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Sound Localization by Cetaceans

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Cetaceans (whales and dolphins) use acoustic cues to determine the locations and identities of environmental stimuli within their underwater habitats. Dolphins evolved unique auditory systems for spatially differentiating ultrasonic signals, whereas the larger baleen whales appear to have evolved different mechanisms for localizing lower frequency sound sources. Many of the cues that terrestrial mammals use to localize sounds in air are less well suited for localizing sounds underwater. Nevertheless, cetaceans can localize sounds as well as or better than most terrestrial mammals. Position-dependent spectral filtering likely plays an important role in sound localization by toothed whales, whereas phase differences between the ears may be important for baleen whales. However, it is exceedingly difficult to determine how filtering and phase differences contribute to spatial hearing by whales and dolphins because, in contrast to terrestrial mammals, the structures through which cetaceans receive sounds are completely internalized (and thus invisible). Computational models of cetacean auditory processing provide one viable approach to generating testable predictions about the mechanisms cetaceans use to localize and identify sound sources.

Ancestors of the order Cetacea began to inhabit aquatic environments about 50 million years ago (early Eocene) and the fossil record of the early Oligocene (around 17 million years later) shows evidence of divergence between the suborders Odontoceti (toothed whales) and Mysticeti (baleen whales). Today, there are at least 65 recognized species of odontocetes, and 11 known mysticetes (Ketten, 1992). All species that have been tested hear exceptionally well, and as a group, exhibit the broadest range of frequency sensitivity in the animal kingdom (Ketten, 2000). Odontocetes' maximum hearing sensitivities are comparable to humans, but shifted higher in frequency (Au, 1993). Dolphins have excellent spectral (Au & Moore, 1990), and temporal (Moore, Pawloski, & Dankiewicz, 1995) resolution, and their frequency discrimination abilities surpass those of most other vertebrates (Herman & Arbeit, 1972; Thompson & Herman, 1975).

Adaptation to an underwater environment was accompanied by an increased dependence on hearing relative to other sensory modalities. Early cetaceans show specialized adaptations for high frequency hearing (Ketten, 1992; Nummela et al., 2004), but it remains unclear what demands drove these adaptations. Regardless of the specific forces that led to auditory adaptations in cetaceans, it is

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clear that good sound localization abilities provide many advantages to both odontocetes and mysticetes. The usefulness of each localization cue will depend on the spectral and temporal characteristics of the sound being received. Hence, the cues mysticetes use to localize low frequency sounds produced by other whales may be quite different from the cues odontocetes use to identify echoes generated by their ultrasonic sounds.

Localization abilities have only been measured in a handful of cetaceans, mainly bottlenose dolphins (*Tursiops truncatus*). A clearer understanding of sound localization mechanisms in modern day cetaceans can elucidate the adaptive specializations that gradually enabled cetaceans to accurately localize sounds underwater. In fact, the need to localize sounds may have been the major selective pressure driving the evolution of hearing in all mammals (Heffner & Heffner, 1992; Masterson, Heffner, & Ravizza, 1969). Consequently, studies of cetacean spatial hearing may also provide insights into how terrestrial mammals perceive sounds.

Utilizing Spatial Information

Localizing Prey, Threats, and Conspecifics

By localizing and identifying acoustic events, cetaceans can potentially (1) track and capture prey (see Au, 1993), (2) locate and avoid obstacles (Clark & Ellison, 2004; Evans & Dreher, 1962; Kellogg & Kohler, 1952), (3) explore the features of objects in their environment (Herzing, 2004; Pack & Herman, 1995), (4) determine water depth (Mercado & Frazer, 1999; Tyack et al., 2004), (5) avoid humans and other possible predators (Richardson et al., 1995), (6) increase their ability to detect acoustic signals (Hirsh, 1948), and (7) track the positions of conspecifics (Frazer & Mercado, 2000; Lammers & Au, 2003; Miller, 2002). Although cetaceans may localize sounds during foraging, navigation, mating, and predator avoidance, the extent to which different species rely on these abilities remains unknown.

Dolphins' use of echolocation during foraging has been studied more extensively than other instances of sound localization by cetaceans (see Herzing, 1996, 2004), but even in this case few data are available. Foraging bottlenose dolphins use both active and passive localization strategies when searching for prey. Dolphins often echolocate only after having passively detected a target (Barros & Wells, 1998; Herzing, 1996). Searching generally involves head and body movements, which likely serve to increase spatial resolution, as they do in humans (Perrett & Noble, 1997; Wightman & Kistler, 1999). Different prey and environmental conditions elicit different searching strategies by dolphins, and dolphins even echolocate differentially depending on the species of nearby predators (Herzing, 2004).

Baleen whales can locate distant conspecifics that are vocalizing (Tyack & Whitehead, 1983; Watkins, 1981), will swim toward or away from sounds projected by an underwater speaker (Clark & Clark, 1980; Cummings & Thompson, 1971; Dalheim, 1990; Mobley, Herman, & Frankel, 1988), and often avoid boats that directly approach them (Watkins, 1986). Some whales avoid stationary industrial activities such as dredging, drilling, and the firing of air guns, or avoid military activities such as the use of sonar (Richardson et al., 1995). These and other findings are consistent with expectations that most cetaceans monitor the locations of sound sources within their environment, but provide only glimpses of the spatial hearing capabilities that they possess. Baleen whales are also believed to rely heavily on sound localization during mating. Male humpback whales (*Megaptera novaeangliae*) produce songs that may serve to attract females and repel competing males (Cerchio, Jacobsen, & Norris, 2001; Clapham, 2000; Tyack & Clark, 2000). Both functions require listening whales to simultaneously determine the spatial positions of multiple singers from long distances, because singing whales are usually alone (Tyack, 1981; Winn & Winn, 1978) and spaced several kilometers apart (Frankel et al., 1995). Humpback whales may also sing to actively generate echoes within their environment, and then use echoes from conspecifics to track their movements (Frazer & Mercado, 2000; Mercado & Frazer, 2001). Similarly, odontocetes may use echoes or vocalizations generated by conspecifics to track their movements (Au, 1996; Lammers & Au, 2003; Miller, 2002).

In addition to providing information about the origins of sounds, sound localization abilities also enable mammals to hear sounds that would otherwise be inaudible. Langmuir (1944, cited in Warren, 1999), reported that when an interfering noise was located at a different azimuth from an underwater sonar signal, the threshold at which human operators could detect that signal was 15 dB lower. This effect is called *masking level differences* (Green & Yost, 1975; Hirsh, 1948). The farther a masking noise source is azimuthally from a source producing a signal of interest, the larger the masking level difference and the lower the threshold for detection. In humans, this effect is especially strong for sounds below one kHz. Masking level differences have been observed in ferrets (Hine, Martin, & Moore, 1994), rabbits (Early et al., 2001), chinchillas (Guo & Burkard, 2003), guinea pigs (Caird, Palmer, & Rees, 1991), and even in birds (Dent, Larsen, & Dooling, 1997), so it seems likely that they also facilitate signal detection by cetaceans. If cetaceans also experience masking levels differences, then the reduction in threshold might be especially important for whales that make extensive use of low frequency sounds, and that may need to attend selectively to individual sound sequences within a chorus of vocalizing whales.

Using Echoes to Differentiate Objects

Although all cetaceans appear to have evolved unique systems for using sound, only odontocetes have definitively been shown to echolocate. The discrimination abilities of odontocete sonar rival any man-made sonar in shallow, high noise environments. For example, bottlenose dolphins can use ultrasonic clicks to detect, discriminate, and recognize objects based on acoustic parameters of their echoes (Au, 1993; Nachtigall, 1980). Furthermore, several studies suggest that bottlenose dolphins can perceive the spatial structure or shape of complex objects through sonar (Azzali, Manzini, & Buracchi, 1995; Harley, Putman, & Roitblat, 2003; Harley, Roitblat, & Nachtigall, 1996; Pack & Herman, 1995; Pack, Herman, & Hoffmann-Kuhnt, 2004; Pack et al., 2002). Herman and colleagues (1998) suggested that to perceive the spatial structure of a complex object using echoes, the dolphin would need to resolve a spatiotemporal array of echoes from the various object features, and integrate information from the echoes to engender a holistic three-dimensional representation. This suggests the dolphin sonar system is well designed for localizing spatial features.

The spectral and temporal characteristics of odontocete biosonar signals vary between species, and appear to be well adapted for localizing echoes in three-dimensional space. During echolocation, dolphins typically emit a series of *clicks*, with a sufficient inter-click interval to receive an echo before emitting a consecutive click. Each click consists of a broadband transient with peak frequencies between 40-140 kHz, durations as short as 40 µs, and peak-to-peak sound pressure levels often exceeding 220 dB re 1 µPa (Au, 1993). The concave shape of the skull, coupled with the focusing properties of the lipid melon, focus the signal forward in a tight beam, elevated about 5° above the rostrum, with a 3 dB beamwidth of approximately 10° in both the vertical and horizontal plane (Au, 1980). Consequently, targets in the forward position will be highly ensonified, enhancing target detection at greater ranges and increasing the signal-to-noise ratio relative to peripheral targets. The high frequency, short duration properties of clicks contribute to the dolphin's ability to resolve fine spatial details and can improve range resolution by limiting overlapping echoes from closely spaced objects. Higher frequencies allow for echoes from small targets, provided the wavelength of the incident signal is less than target's spatial extent (e.g., the wavelength is 1.09 cm at 140 kHz). Fine temporal resolution, demonstrated by an auditory critical interval of 264 µs (Moore et al., 1984), allows dolphins to resolve echoes occurring in close temporal proximity. Although range difference discrimination has been measured between targets highly separated in the horizontal plane (Murchison, 1980), true range resolution, with two sound sources in the same direction of acoustic propagation, has not been studied.

Researchers first investigated the ability of dolphins to localize sound sources in the horizontal and vertical planes through passive listening experiments. The smallest angle at which two sound sources are perceived as being discrete is the minimum audible angle (MAA). Renaud and Popper (1975) measured the MAA of a bottlenose dolphin using sinusoidal pulses and sonar-like clicks. The dolphin was required to station on a horizontal, acoustically "transparent" bite plate. A "buzzer" sound was emitted directly in front of the dolphin, followed by a test sound to the left or right of the buzzer. The dolphin then responded by swimming to a left or right paddle corresponding to the position of the test sound. The angle between the buzzer and the test sound was varied to measure the dolphin's MAA. For sinusoids, MAAs varied between 2° and 4° for both horizontal and vertical presentations. For click stimuli, the MAA was 0.9° in the horizontal and 0.7° in the vertical plane.

Branstetter et al. (2003) investigated a dolphin's ability to resolve angles between multiple targets in the horizontal plane through echolocation. The dolphin was required to echoically discriminate horizontal angular differences between two arrays of vertical, air-filled, PVC rods. A blindfolded dolphin positioned its head within a stationary, vertically oriented hoop, two radial meters from the stimuli, and then indicated whether an array with four rods (S+) was to the left or the right of an array with two rods (S-), by pressing a corresponding paddle. The angular separation between the rods within each array (θ_w) was maintained at 2° but the angular separation between the two arrays (θ_b) was varied to produce angular differences ($\Delta\theta = \theta_b - \theta_w$) ranging between 0.25° to 4°. A modified method of constant stimuli was used to test for angular discrimination ability, yielding a psychometric function having a 75% correct threshold of 1.6° (Figure 1). The results are consistent with the vertical and horizontal MAA measurements report by Renaud and Popper (1975), and with echoic angular discrimination sensitivities observed in bats (Simmons et al., 1983).

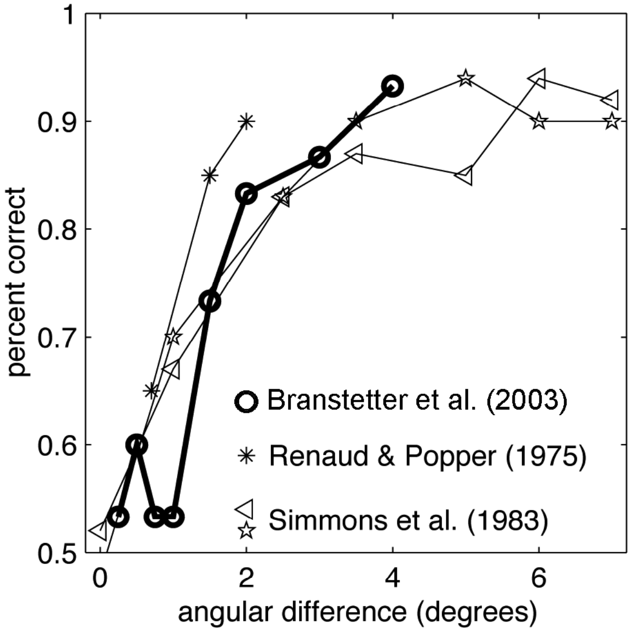

Figure 1. Psychometric functions comparing sound localization abilities between an echolocating dolphin (Branstetter et al., 2003), a passive listening dolphin (Renaud & Popper, 1975), and an echolocating bat (Simmons et al., 1983). Figure adapted from Branstetter et al., 2003, and reproduced with permission from *Bioacoustics.*

MAA measurement through passive listening may reflect the dolphin's ability to localize environmental sounds, but echolocation is a more complex process. During echolocation, dolphins have control over the amplitude, frequency, and number of clicks, as well as the interclick interval (Au, 1993). Thus, dolphins could dynamically optimize signals to improve spatial resolution. On the other hand, the ability to produce click trains that dynamically compensate for target range, target strength, and background noise (Au, 1993) could lead to taxing sound localization constraints by greatly increasing computational demands. Although the high frequency, short duration properties of the dolphin incident signal may aid in detecting small targets, these features cannot account for the dolphin's ability to localize multiple closely spaced objects. Neither the beamwidth of the sonar signal nor the beamwidth of the dolphin's receiving system (13.7° at a signal frequency of 120 kHz at the 3-dB bandwidth; Au, 1993; Au & Moore, 1984) are narrow enough to allow for the excellent angular discrimination capabilities observed during either echolocation or passive listening.

The auditory mechanisms that cetaceans use to determine the locations and identities of environmental stimuli remain unclear. Physiological and behavioral data indicate that cetaceans use a mix of both familiar and exotic sound localization strategies.

Cetacean Auditory Systems

Compared with other mammals, auditory processing in cetaceans is poorly understood. Few researchers have had the opportunity to perform detailed anatomical studies of any sensory system of cetaceans, and even fewer have been able to collect recordings from neurons in auditory pathways. Only a brief description of cetacean auditory systems will be given here (see also Au, 1993; Au, Popper, & Fay, 2000; Thomas, Moss, & Vater, 2004).

Peripheral Reception

Hearing involves converting mechanical energy into electrochemical signals that can be analyzed by the nervous system. Like terrestrial mammals, cetacean use their ears for hearing, but the functional components of cetacean ears are not as well defined. Cetaceans lack an external ear, and the functionality of cetaceans' "middle ear" is debated. The hearing organ of the inner ear is the cochlea, where spectral, temporal and amplitude features of the sound are transduced along the basilar membrane (BM).

The channels through which sound travels from the outside world to the inner ear in cetaceans are bewildering, and those used by baleen whales are entirely different from those used by toothed whales. Cetacean body tissue has similar sound transmission characteristics as seawater, so sounds received underwater could potentially approach the inner ears from any direction (Reysenbach de Haan, 1956). However, because the inner ears are embedded within highly porous bone containing pockets of air, they seem to be shielded from sounds conducted directly through the body. Behavioral studies of bottlenose dolphins indicate that sounds propagate to the inner ear differentially depending on both the direction from which the sound arrives (Au & Moore, 1984), and the frequency content of the sound (Schlundt, Carder, & Ridgway, 2004). For example, a dolphin was able to detect a 60 kHz sound broadcast directly in front of it at levels 20 dB lower than the same sounds generated 45° to the right or left of the dolphin's midline, or 35° above or below the midline (Au & Moore, 1984).

The functions of cetacean middle ears remain unclear. In terrestrial mammals, the ossicular chain of the middle ear serves as a pressure amplification device to overcome impedance mismatch between the air filled sound medium and the fluid filled cochlea. It is not at all clear that this occurs in toothed whales. In fact, physiological experiments showed minimal differences in cochlear responses to sound after most of the middle ear of a dolphin was disconnected from the inner ear (McCormick et al., 1970). However, recent bone models of the odontocete middle ear suggest that the tympano-periotic complex may function as a double lever amplification mechanism responsible for enhancing hearing sensitivity (Hemila, Nummela, & Reuter, 1999, 2001). The bones surrounding the inner ear (tympano-periotic) are dense and massive relative to those of terrestrial mammals, increasing the acoustical contrast between these and other bones (Lees, Hanson, & Page, 1996). In odontocetes, the tympano-periotic is encased in a matrix of lipids, vascularization, ligaments, and air sinuses collectively called the albuminous foam. Because of the density difference between the foam and the tympano-periotic, the complex has been hypothesized to function as an acoustic isolator. The middle ear of baleen whales has a structure that is more similar to what is seen in terrestrial mammals, and therefore ossicular motion seems more likely to be involved in generating round window vibrations. However, the strong connections between the bullae and skull in larger whales suggest that bone conduction of sound may also play an important role. Thus, two possible functions for the middle ear in cetaceans are translational bone conduction of sound vibrations to the cochlea, and more conventional transfer of sound vibrations via ossicular motion.

Cetacean inner ears, where the cochlea is found, are located inside the periotic bullae, bony structures located near the base of the skull (see Ketten, 2000). Due to differential thickness and stiffness of the BM, different locations along the BM resonate at different frequencies, creating a tonotopic map ordered from lowest at the apex to highest at the base (Ketten, 1992). Although most researchers assume that BM deformations are directly sensed by the organ of Corti, anatomical data from dolphins and bats indicate that the BM might alternatively serve to protect the organ of Corti from damage (Braun, 1994). Toothed whales have evolved rigid ligaments and an ossified lamina (rigid bone shelf directly connected to the BM) that stiffen the BM, enhancing membrane responses to ultrasonic frequencies (Braun, 1994; Ketten, 2000; Wever et al., 1971a, 1971b). Baleen whales have instead evolved BMs that are better suited for responding to infrasonic sounds.

Although the basic organization of the cetacean inner ear is comparable to other mammalian inner ears, there are specialized features that may facilitate underwater sound localization. In all cetaceans, the inner ears are positioned outside of the skull (Figure 2A,B). In toothed whales, the bones enclosing the inner ear appear to be acoustically isolated from the skull, whereas in baleen whales, they are tightly connected to the skull (Ketten, 1992). Ketten (2000, p. 68) suggested that, “the relatively broad spread between the ears of cetaceans because of the extracranial relocation of the tympano-periotic complex may be the crucial adaptation that explains their ability to accurately localize underwater sounds.”

Interestingly, in humans the threshold of underwater hearing is determined by bone conduction through the skull (Norman, Phelps, & Wightman, 1971). Ancestral cetaceans might have been similarly constrained upon reentering an aquatic environment, and thus changes in skull features are likely to have had important implications for how they received sounds. Cetacean skulls show evidence of *telescoping*, involving elongation of the jawbones, and extensive modifications to the cranial space (Figure 2C; Ketten, 1992). Cetacean skulls and associated specialized fatty regions (e.g., the dolphin’s melon) may act to channel sound into and out of the cetacean head (Beamish, 1979; Evans, Sutherland, & Beil, 1964; Ketten, 1994; Norris, 1968; Norris & Harvey, 1974). In addition to telescoping, skulls of odontocetes appear to display pronounced asymmetry (Ketten, 2000), consistent with other auditory predators such as the boreal owl (Norgberg, 1978). Many of the anatomical differences between mysticete and odontocete heads and skulls are undoubtedly related to differences in their habitats and foraging strategies, but they may also reflect their relative dependence on low versus high frequency sounds, respectively, because skull properties will affect how different frequencies propagate into a cetacean’s head. Odontocetes, in particular, are believed to receive high frequency sounds through specialized bones and fat channels associated with their lower jawbones (Ketten, 2000; Norris, 1968), but to receive lower frequency sounds (below 30 kHz) through bone-free fat channels just below their eyes, and posterior to their lower jawbones (Brill, Moore, & Helweg, 2001; Ketten, 1994; McCormick et al., 1970; Popov & Supin, 1990). Figure 2B shows areas of a dolphin's head through which sounds are known to propagate well, and which may correspond to the borders of a dolphin's "outer ears."

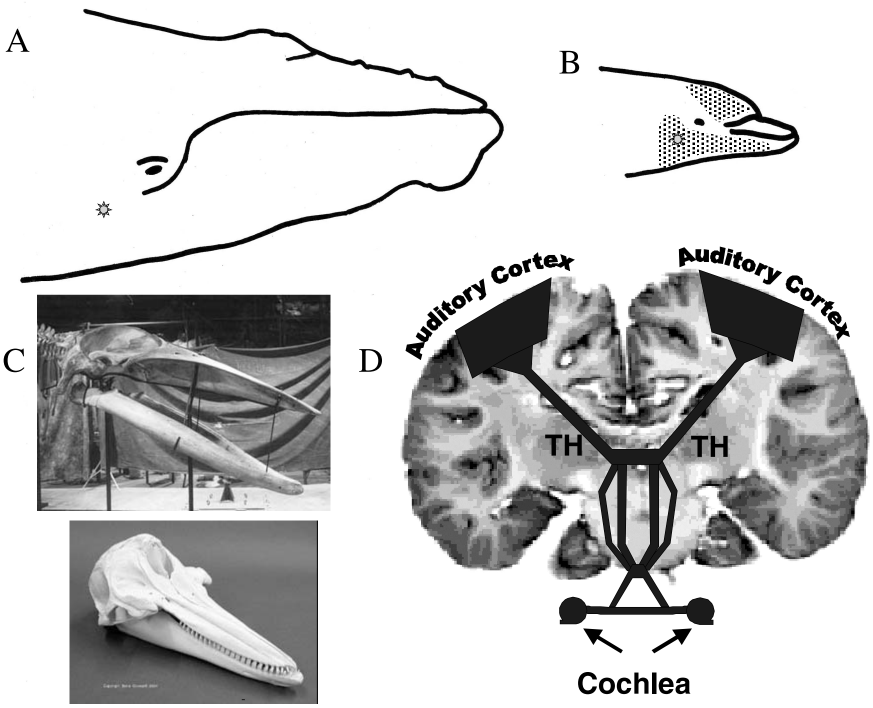

Figure 2. Peripheral reception and auditory pathways in cetaceans. The approximate position of the inner ear (denoted by ✱) is similar in humpback whales (A) and bottlenose dolphins (B), despite large differences in the shapes of their skulls (C; reproduced with permission from Golden Chariot Productions, Canada, and Bone Clones, U.S.A.). Shaded regions in (B) summarize known regions of acoustic sensitivity as reported by Bullock et al. (1968), McCormick et al., 1970, Mohl et al., 1999, and Brill et al., 2001. (D) Schematic of auditory pathways in the dolphin brain. Information from each cochlea interacts at multiple stages before reaching cortical networks; TH = thalamus (reproduced with permission from Wiley & Sons).

Neural Processing of Auditory Information

Sound localization by mammals is constrained by the received signals, as well as by the sensitivity of sensory receptors, but ultimately the ability to localize a sound source is determined by neural circuitry. The vertebrate cochlea is tonotopically organized, and thus does not contain a map of auditory space. Creation of such maps is achieved through complex neural computations. The basic auditory pathways in cetacean subcortical regions follow the general mammalian pattern (Oelschlager & Oelschlager, 2002). Receptor cells in the organ of Corti transmit auditory information to the cochlear nucleus (CN) via auditory nerve fibers. Cells within the CN project to the superior olivary complex (SOC, the main site of binaural convergence), which in turn projects to the inferior colliculus (IC). The IC projects to the thalamus, which projects to the auditory cortex (Figure 2D). Information flow is bidirectional, so cortical neurons can influence thalamic activity, and thalamic neurons can influence IC activity. Auditory information is processed in parallel neural pathways specialized for extracting particular aspects of acoustic events, with extensive interactions between pathways.

Auditory cortex in mammals can be subdivided into several *fields* with differential sensitivities to particular acoustic cues (Merzenich & Schreiner, 1992). Cortical fields are defined based on distinguishing features of their constituent neurons and the interconnections between them, as well as on characteristic stimulus evoked responses. Although the organization of auditory cortical fields is species-specific (reviewed by Aitkin, 1990; Suga, 2004), all mammals show a core auditory field (primary auditory cortex) that is tonotopically organized (Merzenich & Schreiner, 1992)—higher frequency representation areas usually are the largest. In most mammals, secondary auditory fields surround primary auditory cortex. Advanced species typically have more secondary fields; primates have 6-8.

Auditory cortical neurons often respond selectively to complex combinations of acoustic cues that can provide information about the location and movement of sound sources. Combination sensitive neurons are most prevalent in hearing-specialized mammals, such as bats (see Suga, 2004; Suga & Ma, 2003), but are also observed in nonspecialized mammals (Orduna, Mercado, Gluck, & Merzenich, 2001). In mustached bats, maps of combination sensitive neurons are topographically organized, with each field representing a particular cue continuum. Although the basic structural organization within and across auditory cortical fields is species-typical, there are substantial idiosyncratic differences between individuals. Cortical fields in both hemispheres generally respond to signals received at both ears, but most neurons in a particular hemisphere respond best to sounds from contralateral space.

A prominent feature of most components of auditory circuits in cetaceans is that they are much larger and contain more neurons than in terrestrial mammals (Oelschlager & Oelschlager, 2002). The density of receptor cells in the humpback whale cochlea is 2,600 cells/mm compared to a human density of 1,000 cells/mm. Such high densities of auditory receptor cells are very rare in mammals, including bats. Primary afferents are also much more numerous in cetaceans than in terrestrial mammals. The dolphin auditory nerve has many more fibers than the human nerve, and the diameters of fibers are about twice as large as in humans (Bullock & Gurevich, 1979; Ridgway, 2000). Humpbacks have about 156,000 primary afferents, compared to around 31,000 in humans (Ketten, 1997), and humpbacks have a higher density of myelinated fibers within IC than any other cetacean examined, including bottlenose dolphins (Glezer et al., 2004). The IC in bottlenose dolphins is about 40 times larger than in humans, and that of a fin whale is twice as large as a human’s (Glezer et al., 2004). Auditory centers within the dolphin thalamus are about 7 times larger than in humans (Bullock & Gurevich, 1979). These differences do not reflect overall differences in brain size, because bottlenose dolphins and humans have similarly sized brains (Marino, 1998). The specific benefits that enlarged subcortical areas provide remain speculative, but there is little doubt that these adaptations provide cetaceans with the means for sophisticated auditory processing.

Although enlarged subcortical pathways have impressed hearing researchers, it is the massive amounts of cortical tissue within cetacean brains that have most intrigued scientists (reviewed by Marino, 2004). In most terrestrial mammals, auditory cortex is located in temporal regions, but in bottlenose dolphins, it appears to have migrated to a more dorsal position (Bullock & Gurevich, 1979; Bullock & Ridgway, 1972; see Figure 2D). Primary auditory cortex seems to be located on the vertex of each hemisphere, with secondary auditory cortex in a more lateral position. Some evidence suggests that dolphins may have more than one primary auditory cortical area (Bullock & Gurevich, 1979; Bullock & Ridgway, 1972). For example, auditory centers in the thalamus project both to dorsal and temporal regions of cortex, and both of these cortical regions project to subcortical auditory pathways, including the thalamus, SOC, and CN (Bullock & Gurevich, 1979). Auditory cortex in dolphins appears to be larger than other sensory cortices, and thalamo-cortical projections indicate that one third of dolphin cortex may be occupied by auditory-dominant fields (Merzenich & Schreiner, 1992). Much of dolphin auditory cortex appears to be sensitive to ultrasonic frequencies (50-100 kHz; Supin et al., 1978a, as cited in Bullock & Gurevich, 1979), and the expansive dolphin cortex may thus be a result of the sophisticated auditory processing needed to echolocate underwater (Langworthy, 1932; Ridgway, 1990; Wood & Evans, 1980). The large size of the mysticete brain indicates that it has also undergone extensive adaptation, but the organization and physiology of auditory cortex in baleen whales is unknown.

Neural processing for sound localization begins at the subcortical level, and much of the effort to describe these computations has focused on these regions. Neurons in the CN might extract spectral cues used for sound localization (Yu & Young, 2000), and neurons in the SOC are critical for processing binaural cues (Irvine, 1992). In birds, SOC neurons correlate binaural cues related to source position by receiving phase-locked spikes from each CN, detecting coincident spikes, and then producing a graded spike train according to the degree of coincidence (see Konishi, 2003). Neurons in the IC of the barn owl respond only to sounds in a particular position in auditory space, creating an auditory space map (Knudsen, 2002; Knudsen & Konishi, 1978). SOC and IC also subserve binaural processing in mammals, but may involve computations different from those seen in birds (Palmer, 2004).

Auditory cortical lesions severely disrupt sound localization abilities in a wide range of mammals (Heffner & Heffner, 1990; Jenkins & Merzenich, 1984; Kavanagh & Kelly, 1987), suggesting that cortex is essential for normal spatial hearing. There is little evidence of topographical representation of auditory space at the cortical level, however. Instead, auditory cortical processing of spatial position may involve direction-dependent changes in response rates (Ahissar et al., 1992; Fitzpatrick et al., 1997; Middlebrooks et al., 1998; Recanzone et al., 2000), or changes in response latencies (Brugge, Reale, & Hind, 1996; Brugge et al., 2001; Furukawa & Middlebrooks, 2002; Reale, Jenison, & Brugge, 2003).

Experience can shape sensory systems, and many of the idiosyncratic features of auditory cortical organization are thought to arise during sensitive periods of development (Merzenich & Schreiner, 1992). Experience-dependent changes in neural circuits mediating spatial hearing have been studied in bats (Jen, Chen, & Sun, 1998), barn owls (Knudsen, 1998, 1999), and ferrets (King et al., 1988; Mrsic-Flogel et al., 2001). Neuronal sensitivities in the IC, thalamus, and cortex can become reorganized by auditory experience (see Suga & Ma, 2003; Weinberger, 2004). It is also possible to radically change an adult mammal's cortical sensitivities to tones, and even to complex combinations of acoustic features, in a matter of weeks (Kilgard & Merzenich, 1998; Mercado et al., 2001). The adaptive capability of the human auditory localization system was shown in experiments where subjects wore ear molds that modified their pinnae shape (Hofman, Van Riswick, & Van Opstal, 1998; Wightman & Kistler, 1998). Initially these molds disrupted sound localization abilities, but after six weeks of experience localization returned to normal, indicating that spatial processing was recalibrated to accommodate the novel external ears. Compressing a person's visual field also leads to rapid recalibration of sound localization systems (Zwiers, Van Opstal, & Paige, 2003), as does explicit training with localization cues (Javer & Schwarz, 1995; Shinn-Cunningham, Durlach, & Held, 1998a, 1998b; Stouffer, 1975; Wright & Fitzgerald, 2001). Thus, sound localization circuits are dynamically shaped by experience throughout an animal's life (King, Schnupp, & Doubell, 2001), and experience may play a similarly important role in the development and maintenance of sound localization abilities in cetaceans.

Resolving Auditory Space

Sound Localization Mechanisms

Sound source location can be described in terms of azimuth (the angular distance along the horizon), elevation (angular height), and distance. With sufficient time, animals can assess a sound's origin by tracking changes in its position or by scanning the environment with head movements. Over very short periods, however, sound localization requires calculations that are independent of changes in the relative positions of the source and receiver. Evolution has shaped elaborate anatomical structures as well as sophisticated physiological signal processing mechanisms to facilitate such calculations.

Mammals use two general classes of acoustic cues to localize sources: binaural and monaural (see Blauert, 1997; Warren, 1999). Binaural cues include interaural time differences (ITDs) and interaural intensity differences (IIDs). Both ITDs and IIDs are used for localizing sounds in the horizontal plane and, together, are known as the duplex theory of sound localization (Strutt & Rayleigh, 1907). ITDs produced by sound sources off the midsagittal plane depend on the speed of sound and the distance between the auditory receivers; so bigger heads mean larger ITDs. At higher frequencies, ITDs can be determined from envelope characteristics, whereas for lower frequency sinusoids (pure tones) they can be determined from interaural phase differences (IPDs, Stevens & Newman, 1936). Because the wavelengths of sinusoids become progressively smaller as frequency increases, the ability to detect IPDs degrades at higher frequencies. The frequency (f) at which IPDs become physically ambiguous (i.e., several cycles of the sound "fit" between the ears) can be calculated from

$$f = 1 / [6(a/c)\sin(t)]$$

where *a* is the inter-ear distance, *c* is the speed of sound, and *t* is the angle of incidence—this frequency increases as a source approaches the midline (Heffner & Heffner, 1992). The ambiguity of IPD cues at frequencies above *f* can be resolved through neural cross-correlation for sounds that contain multiple frequencies (Konishi, 2003). Spatial information extracted from ITDs related to transient cues such as sound onsets or offsets tends to be more reliable than information obtained from IPDs.

When a sound source is off the median plane, the ears are at different distances R_1 and R_2, from the sound source, resulting in an intensity difference between them equal to

$$\mathrm{IID} = 20[\log(R_1/R_2)]$$

This type of IID results from differences in the distance from each ear to the sound source; consequently, bigger heads mean larger IIDs. The head also reflects sound, casting a significant sound shadow that will result in IIDs when the sound source lies off the median plane. Surprisingly, some mammals with big heads (large IIDs) such as pigs, horses, and cattle seem to have little or no ability to localize sounds using IIDs (Heffner, 1997; Heffner & Heffner, 1992). Lower frequencies produce less salient IIDs, since they tend to bend around the head. Exploiting high frequency IIDs may have been a governing factor selecting for high frequency hearing in the suborder Odontoceti.

Cues such as ITDs and IIDs are useful for localizing sounds in air because the physical structure of the head strongly constrains how sounds reach the ear. The situation differs greatly for aquatic mammals. Underwater sound propagation can profoundly affect the nature of the acoustic stimulus, constraining how useful certain cues will be for deriving spatial information. In particular, the paths through which sounds travel to cetacean ears, both through the ocean and through the head, appear to be highly frequency-dependent (Aroyan, 2001; Supin & Popov, 1993). Thus, the localizability of sounds that are behaviorally relevant to cetaceans is strongly determined by their spectral content. Spectral cues may mediate odontocetes' localization and identification of targets ensonified with ultrasonic clicks, as well as the ability of mysticetes to estimate their distance from other vocalizing whales.

Direction-dependent Spectral Sensitivity

Whereas IIDs and ITDs provide information about the azimuthal position of a source, these cues typically provide no information about source elevation or distance (except in the case of animals with asymmetric ears, like barn owls). In addition, IIDs and ITDs cannot explain a listener's ability to localize sound monaurally (Butler, Humanski, & Musicant, 1990). For terrestrial animals, this type of localization is due to the spectral filtering properties of the outer ear (and to a lesser degree, the head and torso), which behaves as a position-dependent spectral filter. This direction dependent transfer function is known as the head related transfer function (HRTF). If a receiver has knowledge of the sound source spectrum, then any spectral changes in the received sound, other than those attributable to the effects of environmental propagation, will be due to the HRTF. Thus, the position of a sound source can be determined even for monaural listening. Let $f(t)$ and $h(t)$ represent the source signal and the HRTF in the time domain, respectively. Then $F(S)$ and $H(S)$ are their frequency domain Fourier transformations. The received signal $G(S)$ is calculated by

$$G(S) = F(S) * H(S)$$

If the source signal $F(S)$ is species-typical or is known from prior experience, and $G(S)$ is known because it is received, then the HRTF $H(S)$ can be calculated by

$$H(S) = G(S) / F(S)$$

In this formula, $H(S)$ serves as a direct indicator of sound source position, because HRTFs are position-dependent. If $F(S)$ is not familiar to the receiver (i.e., it is a novel sound), then spectrally based localization of the sound requires comparisons between the ears.

Auditory predators (e.g., Chiroptera) often display elaborately convoluted pinnae or asymmetry in external auditory apparatus (e.g., barn owls). Statistical models from two independent human studies suggests HRTF-derived cues are more salient above 5 kHz (Kistler & Wightman, 1992; Middlebrooks & Green, 1992), and when sound sources are broadband. HRTFs from bats (Aytekin et al., 2004) and owls (Keller, Hartung, & Takahashi, 1998) indicate that such cues are increasingly prevalent at ultrasonic frequencies. Researchers hypothesize that broadband sources allow level information from independent peripheral filters to be compared across frequency channels; a direct correlation between bandwidth and sound localization accuracy supports this hypothesis (Wightman & Kistler, 1995). Although most mammals can use both IIDs and ITDs to localize sources, it is less clear to what extent mammals other than humans rely on spectral cues derived from HRTFs.

Echoes generated from odontocete sonar, which are both high frequency and broadband, appear to be ideal for head related spectral filtering. Because HRTF-derived cues work best for high frequency signals, the need to use such cues can act as a selective pressure for the evolution of high frequency hearing (Heffner & Heffner, 1992). When the terrestrial ancestors of cetaceans first began to reenter the oceans, localizing sound sources using HRTF-derived cues would have been problematic because spectral filtering relies on impedance differences between the pinna and air. In an aquatic medium, the impedance difference is negligible. Once the external ear became useless, natural selection favored individuals with increasingly smaller pinna to provide a more streamlined shape to the head, thereby facilitating locomotion. Additionally, immersing a terrestrial mammal in water generally raises its hearing thresholds, so the ancestors of cetaceans likely faced situations where acoustic cues for localization were only detectable to one ear (Nummela et al., 2004). Individuals that could localize sounds using monaural, HRTF-derived cues would thus have a selective advantage. Because the density of water is similar to that of marine mammal tissue (Norris & Harvey, 1974; Reysenbach de Haan, 1956), a spectral filtering mechanism in cetaceans comparable to the pinna would require sound to reflect off internal anatomical structures, or to diffract through structures of differing densities. The particular anatomical structures that could serve as spectral filters for cetaceans remain speculative; however, as noted earlier, the jawbones and the multiple lipid channels along the lower jaw may be good candidates for a dolphin pinna analog (Aroyan, 2001; Ketten, 2000).

Despite the apparent limitations that the aquatic environment initially imposed upon the terrestrial ear of ancestral cetaceans, the fact that sound travels more efficiently in water than most other forms of energy provided a selective advantage to individuals that could exploit acoustic information. In particular, because spectral cues provide information about source distance, elevation, and azimuth, whereas IIDs and ITDs generally only provide information about azimuth, it is likely that cetaceans developed unique specializations to overcome limitations of their terrestrially adapted localization mechanisms. Converging evidence from anatomical (Ketten, 2000), physiological (Supin & Popov, 1993), behavioral (Brill, Moore, & Helweg, 2001) and computer modeling studies (Aroyan, 2001), suggest that modern odontocetes have well developed HRTFs that may play a significant role in their sound localization abilities.

Supin and Popov (1993) used the auditory nerve response (ANR) to investigate direction-dependent spectral sensitivity in an Amazon river dolphin (*Inia geoffrensis*). The ANR is the short latency, first wave of the auditory brain-stem-evoked response (ABR). Supin and Popov measured spectral sensitivity for several frequencies generated from different azimuthal positions. Their results indicated that direction-dependent spectral sensitivity was greater for higher frequencies (above 30 kHz). In addition, each angular position produced a unique pattern of spectral sensitivity indicative of an HRTF. Mohl et al. (1999) suggested that position-dependent variability in ABR strength and latency was consistent with the presence of a shaded receiving transducer, in which inputs are weighted according to the direction of arrival (again indicating an HRTF). Brill et al. (2001) measured a bottlenose dolphin's behavioral auditory sensitivity for 10, 30, 60 and 90 kHz tones. Rather than presenting the tones from an underwater speaker, a small transducer (called a *jawphone*) was placed at 41 positions on the dolphin's head. Thresholds for each frequency at each position were then individually estimated. The results indicated an asymmetric pattern of spectral sensitivity across the head, consistent with the presence of an HRTF.

Aroyan (2001) developed a three-dimensional model of sound propagation based on tissue density and velocity profiles measured from the head of a deceased common dolphin (*Delphinus delphis*). Simulation results revealed receptivity patterns that differed between the ears for different elevation and azimuth locations. These differences were apparent across frequencies and were asymmetric. The results not only indicated that the receptivity pattern within the dolphin's head was complex, but also provided evidence that the jawbones and the fat channels along the lower jaw focus sound toward the tympano-periotic complexes, where the inner ears are located. Thus, the lower jaw and associated fat channels could function as the analog of a terrestrial pinna, focusing sound and functioning as a position-dependent spectral filter.

HRTFs may play a significant and possibly dominant role in echolocation by dolphins. Using a simple two-receiver model, an echolocating dolphin's angular discrimination threshold of 1.6° corresponds to an ITD of 2.6 μs (Branstetter, Mevissen, Herman, Pack, & Roberts, 2003). The smallest reported ITD threshold for a bottlenose dolphin is 7 µs, for click stimuli having a peak frequency of 30 kHz (Moore et al., 1995). For click stimuli with peak frequencies between 60-90 kHz, ITD thresholds increased to between 17-18 µs. The ITD threshold required to support the level of angular discrimination observed by Branstetter et al. is thus several times smaller than the values reported by Moore et al. Additionally, Moore et al. calculated that an ITD necessary for a dolphin to achieve an MAA of 1° was 1.3 µs, again a value several times smaller than was found. There are at least two explanations for the mismatch between empirical and mathematical ITD estimates. First, the geometric models used for calculating the minimal ITDs did not take into account reflective or refractive properties of the dolphin's head, such as those produced by the skull or the lipid channels in the lower jaw. Although these factors possibly increase ITDs, it is unlikely that they would increase by the amount needed to match the ITDs measured by Moore et al. Second, the dolphin may have used IIDs, or binaural and monaural spectral cues, rather than ITDs to make angular discriminations. IIDs are more salient at higher frequencies for terrestrial mammals and also for dolphins (Supin & Popov, 1993). The high degree of sound shadowing produced by the dolphin head (> 20 dB; Supin & Popov, 1993) and the high level of IID sensitivity (< 1dB) measured by Moore et al. suggest IIDs can play a significant and possibly dominant role in sound source localization for fine horizontal angular discrimination.

Although IIDs may be used for horizontal source localization, they are insufficient for localization in the vertical plane. Indeed, if the observed vertical MAA of 0.7° (Renaud & Popper, 1975) is accurate, HRTFs seem the most plausible explanation because simple time and intensity differences should not exist for sound sources along the mid-sagittal plane. Sound sources in the ocean can occur with high probability in almost any spatial position relative to a dolphin. Possessing a sound localization mechanism not restricted to only interaural differences would clearly provide a selective advantage to an individual cetacean.

Range-dependent Spectral Filtering

The exact location of a sound source often can be ambiguous, and in such cases, it may be sufficient to simply determine its approximate location. Acoustic features such as intensity can provide clues about the location of a sound source if the sound is produced at a predictable level - louder usually means the source is closer, and quieter means it is farther. Intensity does not always provide reliable distance information, however, especially when the sounds contain high frequencies or have propagated over long distances. In shallow water environments, such as those frequented by humpback whales and bottlenose dolphins, intensity is only a reliable indicator of range at relatively short distances from a source. Birds that live in dense forests face a similar problem (because vegetation can distort intensity levels), but have overcome these limitations through a process called ranging.

Ranging involves estimating the distance to a source by assessing signal degradation using acoustic cues like frequency-dependent attenuation and reverberation (i.e., environmental echoes) that are independent of both the received level and the source level (Naguib & Wiley, 2001; Richards, 1981). This process requires knowledge of both the environmental conditions (Naguib, 1996), and the undistorted source signals. Birds use such knowledge to compensate for changes in environmental conditions, enabling them to maintain localization performance (Naguib, 1996). Similarly, bats modify their echolocation signals based on environmental constraints (Barclay, Fullard, & Jacobs, 1999; Kalko & Schnitzler, 1993; Obrist, 1995; Wund, 2004), enabling them to actively range targets in a wide variety of conditions.

Humans can detect changes of 5-6% in the distance of a sound source (Stybel & Perrott, 1984), an ability that improves with practice (Little, Mershon, & Cox, 1992; Mershon & King, 1975). Humans can also rapidly calibrate their sound localization estimates to eliminate the influence of echoes within a familiar room (Bronkhorst & Houtgast, 1999; Plenge, 1974). More generally, when *pseudophones* are attached to the ears of adult humans to modify their effective interaural distances (Held, 1955), or HRTFs (Hofman et al., 1998; Wightman & Kistler, 1998), humans usually can adapt to these abnormal cues, indicating that mammalian brains have a great hidden capacity to adjust the neural computations used to localize sound sources. This sort of computational flexibility is necessary for cetaceans and other mammals to be able to take environmental propagation features into account when using spectral cues to estimate the distance that a sound has traveled.

Ranging of sound sources based on signal degradation has yet to be demonstrated in any cetacean. However, simulations of sound propagation in shallow water environments where humpback whales sing suggest that range-dependent spectral degradation of humpback whale songs does occur (Mercado & Frazer, 1999). Sound propagation through the ocean can be simulated as signal transmission through a set of linear, spatiotemporal-varying filters. The effect of propagation on any signal, for every source-receiver configuration, can then be described using a set of filter parameters (known as Green's functions). It is impractical to directly measure Green's functions in real-world environments, but reasonable approximations to these functions can be derived mathematically. Using Green's functions derived for a prototypical humpback whale environment, Mercado and Frazer showed that the ocean channel acts as filter that selectively attenuates specific frequencies within humpback whale songs as a function of distance. Thus, if listening humpback whales have knowledge about the properties of the sounds produced by other whales (as any singing whale would since humpback whales copy the songs of their neighbors; Guinee, Chu, & Dorsey, 1983; Mercado, Herman, & Pack, 2005; Payne & Payne, 1985), then they should be able to estimate the distance those sounds have traveled based on the spectral content of the received signal.

Baleen whales produce loud, low frequency sounds (including infrasonic sounds) that can travel many kilometers in the ocean, and that may be used for long distance communication (Clark & Ellison, 2004; Payne & Webb, 1971; Tyack, 1998). To communicate effectively with such sounds, baleen whales must be able to determine how far a sound they hear has traveled. No mechanisms have been proposed to explain how baleen whales extract this information. Because the speed of sound in seawater is five times that in air, low frequency sounds have extremely long wavelengths (e.g., a 15 Hz sound would have a wavelength of ~100 m). Such long wavelengths would seem to preclude the possibility that either IIDs or monaural cues could play a significant role in sound localization by baleen whales. Thus, the only remaining conventional localization cues are IPDs. It is not known whether large whales rely on IPDs to localize low-frequency sound sources, but if so, then their auditory systems must be exquisitely sensitive to very small pressure gradients. Experimental playback techniques like those used to study ranging by birds may clarify the extent to which humpback whales and other cetaceans make use of environmentally-generated cues when assessing their distance from sound sources.

It is noteworthy that cetaceans are one of the few mammals that can precisely imitate arbitrary sounds (Herman, 2002; Lilly, 1965; Reiss & McCowan, 1993; Richards, Wolz, & Herman, 1984; Sigurdson, 1993). Most explanations of the evolution of vocal mimicry in cetaceans have focused on either sexual selection in the case of baleen whales, or on adaptations for individual and group recognition in toothed whales (Janik & Slater, 1997). Ranging cues are only useful to the extent that the receiver has access to information about the environment and source. Familiarity with time-varying features of the source signal are critical, as evidenced by the fact that humans can accurately judge the distance of normal speech, but are unable to do so when that same speech is time-reversed (McGregor, Horn, & Todd, 1985). Morton (1982) suggested that to accurately judge the distance a sound has traveled, an animal must have the ability to produce that sound. Morton (1996; 1998) further hypothesized that constraints on ranging abilities drove the evolution of song learning in birds. This proposal may also account for the existence of vocal mimicry abilities in both odontocetes and mysticetes. Specifically, vocal learning may have evolved in cetaceans because this enabled them to range sound sources more accurately.

Computational Models of Cetacean Hearing

Behavioral and anatomical data indicate that dolphins, and possibly other cetaceans, may localize sounds based on cues derived from HRTFs. This possibility has never been experimentally investigated, and it would be very difficult to do so, because most studies of HRTF-related cues in terrestrial mammals (including humans) involve either isolating the ears from such cues (by using headphones), or modifying the cues by manipulating the pinnae. Neither of these strategies is well suited for studying localization abilities in dolphins (but see Brill, Moore, & Dankiewicz, 2001; Brill, Sevenich, Sullivan, Sustman, & Witt, 1988). Extensive efforts have been made to develop computational models of mammalian hearing systems, and techniques for modeling auditory processes are rapidly advancing (Colburn, 1996; Hawkins et al., 1996). Computational models of HRTF-based sound localization have proven useful in studies of bats (Muller, 2004; Wotton & Jenison, 1997) and humans (Chung, Carlile, & Leong, 2000; Jin, Schenkel, & Carlile, 2000; Nandy & Ben-Arie, 2001), and may provide unique advantages for examining the role these cues play in the localization abilities of dolphins. Computational models increase the objectivity, efficiency, precision, and repeatability of analyses of cetacean hearing by quantifying properties of the acoustic signals and systems used by cetaceans. Additionally, computational models can reveal the hidden assumptions underlying more qualitative theoretical models. Auditory systems serve two primary functions: (1) to describe patterns of acoustic energy from external sources, and (2) to localize sources of acoustic energy. Most auditory computational modeling to date has focused on the first of these two functions, particularly at the level of the inner ear. The second of these functions depends on the first; all spatial information is inferred from the available descriptions of acoustic patterns. Consequently, all computational models of sound localization abilities must begin with a model of cochlear transduction.

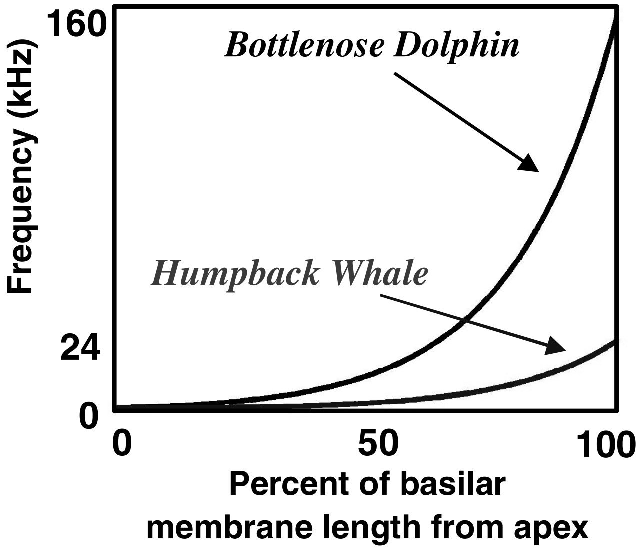

Figure 3. Estimated cochlear frequency position functions for a humpback whale and a bottlenose dolphin.

Cetacean-specific Models of Sound Reception

The peripheral auditory system of mammals is typically modeled as a series of overlapping band pass filters (Fletcher, 1940). Each filter processes frequency information within a restricted range while attenuating the amplitude of adjacent frequencies. Resonance properties of the cochlea vary across species, and so different sets of cochlear filters are needed to model reception, to reflect the physical differences in properties of the BM. If it is assumed that cochlear filters are spaced at equal distances along the BM, then quantitative functions (called cochlear frequency position functions, CFPF) can be used to determine the sensitivities of each filter. CFPFs have been derived from anatomical, physiological and psychophysical measurements of several mammals, including humans and some cetaceans (Glasberg & Moore, 1990; Greenwood, 1961, 1990; Helweg, Houser, & Moore, 2000; Ketten, 1994; Roitblat et al., 1996). Figure 3 shows estimated CFPFs for a humpback whale and a bottlenose dolphin. The dolphin CFPF can be calculated more accurately than the function for any baleen whale, because more is known about the physical structure of the dolphin cochlea, and about their hearing frequency range. Greenwood (1990) developed a general function for describing CFPFs in mammals

$$F = A(10^{ax} - k)$$

where F is the most sensitive frequency at a membrane position (x), and A, a, and k are species-specific constants. Ketten (2000) derived a similar function to characterize cetacean CFPFs

$$F = A(e^{ax})$$

where A is a stiffness coefficient derived from the ratio of BM thickness to BM width, and a is a species-specific constant related to size. These relatively simple functions can be used to estimate several measures of hearing sensitivity, including frequency discrimination thresholds, critical bands, and critical masking ratios (Fay, 1992).

Once the CFPF of a cetacean is calculated, the response properties of particular positions along the cochlea can be modeled mathematically. The outputs of cochlear response models can then be used to create visual representations of acoustic events, as they would be sensed at a particular cetacean's cochlea. For example, sounds produced by a humpback whale will be represented very differently within the cochlea of a bottlenose dolphin than they will be within the cochlea of a humpback whale (Figure 4). It is difficult, if not impossible, to assess how any cetacean cochlea will represent humpback whale sounds based on spectrographic representations, because spectrograms and related time-frequency representations do not incorporate the idiosyncratic processing characteristics of cochlear filters. In some cases, cochlear representations of received sounds can reveal acoustic cues that might not be obvious from either subjective impressions or from visual inspections of spectrograms (Figure 4). Many studies of cetacean sound reception have implicitly assumed that the way cetaceans perceive sounds (including their own vocalizations) is comparable to the way humans perceive them. However, localization cues that are salient to cetaceans are most likely imperceptible to humans. Representations of sounds derived from computational models of cochlear responses (*cochleagrams*) reveal features of sounds that are emphasized by a particular cetacean's ear, and which are thus likely to be salient for a listening whale or dolphin.

Neural Network-based Source Localization

Dolphin cochleagrams provide quantitative estimates of the cochlear response patterns from which dolphins derive all of their auditory spatial representations. It is clear that dolphin auditory systems must perform some calculation that maps cochlear responses onto representations of space. Developing computational models that can achieve comparable levels of spatial resolution based on cochlear response patterns is thus an important step toward identifying what acoustic cues are necessary and sufficient to enable dolphins to resolve certain spatial features. Computational models of auditory localization can also give some sense of the relative complexity of processing required to map acoustic events to spatial positions.

We are developing a series of connectionist models (monaural and binaural) to explore how well dolphins can extract spatial information from HRTF-based acoustic cues. The model incorporates the known anatomical, physiological, and behavioral constraints of the dolphin's auditory system. Connectionist models have been used in the past to model target recognition by echolocating dolphins (Au, 1994; Au et al., 1995; Roitblat et al., 1993), but to our knowledge they have never been used to model sound localization by any cetacean. The major advantage of connectionist models over other possible choices is that they do not require prior knowledge about appropriate mapping functions, but can instead incrementally learn what functions work through training algorithms. The basic model has three main stages, simulating passive filtering by the head of the dolphin, active peripheral filtering at the dolphin cochlea, and experience-based mapping of cochlear responses to positions in two-dimensional space.

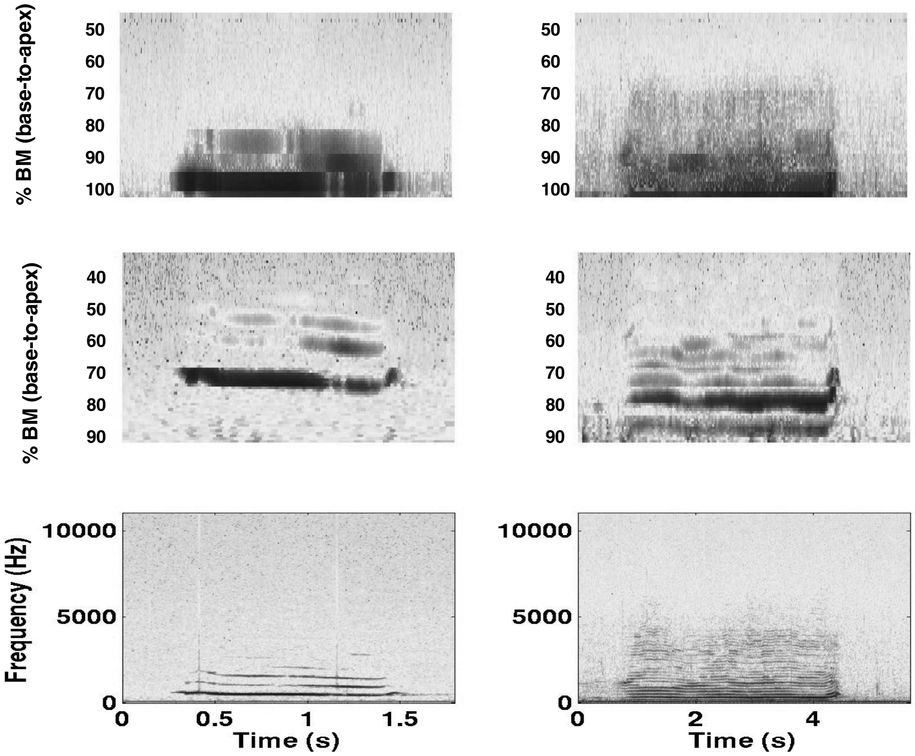

Figure 4. Cetacean-specific cochleagrams of two humpback whale vocalizations. The top row shows how sounds produced by a humpback whale are represented by a bottlenose dolphin's cochlea. The middle row shows how those same sounds are represented by a humpback whale's cochlea, and the bottom row shows spectrograms of these sounds. Images on the left are all representations of one sound produced by a humpback whale, and images on the right represent a different humpback sound. Dolphin and humpback cochleae process the same sound very differently; spectrograms do not clearly reveal features of vocalizations emphasized by species-relevant cochleagrams. For example, the humpback whale cochleagrams in the middle row show transient modulation toward the cochlear base (increases in frequency) at the end of both sounds. These features are not clearly revealed in either spectrograms or dolphin cochleagrams.

Stage 1: Filtering by the Dolphin's Head. Simulated HRTFs can be combined with models of cochlear transduction to create biomimetic representations of received sounds that incorporate all of the acoustic cues currently known to mediate dolphin spatial hearing. The HRTFs provide the localization mechanism for our connectionist model to test the hypothesis that bottlenose dolphins use HRTF-based acoustic cues to localize sound. Because only rudimentary dolphin HRTFs are available (Aroyan, 2001; Brill, Moore, & Helweg, 2001; Supin & Popov, 1993), we initially have chosen to use arbitrary HRTFs. Like actual mammalian HRTFs, the arbitrary HRTFs systematically alter the spectrum of incoming sound as a function of sound source position (Figure 5). No optimization of the HRTFs was attempted. Consequently, model results are considered conservative compared to real HRTFs that have the distinct advantage of evolutionary fine-tuning. The incident signal presented to the HRTFs was a dolphin click used in previous modeling efforts (Au, 1994; Au et al., 1995). The click was sampled at 1 MHz, and lasted ~40 µs with a peak frequency between 100-140 kHz.

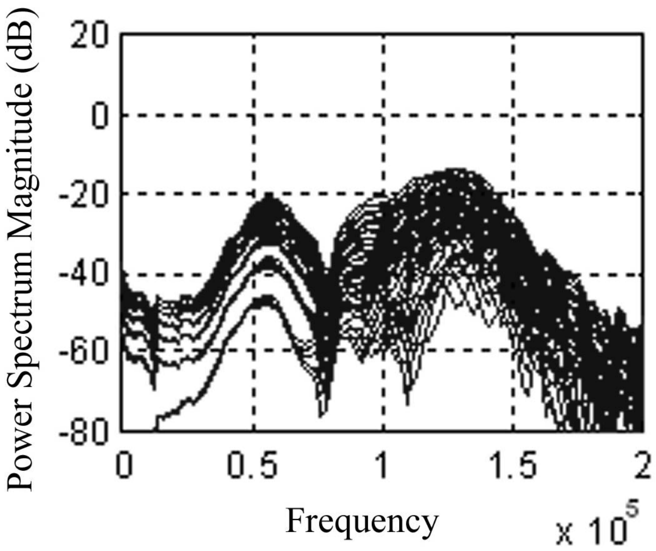

Figure 5. Power spectrum of a dolphin echolocation click filtered by 49 different HRTFs corresponding to 49 different spatial positions.

Stage 2: Filtering by the Dolphin's Cochlea. Although humans (and presumably other mammals) usually perceive a single sound source as arising from a single position, sound waves are always sampled at two positions, corresponding to each cochlea. Consequently, from the perspective of the brain there are always two vibrating sources (the oval windows), and everything else that the brain infers about the space beyond these sources depends on the fidelity of two cochlear representations of sound. Thus, when considering how cetaceans are able to echolocate or passively localize sounds, it is important to keep in mind that there are always effectively two "sounds" to be processed, not one. Differences between the sound waves sampled at each cochlea can provide important clues about the spatial properties of echo generating structures. However, for the current simulation, we used only monaural localization to demonstrate how HRTFs make it possible to localize sound sources with just a single receiver. Because the model uses less information than a binaural model (half the spectral filtering and no binaural comparisons) the model results are considered extremely conservative.

Numerous techniques have been developed to model cochlear filter responses. The current model employs a gammatone filter bank (Branstetter, 1999; Slaney, 1998) to simulate dolphin cochlear responses, where the filter outputs are the impulse response of 40 frequency channels between 5 kHz and 156 kHz. The impulse response can be defined as

$$g_t(t) = at^{(n-1)}\exp(-2\pi bt)\cos(2\pi ft-\phi)$$

where *a*, *n*, and *b* determine ramping and damping in the time domain, and thus the shape of the filters in the spectral domain. The ratio between the center frequency of a filter (f_c) is proportional to the filter bandwidth (Δf) by the equation

$$Q = f_c/\Delta f.$$

A notable feature of the mammalian cochlea is that Q-ratios tend to be constant over the frequency sensitivity range of the cochlea. The constant-*Q* values for bottlenose dolphins have been estimated to be about 12.3 (Au & Moore, 1990). Each filter was logarithmically spaced with respect to its center frequency, and the parameters were adjusted to approximate dolphin Q-values. The output of each filter was half-wave rectified (simulating the response properties of nerve cells in the organ of Corti), and summed to produce a spectral response profile. The output of each frequency channel represented the total energy for that channel. Figure 6 summarizes our model of filtering by the dolphin's HRTF and cochlea.

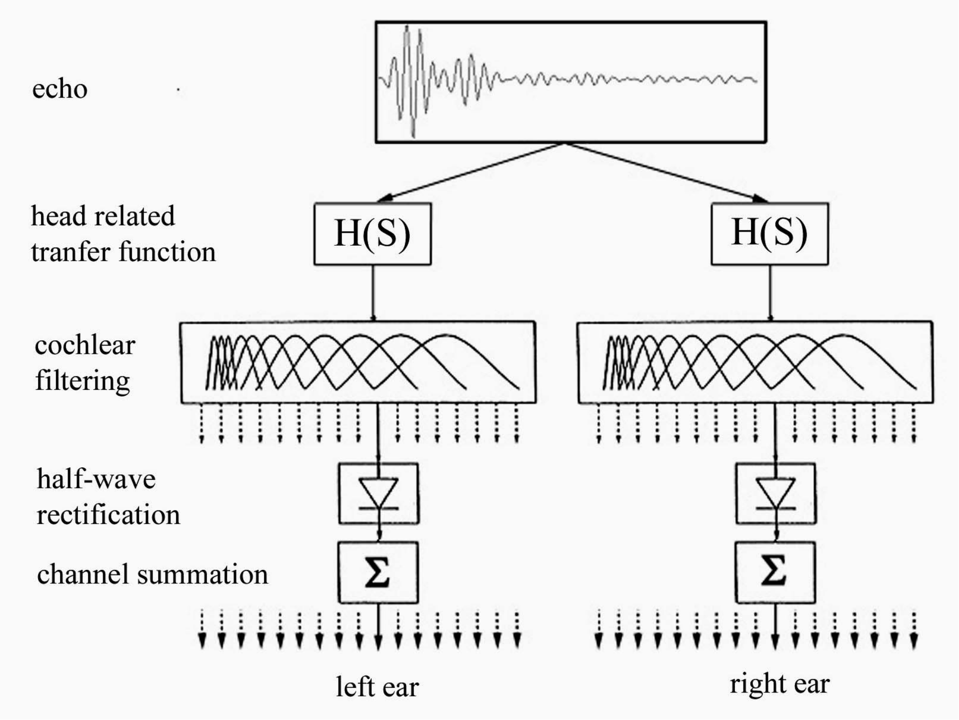

Figure 6. Binaural processing in the active peripheral filtering stages of a computational model of sound localization by a bottlenose dolphin.

Stage 3. Spatial Mapping by the Dolphin's Brain. Spectral response profiles calculated in stage two were presented to a three-layer backpropagation neural network that was trained to associate these spectral profiles with the Cartesian coordinates corresponding to the position of the source in two-dimensional space. The first layer consisted of inputs from the dolphin cochlear filtering stage followed by a hidden layer. Tan-sigmoid transfer functions were used to limit outputs between -1 and 1. The network output space was arranged on a two-dimensional grid to simulate Cartesian coordinates. The architecture of this connectionist network is summarized in Figure 7. It is not known whether such topographic maps are implemented in the cetacean auditory system, but such maps have been described in barn owls (Knudsen, 1983, 1984; Knudsen & Konishi, 1978; Takahashi et al., 2003), cats (Aitkin, Kenyon, & Philpott, 1981), ferrets (King & Hutchings, 1987), and guinea pigs (Binns, Grant, Withington, & Keating, 1992), and topographic maps corresponding to target range exist in the bat auditory system (O'Neill & Suga, 1982; Suga & O'Neill, 1979).

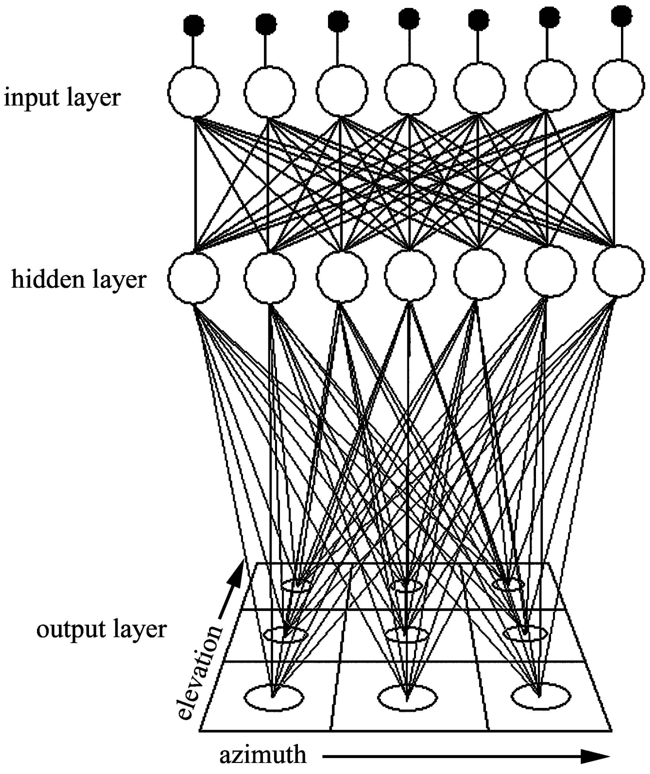

Figure 7. Neural network architecture within a computational model of sound localization by a bottlenose dolphin. This connectionist network simulates mapping of cochlear representations onto a topographic map of auditory space.

The network learned to associate the specific spectral resonance profiles from the gammatone filters with their corresponding spatial location by adjusting the weights of the individual nodes in the network (using the backpropagation learning algorithm) over a series of 5000 iterations, or until the root-mean-square output error fell below a preset parameter value. The connectionist model was able to localize single sound sources in both the horizontal and vertical planes. Figure 8 illustrates how the model processes echoes from two different spatial positions. For simplicity, two examples of monaural processing are presented. Figure 8A shows the echo measured at the sound source. Figure 8, B1 and B2 illustrate the echoes after filtering from two different HRTFs. This stage is equivalent to position-dependent filtering from two different sound source locations. Figure 8, C1 and C2 represent the outputs from the gammatone filters (i.e., dolphin cochleagrams). Low frequencies are at the bottom of these images, and high frequencies are at the top. Figure 8, D1 and D2 show the results of channel summation, which is equivalent to the perceived spectral profile; high frequencies are to the left. Because filter bandwidths are proportional to their center frequencies, low frequency filters are narrower, resulting in a disproportionate amount of filters allocated to lower frequencies. Figure 8, E1 and E2 show responses to the processed echoes in the topographic output layer of the neural network. Peaks indicate the spatial position of the sound source. Although the current example only illustrates how single sound sources can be localized with HRTF-based cues, work is currently in progress modeling how a dolphin may localize multiple sound sources simultaneously and ultimately “image” a complex object.

Summary and Future Directions

Oceanic environments provide reduced opportunities for animals to localize and identify objects using visual or olfactory channels, and as a result the auditory modality plays a dominant role in the sensory world of all cetaceans. Because sound propagates through water differently than it does through air, cetaceans have developed unique mechanisms for generating and sampling acoustic cues from which spatial information can be derived. Cetaceans also have developed unique neural computational approaches to processing localization cues, as evidenced by the ability of bottlenose dolphins to immediately visually recognize objects that they previously have only experienced acoustically (Harley et al., 2003; Pack & Herman, 1995; Pack et al., 2002).

Different ecological constraints have led to vastly different auditory adaptations in odontocetes and mysticetes. The ability to localize small, acoustically cryptic sound sources likely drove the evolution of high frequency, broadband hearing abilities in dolphins, whereas expanded habitat ranges and a need for long-range monitoring of conspecifics and environmental features may have provided advantages for baleen whales with good low frequency localization abilities. IIDs and HRTFs are probably useless for a blue or fin whale attempting to localize another whale producing 12-20 Hz signals, whereas such cues may be critical for a bottlenose dolphin attempting to locate, track, and capture small fish. Conversely, IPDs are unlikely to contribute to echolocation abilities in dolphins, but may be critical for large whales attempting to localize low frequency sources. Because cetaceans come in a wide range of sizes, make use of extreme acoustic regimes, and live in a wide variety of habitats, they provide a unique opportunity for examining how ecological constraints can shape different species’ reliance on particular sound localization strategies across an evolutionary time scale.

Evolutionarily tailored sound production and reception systems are critical for sound localization, but just as critical are the cognitive and perceptual capacities needed to make use of information gained from past experiences. More is known about the cognitive and perceptual capacities of bottlenose dolphins than of

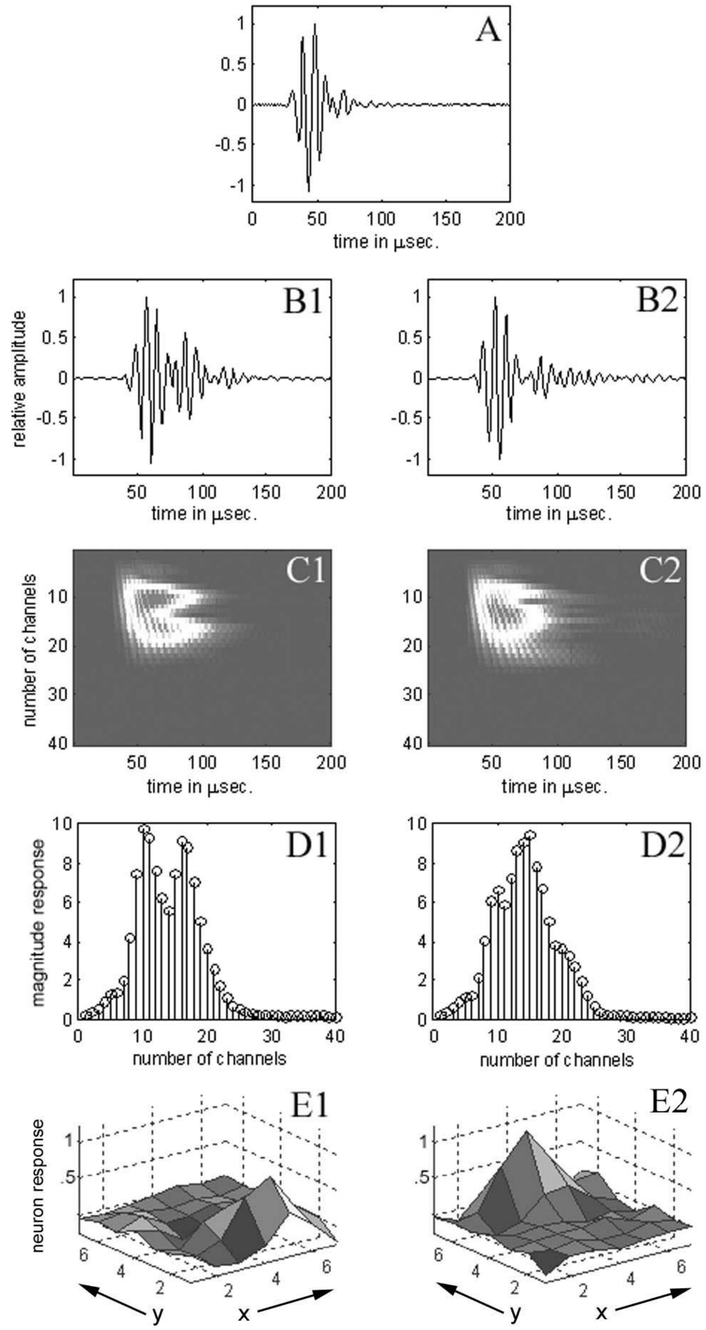

Figure 8. Simulated localization of an echo in a computational model of sound localization by a bottlenose dolphin. (A) echo at sound source; (B1 and B2) echoes from different positions in space have undergone filtration by HRTFs; (C1 and C2) output of gammatone filter bank; (D1 and D2) channel summation; (E1 and E2) neural net response to the echoes identifying the position (elevation and azimuth) from which they originated.

any other cetacean (see Marino, 2002; Reiss, McCowan, & Marino, 1997; Schusterman, Thomas, & Wood, 1986). Almost nothing is known about cognition or perception in humpback whales or any other baleen whale. Several cetacean species, including humpback whales, have demonstrated the ability to flexibly mimic sounds they have heard only a few times as adults (Guinee et al., 1983; Payne & Payne, 1985; Reiss & McCowan, 1993; Richards et al., 1984). A cetacean's ability to vocally imitate may enhance its capacity to determine the distance a sound has traveled, as well as its capacity to identify familiar signals in familiar environments. The limits at which cetaceans lose their ability to localize, range, and spatially differentiate objects in real-world situations are essentially unknown, but can be estimated from general mammalian models of hearing. Researchers can assess the accuracy of such estimates through laboratory studies, but obtaining and maintaining the subjects, facilities, and permits necessary for such work is exceedingly difficult. Computational models provide an alternative way of generating testable hypotheses about cetacean auditory localization abilities, and of determining whether specific acoustic cues are necessary or sufficient for resolving spatial features.

Many questions remain about how different cetacean species sense and perceive sound. Researchers have suggested many potentially unique reception systems that cetaceans might use to transduce sound. For example, odontocetes may receive sound through their teeth (Goodson & Klinowska, 1990), jaws (Norris, 1964, 1968), fat channels (Ketten, 2000), ear canals (Fraser & Purves, 1954, 1960), an acoustic retina behind their melon (Bullock & Gurevich, 1979), and sensory hairs (Lende & Welker, 1972; Ling, 1977). Even today, it is difficult to confidently choose the "correct" subset from these possibilities. Mysticetes may receive sounds through their skulls (Beamish, 1979), ear canals (Fraser & Purves, 1960), sensory hairs (Ridgway, 1997; Yablokov, Bel'kovich, & Borisov, 1974), or resonating air spaces (Barham, 1973). The paths through which sound travel to the ear can provide cues for estimating azimuth, elevation, and even distance, so understanding how these paths vary across cetacean species can clarify the mechanisms odontocetes and mysticetes use for spatial hearing. If dolphins are forming mental images of ensonified objects, then how detailed are those images? How might such images vary as a function of distance, azimuth, and elevation, and how might motion of the source or target affect the images? Can cetaceans (including baleen whales) form lower resolution images using lower frequency sounds? To what extent do active signals act as a "flashlight", providing information that animals other than the sound producer can use (e.g., Xitco & Roitblat, 1996)? How do accumulated experiences affect a cetacean's echolocation abilities? Questions such as these beg further study.

Comparative analyses of auditory perception are relatively rare, especially in the case of marine animals. Cetacean auditory perception of underwater environmental features involves a complex relationship between acoustic events, their neural processing, and the individual's behavior. Unless links can be made between anatomy and perceptual abilities (as revealed through behavior), it will remain difficult to draw inferences about the evolutionary processes driving auditory adaptations in mammals (Stebbins & Sommers, 1992). Comparative studies can shed light on the ecological demands that shaped localization abilities. Without additional comparative anatomical and physiological data, however, it will remain difficult to understand how auditory perception evolved in cetaceans. Computational models provide a theoretical framework for identifying what missing data are most critical to increasing our understanding of cetacean auditory perception, thereby facilitating future progress.

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