Perceptual Soundscapes of Dolphins and Whales

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Thousands of hours of oceanic recordings have revealed whales and dolphins (collectively referred to as cetaceans) to be an exceptionally vociferous group of animals (for examples of vocalizations, see bit.ly/Dosits_Whale). These aquatic mammals produce complex patterns of vocalizations, possibly for communication, social interaction, navigation, or other purposes. However, even after decades of study, many of the sounds that cetaceans produce remain enigmatic.

How would one know if a whale or dolphin is vocalizing to reveal its inner thoughts, to probe its environment, or to pass the time? Simply dropping a hydrophone in the water and recording vocalizations won't reveal what animals are perceiving. Watching how animals behave while vocalizing is also unlikely to shed light on the issue because a cetacean vocalizing to communicate may behave similarly to one vocalizing to echolocate.

In fact, there are three main factors that one needs to consider in detail when attempting to answer questions about how dolphins and whales use sound: (1) How flexibly are the animals varying the physical features of their vocalizations? (2) Do the ways in which sound propagates underwater affect how cetaceans use sound? and (3) How do listening cetaceans encode, perceive, and interpret variations in received sounds? (**Figure 1**).

Figure 1. *Whales and dolphins are immersed in a sea of vibrations. A subset of these vibrations enters the animals' perceptual awareness. Cetaceans may perceive sounds as objects, events, agents, feelings, or in other ways that are unfamiliar to human observers, such as experiencing them as colored waves. Listeners may use their auditory experiences to gain information about vocalizers' movements, identity, emotional states, and potential future actions (Herman, 1980). Vocalizing individuals and groups shape their acoustic environment in ways that depend on how they vocalize, where they vocalize, and on how the surrounding environment reacts to those vocalizations. Predicting the reactions of listeners' brains to vocalizations is particularly critical to understanding how dolphins and whales use sounds in their daily lives.*

One cannot know how cetaceans are using vocalizations without some indication of what perceptual soundscapes they are constructing. The broad range of sound fields that vocalizing dolphins and whales produce afford numerous perceptual possibilities. Sorting vocalizations based on observers' subjective impressions can bias investigation and interpretation of cetacean vocal behavior. Analyzing the full physical spectrum of what happens in oceans and in animals' bodies during and after sound production is key to identifying the properties of sound fields that listening whales and dolphins are encoding and perceiving as well as the perceptually salient scenes and objects that their internal representations of sounds make real.

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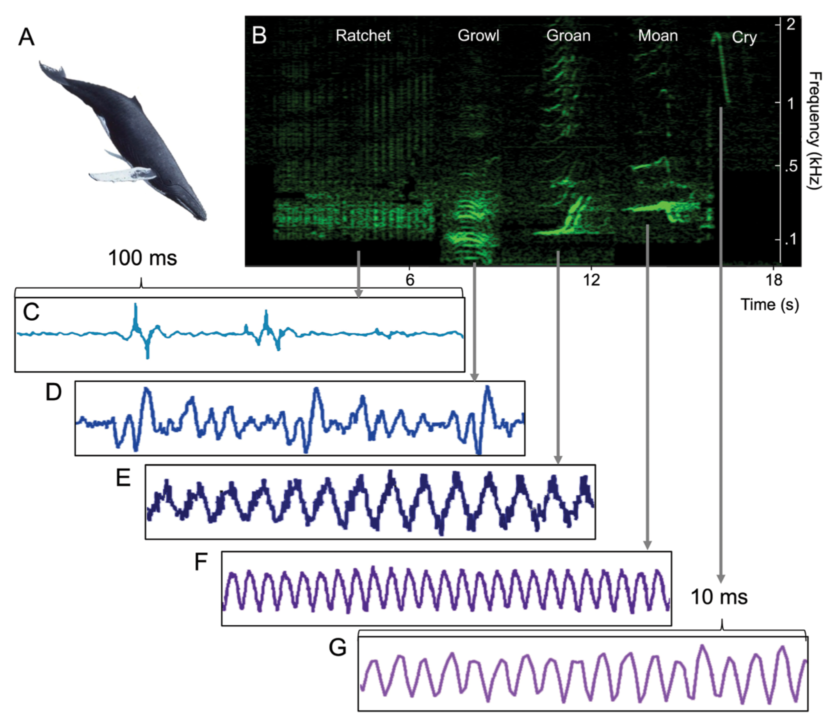
Vocal Flexibility

Whales and dolphins make sounds in many ways. One is to make percussive sounds by striking the water with body parts. They also vocalize by pushing air through vibrating membranes (Reidenberg, 2017). Cetaceans may vocalize reflexively in reaction to internal states (e.g., pain) or external events (e.g., threats). They can also modify properties of their vocalizations based on sounds they have recently heard (Mercado et al., 2014).

Sound Repertoires

Many past descriptions of cetacean vocalizations split them along the lines of the species making them: odontocetes, cetaceans with teeth such as bottlenose dolphins (*Tursiops truncatus*) and sperm whales (*Physeter macrocephalus*), produce clicks, burst-pulse signals, and whistles, whereas mysticetes (toothless whales) produce calls and songs (Au and Lammers, 2014). These categories highlight features that are perceptually salient (i.e., obvious) to human observers. For example, researchers may listen to recordings and sort vocalizations into auditory categories that they learned as a child (e.g., "whistles, "clicks," and "moans"), or may inspect spectrograms (two-dimensional images highlighting the spectral and temporal properties of sounds; see **Figure 2**) and categorize them based on their distinctive visual forms. Sometimes researchers also sort vocalizations based on the context within which the vocalizations were produced, leading to categories like "feeding call." This subjective approach to classifying vocalizations may obscure cross-species similarities that are relevant to understanding how cetaceans perceive or use their vocalizations.

Figure 2. ***A:*** *singing humpback whales produce a wide variety of sounds within their songs. Image by Larry Foster.* ***B:*** *different vocalizations produced by a singing humpback can appear quite distinctive in spectrograms. Researchers often label vocalizations based on preexisting auditory categories (see* ***Multimedia File 1*** *at acousticstoday.org/Mercado-Media).* ***C:*** *the discrete pulses within a "ratchet" are commonly referred to as "clicks" when produced by smaller cetaceans.* ***D:*** *when the duration between pulses is comparable to the pulse duration, then these vibrations are considered continuous. In dolphins, such vocalizations are referred to as "burst pulses."* ***E:*** *as the frequency of pulsation increases, the distinctions between individual pulses decrease, leading to wave patterns that are more regular and triangular. Such vocalizations produced by orcas are called "pulsed calls." Spectrograms of such vocalizations commonly show stacks of horizontal bands.* ***F:*** *further increases in pulse frequency make the waveform of a vocalization appear more regular.* ***G:*** *ultimately, the vocalization begins to approximate a sinusoid. Comparable vocalizations in dolphins are called "whistles."*



Within a species, perceptually distinctive features of signals can be directly related to changes in the vibratory modes of the membranes generating the sounds. This continuum from discrete pulses (clicks) to more sinusoidal tonal sounds (whistles) can be modeled as relaxation oscillations with properties determined by membrane tension and air pressure differences that cause the membranes to vibrate in different ways (Amador and Mindlin, 2023). The vocal repertoires of well-studied cetacean species such as bottlenose dolphins, orcas (*Orcinus orca)*, and humpback whales (*Megaptera novaeangliae*) all include vocalizations spanning the same continuum of membrane oscillations (**Figure 2**) (Murray et al., 1998). A subset of tensions and pressures can lead to more complex membrane movements, producing vocalizations with "nonlinear" features (Cazau et al., 2016).

Communicative Clicks

One category of cetacean vocalizations that has received a disproportionate amount of scientific attention over the last half century are clicks. Many cetaceans produce extended series of clicks in a variety of contexts. In odontocetes, click trains tend to be associated with echolocation (reviewed by Au, 1993). However, studies of stereotyped click trains produced by sperm whales, called codas, have increased awareness that click production and echolocation are not synonymous (Jacobs et al., 2024). Initial reports of click production by mysticetes such as humpback whales and gray whales (*Eschrichtius robustus*) were rare and seldom associated with echolocation (Fish et al., 1974). Mysticetes do not produce ultrasonic clicks. However, they commonly produce short-duration sounds with the impulsive and audible features characteristic of clicks (**Figure 2, B** and **C**) (Stimpert et al., 2007).

When odontocetes use clicks to echolocate, they may time click production such that echoes of interest return during the intervals between clicks or they may produce a burst of clicks, called a packet (Finneran, 2013). Clicks within a series tend to be highly similar, although individuals may vary click features when echolocating in noisy conditions (Au, 1993). Belugas (*Delphinapterus leucas*) and bottlenose dolphins typically switch to using packets when searching for targets at long distances.

Changing Vocalizations Over Time

The vocal repertoires of cetaceans appear to be graded, meaning that their vocalizations vary continuously across one or more acoustic dimensions rather than consisting of a fixed set of stereotyped sounds. Singing humpback whales, for example, continuously morph the acoustic features of individual sounds ("units"), dynamically shifting the pitch, duration, form, and spectral shapes of units as they progress through a song cycle (see **Multimedia File 2** at acousticstoday.org/Mercado-Media). Singers also vary how they morph units from one song to the next (Mercado and Perazio, 2022).

Some of the ways that whales shift the features of their vocalizations accumulate over seasons and years. Blue whales (*Balaenoptera musculus*) around the world have gradually decreased the pitch of units within their songs every year for over a decade (Rice et al., 2022). They vary unit properties while producing them in relatively fixed sequences. Singing humpback whales, in contrast, vary both units and unit sequences from one year to the next (Payne and Payne, 1985). Singers typically produce unit patterns in a predictable order and rhythm, with all singers in a population converging on similar sequences (see **Multimedia File 3** at acousticstoday.org/Mercado-Media). Singing humpbacks progressively and collectively vary the patterns they produce over months and years, with the degree of variation changing from one year to the next (Payne et al., 1983).

Learning to Use Novel Sounds

Like humans, cetaceans possess the rare ability to vocally imitate novel sounds immediately after hearing them. Vocal imitation requires not only flexible control of air pressure and membrane tension but also the capacity to transform perceived sounds into the vocal actions required to reproduce those sounds. Bottlenose dolphins can match not only time-varying changes in the frequency content of individual sounds (Richards et al., 1984) but also the number of sounds in a sequence (Lilly et al., 1968) and the rhythm of sound patterns (Mercado and DeLong, 2010). Both mysticetes and odontocetes sometimes engage in coordinated vocal interactions. Such interactions can even happen across species, leading some to wonder whether it might someday be possible to translate delphinid discussions or engage in interspecies conversations.

Unlike humans, cetaceans are not limited to vocally interacting with a few individuals that they are facing and that are facing them. Instead, cetaceans typically vocalize while

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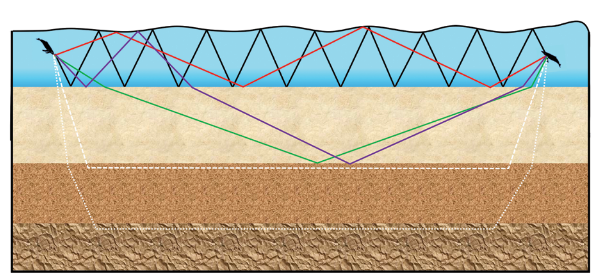
on the move in a fluid, spatially open environment where potential listeners are only occasionally visible. Moreover, cetaceans' movements and selection of sounds can affect how their vocalizations disperse in ways that are much more complex than is true for human speech. A vocalization produced at depth will have different properties from the same vocalization produced near the surface, will produce different echoes, and will reach different subsets of listeners. These are not conditions humans naturally experience. For researchers to understand how cetaceans use sound, it is critical that they identify what listening is like for the individuals using those sounds as well as the various ways that underwater sound transmission has shaped what vocalizing cetaceans hear.

Affordances of Vocalizations

When you hear people vocalizing around you, the specific sounds you hear determine the kinds of reactions you are likely to have. For instance, hearing your name yelled from a distance might provoke you to look in the direction of the caller. Hearing a number called out in a waiting room might lead you to either continue to wait or to initiate an interaction with the caller. Hearing your own voice echoing back from the walls of a canyon might encourage you to yell "Hello!" to yourself. In each case, the sounds you experience set the stage for what you're likely to do next. Psychologists describe the opportunities that objects, events, or environments provide to an individual as *affordances*. Affordances suggest possible future actions. For example, some affordances of beach balls are that they are throwable, rollable, kickable, floatable, deflatable, and huggable.

By vocalizing, cetaceans alter the affordances of their oceanic habitats to better suit their needs. Any sound they make will reveal a host of behaviorally relevant cues to other nearby (and perhaps more distant) group members. A vocalizing cetacean broadcasts where it's located, where it's going, when it's likely to arrive at future locations, and what it's doing. The sound fields they generate make it possible for listening individuals to monitor ongoing events, coordinate actions, identify individuals, corral prey, and recognize the internal states of group members. If the vocalizer is aware of the movements and goals of listeners, then vocalizations can also reveal what the vocalizer expects other individuals to do. Dolphins and whales are using sound to actively construct their perceptual worlds in real time, in ways that guide future actions.

Figure 3. *Shallow water transmission of cetacean vocalizations is more complex than what happens when humans converse or hear birds singing outside a window. Sounds and their echoes will travel through multiple paths, including subterranean channels (Thode et al., 2000). What a listener hears will depend not just on what sounds others are producing but also on where the vocalization was produced relative to the location of the listener. Resulting vocalizations received from long distances will not simply be quieter. They may be distorted in ways that make the original form of the signal unrecognizable.* ***Top to bottom:*** *the four depicted layers (pathways) correspond to seawater, sediments, basalt, and gabbro, each of which differs in its sound transmission properties.*



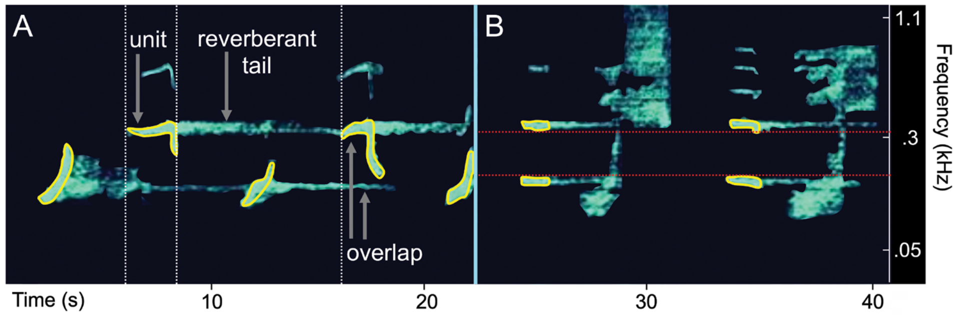


Figure 4. ***A:*** *alternating units produced by a singing humpback whale (****yellow outline****) generate long-lasting reverberant tails. When reverberation from a preceding unit minimally overlaps with the spectral properties of a subsequent unit, the units are spectrally interleaved.* ***B:*** *singers sometimes spectrally interleave tonal units with more broadband, chaotic units. In this example, the singer initiates broadband units at frequencies below those of the preceding unit, then rapidly shifts to higher frequencies. Such patterning may reduce cross-unit interference and/or enhance sound localization. Adapted from Mercado (2021), with permission of the Acoustical Society of America, © 2021.*

Environmental Constraints on Sound Usage

Once a cetacean initiates tissue oscillations within its head, those vibrations will begin propagating into the surrounding seawater. How vocalizations propagate will depend on several factors, including (1) the relationship between the acoustic properties of the vocalization and the anatomy of the vocalizer; (2) the external environment; and (3) the individual's location within that environment. The same click or whistle produced by both a bottlenose dolphin and a beluga will propagate differently based on differences in their bodies, behaviors, and habitats.

A major determinant of how cetacean vocalizations propagate is how intensely the animal vocalizes. That's not the only factor, however. Vocalizations also vary greatly in their directionality and in their susceptibility to degradation during transmission. Propagation gets particularly complicated when the water depth is less than the distances that the vocalizations can travel (**Figure 3**).

Cetaceans can move their bodies in ways that directly influence the form and function of the sound fields they produce and experience (Mercado and Frazer, 1999). For instance, when bottlenose dolphins inspect an object with echolocation, they often move their head from side to side while producing clicks, thereby controlling the properties of echoes that will be generated by the object as well as the acoustic properties that will register at their ears (Au, 1993). The dynamic forms of sound fields that vocalizing cetaceans generate and perceive remain largely unknown. The extent to which vocalizers accommodate, control, or derive useful affordances from such fluctuating fields is similarly obscure.

Vocal Reverberation: Noise or Signal?

Cetaceans' vocalizations sometimes produce significant *reverberation*, reflections that persist within an environment. Reverberation could increase ambient-noise levels, making reception more difficult. However, cetaceans might also use reverberation to guide their actions (Ellison et al., 1987). For example, singing humpback whales often produce consecutive units in ways that minimize overlapping frequencies, a behavior referred to as *spectral interleaving*. Spectrally interleaved units generate reverberation in quite narrow frequency bands that can persist for periods longer than the intervals between units (**Figure 4**). Reverberating units create new affordances for spatially processing sounds that can potentially enable listening whales to more accurately judge their distance from a singer (Mercado, 2016).

The affordances that cetaceans create by vocalizing supplement the oceanic sounds that they experience daily. These affordances are not directly observable from either acoustic recordings or from observations of behavior.

They depend on what cetaceans perceive in the present and on their memories of past acoustic events. Any cetacean's use of sound fields ultimately is a function of the internal neural and mental activity evoked by those fields. This activity, referred to as an individual's *auditory representations* of experienced sounds (Cheung et al., 2016), may differ significantly from what occurs when a terrestrial mammal is exposed to the same sounds.

Cetaceans' Auditory Representations

A soundscape consists of the combination of all sound fields detectable from a specific point in space over some duration (see articles at bit.ly/3yGZoJK). A perceptual soundscape, in contrast, corresponds to what an individual apprehends from a specific vantage point. Identical soundscapes presented to two individuals could evoke radically different perceptual soundscapes. For example, if you were to stick your head underwater as a dolphin echolocates or listen using a hydrophone, you and the dolphin would be exposed to similar soundscapes. However, the dolphin's experience of that received soundscape will differ substantially from yours. These differences arise because the auditory representations that a dolphin constructs as it produces click trains are qualitatively different from those formed by a human exposed to those same clicks.

The full scope of auditory representations and associated perceptual landscapes formed by listening cetaceans remains unknown. Their experiences likely extend beyond the norm for human listeners and other terrestrial animals. For example, sound waves reach sensory receptors within cetaceans' heads through pathways quite different from those typical of terrestrial mammals. Behavioral experiments indicate separate reception channels for ultrasonic versus sonic vocalizations in odontocetes (Norris, 1964). Mysticetes also seem to receive sounds through multiple tissue channels (Yamato et al., 2012). The complexity of pathways through which vocalizations propagate within a cetacean's body likely leads to dynamic interactions between incoming sounds that shape the formation of auditory representations.

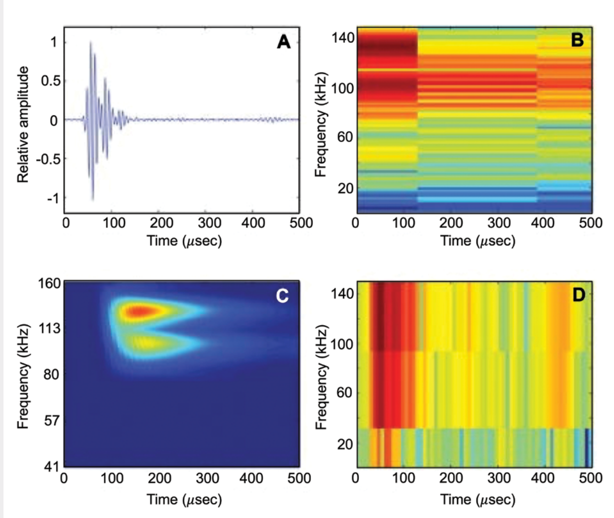
Simulating Sound Reception

One way to reveal aspects of a given species' auditory representations is by simulating cochlear reception of sound and subsequent neural reactions to sensed signals (Branstetter et al., 2007). Representing vocalizations as *cochleagrams*, spectrogram-like images of simulated sensory responses, makes the acoustic features emphasized by the relevant listeners' ears more salient (**Figure 5**).

Mapping Neural Sensitivities

Simulations of sound reception can extend far beyond what happens at the ear. Electrophysiological studies of neural activity have revealed that sensitivities to behaviorally relevant features of vocalizations are spatially organized within sensory cortical networks in the brain. For example, some echolocating bats possess cortical maps organized based on the timing of echo arrivals, emphasizing delays that correspond to distances from which bats track and capture targets while foraging (Moss et al., 2014). Although less is known about cortical maps in cetaceans, the basic principles of auditory cortical processing in other mammals likely generalize to auditory

Figure 5. ***A:*** *an echo from a single click produced by an echolocating dolphin shows rapid oscillations within a short period.* ***B:*** *spectrogram set for fine-frequency resolution reveals periodic structure within these oscillations. In this color scale,* ***red*** *indicates frequencies at which the energy in the echo is most intense and* ***blue*** *corresponds to frequencies where there is little energy.* ***C:*** *cochleagrams display how a dolphin's ear reacts to the echo over time based on theoretical models of inner ear function.* ***D:*** *spectrographic parameters could be set to achieve comparable temporal resolution but at the cost of reduced frequency resolution. Adapted from Branstetter et al. (2007), with permission of the Acoustical Society of America, © 2007.*



representations in whales and dolphins. In particular, whether a whale or dolphin perceives a sound as coming from a friend, foe, or food will depend on how incoming sounds are cortically represented.

The Role of Changing Neural Circuits

The specific auditory representations that any individual forms will also depend on the sounds that individual has heard during development and on how the individual produces and uses similar sounds. Vocalizing cetaceans are not only constantly constructing their personal auditory experiences but also creating the neural infrastructure for auditory perception and cognition in future generations. The collaborative process of vocal repertoire building is evident not only in the shared use of dolphin whistles and orca calls but also in the constantly morphing song sequences produced by singing humpback whales. Use of vocalizations as part of coordinated foraging strategies in humpbacks (Bryngelson and Colonius, 2020) and spinner dolphins (*Stenella longirostris)* (Benoit-Bird and Au, 2009) further suggests that learning experiences not only shape which sounds cetaceans produce but also how and when vocalizations are used during social interactions.

Interpreting Echoic Scenes

Few investigators have considered the perceptual implications of the dynamic, learned vocal repertoires used by cetaceans. Instead, hearing has been treated as analogous to spectrographic analysis, with incoming sounds triggering fixed computations. In reality, however, cetaceans' auditory representations are constantly changing in the short and long term. For example, the songs of blue and humpback whales vary within the lifespans of individuals. Consequently, their auditory representations of songs will change over years. As singing whales change their songs over time, both singers and listeners will need to familiarize themselves with new properties to be able to make best use of the vocalizations that they sense.

The auditory representations that form the foundation for any cetacean's perceptual soundscapes are much more dynamic than the vocalizations that they hear or produce. This asymmetry in complexity and flexibility between produced and received signals is most evident in the case of echolocation. For instance, bottlenose dolphins can repetitively produce highly stereotyped clicks to produce an almost limitless variety of perceptual soundscapes, enabling them to form distinctive representations of complex objects they have never experienced before (Pack and Herman, 1995). These dynamic properties of echoic representations in cetaceans are entirely hidden from outside observers.

Seeking with Sound

Electrophysiological and computational analyses of auditory representations in bats currently provide the best indications of how cetaceans might extract spatial information from echoes. Although there are many differences between the vocalizations used by bats and cetaceans, both groups actively control sound production and reception in ways that affect their ability to resolve the positions and movements of sound sources (Moss et al., 2014). Like dolphins, bats often adjust the timing of their vocalizations while foraging, including producing cries within packets (Mayberry et al., 2019). Both groups also show some ability to form perceptual soundscapes using echoes produced by conspecifics' vocalizations (Xitco and Roitblat, 1996).

As noted in ***Communicative Clicks,*** echolocating cetaceans often vary properties of click trains depending on the echoes that they're experiencing. Some echolocating bats gradually morph the forms of their sonar signals based on the perceptual context, for example, by shifting the frequency content of cries as they approach a target (Moss et al., 2014). Although echolocating dolphins do not change their vocalizations in this way, other cetaceans, such as singing humpback whales, do gradually morph consecutive vocalizations (Mercado et al., 2022). Such vocal variations will shift emitted sound fields in a manner analogous to the changes produced when echolocating bats adjust properties of their cries. Might humpback whales benefit from morphing their vocalizations in the same way that echolocating bats do?

Most mysticetes produce structured vocal sequences (songs), with the complexity of sequences seeming to vary depending on the oceanic conditions within which the sequences are produced (Širović and Oleson, 2022). Mysticetes could potentially use echoes from songs to perceive behaviorally relevant environmental features (Ellison et al., 1987) or to monitor the movements of prey (Yi and Makris, 2016) and conspecifics (Mercado, 2018). The kinds of sound fields and auditory representations that would enable whales to construct echoic soundscapes over vast distances may differ significantly from those that enable dolphins to track and capture fleeing prey. By modulating temporal and spectral features of vocal sequences, mysticetes may selectively enhance aspects of their perceptual soundscapes.

Comparative studies of auditory representations in bats that focus on long-range echolocation and on recognition of faint signals within background reverberation can potentially clarify the auditory mechanisms mysticetes might use to construct spatial scenes from sonic echoes. Bats detect targets from long ranges when they are searching (Moss et al., 2014), and they can recognize faint echoes buried within reverberation when they are foraging from a perch (Neuweiler et al., 1987). During search flights, bats may repetitively produce a stereotyped cry or may alternate between two to three different vocalizations (Jung et al., 2014). Bats that hunt from perches often produce tonal cries in rapid succession, leading researchers to refer to them as high-duty-cycle bats. In both cases, bats generate relatively stable sound fields from which variations in returning echoes can reveal the presence of relevant targets.

The vocal strategies used by perching and searching bats have widely been regarded as irrelevant to analyses of cetacean vocal behavior. It is well-established, however, that singing humpback whales often maintain a relatively stationary position in the water column while singing, sometimes even resting their heads on the ocean floor. Adopting such postures increases the stability of the sound fields the singer generates, providing streams of returning reverberation that are acoustically analogous to the sound fields experienced by high-duty-cycle bats hanging from a perch (Mercado, 2021).

In the past, researchers have assumed that singing humpback whales remain stationary to increase the communicative effectiveness of their songs. The fact that a singer's movements affect the perceptual soundscape that the singer experiences has largely been ignored. Some have argued that humpback whales make no use of the echoes that their songs generate (Au et al., 2001). Without more data on how cetaceans represent the sounds they hear, however, it is difficult to say what they perceive.

Final Remarks

Cetaceans are widely regarded as some of the most vocally versatile animals on the planet. Historically, their sophisticated vocal skills have been linked to the evolution of complex social ecologies requiring the exchange of detailed situation-specific information. No less impressive is their capacity to survey their surroundings using sound. Clarifying what dolphins and whales listen for and how they represent the sounds they hear can reveal new facets of the functions of their vocalizations.

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