

Discussion

Tactile behavior

The first piece of information required by the sea lion during a trial was the localization of a disc. This information was received by the vibrissae situated further posterior in the horizontal rows (D/E 1–4, Fig. 2), which because of their length, were the first to touch the disc. After the localization of a disc, the sea lion proceeded to identify it using only the shorter vibrissae located anteriorly. This functional relationship between the anterior and posterior vibrissae seems to be exactly the opposite in rats (Carvell and Simons 1990).

As relative movements between the tactile organ and the stimulus are absolutely essential for active tactile processes (Krueger 1982), and due to the fact that the sea lion did not, however, actively move the erect vibrissae, it follows that the lateral head movements of the animal must have been decisive for the size measuring process. Insofar as the sea lion moved its head many times to and fro while positioned at the disc, whereby the vibrissae on both sides of the muzzle touched the edges of a disc alternately, it achieved a centered positioning of the head in relation to the disc. This can be clearly seen in that the sea lion's lateral head movements were equidistant to both sides of a disc (see Fig. 6A).

As seen from Fig. 6A the sea lion's lateral head movements were approximately the same for each and every disc compared at threshold. Identical lateral movements of the head, while touching discs of differing sizes in sequence, must have had the consequence that the resistance of the disc with the larger diameter caused a corresponding greater deflection of the vibrissae than did the smaller disc. This functional correlation between 'head movements' and 'disc size' is illustrated in Fig. 7 as a model. The deflection of the outer vibrissal shaft is transmitted to the shorter end of the shaft in the follicle, by which pressure and tractive forces stimulate the mechanoreceptors located there (Wrobel 1965). Therefore, differences in the deflection angle of the vibrissal

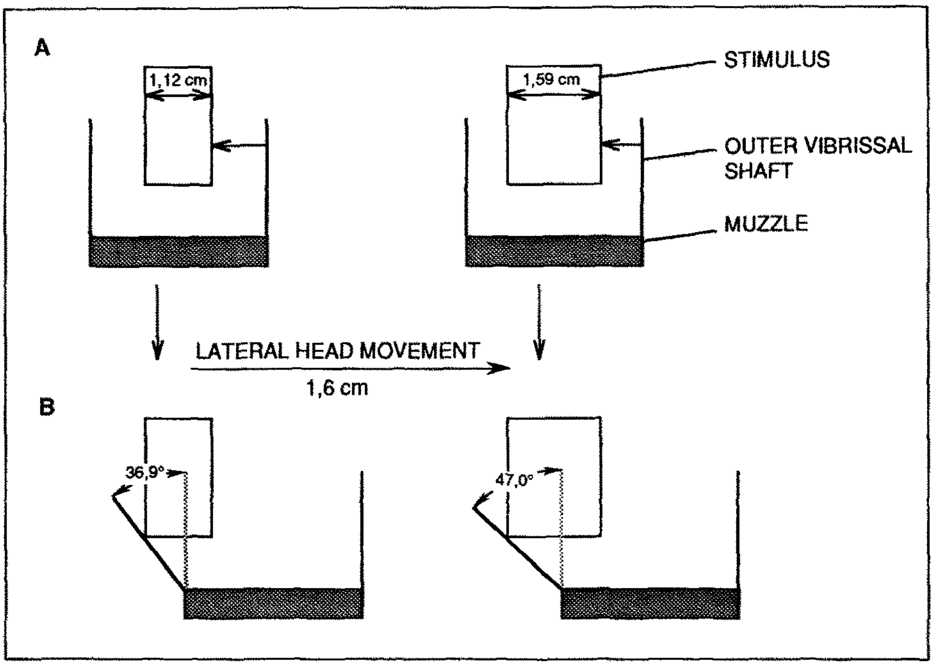


Fig. 7A, B Model for the sea lion's perception of size differences based on its tactile behavior during the comparison of the discs with diameters of 1.12 cm and 1.59 cm. The vibrissae are considered to be rigid levers. **A** Centered positioning of the sea lion's head in relation to the disc. **B** Identical lateral head movements to the extent of 1.6 cm while comparing the two discs with a diameter difference of 0.47 cm cause greater deflections of the outer vibrissal shafts at the disc with the larger diameter (47.0°) than is the case with the smaller disc (36.9°). These different deflections of the vibrissal shafts result in mechanical stimulations of differing intensity inside the follicles which should lead to different responses of the mechanoreceptors located there

shaft result in mechanical stimulations of different intensity inside the follicle, which then lead to a different response of the follicle receptors. The results of various neurophysiological studies support this assumption. For cats (Fitzgerald 1940; Hunt and Mcintyre 1960; Hahn 1971; Gottschaldt et al. 1973; Dykes 1975) as well as for Harbor seals and Grey seals (Dykes 1972, 1975) it has been proved that the recorded discharge rate of impulses in the slowly adapting afferent fibres of the trigeminal nerve rise in proportion to the extent of the vibrissae deflection angle.

Because precisely controlled tactile movements are of central importance to the sea lion's ability to perceive size differences, the part played by kinaesthesis in bringing about the discrimination ability should not be ignored. Gibson (1962) presumes that the tactile sense and kinaesthesis are to be considered as synergistic in nature. This certainly is the case for the discrimination abilities of the sea lion examined in the present study. Von Skramlik (1933) and Pätzold (1934) showed in human subjects that varying tactile movements led to errors in the tactile assessment of stimuli differing in length. Applied to the tactile performances of the sea lion, this means that imprecise tactile movements, carried out during the successive comparison of the stimuli, would have resulted in different deflection angles of the vibrissae which no longer could be explained solely by size differences between the stimuli, but rather could result from insufficient kinaesthetic control.

In humans, measuring the different thickness of metal plates using the thumb and the index finger, the interaction between cutaneous mechanoreception and kinaesthesis seems to be just the opposite to that found for the sea lion (John et al. 1989). The subjects gripped the plates in such a way that the amount of compression applied to the fingerpads was the same for both plates which were to be compared. In this way, the angles of the digital joint were different for the two plates and the discrimination relied on kinaesthesis.

Difference thresholds

Even though the suitability of vibrissae in active touch has been repeatedly described for pinnipeds (Kastelein and van Gaalen 1988; Dehnhardt 1990), and also for rats (Guic-Robles et al. 1989; Carvell and Simons 1990), the relative difference thresholds determined in the present study, allow for the first time, a quantative evaluation of the tactile resolving power of a vibrissal system. Compared to the relative difference thresholds which have been determined for mammals with prehensile tactile organs, carrying out similar tactile size discriminations, the tactile resolving power of the sea lion's vibrissal system is relatively weak (mean c-value=0.26). The raccoon tested by Rensch and Dücker (1963) could resolve size differences with its front paws by a factor of 4 better than the sea lion. The raccoon's performance comes close to that of human experimental subjects, who with the help of the index finger and the thumb achieved an average relative difference threshold of 0.04 (Gaydos 1958; Stevens and Stone 1959; Dietze 1961). The relative difference threshold determined for monkeys (*Macaca mulatta*, Semmes and Mishkin 1965; *Macaca arctoides*, Carlson et al. 1989) averaged 0.1. Because the present study represents a single case analysis, the performance of the California sea lion tested does not necessarily have to be representative of its species. Dietze

(1961), for example, who tested a large number of human subjects, found that the tactile discrimination ability of his most sensitive subject was better by a factor of 3 than that of the subject with the least sensivity.

On the basis of Dykes' (1972, 1975) neurophysiological studies a better tactile resolving power of the sea lion might have been expected. A pressure stimulus which deflected vibrissae of Harbor seals and Grey seals by 11 μm at a distance of 0.5 cm from the skin surface already led to an increased discharge rate in the slowly adapting afferent fibres. However, in comparing these neurophysiological data to the thresholds determined in the present study, the significance of the kinaesthetic sense for active touch has to be considered. The sea lion's size discriminations are based on the interaction of tactile sense and kineaesthesis. In such a synergism the resulting performance level will be determined by the efficiency of the weakest link (Bryant 1968). The vibrissal system of pinnipeds shows a high degree of organisation not only at the receptor level (Dykes 1972, 1975; Stephens et al. 1973; Ling 1977; Hyvärinen 1989), but also at the level of cortical representation (Ladygina et al. 1985). In particular the cortical representation of the vibrissal system does not seem to be any less distinctive than that of the hands of primates (Sur et al. 1982) or the front paws of raccoons (Welker and Seidenstein 1959). Therefore, there is a good reason to assume that differences in the tactile resolving power between the different species can also be attributed to the differences in the performance capability of the kinaesthetic sense. This means that the head movements essential for the sea lion's tactile discriminations were not motor controlled to the extent that the tactile movements of the other species were.

The duration of the touch time could also have had an influence on the perceptive process. It is known from various studies that both the prolonged touching of a single stimulus (Lamb 1983), and a higher number of successive comparisons of two stimuli (Sinclair and Burton 1991) have a positive effect on tactile performance levels. The sea lion did not spend more time in touching individual discs even when discrimination became difficult. Instead, it merely increased the number of successive comparisons. It is likely that a combination of both strategies might have resulted in a better tactile performance.

Weber's law

The results of the determination of four difference thresholds show that the sea lion's tactile perception just as much corresponds to Weber's law as the visual modality described by Wartzok and Ray (1976) regarding the pinniped species *Phoca largha*. Comparing the 4 relative difference thresholds determined for the sea lion, it becomes clear that those determined for the two small standard discs are higher than that determined for the relatively large standard disc with a diameter of 8.74 cm. This effect can be observed in most studies on tactile discrimination, in which relative difference thresholds were determined for several standard stimuli of differing size (Gaydos 1958; Stevens and Stone 1959; Dietze 1961; Sinclair and Burton 1991). However, despite this tendency to show increasing c-values with decreasing stimulus size the relative difference threshold of the sea lion, as demanded by Weber's law, remained approximately constant.

It is generally acknowledged that Weber's law does not apply to the whole range of stimulus sizes (Gescheider 1985). Especially with regard to very small stimulus sizes, which lie within the realm of the detection threshold, the relative difference threshold increases to a large extent. The detection threshold corresponds to the least perceptible absolute difference threshold (ΔD). When ΔD no longer can be reduced further the ratio between ΔD and D has to increase. From the fact that the relative difference threshold in the present study nearly always remained constant (see regression Fig. 3D), it follows that the smallest ΔD value determined (0.33 cm) does not lie within the range of the sea lion's tactile detection threshold.

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References

Bryant PE (1968) Comments on the design of developmental studies of cross-modal matching and cross-modal transfer. Cortex 4:127–137

Carlson S, Tanila H, Linnankoski I, Pertovaara A, Kehr A (1989) Comparison of tactile discrimination ability of visually deprived and normal monkeys. Acta Physiol Scand 135:405–410

Carvell GE, Simons DJ (1990) Biometric analysis of vibrissal tactile discrimination in the rat. J Neurosci 10 (8):2638–2648

Dehnhardt G (1990) Preliminary results from psychophysical studies on the tactile sensitivity in marine mammals. In: Thomas JA, Kastelein RA (eds) Sensory abilities of cetaceans. Plenum Press, New York, pp 435–446

Dietze AG (1961) Kinaesthetic discrimination: the difference limen for finger span. J Psych 51:165–168

Dykes RW (1972) What the seals vibrissae tell the seals brain. Proc Ann Conf Biological Sonar and Diving Mammals, 9th, Stanford Research Institut, Menlo Park, California, pp 123–136

Dykes RW (1975) Afferent fibres from mystacial vibrissae of cats and seals. J Neurophysiol 38:650–662

Fitzgerald O (1940) Discharges from the sensory organs of the cat's vibrissae and the modification in their activity by ions. J Physiol (Lond) 98:163–178

Gaydos HF (1958) Sensitivity in the judgement of size by fingerspan. Am J Psychol 71:557–562

Gellerman LW (1933) Chance orders of alternating stimuli in visual discrimination experiments. J Genet Psychol 42:206–208

Gescheider GA (1985) Psychophysics: Method, theory and application. Lawrence Erlbaum, Hillsdale New Jersey London

Gibson JJ (1962) Observations on active touch. Psych Rev 69 (6):477–491

Gottschaldt KM, Iggo A, Young DW (1973) Functional characteristics of mechanoreceptors in sinus hair follicles of the cat. J Physiol (Lond) 235:287–315

Guic-Robles E, Valdivieso C, Guajardo G (1989) Rats can learn a roughness discrimination using only their vibrissal system. Behav Brain Res 31:285–289

Hahn JF (1971) Stimulus-response relationships in first order sensory fibers from cat vibrissae. J Physiol (Lond) 213:215–226

Hunt CC, Mcintyre AK (1960) Properties of cutaneous touch receptors in cat. J Physiol (Lond) 153:88–98

Hyvärinen H (1989) Diving in darkness: Whiskers as sense organs of the Ringed seal (*Phoca hispida*). J Zool 218:663–678

John KT, Goodwin AW, Darian-Smith I (1989) Tactile discrimination of thickness. Exp Brain Res 78 (1):62–68

Kastelein RA, Gaalen MA van (1988) The sensitivity of the vibrissae of a pacific walrus (*Odobenus rosmarus divergens*) Part I. Aquatic Mammals 14 (3):123–133

Krueger LE (1982) Tactual perception in historical perspective: David Katz's world of touch. In: Schiff W, Foulk E (eds) Tactual perception: A sourcebook. University Press, Cambridge, pp 1–53

Ladygina TF, Popov VV, Supin AYa (1985) Somatotopic projections in the cerebral cortex of the fur seal (*Callorhinus ursinus*). Academy of Siences Moskow 17 (3):344–351

Lamb GD (1983) Tactile discrimination of textured surfaces; psychophysical performance measurements in humans. J Physiol (Lond) 338:551–565

Ling JK (1977) Vibrissae of marine mammals. In: Harrison RJ (ed) Functional anatomy of marine mammals Vol III. Academic Press, London, pp 387–415

Mills F, Renouf D (1986) Determination of the vibration sensitivity of harbour seal (*Phoca vitulina*) vibrissae. J Exp Mar Biol Ecol 100:3–9

Pätzold N (1934) Über die Bedeutung des Zeitfaktors bei Tastwahrnehmungen. Z Sinnesphysiol 64:325–337

Renouf D (1979) Preliminary measurements of the sensitivity of the vibrissae of harbour seals (*Phoca vitulina*) to low frequency vibrations. J Zool Lond 188:443–450

Rensch B, Dücker G (1963) Haptisches Lern- und Unterscheidungsvermögen bei einem Waschbären. Z Tierpsychol 20:608–615

Semmes J, Mishkin M (1965) Somatosensory loss in monkeys after ipsilateral cortical ablation. J Neurophysiol 28:473–486

Sinclair RJ, Burton H (1991) Tactile discrimination of gratings: psychophysical and neural correlates in human and monkey. Somatosensory and Motor Res 8(3):241–248

Skramlik E von (1933) Über die Beeinflussung unserer Tastwahrnehmungen durch Richtung und Schnelligkeit der Tastbewegung. Z Sinnesphysiol 64:97–117

Stephens RJ, Beebe IJ, Poulter TC (1973) Innervation of the vibrissae of the California sea lion, *Zalophus californianus*. Anat Rec 176:421–442

Stevens SS, Stone G (1959) Finger span: ratio scale, category scale, and jnd scale. J Exp Psychol 57:91–95

Sur M, Nelson RJ, Kaas JH (1982) Representation of the body surface in cortical areas 3b and 1 of squirrel monkeys: Comparison with other primates. J Comp Neurol 211 (2):177–192

Wartzok D, Ray GC (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

Welker WJ, Seidenstein S (1959) Somatic sensory representation in the cerebral cortex of the racoon (*Procyon lotor*). J Comp Neurol 111:469–501

Wrobel K-H (1965) Bau und Bedeutung der Blutsinus in den Vibrissen von *Tupaia glis*. Zbl Vet Med A 12:888–899