Tactual discrimination of size and shape by a California sea lion (*Zalophus californianus*)

GUIDO DEHNHARDT

University of Bielefeld, Bielefeld, Germany

and

GERTI DÜCKER

University of Münster, Münster, Germany

We analyzed the capability of a blindfolded California sea lion to discriminate objects differing in size and/or shape by active touch with its mystacial vibrissae. In a two-alternative forced-choice procedure, equilateral triangles and disks with surface areas ranging from 60 to 0.5 cm² served as stimuli. The determination of size difference thresholds (ΔS) for the discrimination of triangles revealed that the animal was capable of discriminating size differences as low as 20%. Presented with triangles and disks having identical surface areas, the sea lions' discriminations relied on the apparent size difference of $\geq 34\%$ between the longest measurable lines of both shapes (side length > diameter). When this size difference was reduced to $\leq 5\%$, the sea lion needed visual information about the shapes before it was able to discriminate them tactually. When the size of these shapes was gradually reduced, the animal was able to make the discrimination down to a longest measurable line of both shapes of 1.70 cm. This tactual performance comes close to that achieved by mammals with prehensile tactile organs.

In pinnipeds, the mystacial vibrissae are the prime organs of the tactile sense, because of their rich endowment with mechanoreceptors (Dykes, 1975; Hyvärinen, 1989; Stephens, Beebe, & Poulter, 1973) as well as their prominent representation in the somatosensory cortex (Ladygina, Popov, & Supin, 1985). Although the mystacial vibrissae are typically considered as vibrotactile sensors (Mills & Renouf, 1986), behavioral studies have shown that they permit pinnipeds to obtain information about objects in their environment through active touch as well. Kastelein and van Gaalen (1988) trained a walrus (*Odobenus rosmarus*) to discriminate between two shapes (equivalent in surface area) decreasing in size. The animal was able to distinguish an equilateral triangle from a disk down to a surface area of 0.4 cm². In transposition tests, the triangle was exchanged for shapes with an increasing number of corners (square, hexagon, octagon, etc.). In the presence of a square, the walrus reacted as if it had perceived a triangle; all other shapes were categorized as disks.

Excellent shape discrimination capabilities by means of mystacial vibrissae have also been shown for a California sea lion (Dehnhardt, 1990). The animal was able to

discriminate between five shapes by means of active touch, with the same accuracy that it had previously reached through vision. For the same animal, size discrimination thresholds have been determined with the use of a psychophysical technique (Dehnhardt, 1994): required to choose the larger of two simultaneously presented disks, the blindfolded sea lion was capable of detecting diameter differences of 22%.

The vibrissal systems of *Odobenus* and *Zalophus* differ considerably. Whereas a walrus has up to 300 relatively short (max. 8–9 cm) and extremely stout (ca. 3 mm in diameter) vibrissae on each side of the snout (King, 1983), the vibrissal pad of *Zalophus* contains just 38 tactile hairs (Dehnhardt, 1994), which can reach a length of >20 cm (posterior vibrissae) and, because of their smaller diameter (max. 1.3 mm; Dehnhardt & Kaminski, 1995), are more pliable.

To obtain comparable data on active touch for these two pinniped species, we investigated in this study the tactile capability of a California sea lion to discriminate between two objects differing in size and/or shape. Since we already knew size difference thresholds of *Zalophus* for the discrimination of disks (Dehnhardt, 1994), Phase 1 dealt with the determination of size difference thresholds for the discrimination of triangles. With some modifications (e.g., a two-alternative forced-choice procedure instead of successive stimulus presentation), Phase 2 was a replication of the Kastelein and van Gaalen (1988) study, requiring the sea lion to discriminate between equilateral triangles and disks both having the same surface area. Disks and equilateral triangles of the same surface area always show a difference in size between their longest

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measurable lines (diameter vs. side length) of $\geq 34\%$. Since Dehnhardt (1994) and Dehnhardt and Kaminski (1995) have shown that size discriminations of a California sea lion and Harbor seals were based on the outer dimension of the stimuli, in Phase 3 the size difference between the longest measurable lines of both shapes was reduced to $\leq 5\%$, which we expected to be imperceptible for the sea lion. These experiments should elucidate at what level the animal is using size or shape as a cue for its discriminations. Another objective was to obtain information about the nature of the sea lion's tactual behavior at different discrimination tasks. Is the animal's tactual behavior adapted to the respective object properties that it has to process during the discrimination? In addition, in Phases 2 and 3 the size of both shapes was reduced successively to bracket a potential threshold down to which the animal could discriminate between both shapes.

METHOD

Subject

Like most studies on the sensory abilities of large mammals, the present investigation was a case study. This is primarily because of the scant availability of suitable test animals as well as the lengthy preparation period required for testing such animals. The experimental animal of the present study was an 11-year-old female *Zalophus* that had previously served as a subject in experiments on tactile shape and size discrimination (Dehnhardt, 1990, 1994). To prevent the sea lion from perceiving any visual information during trials, it was blindfolded with eye caps usually used for human medical purposes (Lohmann, Germany, PZ-No. 1602675). They were covered with waterproof adhesive tape, and a 4-mm-thick rubber lining was fitted on the inside rim. In addition, each cap was fitted with a rubber band, which was used to attach the cap securely to the sea lion's head.

Stimuli and Test Apparatus

Two graded sets of stimuli were used, one consisting of 14 disks and the other of the same number of equilateral triangles, each having the same surface area as did one of the disks (60 cm² down to 0.5 cm²; see Table 1). All stimuli were made of Perspex

Table 1
Performance of the Sea Lion Discriminating Between Disks and Triangles Having the Same Surface Area

Surface Area of Shapes (cm ²)	Disk <i>d</i> (cm)	Triangle <i>a</i> (cm)	<i>a</i> - <i>d</i> (cm)	Choice of Triangle (%)
60.00	8.74	11.77	3.03	87.5
50.00	7.97	10.74	2.77	90.0
40.00	7.13	9.61	2.48	87.5
30.00	6.18	8.32	2.14	82.5
20.00	5.04	6.79	1.75	85.0
10.00	3.56	4.80	1.24	87.5
5.00	2.52	3.39	0.87	87.5
4.00	2.25	3.03	0.78	85.0
3.00	1.95	2.63	0.68	87.5
2.50	1.78	2.40	0.62	85.0
2.00	1.59	2.15	0.56	82.5
1.25	1.26	1.70	0.44	82.5
1.00	1.12	1.52	0.40	80.0
0.50	0.79	1.07	0.28	82.5

Note—The first four columns indicate the different size values of the shapes and the respective difference in size between side length (*a*) and diameter (*d*).

Figure 1. Schematic drawing of the test apparatus (measurements in centimeters). (A) Overview of the back of the apparatus. (B) Detail of the stimulus presentation area.

2 cm thick and were machined with a permissible deviation in diameter or side length of 0.025 mm. Two stimulus carriers were manufactured, each consisting of a crossbar on whose ends vertical metal supports were to be found (Figure 1B). The shorter shank of an iron rod bent into an asymmetrical U shape was welded to the center of the crossbar in such a way as to be at a 90° angle to it. It was possible to screw a stimulus onto the end of the longer shank of the U-shaped rod.

The apparatus consisted of a white polyvinyl chloride (PVC) wall attached to a steel frame (Figure 1A). Two windows were cut out beside each other in the PVC wall. Behind each window there was a U-shaped frame that could be 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 rear of the windows, the elastic pressure of spring-cushioned spheres incorporated at the free end of metal bolts held them in a vertical position. The stimulus carriers could be affixed to the hollow ends of the U-shaped frames (Figure 1B). These could be pushed out of their vertical position by the sea lion's applying a slight amount of pressure with its snout against a stimulus. At the front of the apparatus, a rubber disk was affixed between the two windows, serving as a station for the sea lion before a new trial was started. From this position, the blindfolded sea lion could easily reach the stimuli hanging to both sides of its head.

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 rubber disk. After the sea lion was in this position, its eyes were covered by the eye caps. As soon as the animal was blindfolded, both stimulus carriers were placed in the U-shaped frames. Both frames were then simultaneously brought into a vertical position so that the stimuli were placed in the middle of the windows to each side of the sea lion. The experimenter then gave a short blast of a whis-

tle as a signal for the trial to start. Upon hearing the whistle, the sea lion immediately began to examine both stimuli by touching them alternately. The sea lion was required to indicate its decision by pushing the respective stimulus out of its vertical position (Figure 2). When the sea lion chose the correct stimulus, the experimenter blew a whistle to provide immediate feedback. For each correct response, the sea lion was rewarded with two fishes (sprats, *Sprattus sprattus*). Following each choice, both stimuli were removed from the apparatus before the experimenter pushed back the eye caps from the sea lion's eyes. In this way, the sea lion never received any visual information about the stimuli. In order to rule out olfactory cues, the stimuli were cleaned thoroughly with alcohol before each trial. Each day, one or two sessions consisting of 16 or 20 trials were carried out. During a session, the same two stimuli were presented at both positions of the apparatus, according to pseudorandom schedules (Gellerman, 1933).

The animal's response was filmed with a video camera placed behind the test apparatus. For each trial, the reaction time was measured with a digital clock integrated into the video camera (1/50-sec accuracy). The reaction time was defined as the time that passed between the starting signal and the moment the U-shaped frame of the chosen stimulus fell against the stop block. From a frame by frame analysis of the video recordings, information could be obtained about tactile movements of the sea lion and individual vibrissae involved in the tactile process.

In Phase 1, a modified method of constant stimuli was used to determine size difference thresholds for three standard triangles: (A) 1.52-cm side length, (B) 3.39-cm side length, and (C) 11.77-cm side length. Each test series (A–C) was started with a task in which the animal showed a reliable discrimination between the standard and a comparison triangle (side length of first comparison triangle: series A, 6.79 cm; series B, 1.07 cm; series C, 3.03 cm). After the sea lion had mastered the discrimination between the standard and the first comparison triangle, the size difference between triangles was reduced (next smaller or larger comparison triangle) and the animal was retrained to criterion with this new task. This process was repeated until the animal could no longer discriminate the standard from the comparison triangle. In this way, the upper difference threshold was obtained for the standard triangle A (comparison triangles in descending order; see Table 1), and the lower difference thresholds for the

standard triangles B and C (comparison triangles in ascending order).

The absolute difference threshold ΔS (the difference in side length required to produce a just noticeable difference in sensation) was defined as the difference in side length between standard and comparison triangle at which the test animal performed 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's making 75% correct choices in three consecutive sessions (36 correct choices at 48 trials, binomial test, $p < .001$). When the sea lion showed an increase or decrease in performance of $\geq 10\%$ correct choices between two sessions as well, as in cases wherein 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.

In Phase 2 (replication of the study by Kastelein & van Gaalen, 1988), the sea lion was required to discriminate between two shapes (equilateral triangles and disks) both having the same surface area. The triangle was presented with one corner in an upright position (Figure 1). The size of the surface area of both shapes was reduced successively from 60 cm² down to 0.5 cm² (see Table 1) to bracket a potential threshold down to which the animal could discriminate between both shapes. The animal was presented with each size for at least two sessions. Since these were not psychophysical tests in the classical sense, we defined a more conservative threshold criterion of 80% correct choices over two consecutive sessions each consisting of 20 trials.

In Phase 3, we attempted to determine whether the sea lion used the characteristics of the shapes or the difference in size between diameter and side length for its discrimination. In these tests, the animal was presented with tasks in which the size of the triangle was reduced, so that the difference in size between its side length and the diameter of the corresponding disc was $\leq 5\%$. Again, 80% correct over two consecutive sessions was defined as criterion. These tests alternated with tasks in which the surface area of both shapes was identical, so that a difference in size of about 35% between diameter and side length was available to the sea lion.

RESULTS

Size Difference Thresholds (Phase 1)

Presented with the initial discrimination task of Test Series A (1.52 cm: 6.79-cm side length), the sea lion showed a strong preference for the larger triangle (100% of the choices during one session). In obtaining size difference thresholds, we took advantage of this experimentally unconditioned discrimination by rewarding the animal for its choice of the larger triangle throughout the experiment.

The psychometric function in Figure 3A shows the result of the threshold determination (A) for the standard triangle with 1.52-cm side length. Up to a difference in side length of 1.11 cm, the sea lion differentiated between both stimuli without error. As the difference in side length was gradually reduced to 0.63 cm, performance fell to 83.3% correct choices. Smaller differences in size were no longer identified. The interpolated size of the absolute difference threshold at 75% correct choices was a 0.41-cm side length difference, which corresponds to a Weber fraction (the ratio of the lowest side length difference detected by the seals on 75% of the oc-

Figure 2. The sea lion responding to a disk.

Figure 3. (A) Psychometric function of performance on discriminating size differences of equilateral triangles; percent correct choices plotted versus the side length of comparison triangles. The sea lion was required to choose the larger triangle in each stimulus combination. The horizontal dashed line at 75% correct choices marks the defined difference threshold; the vertical dashed line indicates the size of the interpolated comparison triangle at threshold. Each data point represents the result of 48 trials. (B) Linear regression of the absolute difference thresholds (ΔS) with regard to the corresponding starting stimulus size.

casions to the starting side length, $\Delta S/S$; Laming, 1986) of 0.27.

The results of threshold determinations B and C will not be described in detail. The animal always started with 100% correct choices at the initial task, followed by a more or less linear decrease in performance with increasing difficulty of the discrimination. The interpolated size of ΔS at 75% correct choices was 0.69-cm side length difference (Weber fraction 0.26) for standard triangle B (3.39 cm) and 1.93-cm side length difference (Weber fraction 0.20) for standard triangle C (11.77 cm). A comparison of the absolute difference thresholds determined for the three standard triangles shows that the larger the starting stimulus size, the higher the corresponding value of the absolute difference threshold ΔS . In contrast, the Weber fraction (mean value = 0.24 cm) remained approximately constant. This linear correlation between the starting stimulus size and ΔS is illustrated by the linear regression in Figure 3B. Owing to the low number of threshold values obtained for the sea lion, the linear regression is merely of descriptive significance.

On size discrimination tasks in which the sea lion achieved $\geq 80\%$ correct choices, it explored separately each of the stimuli only once, resulting in a mean reaction time of 1.65 sec ($SD = 0.88$ sec). In tasks on which performance was $\leq 80\%$ but still $\geq 65\%$ correct choices, the reaction time always increased significantly [3.55 sec, $SD = 0.69$ sec; $F(1,574) = 832.60$, $p < .01$], because the sea lion now explored each triangle up to three times. A performance below 65% correct choices can be ex-

plained by the fact that the sea lion developed a position preference without comparing the stimuli any longer. On those tasks, the reaction time was as low as 1.1 sec ($SD = 0.39$ sec).

As long as the sea lion remained in station at the beginning of a trial, its vibrissae lay back close to the snout. When the animal started to touch the stimuli, it brought its vibrissae into the most extreme forward position (see Figure 2). Once it had localized a stimulus, the sea lion immediately centered its head in relation to it, so that the stimulus' edges were covered by the vibrissae of both sides of the snout. The animal then carried out short lateral head movements while the vibrissae themselves remained in a fully protracted state during the tactile process and were not actively moved by the animal. The lateral head movements took place exclusively in the horizontal plane (side to side) and, because of the resistance of the stimulus, caused alternating deflections of the vibrissae of both sides of the snout which were involved in the tactile process.

The extent of these lateral head movements are illustrated in Figure 4 for the standard triangle with 1.52-cm side length, the last three comparison triangles that the animal distinguished from this standard stimulus, and the comparison triangle that the sea lion no longer distinguished from the standard (see Figure 3A for comparison). When touching these smaller triangles (up to 2.63-cm side length), only one or two vibrissae (the most anterior vibrissae C7 and/or D7; see Dehnhardt, 1994) on each side of the snout were involved in the tactile process. An analy-

Figure 4. The extent of the sea lion's lateral head movements while touching the standard triangle with 1.52-cm side length (double frame), the first comparison triangle that the sea lion no longer differentiated from this standard triangle (dashed frame), and the last three comparison triangles that the animal distinguished from the standard triangle (single frames).

sis of variance revealed no effect of direction [left or right; $F(1,318) = 0.500, p > .01$] or stimulus size [$F(9,310) = 0.555, p > .01$] on the extent of the lateral head movements. This supports the observation that the sea lion achieved a centered positioning of the head in relation to the stimulus and indicates that it carried out virtually identical tactile movements on stimuli to be compared.

Shape Discrimination Tasks (Phase 2)

The results of the first shape discrimination tests, on which both shapes always had the same surface area, are described in Table 1. Initially the sea lion was asked to differentiate between a disk and a triangle with 60 cm² of surface area, without differential reinforcement. Since the sea lion spontaneously preferred the triangle (87.5% of the choices during one session), its choice of the triangle was rewarded with two sprats during all shape discrimination tests. When the size of the surface area of

both shapes was reduced successively down to 0.5 cm², the sea lion also achieved $\geq 80.0\%$ correct choices during the first two consecutive sessions of all tasks ($p < .01$, binomial test). During all tasks, the sea lion explored separately each of the stimuli only once so that its reaction time was approximately the same as in Phase 1 (1.72 sec, $SD = 0.56$ sec). Its tactile behavior also did not differ from that described for the size discrimination experiment. The animal showed the same lateral head movements irrespective of whether it touched a triangle or a disk.

Shape Discrimination Tasks (Phase 3)

Once the sea lion was presented with two shapes whose difference in size between diameter and side length was only $\leq 5\%$ (Table 2), it could no longer distinguish between them, regardless of the size of the shapes. In these tests, the animal usually developed a preference for the right-hand position quite quickly, so that it never achieved more than 55% correct choices. When, however, the sea lion was again presented with shapes having identical surface areas it again achieved $\geq 80.0\%$ correct choices (choice of triangle).

Further tests were made to see whether the sea lion was able to learn the discrimination between shapes with a difference in size between diameter and side length of $\leq 5\%$. For this purpose, the animal was again presented with a disk whose surface area was 40 cm², together with a triangle with a surface area of 20 cm². As before, the choice of the triangle was rewarded. Figure 5A shows that even after 10 sessions the sea lion was not able to differentiate between both shapes. The animal touched each of the stimuli only one to two times, so that the reaction time for this discrimination task was not significantly different from that measured for the size discriminations in Phase 1 [1.77 sec, $SD = 0.42$ sec, $F(1,534) = 5.35, p > .01$].

Since the sea lion increasingly exhibited non-test-oriented behavior (e.g., barking), we terminated the tactile experiment after the 10th session. Instead, the shapes

Table 2
Performance of the Sea Lion Discriminating Between Disks and Triangles
When the Difference in Size Between Side Length (a) and
Diameter (d) Was Either $\leq 5\%$ (I) or $\geq 34\%$ (II)

	Surface Area (cm ²) ● : ▲	d (cm) : a (cm) ● : ▲	Difference $ d - a $ (cm)	Choice of Triangle (%)	No. of Sessions
I	40.00 : 20.00	7.13 : 6.79	0.34	55.0	4
II	40.00 : 40.00	7.13 : 9.61	2.48	82.5	1
I	20.00 : 10.00	5.04 : 4.80	0.24	50.0	4
II	20.00 : 20.00	5.04 : 6.79	1.75	85.0	1
I	10.00 : 5.00	3.56 : 3.39	0.17	55.0	4
II	10.00 : 10.00	3.56 : 4.80	1.24	85.0	1
I	5.00 : 2.50	2.52 : 2.40	0.12	50.0	4
II	5.00 : 5.00	2.52 : 3.39	0.87	82.5	1
I	2.50 : 1.25	1.78 : 1.70	0.08	60.0	4
II	2.50 : 2.50	1.78 : 2.40	0.62	87.5	1
I	2.00 : 1.00	1.59 : 1.52	0.07	55.0	4
II	2.00 : 2.00	1.59 : 2.15	0.56	82.5	1
I	1.00 : 0.50	1.12 : 1.07	0.05	50.0	4
II	1.00 : 1.00	1.12 : 1.52	0.40	82.5	1

Figure 5. Learning curves (open circles) for the sea lion's discrimination between a disk of 40 cm² and a triangle of 20 cm² surface area (size difference between diameter and side length $\leq 5\%$). (A) Tactual discrimination without any visual information about the shapes. (B) Visual discrimination. (C) Tactual discrimination after visually learned discrimination. Each point represents 20 decisions by the sea lion. Filled circles with standard deviations indicate the sea lion's mean reaction times for each session.

were now presented to the sea lion as visual discrimination tasks. Despite the fact that the sea lion had not received any visual information about the shapes up to then, its performance, even during the first session, was considerably above that of the last tactile task (Figure 5B). In the third session, the animal chose the triangle 85% of the time, and it achieved 100% correct choices in two further sessions with this task.

The shapes were now presented again for tactual discrimination (blindfolded sea lion). The result is illustrated in Figure 5C. Already in the first session the sea lion fulfilled the criterion, and this performance remained stable at $\geq 80.0\%$ correct choices over four additional sessions. The sea lion changed its tactile behavior after it had learned the discrimination visually. In contrast to the lateral head movements shown during all previous tests, the sea lion's head movements became more gyratory, as if it was trying to follow the contour of a shape. Since these head movements were too complex, the extent of their individual components could not be measured. Compared with the tactual discrimination without visual information (Figure 5A), this tactile behavior was accompanied by a significant increase in the sea lion's reaction time [Figure 5C; 4.84 sec, $SD = 0.62$ sec, $F(1,298) = 2,522.01$, $p < .01$], while the number of successive explorations remained the same.

Following this successful tactual discrimination, the sea lion was presented with all the tasks listed in Table 2 (I), where the difference in size between diameter and side length was $\leq 5\%$, in the same sequential order. The ratio of the surface areas between the disks and the triangles was 2:1 in all stimulus combinations. In these tasks, the sea lion now achieved 80.0% correct choices over two consecutive sessions without training (Figure 6). However, the animal was not able to differentiate between the stimuli of the last two tasks, on which the longest measurable lines of the triangles were 1.52 and 1.07 cm

(longest measurable lines of disks, ca. 5% larger). Even after six sessions with each of these tasks, the sea lion's performance remained at chance level. At the beginning of each of these sessions (Trials 1–3), the animal still compared both shapes. In all further trials, it generally did not compare the stimuli and predominantly chose the right-hand stimulus. This choice behavior is responsible for the short reaction times with high standard deviations. During the preceding tasks, on which the sea lion explored each of the shapes one to two times performing gyratory

Figure 6. Performance of the sea lion (open circles) discriminating shapes gradually reduced in size when the difference in size between diameter and side length was $\leq 5\%$. Filled circles (with standard deviations) indicate the sea lion's reaction times for the respective stimulus combinations. The horizontal dashed line at 80% correct choices marks the defined criterion for a successful discrimination. Each data point represents at least 40 decisions by the sea lion.

head movements, the mean reaction time of 4.68 sec did not differ significantly [$F(1,298) = 2.063, p > .01$] from that measured for the first tactual discrimination after visual experience (Figure 5C).

In tasks on which the size difference between diameter and side length was $\leq 5\%$, both stimuli differed not only in shape, but also with regard to the size of the surface area (disc:triangle = 2:1 cm^2). However, even with the smallest shapes, the sea lion could still discriminate; the few vibrissae involved in the tactile process usually did not touch the front surface of the stimuli, but clasped the outer edges of a shape. If we assume that the animal, irrespective of the absolute size of both shapes, always used the same cue for its discrimination, it is highly improbable that this was the surface area.

DISCUSSION

The results of the size discrimination tests in Phase 1 correspond well to those described by Dehnhardt (1994) for the discrimination of disks. The mean Weber fraction for the detection of size differences of disks in that study was 0.26; in the present study, the sea lion achieved a mean Weber fraction of 0.24. For both types of stimuli, the animal's perception of size differences corresponded as much to Weber's law ($\Delta S/S = \text{constant}$) as has been shown for visual size discriminations of pinnipeds (*Phoca largha*; Wartzok & Ray, 1976).

On the basis of the sea lion's tactile behavior, Dehnhardt (1994) suggested a model describing how the animal actually measured size differences with its mystacial vibrissae. Since the sea lion in the present study showed exactly the same tactile behavior, this model can also be applied to the discrimination of equilateral triangles. When the sea lion carried out short lateral head movements during the tactile examination of a stimulus, the vibrissae on both sides of the snout touched the edges of that stimulus alternately. In this way, the animal achieved a centered positioning of the head in relation to the stimulus (see Figure 4). Since the extents of the sea lion's lateral head movements were approximately the same for the triangles compared, the resistance of the larger triangle must have caused a corresponding greater deflection of the vibrissae than did the smaller triangle. The deflection of the outer vibrissal shaft is translated into a bending of the shorter end of the shaft within the follicle, where the mechanoreceptors are stimulated by the resulting stretch and/or compression of the mesenchymal sheath (Lichtenstein, Carvell, & Simons, 1990; Rice, Mance, & Munger, 1986). Therefore, differences in the deflection angle of the vibrissal shaft result in mechanical stimulations of different intensity inside the follicle, which then lead to a different response of the follicle receptors. It has been repeatedly shown that the discharge rate of impulses in the slowly adapting afferent fibers of the trigeminal nerve rise in proportion to the extent of the vibrissae's deflection angle (Dykes, 1975; Fitzgerald, 1940; Gottschaldt, Iggo, & Young, 1973; Hahn, 1971; Hunt & McIntyre, 1960). When the neural mechanism underly-

ing the size discriminations of the sea lion is the measurement of impulse rates of afferent fibers, the animal used, according to the definition by Johnson and Phillips (1981), a "purely intensive cue" for its discriminations. Since the sea lion's tactile behavior and performance were the same irrespective of whether only two (at small triangles) or more vibrissae were involved in the tactile process, one can assume that spatial information—the exact location of a stimulus within the vibrissal field and the corresponding distribution of activated afferents—was of less significance for the discrimination of size differences.

Because of the mean Weber fraction of 0.24 for the detection of size differences, it must be assumed for the discrimination of shapes with identical surface areas that the respective difference in size of $\geq 34\%$ between diameter and side length was clearly perceptible for the sea lion. Since the animal chose the respectively larger stimulus during the determination of size difference thresholds and showed a spontaneous preference for the triangle when presented with the two different shapes with identical surface areas, it could have applied the same discrimination rule ("choose the larger stimulus") during both test phases. This assumption is confirmed by the results of the tests shown in Table 2 on which the difference between diameter and side length was $\leq 5\%$. Even though the characteristics of the shapes were distinctive in all these tasks and, in addition, a clear difference existed between the respective surface areas of both shapes, the sea lions' performance remained at chance level. However, as soon as shapes with identical surface areas and the corresponding apparent differences in size between diameter and side length were presented, the sea lion again chose the triangle. It therefore clearly discriminated the shapes on the basis of the size difference between their longest measurable lines, which in the case of our discriminanda correspond to their maximal lateral extent. This conclusion is supported by the fact that the animal showed the same tactile behavior (lateral head movements) as it did during Phase 1 irrespective of the kind of the shape.

Kastelein and van Gaalen (1988) do not mention this size difference between shapes with identical surface areas in the discussion of their results. They interpret the walrus' performance as pure shape discrimination, which is not necessarily the case according to the results of the present study. Also, the transposition tests carried out by these authors using geometric shapes with an increasing number of corners cannot be regarded as proof of shape discrimination by their test animal. Once the walrus was presented with a square, a hexagon, or an octagon, it reacted to the square as if it had been presented with a triangle. All other shapes were identified as being "disks." According to Kastelein and van Gaalen, this shows that the cue used by the walrus for its discriminations was the presence or absence of a sharp angle. It is conceivable that identical transposition tests, had they been carried out with our sea lion, would have led to the same result. With regard to the longest measurable line,

the square is still 26% larger than a disk having the same surface area, a difference that is within the sea lion's size difference threshold. In contrast, the longest measurable line of a hexagon is only 19% larger than the diameter of the corresponding disk. This difference would have been imperceptible to the sea lion.

As Figure 5 illustrates, the sea lion was only then able to discriminate the shapes by active touch, when the size difference between the longest measurable lines was $\leq 5\%$, after it had learned to distinguish them visually. At first glance, this concurs with results obtained with primates, whose tactile learning (Wilson, 1965; Wilson, Wilson, & Chiang, 1963) and tactile short-term memory (DiMattia, Posley, & Fuster, 1990), as opposed to their visual information processing, is reported to be generally worse. The inability of the sea lion to discriminate two shapes without previous visual experience can, however, also be explained in a different way.

That the visual impressions of the shapes caused the sea lion to change its tactile behavior (gyratory instead of side-to-side head movements) indicates that the exploratory movements are purposive in nature and are dictated by the object properties that the tactile system is required to process. Lederman and Klatzky (1987) labeled such stereotyped tactile movement patterns related to distinct dimensions "exploratory procedures." An exploratory procedure that is optimal for a certain object property may not provide sufficient information about another dimension (Reed, Lederman, & Klatzky, 1990). This can be seen in that the sea lion's lateral head movements were an appropriate exploratory procedure as long as the object property to be extracted was size (Phases 1 and 2), but they were inadequate for the identification of shapes. In humans, the optimal exploratory procedure for the precise identification of shapes is "contour following," a dynamic movement along the edge of an object (Klatzky, Lederman, & Reed, 1987). Since even with the smallest shapes that the sea lion could still discriminate (Figure 6), the few vibrissae involved in the tactile process usually did not touch the front surface of a stimulus but clasped the outer edges, the gyratory head movements of the animal after visual experience resemble this exploratory procedure. This is supported by the fact that the contour-following procedure is, just as in humans (Reed et al., 1990), a significantly slower process (increased response time, Figure 5C) than the respective exploratory procedure for size.

In contrast to the exploratory procedure applied during size discriminations, the gyratory head movements (though this could not have been analyzed from the video recordings) may have produced a spatial distribution of vibrissae deflections within the mystacial vibrissal field and a corresponding spatial discharge pattern of afferent fibers that was directly related to the respective shape. Whether the neural mechanism underlying the sea lion's shape discrimination was purely spatial (see Johnson & Phillips, 1981) or, as suggested by LaMotte and Srinivasan (1987) for tactile shape discrimination,

was based on a combination of intensive and spatial cues, cannot be decided.

The sea lion was still able to distinguish between a disk and a triangle, when the longest measurable line of both shapes was approximately 1.70 cm. When the size of the shapes was reduced even more, the animal was no longer able to differentiate between them. A similar tactile performance was demonstrated by Rensch and Dürcker (1963) for a raccoon discriminating between spheres and cubes decreasing in size.

In conclusion, the results of the present study indicate that, despite its totally different morphological organization, the suitability of the sea lion's vibrissal system for active touch discriminations is comparable to that of prehensile tactile organs, not only in regard to its sensory capacity, but also to the tactual strategies and their underlying cognitive processes.

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