

Chapter 6

Hydrodynamic Perception in Seals and Sea Lions

Guido Dehnhardt, Wolf Hanke, Sven Wieskotten, Yvonne Krüger and Lars Miersch

Abstract Marine mammals often forage in dark and turbid waters. While dolphins use echolocation under such conditions, pinnipeds seem to lack this sensory system. Instead, species of the families Phocidae (true seals) and Otariidae (eared seals) both possess richly innervated whiskers (synonymously “vibrissae”) representing highly sensitive hydrodynamic receptors that enable these animals to detect fish-generated water movements. The third family of pinnipeds, the Odobenidae (walruses), is less well studied. As water movements in the wake of fishes persist for several minutes, they constitute hydrodynamic trails that should be trackable by piscivorous predators. Hydrodynamic trail following has indeed been shown for the harbor seal (*Phoca vitulina*) and the California sea lion (*Zalophus californianus*). However, in experiments with a sea lion aging of the trails resulted in an earlier decrease in performance. This difference in tracking performance most likely is due to differences in the structure of the respective vibrissal hair shaft. In the harbor seal the high sensitivity and excellent tracking performance is ascribed to the specialized undulated structure of the whiskers that largely suppresses self-generated noise in the actively moving animal. In contrast, the whiskers of a swimming California sea lion, which are smooth in outline, are substantially affected by self-generated noise. However, in the sea lion such self-generated noise contains a characteristic carrier frequency that might allow hydrodynamic reception by being modulated in response to hydrodynamic stimuli impinging on the hair. Thus, in the course of pinniped evolution at least two types of whiskers evolved that realized different mechanisms for the reception of external hydrodynamic information.

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Abbreviations

F-SC	Follicle sinus complex
PIV	Particle image velocimetry
VRGs	Vortex ring generators
HMC	Head-mounted camera
CCD	Charge-coupled device
VIVs	Vortex-induced vibrations
SNR	Signal-to-noise ratio

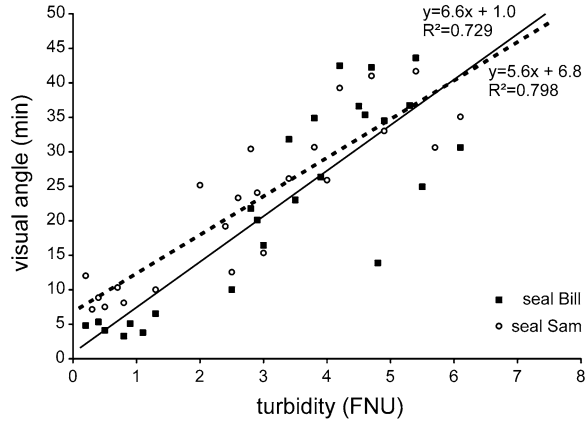
6.1 Introduction

Most marine mammals must search for food under highly variable conditions requiring corresponding sensory specializations. For the detection of distant objects in dark and/or murky waters odontocetes have developed an echolocation system accompanied by exceptional hearing skills at high frequencies (Au 1993). In pinnipeds no sonar system like that of toothed whales has been demonstrated so far, although a sensory modality allowing the localization of prey in the dark has long been debated for these marine mammals.

For decades vision has been suggested to be the predominant source of sensory information in foraging pinnipeds (Walls 1942; Hobson 1966; Lavigne et al. 1977; Levenson and Schusterman 1999). Indeed, the eyes of the pinniped species studied so far are highly adapted for under water vision and to low light intensities encountered so often in the aquatic environment (Hanke et al. 2006a, b, 2008a, b, 2009a, b, 2011; Scholtyssek et al. 2008). A marine mammal relying primarily on vision strongly depends on the transparency of the water. Therefore turbidity is an important ecological factor in aquatic habitats, especially for visual underwater object detection (Aksnes and Giske 1993; Aksnes and Utne 1997). Accordingly, psychophysical experiments indicated a dramatic loss of visual acuity in harbor seals (*Phoca vitulina*) even at moderate levels of turbidity (Fig. 6.1) so that visual object localization is hardly possible under such conditions (Weiffen et al. 2006).

As many fish species produce sounds (see, e.g., Popper and Fay 1993; Akamatsu et al. 2002; Wahlberg and Westerberg 2003; Wilson et al. 2004) pinnipeds searching for pelagic fish may benefit from this acoustic information for prey localization. The high sound localization acuity, particularly with regard to frequencies below 1 kHz, as determined in the California sea lion (*Zalophus californianus*) and the harbor seal (*P. vitulina*), may facilitate the localization of a soniferous fish from a distance (Møhl 1964, 1968; Gentry 1967; Terhune 1974; Moore and Au 1975; Kastak and Schusterman 1998; Bodson et al. 2006, 2007). However, as such signals are generally not continuously produced by a fish, this source of information should not reliably allow a predator to pinpoint its prey.

Fig. 6.1 Visual acuity angles of two harbor seals as a function of water turbidity. Sam *dashed line*, Bill *solid line*. Adapted from Weiffen et al. (2006)



In this paper we provide evidence that pinniped whiskers provide the sensory information for hydrodynamic perception and therewith allow the detection of a swimming fish at a considerable distance as well as its pursuit.

6.2 Morphology and Innervation of Pinniped Whiskers

Pinniped whiskers are generally well developed. They are large in size, have a conspicuous structure, and the follicle sinus complex (F-SC) of each whisker is highly innervated. The term F-SC is derived from the complex sinus system (whiskers are also called “sinus hairs”), a characteristic feature of vibrissal follicles (a third term for these tactile hairs: “vibrissae”) not found in normal body hairs (Stephens et al. 1973; Hyvärinen and Katajisto 1984; Hyvärinen 1989; Marshall et al. 2006).

Although the structure of the sinus system varies considerably across mammalian species, F-SCs of many terrestrial mammals show a ring sinus and a cavernous sinus below it (see, e.g., Ebara et al. 2002). In contrast, pinnipeds seem to be the only group of mammals possessing an additional cavernous sinus situated above the ring sinus (tripartite sinus system, Hyvärinen 1989). In adaptation to the high thermal conductivity and the large potential cooling power of the aquatic environment, this additional and extraordinarily long upper cavernous sinus (60 % of the total follicle length in phocid seals Fig. 6.2) serves the thermoregulation of the system (Dehnhardt et al. 1998a; Mauck et al. 2000) that is essential for the reception of mechanosensory information. Although negative effects of cooling have been described at the receptor level (Bolanowski et al. 1988; Gescheider et al. 1997), increasing stiffness of the F-SC surrounding tissue might be even more important by affecting the transduction of mechanical stimulation via the hair shaft to the main receptor level at and below the ring sinus. However, while seals have been shown to cool down their outermost tissue layers close to ambient

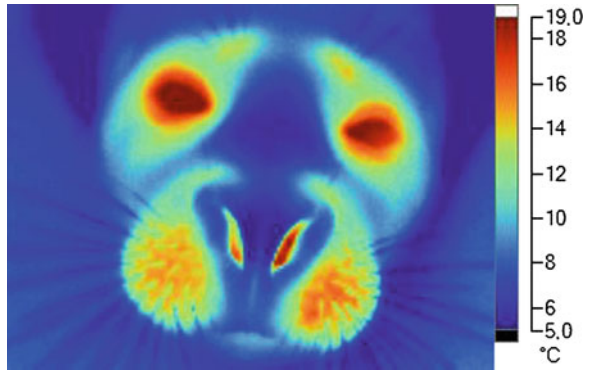


Fig. 6.2 Harbor seals use their mystacial vibrissae in a cold environment. The drawing on the right shows a longitudinal section of a vibrissal follicle of *Phoca hispida* (adapted from Dehnhardt et al. 1998a)

temperature even when exposed to very cold conditions (Irving 1969; Folkow and Blix 1989; Hokkanen 1990; Worthy 1991; Watts et al. 1993; Ryg et al. 1993; Kvadsheim et al. 1997) infrared-thermography demonstrated that the respective pads of mystacial and supraorbital whiskers can show thermal emissions substantially higher than in adjacent skin areas (Fig. 6.3). In phocid seals this regional thermoregulation of vibrissal follicles is accompanied by an excess of low-melting-point monoenoic fatty acids in the adipose tissue surrounding the follicles so that an optimal tissue flexibility and thus mobility of the whiskers inside the follicle should be realized under cold conditions (Käkelä and Hyvärinen 1993, 1996). In accordance with this sophisticated morphological organization of the vibrissal system, psychophysical experiments with harbor seals have shown that their high haptic vibrissal sensitivity for texture differences at water temperatures of about 20 °C remained unaltered even at temperatures close to 0 °C (Dehnhardt et al. 1998a). However, the follicle adaptations that allow active touch to work in a thermally hostile environment may also facilitate hydrodynamic reception.

Compared to terrestrial mammals the degree of innervation found in pinniped F-SCs is also outstanding. Each follicle is innervated by a single “deep vibrissal nerve” of the infraorbital branch of the trigeminal nerve that enters the capsule surrounding the follicle at its base. At the point where the nerve enters the capsule, 1,000–1,600 myelinated axons have been counted in the ringed seal (*Phoca hispida*, Hyvärinen and Katajisto 1984; Hyvärinen 1989) and the bearded seal (*Erignathus barbatus*, Marshall et al. 2006). Thus, the innervation density of vibrissal follicles of these pinniped species exceeds that calculated for richly innervated terrestrial species (Rice et al. 1986) by a factor of 10. Calculated for the bearded seal endowed with 240 single mystacial whiskers, the mystacial vibrissal system is innervated by about 320,000 myelinated nerve fibers.

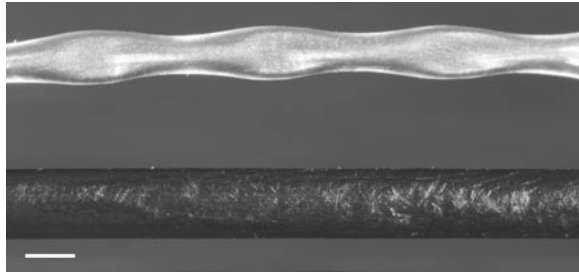
Fig. 6.3 Infrared thermogram showing the typical distribution of temperatures measured on the surface of a seal's face immediately after the animal had left the water



Mechanoreceptors found in a follicle correspond to those typical for the mammalian skin. With about 15,000 per F-SC the Merkel cell–neurite complex is by far the most dominating sensory element (Hyvärinen 1995), although it is not clear yet whether this receptor type can be further differentiated based on ultrastructure and function (Baumann et al. 2003). In addition there are 1,000–4,000 lanceolate endings and 100–400 lamellated endings per F-SC, as well as numerous small free nerve endings at the level of the ring sinus and the lower cavernous sinus (Dehnhardt et al. 2003). As demonstrated for the Northern fur seal (*Callorhinus ursinus*) this high degree of innervation of F-SCs corresponds to a strong and somatotopic representation of the vibrissal system in the somatosensory cortex (Ladygina et al. 1985). It remains to be investigated however, whether the somatosensory cortex shows a barrel-like organization similar to that known from, e.g., rodent species (Woolsey and Van Der Loos 1970).

While we do not understand the system at the neural level yet, it became evident during the last few years that the geometry of the hairs is most crucial for their function as a hydrodynamic sensor. In contrast to the round cross-section of the whiskers of terrestrial mammals, whiskers of sea lions and fur seals (Otariidae) are oval in cross-section, which also applies to the whiskers of the walrus (Odobenidae) and those of some phocid species (*E. barbatus* and *Monachus spp.*, see Fig. 6.4 bottom). However, like a typical hair shaft found in terrestrial mammals, whiskers of these pinniped species are smooth in outline. Whiskers of all other phocid species differ considerably from those of the pinnipeds described above and represent a unique hair type among mammals by being extremely flattened and showing a distinct sinusoidal beaded profile (Watkins and Wartzok 1985; Hyvärinen 1989; Dehnhardt and Kaminski 1995; Ginter and Marshall 2010; Ginter et al. 2012; see Fig. 6.4 top). According to our observations on mystacial whiskers in harbor seals, this beaded profile is present from the shortest to the longest hairs, but diminishes to some degree during the course of a year due to mechanical abrasion. However, different from descriptions by Ling (1966, 1977), harbor seals shed their whiskers during the annual molting season so that most of the year the beaded profile is sufficiently present.

Fig. 6.4 Vibrissae of a harbor seal (*Phoca vitulina*, top) and a California sea lion (*Zalophus californianus*, bottom). Note the undulated outline of the harbor seal vibrissa. Scale bar 1 mm. Adapted from Hanke et al. (2010)

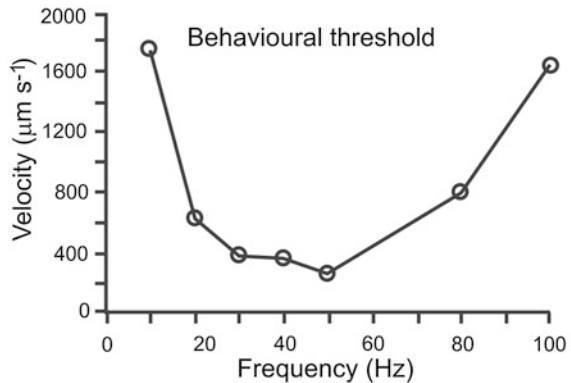
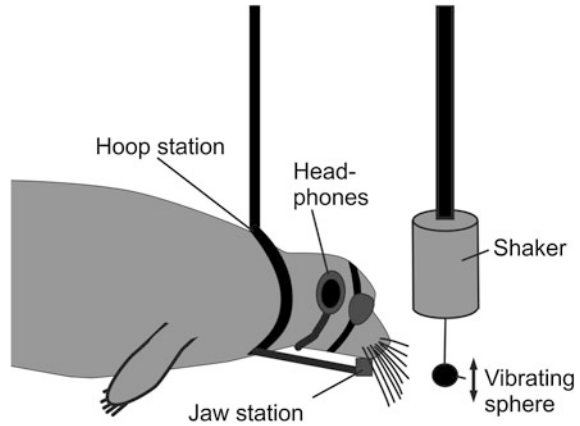


6.3 Hydrodynamic Sensitivity and Trail Following in Harbor Seals and Sea Lions

Based on single unit recordings from the infraorbital branch of the trigeminal nerve of harbor seals, gray seals, and domestic cats, Dykes (1975, p. 650) concluded that these experiments “...did not reveal any way in which the seal’s vibrissae are better adapted to an aquatic environment than the cat’s” and “...their thresholds are too high for most airborne or waterborne vibrations.” Instead, he suggested that whiskers are primarily designed for mechanosensory information obtained by active touch, such as the recognition of surface texture and the shape and size of an object. A number of psychophysical studies supported this hypothesis by showing that the whiskers of the walrus (Kastelein and van Gaalen 1988), the California sea lion (Dehnhardt 1990, 1994; Dehnhardt and Dücker 1996) and the harbor seal (Dehnhardt and Kaminski 1995; Dehnhardt et al. 1997, 1998a; Grant et al. 2013) indeed represent very efficient haptic systems that work in air and under water. However, contradictory to Dykes’ hypothesis a combination of behavioral studies and fluid mechanics has since demonstrated that seal whiskers are highly adapted to the reception of hydrodynamic stimuli that appear as mechanosensory information in the aquatic environment.

After Renouf (1979) and Mills and Renouf (1986) showed that harbor seals respond to a vibrating rod directly contacting the whiskers, Dehnhardt et al. (1998b) used dipole water movements to demonstrate that the whiskers of harbor seals represent a hydrodynamic receptor system analogous to the lateral line of fish (Bleckmann 1994). Dipole water movements were generated at variable distances (5–50 cm) from the whiskers of a stationary harbor seal by means of a constant-volume oscillating sphere. This way, detection thresholds for water movements in the range of 10–100 Hz were determined (Fig. 6.5). Detection thresholds of the harbor seal varied across frequencies with the highest velocity sensitivity of $245 \mu\text{ms}^{-1}$ at 50 Hz. The same experimental approach was used to test a California sea lion (*Z. californianus*) which revealed even lower thresholds at 20 and 30 Hz (Dehnhardt and Mauck 2008). These experiments established the sensory modality of hydrodynamic perception in seals and sea lions. As has been described for other hydrodynamic sensory systems (Bleckmann 1994), the tuning curve of the harbor seal suggests that it responded to particle acceleration at frequencies

Fig. 6.5 Detection of hydrodynamic dipole stimuli by a harbor seal. *Top* experimental setup. A harbor seal was trained to station in a hoop and jaw station. Hydrodynamic stimuli were generated with a sinusoidally oscillating sphere in front of the animal. The animal was trained to leave the station if it detected a hydrodynamic stimulus, and to remain in station otherwise. *Bottom* results. The detection threshold, here in terms of water velocity, is shown as a function of the oscillation frequency of the sphere. Adapted from Dehnhardt et al. (1998b)



<50 Hz and water displacement at frequencies >50 Hz. Further experiments revealed that harbor seals can not only detect but also discriminate the amplitudes of sinusoidal water movements (Dehnhardt and Mauck 2008).

In dipole experiments a seal remains stationary until it receives hydrodynamic stimulation. With respect to natural situations, this resembles the sit-and-wait strategy known, e.g., from antarctic leopard seals (*Hydrurga leptonyx*) sitting in ambush at the ice edge for a penguin that leaves the water or at the breathing hole of a seal. However, the majority of pinniped species forage on pelagic fish (Hauksson and Bogason 1997; Andersen et al. 2004). This requires active predation, including searching for and pursuing prey. As known from canids, active predation in terrestrial predator-prey interactions is often based on olfactory trail following (Hepper and Wells 2005). A similar concept has been established by Hanke et al. (2000) for the aquatic environment which shows that even a small fish generates a wake showing a distinct vortex structure for at least 30 s while water velocities significantly higher than background noise can still be measured 3 min

after a small fish passed by. Thus, a swimming fish leaves a hydrodynamic trail that could be detected and tracked by a piscivorous predator equipped with a hydrodynamic receptor system. Furthermore, the persistence of a fish generated wake may allow the pursuit from a considerable distance. Hydrodynamic trail following was first demonstrated in harbor seals by Dehnhardt et al. (2001). In behavioral experiments hydrodynamic trails were generated with an autonomously operating miniature submarine. The submarine's trail comprised a narrow street of turbulent water movements with velocities similar to those calculated for the wake of a 30 cm long fish. To exclude vision during tests the experimental animal was blindfolded with a stocking mask. After trail detection the harbor seals meticulously tracked the hydrodynamic trails left by the submarine and arrived at its final position in almost 90 % of the trials. However, seals always failed to detect the trail when wearing an additional stocking mask that also covered the mystacial vibrissae. Even delays between the start of the submarine and the start of a seal's search of up to 20 s did not affect a seal's performance. While these delays already simulated trails as long as 40 m, a seal could, hypothetically, continue to follow a hydrodynamic trail indefinitely as long as the traced fish continues swimming and other hydrodynamic events do not disturb the trail. It remains to be shown over which distance a seal can track a hydrodynamic trail under natural conditions.

As mentioned above, the geometry of vibrissal hair shafts of sea lions and fur seals differs from that of most phocid species, like the harbor seal, raising the question whether, e.g., a sea lion is also capable of hydrodynamic trail following. Using the methods applied by Dehnhardt et al. (2001) recent experiments conducted with a California sea lion (*Z. californianus*) demonstrated that this eared seal is, indeed, capable of hydrodynamic trail following (Gläser et al. 2011). The performance was high and comparable to that of harbor seals, provided a linear trail was followed. However, unlike in harbor seals it decreased substantially with trails older than 5–7 s. Particle image velocimetry (PIV) analysis demonstrated that 7 s old trails still contained water velocities higher than 50 mms^{-1} , while water velocities in the 20 s old trails reliably tracked by harbor seals were in the range of 20 mms^{-1} (Wieskotten et al. 2010a). Additionally, although the sea lion showed a significant performance when following curved trails (Gläser et al. 2011) the performance was much lower than that of the harbor seals confronted with the same task (Dehnhardt et al. 2001). In contrast to the finding that stationary animals of both species are similarly sensitive to hydrodynamic dipole stimuli, these results suggest that during forward swimming the structural differences of vibrissal hair shafts of sea lions and harbor seals account for the difference in their capability to use this sensory system for hydrodynamic trail following.

In the wild, fish-generated hydrodynamic trails will not always result from continuous swimming movements, but can be affected by cyclic burst-and-glide swimming, associated with various modifications regarding hydrodynamic parameters of the trail (compare Fig. 3k of Hanke et al. 2000). To test for effects of burst-and-glide swimming, Wieskotten et al. (2010a) used a remote-controlled miniature submarine to investigate the impact of glide phases on the trackability of differently aged hydrodynamic trails in a harbor seal. It was shown that gliding phases during

the generation of a hydrodynamic trail had a negative impact on trackability when trails were ≥ 15 s old. The seal lost a trail more often within the transition zones, where the submarine switched from a burst to a glide phase. PIV revealed that during the gliding phase the smaller dimensions and faster decay of hydrodynamic parameters were responsible for the decrease in performance. Another hydrodynamic parameter that might have affected the seal's ability to track the trail at the gliding section was the change from a rearwards directed stream in the burst phase to a water flow passively dragged behind the submarine during gliding, which might cause a weaker deflection of the vibrissae. Burst-and-glide swimming has been reported for a variety of fish species (Videler and Weihs 1982; Blake 1983; Hinch et al. 2002; Standen et al. 2004), some of which belong to the prey spectrum of harbor seals. These results suggest that gliding in fish not only plays a role in energy saving during locomotion (as discussed in Blake 1983) but might also constitute an anti-predator strategy by interrupting the continuous traceability of hydrodynamic trails. However, as hydrodynamic parameters resulting from this movement style differ considerably between the wakes of fishes and that of the submarine used in the experiment by Wieskotten et al. (2010a), experiments with live fish are needed to arrive at a better understanding of this potential hydrodynamic camouflage against predators capable of hydrodynamic trail following and how in return seals counteract this strategy under natural conditions.

Hydrodynamic trail following provides a conclusive explanation for how pinnipeds may successfully hunt in dark and murky waters. In addition to this predator-prey scenario it could be demonstrated that harbor seals can also detect and follow hydrodynamic trails of conspecifics (Schulte-Pelkum et al. 2007). This may play an important role in, e.g., mate detection and mother-pup cohesion. In this experiment two harbor seals were used, one as the trail generator and the other as the trail follower. In principle hydrodynamic trails generated by the sub-carangiform or thunniform swimming style of phocid seals (Williams and Kooyman 1985; Fish et al. 1988) compare well in structure to those left by many fish species. However, as trail width is also a function of the body size of the trail generator seal trails were about 2 m wide (Schulte-Pelkum et al. 2007). The trail following seal tracked these biogenic hydrodynamic trails with high accuracy. Video analysis revealed that it precisely followed even small deviations from a straight course by sticking exactly to the center of the trail, thus indicating that it was able to analyze the inner structure of the trail. This behavior while following a biogenic hydrodynamic trail as well as the finding that harbor seal whiskers are quite sensitive to amplitude differences of hydrodynamic dipole stimuli suggests that a seal reading a trail obtains qualitative information about the trail generator. Indeed, Hanke and Bleckmann (2004) showed that the velocity profiles of the wakes of different fishes can differ between species. Trails should thus allow a predator to extract information regarding, e.g., the fish species, its size, swimming style, and swimming speed. The characteristic three-dimensional structure of a hydrodynamic trail could be recognized by a seal due to the spatial arrangement of protracted mystacial whiskers that allows simultaneous multiple-point measurements in the wake.

6.4 Qualitative Information Deducible from Hydrodynamic Trails

That a harbor seal can discern information beyond the mere presence of a wake has been shown in a series of psychophysical experiments conducted under PIV-control, this way not only providing information about the discrimination performance of the tested animal, but also about the hydrodynamic parameters it might have used for stimulus discrimination. This was possible because the eyes of the experimental animal were protected against the laser light by the stocking mask while the white and reflecting vibrissae were illuminated by the laser in the same way as the neutrally buoyant particles used for PIV.

After Dehnhardt et al. (2001) provided first indication that a harbor seal can use hydrodynamic cues to determine the swimming direction of a miniature submarine, Wieskotten et al. (2010b) studied how the aging of a hydrodynamic trail affects the directional sensitivity of seals. In the calm water of a closed experimental box situated in the seal's holding pool hydrodynamic trails were generated using a fin-like paddle, moving from left to right or from right to left. PIV measurements revealed that the structure of the hydrodynamic trail generated by the fin-like paddle corresponded well to that found in fish wakes (see Blickhan et al. 1992; Hanke et al. 2000). The blindfolded seal could enter the box through a circular gate up to its pectoral flippers, where it approached the trail with its mystacial vibrissae protracted to the most forward position. Maximum contact time to a trail was less than 0.5 s. In most trials the seal performed a minute head movement toward the moving direction of the fin-like paddle, thus already indicating its correct detection. Then the seal left the box for touching one of two response targets (left target: moving direction of the fin-like paddle, from right to left, right target: moving direction of the fin-like paddle, from left to right). The seal reliably recognized the direction of the paddle movement when the hydrodynamic trail was up to 35 s old. Based on PIV analysis, the contact points of the mystacial whiskers to the hydrodynamic trail suggest that the seal used the rotation direction of the vortex rings and/or the direction of the jet flow between two counter-rotating vortex rings to determine the moving direction of the fin-like paddle (Wieskotten et al. 2010b).

As has been shown in various studies the structure of a fish generated hydrodynamic trail correlates with the size, shape, and swimming style of the species (Hanke et al. 2000; Drucker and Lauder 2002; Nauen and Lauder 2002; Hanke and Bleckmann 2004; Standen and Lauder 2007; Tytell et al. 2008). Consequently, one can assume that a piscivorous predator like a seal is able to distinguish between different trail generators. Based on this assumption, Wieskotten et al. (2011) conducted experiments that elucidated to what extent a seal can obtain information about the size and shape of a moving object from its hydrodynamic trail. For these experiments the same experimental setup and response paradigm was used as for tests on the perception of directional parameters inherent in a hydrodynamic trail. Trails and the whisker contacts to different trail structures were also visualized and measured by PIV.

For trials on shape discrimination trail generating objects consisted of vertically oriented paddles (flat rectangular paddle and flat paddle with undulated edges) and rods (round and triangular in cross section). First, these objects only differed in cross-sectional shape, while the length of all objects was 30 cm and the width 4 cm. However, PIV-data revealed that the lateral extension of the trail strongly correlated with the object shape. Thus, to eliminate the relevance of this cue, object width was randomized from 2–7 cm so that the seal had to rely on the spatial arrangement of the trail for its decision. As long as paddles of equal width were presented, the harbor seal was able to discriminate the flat rectangular paddle from the cylindrical, triangular, and the undulated paddle, as well as the cylindrical paddle from the undulated paddle. In trials where the width of the paddles was randomized the seal could still discriminate rectangular from triangular paddles. PIV measurements showed that vortices detached asymmetrically from the rectangular paddle, while from the triangular paddle they detached symmetrically. This suggests that especially for these two objects discrimination was based on the salient spatial arrangement of vortices in the respective trail.

Size difference thresholds were determined for three rectangular standard paddles that were equal in length (30 cm) and 2, 6 and 8 cm wide, respectively. These were presented against a series of test paddles varying in width from 2–8 cm. Paddles were moved on a horizontal circular path in clockwise direction first at a constant speed of 0.55 ms^{-1} and afterwards at speeds differing from trial to trial between 0.31 and 0.85 ms^{-1} (Fig. 6.6). Speed variation trials were conducted because at constant speed the animal could associate the larger paddles with the greatest water velocities and the widest extension of the area of high velocities within the wake. By varying the speed of the moving paddle the seal could not use these prevailing hydrodynamic parameters but was required to decide on object size on the basis of the mean spatial extension of the trail and/or the diameter of single vortices within the wake. When objects were moved at the same speed, the harbor seal was able to discriminate size differences of trail generating objects of 2.8–3.2 cm. In contrast, if speed was randomized the performance slightly dropped to size differences of 4.1–4.3 cm (Fig. 6.6). As in speed randomization trials the mean spatial extension of the trail and the diameter of single vortices correlated with paddle size these hydrodynamic parameters were identified to be the prime candidates for the seal's trail discrimination. However, as the lateral spread of the trails showed a higher variation between trials than did the size of single vortices, the latter can be expected to be the decisive factor.

All experiments conducted so far on qualitative information deducible from hydrodynamic trails suggest that single vortex structures are most relevant for the ability of a seal to identify the swimming direction, size, or shape of the trail generator. Consequently, recent psychophysical experiments addressed the question whether and to what extent harbor seals can detect and analyze single vortex rings similar to those found in trails generated by swimming fish (Krüger et al. unpublished). Vortex rings of predefined size, velocity, and acceleration were generated by custom made vortex ring generators (VRGs). VRGs consisted of $20 \times 20 \times 20$ cm cubes with a 2 cm circular aperture on one side. On top of the

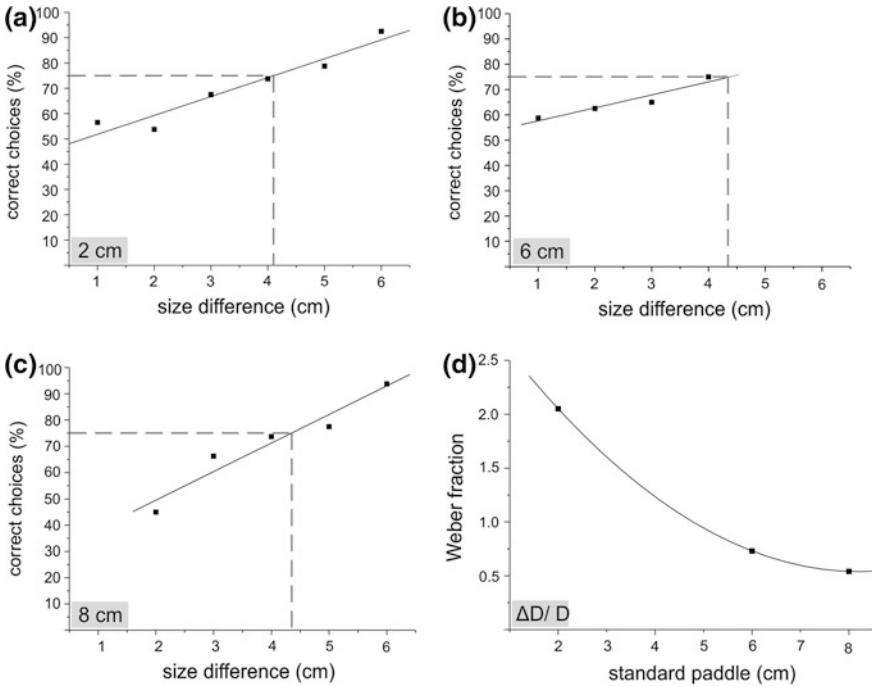


Fig. 6.6 Psychometric functions of a harbor seal's performance on discriminating different sized objects moving with different speeds ranging from 31 up to 85 cm s^{-1} . **a–c** Percentages of correct choices are plotted against differences in size between standard objects ranging from 2 to 8 cm and different sized comparison objects. The *dashed lines* at 75 % correct choices mark difference thresholds. Each data point represents the result of 80 single trials. **d** Weber function showing the relationship between Weber fractions (the ratio of the size difference at threshold ΔD to the size of the comparison object D) and comparison object size (D)

cube, a 10 cm diameter vertical pipe was mounted in which a plunger was moved by a linear motor. A vortex ring was generated by the plunger moving down, this way expelling water through the aperture (see Fig. 6.7). PIV was used to quantify the hydrodynamic parameters of vortex rings generated this way.

In a first set of experiments the ability of blindfolded stationary harbor seals to perceive and detect the direction of single vortex rings was investigated. Two VRGs were fixed on a semicircular horizontal profile on either side of a point directly ahead of the animal's snout. For every trial, one of the two VRGs was oriented toward the animal in order to produce a vortex ring travelling to the seal's mystacial vibrissal pad (see Fig. 6.7). The second vortex ring generator simultaneously produced a vortex ring that travelled away from the seal and was operated in the same way as the first VRG to avoid acoustical directional cues. Seals were trained to indicate the direction from which a vortex ring impinged on their vibrissae by touching a left or right response target.

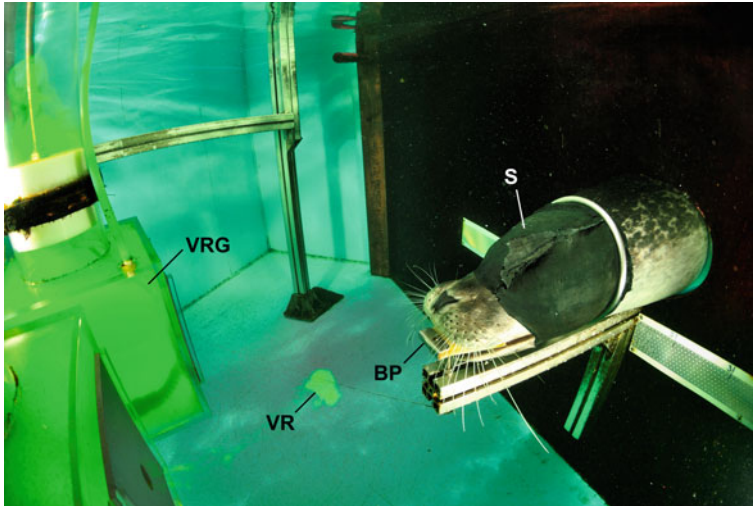


Fig. 6.7 Experimental setup for investigating the ability of harbor seals to detect and analyze single vortex rings. For visualization purpose the water in the VRGs was dyed. *VRG* vortex ring generator, *VR* single vortex ring, *BP* bite plate, *S* stocking mask. Picture: E. Krumpholz (<http://www.photos-subjektiv.de>)

The two test animals spontaneously detected the direction of a vortex ring, either coming from the right or the left side at an angle of 60° to the midline of the animal. The minimum angle from which the direction of a vortex ring is still detectable by the vibrissal system was determined by gradually decreasing the angle between the VRGs. The harbor seals could still detect the direction of a vortex ring coming from an angle of $\pm 5.7^\circ$ to the body midline. Although the seals performance was highly significant at this angle, the distance of the VRGs could not be reduced further so that a threshold could not be determined yet. However, in these still ongoing experiments many further questions concerning the detectability and discrimination of single vortex rings will be addressed.

6.5 Mechanisms of Hydrodynamic Reception in Seals and Sea Lions

When in search of hydrodynamic information, a seal usually keeps its moveable mystacial vibrissae in an abducted position largely perpendicular to its swimming direction. This means that while the seal is swimming with a velocity of about 1 ms^{-1} the vibrissae are maximally exposed to the resulting flow effects. Although the vibrissal hair shafts of seals and sea lions are much stiffer than the hair shafts of normal body hair, they are quite flexible structures. This is especially true for phocid vibrissae and here in particular while these hygroscopic hairs are immersed in water, although the degree of soaking has not been quantified for this hair type

yet. These observations raise the question of how harbor seals and California sea lions, both capable of hydrodynamic trail following, counter the flow effects acting on their vibrissae like bending and vibrations resulting from vortex shedding while the hair is dragged through the water. For the harbor seal this has been studied by different experimental approaches by Hanke et al. (2010).

First, a head-mounted camera (HMC) system was developed to record the posture and potential movements of vibrissae within the right vibrissal pad while a seal was following the hydrodynamic trail of a remote controlled miniature submarine. An analog charge-coupled device (CCD) camera module was integrated into the stocking mask used to blindfold the seal, while the recording system and its power supply was mounted in a waterproof housing on the back of the seal. Immediately after blindfolding, the still stationary seal abducted its vibrissae to the most forward position. The video recordings revealed that the seal kept the vibrissae in that position while tracking the trail at swimming speeds of about 1 ms^{-1} . Despite their flexibility the vibrissae neither showed significant bending nor did they vibrate to a degree that was resolved by the recording system. These first data obtained on the organismic level already demonstrated that the vibrissal hair shafts of a harbor seal do not respond to laminar flow. It was suggested that the special hair structure characterized by the flat elliptical cross-section and the sinusoidal beaded longitudinal profile is responsible for this effect. To elucidate this effect the wake flow of harbor seal vibrissae was studied by a combination of micro-stereo-PIV and 3D direct numerical simulation (Hanke et al. 2010; Witte et al. 2012). These studies revealed that the primary vortex structure in the wake flow of an isolated whisker differs considerably from that of a circular cylinder. In comparison to the typical Kármán-vortex-street in the wake of a cylinder, two counter rotating vortex-segments shed simultaneously from the whisker, but they are shifted spanwise (Fig. 6.8), reducing the fluid-structure interaction. These vortex rings shedding from a whisker are more unstable so that no side alternating forces act on the structure. In fact, the fluctuating lift and drag forces acting on the hair are reduced by more than 90 % as compared to a cylinder (Fig. 6.9). This effective suppression of the periodic forces acting on the whisker provokes that vortex induced vibrations (VIVs) are almost eliminated while the hair is dragged through the water. Thus, as already indicated by data obtained by the HMC-system, the harbor seal's vibrissae move almost quiescent through the water, e.g., while searching for relevant hydrodynamic information.

The specialized whisker type of harbor seals explains how these pinnipeds cope with the flow effects affecting their vibrissae while extracting hydrodynamic information from their environment at considerable swimming speed. However, the fact that a California sea lion is also capable of hydrodynamic trail following raised the question how this is possible with a whisker that is much more cylindrical and lacks the undulated surface structure. Miersch et al. (2011) therefore compared the capability of isolated vibrissae of the harbor seal and the California sea lion in a rotational flow channel to decode vortex trails shedding from a

Fig. 6.8 Numerical simulation of the vortex street behind a harbor seal vibrissa, Reynolds number $Re = 500$ (corresponding to a swim speed around 0.5 ms^{-1}). *Left side* the vibrissa and its surface flow, showing a wavy separation line. *Right side* the separated flow behind the vibrissa, vortex cores depicted as iso-surfaces using the Q -criterion. *Shades of gray* cross-stream vorticity Ω_z . Vortices develop at some distance from the vibrissa; clockwise and counterclockwise rotating vortices are staggered spanwise (adapted from Hanke et al. 2010)

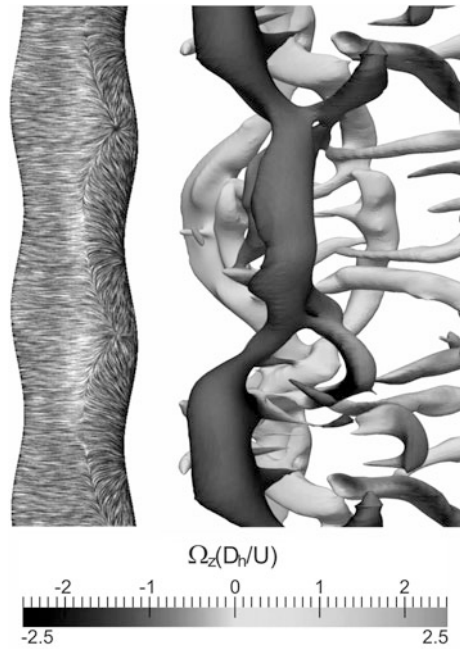
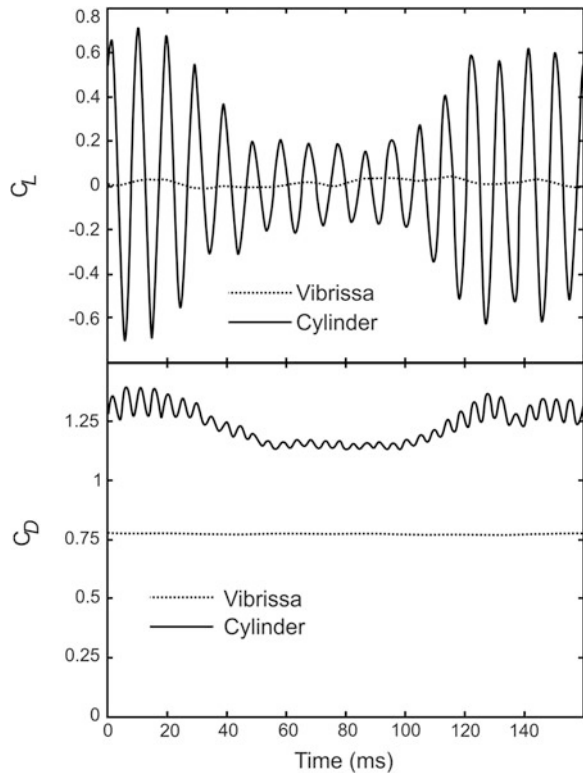


Fig. 6.9 Time history of the lift coefficient C_L and the drag coefficient C_D . The *dashed line* shows the results for the vibrissa, the *solid line* for a cylinder of equal hydraulic diameter (adapted from Hanke et al. 2010)



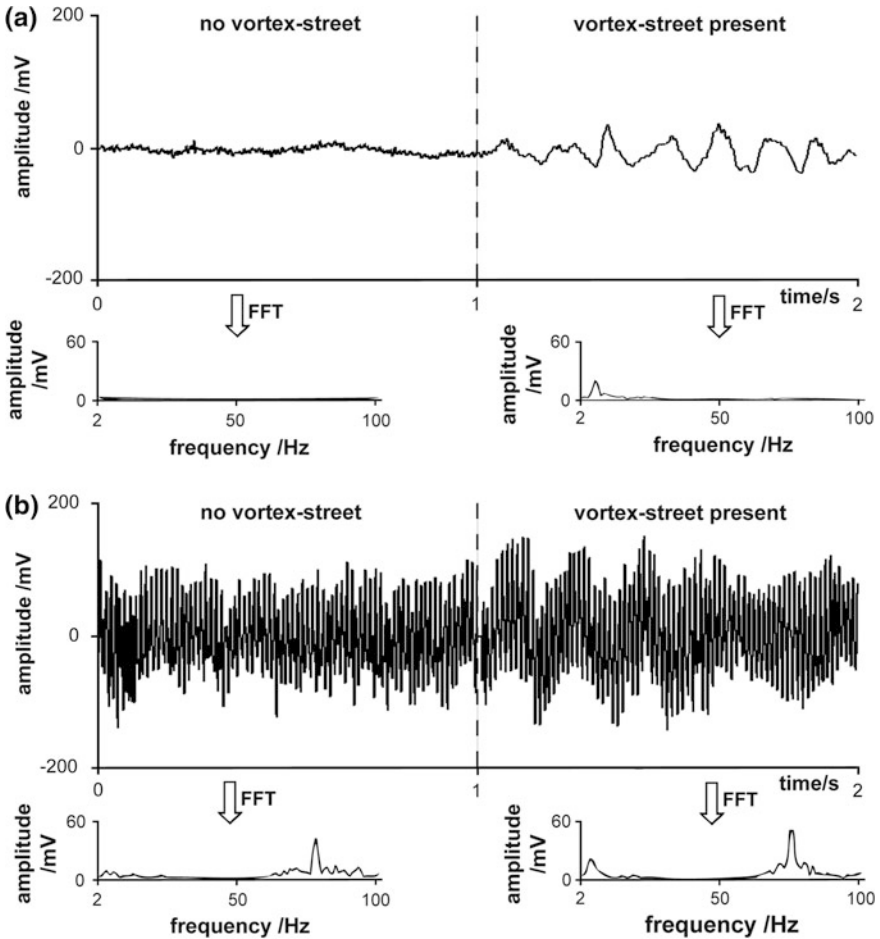


Fig. 6.10 The vibrations of a seal whisker **(a)** and a sea lion whisker **(b)** are plotted in the time domain and below the respective frequency spectrums. The *left* parts were recorded while the vibrissae were exposed to laminar flow. In the *right* parts a hydrodynamic disturbance was added upstream the whisker in form of a Kármán vortex street generated by an immersed cylinder. **a** Demonstrates the direct measurement of the vortex street (flow speed: 35 cm s^{-1} ; cylinder diameter: 8 mm) with a frequency of vortex shedding $f_{VS} = 7 \text{ Hz}$ (*right part*) and the absence of any vortex-induced vibrations (VIV) during laminar flow (*left part*). **b** Reveals the occurrence of VIVs during laminar flow (*left part*) with a frequency of 75 Hz and the additional modulation of that kind of carrier frequency by the vortex shedding of the Kármán vortex street $f_{VS} = 7 \text{ Hz}$ (flow speed: 34 cm s^{-1} ; cylinder diameter: 8 mm) (*right part*)

cylinder immersed in the flow tank. Above the water surface a single whisker was attached to a piezoceramic holder so that the hair extended into the water. The piezoceramic holder transformed mechanical vibrations into an electrical signal. Although both whisker types were able to detect the vortex shedding frequency generated by the cylinder, the signal detected by sea lion whiskers was

considerably masked by noise (Fig. 6.10b). In contrast, harbor seal whiskers showed a much higher signal-to-noise ratio (SNR) due to largely reduced noise (Fig. 6.10a), which is consistent with the findings by Hanke et al. (2010) and Witte et al. (2012). However, a further analysis of the high noise signals of sea lion whiskers revealed that each noise signal contained a dominant frequency that correlated with flow velocity. Thus instead of being noise, this steady fundamental frequency may serve as a carrier signal that is modulated by each hydrodynamic event impinging on the hair. This modulation may be the crucial information used by sea lions and is suggested to represent the mechanism underlying hydrodynamic reception in the fast swimming sea lion.

Apparently, two types of hydrodynamic sensors developed in the course of pinniped evolution and it seems that the harbor seal whisker is the more effective one. In sea lions and perhaps other eared seals each hydrodynamic event should cause the deterioration of the carrier signal, which has to recover before a new modulation can occur so that the temporal resolution of the whisker should be reduced. Moderate temporal resolution should result in an impaired spatial resolution of, e.g., vortex patterns in a moving sea lion. This might explain why hydrodynamic trail following in the California sea lion is more affected by the aging of trails (Gläser et al. 2011). However, as the carrier frequency changes with the animal's swimming speed, it may provide information that enables the animal to determine its swimming velocity. Knowing its own swimming speed might be advantageous for underwater orientation. Thus, in the sea lion the mechanism underlying hydrodynamic reception might be a trade-off between these different functions. However, more results are needed to elucidate the mechanism of hydrodynamic reception in seals possessing the otarid-like vibrissal hair shaft.

The investigation of hydrodynamic perception as a sensory modality in seals is a new topical research field recently started with the dipole study of Dehnhardt et al. (1998b). Taking the extensive afferent innervation of the vibrissae into account, and considering that in the seal's environment hydrodynamic detection may often be crucial for finding food, we believe that we have only started to understand what kinds of hydrodynamic stimuli a seal can sense, analyze, and discriminate with its vibrissae.

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