Vibrissal touch sensing in the harbor seal (*Phoca vitulina*): How do seals judge size?

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Abstract

"Whisker specialists" such as rats, shrews and seals actively employ their whiskers to explore their environments and extract object properties such as size, shape and texture. It has been suggested that whiskers could be used to discriminate between different sized objects in one of two ways: i) to use whisker positions, such as angular position, spread or amplitude to approximate size; or ii) to calculate the number of whiskers that contact an object. This study describes in detail how two adult harbor seals use their whiskers to differentiate between three sizes of disc. The seals judged size very fast, taking less than 400 milliseconds. In addition, they oriented their smaller, most rostral, ventral whiskers to the discs, so that more whiskers contacted the surface, complying to a maximal contact sensing strategy. Data from this study supports the suggestion that it is the number of whisker contacts that predict disc size, rather than how the whiskers are positioned (angular position), the degree to which they are moved (amplitude) or how spread out they are (angular spread).

Keywords: whiskers, haptic, active touch, aquatic, maximal contact
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Introduction

The majority of behavioral studies in vibrissal touch have been directed at rats and mice, however all mammals, apart from some primates and humans, have whiskers at some point in their lives (Ahl 1986). In pinnipeds each whisker is richly endowed with mechanoreceptors and 1000-1600 nerve fibers, which is about ten-fold greater than those in other mammals (Hyvärinen 1989). In accordance with this high degree of innervation the whiskers have a large representation in the somatosensory cortex (Ladygina et al. 1985). Not only are pinniped whiskers well-equipped for active touch sensing and employed to perform tasks such as discriminating object textures, shape and size (Dykes 1975), they are also used to detect water movements such as simulated fish hydrodynamic trails (Dehnhardt et al. 2001; Wieskotten et al. 2010a; Wieskotten et al. 2010b).

Using their whiskers to touch stimuli, harbor seals are able to judge differences between widths of textured grooves as small as 0.18 mm (9% stimulus difference). Their high level of performance is unaffected by changes in water temperature (Dehnhardt et al. 1998), unlike humans who have a reduced tactile performance when their skin temperature is less than 15 degrees (Dehnhardt et al. 1998). As well as being robust texture sensors, pinniped vibrissae are also excellent shape detectors. A Pacific walrus (*Odobenus rosmarus divergens*) can distinguish between circular and triangular objects, with surface area differences between the two shapes as small as 0.4 cm^2 (50% stimulus difference in surface area, Kastelein et al. 1990). A study in the California sea lion (*Zalophus californianus*) showed that this animal could distinguish between five shapes using its vibrissal sense of touch, and was able to reach the same level of accuracy that it had previously reached using vision (Dehnhardt 1990). California sea lions could also distinguish between circles and triangles with surface area differences down to 0.5 cm^2 (34% stimulus difference in surface area, Dehnhardt and Dücker 1996), which is comparable to the Pacific walrus. Pure size discrimination tasks in pinnipeds have also been very well described. A California sea lion (*Zalophus californianus*) can differentiate between triangles that are 0.63 cm different (20% stimulus difference in surface area, Dehnhardt and Dücker 1996) and harbor seals have been found to distinguish between discs that are 1.08 cm different (individual 1, male harbor seal) and 0.65 cm different (individual 2, female harbor seal) (interpolated value; 14% and 8% stimulus difference in surface area, respectively, Dehnhardt and Kaminski 1995) and even as little as 2 mm different both on land and under water (5% stimulus difference in surface area, Dehnhardt et al. 1997).

As the pinniped whisker was first thought of as a vibrotactile sensor (Dykes 1975), it might be understandable that pinnipeds can detect texture differences; however, how can a simple whisker array detect size, or shape? This paper will focus on size differentiation, as perhaps the more simple of these two object properties. In rats, Brecht et al. (1997) suggested that the whisker row could act as a size or distance detector, such that the most caudal untouched whisker could code for size, and also the minimal distance to the object. However, in humans, it is the spread (or span) of their thumb and fingers that codes for size (Stevens and Stone 1959; John et al. 1989; Santello and Soechting 1997). Knutsen et al. (2006) have found that rodents can judge gap sizes with only one whisker intact, and suggest that they may encode size using the angular position (amount of protraction) of their whiskers (Knutsen et al. 2008; Horev et al. 2011), which might be a similar measure to the finger span in humans. This paper investigates whether the angular changes in the whisker positions, or the number and identity of contacts, contributes most to the prediction of size in the case of large size differences.

Studies in walrus, sea lion and harbor seal have all described that the animal orients to the stimuli, such that it can be touched by vibrissae on both sides of the head, and that the animal may also move its whiskers against or over the stimuli (Kastelein et al. 1990; Dehnhardt 1994; Dehnhardt and Dücker 1996). However, descriptions and quantification of pinniped whisker movements currently lack the level of detail seen in the rodent literature. Furthermore, since the number, arrangement, size, stiffness and structure of the whiskers vary significantly between pinnipeds (Ling 1977; Watkins and Wartzok 1985), observations from walruses and sea lions might not hold for other pinnipeds, especially phocids, such as the harbor seal. Therefore, this study focuses on describing vibrissal behavior in the harbor seal (*Phoca vitulina*) using a simple size differentiation task that has previously been used in both harbor seals (Dehnhardt and Kaminski 1995) and a California sea lion (Dehnhardt 1994). Video analysis techniques were employed to measure the head and whisker movements of harbor seals during the size differentiation task, and characterize their behaviors using metrics that allow comparison with rodent studies. These are important first steps in understanding vibrissal touch sensing in the harbor seal.

Materials and methods

Animals

The study was conducted at the Marine Science Center, Rostock, Germany. Two male harbor seals (*Phoca vitulina*) were studied; 5-year-old Moe and 29-year-old Marco. Both seals were familiar with a variety of psychophysical experiments. The animals were kept within a group of seven other male harbor seals and one South African fur seal (*Arctocephalus pusillus*) within a large seawater enclosure in the Baltic Sea, with dimensions of 60x30 meters and 5 meters deep.

Apparatus

Experiments on land were carried out in a chamber on a dry platform adjacent to the seal enclosure, while experiments in the water were carried out in a separate pool that was also adjacent to the main enclosure. The test apparatus (Fig.1) consisted of a MiniTec™ frame in three sections. The middle section contained a yellow ball, about 35 cm from the ground, which was a stationing point for the seals. Sections to the left and right contained the tactile stimuli and were angled at 140 degrees from the middle section. These were positioned around 30 cm from the ground, 15 cm in front of the frame. The stimuli were slotted into the MiniTec™ frame in blocks, which could fold back to an angle of 45 degrees (see the left hand side of the set-up in Fig. 1a).

Two video cameras were positioned to film the right-hand stimuli. The first, giving a top-down view, was a Canon XL-2 recording at 25 frames per second (fps), and the second was a Sony Handicam, recording at 30 fps, which was positioned behind the right-hand stimuli, giving a front-on view (Fig. 1b and c). This enabled the angular positions of the whiskers to be viewed, from on top, while also observing the whiskers that were contacting the stimuli, from behind the stimuli. Observing the whiskers from a top-down view is common in the rodent literature (Voigts et al. 2008; Grant et al. 2009; Mitchinson et al. 2011). The cameras were calibrated in space using a custom-made calibrator of known size and, in time, using the whistle signal in the audio recording. However, the data presented in this study used the two cameras to extract different whisker measures and did not require this level of calibration. When the apparatus was placed into the water, it was lowered until the top bar of the frame was 20 cm below the water surface. The cameras were placed into waterproof housings and positioned in the same way as described for experiments on land (Fig. 1d-f). The apparatus was hung in the water over MiniTec™ fittings and wooden boards. An additional station (red ball in Fig. 1d) was added to the set-up so that the experimenter could access the seal above the water to put on its mask and headphones. During both experiments on land and in the water, the experimenter was positioned on the dry platform behind the set-up in order to have good access to both the stimuli and the animal.

Stimuli selection

The stimuli were perspex discs of 2, 4 and 6 cm in diameter, and a depth of 1.5 cm, giving front surface areas of 3.14, 12.57 and 28.27 cm^2, respectively. The distance between whisker follicles ranged from 0.7-1 cm (calculated from video footage). These disc sizes were chosen to have relatively large differences in surface area. This study is not concerned with finding size discrimination thresholds, but rather measuring the whisker parameters (such as number of contacts and whisker positions) that change with an increase in stimulus size. Looking at large differences in stimuli would address these behavioral changes best. Large size differences have been used previously in discrimination tasks with three stimuli and have been found suitable to assess behavioral parameters in both visual (Segev et al. 2007) and tactile (Harvey et al. 2001) active sensing.

Experimental procedure

During training and experimental sessions, Moe and Marco were separated from the other animals and tested individually in a chamber (on land) or in a separate pool (under water). Prior to data acquisition, training sessions were carried out once daily, typically 5 days a week for 10 to 20 weeks, until a learning criterion of 80% correct choices in three consecutive sessions was achieved. Video clips were also collected during training to check the set-up and camera positions. Experimental sessions with formal data acquisition (video filming) were conducted once or twice per day, typically 5 days a week, for around 6 weeks in total and usually consisted of 12-18 trials. During a typical session each animal received approximately 40% of its daily amount of food in the form of freshly thawed cut herring or whole sprats.

Experiments were based on a two alternative forced choice paradigm. At the beginning of each trial the seal positioned itself in front of the apparatus and pressed its nose against the stationing ball. With the seal properly positioned at the station ball in the middle of the setup, the experimenter covered its eyes with a blindfold, which could either be a latex stocking mask (Wieskotten et al. 2011) or eye caps (Dehnhardt 1994), and placed headphones over its ears. Two disc stimuli differing in size were selected and placed into the left and right sections of the frame. They were brought simultaneously to a vertical position such that the discs were placed into the middle of the windows on each side of the seal. The experimenter then removed the headphones from the seal and indicated that the trial was to start using a verbal command. The seal then immediately left the station ball and examined both discs by touching them alternately. The seal was required to respond by pressing its nose against one of the two discs and deflecting it back. The blindfold could then be removed. If the seal had chosen correctly, the experimenter whistled for one second and rewarded the seal with a fish. If the seal had chosen incorrectly, no whistle sounded and no fish was given. Following a choice both discs were removed from the apparatus and the seal stationed back at the stationing ball. In order to rule out olfactory cues the discs were cleaned thoroughly between sessions. The discs could be presented in any combination (big and small, small and big, medium and big, big and medium, medium and small, small and medium) and were presented in a pseudo-random order (Gellermann 1933), with each combination presented two or three times per session. Once the seals were trained in the task (achieving 80% correct choice in three consecutive sessions) they were filmed in subsequent sessions.

Biases and controls

Before being trained on the task, the seals were introduced to the stimuli and the set-up to observe their natural preferences for disc size and side. Moe displayed a natural preference for the biggest disc, and pushed it over many times. Marco displayed a natural preference for the smallest disc, and pushed it over and mouthed it repeatedly. These size biases caused us to train Moe to choose the biggest disc presented to him and Marco the smallest.

The respective right-hand stimulus was chosen for filming as in over 99% of all the trials the seal went to the right stimulus first, indicating that they had a natural preference for the right-hand stimuli. The direction of movements can be seen in Table 1, and these movement patterns could be observed even during training. This meant that for the medium disc of 4 cm, the seals typically explored it twice when it was paired with a disc that was not the target disc (i.e. when it was paired with a smaller disc for Moe, and a bigger one for Marco). This pattern indicates that the seals learned to differentiate absolute, rather than relative, sizes. Indeed, past studies have found that the number of times seals revisit stimuli remain at low levels even when disc diameters are very similar (Dehnhardt and Kaminski 1995). For the rest of this article the 6 cm disc is referred to as *big*, the 4 cm disc as *medium* and the 2 cm disc as *small*. If the animal returned to explore the medium disc a second time during a trial, this will be referred to as *medium-2*. These biases for disc and side do not affect the results from this study because the focus of the experiment is on the exploration of the discs, rather than the learning of the task. The animals also achieved high scores in each session (>80% correct choices) during the test stages of the experiment.

Data selection and video analyses

All the video clips collected during the trials were reviewed for analysis. Clips were selected when: i) both whisker fields could clearly be observed by the cameras in both views throughout the clip; ii) lighting was sufficient to see the whisker follicles in the front-on view; iii) the seal did not make significant head pitching or rolling movements and iv) the seal made the correct choice (note, there were not enough incorrect choices to analyze incorrect choices further). In total, 241 video clips were selected, 120 recorded in air and 121 under water. 123 of these clips featured Moe and 118 clips Marco. There were a total of 68 clips featuring the big disc, 70 for the medium disc, 32 for medium-2, and 71 for the small disc.

Whisker tracking

In each clip selected for tracking, three whiskers on each side of the face were manually tracked in every video frame using uncompressed video footage and a purpose-built whisker-tracking tool written in Matlab (Mitchinson et al. 2007; Grant et al. 2009). The clips were tracked from the frame of the first contact with the target disc to the frame prior to the seal either turning its head away or pushing the disc over. These were termed the *first contact* frame and the frame *after orienting* and were identified by eye by a trained observer. Tracking used only the overhead camera view, which is a standard way to track whisker positions when head pitch or roll is low (i.e. Voigts et al. 2008; Grant et al. 2009; Mitchinson et al. 2011; Grant et al. 2012a). Two points were tracked on each whisker, one near the base, the other around two-thirds of the way out along the whisker shaft. Fig. 2 shows the points (in red) that were identified by visual inspection of this frame and selected by a mouse click at the appropriate cursor position. This process was performed in every tracked frame and this data was then used to calculate a summary measure of the angular position of the left and right whisker fields (θ for the left-hand caudal-most tracked whisker can be seen in Fig. 2). The head orientation was also calculated from a point on the nose and head, and the instantaneous angular head velocity was calculated in each frame, for each clip.

Next, this angular position data were used to calculate estimates of whisker *angular position*, *angular spread* and *amplitude*, all measured in degrees. Angular positions for the left and right were calculated by averaging between the three tracked whiskers on each side. Angular spread was calculated by finding the difference in angular positions between the rostral and middle whisker (*rostral spread*) and the middle and caudal whisker (*caudal spread*), and was averaged between the two sides. Amplitude was calculated, in degrees, as the maximum movement of the whiskers throughout the clip. The angular positions of the three whiskers on each side were averaged, and the maximum angular position was subtracted from the minimum angular position; the overall amplitude was calculated as an average between the two sides. Angular position and angular spread were measured at two time points: i) first contact and ii) after orienting, whilst amplitude was measured throughout the clip. The *decision time* was also estimated by calculating the time from first contact to the time after orienting.

Further video analyses

In addition to measuring whisker movement variables from the overhead view, the corresponding front-on video view was used to count whisker contacts. The front-on videos were manually inspected and the identities of the whisker contacts were recorded. In Fig. 2b, the left hand whiskers are touching the big disc, identified as whiskers G3-G8 and F3-F8 (using the identification grid in Fig. 2c). Therefore, whisker identities were recorded for the first contact and after orienting, and presented as a proportion of all the contacts on that disc (see Electronic Supplementary Material, Online Resource 1 for all the proportions of contacts for each whisker). Figures 6 and 7 show the whiskers that are contacted in >15% of these trials. Raw data of these proportions can be seen in the Electronic Supplementary Material, Online Resource 1. The contact numbers were also summed to calculate the total *number of whisker contacts* at first contact and after orienting.

Statistical considerations

In the following section results are expressed in the form mean±sd. A MANOVA was carried out on the whisker position measures (angular position, angular spread, amplitude), with disc size as the between variable. Individual mixed model ANOVAs were carried out on these variables with disc size as the between variable. All data were checked to ensure normal distributions (Kolmogorov-Smirnov Test) and equal variances (Levene's Test) before running the ANOVAs. The effect of whether the experimental session took place on land or under water, and also differences between animals were checked by adding these as additional between-variables. These effects will also be referred to in the text. More information of the individual ANOVA analyses can be found in Table 2. Angular positions, angular spread, amplitude and the number of whisker contacts are all presented in bar graphs with standard error bars in the results section (Fig. 4).

The instantaneous angular head velocity and bilateral asymmetry were correlated (scattergram can be seen in Electronic Supplementary Material, Online Resource 1) and this data was also checked to ensure normal distributions using a Kolmogorov-Smirnov Test.

Results

Training the task

The task was to select one target disc from two presented discs, such that Moe had to find the biggest presented disc, and Marco, the smallest. The presented discs could be either 2, 4 or 6 cm in diameter. The seals learnt this task relatively quickly; it took 45 to 50 sessions to learn the task on land, and only 3-6 sessions to then apply this task under water. Fig. 3a, b show the learning curves of the two seals being trained to complete the task with three stimuli. The learning criterion was 80% correct choices in three consecutive sessions, but this could only be reached in the complete task when all the equipment was in place. Pre-training occurred on land and included a number of steps, such as training with two discs without a mask, with a mask and with head phones. The data presented here in the first learning stage on land (Fig. 3, stage 1) was collected from the first time the seals were trained with all three disc stimuli present. The headphones and mask were then added in subsequent sessions. Some sessions were solely aimed at training core skills such as putting on the mask, or stationing, therefore these would not have a percentage correct output associated with them. Moving from one training step to another (i.e. introducing the mask to the experiment) did not necessarily mean that the percentage of correct answers decreased below the 80% limit (Fig. 3, stage 1). In the water, training steps included habituating to the set-up in the water and learning to station with the mask and headphones (Fig. 3, stage 3). Data collection was carried out on land and under water in stages two and four, respectively (Fig. 3).

Both in training and post-training the seals had a systematic bias towards the right hand side. They turned towards the right-hand disc first in 99% of all trials.

How do the seals judge size?

Both seals made decisions about disc size very fast. Indeed, the time from the first contact to the decision (whether to push the disc or explore the next one) was 0.17±0.07 seconds overall (including data on land and under water, Fig. 3). All the decision times were well under 0.4 seconds and did not change significantly with disc size. There were also no differences in decision time between the two animals, however they both generally took approximately 0.02 seconds longer under water.

Whisker positions

A MANOVA run on the whisker position measures (angular positions, angular spread and amplitude) showed that there was no overall significant effect of disc size on these measures (MANOVA results: F(15,643.612)=0.873, p=0.595). Each of these measures will now be considered in turn.

Fig. 4a shows the angular position of the whiskers. The whiskers were less protracted after orienting (just prior to the decision to leave or push the disc), compared to at first contact. From reviewing the video footage it appeared that when the whiskers contacted the disc they were forced backwards against the disc surface, which explains this decrease in angular positions (Fig. 5a). Angular positions were slightly smaller on the big disc and slightly larger on the smallest disc after orienting. This can be seen in Fig. 4a by comparing the lightest bars for the big and small disc (means are 130.40±19.58 for the biggest disc, and 133.60±17.35 for the smallest disc), and might indicate that more whiskers were forced backwards by the bigger disc, after orienting. Indeed, Fig. 5a shows many whiskers on the left hand side being deflected strongly against the big disc (compare with Fig. 5 b-d). There were no differences in angular positions of the whiskers on land versus under water or between animals. The graph in Fig. 4a also shows that seals positioned their whiskers on the block asymmetrically, with left-hand whiskers being more protracted forward than right-hand whiskers. The whiskers were more asymmetric on the first contact than after orienting, and the disc size did not have an effect on the amount of asymmetry. The whiskers were more asymmetric under water, and Marco had more asymmetric whisker positions than Moe. Anecdotally, Marco tended to tilt his head more, and contacted the discs at more obtuse angles than Moe by contacting the disc at the side, rather than straight-on (see, for example, Fig. 5d). Further analyses on asymmetry can be found in the Electronic Supplementary Material, Online Resource 1.

Fig. 4b shows the angular spread of the whiskers. The seals had more spread out whiskers after orienting and the rostral whiskers were more spread out than the caudal whiskers. The seals did not change their whisker spread in response to the different sizes of disc, and there were no differences in whisker spread between the two seals. The whiskers were, however, less spread out under water.

Fig. 4c shows the amount the seals moved their whiskers (whisker amplitude) during the contact. There were no significant changes in this angular displacement between the different disc sizes, and no difference between the two animals. The whiskers did, however, move more (with higher amplitudes) under water than on land.

Whisker contacts

Fig. 4d shows the number of whiskers that contacted the discs. The number of whisker contacts changed significantly with disc size (Mixed model ANOVA results: $F(3,237)=7.540$, $p<0.001$), such that a Bonferroni posthoc test indicates that the big disc had more whisker contacts than the medium disc (after orienting on its first explore), which had more whisker contacts than the smallest disc. Doing the task under water did not affect the number of whisker contacts, but Moe tended to contact more whiskers, on all the discs, than Marco. The number of contacts significantly increased following the orientation movement.

Looking in detail at which whiskers contacted the disc after orienting, it can be seen that the seal usually contacted the right-hand disc unilaterally first, with 81% of trials containing unilateral touches on a first contact frame, and 66% of all trials containing unilateral first contact on right-hand whiskers. Following a first contact, the seal then continued to orient towards the disc, which usually involved making bilateral whisker contacts; 74% of trials contained bilateral whisker contacts after orienting.

Figures 6 and 7 show the whiskers that most commonly contacted each disc. These are the whiskers that contacted in >15% of all trials; raw data and a description of these can be found in the Electronic Supplementary Material, Online Resource 1. Fig. 6 shows the whiskers that most commonly contacted each disc during a first touch. Whiskers on the right hand side touched the disc more than those on the left, and contacts occurred across the entire whisker pad. Fig. 7 then shows whiskers that most commonly contacted each disc after orienting. These were quite different from the first contacts. Firstly, the seal touched the disc with its more rostral and ventral whiskers. These are the most densely packed whiskers in the pad. Secondly, it is clear to see from Fig. 7 that more whiskers contacted the big disc than the medium disc (on both first and second explorations), and more whiskers contacted the medium disc than the small disc. This is consistent with the data shown in Fig. 4d.

Discussion

Size differentiation using whisker contacts

Humans code for object size by calculating the spread (or span) of their thumb and fingers (Stevens and Stone 1959; John et al. 1989; Santello and Soechting 1997). Accordingly, this study measured the angular positions and spread of the whiskers to see if these could also encode size. However, there were no distinct changes in the whisker positions and spread in response to the different sized discs. Rather, it became apparent that larger discs contacted more whiskers than smaller discs. Data from this study, therefore, suggests that it is the number of whisker contacts that indicate the size of an object. In addition, it appears that the seals have learnt the absolute size of the discs in this experiment, rather than the relative size. If the seal contacted the target disc first (biggest for Moe, and smallest for Marco), it chose that one before even exploring the other disc. This can be seen in Table 1, and in 99% of the trials. Dehnhardt and Kaminski (1995) observed a similar pattern in a size discrimination task in harbor seals, when they were finding the discrimination threshold. Even when the diameters of the discs were very similar (0.33 cm difference in diameter), the male seal did not make more subsequent comparisons between the stimuli (Dehnhardt and Kaminski 1995). As there were only three discs, and the seals were extremely well trained, it would be an efficient strategy to judge absolute size. As the target stimuli differed only in size, this task is still considered a size differentiation task, rather than a simple object recognition task. In addition, the target stimuli did vary between trials, namely between big and medium discs (for Moe), and small and medium discs (for Marco). Further work is needed to find the threshold between absolute and relative size differentiations.

Video footage collected in this study clearly shows that the seal consistently oriented its more rostral, ventral whiskers to the discs. Orienting the whiskers can increase the sampling resolution in such a size differentiation task. The rostral and ventral whiskers are shorter and more closely packed, so orienting to these whiskers gives higher resolution touches, such that more whiskers contact the disc. For example, touching the big disc to the more caudal, spaced-out whisker would contact as many whiskers as touching the small disc to the more rostral whiskers. Positioning the stimuli centrally to the face, so that the whiskers can contact an object bilaterally, has been observed in a California sea lion (Dehnhardt and Dücker 1996), a Pacific walrus (Kastelein et al. 1990) and also previously in harbor seals (Dehnhardt 1994). Kastelein et al. (1990) also observed that, during a shape differentiation task with a Pacific walrus, the animal strived to touch objects with its short central vibrissae; they suggested that these whiskers have a higher resolving power than the lateral vibrissae that are perhaps used for contact detection. Data from our study lends support to this idea.

Differences on land and under water

Under water, the seals took a bit longer to judge size (approximately 170 milliseconds more), their whiskers were less spread out and they had more variability in angular position between the two sides. This might be because the underwater environment is more noisy due to water movements and underwater drag, which will cause small changes in whisker movements and thus might let them take them longer to judge size. This has not been found previously in the literature; indeed Dehnhardt et al. (1997) found the opposite was true, that one of their seals could in fact perform a size experiment quicker in the water. Contrasts between these two studies could have arisen from differences between the animals, especially in terms of their prior exposure to performing in underwater experiments and their training experiences, or from differences in hydrodynamic background flow.

Differences between seals

There were also small differences between the two seals as Marco made more asymmetric movements and less whisker contacts than Moe. These differences occur as Marco often contacted the edge of the disc and could make decisions about the disc size just from an edge contact (Fig. 5d). As harbor seals have been found to judge size differences to as low as 2 mm (Dehnhardt et al. 1997), it was a relatively easy task for the seals to judge size in this experiment, even just from an edge contact, as the discs differed by 2 cm in diameter.

Additional Observations

There is evidence for orienting responses in this data (as detailed above), which complies to a 'maximal contact' sensing strategy (Mitchinson et al. 2007). In addition, the harbor seal whiskers were often forced into the disc and deformed against its surface, so much that the overall angular positions of the whiskers are reduced (Fig. 5). This is in contrast to what has been observed previously in rodents (Mitchinson et al. 2007) and sea lions (Dehnhardt 1994) who both make gentle touches with their whisker tips (termed *minimal impingement* (Mitchinson et al. 2007)). There was also strong asymmetry in the whisker fields, such that the left-hand whiskers had larger angular positions (were protracted more forward) than the right-hand whiskers. If the asymmetry observed in this investigation was caused by contacting the disc, termed *contact-induced asymmetry* (Mitchinson et al. 2007; Mitchinson et al. 2011; Grant et al. 2012a), it would likely be larger after orienting, and also larger on the big disc. That this is not the case suggests that the bilateral asymmetry might well be as a result of a head rotation, termed *head-turning asymmetry* (Towal and Hartmann 2006; Mitchinson et al. 2011; Grant et al. 2012a). This data-set is not really suitable for testing head-turning asymmetry, as the footage was collected during whisker contacts and without much rotational movement of the head. However, comparing the amount of bilateral asymmetry in our clips to the rotational head velocity does give a very small correlation result ($r=0.0461$, $p=0.0908$, see also Electronic Supplementary Material, Online Resource 1 for more details). A future study comparing rotational head velocity and bilateral asymmetry using longer clips without whisker contacts may well provide evidence for a correlation effect.

Orienting to the stimuli in such a way that the closely packed whiskers touch the object will improve the pinniped's ability to judge size. However, how can they successfully judge sizes as low as 2 mm (as shown in Dehnhardt et al. 1997), when their whisker follicles are more spaced out than that?

Studies in rodents may shed some light on this. Following a whisker contact, rodents orient to their small microvibrissae (Brecht et al. 1997; Hartmann 2001; Grant et al. 2012b), and then they dab their microvibrissae at 8 Hz on to the surface to gather higher resolution data (Hartmann 2001; Grant et al. 2012b). Dehnhardt (1994) has also described "multiple short lateral head movements" in a California sea lion, following orienting its whiskers to the stimulus. Fig. 8

shows that the seals also move their whiskers against the disc. The left panel in Fig. 8 shows Moe exploring the medium disc on land. The pictured video-still is the final tracked video frame after orienting. The nose tracking for previous video frames is shown in red. Around the nose there is a circular red line, showing a dab against the front of the disc. Similarly, the right panel in Fig. 8 shows Marco exploring the medium disc under water. The red line, again, corresponds to previous nose positions and the horizontal red line by the nose is a dabbing movement against the side of the disc. By moving the whiskers over the disc surface in this dabbing motion, the seal will be able to detect size differences that are smaller than the spacing of its vibrissal follicles, which will account for the seal being able to detect differences as small as 2 mm in disc sizes in previous studies (Dehnhardt et al. 1997). These clips can be seen in full in the Electronic Supplementary Material, Online Resource 2 and 3. While this study does not aim to address the question of judging disc sizes that are smaller than whisker follicle spacings (i.e. hyperacuity) as hyperacuity is not needed to differentiate between the disc sizes used in this study, these observations are useful first descriptions of this behavior. The seal would greatly improve their ability to distinguish between disc sizes by making these small head movements, which are similar to those that have been observed in rodent studies. However, to describe dabbing further, high-speed video clips should be collected from the seals using discs that are less than 5 mm different.

Conclusions

Harbor seals can perform a size differentiation task extremely quickly (<400 msec decision time) and efficiently. They can judge the size of discs by recognizing how many whiskers are contacted and can maximize contacts by orienting to a whisker touch and touching their more ventral, rostral whiskers to the disc. This means they get more whisker contacts at higher resolutions, since these whiskers are smaller and more densely packed. They may then move (or dab) these whiskers on to the disc after orienting, to gather even more information from the surface.

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FIGURE LEGENDS

Fig. 1 Experimental apparatus. **a** The set-up consisted of a metal frame containing three sections, the middle stationing section and then two sections containing the disc stimuli. The big (6 cm) and medium (4 cm) disc can be seen. The experimenter sits behind the set-up. Two video cameras are arranged on the right-hand stimulus to film an overhead image (panel **b**) and a front-on view (panel **c**). **d** To do the experiment under water, the apparatus was placed in to the water and suspended on wooden planks, the experimenter sits on the wooden plank behind the set-up. The cameras are put in waterproof casings to get the overhead (panel **e**) and front-on (panel **f**) images.

Fig. 2 Examples of clip analyses. **a** An example over-head video-still showing Moe exploring the medium disc under water, the red dots correspond to the manually tracked points of the whiskers and theta is the angular position of the most caudal left tracked whisker. **b** A front-on video showing Moe exploring the big disc, the contacting whiskers can clearly be seen behind the perspex disc, and can be identified, using the grid (panel **c**), which has been taken from Dehnhardt and Kaminski (1995) (Figure 1, pg. 2318). Rostral (r) and caudal (c) directions are indicated on panels a and c, and dorsal (d) and ventral (v) on panel c.

Fig. 3 Learning during the experiment. **a** The learning curve (percentage correct) of Moe during the experiment; **b** The learning curve of Marco (percentage correct) during the experiment. The learning criterion was set as > 80% correct, for three consecutive sessions. Pre-training included a number of steps, such as introducing the mask, learning to station, introducing the headphones and learning the task on two stimuli. The learning data presented here is in four stages: 1: training on land: including a number of training steps, such training on three stimuli and adding the mask and headphones. 2: test phase on land; 3: training under water, 4: test phase under water. The red lines correspond to the filming (test phase) sessions. **c** The decision time (from first contact to after orienting) on land and under water. Seals took longer to make a decision under water.

Fig. 4 Whisker variables changing during the task; **a** Angular positions of the whiskers for the three discs and re-visit to the medium disc. Black bars represent the left whisker field angular positions at the first contact, dark grey bars represent the right whisker field angular positions at first contact. The light grey bars, and white bars represent the left and right hand whisker field angular positions after the orient, respectively. Angular positions do not change with disc size, but there are large asymmetries in the whisker field, with left whiskers pushed much further forward than right whiskers; **b** Angular whisker spread of the whiskers for the three discs and re-visit to the medium disc. Black and dark grey bars represent the rostral and caudal whisker spread at the first contact, and light grey and white bars represent the rostral and caudal whisker spread after orienting, respectively. Whisker spread does not change with disc size, the whiskers tend to be more spread out after orienting, especially in the more rostral whiskers; **c** Whisker amplitude during inspection of the three discs and re-visit to the medium disc. Black bars represent the left hand whisker amplitudes and grey bars the right. Amplitude does not change with disc size; **d** Number of whiskers contacting the three discs and also on the re-visit to the medium disc. Grey bars represent the number of whisker contacts at the first contact, and black bars represent the number of whisker contacts after orienting. Following orienting there are more whisker contacts on the discs, in particular there are more whisker contacts on bigger discs, and also on the re-visit to the medium disc.

Fig. 5 Video-stills from the over-head camera. Red arrows are pointing out the deformed whiskers that are pressed against the disc. **a** Moe, on land, exploring the big disc. Right whiskers are pressed down beneath the disc and left whiskers are pushed back; **b** Moe, under water, exploring the small disc. Left whisker is deformed and deflected across the whole of the disc; **c** Marco, on land, exploring the medium disc.

Rostral whiskers on the right and left are pressed against the disc; **d** Marco, under water exploring the small disc. Right whiskers are deflected ventral and rostral to the side of the disc.

Fig. 6 Most common whisker contacts during a first contact. The most common whisker contacts are defined as the whiskers which contact in >15% of all the clips. The most common whisker contacts are marked in red on the diagrams, for the big disc, medium disc, the medium disc when it is explored for the second time, and the small disc. As this is data from discs on the right-hand side of the seal, first contacts tend to touch the right hand side of the pad. See Electronic Supplementary Material, Online Resource 1 for the exact number of proportions for each whisker.

Fig. 7 Most common whisker contacts after orienting. The most common whisker contacts are defined as the whiskers which contact in >15% of all the clips. The most common whisker contacts are marked in red on the diagrams, for the big disc, medium disc, the medium disc when it is explored for the second time, and the small disc. After orienting, the more rostral and ventral whiskers are contacted, and bigger discs contact more whiskers. See Electronic Supplementary Material, Online Resource 1 for the exact number of proportions for each whisker.

Fig. 8 Two examples video-stills with the nose tracking overlaid. Left: Moe exploring the medium disc on land; and Right: Marco exploring the medium disc under water.

TABLE CAPTIONS

Table 1 movement direction of the seals in response to the discs. 99% of the trials, both pre and post training, conform to this pattern.

Table 2 Statistical results from measuring amplitude, decision time, angular position, spread, the number of whisker contacts and bilateral asymmetry. ANOVAs were run on all the variables (details can be found below), with disc size, animal and land/under water as between variables. Significance levels are indicated by *for $p<0.05$ and ** for $p<0.01$.

1. Between ANOVA of measures (Amplitude and Decision Time), with animal and land/under water as the between variables.
2. A mixed-model ANOVA was run with Angular Position: i) at first contact and after orienting; ii) on the left and right sides, as the two within variables and disc size as the between-variable. Animal (Marco/Moe) and land/under water were then added as between variables.

3. A mixed-model ANOVA was run on Angular Spread: i) at first contact and after orienting; ii) on the rostral and caudal whiskers, as the two within variables and disc size as the between-variable. Animal (Marco/Moe) and land/under water were then added as between variables.
4. A mixed-model ANOVA was run on these measures (Number of Whisker Contacts and Bilateral Asymmetry) at first contact, and after orienting, as the within variables and disc size as the between-variable. Animal (Marco/Moe) and land/under water were then added as between variables.

TABLES

TABLE 1

Moe:			**Marco:**		
Arrangement of discs		**Movement direction**	**Arrangement of discs**		**Movement direction**
right	**left**		**right**	**left**	
2cm	4cm	Right, left	2cm	4cm	Right
2cm	6 cm	Right, left	2cm	6 cm	Right
4cm	2cm	Right, left, right	4cm	2cm	Right, left
4cm	6cm	Right, left	4cm	6cm	Right, left, right
6cm	2cm	Right	6cm	2cm	Right, left
6cm	4cm	Right	6cm	4cm	Right, left

TABLE 2

	Differences from first contact and after orienting		**Differences between disc sizes**		**Additional significant effects of:**		
	$F(df_1, df_2)=$	**p**	**$F(df_1, df_2)=$**	**p**	**Animal**	**on land/**	**Other**

						under water	
Angular Position [1] **(degrees)**	(1,237)= 25.494	<0.001**	(3,237)= 7.628	<0.001 **	n.s.	n.s.	left>right
Angular Spread [2] **(degrees)**	(1,237)= 7.787	0.006**	(3,237)= 2.171	0.092	n.s.	land> under water	rostral> caudal
Amplitude (degrees) [3]			(3,237)= 1.293	0.278	n.s.	under water>land	left>right
No. Whisker Contacts [4] **(count)**	(1,237)= 368.316	<0.001**	(3,237)= 7.540	<0.001 **	Moe> Marco	n.s.	