# Chapter 16
# The Sensory World of Otariids

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**Abstract** Otariids face many unique challenges with respect to lifestyle and habitat. They need to find suitable foraging areas in the open ocean, detect and capture moving prey in near darkness, identify suitable mating partners in traditional terrestrial breeding areas, and relocate their pups following extended separations. Above all, otariids have to cope with the different physical properties of air and water. This chapter illustrates how the challenges of amphibious living have shaped the sensory systems considered to be the 'antennae' through which otariids gather information about the surrounding world. Our current understanding of the sensory capabilities of otariids comes from studies of both structure (anatomy, neurobiology) and function (sensitivity, performance) of specific sensory modalities. This information helps us to describe what the senses are specialized for and to identify the particular biological tasks they are probably involved in. However, future studies need to explicitly link the senses, behavior, and ecology. Altogether, this knowledge will be informative to behavioral ecologists in their attempts to determine why an otariid behaves the way it does.

**Keywords** Sea lions · Fur seals · Vision · Audition · Chemoreception · Olfaction · Gustation · Mechanoreception · Sensory adaptation

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## 16.1   Introduction

Behavioral ecology, the topic of this book, is focused on the interactions between animals and their environment (Krebs and Davies 1981). A key role herein is played by the sensory systems—as they are an individual's interface to the physical environment, providing the information that enables and guides specific behaviors. For otariids (as for all animals), sensory biology is thus fundamental to behavior.

Otariids represent a fascinating case of animals evolved to operate with precision within, and to transit effortlessly between, two sensory worlds. They show impressive capability at solving ecological and social problems both in their aquatic and terrestrial habitats—from foraging alone or in multi-species aggregations on an assortment of marine prey to providing extended maternal care in crowded coastal colonies. For the amphibious pinnipeds including the otariids, the competing demands of terrestrial and aquatic environments have strongly shaped their sensory systems and led to adaptations that allow them to efficiently receive relevant airborne and waterborne sensory cues. This is a remarkable feat, as the vastly different physical properties of air and water make it extremely difficult to build a sensor or instrument that is equally effective in both media.

Here, we review much of what is known about the sensory processing abilities of otariids, and contrast their sensory adaptations with those of other marine mammals as well as with terrestrial carnivores. A strong emphasis is placed on the California sea lion (*Zalophus californianus;* Fig. 16.1) as it is the best studied species among otariids with respect to sensory biology. Of course, sensory abilities are closely tied to cognitive operations, which will be described in more detail in the following chapter (Chap. 17). Together, these accounts of information gathering and information processing in otariids should provide behaviorists with an appropriate sensory perspective with which they can better understand the behaviors and strategies of free-ranging animals.
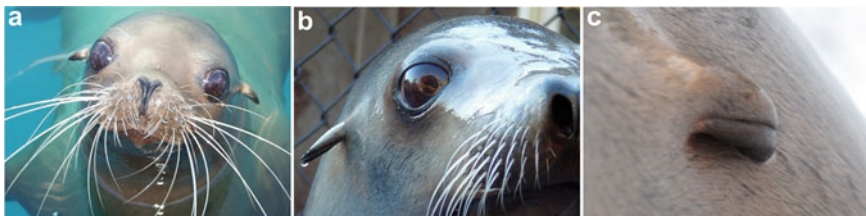


**Fig. 16.1** (**a**) The California sea lion *(Zalophus californianus)* is a model species among otariids regarding sensory and cognitive research. The image illustrates the visible sensory structures including the large eyes, two types of vibrissae (mystacial and supraorbital), the external ear, and the nose, which remains tightly closed aside from breathing and sniffing in air. Image: C. Reichmuth/NMFS 14535. (**b**) The right eye of a sea lion showing the central flat region of the cornea. The image also offers a close-up of the mystacial vibrissae which are smooth and stiff. Image: C. Reichmuth/NMFS 14535. (**c**) The left ear of a sea lion showing the outer ear, the pinna. Image: MSC

## 16.2 The Visual System

The eyes are perhaps the most noticeable sensory structures in sea lions and fur seals (Fig. 16.1a, b). Otariids have large, bulging eyes with axial eye diameters from 30 to 44 mm (Mass and Supin 2005; Miller et al. 2010; Pütter 1903; Turner et al. 2017; West et al. 1991). Pinnipeds have orbits that are proportionally larger than those of related terrestrial species (Debey and Pyenson 2013). Among otariids, there is an interesting correlation between orbit size and body mass, with body mass in turn correlated to maximum diving depth; this correlation points to the fact that large eyes can be considered an adaptation to low light conditions experienced during diving. In California sea lions, several parameters of the visual system generally reflect the rather shallow dive depth of this species (usually less than 80 m; Feldkamp et al. 1989). These include a smaller pupillary range (Levenson and Schusterman 1997) and slower dark adaptation rate (~16 min) than deeper diving seals (Levenson and Schusterman 1999).

Despite not traveling to the depths explored by some other marine mammal species, otariids have eyes that are adapted to function under low ambient illumination. The eye itself is large, which allows the vertical, slit-shaped pupil to dilate widely to capture even small amounts of light. Like many predators that hunt in low-light conditions, otariids have a well-developed reflective layer, the *tapetum lucidum*, underlying the retina in the eye fundus. This tapetum maximizes photon absorbance by reflecting photons that were not absorbed by the photoreceptors at first passage through the retina, thus allowing absorbance at second passage (Miller et al. 2010; Pütter 1903; Turner et al. 2017; West et al. 1991). The tapetum of otariids lines the entire fundus (Miller et al. 2010) to maximize absorbance of photons reaching the eye from all directions, which is crucial for an animal that can rotate its head and body along all axes underwater. Otariids also appear sensitive to small differences in brightness contrasts. A brightness discrimination study of Scholtyssek and Dehnhardt (2013), in contrast to the study of Busch and Dücker (1987), revealed that a South African fur seal *(Arctocephalus pusillus)* was able to perceive brightness differences of $\leq 10$ %, which is slightly better than the performance of previously tested phocid pinnipeds (14%; Scholtyssek and Kelber 2008) and even humans (11–14%; Cornsweet and Pinsker 1965; Griebel and Schmid 1997). Finally, the photoreceptors that line the otariid retina are predominantly light-sensitive rods with a wavelength of maximum absorbance at 497–501 nm, within the blue-green portion of the light spectrum that dominates under water (Crescitelli 1958; Lavigne and Ronald 1975a, b; Levenson et al. 2006).

In general, the retina of otariids is densely packed with photoreceptors, about 220,000 cells/mm$^2$ (Landau and Dawson 1970), a density higher than that of many terrestrial mammals including humans (120,000–160,000 cells/mm$^2$), although less than that found in fully aquatic mammals such as cetaceans (cell density in the bottlenose dolphin is ~400,000 cells/mm$^2$; Wartzok and Ketten 1999). Only a tiny fraction of the receptor population are cones (Peichl et al. 2001). Among the cones, only L-cones, with a wavelength of maximum absorbance of 560 nm, are present in

California sea lions (Levenson et al. 2006); no S-cones were found in this species (Peichl et al. 2001). Because of this, cone-based color vision may not be possible. One possibility for otariids to perceive colors would be by comparing the responses of cones and rods under light conditions when both receptor types are active, called mesopic light conditions. Unfortunately, color vision tests to address either cone-based (Busch and Dücker 1987; Griebel and Schmid 1992) or mesopic color vision (Oppermann et al. 2016) have failed thus far to fully control for ambient illumination. Consequently, the conclusion that California sea lions, South African fur seals, and South American fur seals *(Arctocephalus australis)* are able to perceive colors must be considered with caution.

The eyes of otariids show some characteristics reflecting their predatory nature. The viewing axes point to the front (Fig. 16.1a, b), and the visual fields of both eyes most likely overlap to some extent, which is a prerequisite for binocular depth perception. Additionally, otariids have good aerial and underwater visual acuity (Schusterman 1972; Schusterman and Balliet 1970, 1971) that is comparable to terrestrial carnivores (Rahmann 1967). Normally one would expect to find the amphibiously living otariids to be emmetropic (normal-sighted) in one medium and ametropic (short- or far-sighted) in the other, resulting in an inferior visual acuity in one medium. For the pinnipeds, it is usually assumed that they are emmetropic under water, supporting precise visual assessments such as prey localization during hunting. To provide a well-resolved image of the marine environment, all otariids have a spherical lens (Miller et al. 2010; West et al. 1991) which resembles the lenses of fish and differs from the more oblong lens shape of terrestrial mammals. The cornea, which provides focusing power in air, is ineffective at refracting light in water. In terrestrial environments, an eye with a lens adapted to underwater vision should result in myopic (near-sighted) vision due to the combined effects of both the spherical, highly refractive lens and the curved cornea in the aerial medium. A careful examination of the cornea of California sea lions however reveals an ingenious solution to this problem—a completely flattened region of the cornea (~ 6.5 mm diameter; Fig. 16.1b; Dawson et al. 1987; Miller et al. 2010). In contrast to a more typically curved mammalian cornea, this flattened cornea does not contribute much to the overall refractive power of the eye. Instead, this feature renders the cornea optically ineffective in air, allowing light to pass directly into the eye with only the circular lens focusing the light rays as in water. Visual performance reflects this remarkable anatomical adaptation. Behavioral measurements obtained from trained sea lions tested both in air and under water in bright light reveal visual acuity values of 5.5–5.7 cycles/deg in the California sea lion (Schusterman 1972; Schusterman and Balliet 1971) comparable to the visual acuity of felid carnivores (for example, visual acuity in cats: 6–9 cycles/deg; Peichl 1997; Rahmann 1967). Visual acuity was also assessed in behavioral experiments conducted under water in the Steller sea lion *(Eumetopias jubatus)* as 4.2 cycles/deg (Schusterman 1972; Schusterman and Balliet 1970), and in air in the South America fur seal as 4.2 cycles/deg and the South African fur seal as 4.5 cycles/deg (Busch and Dücker 1987). When ambient light levels decline, aerial visual acuity decreases faster than underwater visual acuity (Schusterman and Balliet 1971). Thus, visual adaptations

allow sea lions to see clearly in both media with the exception of in dim conditions while on shore.

Behavioral measures of visual acuity obtained from experiments with trained sea lions are in the same range as measures of retinal resolution calculated on the basis of neural anatomy, that is, on the basis of the density of ganglion cells in the best vision zone of the retina, the *area centralis*. Both Steller sea lions and northern fur seals *(Callorhinus ursinus)* have maximum ganglion cell densities corresponding to a resolution of 5.3–5.5 cycles/deg in air and 7.1–7.2 cycles/deg in water (Mass 1992; Mass and Supin 2005). In addition to these species, the density and topography of ganglion cells in the retina was also assessed for the California sea lion (Landau and Dawson 1970). If, in the future, the internal geometry of the sea lions' eyes is characterized, the maximum ganglion cell density of 5,000 cells/mm$^2$ documented in the latter study can be used to estimate retinal resolution in California sea lions for further comparison with behavioral visual acuity measurements.

In other otariids, at least 260,000 ganglion cells were found in the retinae of northern fur seals (Mass and Supin 1992) and 177,500 ganglion cells in the retinae of Steller sea lions (Mass and Supin 2005). As in all pinnipeds, giant ganglion cells reaching a diameter of up to 50μm in some species (Mass and Supin 1992) accounted for 8–10% of the whole ganglion cell population in otariids (Mass and Supin 2007); these giant cells may serve to mediate motion information as hypothesized by Dawson et al. (1982). The ganglion cells give rise to the optic nerve, which transports the visual information to higher brain regions. The optic nerve of California sea lions comprises 130,000 myelinated axons (Turner et al. 2017). Only a single study has so far described the higher brain areas in sea lions which are involved in the processing of optical stimuli, such as the superior colliculus, the lateral geniculate nucleus, and the visual cortex (Turner et al. 2017). In contrast, many behavioral experiments concerning cognitive processing of visual information have been conducted; the visual stimuli used in these studies have included moving gestural cues given by experimenters, black-and-white two-dimensional shapes presented in air and underwater, and more complex, three-dimensional objects. These experiments are summarized by Cook et al. (Chap. 17).

The visual system of otariids is well-adapted to function in air as well as under water and shows many adaptations for vision under low light conditions. Underwater, predatory otariids may use vision to detect their prey when visibility is high but also under low contrast conditions. Observations of free-ranging individuals have revealed that sea lions mainly approach their swimming prey from below, suggesting that sea lions may silhouette the fish against the bright(er) water surface (Bonnot 1932; Hobson 1966). In this foraging context, future studies on motion vision will be highly informative. In the social domain, visual cues contribute to the recognition of individuals, as summarized by Charrier (Chap. 7) and Sinclair (Chap. 13), and may further function to support recognition of familiar places, an aspect left to be demonstrated in the future.

## 16.3 Mechanoreception

### 16.3.1 Haptics and Hydrodynamics

Besides the eyes, the face of otariids is dominated by long vibrissae (colloquially referred to as whiskers; Fig. 16.1a, b). Otariids have 20–40 vibrissae on each side of the snout, called mystacial vibrissae, and 1–2 vibrissa(e) above each eye, called supraorbital vibrissae (Fig. 16.1a, b; King 1983). The vibrissae of otariids are thicker, longer, and stiffer than those of terrestrial carnivores. In California sea lions, the longest of the 38 mystacial vibrissae (Dehnhardt 1994; Sawyer et al. 2016; Sprowls and Marshall 2019) reach a length of at least 12 cm (McHuron et al. 2020; Sawyer et al. 2016), whereas, among the otariids, the longest vibrissae (>48 cm) can be found in South Georgia Antarctic fur seals (*Arctocephalus tropicalis gazelle*; Bonner 1968) and Steller sea lions (C. Reichmuth, unpublished data). In contrast to the phocids, otariids do not have vibrissae close to the nose, called rhinal vibrissae (Ling 1977), and their vibrissae are smooth instead of undulated and slightly compressed in cross-section (oval rather than round; Hanke et al. 2010; Miersch et al. 2011). Comparative morphometric descriptions of otariid vibrissae were published by Ginter et al. (2012).

The vibrissae are composed of non-living keratinized tissue and emerge from follicle sinus complexes (FSCs) in the skin. As in other pinnipeds (Hyvärinen et al. 2009; Marshall et al. 2006; Mattson and Marshall 2016; McGovern et al. 2015), these FSCs have several distinguishing features. In California sea lions, FSCs are long with an upper cavernous sinus in addition to the ring and lower cavernous sinus (Sprowls and Marshall 2019; Stephens et al. 1973). The upper cavernous sinus, usually considered to support the function of the vibrissae in cold temperatures (Mauck et al. 2000), is shorter than in phocids, reflecting that sea lions inhabit temperate waters and are shallow divers. The follicle is innervated by the deep vibrissal nerve, and the innervation per follicle is higher than in terrestrial carnivores, although not as high as in phocid pinnipeds. For comparison, California sea lions have ~86,000 axons per vibrissal pad, while a terrestrial carnivore, the pole cat, has only ~7,500 axons per vibrissal pad (Hyvärinen et al. 2009), and seal species have 60,000–160,000 axons per vibrissal pad (Hyvärinen et al. 2009; Marshall et al. 2006; Mattson and Marshall 2016; McGovern et al. 2015). Sprowls and Marshall (2019) took differences in innervation of different vibrissae in the vibrissal pad into account and thus offer a more conservative estimate in comparison to the estimate provided by Sawyer et al. (2016). The extensive and highly organized neural investment along the pathway that extends from an individual vibrissa to somatosensory regions of the brain suggests significant information transfer. In the California sea lion as well as in the northern fur seal, the brain areas that receive and process this information are enlarged and spatially structured, with the neural tissue somatotopically mapped in the central nervous system (Ladygina et al. 1985, 1992; Sawyer et al. 2016). However, how otariids integrate the incoming information flow

from individual vibrissae to develop a sensory representation based on the full sensory array remains poorly understood.

When otariids explore the world, they often protract their vibrissae to bring them into contact with objects in the environment. With their pliable vibrissae, California sea lions can rapidly respond to moving stimuli (Milne and Grant 2014) and discriminate objects on the basis of size and shape by using active touch (Dehnhardt 1990, 1994; Dehnhardt and Dücker 1996). For example, when presented with discs differing in diameter, a trained sea lion wearing a blindfold could reliably detect a size difference of 22% (Dehnhardt 1994); when presented with triangles differing in size, the same sea lion performed similarly well in a discrimination task (Dehnhardt and Dücker 1996). Shape discrimination between triangles and discs with identical surface areas is possible on the basis of the size difference between the longest measurable lines (Dehnhardt and Dücker 1996); after the sea lion had learned to perform this shape choice task visually, she was able to discriminate the objects using only her whiskers even when the size difference was less than 5%, corresponding to an absolute size difference of less than 2 cm. During such difficult size and shape discrimination tests, sea lions use short lateral head movements with protracted vibrissae to investigate and compare objects (Dehnhardt 1994; Dehnhardt and Dücker 1996).

While in water, the vibrissae of otariids seem to function as hydrodynamic sensors, as they do in phocids (Dehnhardt et al. 2014; Hanke et al. 2013), enabling the animals to sense water movements. Preliminary measurements conducted with a trained California sea lion revealed the vibrissae to be very sensitive to water movements generated by a dipole vibrating at 20 and 30 Hz (Dehnhardt and Mauck 2008); the sea lion was even more responsive than a trained harbor seal *(Phoca vitulina)* performing the same task at the same frequencies (Dehnhardt et al. 1998). Like harbor seals, a trained sea lion can find and follow the hydrodynamic trail left behind by a remote-controlled submarine (Gläser et al. 2011). However, the performance of the sea lion was reduced in comparison to harbor seals when tasked with following hydrodynamic trails including directional changes or when following hydrodynamic trails after increasing delay periods (Gläser et al. 2011); this experimental procedure mimics a situation in which a sea lion encounters a hydrodynamic trail of a fish that had swum by some time ago. The vibrissae of otariids are able to transmit external events such as a hydrodynamic trail left behind by a fish or a conspecific, as phocids do; however, structural differences result in noise being substantially reduced in the seal in comparison to the sea lion vibrissa (Hanke et al. 2010; Witte et al. 2012). Nevertheless, both types of vibrissae are able to detect external events; the proposed mechanism is described by Miersch et al. (2011).

From the few experimental studies conducted so far on the ability of California sea lions to perceive haptic and hydrodynamic information, we can confirm a role for active touch, the exploration of objects when in direct contact with surfaces, and for the detection and localization of swimming prey using hydrodynamic cues. Vibrissae may have other important roles as well, for example in nursing behavior or benthic feeding. In social contexts, the vibrissae are part of facial expressions and

may signal arousal and provide other important communicative cues (Miller 1975). For example, the whiskers of male Steller sea lions extend forward and touch those of territorial neighbors during boundary displays, and serve as key components of multi-modal communication (Chap. 7).

## 16.3.2   Audition

Otariids have a visible outer ear, a pinna (Fig. 16.1a, c), which clearly distinguishes them from the phocids (and grants them the moniker of 'eared' seals). The pinna is small and tightly rolled, which reduces both drag and heat loss in water. The bony anatomy of the ear is comparable to that of terrestrial carnivores, with a few exceptions (Nummela 2008; Repenning 1972). The middle ear ossicles (bones) are not enlarged, as they are in other diving mammals (Nummela 1995). Other modifications in comparison to terrestrial animals include the increased size of the round window of the cochlea in comparison to the oval window, a small tympanic membrane and small middle ear cavity (Repenning 1972). As in phocids (and in contrast to terrestrial carnivores), the auditory canal and middle ear cavity are lined with cavernous tissue that apparently engorges with blood to counteract pressure changes during diving (Odend'hal and Poulter 1966; Repenning 1972). Repenning (1972) concluded that the otariid ear is best suited for hearing by bone and tissue conduction under water. In air, hearing seems to be mediated by the normal mammalian auditory pathway via the ear canal and middle ear ossicles.

As with other sensory modalities, most of what is known about the auditory sense in otariids comes from studies of California sea lions. Several studies have described the hearing ability of California sea lions (Fig. 16.2); these include studies using behavioral methods with trained individuals in air and under water, as well as electrophysiological methods with anesthetized individuals in air. Terrestrial hearing (Fig. 16.2a) is most sensitive within the frequency range between 1 and 23 kHz; hearing ability declines below 2 kHz and above 16 kHz, with an upper-frequency hearing limit around 38 kHz (Kastak and Schusterman 1998; Moore and Schusterman 1987; Mulsow et al. 2011; Reichmuth et al. 2013; Reichmuth et al. 2017; Schusterman 1974). While the hearing profile is generally similar to that of other carnivores, the lowest hearing thresholds (~ 0 dB re 20µPa, measured at 12 kHz) are slightly above those of both phocids (as low as –12 dB re 20µPa; Sills et al. 2015) and terrestrial carnivores (as low as –24 dB re 20µPa; Fay 1988); this difference may be due to attenuation by cartilaginous structures of the pinna and auditory canal that keep water from penetrating into the ears. Audiograms that are markedly similar to those measured for California sea lions have been obtained for northern fur seals (Babushina et al. 1991; Moore and Schusterman 1987) and Steller sea lions (Mulsow and Reichmuth 2010). As these three species span both the size range and greatest evolutionary distance among living otariids, it is likely that all otariids share similar hearing abilities (Mulsow and Reichmuth 2010; Southall et al. 2019). The finding that otariids have retained sensitive hearing for airborne sounds

**Fig. 16.2** Amphibious hearing profiles for California sea lions tested (**a**) in air (Reichmuth et al. 2017) and (**b**) under water (Reichmuth and Southall 2012), highlighting similar hearing abilities and range of hearing in both media. Panel b further shows sensitivity to sounds above the 'functional' high-frequency hearing limit (dotted line); at high levels, sea lions can detect ultrasound above 40 kHz, and as high as 180 kHz (Cunningham and Reichmuth 2016). Figure drawing: R. Jones
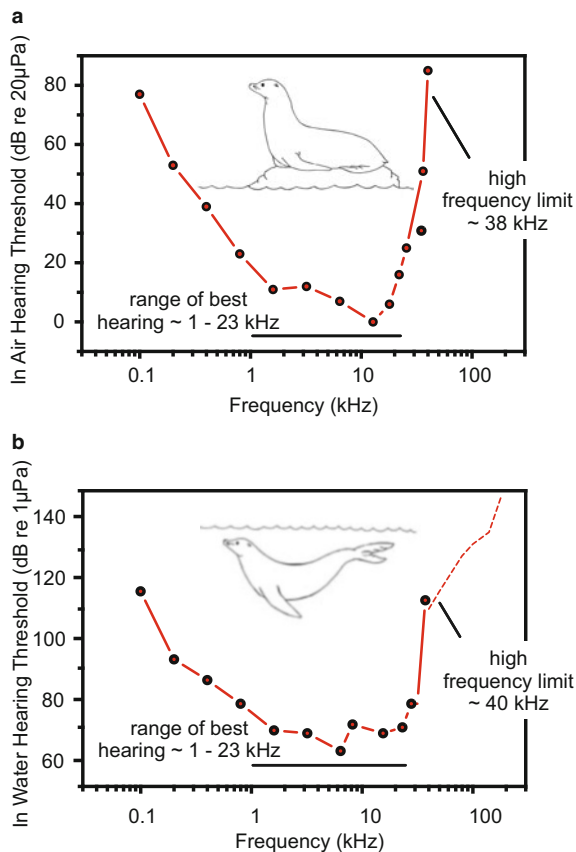


reflects that these species spend considerable amounts of time on land, and most of their social behavior occurs while on shore.

Underwater hearing in California sea lions (Fig. 16.2b) is similar to aerial hearing in terms of frequency sensitivity: audiograms obtained from trained individuals show best hearing between 1 and 23 kHz, with hearing rolling off gradually below 2 kHz and sharply above 30 kHz (Kastak and Schusterman 1998; Mulsow et al. 2012; Reichmuth et al. 2013; Reichmuth and Southall 2012; Schusterman et al. 1972; Southall et al. 2005). The lowest hearing thresholds in water (~ 62 dB re 1μPa, measured at 6 kHz) are less sensitive than those of both phocids (as low as 49 dB re 1μPa; Sills et al. 2015) and fully aquatic cetaceans (as low as 41 dB; Johnson 1967), suggesting that otariids are not quite as adapted for hearing under water. The 'functional' high-frequency limit of hearing in water is similar to that observed in air, around 40 kHz; unlike phocids, otariids do not show an extended range of acute high-frequency underwater hearing (see Reichmuth et al. 2013). Hemilä et al. (2006) proposed that high-frequency hearing in otariids is limited by cochlear constraints, as their hearing range in water is comparable to that of similar-sized carnivores in air.

Interestingly, and despite this constraint, sea lions can detect 'ultrasound' at frequencies extending from 40 to >180 kHz when underwater sounds are of high intensity (Fig. 16.2b; Cunningham and Reichmuth 2016). While otariids cannot discriminate between sound frequencies within this range (Schusterman and Moore 1978), they are still able to detect sounds above their true hearing range in water. Such sounds may include the echolocation clicks of killer whales, *Orcinus orca*, the output of various commercial echosounders, and 'ultrasonic' acoustic tags used to track the movements of fish (Cunningham et al. 2014).

Many other aspects of hearing in otariids have been studied, including temporal processing and sound localization. Perhaps not surprisingly, sea lions and other pinnipeds cannot resolve the temporal separation of sounds at rates as high as echolocating odontocete cetaceans can differentiate, and their temporal processing abilities are instead more similar to those of canids (Mulsow and Reichmuth 2007). The data available thus far suggest that northern fur seals can resolve the spatial origin of underwater sounds in the region of best hearing to within 8° of the source (Babushina and Poliakov 2004), close to the estimate by Gentry (1967) for California sea lions. In air, despite the absence of a true sound-ducting pinna, sound localization performance is even better, with an accuracy of < 5° in the horizontal plane (Holt et al. 2004, 2005; Moore 1975; Moore and Au 1975), comparable to the performance of cats, pigs, and rhesus macaques (5.7°, 4.6°, and 5.0°, respectively; Heffner and Heffner 1992).

A number of studies have examined the effects of noise on otariid hearing in air and under water. The ability of California sea lions and northern fur seals to detect simple and complex signals in the presence of masking noise has been reviewed elsewhere (Erbe et al. 2016; Reichmuth 2012). Studies concerning the temporary and permanent effects of noise exposure on hearing in sea lions have been thoroughly described by Finneran (2015) and Southall et al. (2019). Given high and fluctuating levels of noise in the coastal habitats used by otariids, such research has relevance to assessing risks from human-generated noise exposure, improving knowledge of auditory adaptations, and increasing understanding of how otariids operate in complex soundscapes.

Otariids can rely on their sense of hearing in air to detect threats and support long- and short-range social communication in noisy coastal rookeries (Charrier, Chap. 14). Their acute hearing abilities in water likely aid in alerting them to swimming movements and sounds generated by potential predators and prey, as fish emit sounds (Kasumyan 2008; Wilson et al. 2004) and some predators emit vocalizations and echolocation clicks. Otariids also produce some social sounds under water; for example, territorial male California sea lions bark under water when their territories are tidally submerged, and similar sounds can sometimes be detected at significant depths far offshore (Schusterman and Balliet 1969). In both terrestrial and aquatic environments, orientation and navigation are facilitated by a broad sense of the surrounding acoustic scene (Bregman 1990); this is especially true in the dark, three-dimensional underwater realm where distant acoustic cues may support a sense of space relative to the water surface (Schusterman et al. 2000).

## 16.4 Chemoreception

In general, the chemoreceptive senses, olfaction and gustation, are the least studied senses in otariids. Regarding olfaction, the external olfactory system and the olfactory bulb are reduced in California and Steller sea lions as well as in northern fur seals in comparison to terrestrial carnivores (Reep et al. 2006). However, Steller sea lions have maintained their olfactory receptor multigene family (Kishida et al. 2007). In line with this finding, Laska et al. (2008) successfully trained South African fur seals to discriminate between olfactory stimuli. The fur seals were able to discriminate between structurally similar chemical compounds, including related aliphatic odorants which differ in the length of their carbon chain (Laska et al. 2010) and between many of the presented enantiomers (Kim et al. 2013). This experimental evidence for sensitivity to airborne olfactory cues is entirely in line with observations of free-ranging otariids, many of which are described by Charrier (Chap. 15). Scent recognition is a critical component of individual recognition, including recognition of dependent pups by their mothers (Pitcher et al. 2011; Wierucka et al. 2018). Among other social contexts, olfactory cues have been shown in field observations and experiments to play a role in reproductive behavior; olfaction is used by adult males to detect the onset of estrous in breeding females, and territorial males emit strong odor cues (Gentry 1998). These data suggest an important role for scent cues in otariid behavior.

Regarding gustation, the apex of the tongue of California sea lions and northern fur seals is divided in two parts, and the two tips of the tongue are rounded (Kubota 1968; Sonntag 1923; Tuckerman 1890), the number of taste buds on the tongue is reduced, and the buds are modified in structure compared to terrestrial mammals. Nevertheless, the California sea lion (Friedl et al. 1990) and Steller sea lion (Kuznetzov 1990) can apparently perceive the primary tastes salty, sour, and bitter, except for sweet, albeit at a substantially higher concentration in comparison to humans. For example, a concentration of 3.6 parts per thousand (ppt) was needed to produce a sensation in one trained California sea lion (Friedl et al. 1990) while humans can perceive the same primary tastes at concentrations as low as 0.18 ppt (Pfaffmann et al. 1971). It remains unknown if the sense of taste is relevant to marine mammals when navigating in the ocean or when consuming fish under water; however, the apparent food preferences of captive individuals and aversion to substances hidden in food (C. Reichmuth, unpublished data) suggest that taste remains an important sense to otariids despite their adaptations for marine living.

## 16.5 Other Senses

Early research with California sea lions concentrated on putative echolocation abilities. However comprehensive experiments, summarized by Schusterman et al. (2000) and Cook et al. (Chap. 17), failed to demonstrate echolocation in sea lions. So

far, there have been no studies on additional possible sensory modalities, such as on magneto- or electroreception, other than those mentioned in the previous paragraphs of this chapter. Although not a sensory dimension *per se*, a recent investigation revealed the ability of a South African fur seal to discriminate time intervals lasting milliseconds to seconds, with precision (Heinrich et al. 2020). A well-developed sense of time might support the classical sensory systems when otariids are making foraging decisions or need to estimate travel duration or distance.

## 16.6 Conclusions

From this review of available studies concerning the sensory systems of otariids, we find substantial information about the anatomy and function of some of the sensory modalities, especially of vision and audition, whereas others, such as chemoreception, remain poorly studied. The model species among otariids is the California sea lion (*Zalophus californianus*; Fig. 16.1), and there is only limited information available about sensory biology for other sea lions and fur seals. For the future, new insights into the adaptations of the sensory systems could be obtained by intensifying comparative research on otariids with different evolutionary, ecological, and life history characteristics.

Despite the gaps, we have tried to link the current knowledge of sensory processes in otariids to aspects of their ecology and behavior. It is clear that otariid evolution has produced a range of remarkable adaptations. By studying the structure and function of these adaptations we can better understand the environmental cues that support amphibious behavior.

The links between structure, function, and behavior provided in this chapter are mostly preliminary, often speculative hypotheses. We still await the design of new experiments that will relate measures of perception to natural behavior and allow us to consider the most promising paths forward for research. In our view, further developing the sensory ecology approach—which combines sensory physiology and behavioral ecology —should reveal the types of information otariids can obtain from the environment, how they gather and use this information, the role that ecology plays in shaping sensory systems to best acquire and process information, and how sensory abilities influence observed behavior (Dusenbery 1992; Stevens 2013). In addition, continued research to better connect sensory acquisition with sensory processing, perception, and cognition in general will be informative (see Chap. 17 by Cook et al.).

Behavior and cognition are both supported and limited by the sensory world (or 'Umwelt') of an animal (Barett 2011). With this in mind, it may someday be possible to understand how sea lions and other otariids form a multi-modal representation of the external world (whether it be terrestrial or aquatic) through sensory integration. This is one of the key questions of sensory biology (Johnsen 2017) and is of particular interest to neuroscientists studying brain organization, development, and evolution (Ghazanfar et al. 2005). New tools may advance this goal, such as

using functional brain imaging to map the connections between different sensory regions and to visualize activated brain areas during multimodal stimulation. Research that enables us to access the perceptual worlds inhabited by amphibious marine mammals is of interest to sensory biologists and behavioral ecologists, but also for neurobiologists, as such studies provide insight into how otariid carnivores have adapted to a lifestyle spanning the shore and the sea.

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