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REVIEW

Communication with self, friends and foes in active-sensing animals

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ABSTRACT

Animals that rely on electrolocation and echolocation for navigation and prey detection benefit from sensory systems that can operate in the dark, allowing them to exploit sensory niches with few competitors. Active sensing has been characterized as a highly specialized form of communication, whereby an echolocating or electrolocating animal serves as both the sender and receiver of sensory information. This characterization inspires a framework to explore the functions of sensory channels that communicate information with the self and with others. Overlapping communication functions create challenges for signal privacy and fidelity by leaving active-sensing animals vulnerable to eavesdropping, jamming and masking. Here, we present an overview of active-sensing systems used by weakly electric fish, bats and odontocetes, and consider their susceptibility to heterospecific and conspecific jamming signals and eavesdropping. Susceptibility to interference from signals produced by both conspecifics and prey animals reduces the fidelity of electrolocation and echolocation for prey capture and foraging. Likewise, active-sensing signals may be eavesdropped, increasing the risk of alerting prey to the threat of predation or the risk of predation to the sender, or drawing competition to productive foraging sites. The evolutionary success of electrolocating and echolocating animals suggests that they effectively counter the costs of active sensing through rich and diverse adaptive behaviors that allow them to mitigate the effects of competition for signal space and the exploitation of their signals.

KEY WORDS: Weakly electric fish, Bat, Odontocete, Electrolocation, Echolocation, Jamming avoidance response, Social signals

Introduction: an overview of active sensing

Most animals rely on some form of active sensing (see Glossary) to facilitate behaviors such as navigation, foraging and predator evasion. Active sensing falls into two broad categories: alloactive sensing and homeoactive sensing (see Glossary). In alloactive sensing, the animal moves its sensors to inspect and interact with the environment. Eye movements, manual object manipulation and rodent whisking are examples of alloactive sensing. Homeoactive sensing is characterized by the generation of stimulus energy to detect, localize and discriminate objects in the environment. A detailed disambiguation of the types of active sensing can be found in a recent review by Zweifel and Hartmann (2020). Here, we consider two broad examples of homeoactive sensing that have been featured in neuroethological research for decades and continue to generate new discoveries: electrolocation and echolocation.

Homeoactive-sensing animals that use electrolocation and echolocation actively generate signals to determine the distance, direction, size and features of nearby objects. For weakly electric fish that rely on electrolocation, and bats and odontocetes that rely on echolocation, active sensing allows them to operate in dark environments and to garner information from their immediate surroundings (Griffin, 1958; Heiligenberg, 1991). Both electrolocation and echolocation allow for the control of stimulus parameters critical to executing ecologically relevant tasks without light and with relatively low energetic costs (Crampton, 2019; Currie et al., 2020; Salazar et al., 2013; Speakman and Racey, 1991; Voigt and Lewanzik, 2012).

Homeoactive sensing and communication

The comparatively low cost of echolocation and electrolocation systems, combined with their sophistication and adaptability, makes them excellent channels for multiple forms of communication. In the case of active-sensing animals, the sender and receiver can be the same individual, conspecifics or heterospecifics. Thus, animals relying on electrolocation or echolocation exhibit different types of communication. They regularly engage in the generally accepted form of communication, information exchange with others, which comes with its own challenges (Brenowitz, 1986). However, animals that exploit homeoactive sensing systems also engage in a form of autocommunication, or communication with the self, by which they transmit signals into their environment and receive modified versions of those signals to gather information about the state of their surroundings (Bradbury and Vehrencamp, 1998). Although this definition of 'autocommunication' is refuted by those who posit that communication involves the transfer of symbolic information (see Hauser and Konishi, 1999), we find that this term provides a useful framework for considering challenges to homeoactive sensing. Specifically, many of the behaviors discussed in this Review (e.g. eavesdropping and jamming) reveal common features of autocommunication and animal-to-animal communication, as well as behavioral strategies to mitigate vulnerabilities.

The purpose of this Review is to consider the features of homeoactive sensory systems that jointly enable communication with self and others. Fig. 1 illustrates the communicative functions that drive adaptive signal design in homeoactive-sensing animals. We begin with a general overview of the mechanisms and functions of homeoactive sensing in weakly electric fish, bats and odontocetes. Then, we compare and contrast social communication, signal jamming, adaptive signal adjustments (ASAs; see Glossary), and eavesdropping in examples of electrolocating and echolocating species that are subject to specific penalties imposed by conspecifics and heterospecifics operating in the same sensory space. We further discuss how these penalties can be mitigated by

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Glossary

Active sensing
The use of sensory systems that make use of motor commands to collect and refine the reception of sensory signals. Can be categorized into alloactive and homeoactive sensing.

Alloactive sensing
The use of actions to move sensors (e.g. eyes, ears, whiskers) to better interact with sensory stimuli.

Adaptive signal adjustments (ASAs)
Adjustments in homeoactive signals in response to environmental stimuli, which includes but is not limited to jamming avoidance responses (JAR), defined below.

Communication
The act of transmitting information from a sender to a receiver through the environment, using optic, acoustic, chemical and electric signals.

Constant frequency-frequency modulated (CF-FM) calls
Sonar sounds used by some species of echolocating bats, which combine tonal and sweep components. CF components are well suited to convey information about velocity (through Doppler shift), and FM components are well suited to convey information about target distance (through echo arrival time).

Eavesdropping
Exploiting sensory signals intended for another individual or group.

Frequency-modulated (FM) calls
Sonar sounds containing frequency sweeps (typically, but not exclusively, downward) used by many species of echolocating bats.

Homeoactive sensing
The generation of external signals (sound, electricity) to probe the environment.

Jamming avoidance response (JAR)
A term first coined by Bullock et al. (1972) to describe shifts in the signal frequency generated by weakly electric knifefish in response to an external electrical signal close in frequency. The term JAR has been extended to echolocating animals, with the suggestion that adjustments in sonar signal design in the presence of echolocating conspecifics enable the parsing of sensory information collected from self-generated signals. JARs may involve changes in the timing or frequency content of emitted signals, or other strategies, such as pausing signal emission altogether.

Masking
Interference in the detection or discrimination of a signal that arises from environmental stimuli, such as sounds produced by running water, or signals produced by other animals.

Melon
Large, lipid-filled organ located in the forehead of odontocetes that acts as a sound transduction mechanism.

Signal jamming
The disruption of information transfer by an outside signal. This interference may be active (targeted to deliberately disrupt a sender) or passive (incidental disruption through two senders in close proximity).

Terminal buzz
The final portion of the prey capture echolocation sequence, when sounds are produced at the highest rate.

adaptive behaviors and propose a framework for future research on homeoactive sensing.

Electrolocation in weakly electric fish

Weakly electric fish are a group of aquatic animals that populate cluttered and often murky freshwater systems with low visibility. Three clades, the Gymnotiforms (native to Central and South America), the Mormyrids and Syndontids (both native to Africa) independently evolved organs that produce weak (<1 V) electric fields (Lavoué et al., 2012; Day et al., 2013). This Review focuses primarily on the well-described electrolocation and communication behaviors of the Gymnotiform and Mormyrid clades. Weakly electric fish use their electric organ discharges (EODs) to generate an electric signal and sense via electric receptors the resulting distortions in that signal introduced by nearby objects (Fig. 2A). Electric receptors are located in the epidermis, and sense changes in current flow that create an electric image across the fish's skin, encoding varying properties of nearby objects, such as conductivity, size, shape and distance. In addition to active electroreception, weakly electric fish can also rely on passive electroreception, detecting small electrical charges usually associated with muscle contractions of prey items or the signals produced by conspecifics. Weakly electric fish use electrolocation to navigate obstacles in their cluttered, low-visibility environments, detect and capture prey, and locate and communicate with conspecifics. Extensive reviews of electrolocation can be found in Bullock, 1982; von der Emde, 1999; Heiligenberg, 1991; Metzner and Viete, 1996.

Echolocation in bats and odontocetes

Many animals, including some birds (Griffin, 1958), use information carried by echoes; however, only echolocating bats and the toothed whales are able to adapt the features of their ultrasonic signals to accurately detect, localize and discriminate objects in the environment and pursue prey items. Adaptive sonar signal design, coupled with acute hearing in ultrasonic ranges, allows for tracking objects in three-dimensional environments while moving at high speeds. These two groups convergently evolved echolocation, and in the following sections we outline the basic mechanisms of signal production and adaptive signal designs.

Bats

Most bat species forage under conditions where their visual systems are ineffective, and thus use echolocation for foraging and obstacle avoidance. Most echolocating bats produce brief, high-frequency calls with the larynx, which they emit through the nose or open mouth (Fig. 2C), often at high intensities. They then extract information about their surroundings from echoes reflecting off nearby objects or potential prey items (Busnel and Fish, 1980; Griffin, 1958; Nachtigall and Moore, 1988; Popper and Fay, 2012; Thomas et al., 2004). Echolocation allows bats to orient in complex environments, identify and navigate to roost sites, and forage for food such as insects, small vertebrates, nectar and fruit. The variety of tasks supported by echolocation is possible because of the impressive diversity and flexibility of the emitted signals, whose features are influenced by ecology, allometric scaling, phylogeny and the animal's immediate surroundings. Several comprehensive reviews are available on bat echolocation (Fenton, 2003; Moss and Surlykke, 2010; Neuweiler, 1990; Schnitzler and Kalko, 2001).

Odontocetes

The odontocetes, commonly called toothed whales, are a large group of cetaceans encompassing superfamilies of oceanic dolphins, river dolphins, beaked whales, sperm whales and porpoises. It appears that all toothed whales have the capacity for echolocation (Surlykke et al., 2014). They use echolocation to hunt, with prey ranging from small fish and squid to other odontocetes. Odontocete habitats can present a variety of challenges: sea floors may be cluttered with corals and grasses, large groups of non-prey animals may scatter sonar reflections, and murky rivers or deep-ocean settings may transmit little or no light, reducing or eliminating visual information. There are species-specific anatomical and signal adaptations for echolocation based on foraging environment and prey type, as well as body size (Fenton et al., 2014; Jensen et al., 2018). Descriptions of head and jaw features across species, as well as detailed accounts of odontocete echolocation functions, are

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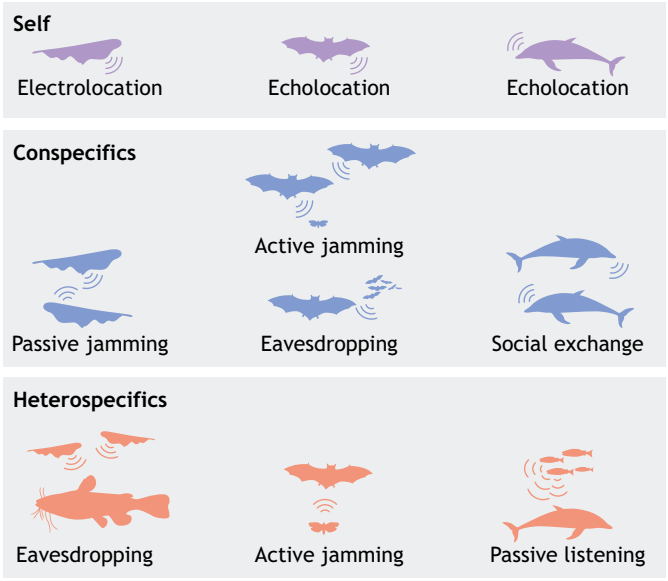

Fig. 1. Schematic illustration of communication with self, conspecifics and heterospecifics in homeoactive-sensing animals. Homeoactive sensing can be considered a form of communication, whereby the sender and receiver are the same individual. This specialized form of communication can also be impaired (unintentionally and intentionally) or intercepted by both conspecifics and heterospecifics. Here, we show several examples of potential communication interactions that arise from the use of active sensing. This is not an exhaustive list of all possible interactions, but merely examples of well-reported communication exchanges in homeoactive-sensing animals. Top panel: examples of self-communication (electrolocation and electrolocation). Middle panel: conspecific–self communication may be either intentional (active jamming, eavesdropping on conspecifics and social exchanges) or unintentional (passive jamming). Bottom panel: heterospecific–self communication can involve homeoactive-sensing animals as senders (eavesdropping by predators or prey) or receivers (jamming by prey, passively listening for prey generated sounds).

discussed in the book *Biosonar*, edited by Surlykke et al. (2014). Additionally, in-depth comparisons between bat and toothed whale echolocation can be found in reviews by Au (1993, 2004), Au and Simmons (2007), and Madsen and Surlykke (2014).

Comparative homeoactive sensing

Bats, dolphins and weakly electric fish adapt their signals actively to adjust for tasks and conditions, and marked similarities in production patterns have emerged. Examples of such similarities include increased signal production rate during active target inspection (seen in odontocetes, bats and weakly electric fish, Moss and Surlykke, 2010; von der Emde, 1992; Penner, 1988) and inspection behaviors, such as using specific head and body movements to control signal reception, and to separate target from clutter (observed in weakly electric fish and bats, Babineau et al., 2007; Moss et al., 2006; Surlykke et al., 2009; Taub and Yovel, 2020; von der Emde, 2006). The primary distinction between these animal groups revolves around their operation in different media, under water and in air, which affects signal generation and transmission in the environment. The similarities in active-sensing behaviors across weakly electric fish, bats and odontocetes, despite differences in media and mechanisms, make these groups rich sources for comparative studies of sensory ethology (Fig. 2C).

Adaptive signal adjustments to maintain robust homeoactive sensing

Homeoactive-sensing animals that operate in groups face the challenge of separating their own signals from those of conspecifics. Signal jamming or interference (see Glossary) may arise from the overlap in time and/or frequency of homeoactive signals with those produced by conspecifics (see Fig. 3). The presence of signals produced by other animals may interfere with the ability of homeoactive-sensing animals to extract information from returns of their own, via masking (see Glossary), degrading or canceling out their signals. A variety of behavioral reactions employed by homeoactive-sensing animals are posited to mitigate signal interference and are commonly referred to as jamming avoidance responses (JARs, see Glossary). The term JAR was originally coined to describe frequency adjustments made by weakly electric fish to avoid interference by conspecifics and use of this term has been extended to echolocating bats and cetaceans. Although there is some evidence that signal jamming interferes with behavior of Gymnotiform electric fish (Heiligenberg, 1973), such evidence is lacking in Mormyrid electric fish (Schumacher et al., 2016) and is sparse in echolocating bats (Corcoran et al., 2009; Corcoran and Conner, 2014). Ambiguity in separating signal adjustments based on active control (to explicitly avoid jamming) and effects (improved performance on sensory tasks) has obfuscated past work on jamming avoidance. Indeed, we currently lack data demonstrating the effects of failing to make signal adjustments on behavioral performance. Therefore, we propose the use of broader term, adaptive signal adjustments (ASAs), to capture what may be JARs, along with other behavioral responses to stimuli in an animal's surroundings.

Weakly electric fish

Early work on electric discharge adjustments in weakly electric fish has influenced criteria for assessing JARs or ASAs in other species. Both spectral and temporal JARs in weakly electric fish have evolved independently at least twice (Heiligenberg, 1976, 2012; Kawasaki and Guo, 1996), suggesting the importance of maintaining signal separation from nearby conspecifics for robust electrolocation. Table S1 summarizes behavioral studies of JARs in weakly electric fish.

Weakly electric fish exhibit two discharge types. Wave-type species emit near-constant quasi-sinusoidal electric fields and measure amplitude shifts in the field to represent electric images. Wave-type fish produce EODs in species-specific frequency ranges (Hopkins and Heiligenberg, 1978). When two conspecifics with similar EOD frequencies interact, their signals may jam each other through deconstructive interference, or antiphase signals, which nullify the electric field for both individuals (Fig. 3A). Posited to minimize the risk of jamming, most wave-type fish placed within detection range of each other will shift the frequency of their EODs either up or down to maximize the EOD frequency distance between individuals (Bullock et al., 1972; Watanabe and Takeda, 1963).

Pulse-type fish produce isolated electric pulses rather than constant fields of electricity. Thus, for these fishes, the risk of jamming arises from temporal overlap of individual pulses rather than spectral overlap. Thought to minimize jamming, fish alter the inter-pulse interval of their EOD when operating in pairs or groups (Westby, 1988). Individuals are hypothesized to track inter-pulse intervals of the fish around them and respond to the signals of conspecifics by either increasing or decreasing their own EOD rate, presumably to minimize the probability of overlapping their EOD pulses with those of neighbors (Baker, 1980; Heiligenberg, 1974; Westby, 1988).

Some populations of fish do not exhibit JARs, even under conditions that typically evoke signal adjustments in other species (Fortune et al., 2020). Laboratory studies of jamming show reduced

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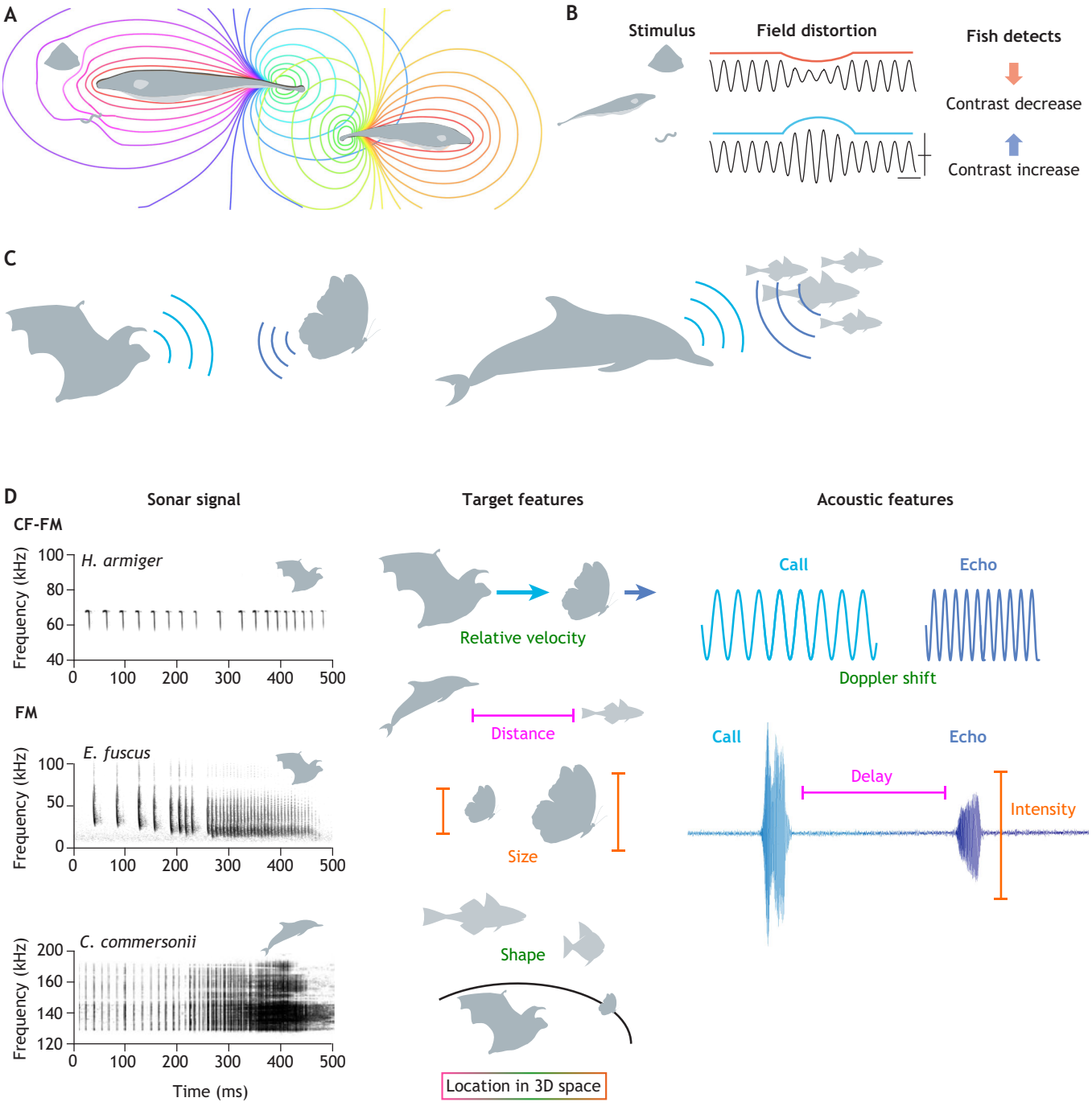

Fig. 2. Electrolocation and echolocation. (A) Weakly electric fish produce electric fields originating from an electric organ located in the tail. Objects and conspecifics in the environment modulate the field, allowing the fish to detect prey, obstacles, mates and competitors. (B) An isolated fish detects changes in self-generated field amplitude when encountering a rock (resistive) or prey item (conductive); these create electric field amplitude decreases (red arrow) or increases (blue arrow), respectively. Scale bars are approximate. Vertical: –2.5–2.5 mV, horizontal: 5 ms. (C) Both bats and odontocetes produce high-intensity ultrasonic acoustic signals and listen for returning echoes to detect, localize and discriminate objects in their environment. Bats produce sonar sounds with their larynx or tongue and emit signals through their mouth or nose that are reflected from objects, such as prey items. Odontocetes use a specialized set of phonic lips located beneath the blowhole to produce sonar clicks, which are amplified through the melon. These clicks are reflected by the swim bladders of target prey items. (D) Different sonar signal structures of bats (*Hipposideros amiger, Eptesicus fuscus*) and odontocetes are (*Cephalorhynchus commersonii*) shown in the left panel. A CF-FM call (top) contains a constant tone combined with a frequency sweep, whereas an FM call (middle) contains a frequency sweep alone. Most odontocetes produce brief broadband ultrasonic clicks for echolocation. Representative dolphin click train (bottom panel) based on Reyes et al. (2015). The middle panel illustrates target features, such as relative velocity, distance, size, shape and 3D location that are represented by features of echoes. Acoustic features of echoes, such as Doppler shift (navy compressed waveform), delay (pink time axis bar) and intensity (orange amplitude bar), are illustrated in the bottom right panel.

target discrimination accuracy in the presence of spectrally overlapping signals (Fortune, 2006). However, in the wild, fish may be more likely to mitigate interference from another animal's signals by physically moving away from a jamming signal rather than shifting the frequency of its own, or by increasing reliance on passive electroreception of environmental electric signals instead of

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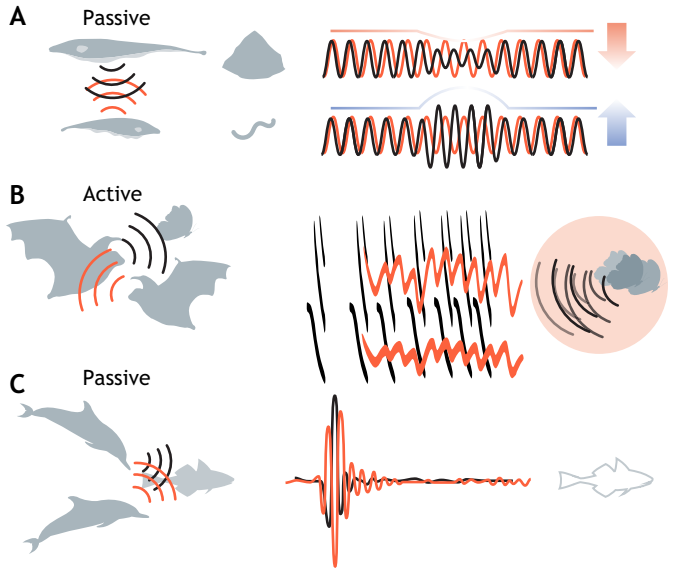

Fig. 3. Passive and active jamming. (A) Two weakly electric fish with similar discharge frequencies passively create deconstructive signal interference by overlapping out-of-phase electric organ discharges. The result is a reduced contrast electric field, making it difficult to detect field amplitude increases (blue arrow) and decreases (red arrow). (B) A bat actively jams another by producing a call (left) that overlaps temporally and spectrally with the foraging bat's terminal buzz (middle, echolocation sequence in black, jamming call in orange); based on Corcoran and Conner (2014). Some insects produce ultrasound that may jam bat sonar (right), see Corcoran et al. (2010). These signals potentially interfere with a bat's localization of a prey item. (C) Two dolphins produce off-axis clicks (left) that may overlap temporally while inspecting the same target. This hypothetical scenario potentially reduces returning echo intensity (middle) and interferes with target detection (right). Based on Kloepper and Branstetter (2019). Note that these examples represent posited behaviors in different species reported in the literature. Alternative interpretations have also been suggested.

active electrolocation. Indeed, it may be that spectral changes in electric signals often serve social functions, as appeasement or 'good manners' for fish populations living in groups or in close proximity, where increasing physical distance from a conspecific's signal is not possible.

In pulse species, researchers have speculated whether there is a clear distinction between jamming avoidance behaviors and communication. Mormyrid fish show shifts in electrolocation signals that might serve communicative functions and reinforce school cohesion, rather than active avoidance of temporal signal overlap (Carlson, 2002; Moller, 1980; Worm et al., 2018), particularly because there is evidence that object discrimination is not reliably impaired by overlapping conspecific signals (Schumacher et al., 2016). In gymnotiform pulse fish, turn-taking and signal synchronization has long been speculated to play a role in establishing social hierarchies (Westby, 1979). Active targeted jamming in weakly electric fish that use pulse signals has also been recently posited: *Microsternarchus* and *Steatogenys* fishes interacting with a playback stimulus (mimicking a conspecific in the lab) frequently timed their EOD modulations to maximize overlap between their own signals and the mimic (Field et al., 2019). The purpose of this behavior is as yet unknown, but may serve as an assertion of social rank, a measure of competitiveness, or any number of other complex communicative functions. These findings have yet to be quantified in freely interacting fish in more naturalistic settings, but it appears that some signaling behaviors characterized as targeted jamming may in fact serve a communication function during conspecific encounters. The communicative function of targeted jamming has also been suggested for some species of echolocating bats (see below).

Bats

Because bat echolocation relies on information obtained from spectral and temporal echo features, hypotheses about jamming avoidance in these animals have been guided by work on weakly electric fish, which shows shifts in signal frequency or pulse timing, as described above, even though these well-established patterns fail to encompass weakly electric fishes' full range of behaviors, particularly in their natural habitats (Fortune et al., 2020; Benda, 2020). Given the greater flexibility in signal production exhibited by laryngeal echolocators compared with weakly electric fish, we use the term adaptive signal adjustments (ASAs) to refer to call shortening or lengthening, a cessation of calling or spectral changes evoked by the presence of conspecifics, as well as responses to echoes from objects in the environment.

The gregarious nature of many bat species often leads to acoustically crowded foraging sites. Fortunately, there are several features of bat echolocation systems that allow them to readily overcome conspecific acoustic interference, such as changing emission rates (Amichai et al., 2015), exploiting the directionality of sonar emissions and hearing (Adams et al., 2019; Chiu et al., 2010; Ghose and Moss, 2003; Grinnell and Schnitzler, 1977; Jakobsen and Surlykke, 2010; Schnitzler and Grinnell, 1977; Surlykke et al., 2009), and relying on naturally occurring individual differences in signal design (Brigham et al., 1989; Kazial et al., 2001; Masters et al., 1991, 1995; Obrist, 1995; Siemers and Kerth, 2006; Siemers et al., 2005; Chiu et al., 2009). In addition, there is evidence that bats adjust call duration, bandwidth and intensity in response to the surrounding environmental stimuli (Grinnell, 1995; Hiryu et al., 2010; Moss and Surlykke, 2001, 2010). Some species, however, face additional proximity-related challenges arising from competition for resources, which may evoke the production of communication sounds intermingled with echolocation, as described below (Corcoran and Conner, 2014; Wright et al., 2014). Table S2 summarizes ASA (also referred to as JAR) studies in bats.

Numerous studies have demonstrated that bats alter sonar signal parameters in response to environmental sounds and signals produced by conspecifics, and the specific adjustments to potential acoustic interference appear to be highly context-dependent (Fenton et al., 2004; Kazial et al., 2001; Masters et al., 1995; Pearl and Fenton, 1996; Siemers and Schnitzler, 2004; Yovel et al., 2009). For spectral examples, data show that bats bidirectionally shift their call frequencies away from a pure tone (Bates et al., 2008; Gillam and Montero, 2016; Ulanovsky, 2004), adjust call frequencies up or down in response to signals from nearby conspecifics (Ulanovsky, 2004) and alter call peak frequencies, potentially to maximize individual differences (Bartonička et al., 2007; Corcoran and Conner, 2014; Ibáñez et al., 2004; Necknig and Zahn, 2011; Ratcliffe et al., 2004). In some species, such as *Eptesicus fuscus*, one bat in a pair may cease echolocating altogether for short periods (Chiu et al., 2008). This example of an ASA strategy may also serve a communicative function, i.e. 'keeping the channel clear' minimizes signal overlap while also potentially conveying social hierarchy. Chiu et al. (2008) reported that bats exhibiting 'silent behavior' in a competitive foraging context were typically dominant males that were also victors in prey capture. Bats have also been observed to alter their emission rates (Adams et al., 2017; Jarvis et al., 2010, 2013), duration (Amichai et al., 2015; Corcoran et al., 2011; Gillam et al.,

2007; Obrist, 1995; Tressler and Smotherman, 2009) and intensity (Amichai et al., 2015; Fawcett et al., 2015; Schmidt and Joermann, 1986) when other bats are nearby. Takahashi et al. (2014) reported bats using frequency-modulated (FM) sonar signals (see Glossary) alter the timing of their calls to minimize overlap with band-limited noise bursts that are similar to the JAR seen in pulse-type weakly electric fish. Although some reports claim that these behaviors represent a JAR, others suggest that the call modifications can be explained by other factors, such as attention to objects in the animal's surroundings (Cvikel et al., 2015a,b; Götze et al., 2016), which prompted us to introduce the broader term, adaptive signal adjustment. Whether adjustments in echolocation call parameters in response to acoustic signals produced by neighboring animals constitute a JAR or a non-specific reaction remains a topic of debate. In order to address this issue, we critically need data demonstrating the behavioral consequences of animals failing to adjust their signal parameters in response to conspecific signals.

Odontocetes

Although some odontocetes are solitary foragers unlikely to face conspecific jamming (Connor et al., 1998), many species of odontocete are highly social, cooperative foragers that might coordinate signal production to reduce overlapping echolocation signals among individuals in a pod. Whereas foraging bats have been documented both to direct sonar emissions towards (Corcoran and Conner, 2014) and away from conspecifics (Chiu et al., 2010), dolphins have been reported to behave in a 'mannerly' fashion, although this has yet to be systematically explored. Accounts published in the book *Dolphin Days* detail the interactions between captive Hawaiian spinners (*Stenella longirostris*) that were never documented to 'spray each other with loud sounds' because they swam in formations that would not result in pointing their sonic beams at their tank mates (Norris, 1991). There have been no quantitative measurements of sonar beam aim-directing behaviors in group-swimming dolphins to support this. However, there have been reports of aggressive behaviors, including the use of seemingly directed sonic pulses of bottlenose dolphins, *Tursiops truncatus* (Blumquist and Amundin, 2004), which may be the cause of high-frequency hearing loss observed in adult males (Mann et al., 2010).

Despite 'polite' echolocating behaviors and the microsecond duration of clicks, making temporal overlap a low probability occurrence, the large group size and high click rate of some group-hunting dolphins may be subjected to some acoustic interference from conspecifics. The extent to which signals from conspecifics affect odontocete echolocation in the wild is not known. To date, a single study of *Tursiops truncatus* responses to interfering signals has been published (Kloepper and Branstetter, 2019). Researchers tested two male dolphins performing a phantom target detection task under quiet conditions and in the presence of interference signals. Both dolphins were able to maintain 100% detection rate under all conditions, but they did exhibit changes in the parameters of their own click emissions. These changes, however, were not consistent between the two individuals; for example, dolphin 1 decreased the interval between successive clicks as the interfering stimulus click rate was increased, whereas the opposite effect was observed in dolphin 2. It is difficult to assess whether this represents individual strategies for overcoming interference or whether these effects were related to hearing loss suffered by dolphin 1. This study, like many bat studies, shows that the external stimulus does not necessarily impair task performance, and thus poses the question of whether adaptive responses in signal design should be attributed to jamming avoidance or the animal's individual natural reaction to sounds in its surroundings.

In contrast, other group-foraging odontocetes such as beaked whales, do not show any behavioral changes in their click emissions with increased group size (Alcázar-Treviño et al., 2021). This suggests that species may differ in their susceptibility to interference – possibly owing to the directionality of their signals – or may exhibit other behaviors to mitigate interference, such as maintaining separation from conspecifics.

Interpretation of signal adjustments in homeoactive-sensing animals

Heterospecific and conspecific signal interference present acoustic challenges that homeoactive-sensing animals must overcome through adaptive behaviors. In the literature on weakly electric fish reviewed above, we see that adjustments in signal design by animals in close proximity can serve both JAR and social functions, but the more stereotyped signal adjustments associated with JAR have received far more research attention. Within the bat bioacoustics research community, reports of signal jamming and JARs have stimulated a controversy. We distil this controversy into two primary arguments.

First, some stand strictly by the definition of JAR originally established in weakly electric fish that refers to an increased or decreased signal frequency or temporal repetition rate to increase separation from the jamming signal. Following this definition, we might expect experimental studies to show responses to interfering signals tied to species-specific call structures, whereby bats may either shift signal frequency in response to jamming signals, similar to the frequency shifts of wave-type weakly electric fish, or adjust the timing of their calls in response to jamming signals, as seen in pulse-type weakly electric fish. Few experiments to date have reported robust and consistent call adjustments to mitigate acoustic interference in bats using either FM or CF-FM calls (see Glossary).

Second, some assert that adjustments in bat echolocation behavior that have been characterized as JARs actually arise from shifts in the animal's attention and as a response to echoes returning from nearby conspecifics (Cvikel et al., 2015a,b, Götze et al., 2016). These researchers further argue that evidence is lacking to demonstrate that shifts in echolocation signal design in reaction to sounds in the environment constitutes jamming avoidance. Careful analysis of echolocation call features in events where bats crash or fail to capture prey may shed light on this issue.

Targeted signal jamming

As noted above, there are many sources of signal interference that challenge homeoactive sensing, but in this section, we focus specifically on 'active' interference, or 'intentional' signal jamming, in which conspecifics or heterospecifics interfere with the information used by homeoactive-sensing animals. The distinguishing feature of active signal jamming is that the interfering signals are used with the intention of disrupting normal homeoactive sensing.

We consider targeted signal jamming and its elicited responses to be a special form of communication that can occur between both conspecifics and heterospecifics. This type of communication can occur when conspecifics share a similar set of signals to compete for limited sensory space, or it can act as a defensive mechanism used by prey to evade predation.

Weakly electric fish

Canonically, the gymnotiform JAR has been reported as a stereotyped, almost reflex-like, behavior (Viete and Heiligenberg,

1991). The beauty of the electric fish system is its tractability in laboratory settings, where artificial stimuli can be tightly controlled and evoke consistent and reproducible behaviors. In this animal system, there are numerous reports of frequency shifts resembling the JAR and even its inverse, targeted jamming, which appears to serve a conspecific communication role in weakly electric fish. Instances of targeted jamming as a feature of agonistic encounters have been observed in controlled laboratory settings where female *A. leptorhynchus* may establish rank via frequency matching, the opposite of JAR behavior, when a weakly electric fish raises its EOD frequency to match that of another individual. Females in particular may engage in this behavior rather than producing discrete communication signals, such as chirps (transient, upward frequency modulations) or exhibiting physical aggression (Tallarovic and Zakon, 2005). It is more difficult to categorize and quantify the behaviors of weakly electric fish interacting in the wild, but with improved long-term recording technology, reports of diverse signaling behaviors are emerging. There is evidence from field studies, for example, that agonistic frequency rises in signals produced by weakly electric fish may be used for purposeful jamming; although it is currently unknown whether this behavior is restricted to females or used by both sexes (Benda, 2020).

Bats

Insectivorous bats do not cooperate when they forage. Rather, group foraging often leads to competition for resources that can evoke agonistic signaling, such as the production of 'food-claiming calls', which can drive competitors from a prey item (Wright et al., 2014). In addition to food-claiming communication behaviors, there is a report that foraging insectivorous bats actively jam conspecifics. Corcoran and Conner (2014) published an account of bats appearing to jam the sonar of other bats when competing for prey. *Tadarida brasiliensis* produces sinusoidal frequency-modulated (sinFM) calls directed toward conspecifics approaching a selected prey item, often resulting in the competing individual failing to make a successful capture. During playback experiments, sinFM calls were broadcast via a loudspeaker as bats attempted to capture tethered moths, and under these conditions, bats exhibited decreases in capture success, especially when sinFM calls overlapped the terminal buzz (see Glossary) portion of the attacking bats' echolocation sequence. Whether this represents true jamming deserves additional consideration, as *E. fuscus* presented with this same *T. brasiliensis* sinFM signal did not fail to capture prey, although they did alter their echolocation call structure (Jones et al., 2018). It is therefore plausible that the sinFM calls produced by *T. brasiliensis* serve a social function similar to the food-claiming calls produced by *E. fuscus* in a competitive foraging context, and additional experiments should be conducted to disambiguate the functionality of these calls.

An additional source of jamming in bat echolocation comes from their insect prey. Some moth species evolved an acoustic defensive strategy against bat predators following the evolution of hearing structures. As they are able to hear the echolocation calls of approaching bats, arctiid moths respond by producing their own high-frequency clicks that reduce the capture success of the bats targeting them (Barber and Conner, 2006; Blest et al., 1963; Corcoran et al., 2010; Dunning, 1968). Multiple hypotheses have been proposed to explain the functionality of these moth clicks (Edmunds, 1974; Fullard et al., 1979, 1994; Hoy et al., 1989; Møhl and Surlykke, 1989; Troest and Møhl, 1986), and one prominent explanation is the 'ranging interference' hypothesis (Corcoran et al., 2011; Masters and Raver, 1996; Miller, 1991), wherein moth-generated clicks degrade the bats' ability to accurately determine the distance to the target.

Odontocetes

The literature is largely speculative on the topic of targeted jamming in marine mammals. Pulsed sounds, in addition to the commonly studied odontocete whistles, are thought to function in intraspecific communication in toothed whales (Tyack, 1986). Social sounds have been documented in Hector's dolphin (*Cephalorhynchus hectori*) when exhibiting aggressive behaviors (Dawson, 1991) and in harbor porpoises (*Phocoena phocoena*) that are in distress or engaging in agonistic encounters (Clausen et al., 2010). Bottlenose dolphins (*Tursiops truncatus*) also emit pulsed sounds during aggressive behaviors (Overstrom, 1983), and when individuals were separated by a net permitting acoustic and visual, but not physical, contact, they were observed to act aggressively towards each other (Thomas et al., 2004) in the form of directed bursts of pulse sound types in conjunction with aggressive physical gestures. The emitted pulses resembled typical echolocation sounds but were produced at higher pulse repetition rates, up to 940 pulses per second (with intervals of just over 1 ms). However, it is unclear whether the setup of the study itself, a net placed in a narrow channel between two pools, could have contributed to or escalated the aggressive interactions by creating an environment that made them more likely to occur, as the dolphins were captive, genetically related animals that routinely swam freely together. Whether free-living dolphins use sound production to actively interfere with the echolocation of another dolphin is not known.

Eavesdropping on echolocation and electrolocation signals

In communication, eavesdropping (see Glossary) occurs when one animal intercepts signals of another to glean useful information. This might involve scenarios in which homeoactive-sensing animals listen to the signals of conspecifics to glean information (Barber et al., 2003; Razak, 2018; Madsen et al., 2002), predators listen to the signals produced by homeoactive-sensing animals to find prey (Stoddard, 1999), or prey listen to signals produced by homeoactive-sensing animals to evade predation (Fullard, 1998).

Weakly electric fish

There is little published evidence for conspecific eavesdropping in weakly electric fish. In mormyrid fish, the negative image efference copy of self-generated EODs disambiguates self-signals from social signals (Bell, 1982; Fukutomi and Carlson, 2020; Xu-Friedman and Hopkins, 1999) and enhances stimulus detection (Enikolopov et al., 2018), making eavesdropping less useful than self-generated signals. Wave-type gymnotiforms lack the negative self-efference of mormyrids, but rely on inhibitory feedback and the geometry of their electrosensory fields to disambiguate self from conspecific signals (Carr et al., 1982; Shumway and Maler, 1989). Moreover, because the self-generated signals of wave-type fish are constant, it is difficult to conjure a natural scenario where eavesdropping could occur. Pulse-type gymnotiforms may benefit from eavesdropping on conspecific signals, but this has not been reported. However, these weakly electric fish face a different dilemma, namely eavesdropping by predators (Stoddard, 1999; Stoddard and Markham, 2008).

Weakly electric fish are the prey of larger electroreceptive predators such as the electric eel (Westby, 1988) and electroreceptive catfish (Hanika and Kramer, 1999, 2000). Both lineages of weakly electric fish are prey to electroreceptive predators and thus are subject to similar levels of evolutionary pressure to maintain signal crypsis

(Stoddard et al., 2019) by avoiding the electric discharge frequencies to which predators are tuned. The ampullary electroreceptors used by these predators are common in passively electroreceptive animals (von der Emde, 2013) and are most sensitive to low-frequency electric signals characteristic of muscle contractions (Kalmijn, 1988). Weakly electric fish can exploit this limitation by using high frequencies to maintain conspecific communication while remaining inconspicuous to predators. Low-frequency, monophasic pulses appear to be the basal condition of active electroreception (Albert and Crampton, 2005; Bass, 1986), but are comparatively rare in both mormyrids and gymnotiforms (Catania, 2019; Stoddard et al., 2019). Weakly electric fishes that are more likely to serve as prey than act as predators are under strong selective pressure to produce complex EOD pulses with multiple phases and voltage symmetry to minimize low-frequency components of the emission spectra, which keeps their signals out of the sensitivity ranges of ampullary receptors used by predators (Stoddard, 2002; Stoddard and Markham, 2008; Stoddard et al., 2019). These complex, high-frequency EODs are less likely to be detected by both catfish and eels (Hanika and Kramer, 1999, 2000; Stoddard, 1999). Supporting this crypsis hypothesis, fishes in high-predation areas exhibit high-shifted frequency peaks compared with fishes from lower-predation areas (Stoddard et al., 2019).

An exception to the shift into higher EOD frequencies to evade predation is exhibited by males of several genera, both gymnotiform and mormyrid, during courtship behaviors. Weakly electric fish in breeding condition elongate the final EOD phase, thus shifting frequencies lower and back into the signal detection range of predators (Franchina et al., 2001; Hagedorn, 1995). This potentially risky behavior may serve to convey mate quality in the face of predation risk (Zahavi, 1975), especially because it is frequently observed in the presence of females and competing males (Gavassa et al., 2013).

Bats

Although they are not cooperative foragers, insectivorous bats still have a propensity to aggregate, likely attracted by the echolocation sounds associated with feeding and increased detection distance of insect swarms (Boonman et al., 2019; Cvikel et al., 2015a,b; Dechmann et al., 2009; Gillam, 2007). Despite rapid attenuation in air, high-frequency echolocation calls can be detectable by bats at distances of many meters. A 20 kHz sonar call has the potential to be heard by conspecifics over 100 m away, and the echo of a large insect from that call could be detectable by a bat at a range of approximately 11 m (outlined in Jones and Siemers, 2011). Eavesdropping on others can increase an individual's success in finding abundant food sources. Naturally, increased competition drives the sharing of resources, and we might predict that animals alter their signal design to elude potential eavesdroppers, as suggested by the production of micro-calls of foraging hoary bats (Corcoran and Weller, 2018). However, stereotypical echolocation patterns persist during foraging of most bat species, regardless of the presence of competitors. This suggests that eavesdropping on the calls of foraging bats could offer a powerful survival strategy.

In laboratory experiments, paired *E. fuscus* competing for a single prey item may eavesdrop on conspecifics. Data show that this species exhibits following behaviors, in which one bat flies closely behind the other and ceases echolocating (Chiu et al., 2008). This silent behavior occurs on average 40% of the time when the bats are less than 1 m apart. Without their own echolocation to guide them, silent bats can rely on passively listening to their conspecific's vocalizations to localize their competitor and track its foraging activity. Flying in silence, combined with spatial memory (Barchi et al., 2013; Ulanovsky and Moss, 2008), allows bats to orient in the dark without homeoactive sensing. Chiu et al. (2008) proposed that bats with similar echolocation structures may also be able to exploit the echoes of another bat's sonar signals to localize objects. Evidence lies in findings from laboratory experiments demonstrating that bats can interpret 'phantom echoes' to discriminate the distance (or arrival time) of sonar call playbacks (Masters and Jacobs, 1989; Masters et al., 1997; Moss and Schnitzler, 1989, 1995).

Eavesdropping on echolocation calls can also serve as a method of animal identification, with an individual's vocal signature encoding important social information that is conveyed to listeners (Jones, 2008). For example, in one study, the lesser bulldog bat (*Noctilio albiventris*) was presented echolocation signals from conspecifics known to the experimental individual, along with those of unfamiliar conspecifics and heterospecifics sharing roost space (Voigt-Heucke et al., 2010). The bats reacted most often to unfamiliar conspecifics and least often to cohabitating heterospecifics, suggesting that the bats are capable of distinguishing the calls of different species and known individuals within their species. This kind of eavesdropping can also facilitate basic needs, such as recruiting additional members of a species to a roost site to increase thermoregulatory efficiency (Kerth and Reckardt, 2003). Additionally, free-living *Saccopteryx bilineata* can identify the sex of an approaching bat based on its echolocation calls, and individuals exhibit differential responses to males and females (Knörnschild et al., 2012); female *E. fuscus* can discriminate between male and female echolocation calls of unfamiliar bats from playbacks, as indicated by alterations to their own call rate (Kazial and Masters, 2004).

Many insect prey can detect the high-intensity echolocation calls of bats. The ability to hear an approaching bat and thus undertake measures to evade capture appears to be a common strategy employed by insects. Thus, eavesdropping on echolocation by potential prey has driven an evolutionary arms race between bats and their quarry. Many insects are highly sensitive to ultrasonic frequencies and exhibit strong negative phonotaxis to sounds in the >20 kHz range (Hoy et al., 1989; Mason et al., 1998; Yager and May, 1990; Forrest et al., 1995; Miller and Surlykke, 2001). Lepidopterans (moths and butterflies) in particular have evolved ultrasonic hearing specialized for detecting echolocation calls (Yack and Fullard, 2000), and they undertake dramatic evasive maneuvers in flight in response to ultrasound to avoid capture (Miller and Surlykke, 2001). This leads some bats to adopt very low-intensity echolocation calls to avoid detection by prey (Goerlitz et al., 2010). Eavesdropping on heterospecific echolocation may be a particularly valuable defense strategy for bats that are subject to predation by carnivorous species of bats, although reports of evasive movements after hearing predatory bat echolocation calls are scarce (Lima and O'Keefe, 2013).

Odontocetes

It has also been proposed that dolphins are able to rely on the echolocation clicks and echoes from nearby conspecifics. This type of eavesdropping is referred to as the 'echoic eavesdropping hypothesis' (Gregg et al., 2007) in dolphins. Evidence of cooperative eavesdropping is found in rough-toothed dolphins (*Steno bredanesis*). In wild pods, groups of individuals swimming in close proximity in coordinated subgroups are often silent, with a single dolphin echolocating in approximately 80% of observed swims (Götz et al., 2006). When the dolphins swim in a less tightly coordinated manner, multiple dolphins tend to be echolocating. This

suggests that dolphins may purposely coordinate their group behaviors to facilitate eavesdropping and simultaneously reduce their likelihood of interfering with another dolphin's echolocation.

Early studies by Scronce and Johnson (1976) demonstrated that captive dolphins prevented from using their own sonar were able to detect the presence of targets using only echoes from an ensonified sphere. Twenty years later, two dolphins positioned along the same axis (Xitco and Roitblat, 1996) were tested in an acoustic match-to-sample task. The eavesdropper's melon (see Glossary) was above the water's surface, preventing the use of echolocation (but permitting sound reception), whereas the other was fully submerged directly in the water and allowed to probe sonar targets. The eavesdropping dolphin performed at levels above chance and similar to that of its companion.

Eavesdropping by prey is also a driver of foraging behavior among odontocetes. Several species of fish are sensitive to ultrasound, including dolphin clicks (Mann et al., 2001) and may undertake evasive maneuvers when hearing a predator approach. Orcas that specialize in feeding on seals, which are sensitive to ultrasonic frequencies, tend to hunt 'silently'. While approaching prey, orcas produce very few echolocation clicks to avoid alerting prey to their approach (Deecke et al., 2011). Sonar hunting behavior may also increase competition from other species drawn to productive hunting grounds, as playback experiments indicate that orca signals recorded during a hunting bout are attractive to pilot whales, although this behavior may also be explained as a mobbing defense strategy by the pilot whales against orcas (Curé et al., 2012).

Eavesdropping by acoustically sensitive prey and competitors is a fundamental weakness of reliance on echolocation for hunting. The evolution of ultrasonic hearing among animals that serve as prey to both bats and odontocetes indicates that having an early warning system for a predatory approach is a highly effective protector. Behavioral strategies of both predators and prey to counter the success of opponents continue to be exciting avenues for further research.

Perspectives and conclusions

This Review considers the benefits and vulnerabilities of homeoactive sensory systems and highlights the dynamic interplay between social communication, eavesdropping and signal interference in weakly electric fish, odontocetes and bats. Specifically, we lay out a framework for considering the intersection of ASA, social communication and predator–prey interactions in animals that generate signals to probe their surroundings.

We aim to inspire readers of this Review to consider the diverse behavioral tasks, coupled with evolutionary and ecological factors, that drive homeoactive-sensing animals to adapt their signals to acquire robust stimuli from their surroundings. For example, weakly electric fish have been well studied in the laboratory; however, because of their remote origins and the difficulty of coordinating unobtrusive long-term electrical observations, comparatively little is known about how electric signal communication, jamming and jamming avoidance manifests in the wild. Field studies have the potential to shed new light on the story of their social, jamming and JAR interactions. Recent advances in technology such as large-scale, long-term recording arrays and computational methods for tracking individuals (Henninger et al., 2020) are just now allowing researchers to glimpse the nuances of communication in the wild. Likewise, studies of bats and odontocetes suggest that these animals have the potential to glean information from the echolocation signals of others, but it is unclear how this information is encoded, how reliable the encoded information is and whether bats actually use this information to operate in the natural environment (see Balcombe and Fenton; Barclay, 1982; Gillam, 2007).

Despite being remarkably social and sophisticated animals, the lack of experimental data on the natural sources of ASAs in weakly electric fish, bats and odontocetes makes it difficult to draw direct comparisons among species in these very diverse groups. This challenge is augmented by the need for appropriate definitions of adaptive responses to environmental stimuli that reflect the complex interplay of jamming avoidance, social signaling and predator–prey interactions that act upon the same sensory modality. To address this issue, we propose that adaptive responses to environmental signals be evaluated with species-specific operational definitions, and with consideration of signal domain, design and production constraints. Adoption of this approach will help to establish a unifying framework for the study of social communication and ASAs in homeoactive-sensing animals in natural settings.

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References

Adams, A. M., Davis, K. and Smotherman, M. (2017). Suppression of emission rates improves sonar performance by flying bats. *Sci. Rep.* **7**, 41641.

Adams, A. M., Patricio, A., Manohar, R. and Smotherman, M. (2019). Influence of signal direction on sonar interference. *Anim. Behav.* **155**, 249-256. doi:10.1016/j.anbehav.2019.05.024

Albert, J. S. and Crampton, W. G. R. (2005). Diversity and phylogeny of neotropical electric fishes (Gymnotiformes). In *Electroreception* (ed. T. H. Bullock, C. D. Hopkins, A. N. Popper and R. R. Fay), pp. 360-409. New York, NY: Springer New York.

Alcázar-Treviño, J., Johnson, M., Arranz, P., Warren, V. E., Pérez-González, C. J., Marques, T., Madsen, P. T. and Aguilar de Soto, N. (2021). Deep-diving beaked whales dive together but forage apart. *Proc. R. Soc. B* **288**, 20201905.

Amichai, E., Blumrosen, G. and Yovel, Y. (2015). Calling louder and longer: how bats use biosonar under severe acoustic interference from other bats. *Proc. R. Soc. B Biol. Sci.* **282**, 20152064. doi:10.1098/rspb.2015.2064

Au, W. W. L. (1993). *The Sonar of Dolphins*. New York: Springer-Verlag.

Au, W. W. L. (2004). A comparison of the sonar capabilities of bats and dolphins. In *Echolocation in Bats and Dolphins* (ed. J. Thomas, C. Moss and M. Vater), pp. 76-98. Chicago: University of Chicago Press.

Au, W. and Simmons, J. (2007). Echolocation in dolphins and bats.

Babineau, D., Lewis, J. E. and Longtin, A. (2007). Spatial acuity and prey detection in weakly electric fish. *PLOS Comput. Biol.* **3**, e38.

Baker, C. L. (1980). Jamming avoidance behavior in Gymnotoid electric fish with pulse-type discharges: Sensory encoding for a temporal pattern discrimination. *J. Comp. Physiol.* **136**, 165-181. doi:10.1007/BF00656910

Balcombe, J. P. and Fenton, M. B. (1988) Eavesdropping by Bats: The influence of echolocation call design and foraging strategy. *Ethology* **79**, 158-166.

Barber, J. R. and Conner, W. E. (2006). Tiger moth responses to a simulated bat attack: timing and duty cycle. *J. Exp. Biol.* **209**, 2637-2650. doi:10.1242/jeb.02295

Barber, J. R., Razak, K. A. and Fuzessery, Z. M. (2003). Can two streams of auditory information be processed simultaneously? Evidence from the gleaning bat Antrozous pallidus. *J. Comp. Physiol. [A]* **189**, 843-855. doi:10.1007/s00359-003-0463-6

Barchi, J. R., Knowles, J. M. and Simmons, J. A. (2013). Spatial memory and stereotypy of flight paths by big brown bats in cluttered surroundings. *J. Exp. Biol.* **216**, 1053-1063. doi:10.1242/jeb.073197

Barclay, R. M. R. (1982). Interindividual use of echolocation calls: eavesdropping by bats. *Behav. Ecol. Sociobiol.* **10**, 271-275. doi:10.1007/BF00302816

Bartonička, T., Řehák, Z. and Gaisler, J. (2007). Can pipistrelles, *Pipistrellus pipistrellus* (Schreber, 1774) and *Pipistrellus pygmaeus* (Leach, 1825), foraging in

a group, change parameters of their signals? *J. Zool.* **272**, 194-201. doi:10.1111/j.1469-7998.2006.00255.x
Bass, A. H. (1986). Electric organs revisited: evolution of a vertebrate communication and orientation organ. In Electroreception (ed. T. H. Bullock, W. Heiligenberg), pp. 13–70. New York, John Wiley and Sons.
Bates, M. E., Stamper, S. A. and Simmons, J. A. (2008). Jamming avoidance response of big brown bats in target detection. *J. Exp. Biol.* **211**, 106-113. doi:10.1242/jeb.009688
Bell, C. C. (1982). Properties of a modifiable efference copy in an electric fish. *J. Neurophysiol.* **47**, 1043-1056. doi:10.1152/jn.1982.47.6.1043
Benda, J. (2020). The physics of electrosensory worlds. In *The Senses: A Comprehensive Reference* (ed. B. Fritzsch and H. Bleckmann), pp. 228-254. Elsevier.
Blest, A. D., Collett, T. S. and Pye, J. D. (1963). The generation of ultrasonic signals by a New World arctiid moth. *Proc. R. Soc. Lond. B Biol. Sci.* **158**, 196-207. doi:10.1098/rspb.1963.0042
Blumquist, C. and Amundin, M. (2004). High-frequency burst-pulse sounds in agonistic/aggresive interactions in bottlenose dolphins, *Tursiops truncatus*. In *Echolocation in bats and dolphins* (ed. Thomas, Moss and Vater), pp. 425-431. The University of Chicago Press.
Boonman, A., Fenton, B. and Yovel, Y. (2019). The benefits of insect-swarm hunting to echolocating bats, and its influence on the evolution of bat echolocation signals. *PLoS Comput. Biol.* **15**, e1006873. doi:10.1371/journal.pcbi.1006873
Bradbury, J. W. and Vehrencamp, S. L. (1998). *Principles of Animal Communication*. Sunderland, MA: Sinauer Associates.
Brenowitz, E. A. (1986). Environmental influences on acoustic and electric animal communication. *Brain Behav. Evol.* **28**, 32-42. doi:10.1159/000118690
Brigham, R. M., Cebek, J. E. and Hickey, M. B. C. (1989). Intraspecific variation in the echolocation calls of two species of insectivorous bats. *J. Mammal.* **70**, 426-428. doi:10.2307/1381534
Bullock, T. H. (1982). Electroreception. *Annu. Rev. Neurosci.* **5**, 121-170. doi:10.1146/annurev.ne.05.030182.001005
Bullock, T. H., Hamstra, R. H. and Scheich, H. (1972). The jamming avoidance response of high frequency electric fish. *J. Comp. Physiol.* **77**, 1-22. doi:10.1007/BF00696517
Bullock, T. H., Behrend, K. and Heiligenberg, W. (1975). Comparison of the jamming avoidance responses in gymnotoid and gymnarchid electric fish: a case of convergent evolution of behavior and its sensory basis. *J. Comp. Physiol.* **103**, 97-121. doi:10.1007/BF01380047
Busnel, R.-G. and Fish, J. F. (eds) (1980). *Animal Sonar Systems*. New York: Plenum Press.
Carlson, B. A. (2002). Electric signaling behavior and the mechanisms of electric organ discharge production in mormyrid fish. *J. Physiol. Paris* **96**, 405-419. doi:10.1016/S0928-4257(03)00019-6
Carr, C. E., Maler, L. and Sas, E. (1982). Peripheral organization and central projections of the electrosensory nerves in gymnotiform fish. *J. Comp. Neurol.* **211**, 139-153. doi:10.1002/cne.902110204
Catania, K. C. (2019). The Astonishing Behavior of Electric Eels . *Front. Integr. Neurosci.* **13**, 23. doi:10.3389/fnint.2019.00023
Chiu, C., Xian, W. and Moss, C. F. (2008). Flying in silence: echolocating bats cease vocalizing to avoid sonar jamming. *Proc. Natl. Acad. Sci.* **105**, 13116-13121. doi:10.1073/pnas.0804408105
Chiu, C., Xian, W. and Moss, C. F. (2009). Adaptive echolocation behavior in bats for the analysis of auditory scenes. *J. of Exp. Biol,* **212**, 1392-1404. doi:10.1242/jeb.027045
Chiu, C., Reddy, P. V., Xian, W., Krishnaprasad, P. S. and Moss, C. F. (2010). Effects of competitive prey capture on flight behavior and sonar beam pattern in paired big brown bats, Eptesicus fuscus. *J. Exp. Biol.* **213**, 3348-3356. doi:10.1242/jeb.044818
Clausen, K. T., Wahlberg, M., Beedholm, K., DeRuiter, S. and Madsen, P. T. (2010). Click communication in harbour porpoises (Phocoena phocoena). *Bioacoustics* **20**, 1-28.
Connor, R. C., Mann, J., Tyack, P. L. and Whitehead, H. (1998). Social evolution in toothed whales. *Trends Ecol. Evol.* **13**, 228-232. doi:10.1016/S0169-5347(98)01326-3
Corcoran, A. J. and Conner, W. E. (2014). Bats jamming bats: food competition through sonar interference. *Science* **346**, 745-747. doi:10.1126/science.1259512
Corcoran, A. J. and Weller, T. J. (2018). Inconspicuous echolocation in hoary bats (Lasiurus cinereus). *Proc. R. Soc. B* **285**, 20180441. doi:10.1098/rspb.2018.0441
Corcoran, A. J., Conner, W. E. and Barber, J. R. (2010). Anti-bat tiger moth sounds: form and function. *Curr. Zool.* **56**, 358-369. doi:10.1093/czoolo/56.3.358
Corcoran, A. J., Barber, J. R., Hristov, N. I. and Conner, W. E. (2011). How do tiger moths jam bat sonar? *J. Exp. Biol.* **214**, 2416-2425. doi:10.1242/jeb.054783
Corcoran, A. J., Barber, J. R. and Conner, W. E. (2009). Tiger moth jams bat sonar. *Science* **325**, 325-327.
Crampton, W. G. R. (2019). Electroreception, electrogenesis and electric signal evolution. *J. Fish Biol.* **95**, 92-134. doi:10.1111/jfb.13922
Curé, C., Antunes, R., Samarra, F., Alves, A. C., Visser, F., Kvadsheim, P. H. and Miller, P. J. (2012). Pilot whales attracted to killer whale sounds: acoustically-mediated interspecific interactions in cetaceans. *PloS one, 7,* **12**, e52201. doi:10.1371/journal.pone.0052201
Currie, S. E., Boonman, A., Troxell, S., Yovel, Y. and Voigt, C. C. (2020). Echolocation at high intensity imposes metabolic costs on flying bats. *Nat. Ecol. Evol.* **4**, 1174-1177. doi:10.1038/s41559-020-1249-8
Cvikel, N., Egert Berg, K., Levin, E., Hurme, E., Borissov, I., Boonman, A., Amichai, E. and Yovel, Y. (2015a). Bats aggregate to improve prey search but might be impaired when their density becomes too high. *Curr. Biol.* **25**, 206-211. doi:10.1016/j.cub.2014.11.010
Cvikel, N., Levin, E., Hurme, E., Borissov, I., Boonman, A., Amichai, E. and Yovel, Y. (2015b). On-board recordings reveal no jamming avoidance in wild bats. *Proc. R. Soc. B* **282**, 20142274. doi:10.1098/rspb.2014.2274
Dawson, S. M. (1991). Clicks and Communication: The Behavioural and Social Contexts of Hector's Dolphin Vocalizations. *Ethology* **88**, 265-276.
Day, J. J., Peart, C. R., Brown, K. J., Friel, J. P., Bills, R. and Moritz, T. (2013). Continental diversification of an African catfish radiation (Mochokidae: Synodontis). *Systematic Biology,* **62**, 351-365. doi:10.1093/sysbio/syt001
Dechmann, D. K. N., Heucke, S. L., Giuggioli, L., Safi, K., Voigt, C. C. and Wikelski, M. (2009). Experimental evidence for group hunting via eavesdropping in echolocating bats. *Proc. R. Soc. Lond. B Biol. Sci.* **276**, 2721-2728.
Deecke, V. B., Nykänen, M., Foote, A. D. and Janik, V. M. (2011). Vocal behaviour and feeding ecology of killer whales Orcinus orca around Shetland, UK. *Aquatic Biology,* **13**, 79-88. doi:10.3354/ab00353
Dunning, D. C. (1968). Warning sounds of moths. *Z. Für Tierpsychol.* **25**, 129.
Dye, J. (1987). Dynamics and stimulus-dependence of pacemaker control during behavioral modulations in the weakly electric fish, Apteronotus. *J. Comp. Physiol. A* **161**, 175-185. doi:10.1007/BF00615239
Edmunds, M. (1974). *Defence in Animals: A Survey of Anti-predator Defences*. Longman.
Enikolopov, A. G., Abbott, L. F. and Sawtell, N. B. (2018). Internally generated predictions enhance neural and behavioral detection of sensory stimuli in an electric fish. *Neuron* **99**, 135-146.e3. doi:10.1016/j.neuron.2018.06.006
Fawcett, K., Jacobs, D. S., Surlykke, A. and Ratcliffe, J. M. (2015). Echolocation in the bat, *Rhinolophus capensis*: the influence of clutter, conspecifics and prey on call design and intensity. *Biol. Open* **4**, 693-701. doi:10.1242/bio.201511908
Fenton, M. B. (2003). Eavesdropping on the echolocation and social calls of bats. *Mammal. Rev.* **33**, 193-204. doi:10.1046/j.1365-2907.2003.00019.x
Fenton, M. B. and Bell, G. P. (1981). Recognition of species of insectivorous bats by their echolocation calls. *J. Mammal.* **62**, 233-243. doi:10.2307/1380701
Fenton, M. B., Jacobs, D. S., Richardson, E. J., Taylor, P. J. and White, W. (2004). Individual signatures in the frequency-modulated sweep calls of African large-eared, free-tailed bats *Otomops martiensseni* (Chiroptera: Molossidae). *J. Zool.* **262**, 11-19. doi:10.1017/S095283690300431X
Fenton, M. B., Jensen, F. H., Kalko, E. K. V. and Tyack, P. L. (2014). Sonar Signals of Bats and Toothed Whales. In *Biosonar* (ed. A. Surlykke, P. E. Nachtigall, R. R. Fay and A. N. Popper), pp. 11-59. New York, NY: Springer.
Field, C. E., Petersen, T. A., Alves-Gomes, J. A. and Braun, C. B. (2019). A JAR of chirps: the gymnotiform chirp can function as both a communication signal and a jamming avoidance response. *Front. Integr. Neurosci.* **13**, 55. doi:10.3389/fnint.2019.00055
Forrest, T. G., Farris, H. E. and Hoy, R. R. (1995). Ultrasound acoustic startle response in scarab beetles. *The Journal of experimental biology, 198,* **12**, 2593-2598. doi:10.1242/jeb.198.12.2593
Fortune, E. S. (2006). The decoding of electrosensory systems. *Curr. Opin. Neurobiol.* **16**, 474-480. doi:10.1016/j.conb.2006.06.006
Fortune, E. S., Andanar, N., Madhav, M., Jayakumar, R. P., Cowan, N. J., Bichuette, M. E. and Soares, D. (2020). Spooky interaction at a distance in cave and surface dwelling electric fishes. *Front. Integr. Neurosci.* **14**, 561524. doi:10.3389/fnint.2020.561524
Franchina, C. R., Salazar, V. L., Volmar, C. H. and Stoddard, P. K. (2001). Plasticity of the electric organ discharge waveform of male Brachyhypopomus pinnicaudatus. II. Social effects. *J. Comp. Physiol. [A]* **187**, 45-52. doi:10.1007/s003590000176
Fukutomi, M. and Carlson, B. A. (2020). A history of corollary discharge: contributions of mormyrid weakly electric fish . *Front. Integr. Neurosci.* **14**, 42. doi:10.3389/fnint.2020.00042
Fullard, J. H. (1998). The sensory coevolution of moths and bats. In *Comparative Hearing: Insects*, (ed. R. R. Hoy, A. N. Popper and R. R. Fay) pp. 279-326. New York, NY: Springer.
Fullard, J. H., Fenton, M. B. and Simmons, J. A. (1979). Jamming bat echolocation: the clicks of arctiid moths. *Can. J. Zool.* **57**, 647-649. doi:10.1139/z79-076
Fullard, J. H., Simmons, J. A. and Saillant, P. A. (1994). Jamming bat echolocation: the dogbane tiger moth *Cycnia tenera* times its clicks to the terminal attack calls of the big brown bat *Eptesicus fuscus*. *J. Exp. Biol.* **194**, 285-298. doi:10.1242/jeb.194.1.285
Gavassa, S., Roach, J. P. and Stoddard, P. K. (2013). Social regulation of electric signal plasticity in male Brachyhypopomus gauderio. *J. Comp. Physiol. A*

Neuroethol. Sens. Neural. Behav. Physiol. **199**, 375-384. doi:10.1007/s00359-013-0801-2
Ghose, K. and Moss, C. F. (2003). The sonar beam pattern of a flying bat as it tracks tethered insects. *J. Acoust. Soc. Am.* **114**, 1120-1131. doi:10.1121/1.1589754
Gillam, E. H. G. H. (2007). Eavesdropping by bats on the feeding buzzes of conspecifics. *Can. J. Zool.* **85**, 795-801. doi:10.1139/Z07-060
Gillam, E. H. and Montero, B. K. (2016). Influence of call structure on the jamming avoidance response of echolocating bats. *J. Mammal.* **97**, 14-22. doi:10.1093/jmammal/gyv147
Gillam, E. H., Ulanovsky, N. and McCracken, G. F. (2007). Rapid jamming avoidance in biosonar. *Proc. R. Soc. B Biol. Sci.* **274**, 651-660. doi:10.1098/rspb.2006.0047
Goerlitz, H. R., ter Hofstede, H. M., Zeale, M. R., Jones, G. and Holderied, M. W. (2010). An aerial-hawking bat uses stealth echolocation to counter moth hearing. *Current Biology, 20,* **17**, 1568-1572. doi:10.1016/j.cub.2010.07.046
Götz, T., Verfuß, U. K. and Schnitzler, H.-U. (2006). 'Eavesdropping' in wild rough-toothed dolphins (*Steno bredanensis*). *Biol. Lett.* **2**, 5-7.
Götze, S., Koblitz, J., Denzinger, A. and Schnitzler, H.-U. (2016). No evidence for spectral jamming avoidance in echolocation behavior of foraging pipistrelle bats. *Sci. Rep.* **6**, 30978. doi:10.1038/srep30978
Gregg, J. D., Dudzinski, K. M. and Smith, H. V. (2007). Do Dolphins eavesdrop on the echolocation signals of conspecifics? *Int. J. Comp. Psychol.* **20**, 65-88.
Griffin, D. R. (1958). *Listening in the Dark: The Acoustic Orientation of Bats and Men*. Oxford, England: Yale University Press.
Grinnell, A. D. (1995). Hearing in bats: an overview. In *Hearing by Bats*, pp. 1-36. New York, NY: Springer New York.
Grinnell, A. D. and Schnitzler, H.-U. (1977). Directional sensitivity of echolocation in the Horseshoe bat, *Rhinolophus ferrumequinum*. *J. Comp. Physiol. A Neuroethol. Sens. Neural. Behav. Physiol.* **116**, 63-76. doi:10.1007/BF00605517
Habersetzer, J. (1981). Adaptive echolocation sounds in the bat *Rhinopoma hardwickei*: a field study. *J. Comp. Physiol. A* **144**, 559-566. doi:10.1007/BF01326841
Hagedorn, M. (1995). The electric fishv*Hypopomus occidentaliscan* rapidly modulate the amplitude and duration of its electric organ discharges. *Anim. Behav.* **49**, 1409-1413. doi:10.1006/anbe.1995.0174
Hanika, S. and Kramer, B. (1999). Electric organ discharges of mormyrid fish as a possible cue for predatory catfish. *Naturwissenschaften* **86**, 286-288. doi:10.1007/s001140050616
Hanika, S. and Kramer, B. (2000). Electrosensory prey detection in the African sharptooth catfish, Clarias gariepinus (Clariidae), of a weakly electric mormyrid fish, the bulldog (Marcusenius macrolepidotus). *Behav. Ecol. Sociobiol.* **48**, 218-228. doi:10.1007/s002650000232
Hauser, M. D. and Konishi, M. (eds) (1999). *The Design of Animal Communication*. MIT press.
Heiligenberg, W. (1973). Electrolocation of objects in the electric fish Eigenmannia (Rhamphichthyidae, Gymnotoidei). *J. Comp. Physiol.* **87**, 137-164. doi:10.1007/BF01352158
Heiligenberg, W. (1974). Electrolocation and jamming avoidance in a Hypopygus (Rhamphichthyidae, Gymnotoidei), an electric fish with pulse-type discharges. *J. Comp. Physiol.* **91**, 223-240. doi:10.1007/BF00698054
Heiligenberg, W. (1976). Electrolocation and jamming avoidance in the mormyrid fish *Brienomyrus*. *J. Comp. Physiol.* **109**, 357-372. doi:10.1007/BF00663615
Heiligenberg, W. F. (1991). *Neural Nets in Electric Fish*. Cambridge, MA: MIT Press.
Heiligenberg, W. (2012). *Principles of Electrolocation and Jamming Avoidance in Electric Fish: A Neuroethological Approach*, Vol. 1. Springer Science & Business Media.
Henninger, J., Krahe, R., Sinz, F. and Benda, J. (2020). Tracking activity patterns of a multispecies community of gymnotiform weakly electric fish in their neotropical habitat without tagging. *J. Exp. Biol.* **223**, jeb206342.
Hiryu, S., Bates, M. E., Simmons, J. A. and Riquimaroux, H. (2010). FM echolocating bats shift frequencies to avoid broadcast-echo ambiguity in clutter. *Proc. Natl. Acad. Sci. USA* **107**, 7048-7053. doi:10.1073/pnas.1000429107
Hopkins, C. D. and Heiligenberg, W. F. (1978). Evolutionary designs for electric signals and electroreceptors in gymnotoid fishes of Surinam. *Behav. Ecol. Sociobiol.* **3**, 113-134. doi:10.1007/BF00294985
Hoy, R., Nolen, T. and Brodfuehrer, P. (1989). The neuroethology of acoustic startle and escape in flying insects. *J. Exp. Biol.* **146**, 287-306. doi:10.1242/jeb.146.1.287
Ibáñez, C., Juste, J., López-Wilchis, R. and Núñez-Garduño, A. (2004). Habitat variation and jamming avoidance in echolocation calls of the sac-winged bat (*Balantiopteryx plicata*). *J. Mammal.* **85**, 38-42. doi:10.1644/1545-1542(2004)085<0038:HVAJAI>2.0.CO;2
Jakobsen, L. and Surlykke, A. (2010). Vespertilionid bats control the width of their biosonar sound beam dynamically during prey pursuit. *Proc. Natl. Acad. Sci.* **107**, 13930-13935. doi:10.1073/pnas.1006630107
Jarvis, J., Bohn, K. M., Tressler, J. and Smotherman, M. (2010). A mechanism for antiphonal echolocation by free-tailed bats. *Anim. Behav.* **79**, 787-796. doi:10.1016/j.anbehav.2010.01.004
Jarvis, J., Jackson, W. and Smotherman, M. (2013). Groups of bats improve sonar efficiency through mutual suppression of pulse emissions. *Front. Physiol.* **4**, 140. doi:10.3389/fphys.2013.00140
Jensen, F. H., Johnson, M., Ladegaard, M., Wisniewska, D. M. and Madsen, P. T. (2018). Narrow acoustic field of view drives frequency scaling in toothed whale biosonar. *Curr. Biol.* **28**, 3878-3885. doi:10.1016/j.cub.2018.10.037
Jones, G. (2008). Sensory ecology: echolocation calls are used for communication. *Curr. Biol.* **18**, R34-R35. doi:10.1016/j.cub.2007.10.056
Jones, G. and Siemers, B. M. (2011). The communicative potential of bat echolocation pulses. *J. Comp. Physiol. A* **197**, 447-457. doi:10.1007/s00359-010-0565-x
Jones, T. K., Wohlgemuth, M. J. and Conner, W. E. (2018). Active acoustic interference elicits echolocation changes in heterospecific bats. *J. Exp. Biol.* **221**, jeb176511.
Kalmijn, Ad. J. (1988). Detection of weak electric fields. In *Sensory Biology of Aquatic Animals* (ed. J. Atema, R. R. Fay, A. N. Popper and W. N. Tavolga), pp. 151-186. New York, NY: Springer.
Kawasaki, M. and Guo, Y. X. (1996). Neuronal circuitry for comparison of timing in the electrosensory lateral line lobe of the African wave-type electric fish Gymnarchus niloticus. *J. Neurosci.* **16**, 380-391.
Kazial, K. A. and Masters, W. M. (2004). Female big brown bats, *Eptesicus fuscus*, recognize sex from a caller's echolocation signals. *Anim. Behav.* **67**, 855-863. doi:10.1016/j.anbehav.2003.04.016
Kazial, K. A., Burnett, S. C. and Masters, W. M. (2001). Individual and group variation in echolocation calls of big brown bats, *Eptesicus fuscus*. *J. Mammal.* **82**, 339-351. doi:10.1644/1545-1542(2001)082<0339:IAGVIE>2.0.CO;2
Kerth, G. and Reckardt, K. (2003). Information transfer about roosts in female Bechstein's bats: an experimental field study. *Proc. R. Soc. B Biol. Sci.* **270**, 511-515. doi:10.1098/rspb.2002.2267
Kloepper, L. N. and Branstetter, B. K. (2019). The effect of jamming stimuli on the echolocation behavior of the bottlenose dolphin, *Tursiops truncatus*. *J. Acoust. Soc. Am.* **145**, 1341-1352. doi:10.1121/1.5093636
Knörnschild, M., Jung, K., Nagy, M., Metz, M. and Kalko, E. (2012). Bat echolocation calls facilitate social communication. *Proc. R. Soc. B Biol. Sci.* **279**, 4827-4835. doi:10.1098/rspb.2012.1995
Kramer, B. (1978). Spontaneous discharge rhythms and social signalling in the weakly electric fish Pollimyrus isidori (Cuvier et Valenciennes) (Mormyridae, Teleostei). *Behav. Ecol. Sociobiol.* **4**, 61-74. doi:10.1007/BF00302561
Lavoué, S., Miya, M., Arnegard, M. E., Sullivan, J. P., Hopkins, C. D. and Nishida, M. (2012). Comparable ages for the independent origins of electrogenesis in African and South American weakly electric fishes. *PLoS one* **7**, e36287. doi:10.1371/journal.pone.0036287
Lima, S. L. and O'Keefe, J. M. (2013). Do predators influence the behaviour of bats? *Biological Reviews* **88**, 626-644. doi:10.1111/brv.12021
Mann, D. A., Higgs, D. N., Tavolga, W. N., Souza, M. J. and Popper, A. N. (2001). Ultrasound detection by clupeiform fishes. *J. Acoust. Soc. Am.* **109**, 3048-3054.
Mann, D., Hill-Cook, M., Manire, C., Greenhow, D., Montie, E., Powell, J., Wells, R., Bauer, G., Cunningham-Smith, P., Lingenfelser, R., et al. (2010). Hearing loss in stranded odontocete Dolphins and whales. *PLoS ONE* **5**, e13824. doi:10.1371/journal.pone.0013824
Madsen, P. T., Surlykke, A. (2014). Echolocation in air and water. In *Biosonar* (ed. A. Surlykke, P. E. Nachtigall, R. R. Fay and A. N. Popper), pp. 257-304. New York, NY: Springer.
Madsen, P. T., Wahlberg, M. and Møhl, B. (2002). Male sperm whale (Physeter macrocephalus) acoustics in a high-latitude habitat: implications for echolocation and communication. *Behav. Ecol. Sociobiol.* **53**, 31-41. doi:10.1007/s00265-002-0548-1
Mason, A. C., Forrest, T. G. and Hoy, R. R. (1998). Hearing in mole crickets (Orthoptera: Gryllotalpidae) at sonic and ultrasonic frequencies. *J. Exp. Biol.* **201**, 1967-1979. doi:10.1242/jeb.201.12.1967
Masters, W. M. and Jacobs, S. C. (1989). Target detection and range resolution by the big brown bat (*Eptesicus fuscus*) using normal and time-reversed model echoes. *J. Comp. Physiol. A Neuroethol. Sens. Neural. Behav. Physiol.* **166**, 65-73. doi:10.1007/BF00190211
Masters, W. M. and Raver, K. A. S. (1996). The degradation of distance discrimination in big brown bats (*Eptesicus fuscus*) caused by different interference signals. *J. Comp. Physiol. A* **179**, 703-713. doi:10.1007/BF00216134
Masters, W. M., Jacobs, S. C. and Simmons, J. A. (1991). The structure of echolocation sounds used by the big brown bat *Eptesicus fuscus*: Some consequences for echo processing. *J. Acoust. Soc. Am.* **89**, 1402-1413. doi:10.1121/1.400660
Masters, W. M., Raver, K. A. S. and Kazial, K. A. (1995). Sonar signals of big brown bats, *Eptesicus fuscus*, contain information about individual identity, age and family affiliation. *Anim. Behav.* **50**, 1243-1260. doi:10.1016/0003-3472(95)80041-7
Masters, W. M., Raver, K. A. S., Kornacker, K. and Burnett, S. C. (1997). Detection of jitter in intertarget spacing by the big brown bat Eptesicus fuscus. *J. Comp. Physiol. [A]* **181**, 279-290. doi:10.1007/s003590050114

Matsubara, J. and Heiligenberg, W. (1978). How well do electric fish electrolocate under jamming? *J. Comp. Physiol.* **125**, 285-290. doi:10.1007/BF00656862
Metzner, W. (1993). The jamming avoidance response in Eigenmannia is controlled by two separate motor pathways. *J. Neurosci.* **13**, 1862-1878. doi:10.1523/JNEUROSCI.13-05-01862.1993
Metzner, W. and Viete, S. (1996). The neuronal basis of communication and orientation in the weakly electric fish, eigenmannial. communication behavior or: seeking a conspecific's response. *Naturwissenschaften* **83**, 6-14.
Miller, L. A. (1991). Arctiid moth clicks can degrade the accuracy of range difference discrimination in echolocating big brown bats, *Eptesicus fuscus*. *J. Comp. Physiol. A* **168**, 571-579. doi:10.1007/BF00215079
Miller, L. A. and Surlykke, A. (2001). How some insects detect and avoid being eaten by bats: Tactics and countertactics of prey and predator. *Bioscience* **51**, 570-581. doi:10.1641/0006-3568(2001)051[0570:HSIDAA]2.0.CO;2
Møhl, B. and Surlykke, A. (1989). Detection of sonar signals in the presence of pulses of masking noise by the echolocating bat, *Eptesicus fuscus*. *J. Comp. Physiol. A Neuroethol. Sens. Neural. Behav. Physiol.* **165**, 119-124. doi:10.1007/BF00613805
Moller, P. (1980). Electroreception and the behaviour of mormyrid electric fish. *Trends Neurosci.* **3**, 105-109. doi:10.1016/0166-2236(80)90041-7
Moss, C. F. and Schnitzler, H.-U. (1989). Accuracy of target ranging in echolocating bats: acoustic information processing. *J. Comp. Physiol. A* **165**, 383-393. doi:10.1007/BF00619357
Moss, C. F. and Schnitzler, H.-U. (1995). Behavioral Studies of Auditory Information Processing. In *Hearing by Bats* (ed. A. N. Popper and R. R. Fay), pp. 87-145. New York, NY: Springer.
Moss, C. F. and Surlykke, A. (2001). Auditory scene analysis by echolocation in bats. *J. Acoust. Soc. Am.* **110**, 2207-2226. doi:10.1121/1.1398051
Moss, C. F. and Surlykke, A. (2010). Probing the natural scene by echolocation in bats. *Front. Behav. Neurosci.* **4**, 33. doi:10.3389/fnbeh.2010.00033
Moss, C. F., Bohn, K., Gilkenson, H. and Surlykke, A. (2006). Active listening for spatial orientation in a complex auditory scene. *PLoS Biol.* **4**, e79. doi:10.1371/journal.pbio.0040079
Nachtigall, P. E. and Moore, P. W. B. (eds.) (1988). *Animal Sonar: Processes and Performance*. Springer US.
Necknig, V. and Zahn, A. (2011). Between-species jamming avoidance in Pipistrelles? *J. Comp. Physiol. A* **197**, 469-473. doi:10.1007/s00359-010-0586-5
Neuweiler, G. (1990). Auditory adaptations for prey capture in echolocating bats. *Physiol. Rev.* **70**, 615-641. doi:10.1152/physrev.1990.70.3.615
Norris, K. S. (1991). *Dolphin Days: The Life and Times of the Spinner Dolphin*. W. W. Norton, Incorporated.
Obrist, M. K. (1995). Flexible bat echolocation: the influence of individual, habitat and conspecifics on sonar signal design. *Behav. Ecol. Sociobiol.* **36**, 207-219. doi:10.1007/BF00177798
Overstrom, N. A. (1983). Association between burst-pulse sounds and aggressive behavior in captive Atlantic bottlenosed dolphins (Tursiops truncatus). *Zoo Biol.* **2**, 93-103. doi:10.1002/zoo.1430020203
Partridge, B. L. and Heiligenberg, W. (1980). Three's a crowd? Predicting Eigenmannia's responses to multiple jamming. *J. Comp. Physiol. A* **136**, 153-164.
Pearl, D. L. and Fenton, M. B. (1996). Can echolocation calls provide information about group identity in the little brown bat (*Myotis lucifugus*)? *Can. J. Zool.* **74**, 2184-2192. doi:10.1139/z96-247
Penner, R. H. (1988). Attention and detection in dolphin echolocation. In *Animal Sonar*, pp. 707-713. Boston, MA: Springer.
Petzold, J. M., Alves-Gomes, J. A. and Smith, G. T. (2018). Chirping and asymmetric jamming avoidance responses in the electric fish D*istocyclus conirostris*. *J. Exp. Biol.* **221**, jeb178913. doi:10.1242/jeb.178913
Popper, A. N. and Fay, R. R. (eds.) (2012). *Hearing by Bats*. Springer-Verlag New York, Inc.
Ratcliffe, J. M., ter Hofstede, H. M., Avila-Flores, R., Fenton, M. B., McCracken, G. F., Biscardi, S., Blasko, J., Gillam, E., Orprecio, J. and Spanjer, G. (2004). Conspecifics influence call design in the Brazilian free-tailed bat, *Tadarida brasiliensis*. *Can. J. Zool.* **82**, 966-971. doi:10.1139/z04-074
Razak, K. A. (2018). Adaptations for substrate gleaning in bats: the pallid bat as a case study. *Brain. Behav. Evol.* **91**, 97-108. doi:10.1159/000488873
Reyes, M. V., Iñíguez, M. A., Hevia, M., Hildebrand, J. A. and Melcón, M. L. (2015). Description and clustering of echolocation signals of Commerson's dolphins (Cephalorhynchus commersonii) in Bahía San Julián, Argentina. *J. Acoust. Soc. Am.* **138**, 2046-2053. doi:10.1121/1.4929899
Russell, C. J., Myers, J. P. and Bell, C. C. (1974). The echo response in Gnathonemus petersii (Mormyridae). *J. Comp. Physiol.* **92**, 181-200. doi:10.1007/BF00694505
Salazar, V. L., Krahe, R. and Lewis, J. E. (2013). The energetics of electric organ discharge generation in gymnotiform weakly electric fish. *J. Exp. Biol.* **216**, 2459-2468.
Schmidt, U. and Joermann, G. (1986). The influence of acoustical interferences on echolocation in bats. *Mammalia* **50**, 379-390.
Schnitzler, H.-U. and Grinnell, A. D. (1977). Directional sensitivity of echolocation in the horseshoe bat, *Rhinolophus ferrumequinum*: I. Directionality of sound emission. *J. Comp. Physiol. A* **116**, 51-61. doi:10.1007/BF00605516
Schnitzler, H.-U. and Kalko, E. K. (2001). Echolocation by insect-eating bats. *Bioscience* **51**, 557-569. doi:10.1641/0006-3568(2001)051[0557:EBIEB]2.0.CO;2
Schumacher, S., Burt de Perera, T. and von der Emde, G. (2016). Object discrimination through active electrolocation: Shape recognition and the influence of electrical noise. *J. Physiol. Paris* **110**, 151-163. doi:10.1016/j.jphysparis.2016.11.008
Scronce, B. L. and Johnson, C. S. (1976). Bistatic target detection by a bottlenosed porpoise. *J. Acoust. Soc. Am.* **59**, 1001-1002. doi:10.1121/1.2180997
Shumway, C. A. and Maler, L. (1989). GABAergic inhibition shapes temporal and spatial response properties of pyramidal cells in the electrosensory lateral line lobe of gymnotiform fish. *Journal of Comparative Physiology A* **164**, 391-407. doi:10.1007/BF00612998
Siemers, B. M. and Kerth, G. (2006). Do echolocation calls of wild colony-living Bechstein's bats (*Myotis bechsteinii*) provide individual-specific signatures? *Behav. Ecol. Sociobiol.* **59**, 443-454. doi:10.1007/s00265-005-0068-x
Siemers, B. M. and Schnitzler, H.-U. (2004). Echolocation signals reflect niche differentiation in five sympatric congeneric bat species. *Nature* **429**, 657-661. doi:10.1038/nature02547
Siemers, B. M., Beedholm, K., Dietz, C., Dietz, I. and Ivanova, T. (2005). Is species identity, sex, age or individual quality conveyed by echolocation call frequency in European horseshoe bats? *Acta Chiropt.* **7**, 259-274.
Speakman, J. R. and Racey, P. A. (1991). No cost of echolocation for bats in flight. *Nature* **350**, 421-423. doi:10.1038/350421a0
Stamper, S. A., Madhav, M. S., Cowan, N. J. and Fortune, E. S. (2012). Beyond the Jamming Avoidance Response: weakly electric fish respond to the envelope of social electrosensory signals. *J. Exp. Biol.* **215**, 4196-4207. doi:10.1242/jeb.076513
Stoddard, P. K. (1999). Predation enhances complexity in the evolution of electric fish signals. *Nature* **400**, 254-256. doi:10.1038/22301
Stoddard, P. K. (2002). The evolutionary origins of electric signal complexity. *J. Physiol. Paris* **96**, 485-491. doi:10.1016/S0928-4257(03)00004-4
Stoddard, P. K. and Markham, M. R. (2008). Signal cloaking by electric fish. *Bioscience* **58**, 415-425. doi:10.1641/B580508
Stoddard, P. K., Tran, A. and Krahe, R. (2019). Predation and crypsis in the evolution of electric signaling in weakly electric fishes. *Front. Ecol. Evol.* **7**, 264. doi:10.3389/fevo.2019.00264
Surlykke, A., Ghose, K. and Moss, C. F. (2009). Acoustic scanning of natural scenes by echolocation in the big brown bat, Eptesicus fuscus. *J. Exp. Biol.* **212**, 1011-1020. doi:10.1242/jeb.024620
Surlykke, A., Nachtigall, P. E., Fay, R. R. and Popper, A. N. (eds.) (2014). *Biosonar*. New York: Springer-Verlag.
Takahashi, E., Hyomoto, K., Riquimaroux, H., Watanabe, Y., Ohta, T. and Hiryu, S. (2014). Adaptive changes in echolocation sounds by *Pipistrellus abramus* in response to artificial jamming sounds. *J. Exp. Biol.* **217**, 2885-2891. doi:10.1242/jeb.101139
Tallarovic, S. and Zakon, H. (2005). Electric organ discharge frequency jamming during social interactions in brown ghost knifefish, Apteronotus leptorhynchus. *Anim. Behav.* **70**, 1355-1365. doi:10.1016/j.anbehav.2005.03.020
Taub, M. and Yovel, Y. (2020). Segregating signal from noise through movement in echolocating bats. *Sci. Rep.* **10**, 1-10. doi:10.1038/s41598-019-57346-2
Thomas, J. A., Moss, C. and Vater, M. (eds.) (2004). High-frequency burst-pulse sounds in agonistic/aggressive interactions in bottlenose Dolphins, *Tursiops truncatus*. In *Echolocation in Bats and Dolphins*, pp. 425-431. Chicago: The University of Chicago Press.
Tressler, J. and Smotherman, M. S. (2009). Context-dependent effects of noise on echolocation pulse characteristics in free-tailed bats. *J. Comp. Physiol. A* **195**, 923-934. doi:10.1007/s00359-009-0468-x
Troest, N. and Møhl, B. (1986). The detection of phantom targets in noise by serotine bats; negative evidence for the coherent receiver. *J. Comp. Physiol. A Neuroethol. Sens. Neural. Behav. Physiol.* **159**, 559-567. doi:10.1007/BF00604175
Tyack, P. (1986). Population biology, social behavior and communication in whales and dolphins. *Trends Ecol. Evol.* **1**, 144-150. doi:10.1016/0169-5347(86)90042-X
Ulanovsky, N. (2004). Multiple time scales of adaptation in auditory cortex neurons. *J. Neurosci.* **24**, 10440-10453. doi:10.1523/JNEUROSCI.1905-04.2004
Ulanovsky, N. and Moss, C. F. (2008). What the bat's voice tells the bat's brain. *Proc. Natl. Acad. Sci. USA* **105**, 8491-8498. doi:10.1073/pnas.0703550105
Viete, S. and Heiligenberg, W. (1991). The development of the Jamming Avoidance Response (JAR) in Eigenmannia: An innate behavior indeed. *J. Comp. Physiol. A* **169**, 15-23. doi:10.1007/BF00198169
Voigt, C. C. and Lewanzik, D. (2012). "No cost of echolocation for flying bats" revisited. *J. Comp. Physiol. [B]* **182**, 831-840. doi:10.1007/s00360-012-0663-x
Voigt-Heucke, S. L., Taborsky, M. and Dechmann, D. K. N. (2010). A dual function of echolocation: bats use echolocation calls to identify familiar and unfamiliar individuals. *Anim. Behav.* **80**, 59-67. doi:10.1016/j.anbehav.2010.03.025
von der Emde, G. (1992). Electrolocation of capacitive objects in four species of pulse-type weakly electric fish. *Ethology* **92**, 177-192.

von der Emde, G. (1999). Active electrolocation of objects in weakly electric fish. *J. Exp. Biol.* **202**, 1205-1215. doi:10.1242/jeb.202.10.1205

von der Emde, G. (2006). Non-visual environmental imaging and object detection through active electrolocation in weakly electric fish. *J. Comp. Physiol. A Neuroethol. Sens. Neural. Behav. Physiol.* **192**, 601-612. doi:10.1007/s00359-006-0096-7

von der Emde, G. (2013). Electroreception. In *Neurosciences - From Molecule to Behavior: A University Textbook* (ed. C. G. Galizia and P.-M. Lledo), pp. 409-425. Berlin, Heidelberg: Springer Berlin Heidelberg.

Watanabe, A. and Takeda, K. (1963). The change of discharge frequency by A.C. Stimulus in a weak electric fish. *J. Exp. Biol.* **40**, 57.

Westby, G. W. M. (1979). Electrical communication and jamming avoidance betwen resting Gymnotus carapo. *Behav. Ecol. Sociobiol.* **4**, 381-393. doi:10.1007/BF00303244

Westby, G. W. M. (1988). The ecology, discharge diversity and predatory behaviour of gymnotiforme electric fish in the coastal streams of French Guiana. *Behav. Ecol. Sociobiol.* **22**, 341-354.

Worm, M., Landgraf, T., Prume, J., Nguyen, H., Kirschbaum, F. and von der Emde, G. (2018). Evidence for mutual allocation of social attention through interactive signaling in a mormyrid weakly electric fish. *Proc. Natl. Acad. Sci.* **115**, 6852-6857. doi:10.1073/pnas.1801283115

Wright, G. S., Chiu, C., Xian, W., Wilkinson, G. S. and Moss, C. F. (2014). Social calls predict foraging success in big brown bats. *Curr. Biol.* **24**, 885-889.

Xitco, M. J. and Roitblat, H. L. (1996). Object recognition through eavesdropping: Passive echolocation in bottlenose dolphins. *Anim. Learn. Behav.* **24**, 355-365. doi:10.3758/BF03199007

Xu-Friedman, M. A. and Hopkins, C. D. (1999). Central mechanisms of temporal analysis in the knollenorgan pathway of mormyrid electric fish. *J. Exp. Biol.* **202**, 1311-1318.

Yack, J. E. and Fullard, J. H. (2000). Ultrasonic hearing in nocturnal butterflies. *Nature* **403**, 265-266. doi:10.1038/35002247

Yager, D. D. and May, M. L. (1990). Ultrasound-triggered, flight-gated evasive maneuvers in the praying mantis, *Parasphendale agrionina* (Gerst.). II: tethered flight. *J. Exp. Biol.* **152**, 41-58.

Yovel, Y., Melcon, M. L., Franz, M. O., Denzinger, A. and Schnitzler, H.-U. (2009). The voice of bats: how greater mouse-eared bats recognize individuals based on their echolocation calls. *PLoS Comput. Biol.* **5**, e1000400. doi:10.1371/journal.pcbi.1000400

Zahavi, A. (1975). Mate selection—A selection for a handicap. *J. Theor. Biol.* **53**, 205-214. doi:10.1016/0022-5193(75)90111-3

Zakon, H., Oestreich, J., Tallarovic, S. and Triefenbach, F. (2002). EOD modulations of brown ghost electric fish: JARs, chirps, rises, and dips. *J. Physiol. Paris* **96**, 451-458. doi:10.1016/S0928-4257(03)00012-3

Zweifel, N. O. and Hartmann, M. J. Z. (2020). Defining “active sensing” through an analysis of sensing energetics: homeoactive and alloactive sensing. *J. Neurophysiol.* **124**, 40-48. doi:10.1152/jn.00608.2019