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On route with harbor seals – how their senses contribute to orientation, navigation and foraging

Summary: Seals and sea lions are well-oriented in their habitat, the coastal regions and oceans, and are, moreover, successful hunters. During their movements between haul-out places and foraging grounds as well as during foraging, the sensory systems of seals and sea lions provide useful information, although the animals, and thus their sensory systems, face considerable challenges in their habitat and due to their amphibious lifestyle. In this review, in the first chapter, we compiled and later (chapter 4) discuss the information on the senses of seals and sea lions in general and their specific adaptations to habitat and lifestyle in particular. We hereby focus on the senses of harbor seals. Harbor seals turned into a model organism regarding the sensory systems due to intensive sensory research of the last decades. In the second and third chapter, the sensory basics are put into the context of orientation, navigation, and foraging. This allows formulating new research questions, such as where and how the information from different senses is integrated.

Keywords: Vision; audition; olfaction; gustation; haptics; hydrodynamics

Seals and sea lions inhabit the coasts and oceans almost world-wide. At the German coasts, we can find harbor seals and gray seals. By the attachment of tags on to the shoulder region of these animals, their movements between the coast and the open ocean can be inferred. The tagging data reveal that harbor seals cover up to 50 km when moving towards the open ocean, and sometimes they even spend several days offshore (Thompson and Miller, 1990). Scientists also obtained interesting movement patterns from gray seals from the Channel; the seals crossed the Channel in slightly less than two days on a direct route (Chevaillier et al., 2014). Generally the tracks obtained from tagging

studies clearly demonstrate that the animals are well orientated in their habitat; they leave their haul-out places at or near the coast, swim towards the open ocean for foraging, and return straight to their haul-out places. Although these tracks were recorded over years, we still lack a profound understanding of the underlying mechanisms of orientation, and navigation as well as foraging. These behaviors require information from the environment that can be obtained from the sensory systems. Due to this reason, the sensory abilities of seals and sea lions were intensively investigated. In this review, the findings of these sensory experiments are summarized and discussed regarding orientation, navigation, and foraging. We will focus on harbor seals as they turned into model organisms regarding the bespoken behaviors as a result from research from the last decades.

1 The sensory systems of harbor seals

1.1 The visual system

Harbor seals possess large eyes with a diameter of ~40 mm in adult animals (Jamieson and Fisher, 1972; Fig.1a-c). For comparison, the human eye has a diameter of ~24 mm (Augusteyn e al., 2012); however it is inserted into a skull that is slightly larger in length, width, and height in comparison to the seal skull. The seal eyes show specific adaptations to the amphibious lifestyle, the continuous transition between water and air, as well as to the change between high and low ambient luminance (Hanke et al., 2009a). The cornea of the harbor seal eye displays a high degree of astigmatism (Hanke et al., 2006a; Jamieson, 1971; Fig.1c), the refractive powers of the vertical and horizontal meridian are different. This astigmatism has its origin in a corneal flattening in the vertical meridian. It is suggested that the combination of the slit-pupil (Fig.1a) with the corneal flattening solves the main problem of the amphibious lifestyle, the loss of the refractive power of the cornea underwater. If ambient luminance is high and the slit-pupil is closed to a vertical slit (Fig.1a), only light passing the corneal flattening is entering the eye. Due to

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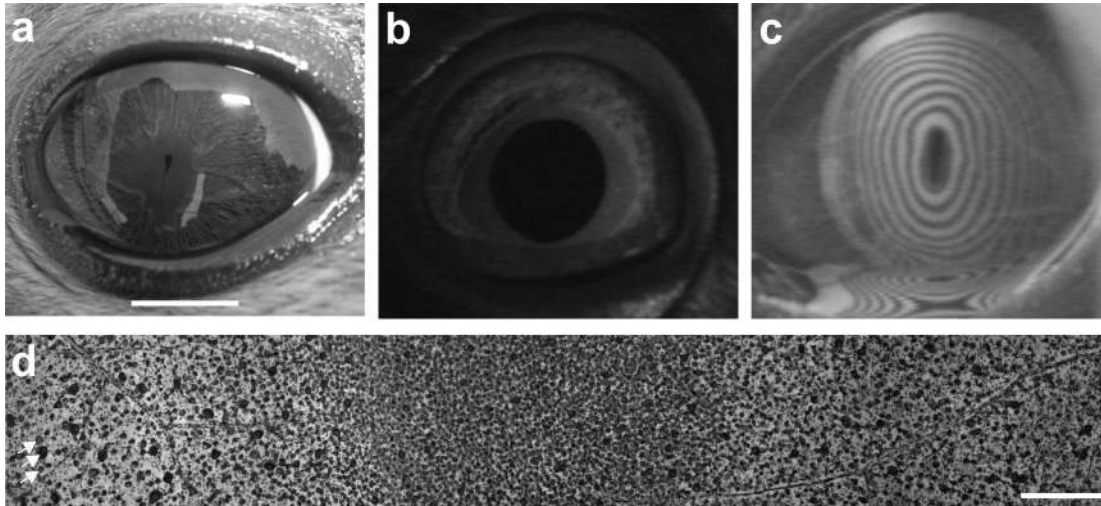
Fig. 1: The visual system of harbor seals. a The seal's pupil closes to a pinhole in bright light. Scale 10mm. b The seal eye with dilated pupil in darkness. c Visualisation of the astigmatism of the seal's cornea with a Placido's disc, the concentric rings are distorted when reflected on the cornea due to the astigmatism. d The distribution of ganglion cells of the seal retina. In a central horizontal streak, an increased ganglion cell density can be found (visual streak; central in this figure). Dorsal to the right, ventral to the left, temporal at the top, nasal at the bottom. At the very left of the figure, three ganglion cells were marked with arrows. Scale 250µm

the corneal flattening, this light is only weakly refracted at the cornea, thus the optical situation in air resembles the optical situation underwater. Measurements of visual acuity support the fact that the aerial visual acuity in bright light amounting to 5.6 cycles/deg is comparable to the underwater visual acuity (Hanke and Dehnhardt, 2009; Jamieson and Fisher, 1970; Schusterman and Balliet, 1970; Weiffen et al., 2006). In air, the visual acuity seems to be mainly affected by ambient luminance. Underwater the visual acuity is also affected by turbidity; if turbidity is increasing, visual acuity is drastically decreasing (Weiffen et al., 2006).

The retina of harbor seals is dominated by rods (Jamieson and Fisher, 1971; Landau and Dawson, 1970; Peichl et al., 2001; Peichl and Moutairou, 1998). The less light-sensitive photoreceptors, the cones, can only be found in low numbers; in ringed seals *(Phoca hispida)*, a seal species closely related to harbor seals, 1.5 % of the photoreceptors were found to be cones (Peichl and Moutairou, 1998). Interestingly all marine mammals, excluding manatees (Cohen et al., 1982; Newman and Robinson, 2006), possess only one cone type. This cone absorbs maximally in green light (Crognale et al., 1998; Fasick and Robinson, 2000; Lavigne and Ronald, 1975; Levenson et al., 2006; Newman and Robinson, 2005). Therefore harbor seals do not have cone-based color vision present in humans and many mammals. Even color vision on the basis of rods and cones under mesopic light conditions, under which rods and cones are active, could not be shown experimentally

(Scholtyssek et al,. 2015). Thus the multifocal, spherical lens (Hanke et al., 2008b), meaning that the lens possesses distinct areas that refract light of different wavelength differently, cannot be considered an adaptation for color vision. Instead the multifocal lens could increase depth of focus in dim ambient light, when the pupil is circularly dilated (Fig.1b).

The advantage of a rod-dominated retina is that it renders the eye very light sensitive. High light sensitivity is important for harbor seals under low ambient luminance; a condition that they experience if they are active at night or when they are diving to deep waters. Parameters that additionally increase the sensitivity of the eye are: (a) The tapetum lucidum (Jamieson and Fisher, 1971; Johnson, 1901; Walls, 1942), which reflects back photons, that were not absorbed during the first passage of the retina, allowing absorbance during the second passage; (b) The pupil (Hanke et al., 2009a; Levenson and Schusterman, 1997), which can dilate from a vertical slit (Fig.1a) to a full circle (Fig.1b). Thereby a fast adaptation to the low light levels during descent can be achieved (Levenson and Schusterman, 1999).

On the level of the retinal ganglion cells, the neurons that are sending the optic information to higher brain centers, a visual streak (Fig.1d) can be found. This visual streak samples events occurring along the horizon, such as the water surface or the sea floor, with increased resolution (Hanke et al., 2009b). Furthermore an area centralis is present that mediates a visual resolution in good agree-

ment with the values obtained in the behavioral experiments (Hanke and Dehnhardt, 2009; Hanke et al., 2009b; Jamieson and Fisher, 1970; Schusterman and Balliet, 1970; Weiffen et al., 2006). In the optic nerve formed by the axons of the ganglion cells, ~ 200,000 axons were counted in harbor seals (Pütter, 1903; Wohlert et al., 2016). A first examination of the decussation pattern present at the optic chiasm of harbor seals (Kröger, 2012) is indicative of a partial decussation as was found in hooded seals *(Cystophora cristata)*, another phocid species (Cystophora cristata; Dohmen et al., 2015).

The eyes are highly mobile; eye movements especially extend the dorsal visual field drastically (Hanke et al., 2006b). Moreover they stabilize external motion (Hanke et al., 2008a). Motion vision is well-developed in harbor seals. They are very sensitive to whole-field motion (Weiffen et al., 2014) occurring for example if a harbor seal is swimming through a cloud of particles generating optic flow. Optic flow perception was recently demonstrated in harbor seals (Gläser et al., 2014). Consequently the significance of particles dissolved in the water needs to be reassessed. In former times, particles were only referred to as visual limitations. Contrary to this opinion, harbor seals can rely on a rich source of optic information, optic flow, when swimming through water with particle load. Optic flow can potentially be used for numerous behaviors such as collision avoidance documented for example for insects (Serres and Ruffier, 2017).

1.2 Mechanoreception

1.2.1 Haptics and hydrodynamics

Harbor seals possess vibrissae at the snout (mystacial vibrissae), on top of the nose (rhinal vibrissae) and above the eyes (supraorbital vibrissae; Fig.2a). The vibrissae of harbor seals and generally the vibrissae of most phocids are undulated, meaning that the hair is showing a wave-like structure (Hanke et al., 2010; Miersch et al., 2011). Due to this undulation, vortices are shedding from the vibrissae if the vibrissae are moving through the water. However, these vortices are destroyed right after their generation, which allows the vibrissae to remain motionless (Hanke et al., 2010; Miersch et al., 2011). This fact is advantageous when external stimuli are to be detected. Then the movement of the vibrissae itself does not need to be considered, instead the external event can directly be measured.

The vibrissa is inserted into a dermal follicle. The follicles of seals show some specific adaptations to the aquatic medium (Hyvärinen, 1989; Hyvärinen and Kata-
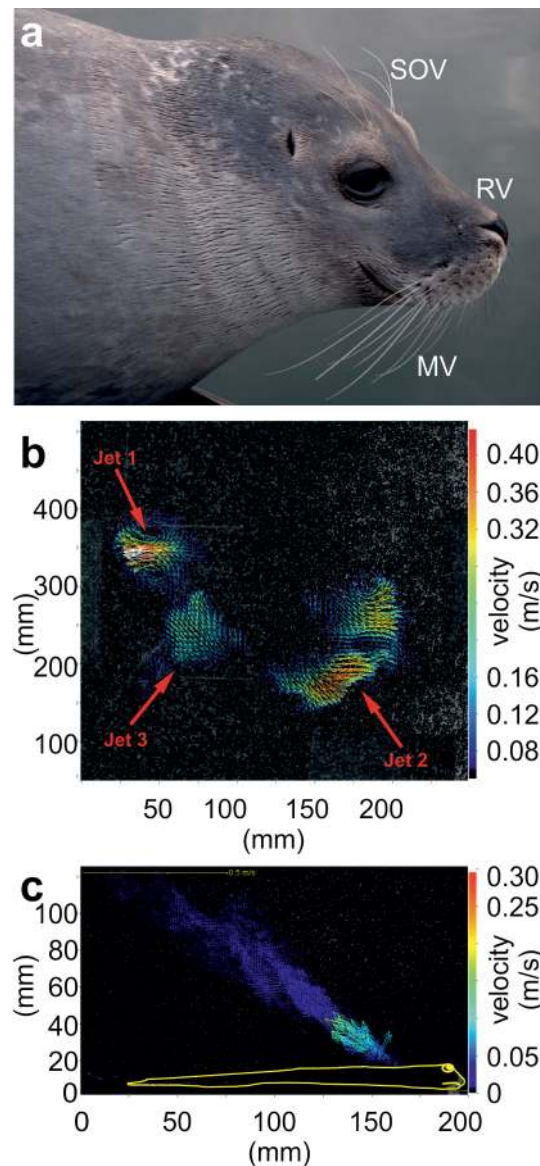

Fig. 2: The vibrissal system of harbor seals. a Harbor seals possess supraorbital vibrissae (SOV), a pair of rhinal vibrissae (RV) and mytacial vibrissae (MV). b Escape reaction of a fish. The water movements were visualized by recording and analyzing the movement of particles added to the water and illuminated with a laser over time. The arrows indicate the movement direction, the velocity of the water movement in m/s is color-coded; these conventions also apply for section c of this figure. During this escape reaction, a C-start, during which the fish escapes by bending its body in a C-shape, jet 1 for example is a single vortex ring. Such a single cortex ring can be perceived and interpreted regarding its movement direction and size by a harbor seal. c Breathing current of a flounder (fish drawn in yellow). The water movements elicited during breathing are within the detection threshold of harbor seals

jisto, 1984; Hyvärinen et al., 2009): (a) In comparison to terrestrial mammals (Ebara et al., 2002), the follicle possesses an additional blood sinus. This sinus amounts to ~ 60 % of the total length of the follicle and is surrounding the upper part of the follicle. Consequently, the region in which the mechanoreceptors can be found is inserted into the skin deeply. Additionally, the blood sinus is heating the sensory system (Mauck et al., 2000). Therefore the vibrissal system is less sensitive to temperature changes in the surrounding medium (Dehnhardt et al., 1998b); (b) The follicle of seals shows a dense innervation (see for example Hyvärinen, 1995; Marshall et al., 2006; McGovern et al., 2015). It augments the innervation density of the follicle of terrestrial mammals (Rice et al., 1986) tenfold or more; in ringed seals, the vibrissae are innervated by 160,000 nerves (Hyvärinen, 1995), whereas in bearded seals *(Erignathus barbatus)*, 320,000 nerves innervating the vibrissae can be found (Marshall et al., 2006).

With the help of their vibrissae, harbor seals are able to actively touch upon objects (haptics; Dehnhardt and Kaminski, 1995; Dehnhardt et al., 1998b; Dehnhardt et al., 1997; Dehnhardt et al., 2014). Moreover they can perceive and interpret water movements via the vibrissae (hydrodynamics; see for example Dehnhardt et al., 1998a; Dehnhardt et al., 2001; Dehnhardt and Mauck, 2008; Fig.2b,c). The function of the vibrissae regarding haptics and hydrodynamics will be extensively described in chapter 3 Foraging.

1.2.2 Audition

Probably the most prominent characteristic of phocids in respect to their ears, generally and in comparison to eared seals, is the lack of an external ear (Fig.3). The external ear was most likely reduced during evolution to increase the streamlined shape of the body. Consequently, the well-documented sound localization abilities in the median plane, judging if a sound is reaching the ear from below or above or from exactly from behind or exactly from in front, in air as well as underwater (Byl, 2017; Byl et al., 2016) cannot be explained by mechanism involving the external ear as in humans (Blauert, 1997; Muller and Bovet, 1999; Wightman and Kistler, 1997).

The ear of harbor seals shows some clear anatomical differences in comparison to terrestrial mammals (Hemilä et al., 2006; Nummela, 2008; Repenning, 1972; Wartzok and Ketten, 1999): (a) The bones of the middle ear of harbor seals are larger, ten times more heavy and also more dense than those of land mammals with comparable skull size (Nummela, 1995). (b) A cavernous tissue is lining the middle ear and the outer ear canal which most likely serves to equilibrate differences in pressure during diving (Mohl, 1967). (c) The tympanic membrane and the oval window with 82.5 mm^2 and 4.94 mm^2 are enlarged (Hemilä et al., 1995). (d) The outer ear canal is lying parallel to the skull which results in the ear canal being oriented backwards (Boenninghaus, 1903).

In general, the experimental evidence gathered in respect to hearing in harbor seals reflects the amphibious lifestyle, and demonstrates that harbor seals can hear well both in air and underwater (Reichmuth et al., 2013). In air, the ear canal is open, and sound is transmitted to the inner ear via the middle ear, which is the general sound transmission pathway in mammals. This enables harbor seals to hear from 100 Hz to ~ 30 kHz with the highest sensitivity at 2–12 kHz (Kastak and Schusterman, 1998; Mohl, 1968; Reichmuth et al., 2013; Terhune, 1974). They are also able to localize sound with the lowest thresholds of 4.1 deg at 1 kHz and of 3.8 deg at 16 kHz (Holt et al., 2005; Holt et al., 2004). To obtain these thresholds, the animal was asked to indicate if a sound was coming from the right or from the left; the threshold can then be calculated as the azimuth value of the angle corresponding to 75 % correct choices averaged from right and left angles.

Underwater, the ear is closed by muscles. In this medium, the mechanism of sound transmission to the inner ear is unresolved. Mostly scientists propose bone conduction, however, this is contradicted by for example the good sound localization abilities of harbor seals (Bodson et al., 2007; Bodson et al., 2006; Byl et al., 2016). Generally, harbor seals hear better underwater than in air (Watkins and Wartzok, 1985). Hearing ranges up to ~ 100 kHz with a range of best hearing between 4–16 kHz (Kastak and Schusterman, 1998; Kastelein et al., 2009; Mohl, 1968; Reichmuth et al., 2013; Southall et al., 2005; Terhune, 1988; Wolski et al., 2003). The lowest hearing thresholds in sound localization of ~ 2.5 – 5.5 deg can be found between 0.2–1 kHz (Bodson et al., 2007; Bodson et al., 2006; Byl et al., 2016).

1.3 Chemoreception

Up to now, chemoreception in seals and sea lions has not attracted much attention. Generally the significance of olfaction and olfactory discrimination abilities have been examined better in eared seals (see for example Kim et al., 2013; Kishida et al., 2007; Laska et al., 2010; Laska et al., 2008; Pitcher et al., 2011). Phocids and harbor seals in particular can smell in air, whereas the nose is closed underwater. The olfactory bulbus being smaller relative to
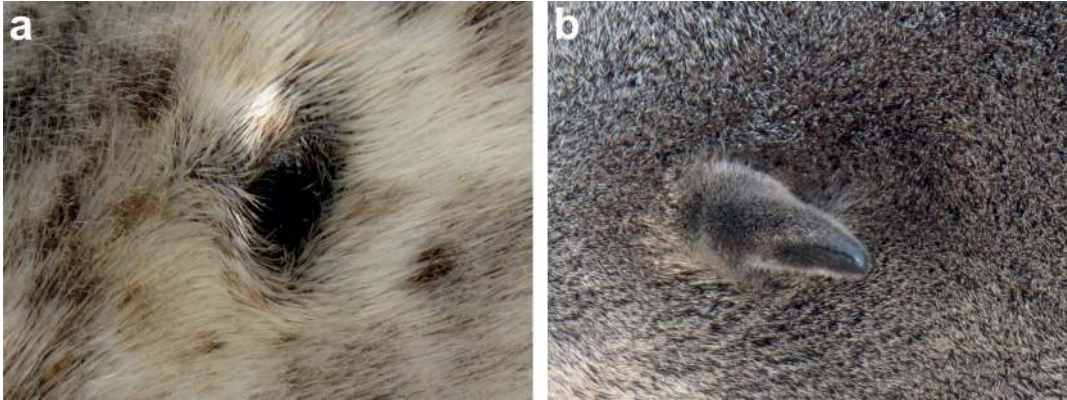
Fig.3: The ears of seals and sea lions. a The ear of the harbor seal, a phocid, lacks an external ear. b The ear of a fur seal, an otariid seal, possess a lappet-like external ear in contrast

the olfactory bulbus in terrestrial mammals suggests less developed olfaction (Reep et al., 2006; Spitzka, 1890). In contrast, the ethmoid bone resembles that of terrestrial mammals (Philström et al., 2005); this good agreement could result in a comparable olfactory sensitivity. Harbor seals are very sensitive to dimethylsulfide (DMS; Kowalewsky et al., 2006; Tab.1) which is a byproduct produced when zooplankton is grazing phytoplankton; the perception of DMS will be discussed in the context of detecting foraging areas (see chapter 2 Orientation and navigation). In phocids, olfaction also seems to play a role in mother-pup-interaction (Burton et al., 1975; Kovacs, 1995) and in reproduction (Hardy et al., 1991).

Concerning gustation of seals, Sonntag (1923) describes, among others, the anatomy of the harbor seal's tongue. He resumes that, among the pinnipeds, harbor seals possess the best-developed taste buds. With their help, harbor seals are able to perceive salinity differences; at a salinity of 30 promille, which naturally occurs in their environment, they can detect a salinity difference of ≥4 % (Sticken and Dehnhardt, 2000; Tab.1). We will focus on this ability in the context of orientation and the detection of frontal systems (see chapter 2 Orientation and navigation).

2 Orientation and navigation

Orientation describes the ability of an individual to detect and keep a direction. Navigation implies that an animal is determining a direction relative to a goal and keeps or adjusts that direction during its movement towards the goal. For the latter, the animal needs information about its current position in relation to the goal.

The visual system could contribute to orientation and navigation manifold. Astronavigation seems plausible as studies could show that harbor seals can perceive artificial as well as natural stars down to 4.4 apparent stellar magnitude (Mauck et al., 2005) and that they can swim towards a single star comparable to a load star in the presence of the whole starry sky (Mauck et al., 2008; Fig.4). Harbor seals do not seem to have access to the polarization quality of light (Hanke et al., 2013). But it remains to be investigated if the sun or the moon itself can be used as orientation cue. Orientation based on landmarks as present close to the coast should also be investigated in future experiments.

A fascinating area of research in respect to visual navigation is optic flow perception described in 2014 (Gläser et al., 2014; Fig.4). Using optic flow, harbor seals could for example determine how far they have swum. The estimation of distances is an important element of path integration (Etienne and Jeffrey, 2004; Mittelstaedt and Mittelstaedt, 1982) among others. This navigation mechanism would allow the animals to return to the starting point or to any point along their journey by integrating over all distances swum and directions covered up to the point of return. Path integration is promising in respect to marine mammals as it can be based on external information, but also solely on the basis of idiothetic information, information derived from self-motion, which can be of significance in the seals' seemingly structurless environment.

So far only the classic sensory systems were focused on regarding orientation and navigation in marine mammals. Besides these, the parameters time and space could play a role during the movements in their habitat. A first examination revealed that harbor seals possess a well-developed sense of time and are able to discriminate time intervals ranging from a few milliseconds up to half a minute (Heinrich et al., 2016; Heinrich et al., unpublished
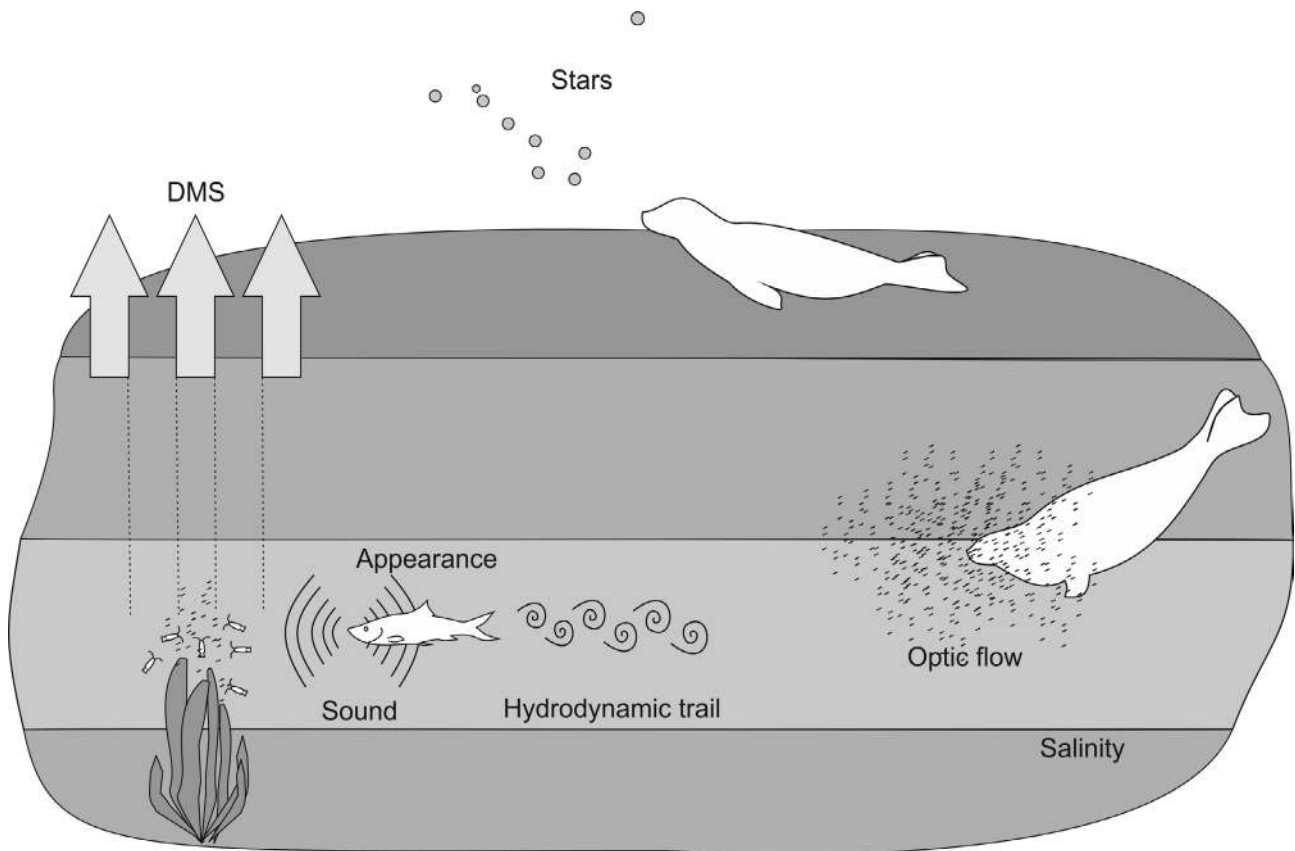
Fig.4: Overview of the mechanisms of orientation, navigation, and foraging of harbor seals with an already investigated sensory basis. These mechanisms include (a) olfactory perception of dimethyl sulphide (DMS), which is a byproduct produced where zooplankton grazes phytoplankton, (b) visual perception of stars, optic flow induced by swimming through particles or directly viewing of the prey, (c) auditory perception of prey, (d) the perception of hydrodynamic trails or breathing currents generated either during swimming or breathing of the prey as well as (e) gustatory perception of salinity with salinity varying in horizontal layers in this figure

data). Assuming that their sense of time is also providing reliable information for longer time intervals, harbor seals could judge how long or, considering additionally their swimming velocity, how far they have travelled in one direction.

So far scientists have only speculated about a hydrodynamic or acoustic orientation mechanisms. It is conceivable that harbor seals sense currents underwater to determine or modify their movement direction. The prerequisite would be that the ocean currents show a temporal or permanent course or change systematically with for example external parameters. The inflow and outflow of water with the tide could provide important hydrodynamic cues for orientation. The underwater acoustic landscape could fulfill the same task as already suggested by Norris (1967) for whales.

Regarding chemosensoric orientation, plausible scenarios have already been developed. Even the sensory basis for these mechanisms was investigated. One scenario is based on the finding that foraging areas are characterized by high concentrations of DMS in the atmosphere (Andreae et al., 1994; Bürgermeister et al., 1990). Where there is a high DMS concentration, there are also many fishes according to the trophic pyramid. As fishes are the prey of harbor seals, these areas are in turn also interesting for harbor seals. To localize these areas rich in fish on the basis of their increased DMS concentration (Fig.4), DMS has to be perceived; a capability that has already been thoroughly investigated in sea birds (for review see Nevitt 2008; Tab.1). Kowalewsky et al. (2006) demonstrated that harbor seals are indeed able to perceive this odor and, moreover, are sensitive for very small DMS concentrations. In a second step, it would need to be demonstrated that harbor seals are able to localize DMS and accordingly are attracted by DMS plumes.

Foraging areas are also characterized by salinity. High productivity areas were found at salinity fronts (Bowman and Esaias, 1978; Floodgate et al., 1981; Fig.4) characterized by steep salinity gradients. With the help of their high sensitivity for salinity (Sticken and Dehnhardt, 2000;

Tab.1), harbor seals possess the sensory basis to locate the foraging areas at salinity fronts. It was shown for fishes that they use specific layers of salinity for long-distance orientation (Atema, 1988; Westerberg, 1984). Therefore it would be interesting to correlate the movement pattern of wild harbor seals with the parameter salinity to reveal a possible influence of salinity on the behavior of harbor seals.

Many organisms such as turtles, mole rats, sharks, and birds use the earth magnetic field for orientation and navigation (see for example Kalmijn, 1982; Kimchi and Terkel, 2001; Kirschvink et al., 2001; Lohmann and Lohmann, 1996; Mouritsen and Ritz, 2005; Wiltschko and Wiltschko, 2006). Already in the 1990ties, Renouf (1991) examined if harbor seals were able to perceive magnetic fields, however, without success. Hanke et al. (unpublished data) took on this topic. Although the topic was approached with a variety of experimental procedures including large and small coils as well as bar magnets, no learning effect could be documented regarding the perception of magnetic fields and magnetic anomalies by harbor seals in our research group. In conclusion, it has to be assumed at the moment that harbor seals are not able to orient or navigate with the help of the earth magnetic field.

3 Foraging

In many instances, harbor seals are swimming towards the open ocean in search for their prey. When the seals will have reached a foraging ground, their task is to localize their prey. Under good light conditions, harbor seals can directly see and hunt its prey (Kilian et al., 2015). Hunting based on vision is also possible if the lighting conditions are not optimal but if the seals are close to the prey item, meaning shortly before prey capture. Evidence that the visual system is indeed adapted to see objects at close vicinity has been gathered in many studies on the visual system of harbor seals (Hanke et al., 2009a; Hanke et al., 2011; Scholtyssek et al., 2008; Weiffen et al., 2006).

If, however, vision is limited due to turbidity or under low light conditions or if the seals are not close to the prey, other sensory systems have to fulfil the task of detecting prey. Many fish species emit sounds (Kasumyan, 2008; Wilson et al., 2004), thus a localization of fish could be possible via audition (Fig.4).

If a prey fish is swimming in the open water, it leaves a hydrodynamic trail, a trail of vortices, behind itself (Fig.4). When encountering such a hydrodynamic trail, harbor seals are able to not only detect this water disturbance but also to actively follow the trail (Dehnhardt et al., 2001; Dehnhardt and Mauck, 2008). This so-called hydrodynamic trail-following was shown in experiments including remote-controlled submarines (Dehnhardt et al., 2001), a conspecific (Schulte-Pelkum et al., 2007), and artificial fish (Kilian, 2010) as trail-generators. The animals were able to follow the hydrodynamic trail right after generation. However, they also followed successfully, if the hydrodynamic trail was more than 30s old, which simulated a situation in which the fish has already passed the specific point in space, or if the trail included gliding phases (Wieskotten et al., 2010b). A hydrodynamic trail seems to convey additional information about the trail generator such as its size and form (Wieskotten et al., 2010a; Wieskotten et al., 2011). Even if single vortices, which every hydrodynamic trail contains or which are generated during escape reactions (Niesterok and Hanke, 2013; Tytell and Lauder, 2008; Fig.2b), are presented, a harbor seal can determine the movement direction and the size of the vortex ring (Krüger, 2017; Krüger et al., 2018). This ability would allow harbor seals to make decisions for example on its future swimming direction upon encountering a hydrodynamic trail. It remains to be investigated if harbor seals can follow the hydrodynamic trail of a real fish and under natural conditions, for example if natural currents are present.

Harbor seals, however, occasionally ingest only a very small percentage of pelagic fish. Examinations of the stomach content of dead harbor seals revealed that in some places they feed almost exclusively on flatfish (see for example Härkönen, 1987; Pierce et al., 1991; Tollit and Thompson, 1996). Flatfish mostly bury themselves in the sand to which they are perfectly camouflaged. Visual detection is not plausible, even if it was possible to detect these fish on the coherent movement of the various body parts (Lui et al., 2012; Weiffen et al., 2014). An electroreceptive detection of the fish was also excluded, as there is no evidence for electroreception in harbor seals up to date. So far it was assumed that harbor seals detect these flatfish when they are in direct contact with these with their vibrissae, meaning they detect the flatfish haptically. Via haptics, harbor seals could indeed infer the form, size or texture of a fish (Dehnhardt and Kaminski, 1995; Dehnhardt et al., 1998b; Dehnhardt et al., 1997). However, on videos recording the behavior of wild harbor seals during foraging, a direct contact of the vibrissae with the prey was not discernable. The seals are rather swimming at some distance to the sea floor. Taking this into account, Niesterok et al. (Niesterok et al., 2017a; Niesterok et al., 2017b) hypothesized that harbor seals are able to detect flatfish on the basis of the water currents generated during

breathing (Bublitz, 2010; Fig.2c). This hypothesis was supported by: (a) a detailed analysis of these breathing currents, which elicit water movements with velocities well within the detection range of harbor seals; (b) behavioral experiments, in which harbor seals were able to localize an artificial breathing current with characteristics similar to natural breathing currents spaced out in a large area. Thus a hydrodynamic detection of benthic fish seems possible.

4 Discussion and perspective

Research of the last decades has ameliorated our understanding of the sensory systems of harbor seals and of seals and sea lions in general. Nevertheless, as already indicated in the previous chapters, many aspects still need to be investigated to close existing gaps in our understanding of the sensory systems themselves and of the mechanisms of orientation, navigation, and foraging.

This review has largely focused on experimental evidence gathered in harbor seals. Before the harbor seal turned into a model organism concerning its sensory systems by systematic research in this field, only some information on the sensory systems of a multitude of pinniped species were available. Thus often researcher generalized across species. This generalization, however, carries risks as all pinnipeds show very specific adaptations to their habitat and lifestyle. However now that more detailed information on the sensory systems of one seal species is available, comparative studies regarding selected sensory aspects that include other pinnipeds would be interesting. To give an example, future studies could continue (Gläser et al., 2011, Miersch et al., 2011) to work on the structural difference of the vibrissae, undulated versus smooth. Moreover the finding of completely and partially flattened corneae in pinnipeds (Dawson et al., 1987, Hanke et al., 2006a) leads to the question if even other corneal types are present or if there is a systematic difference between otarid and phocid seals.

Exciting research questions could also be derived by having a comparative look at species that for examples share the aquatic environment or live in a habitat with comparable characteristics. Concerning the latter, it is interesting to look at for example the desert ant that inhabits a structurless environment comparable to the open ocean. The desert ant is a successful path integrator; in our opinion, path integration could be a navigational mechanism of marine mammals promising to investigate. In uneven terrain, the desert ant calculates its homing

vector guiding the ant back to its nest after foraging not on the basis of the distance actually travelled. Instead the ants take the distance into account that corresponds to the horizontal projection of the path segments (Wohlgemuth et al., 2001). Marine mammals could show a comparable behavior as, due to diving, the distance actually travelled can deviate from the ground distance.

Previous studies on the sensory systems of pinnipeds were conducted comparable to classical lab experiments. Therefore the experimental conditions were well-controlled which is a prerequisite to obtain a fundamental understanding of for example the function of the sensory systems. These lab experiments, however, only partially mimic the situation encountered by the animals in their natural habitat. In the future, it would be desirable to conduct experiments under natural conditions for example directly in the seals' habitat. An essential characteristic of these open-field experiments is that they are not space-limited; thus orientation and navigation experiments could be run without spatial limitations that prohibited the direct investigation of orientation and navigation in the past.

Although our knowledge of the pinnipeds' sensory abilities has increased over time, it has so far been neglected that the senses interact, they complement or substitute each other. Therefore we think that studies focusing on multimodality and sensory integration are promising. Sensory integration could be approached with functional magnetic resonance imaging. This technique can also close the gap between the sensory systems and the central nervous system, which has not been thoroughly worked on in our model animal. Generally, the examination of a complex central nervous system of a mammal that has adapted to the aquatic medium for ~ 30 Mio years, promises many new and interesting insights.

To obtain a fundamental understanding of the mechanisms of orientation and navigation of pinnipeds, it is essential to close the gap between the sensory abilities that were examined in laboratory animals and the behavior of wild animals. Both disciplines can grow together: on the one hand, the documented sensory abilities can help to describe the behavior of wild animals. On the other hand, the behavior of wild animals can lead to hypotheses to be tested in controlled laboratory experiments.

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Appendix

Tab.1: Overview of the chemosensoric thresholds of harbor seals in comparison to other species

Species	Threshold for DMS	Reference
Harbor seal	13–20 pmol/m^{-3}	Kowalewsky et al. 2006
Blue petrel *(Halobaena caerulea)*	<10 pmol/l	Bonadonna et al. 2006
Antarctic prion *(Pachyptila desolata)*	~3–4nM	Nevitt and Bonadonna 2005
Human	0.0026–1 µg/l	e. g. Leonardos et al. 1969 Belitz and Grosch 1982

Species	Threshold for seawater/NaCl	Reference
Harbor seal	<4 % bei 30 ppt (best difference threshold)	Sticken and Dehnhardt 2000
California sea lion *(Zalophus californianus)*	3.6 ppt (absolute threshold)	Friedl et al. 1990
Pacific bottlenose dolphin *(Tursiops truncatus gilli)*	1.6 ppt (absolute threshold)	Friedl et al. 1990
Black sea bottlenose dolphin *(Tursiops truncatus ponticus)*	5.4 ppt (absolute threshold)	Kuznetsov 1978 (cited after Friedl et a. 1990)
Human	18 % bei 20 ppt (best difference threshold	Sticken and Dehnhardt 2000
	0.18 ppt (absolute threshold)	Pfaffmann et al. 1971

Bionotes

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Frederike D. Hanke studied biology at the University of Freiburg with majors in Animal physiology/Neurobiology, Ecology/Evolution, Genetics and Animal Behavior/Psychology. She was awarded a PhD from the International Graduate School of Biosciences of the University of Bochum. During her PhD as well as during the subsequent postdoctoral phase, she has had the opportunity to conduct research projects at many research institutions in Germany and abroad. Just recently, she successfully completed her habilitation at the University of Rostock. During her scientific career, Frederike Hanke enjoyed working with many different and exciting species such as honeybees, corvids, fish, and bears. However, her main experimental animals are pinnipeds and cephalopods. In her research, she is focusing on their sensory systems, mainly on vision. Frederike Hanke is interested in all kinds of aspects of vision including the adaptation of the visual system to the species-specific lifestyle and habitat up to motion and polarization vision, visual orientation and visual cognition as well as visual neuroanatomy.

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Guido Dehnhardt studied Biology, and Geography at the University of Münster. Already during his studies, he focused on marine mammals and therefore also visited the Kewalo Basin Marine Mammal Laboratory, University of Hawaii, and the Naval Ocean Systems Center. He continued with a PhD in marine mammal science that he was awarded from the University of Münster. After a postdoc at the University of Bielefeld, Guido Dehnhardt changed to the University of Bonn. During his time in Bonn, he also stayed for research projects at the University of Joensuu, Finland, and at the University of Newfoundland, Canada, before he successfully completed his habilitation. Very intensive years of research at the University of Bochum followed before he was awarded a Lichtenberg professorship from the VolkswagenStiftung to be realized at the University of Rostock. In Rostock, he founded the well-known Marine Science Center, the largest seal research station worldwide. Guido Dehnhardt's research interests are sensory and cognitive abilities in the context of marine mammal orientation. He is famous in particular for his research on the function of vibrissae as a haptic and hydrodynamic system.