The tactile sensitivity of the mystacial vibrissae of a Pacific Walrus (*Odobenus rosmarus divergens*). Part 2: Masking

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Summary

At night, at great depth and in murky water, Walruses are able to distinguish irrelevant objects from bentic prey. This is thought to be achieved by tactile investigation of the environment with their mystacial vibrissae. Recently a psychophysical test showed that a blindfolded Walrus could discriminate between 3 mm thick circular and triangular objects with surface areas of 0.4 cm², which were mounted on a smooth background. The animal seemed to use its long lateral vibrissae to detect and locate the objects, and its short central vibrissae for identification. Because Walruses have to identify their prey in an inhomogenous substrate, the task was made more realistic by mounting the test-objects on a rough background. Even with this background the animal was able to identify the 3 mm thick circular and triangular objects down to a surface area of 0.4 cm².

To verify the different use of regions of the mystacium, the objects were offered in such a way that the animal had difficulty reaching the objects with its central vibrissae. The animal made a great effort to touch the objects with its short central vibrissae. The present study shows that the central vibrissae have more resolving power (mainly used for identification) than the lateral vibrissae (mainly used for detection), and that the Walrus is able to discount irrelevant signals.

Introduction

Walruses mainly consume benthic organisms, which they find by digging in the substrate (Fay, 1982). Sonar recordings of the ocean floor in their distribution area have revealed 40 cm wide furrows apparently dug by Walruses (Nelson & Johnson, 1987). The position of the eyes on the head and the width of the mystacium make it impossible for a Walrus to see small objects just in front of its mouth. These morphological limitations, and the fact that the Walrus makes the water murky by digging and also forages at night, raise the question of how a Walrus can discriminate between food items and other small objects that it comes across in the substrate, such as stones.

Rooting marks of Walruses in the sediment indicate that discrimination between items is probably carried out by means of the large mystacial vibrissae. Walruses probably swim upside-down in a vertical position along the ocean floor and root up the substrate with a thick skin ridge just above the vibrissae. After it contacts an object the Walrus probably tries to identify it by tactile investigation with its mystacial vibrissae (Ling, 1977; Fay, 1982). Then, the object is probably excavated by expulsion of jets of water from the Walrus's mouth, which leaves excavation pits in the ocean floor. This is a rapid process, a Walrus can excavate and consume at least 6 scattered bivalve molluscs per minute (Oliver *et al.*, 1983). This hypothesis concerning the rooting, identification and excavation techniques has been tested and confirmed by experiments in a pool (Kastelein *et al.*, 1989; Kastelein & Wiepkema, 1989; Kastelein & Mosterd, 1989).

In part 1 of this study, the tactile sensitivity of Walrus mystacial vibrissae was tested using a psychophysical technique (Kastelein & van Gaalen, 1988). A blindfolded Walrus was asked to use its vibrissae to identify circular and triangular objects that were mounted on a smooth background. This discriminatory task was probably unrealistic since the prey of Walruses are buried in the substrate, which can have a rough texture. The first aim of the present portion of the study was to create a more realistic test situation, in which a Walrus had to discriminate between two different objects that were mounted on a rough background to mask their contours. A smooth plate was modified to create the various background.

In part 1 of this study (Kastelein & van Gaalen, 1988), the animal moved its head in such a way that the final contact with the test object was made with the central vibrissae of the mystacium. This seems to indicate that the central vibrissal area has a higher resolving power than the periphery. The second aim of the present part of the study was to further investigate possible regional differences in sensitivity of the mystacial vibrissae.

Materials and methods

Study animal and training
A male Pacific Walrus (*Odobenus rosmarus divergens*, code: OrZH003) was used in this study.
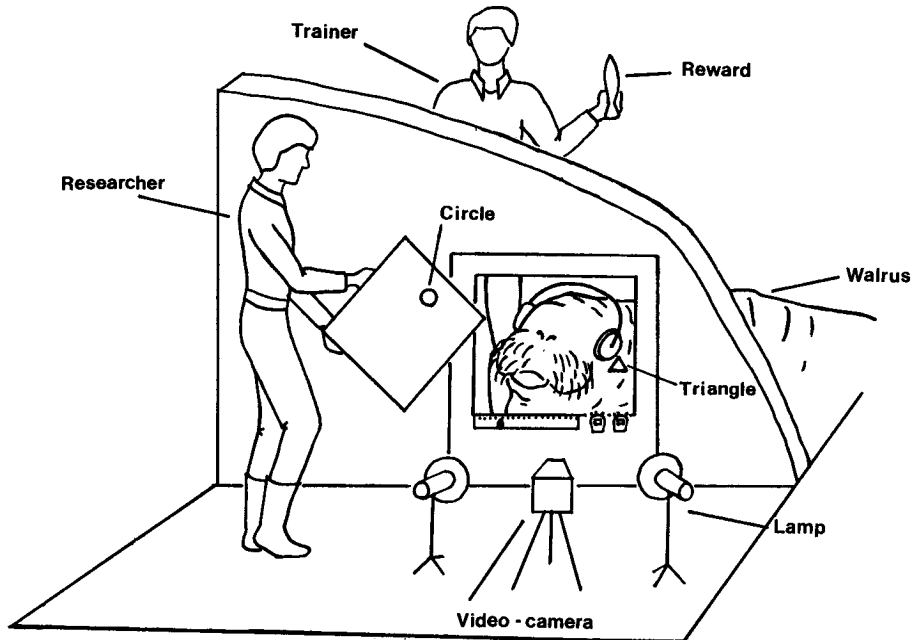
Figure 1. The study area showing the researcher and equipment on one side, and the trainer and Walrus on the other side of the wall. Note the position of the trainer and the location of the triangle on the glass plate.

The animal was born in 1982 and arrived at the Harderwijk Marine Mammal Park in February 1985. Since May 1986 he has been trained to perform in an educational show. The present study was performed in December 1988.

The same animal was used in part 1 of this study (Kastelein & van Gaalen, 1988). The animal had been trained to discriminate by touch, while blindfolded, between objects which were mounted on a smooth background. The objects were classified in sets, each set consisting of a circular and an equilateral triangular object of equal surface area. The animal showed recognition by nodding when it felt a circular object, and by shaking its head when it felt a triangular object.

Test situation

The test situation was the same as in part 1 of this study (Kastelein & van Gaalen, 1988). A square opening was made in a door leading to a covered area. The sides of the opening had slits into which the researcher could slide bulletproof glass plates (50 × 50 cm). By means of a bolt through a hole in the plates, test objects could be mounted.

The blindfolded animal was trained to sit outside the door next to the trainer. On the inside a researcher would place a glass plate with a test object in the frame (Fig. 1). The trainer would ask the

Walrus to investigate the object with its vibrissae. While doing so, the Walrus would then shake its head or nod and, if it answered correctly, be rewarded. This sequence of events was called a trial. Two sessions of 20 trials were held daily in the afternoon at 14.15 and 15.00 hrs. Each session lasted approximately 8 minutes. Twenty times in each session the animal was offered one of 2 test objects (see below) at random. If the animal had no motivation, which it showed by leaving the study area, or by pressing hard against the glass plates, the session was abandoned.

From the inside, the animal's investigation and its response were filmed with a video camera that covered part of the glass plate. Information about the date, time, trial number, background, the shape's configuration, surface area, and position were also recorded on the video tape.

Rough background

To refresh its memory, the animal was offered a thick (20 mm) set of a perspex circle and a triangle, both with a surface area of 3.1 cm², on a smooth background for the first session (20 trials). Then, the animal was offered the same easily identifiable set of objects on a rough background for one session. The rough background was devised to mask the contours of the test objects and was created by pouring transparent resin onto a smooth bulletproof glass plate.

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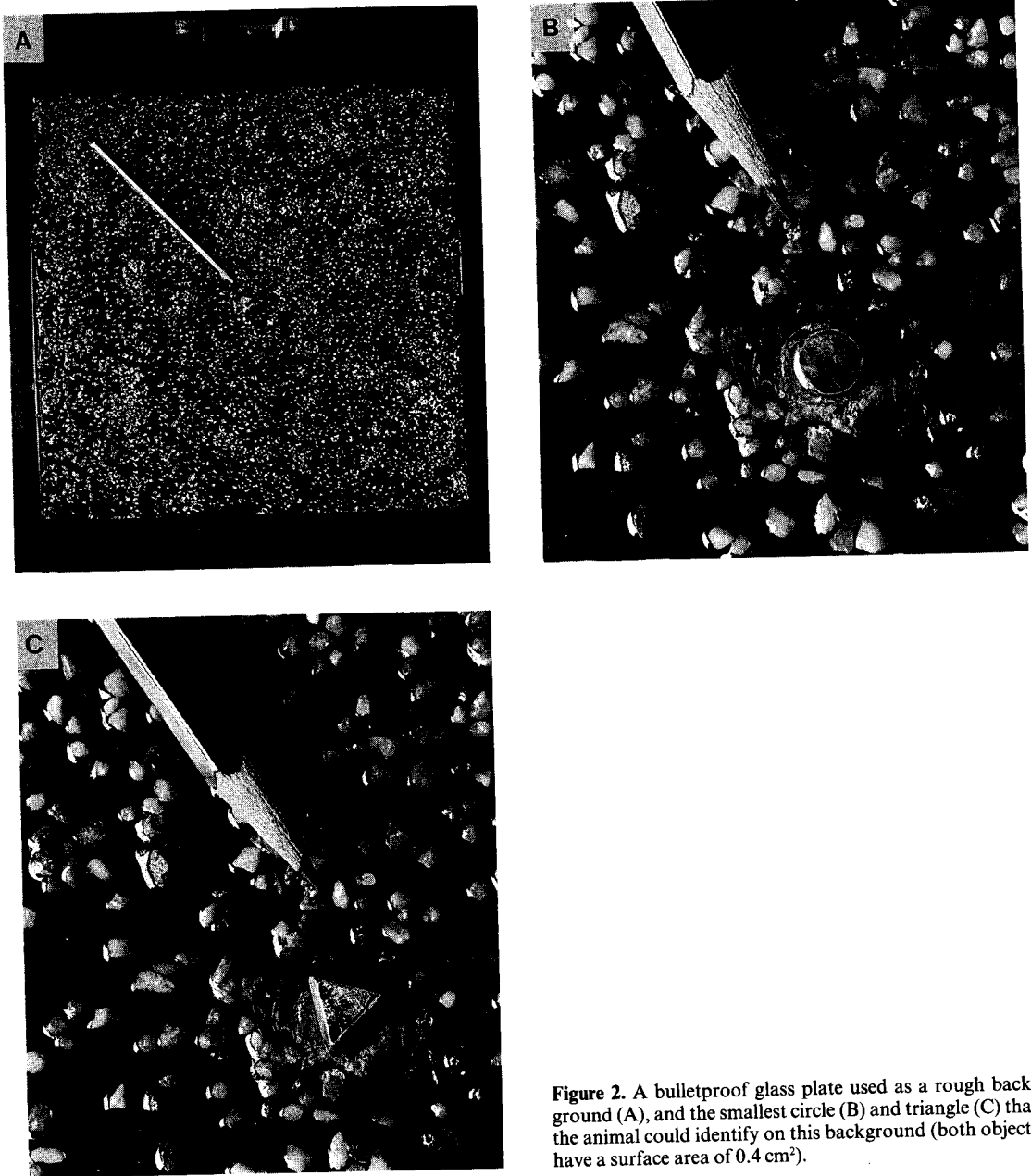
Figure 2. A bulletproof glass plate used as a rough background (A), and the smallest circle (B) and triangle (C) that the animal could identify on this background (both objects have a surface area of 0.4 cm^2).

Sand (average diameter: 2.0 mm; range: 1.5–2.5 mm) was distributed evenly (average density: 6 particles/ cm^2; range: 4–9 particles/cm^2) over this plate while the resin was still wet (Fig. 2).

When the animal had become familiar with a rough background, thinner (3 mm) sets of perspex circles and triangles were offered. The 2 objects in each set had equal surface areas (28.3, 12.6, 3.1, 0.8, 0.4, and 0.2 cm^2). The 2 smallest sets were made of stainless steel. The objects were offered in order of decreasing surface area (Fig. 3). Down to the size of 3.1 cm^2 the glass plates were positioned in the door frame. The 3 smallest sets (0.8, 0.4 and 0.2 cm^2) were offered to the animal by hand, but still on the rough
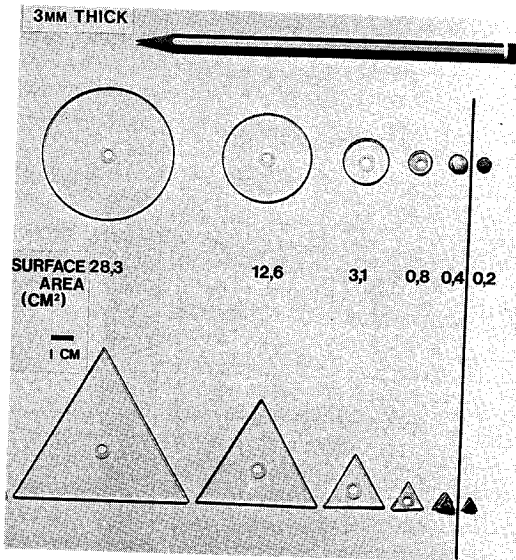
Figure 3. The 6 sets of 3 mm thick triangles and circles; each set being 2 objects of equal surface area. The vertical line indicates the discrimination threshold on the rough background.

plates, and were held in such a way that the objects were close to the centre of the Walrus's mystacium (Fig. 4).

Each size was offered for a number of sessions until the animal's percentage of correct identifications in 2 consecutive sessions was above the set level of coincidence. The percentage of correct responses in the last 2 sessions (40 trials) for each set of objects was calculated and compared to a 50% correct response score (which would mean that the animal could not distinguish the test objects) by means of a G-test. Because of the small number of trials the Wilson-correction was applied to the G-test (Sokal & Rohlf, 1981). As a critical value $p \leqslant 0.005$ was used.

Laterally positioned objects

In 2 sessions, the centre of the test objects (3.1 and 0.8 cm^2) was located 7.0 cm from the side of smooth bullet proof plates (Fig. 5). The video recordings of these trials were used to investigate the touch time (the time spent feeling the shape before responding). With a digital video recorder it was possible to view the recordings frame by frame. This was done for 13 (3.1 cm^2) and 12 (0.8 cm^2) trials, chosen from each session for their image quality. Only trials with a correct response were used. For each trial, the number of frames between the first contact of the vibrissae with the shape and the response was counted. Each frame corresponded with 1/25 sec.

To determine the touch path and which vibrissae were used most during the different stages of a trial, the mystacium was divided into 3 areas at either side
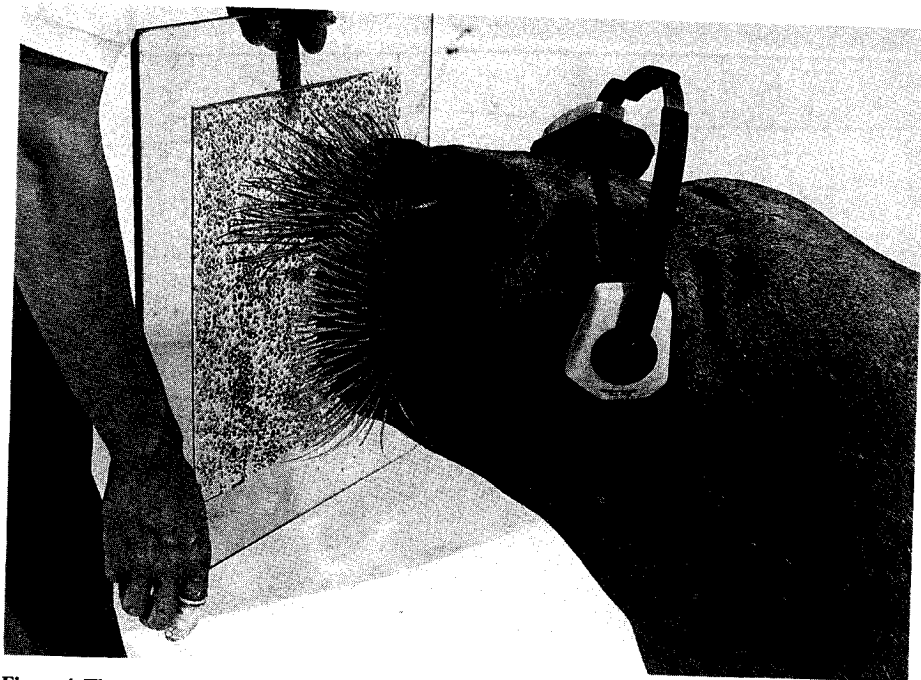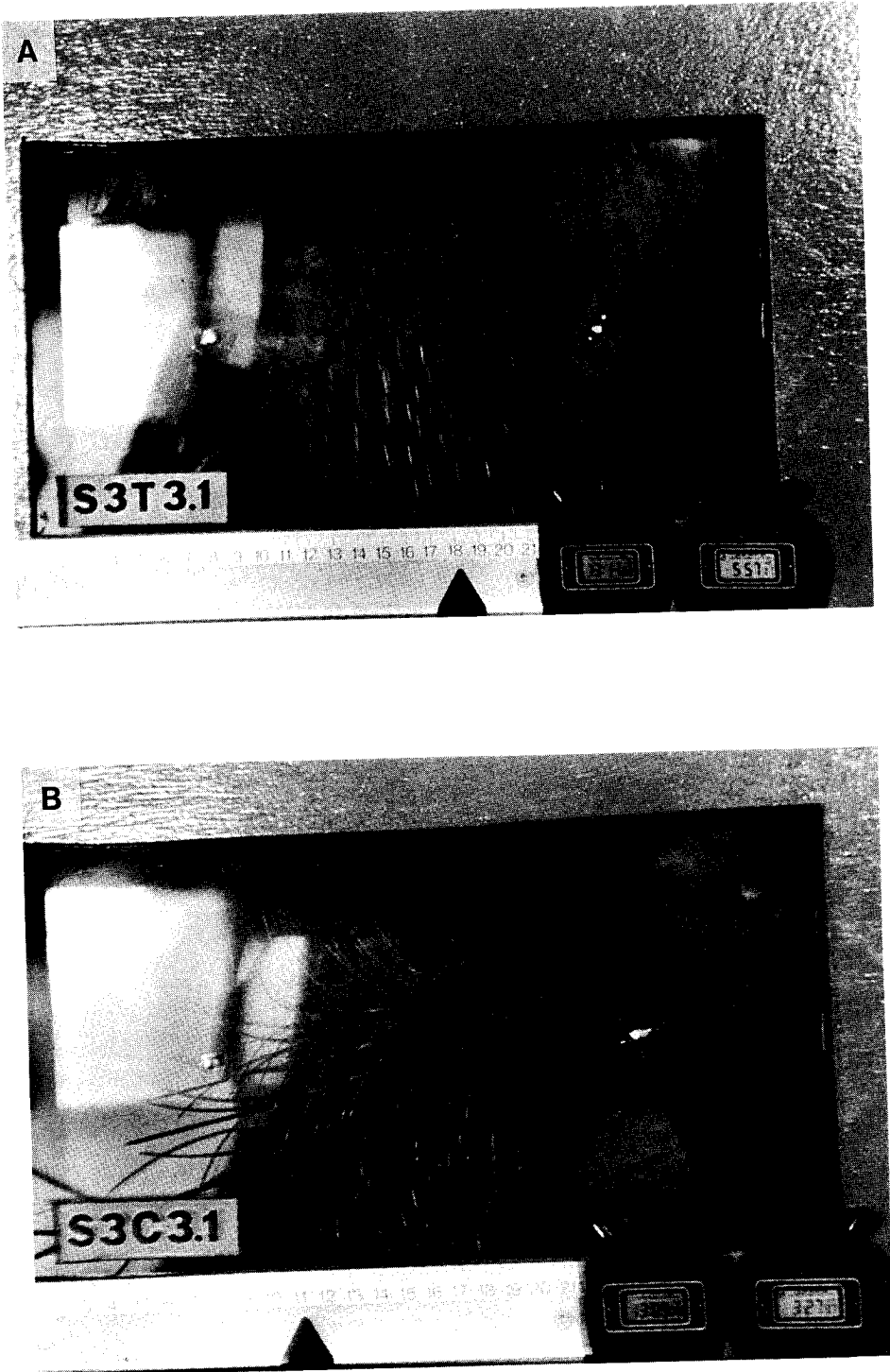

Figure 4. The method of presentation of the rough plates with the objects with a surface area of 0.8, 0.4 and 0.2 cm^2.

Figure 5. The view as recorded by the video camera showing (A) a perspex triangle, and (B) a circle. Both have surface areas of 3.1 cm² and a thickness of 3 mm and were placed 7.0 cm from the side of the bulletproof glass plate.

Table 1. The number of sessions and the percentages of correct responses of the last 2 sessions of each set with objects on a rough background. Plates were hand-held in sessions indicated with *. The threshold is 72% (p ≤ 0.005)

Thickness (mm)	Surface area (cm²)	No. of sessions	Mean percentage of correct responses of last 2 sessions
3	28.3	3	100
3	12.6	2	92.5
3	3.1	3	85
3	0.8	6*	82.5
3	0.4	2*	82.5
3	0.2	4*	65

of the mid-line. These areas were traced onto a transparent sheet which stuck to the monitor screen due to the static electric field. The position of the centre of a shape on the vibrissae pads was determined for the frames during which the vibrissae were in contact with the objects. The total touch time of a trial was divided into 3 periods (first contact—0.24 sec, 0.24– 0.48 sec, and 0.48—last contact). The total score of usage of each vibrissae area was calculated for these 3 periods (only trials with a correct response were examined).

The average scanning speed of the Walrus head was calculated for each of 4 vibrissae areas by measuring the distance travelled by the head relative to the centre of the objects per 0.04 second time period (= time period of 1 video frame).

Results

Rough background

Touch time
Unfortunately, in the sessions with the rough background, the quality of the video images was poor due to light reflection on the sand particles. Therefore, the exact touch time could not be determined. However, the touch time of the animal was roughly estimated at between 1 and 2 seconds.

Sensitivity threshold
The correct response percentages of the last 2 sessions with each set of test objects are compiled in Table 1. Most of the mistakes (88.9%) were incorrect identifications of circles. Initially the animal could only discriminate between the 2 objects down to a surface area of 3.1 cm², but when the plates were hand-held, it could identify them down to a surface area of 0.4 cm² (Figs 2B and 2C). The animal's performances were below the p ≤ 0.005 threshold for the 0.2 cm² set of objects. Therefore the discrimination

threshold for circular and triangular objects on this rough background must be between a surface area of 0.2 and 0.4 cm² (the vertical line in Fig. 3).

Laterally positioned objects

Touch area
The animal located the objects with the lateral vibrissae on its left side, and then moved its head further towards its left to touch the objects with the central vibrissae before responding (Figs 6B and 6C). In order to reach the objects with its central vibrissae, the animal had to press its left lateral vibrissae against the side of the door (Fig. 5). Because the animal was rewarded by the trainer from its right side only (Fig. 1), the first contact of the vibrissae with the objects was always made with the left mystacial pad (Fig. 6A).

Scanning speed
The first laterally placed set of objects had a surface area of 3.1 cm². The average scanning speed of the head in area 1 was 27 cm/sec (Fig. 6.1A). The scanning speed increased in area 2 and finally decreased in area 3 just before the animal responded.

The second set of laterally placed objects had a surface area of 0.8 cm². The scanning speed of the head in area 1 was 32 cm/sec (Fig. 6.2A) and dropped to around 25 cm/sec in areas 2, 3 and 4.

Touch time
The average touch time of this Walrus for laterally placed objects with surface areas of 3.1 cm² (13 trials) was 0.75 seconds, and for objects with a surface area of 0.8 cm² (12 trials), 0.95 seconds (Fig. 7).

Discussion and conclusions
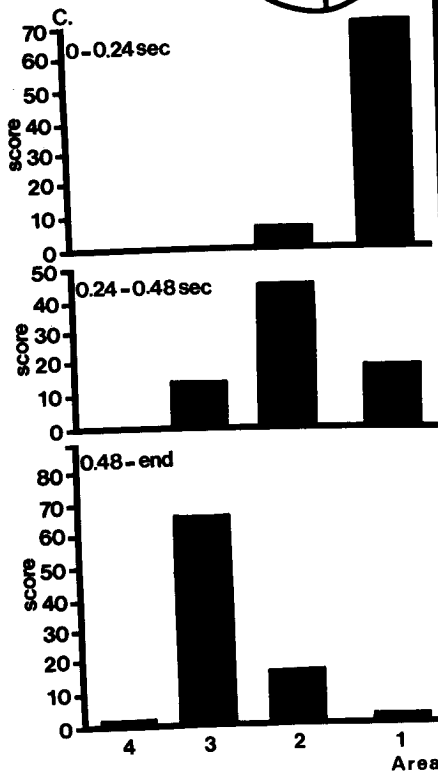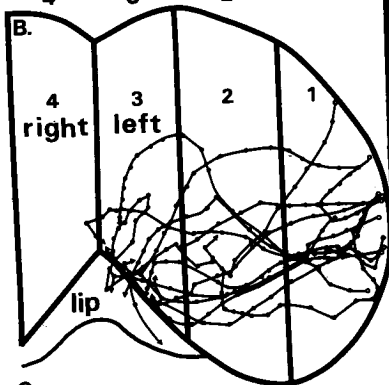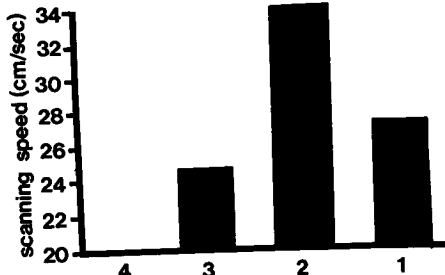
Rough background

Touch time
The touch time for objects on a rough background (estimated at between 1 and 2 seconds) was more than the touch time for the same objects on a smooth background (less than 1 second, Kastelein & van Gaalen, 1988). This was probably due to the masking effect of the sand on the background. It was probably more difficult for the animal to find the objects among the sand particles. Because of the poor transparency of the testing plate, it was impossible to determine when the animal made first contact with the objects.
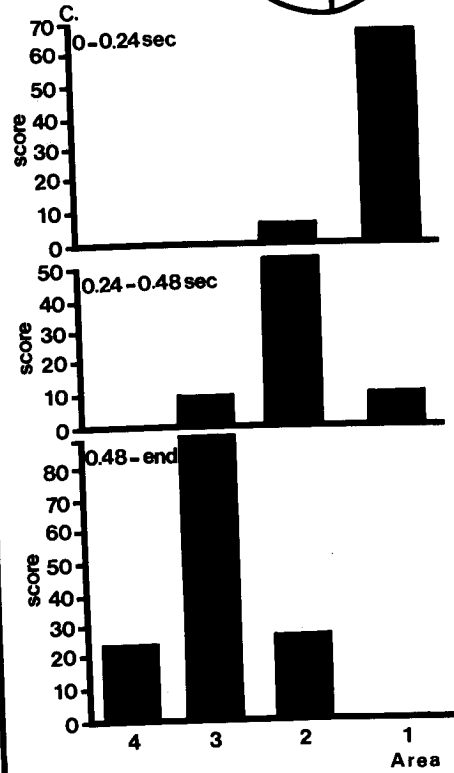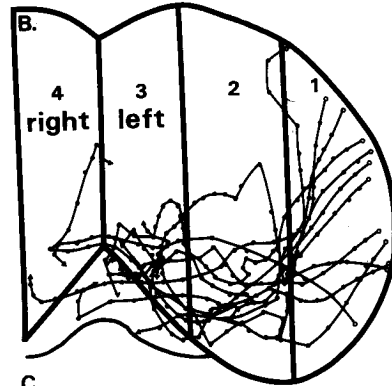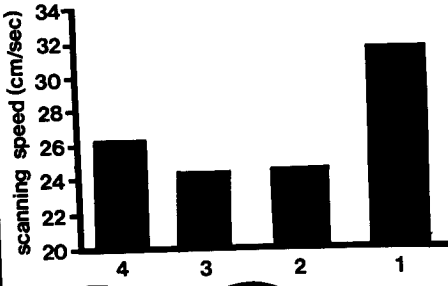
Sensitivity threshold
The animal had no problems discriminating between circles and triangles down to a surface area of 3.1 cm². The animal had considerable problems with

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6.1 A. surface area: 3.1 cm²

scanning speed (cm/sec)

34
32
30
28
26
24
22
20

4   3   2   1

6.2 A. surface area: 0.8 cm²

scanning speed (cm/sec)

34
32
30
28
26
24
22
20

4   3   2   1

B.

4   3   2   1
right left

lip

B.

4   3   2   1
right left

C.

score

70
60
50
40
30
20
10
0

0–0.24 sec

C.

score

70
60
50
40
30
20
10
0

0–0.24 sec

score

50
40
30
20
10
0

0.24–0.48 sec

score

50
40
30
20
10
0

0.24–0.48 sec

score

80
70
60
50
40
30
20
10
0

0.48–end

4   3   2   1
Area

score

80
70
60
50
40
30
20
10
0

0.48–end

4   3   2   1
Area

Figure 7. The mean touch time for 2 sets (3.1 and 0.8 cm²) of 3 mm thick objects that were mounted laterally (L) on a smooth glass plate in part 2 (this paper), and of the same objects mounted centrally (C) on a smooth plate in part 1 (Kastelein & van Gaalen, 1988). The bars indicate the standard deviation.

too long, to a smooth background (Kastelein & van Gaalen, 1988) on which it needed only a maximum of 0.88 seconds to touch and to make a decision. With objects on a rough background the animal had problems in concentrating longer than it needed to do with a smooth background.

In part 1, with the smooth background (Kastelein & van Gaalen, 1988), the animal made an equal number of mistakes when confronted with circles or triangles. With the rough background almost all mistakes were made when identifying circles. The jagged sand on the background probably resembled the sharp corners of the triangles. When the animal had to identify a circle, he probably interpreted the sharp edges of the sand (which he touched first, before moving the central vibrissae towards the object) as the corners of a triangle.

Kastelein & van Gaalen (1988) showed that the centre of the mystacium was usually the end-point of a touch movement, and it was presumed in part 1 that this area has the best resolving power. When the rough background plates with objects of 0.8, 0.4 and 0.2 cm² were offered by hand in such a way that there was immediate contact with the centre of the mystacium (Fig. 4), the animal was able to discriminate between circles and triangles down to a surface area of 0.4 cm². This showed that the Walrus could identify very small objects mounted on a rough or smooth surface with the same accuracy. It is somehow able to compensate for the masking effect of the rough background. When touching a shape with some of the central vibrissae, lateral vibrissae were stimulated at the same time by the sand particles. Maybe signals from the central vibrissae are processed differently from signals from the lateral vibrissae, enabling the animal to filter out irrelevant (lateral) signals from more relevant (central) signals when an object is moved closer to the mouth.

the objects of 0.8 cm². It became frustrated and several sessions had to be abandoned. Because the animal was rewarded from the side, its head moved sideways when searching for the objects on the rough plates. As soon as the lateral vibrissae touched the rough plate, the animal started to shake its head, as it would if it felt a triangle. It did not touch more carefully for a longer period of time. Perhaps the Walrus became frustrated because it was accustomed, for

Laterally positioned objects

Touch area
This study showed that the animal made a great effort to move its head so that the final contact with the test objects was with its central vibrissae just above the upper lip. In some cases the Walrus ended the investigation by touching the objects with its

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Figure 6.1. Touch parameters, during 13 trials with a correct response, when investigating laterally placed objects with a surface area of 3.1 cm².

Figure 6.2. Touch parameters, during 12 trials with a correct response, when investigating laterally placed objects with a surface area of 0.8 cm².

(A) The average scanning speed in 4 vibrissae areas (an imaginary grid divides the total vibrissae surface into 6 areas, of which 4 are shown).

(B) The touch path on the vibrissae endings and upper lip. The beginnings of the touch paths are indicated by open circles and the ends by triangles.

(C) The touch direction indicated by the object's position during 3 time intervals.

upper lip. This confirms the suggestion in part 1 (Kastelein & van Gaalen, 1988) that the long lateral vibrissae are used mainly for detection and the short central ones for identification. It is possible that the upper lip is even more sensitive than the central vibrissae. Although the scanning technique seems like a rough head movement at first, the direction and end of the movement are precisely determined. In contrast, head movements are minimized during whisking of the vibrissae in rats (Gustafson & Felbain-Keramidas, 1977) and hamsters (Winenski, 1983).

Scanning speed
The laterally placed objects with a surface area of 3.1 cm^2 were the first laterally placed objects the animal ever encountered during the study. The animal had to detect the objects first, and therefore moved its head slowly (area 1 in Fig. 6.1A). Once the objects were found, the animal moved its head quickly in order to make contact with the central vibrissae (area 2 in Fig. 6.1A). When the central vibrissae reached the object, the animal slowed down the movement of its head.

During the second session with laterally placed objects (0.8 cm^2) the animal was used to the position of the objects, and quickly moved its head into the correct position. Probably because of this, the average scanning speed in the area of the long vibrissae (area 1 of Fig. 6.2A) was very high. This test indicates the animal's capacity for learning and memorizing.

Touch time
It took the animal longer (Wilcoxon, $p \leqslant 0.05$) to identify laterally placed objects (3.1 cm^2 and 0.8 cm^2 sets) than centrally placed objects (Fig. 7). This difference is probably due to the fact that the left lateral vibrissae would have hit the edge of runway of the glass plates hard if the animal would have moved its head too fast or too far to its left (Fig. 5).

Vibrissae of otarids and phocids serve to detect vibrations in their environment such as caused by swimming fish or holes in the ice (Renouf, 1979, 1980; Sonafrank et al., 1983; Mills & Renouf, 1986) and to actively investigate the surface texture of prey (Dykes, 1965; Schusterman, 1968; Oliver, 1978). The present study only investigated the Walrus's sensitivity when it was actively touching the objects under investigation. Whether its vibrissae are also sensitive to vibrations in the water or in the substrate has not been determined. However, because Walruses do not eat fast-swimming fish which create vibrations in the water, but plough through the substrate in order to find bentic prey, a high sensitivity for vibrations (= rapidly adapting afferent fibres) seems unnecessary, unless Walruses use the water current which is created by a disturbed (siphon retracting) clam to locate the bivalve molluscs. Walruses probably have

slowly adapting fibres which can provide information about shape and size (Mountcastle & Darian-Smith, 1968; Iggo & Muir, 1969). The Walrus' method of identifying prey in the substrate resembles that of ducks foraging for food on and in the substrate. They also rely on tactile information to identify prey since the edges of the bills of birds contain many mechano-receptors (Berkhoudt, 1980; Dubbeldam, 1980).

The results of the present study should be interpreted carefully since they concern the vibrissal sensitivity of only one Walrus. There may be individual differences in discriminatory abilities due to the individual variation in the number of vibrissae of each Walrus (Fay, 1982), and also due to individual differences in the length, diameter and stiffness of the vibrissae (Yablokov & Klevezal, 1964; Kastelein & van Gaalen, 1988).

The differences in sensitivity between areas of the vibrissae pads can be partially explained by the morphological differences mentioned above, but anatomical differences probably exist also. These could be differences in the type of follicles (Melaragno & Montagna, 1953; Ling, 1966, 1972), the type of mechano-receptors (Dykes, 1965; Andres, 1966) and number of mechano-receptors at the base of the vibrissae (Stephens et al., 1973). Also the type and number of nerve fibres leading from one vibrissa (Dykes, 1975), the nerve connections between vibrissae (Dörfl, 1985) and the central projection and analysis of the signals can influence the amount of information obtained from an individual vibrissa (Woolsey & Van der Loos; Van de Loos & Welker, 1985; Van der Loos, 1985; Welker & Van der Loos, 1986; Ladygina et al., 1985). Neuroanatomical research is presently being carried out by the Harderwijk Marine Mammal Park and the Erasmus University in Rotterdam to address these questions.

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