Neuroethology of sound localization in anurans

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Abstract

Albert Feng pioneered the study of neuroethology of sound localization in anurans by combining behavioral experiments on phonotaxis with detailed investigations of neural processing of sound direction from the periphery to the central nervous system. A main advantage in these studies is that many species of female frogs readily perform phonotaxis towards loudspeakers emitting the species-specific advertisement call. Behavioral studies using synthetic calls can identify which parameters are important for phonotaxis and also quantify localization accuracy. Feng was the first to investigate binaural processing using single-unit recordings in the first two auditory nuclei in the central auditory pathway and later investigated the directional properties of auditory nerve fibers with free-field stimulation. These studies showed not only that the frog ear is inherently directional by virtue of acoustical coupling or crosstalk between the two eardrums, but also confirmed that there are extratympanic pathways that affect directionality in the low-frequency region of the frog's hearing range. Feng's recordings in the midbrain also showed that directional information is enhanced by cross-midline inhibition. An important contribution toward the end of his career involved his participation in neuroethological research with a team of scientists working with frogs that produce ultrasonic calls.

Keywords

Albert Feng Sound localization Binaural input requirement Pressure-difference system Cross-midline inhibition

Introduction

Frogs and toads are among the most vocal vertebrates. Many species call at night from huge aggregations – choruses – and others that routinely call in daylight may do so from solitary locations in dense forests. Males are responsible for most long-range calling in nearly all species; and because visual information about a signaler's location is poor at best, females have the task of locating individual males by sound. In territorial species, males may also use sound to locate rivals. Gravid females of many species that have not yet spawned are often highly responsive to playbacks of male advertisement calls or synthetic versions of these signals and they readily move to and contact a loudspeaker broadcasting such signals. Quantifying their path to a speaker and observing other behaviors such as head scanning have been used to assess their sound localization abilities in the field and laboratory. Playbacks of synthetic calls not only provide information about what physical properties of their calls are used for choosing an appropriate mate but also show what properties affect quantitative aspects of their phonotactic behavior. These behavioral data are important for guiding studies of the underlying mechanisms of sound pattern recognition and localization and for testing ideas and hypotheses that arise from mechanistic studies. As a neuroethologist, Albert Feng spent much of his professional career integrating behavioral and electrophysiological studies to elucidate the mechanisms of sound localization in frogs and the neural processing contributing to the behavioral response.

Feng's training was in electrical engineering, and his Ph.D. dissertation (Feng 1975) and many of his subsequent publications reported the results of neurophysiological studies that addressed mechanisms of anuran sound localization as well as receiver preferences. In 1970 he was a graduate student and one of us (Gerhardt) was a postdoc in Robert Capranica's laboratory at Cornell University. They first worked together after Feng had completed some neurophysiological experiments on sound localization in frogs (Feng and Capranica 1976) and wanted to test the common-sense expectation that frogs use both ears to locate sounds. This hypothesis was supported by observing that females of the American green treefrog (*Hyla cinerea*) and barking treefrog (*Hyla gratiosa*) were unable to locate a speaker playing back male advertisement calls when one of their external tympanic membranes was covered with a thin layer of grease (Fig. 1). Although moving in the general direction of the speaker, they continually circled in the direction of the uncovered ear (Feng et al. 1976). This was to our knowledge Feng's first extended field work with frogs, and he braved encounters with snakes and alligators in swamps and ponds near Savannah, Georgia, USA to collect test subjects. Subsequently he conducted field work in many other parts of the world including Chile, Malaysia, Indonesia, and China.

Feng's main contributions to understanding the mechanisms underlying vocal communication in frogs and other animals were centered on electrophysiological recordings from cells or groups of cells in the auditory pathway from the auditory nerve to the thalamus. His work also addressed directly and indirectly issues concerning the structure and function of the frog ear, mechanisms of sound localization, sound pattern recognition of species and individuals and how recognition is achieved in the noisy conditions in which most species communicate. Here we highlight some of these contributions in a semi-chronological way along with the results of the studies of other individuals who influenced him. Sound localization and related phenomena important for acoustic communication in natural environments are the subjects of numerous comprehensive reviews (Feng and Ratnam 2000; Gerhardt and Huber 2002; Christensen-Dalsgaard 2005, 2011; Feng and Schul 2007; Gerhardt and Bee 2007; Schwartz and Bee 2013; Bee 2015; Bee and Christensen-Dalsgaard 2016). We will summarize much of the behavioral information in these reviews after presenting a summary of Feng's neurophysiological work and before describing the comprehensive research he and his colleagues conducted over the last two decades with frogs that produce ultrasonic signals.

Besides his significant contributions to our knowledge about mechanisms underlying acoustic communication in frogs and other animals, Feng was enthusiastic about showing the relevance of these mechanisms to behavior in natural settings. Indeed, the titles of two of his reviews cited above (Feng and Ratnam 2000; Feng and Schul 2007) refer to hearing and sensory processing in "real-world" situations or environments. Moreover, throughout his long and highly productive career, Feng continued a research strategy combining the results of studies of neurophysiology and neuroanatomy with results from behavioral research whether his own or that of other scientists.

Neurophysiological Studies

Following an outstanding paper on auditory single neurons in the American bullfrog, *Lithobates catesbeianus* (formerly *Rana catesbeiana*) (Feng et al. 1975), two important papers concerned with the neural bases of sound localization in frogs came out of Feng's thesis work at Cornell University (Feng 1975). His first paper reports data from single auditory neurons in the dorsal medullary nucleus (DMN) of the American bullfrog (Feng and Capranica 1976) using closed-coupler stimulation and carefully controlling for acoustic crosstalk between the two ears. Nearly half of the neurons in this first hindbrain nucleus received binaural inputs from the periphery, unlike in amniotes (reptiles, birds, and mammals) where the second nucleus, the superior olivary nucleus (SON), is the first structure to receive binaural input. Most of the binaural cells (examples in Fig. 2) were excited (E) by acoustic input from the contralateral ear and inhibited (I) by sound of the same frequency from the ipsilateral ear (EI units), and responses were generally modified by differences in binaural intensity and arrival time. Comparable results corroborating the prominence of EI units in the DMN were later reported by Christensen-Dalsgaard and Kanneworff (2005) in their study of the grass frog (*Rana temporaria*).

In his second paper, single unit recordings in green treefrogs from the SON, the next station in the ascending pathway, revealed that nearly all of the binaural cells he recorded (42% of all cells) were also EI units (Feng and Capranica 1978) and most binaural cells had similar response characteristics to the DMN cells (Feng and Capranica 1976). While subsequent papers described basic firing patterns of single cells in the SON in anurans (Condon et al. 1991, 1995), this early paper (Feng and Capranica 1978) was his only study concerned with its function in sound localization. It is noteworthy that unlike in frogs, neurophysiological studies of birds and mammals revealed sharpening of directionality or separation in time and intensity pathways, showing that the processing of binaural inputs is different in frogs (Christensen-Dalsgaard 2005).

In both their 1976 and 1978 papers, Feng and Capranica related the binaural sensitivity and sharpening afforded by EI cells to the possibility that they could serve to magnify small external binaural cues in the form of interaural time differences (ITD) and interaural level differences (ILD) at the exterior surfaces of the tympanic membranes of these frogs, including the green treefrog, which is much smaller than the American bullfrog. This possibility was later discounted by behavioral studies of sound localization in the green treefrog and other treefrogs as well as a miniature dendrobatid frog, the Boquete rocket frog (*Silverstoneia nubicola*, formerly *Colostethus nubicola*)(Rheinlaender et al. 1979; Gerhardt and Rheinlaender 1980, 1982). The methodology and results will be presented below. But the important point is that the response properties of EI and other binaurally driven cells characterized by Feng and Capranica (1976, 1978) can enhance directional resolution regardless of how differences in intensity and time are generated between the two tympanic membranes.

Directionality based on acoustic coupling

The experiments by Rheinlaender et al. (1979) suggested that a special property of the anuran ear, the internal acoustical coupling of the eardrums, greatly enhance the small external cues. The acoustical coupling in frogs connects the two middle ear cavities through wide Eustachian tubes that are permanently open in most species (but see Gridi-Papp et al. 2008) and allow sound to reach both surfaces of the eardrums. This property increases directionality since eardrum vibration will depend on the phase differences between the external and internal sound component. Since these early experiments internal coupling has been demonstrated in all frog species investigated, so it is a general property in frogs (and most other non-mammalian tetrapods) (Christensen-Dalsgaard 2005; Shofner 2015; van Hemmen et al. 2016). The directionality depends on frequency and on attenuation of the internal sound component, and

Feng (1980) was able to quantify the coupling by closed-coupler stimulation of the two eardrums while recording from auditory nerve fibers in one auditory nerve (Fig. 3). The minimal crosstalk, the difference between ipsilateral and contralateral stimulation, was around -4 dB at around 1 kHz in the northern leopard frog (*Lithobates pipiens*). Crosstalk in the same range has been found by laser vibrometry measurements in the grass frog (*Rana temporaria*) (-4 to -8 dB, Vlaming et al. 1984). Theoretically, a crosstalk of -4 dB can generate a maximal directionality of 12 dB (Feng and Christensen-Dalsgaard 2008), which corresponds well to the directionality of the eardrum and of the auditory nerve fibers (see below). Such systems are characterized as “pressure-difference” systems as opposed to the “pressure” systems of larger animals in which directionality results from comparisons of sounds impinging on the external surfaces of the tympanic membranes.

Auditory nerve directionality

In the very important paper on directional properties of auditory nerve fibers (Feng 1980), Feng was able to expose the auditory nerve from the dorsal side, allowing naturalistic, free field stimulation of the frog. He recorded from 158 nerve fibers and could divide the responses in two very distinct types: fibers with low-frequency best frequencies (BFs of 100-300 Hz) showed a ‘figure-eight’ characteristic with a pronounced ‘frontal null’ (Fig. 4a), whereas the response of units with higher best frequencies was ovoidal (Fig. 4b).

Comparable studies were conducted with the grass frog (*Rana temporaria*) in Denmark almost twenty years later (Jørgensen and Christensen-Dalsgaard 1997a, b; Christensen-Dalsgaard et al. 1998). Because the directionality was highly intensity-dependent and the dynamic range of each cell was narrow, spike rates could be recalculated as equivalent decibel values by converting spikes rates to levels using the fiber’s rate-level curve, measured with ipsilateral stimulation (Feng 1980). This was justified because of the large dynamic range of the entire population of cells so that resulting estimates of directivity reflect that of the entire acoustic periphery. For units tuned to relatively high frequencies, these plots are comparable to the directivity of the tympanum as analyzed with laser vibrometry in treefrogs (Fig. 5, Table 1; Michelsen et al. 1986; Jørgensen 1991). Laser vibrometry measurements in frogs generally show an ovoidal response with a maximal directionality of approximately 10 dB (reviews in Christensen-Dalsgaard 2005; Bee and Christensen-Dalsgaard 2016). For high-frequency fibers, the maximal directional difference between ipsilateral and contralateral stimulation in equivalent decibels was 5 to 10 dB in northern leopard frogs (Feng 1980) and 10 dB in grass frogs (Jørgensen and Christensen-Dalsgaard 1997a); maximal differences in low-frequency tuned fibers were 1 to 8 dB and 15 dB in the two species, respectively. Christensen-Dalsgaard (2004) presented data from single units in the auditory nerve of gray treefrogs (*Hyla versicolor*) that showed comparable directional patterns (see examples in Bee and Christensen-Dalsgaard 2016).

Extratympanic directionality

The figure-of-eight directivity pattern observed at low frequencies in Feng's (1980) study was difficult to explain based on vibrometry measurements that generally show low sensitivity and omnidirectional or slightly ovoidal directivity of the eardrum at low frequencies (Fig. 5, Table 1; Michelsen et al. 1986; Jørgensen 1991). This pattern is now thought to be caused by extratympanic pathways that bypass the eardrum and stimulate the inner ear in a fashion analogous to human bone conduction (Wilczynski et al. 1987; Capshaw et al. 2022). Studies in the Feng laboratory concluded that 55% of the cells show some degree of extratympanic directionality (Feng 1980; Feng and Shofner 1981; see also Wang et al. 1996). The potential sources of extratympanic input are still not definitively identified, but one likely component at low frequencies is simply that the frog is moved by the sound wave, ultimately vibrating the fluid in the inner ear and stimulating the amphibian papilla (Jørgensen and Christensen-Dalsgaard 1997b; Capshaw et al. 2022). Detailed reviews regarding the structure and function of the anuran ear are provided by Narins (2016), Lewis and Narins (1999), Christensen-Dalsgaard (2005, 2011) and Bee and Christensen-Dalsgaard (2016). One obvious conclusion is that frogs lack the evolutionary inventions in small mammals that tend to isolate the middle ear and close the Eustachian tubes with the result that the eardrum's vibrations are dominantly or solely driven by sounds impinging on its external surface (Christensen-Dalsgaard 2011).

Later investigations highlighted the importance of directional timing cues in the auditory nerve response. These cues are generated by arrival-time differences of the sound wave (like mammalian ITDs), but additionally, the acoustical coupling increases the interaural time differences (Christensen-Dalsgaard 2011). An even larger effect is produced by the directional sensitivity of the ear due to intensity-latency trading that results from decreases in spike latency that occur with increases in sound intensity (Feng 1982). Feng showed that concomitant with a spike rate increase of 15 spikes/s/dB there could be latency decrease of up to 1.5 ms/dB, so the 10 dB directional difference of the eardrum can result in large time differences that will depend on the steepness of the sound envelope. Thus, amplitude modulated sounds like natural calls will produce large directional differences in neural spike timing (up to 2 ms, Klump et al. 2004). These temporal cues are easily processed by binaural neurons in the DMN and SON, where responses to ITDs is graded over a range of ±0.5 ms (Fig. 6; Feng and Capranica 1976, 1978). For example, the 30˚ acuity observed in behavioral experiments corresponds to a spike-time difference of approximately 0.27 ms in the experiments by Klump et al. (2004), well within the range of time differences processed by binaural neurons in the DMN and SON (Fig. 6).

Central processing of directionality

Feng and his colleagues also explored neural correlates of sound localization and temporal pattern recognition in a complex midbrain structure, the torus semicircularis (TS), which is a homolog of the inferior colliculus of mammals. Numerous other laboratories have described single- and multiunit activity because of the relative ease of access to auditory nuclei in this structure. Feng's initial paper identified different classes of binaurally driven neurons in the TS of northern leopard frogs (Feng 1981). Type I cells were equally well excited by sounds coming from the right or left but maximally excited by sounds from the frontal field; Type II cells, which were the most common type, were maximally excited by sounds from the contralateral field and showed little response to sounds from the ipsilateral field. Unlike the responses of auditory nerve cells, these response patterns were uncorrelated with the frequency sensitivity of the cell. This paper also confirmed the conclusions of the behavioral study of localization in green treefrogs (Feng et al. 1976) in that the directional responses of these cells were significantly reduced when one of the auditory nerves was cut. Finally, this paper reinforced the importance of quantifying latency (phase) shifts in response to changes in sound direction, which encouraged the use of this metric in a study of auditory nerve cells by Klump et al. (2004). Thus, Feng's contention that directivity patterns present in the responses of auditory nerve fibers could be sharpened by binaural interactions taking place in higher stations in the auditory pathway has been well supported. Although some evidence for a role in sound pattern recognition (e..g., Hall and Feng 1987; Mudry and Capranica 1987) was confirmed in a lesion study of the auditory thalamus in the forebrain by Endepols et al. (2003), there was little or no effect on sound localization, as opposed to a motivational role for phonotaxis, and these authors concluded that the TS plays a crucial role for this function. There is also no clear evidence for a map of auditory space in the TS (Christensen-Dalsgaard 2005). Instead, sound direction appears to be processed by comparisons of activity in the two hemispheres (probably in separate frequency channels), and the lateralization is enhanced by contralateral inhibition (Zhang et al. 1999). Interestingly, a study by Ponnath and Farris (2014) showed that thalamic stimulation can modulate the binaural responses in the TS. The modulation increases the ipsilateral-contralateral difference and may show how attention can selectively enhance sound from a particular location.

Feng and his colleagues repeatedly emphasized the role of source localization in improving the detection of sounds in the presence of noise, a common occurrence in vocal communication in frogs. Early behavioral evidence for a psychoacoustic phenomenon called "spatial release from masking" in frogs was provided by Schwartz and Gerhardt (1989; see also Bee 2007b, 2008; Nityananda and Bee 2012; Ward et al. 2013) and was followed by the discovery of correlates of this and other masking-related phenomena in the TS (e.g., Gooler et al. 1993; Schwartz and Gerhardt 1995; Xu et al. 1996; Ratnam and Feng 1998; Feng and Ratnam 2000; Lin and Feng 2001, 2003; Goense and Feng 2012). For example, Goense and Feng (2012) showed that some TS neurons had lower response thresholds in the presence of "comodulated" noise (i.e., amplitude-modulated wideband noise with temporal correlations across frequency) and speculated that such neurons might contribute to a psychoacoustic phenomenon called "comodulation masking release" (Verhey et al. 2003). Lee et al. (2017; see also Bee and Vélez 2018) subsequently confirmed that chorus noise exhibits comodulation and that frogs, like humans, experience comodulation masking release when listening to advertisement calls in comodulated noise. Below we briefly review the behavioral evidence related to sound source localization and touch on other widespread psychoacoustic phenomena that depend on directional hearing such as the detection of more than one calling male in a chorus.

Behavioral Studies

Quantifying localization accuracy in the horizontal and vertical planes

Most of the behavioral work on sound localization and related processes has been conducted with four species of North American treefrogs (genus *Hyla*), including the green and barking treefrogs first in the pioneering study by Feng et al. (1976) (Fig. 1). Juergen Rheinlaender's research while in Capranica's laboratory resulted in the first study to quantify the accuracy of phonotaxis in *H. cinerea* (Rheinlaender et al. 1979). As in most other studies, the deviations from a straight-line between the frog's position and a loudspeaker were measured from videos of their approach from a release point, usually from more than a meter away. Typically, frogs showed a zig-zag pattern of hopping in which they repeatedly deviated from the direct path on one side and overcorrected slightly until they reached the speaker (see Fig. 1). The majority of head orientation angles (α) and jump error angles (γ) when females engaged in head scanning behavior during phonotaxis were less than 10° to 15° (Fig. 7), indicating high localization accuracy. Allowing the frogs to move toward the sound source gave the frogs the possibility of updating information about its location after every hop or crawl and also to use the change in sound pressure level to assess if they were getting closer to the sound source. Such experiments are defined as having a "closed-loop" design. One of these cues was eliminated in a study of eastern gray treefrogs (*Hyla versicolor*) by stopping the playback after each hop or crawl and adjusting the sound pressure level to the same value at the initial release point (Jørgensen and Gerhardt 1991). Two "open-loop" studies with barking treefrogs (*H. gratiosa*) and Cope's gray treefrog (*H. chrysoscelis*) only measured the deviation of the first movement, thus eliminating the possibility of updating information with a hop from its starting position (Klump and Gerhardt 1989; Caldwell and Bee 2014). Localization accuracy in both studies (Fig. 8) was comparable to that estimated from closed-loop studies thus indicating that the frogs had the capability of true angle discrimination rather than mere lateralization. Barking treefrogs showed reduced accuracy when the sound source was directly in front of them, and Cope's gray treefrogs showed extremely poor accuracy when the sound source was located in the rear hemi-field. In Cope's gray treefrog, the presence of noise had negligible impacts on sound localization accuracy across the frontal field in open loop tests, though noise caused some degradation of localization accuracy in closed loop tests, but only at the most challenging signal-to-noise ratio tested (+3dB).

Most of the treefrog studies also used synthetic advertisement calls, which allowed the researchers to assess how stimulus frequency affects the accuracy of sound localization and even to test the effect of presenting audible frequencies that are not emphasized in natural vocalizations. For example, Rheinlaender et al. (1979) showed that localization accuracy was somewhat poorer when synthetic calls had just the high-frequency peak alone rather than only the low-frequency peak or both peaks as in natural calls. Jørgensen and Gerhardt (1991) showed that a frequency between the two spectral peaks (1.4 kHz) typical of the conspecific call was more poorly localized than predicted by directional patterns estimated with laser vibrometry. This frequency range corresponds to the spectrum of input to the internal surfaces of the tympanic membranes from frog's lung, and it has recently been hypothesized that this input could serve to improve detection of conspecific calls in mixed-species choruses rather than affecting sound localization (Christensen-Dalsgaard et al. 2020; Lee et al. 2021).

So far, we have only considered localization in the horizontal plane, but frogs, and especially most treefrogs, also locate mates calling from elevated positions. Localization in elevation has been studied in green treefrogs (Fig. 9; Gerhardt and Rheinlaender 1982), painted reed frogs (*Hyperolius marmoratus*) (Passmore et al. 1984), and eastern gray treefrogs (Jørgensen and Gerhardt 1991). There were species differences in the accuracy of the location of elevated speakers relative to the horizontal accuracy discussed above. Green treefrogs were less accurate despite the observation that they frequently did head scanning before a jump or climb, whereas the accuracy was nearly the same in gray treefrogs which rarely showed head scanning.

Localization of breeding sites

Many frog species do not live close to their breeding site and others use temporary sites that fill with water after heavy rains. Individuals may use any number of non-auditory cues to return to a permanent site where they lived as a tadpole and metamorphosed, but if the site is semi-permanent or temporary, then the presence of a chorus provides potentially useful auditory information about its present suitability, location, and presence of potential mates. Gerhardt and Klump (1988) showed that gravid females of barking treefrogs, which usually breed in semi-permanent bodies of water in otherwise dry areas, oriented and moved toward a speaker broadcasting a recording of a chorus of males that was made at a distance of 160 meters and played back at less than 50 dB SPL at the release point of the female. American toads (*Anaxyrus* [formerly *Bufo*] *americanus*) and Cope's gray treefrogs oriented in the laboratory to playbacks of chorus sounds recorded at 0, 20, and 40 m, but not at 80 or 160 m (Swanson et al. 2007), and eastern gray treefrogs oriented to choruses of conspecific males at as far as 100 m distant when tested in the field (Christie et al. 2010). Wood frogs (*Lithobates sylvaticus*) are explosive breeders with a season usually lasting only a few days. Males in a laboratory setting were attracted to playback a chorus recording made at about 10 m from a cluster of conspecific callers and discriminated against a simultaneous playback of a chorus of mink frogs (*Lithobates septentrionalis*) recorded at a similar distance (Bee 2007a).

Barking treefrog females also responded preferentially to a recording of a mixed species chorus of conspecific males and green treefrogs rather than to a chorus of green treefrogs alone (Gerhardt and Klump 1988). Nevertheless, field studies showed that just as many females and males of the barking treefrog arrived at breeding ponds on favorable nights whether or not a full chorus was allowed to form; furthermore, there was no difference in the sex ratio between nights with and without a full chorus (Murphy 2003). Clearly males and females attended to the same environmental variables to determine when to breed and they did not need auditory cues from conspecific males to locate the breeding pond. The same is probably true of the other species shown to orient toward playbacks of conspecific choruses.

Detection and localization of calling males in choruses

Whereas choruses may sometimes augment other cues for locating active breeding areas, much more attention has focused on the difficulties the chorus background poses for males trying to attract mates and deal with rivals and for females trying to locate calling males of their own species. Schwartz and Bee (2013) provide an extensive review of the diverse tactics used by calling males during vocal interactions with nearby rivals or even males of other species with similar calls in some species. Rough matches between call frequency and auditory tuning and their weak inverse correlation with body size can provide some reduction in acoustic masking between species, and such correlations may also affect size-dependent female preferences within species (Feng and Schul 2007; Schwartz and Bee 2013). Interspecific differences in this context are usually best interpreted as incidental consequences of selection in other contexts, and the ability of individual frogs to change call amplitude or frequency in nearly all species of frogs is extremely limited (Schwartz and Bee 2013). Some exceptions will be discussed in the last section of this review.

The ability to hear the calls of individuals comprising the chorus appears to be important in some species. In Cope's gray treefrogs and green treefrogs, for example, the timing and temporal structure of individual calls in the chorus noise were necessary cues for eliciting phonotaxis. Females did not exhibit phonotaxis in response to chorus noise having the long-term frequency spectrum and amplitude-modulation spectrum of natural choruses, but lacking information on the timing and temporal structure of individual calls (Vélez et al. 2017). Reliable attraction of female gray treefrogs to a chorus from distances of about 30 m or more depends on the detection of species-identifying call properties (pulse-repetition rate in Cope's gray treefrogs and pulse duration and interpulse interval in eastern gray treefrogs; Schul and Bush 2002). Attraction at this distance and sometimes at longer distances depends on hearing a sufficient number of pulses in the advertisement calls of one or a few males with the correct values, either in low density choruses or during lulls in chorus activity in dense choruses (so-called "dip listening"; Vélez and Bee 2010, 2011). These conclusions have been based on numerous field and laboratory experiments with these species using recordings of choruses at various distances as well as broad-band noise or noise with a frequency spectrum similar to that of a chorus, either continuous or fluctuating sinusoidally. For example, Feng and his colleagues used recordings of single focal males of eastern gray treefrogs calling on the edge of choruses at distances ranging from 1 to 100 m to assess the probability of positive phonotaxis and accuracy of localization in gravid females relative to these metrics in response to an unmasked synthetic call (Christie et al. 2019). The negative effects of the chorus background were already evident at 1 m (Fig. 10). Differences in the effects of distance on the acoustic properties of the chorus and playback levels in the laboratory led Christie et al. (2019) to conclude that the environmental degradation of temporal properties (e.g., Wiley and Richards 1978; Ryan and Sullivan 1989; Kuczynski et al. 2010) was a more important factor than the drop in intensity with distance.

Another contribution of Christie et al. (2019) is their thorough review of the literature regarding the problems and possible solutions to the negative effects of a dense chorus background on female preferences in treefrogs, and their paper closes with some of the neurophysiological results showing that the binaural interactions in the central nervous system could boost directional hearing and hence the detectability and localization of signals in a noisy environment. Recall from the first part of our review that Feng proposed this hypothesis in many of his first papers as well as in his subsequent studies throughout the anuran auditory system. As mentioned above, the behavioral correlates refer to a psychoacoustic phenomenon termed "spatial release from masking" and probably facilitate the detection of more than a single conspecific caller provided their separation in space is adequate (Schwartz and Del Monte 2019). These phenomena are generally treated as the "cocktail party effect" (Cherry 1953), a term used by Feng in his first (Fay and Feng 1987) and subsequent reviews (Feng and Ratnam 2000; Feng and Schul 2007). A thorough treatment of Feng's contributions to understanding release from masking and other solutions to cocktail-party-like problems is provided by Lee et al. (this special issue).

Conclusion

Albert Feng had a long and remarkable career, and the neuroethological approach applied to his first studies of sound localization in frogs served him well in this field and the other research highlighted in this issue. More than anyone, he and his students and postdocs are responsible for discovering through rigorous experimentation what we currently know about the mechanisms of sound localization in frogs. His contributions to the field remain valuable and serve as a solid foundation for future research. Moreover, his findings from basic research have also led to applied improvements in the design of sound processing for hearing aids (Liu et al. 2000, 2001). But certainly, what must be considered one of his most significant and fascinating contributions to the field stems from work he conducted near the conclusion of his scientific career on ultrasonic hearing and communication in frogs. We conclude this article by turning briefly to this important work (see other contributions in this special issue for additional treatments of this topic).

A new frontier at the conclusion of a career

At the beginning of a remarkable series of discoveries, Feng et al. (2002) described the highly variable calls of the concave-eared torrent frog (*Odorrana tormota*, formerly *Amolops tormotus*), which lives in the vegetation along fast-flowing, noisy streams in mountains and hills in Zhejiang Province in China. Not only did the calls vary remarkably among individuals in the degree and directions of the modulation of frequency and presence or absence of harmonics, but they also varied significantly within males to the extent that Feng and his colleagues did not find any "identical" calls in recordings of a single male. Many of the harmonics of these calls had frequencies well into the ultrasonic range. Zhang et al. (2017) later showed that females, which do not call very often, have the same signal morphology as males. In the years leading up to his retirement from academia in 2010, Feng and his colleagues explored mechanisms underlying the production of ultrasonic calls in this species and their ability to hear such signals (Narins et al. 2004; Feng et al. 2006; Suthers et al. 2006; Feng and Narins 2008; Gridi-Papp et al. 2008; Arch et al. 2012). Perhaps the most remarkable behavioral discovery about this species is the apparent accuracy of male phonotaxis to a speaker playing back female courtship calls (closed loop): a horizontal azimuthal error of less than 1° (Shen et al. 2008). This level of acuity is at least 10 to 15 times better than that of "normal" frogs and, as the authors point out, comparable to that of bats, elephants, dolphins and humans.

The female calls have a fundamental frequency from 7 kHz to 10 kHz and multiple harmonics extending into the ultrasonic range. The precise mechanisms underlying the extraordinary localization acuity are still unknown and represent a current frontier in studies of animal hearing and acoustic communication. Elucidating these mechanisms will certainly challenge future researchers working on sound localization in frogs and other small vertebrates. We believe insights and inspiration from Albert Feng's work on the neuroethology of sound localization in anurans will serve as a lasting guide for those who choose to take up this challenge.

Acknowledgements

We are grateful to Albert Feng for his many contributions to research on hearing and sound communication in frogs and to Peter Narins for inviting us to contribute to this special issue.

Author contributions HCG: wrote an initial draft of the manuscript. MAB and JC-D: contributed text and created figures and tables. HCG, MAB, and JC-D: edited and prepared the final draft of the manuscript.

Funding MAB was supported by a grant from the National Science Foundation (IOS-2022253) during the preparation of this article.

Declarations

Conflicts of interest The authors declare no competing or financial interests.

Ethical approval No ethical approval was required for this work.

References

Arch VS, Simmons DD, Quinones PM, Feng AS, Jiang JP, Stuart BL, Shen JX, Blair C, Narins PM (2012) Inner ear morphological correlates of ultrasonic hearing in frogs. Hear Res 283 (1-2):70-79. doi:https://doi.org/10.1016/j.heares.2011.11.006

Bee MA (2007a) Selective phonotaxis by male wood frogs to the sound of a chorus. Behav Ecol Sociobiol 61 (6):955-966. doi:https://doi.org/10.1007/s00265-006-0324-8

Bee MA (2007b) Sound source segregation in grey treefrogs: Spatial release from masking by the sound of a chorus. Anim Behav 74:549-558. doi:https://doi.org/10.1016/j.anbehav.2007.10.032

Bee MA (2008) Finding a mate at a cocktail party: Spatial release from masking improves acoustic mate recognition in grey treefrogs. Anim Behav 75:1781-1791. doi:https://doi.org/10.1016/j.anbehav.2007.10.032

Bee MA (2015) Treefrogs as animal models for research on auditory scene analysis and the cocktail party problem. Int J Psychophysiol 95 (2):216-237. doi:https://doi.org/10.1016/j.ijpsycho.2014.01.004

Bee MA, Christensen-Dalsgaard J (2016) Sound source localization and segregation with internally coupled ears: The treefrog model. Biol Cybern 110:271-290. doi:https://doi.org/10.1007/s00422-016-0695-5

Bee MA, Vélez A (2018) Masking release in temporally fluctuating noise depends on comodulation and overall level in Cope's gray treefrog. J Acoust Soc Am 144 (4):2354-2362. doi:https://doi.org/10.1121/1.5064362

Caldwell MS, Bee MA (2014) Spatial hearing in Cope's gray treefrog: I. Open and closed loop experiments on sound localization in the presence and absence of noise. J Comp Physiol A 200 (4):265-284. doi:https://doi.org/10.1007/s00359-014-0882-6

Caldwell MS, Lee N, Schrode KM, Johns AR, Christensen-Dalsgaard J, Bee MA (2014) Spatial hearing in Cope's gray treefrog: II. Frequency-dependent directionality in the amplitude and phase of tympanum vibrations. J Comp Physiol A 200 (4):285-304. doi:https://doi.org/10.1007/s00359-014-0883-5

Capshaw G, Christensen-Dalsgaard J, Carr CE (2022) Hearing without a tympanic ear. 225 (12). doi:https://doi.org/10.1242/jeb.244130

Cherry EC (1953) Some experiments on the recognition of speech, with one and with two ears. J Acoust Soc Am 25 (5):975-979. doi:https://doi.org/10.1121/1.1907229

Christensen-Dalsgaard J (2004) Directionality of auditory nerve fibers in the gray treefrog, *Hyla versicolor*. Association for Research in Otolaryngology Abstracts:#202

Christensen-Dalsgaard J (2005) Directional hearing in nonmammalian tetrapods. In: Popper AN, Fay RR (eds) Sound source localization, vol 25. Springer Handbook of Auditory Research. Springer, New York, pp 67-123. doi:https://doi.org/10.1007/0-387-28863-5_4

Christensen-Dalsgaard J (2011) Vertebrate pressure-gradient receivers. Hear Res 273 (1-2):37-45. doi:https://doi.org/10.1016/j.heares.2010.08.007

Christensen-Dalsgaard J, Jørgensen MB, Kanneworff M (1998) Basic response characteristics of auditory nerve fibers in the grassfrog (*Rana temporaria*). Hear Res 119 (1-2):155-163. doi:https://doi.org/10.1016/S0378-5955(98)00047-1

Christensen-Dalsgaard J, Kanneworff M (2005) Binaural interaction in the frog dorsal medullary nucleus. Brain Res Bull 66 (4-6):522-525. doi:https://doi.org/10.1016/j.brainresbull.2005.03.005

Christensen-Dalsgaard J, Lee N, Bee MA (2020) Lung-to-ear sound transmission does not improve directional hearing in green treefrogs (*Hyla cinerea*). J Exp Biol 20:jeb232421. doi:https://doi.org/10.1242/jeb.232421

Christie K, Schul J, Feng AS (2010) Phonotaxis to male's calls embedded within a chorus by female gray treefrogs, *Hyla versicolor*. J Comp Physiol A 196 (8):569-579. doi:https://doi.org/10.1007/s00359-010-0544-2

Christie KW, Schul J, Feng AS (2019) Differential effects of sound level and temporal structure of calls on phonotaxis by female gray treefrogs, *Hyla versicolor*. J Comp Physiol A 205 (2):223-238. doi:https://doi.org/10.1007/s00359-019-01325-5

Condon CJ, Chang SH, Feng AS (1991) Processing of behaviorally relevant temporal parameters of acoustic stimuli by single neurons in the superior olivary nucleus of the leopard frog. J Comp Physiol A 168 (6):709-725. doi:https://doi.org/10.1007/BF00224360

Condon CJ, Chang SH, Feng AS (1995) Classification of the temporal discharge patterns of single auditory neurons in the frog superior olivary nucleus. Hear Res 83 (1-2):190-202. doi:https://doi.org/10.1016/0378-5955(95)00005-O

Endepols H, Feng AS, Gerhardt HC, Schul J, Walkowiak W (2003) Roles of the auditory midbrain and thalamus in selective phonotaxis in female gray treefrogs (*Hyla versicolor*). Behav Brain Res 145 (1-2):63-77. doi:https://doi.org/10.1016/S0166-4328(03)00098-6

Fay RR, Feng AS (1987) Mechanisms for directional hearing among nonmammalian vertebrates. In: Yost WA, Gourevitch G (eds) Directional hearing. Proceedings in Life Sciences. Springer, New York, pp 179-213. doi:https://doi.org/10.1007/978-1-4612-4738-8_77

Feng AS (1975) Sound localization in anurans: An electrophysiological and behavioral study. Ph.D. Dissertation, Cornell University,

Feng AS (1980) Directional characteristics of the acoustic receiver of the leopard frog (*Rana pipiens*): A study of 8th nerve auditory responses. J Acoust Soc Am 68 (4):1107-1114. doi:https://doi.org/10.1121/1.384981

Feng AS (1981) Directional response characteristics of single neurons in the torus semicircularis of the leopard frog (*Rana pipiens*). J Comp Physiol 144 (3):419-428. doi:https://doi.org/10.1007/BF00612574

Feng AS (1982) Quantitative analysis of intensity-rate and intensity-latency functions in peripheral auditory nerve fibers of northern leopard frogs (*Rana pipiens*). Hear Res 6 (3):241-246. doi:https://doi.org/10.1016/0378-5955(82)90057-0

Feng AS, Capranica RR (1976) Sound localization in anurans. I. Evidence of binaural interaction in dorsal medullary nucleus of bullfrogs (*Rana catesbeiana*). J Neurophysiol 39 (4):871-881. doi:https://doi.org/10.1152/jn.1976.39.4.871

Feng AS, Capranica RR (1978) Sound localization in anurans II. Binaural interaction in superior olivary nucleus of the green tree frog (*Hyla cinerea*). J Neurophysiol 41 (1):43-54. doi:https://doi.org/10.1152/jn.1978.41.1.43

Feng AS, Christensen-Dalsgaard J (2008) Interconnections between the ears in nonmammalian vertebrates. In: Masland RH, Albright TD, Albright TD et al. (eds) The senses: A comprehensive reference. Academic Press, New York, pp 217-224. doi:https://doi.org/10.1016/B978-012370880-9.00019-0

Feng AS, Gerhardt HC, Capranica RR (1976) Sound localization behavior of the green treefrog (*Hyla cinerea*) and the barking treefrog (*Hyla gratiosa*). J Comp Physiol 107 (3):241-252. doi:https://doi.org/10.1007/BF00656735

Feng AS, Narins PM (2008) Ultrasonic communication in concave-eared torrent frogs (*Amolops tormotus*). J Comp Physiol A 194 (2):159-167. doi:https://doi.org/10.1007/s00359-007-0267-1

Feng AS, Narins PM, Capranica RR (1975) Three populations of primary auditory fibers in the bullfrog (*Rana catesbeiana*): Their peripheral origins and frequency sensitivities. J Comp Physiol A 100 (3):221-229. doi:https://doi.org/10.1007/BF00614532

Feng AS, Narins PM, Xu CH (2002) Vocal acrobatics in a Chinese frog, *Amolops tormotus*. Naturwissenschaften 89 (8):352-356. doi:https://doi.org/10.1007/s00114-002-0335-x

Feng AS, Narins PM, Xu CH, Lin WY, Yu ZL, Qiu Q, Xu ZM, Shen JX (2006) Ultrasonic communication in frogs. Nature 440 (7082):333-336. doi:https://doi.org/10.1038/nature04416

Feng AS, Ratnam R (2000) Neural basis of hearing in real-world situations. Annu Rev Psychol 51:699-725. doi:https://doi.org/10.1146/annurev.psych.51.1.699

Feng AS, Schul J (2007) Sound processing in real-world environments. In: Narins PA, Feng AS, Fay RR, Popper AN (eds) Hearing and sound communication in amphibians, vol 28. Springer, New York, pp 323-350. doi:https://doi.org/10.1007/978-0-387-47796-1_11

Feng AS, Shofner WP (1981) Peripheral basis of sound localization in anurans: Acoustic properties of the frog's ear. Hear Res 5 (2-3):201-216. doi:https://doi.org/10.1016/0378-5955(81)90046-0

Gerhardt HC, Bee MA (2007) Recognition and localization of acoustic signals. In: Narins PM, Feng AS, Fay RR, Popper AN (eds) Hearing and sound communication in amphibians, vol 28. Springer Handbook of Auditory Research. Springer, New York, pp 113-146. doi:https://doi.org/10.1007/978-0-387-47796-1_5

Gerhardt HC, Huber F (2002) Acoustic communication in insects and anurans: Common problems and diverse solutions. Chicago University Press, Chicago

Gerhardt HC, Klump GM (1988) Phonotactic responses and selectivity of barking treefrogs (*Hyla gratiosa*) to chorus sounds. J Comp Physiol A 163 (6):795-802. doi:https://doi.org/10.1007/BF00604056

Gerhardt HC, Rheinlaender J (1980) Accuracy of sound localization in a miniature dendrobatid frog. Naturwissenschaften 67 (7):362-363

Gerhardt HC, Rheinlaender J (1982) Localization of an elevated sound source by the green tree frog. Science 217 (4560):663-664. doi:https://doi.org/10.1126/science.217.4560.663

Goense JBM, Feng AS (2012) Effects of noise bandwidth and amplitude modulation on masking in frog auditory midbrain neurons. PLoS ONE 7 (2):e31589. doi:https://doi.org/10.1371/journal.pone.0031589

Gooler DM, Condon CJ, Xu JH, Feng AS (1993) Sound direction influences the frequency-tuning characteristics of neurons in the frog inferior colliculus. J Neurphysiol 69 (4):1018-1030. doi:https://doi.org/10.1152/jn.1993.69.4.1018

Gridi-Papp M, Feng AS, Shen JX, Yu ZL, Rosowski JJ, Narins PM (2008) Active control of ultrasonic hearing in frogs. Proc Natl Acad Sci USA 105 (31):11014-11019. doi:https://doi.org/10.1073/pnas.0802210105

Hall JC, Feng AS (1987) Evidence for parallel processing in the frog's auditory thalamus. J Comp Neurol 258 (3):407-419. doi:https://doi.org/10.1002/cne.902580309

Ho CCK, Narins PM (2006) Directionality of the pressure-difference receiver ears in the northern leopard frog, *Rana pipiens pipiens*. J Comp Physiol A 192 (4):417-429. doi:https://doi.org/10.1007/s00359-005-0080-7

Jørgensen MB (1991) Comparative studies of the biophysics of directional hearing in anurans. J Comp Physiol A 169 (5):591-598. doi:https://doi.org/10.1007/BF00193548

Jørgensen MB, Christensen-Dalsgaard J (1997a) Directionality of auditory nerve fiber responses to pure tone stimuli in the grassfrog, *Rana temporaria*. I. Spike rate responses. J Comp Physiol A 180 (5):493-502. doi:https://doi.org/10.1007/s003590050066

Jørgensen MB, Christensen-Dalsgaard J (1997b) Directionality of auditory nerve fiber responses to pure tone stimuli in the grassfrog, *Rana temporaria*. II. Spike timing. J Comp Physiol A 180 (5):503-511. doi:https://doi.org/10.1007/s003590050066

Jørgensen MB, Gerhardt HC (1991) Directional hearing in the gray tree frog *Hyla versicolor:* Eardrum vibrations and phonotaxis. J Comp Physiol A 169 (2):177-183. doi:https://doi.org/10.1007/BF00215864

Jørgensen MB, Schmitz B, Christensen-Dalsgaard J (1991) Biophysics of directional hearing in the frog *Eleutherodactylus coqui*. J Comp Physiol A 168 (2):223-232. doi:https://doi.org/10.1007/BF00218414

Klump GM, Benedix JH, Gerhardt HC, Narins PM (2004) AM representation in green treefrog auditory nerve fibers: Neuroethological implications for pattern recognition and sound localization. J Comp Physiol A 190 (12):1011-1021. doi:https://doi.org/10.1007/s00359-004-0558-8

Klump GM, Gerhardt HC (1989) Sound localization in the barking treefrog. Naturwissenschaften 76 (1):35-37. doi:https://doi.org/10.1007/BF00368312

Kuczynski MC, Vélez A, Schwartz JJ, Bee MA (2010) Sound transmission and the recognition of temporally degraded sexual advertisement signals in Cope's gray treefrog (*Hyla chrysoscelis*). J Exp Biol 213 (16):2840-2850. doi:https://doi.org/10.1242/jeb.044628

Lee N, Christensen-Dalsgaard J, White LA, Schrode KM, Bee MA (2021) Lung mediated auditory contrast enhancement improves the signal-to-noise ratio for communication in frogs. Curr Biol 31 (7):1488-1498. doi:https://doi.org/10.1016/j.cub.2021.01.048

Lee N, Ward JL, Vélez A, Micheyl C, Bee MA (2017) Frogs exploit statistical regularities in noisy acoustic scenes to solve cocktail-party-like problems. Curr Biol 27 (5):743-750. doi:https://doi.org/10.1016/j.cub.2017.01.031

Lewis ER, Narins PM (1999) The acoustic periphery of amphibians: Anatomy and physiology. In: Fay RR, Popper AN (eds) Comparative hearing: Fish and amphibians, vol 11. Springer Handbook of Auditory Research. Springer, New York, pp 101-154. doi:https://doi.org/10.1007/978-1-4612-0533-3_4

Lin WY, Feng AS (2001) Free-field unmasking response characteristics of frog auditory nerve fibers: Comparison with the responses of midbrain auditory neurons. J Comp Physiol A 187 (9):699-712. doi:https://doi.org/10.1007/s00359-001-0241-2

Lin WY, Feng AS (2003) GABA is involved in spatial unmasking in the frog auditory midbrain. J Neurosci 23 (22):8143-8151. doi:https://doi.org/10.1523/JNEUROSCI.23-22-08143.2003

Liu C, Wheeler BC, O'Brien WD, Bilger RC, Lansing CR, Feng AS (2000) Localization of multiple sound sources with two microphones. J Acoust Soc Am 108 (4):1888-1905. doi:https://doi.org/10.1121/1.1290516

Liu C, Wheeler BC, O'Brien WD, Lansing CR, Bilger RC, Jones DL, Feng AS (2001) A two-microphone dual delay-line approach for extraction of a speech sound in the presence of multiple interferers. J Acoust Soc Am 110 (6):3218-3231. doi:https://doi.org/10.1121/1.1419090

Michelsen A, Jørgensen MB, Christensen-Dalsgaard J, Capranica RR (1986) Directional hearing of awake, unrestrained treefrogs. Naturwissenschaften 73 (11):682-683. doi:https://doi.org/10.1007/bf00366697

Mudry KM, Capranica RR (1987) Correlation between auditory thalamic area evoked responses and species-specific call characteristics II. *Hyla cinerea* (Anura: Hylidae). J Comp Physiol A 161 (3):407-416. doi:https://doi.org/10.1007/BF00603966

Murphy CG (2003) The cause of correlations between nightly numbers of male and female barking treefrogs (*Hyla gratiosa*) attending choruses. Behav Ecol 14 (2):274-281. doi:https://doi.org/10.1093/beheco/14.2.274

Narins PM, Feng AS, Lin WY, Schnitzler HU, Denzinger A, Suthers RA, Xu CH (2004) Old World frog and bird vocalizations contain prominent ultrasonic harmonics. J Acoust Soc Am 115 (2):910-913. doi:https://doi.org/10.1121/1.1636851

Nityananda V, Bee MA (2012) Spatial release from masking in a free-field source identification task by gray treefrogs. Hear Res 285 (1-2):86-97. doi:https://doi.org/10.1016/j.heares.2012.01.003

Passmore NI, Capranica RR, Telford SR, Bishop PJ (1984) Phonotaxis in the painted reed frog (*Hyperolius marmoratus*): The localization of elevated sound sources. J Comp Physiol 154 (2):189-197. doi:https://doi.org/10.1007/BF00604984

Ponnath A, Farris HE (2014) Sound-by-sound thalamic stimulation modulates midbrain auditory excitability and relative binaural sensitivity in frogs. Front Neural Circuits 8:85. doi:https://doi.org/10.3389/fncir.2014.00085

Ratnam R, Feng AS (1998) Detection of auditory signals by frog inferior collicular neurons in the presence of spatially separated noise. J Neurophysiol 80 (6):2848-2859. doi:https://doi.org/10.1152/jn.1998.80.6.2848

Rheinlaender J, Gerhardt HC, Yager DD, Capranica RR (1979) Accuracy of phonotaxis by the green treefrog (*Hyla cinerea*). J Comp Physiol 133 (4):247-255. doi:https://doi.org/10.1007/BF00661127

Ryan MJ, Sullivan BK (1989) Transmission effects on temporal structure in the advertisement calls of two toads, *Bufo woodhousii* and *Bufo valliceps*. Ethology 80 (1-4):182-189. doi:https://doi.org/10.1111/j.1439-0310.1989.tb00738.x

Schul J, Bush SL (2002) Non-parallel coevolution of sender and receiver in the acoustic communication system of treefrogs. Proc Roy Soc Ser B 269 (1502):1847-1852. doi:https://doi.org/10.1098/rspb.2002.2092

Schwartz JJ, Bee MA (2013) Anuran acoustic signal production in noisy environments. In: Brumm H (ed) Animal communication and noise. Animal Signals and Communication. Springer, New York, pp 91-132. doi:https://doi.org/10.1007/978-3-642-41494-7_5

Schwartz JJ, Del Monte MES (2019) Spatially-mediated call pattern recognition and the cocktail party problem in treefrog choruses: Can call frequency differences help during signal overlap? Bioacoustics 28 (4):312-328. doi:https://doi.org/10.1080/09524622.2018.1443836

Schwartz JJ, Gerhardt HC (1989) Spatially mediated release from auditory masking in an anuran amphibian. J Comp Physiol A 166 (1):37-41. doi:https://doi.org/10.1007/BF00190207

Schwartz JJ, Gerhardt HC (1995) Directionality of the auditory system and call pattern recognition during acoustic interference in the gray treefrog, *Hyla versicolor*. Aud Neurosci 1:195-206

Shen JX, Feng AS, Xu ZM, Yu ZL, Arch VS, Yu XJ, Narins PM (2008) Ultrasonic frogs show hyperacute phonotaxis to female courtship calls. Nature 453 (7197):914-916. doi:https://doi.org/10.1038/nature06719

Shofner WP (2015) Acoustic analysis of the frequency-dependent coupling between the frog’s ears. J Acoust Soc Am 138: 1623–1626. doi: https://doi.org/10.1121/1.4929746

Suthers RA, Narins PM, Lin WY, Schnitzler HU, Denzinger A, Xu CH, Feng AS (2006) Voices of the dead: Complex nonlinear vocal signals from the larynx of an ultrasonic frog. J Exp Biol 209 (24):4984-4993. doi:https://doi.org/10.1242/jeb.02594

Swanson EM, Tekmen SM, Bee MA (2007) Do female frogs exploit inadvertent social information to locate breeding aggregations? Can J Zool 85:921-932. doi:https://doi.org/10.1139/Z07-074

van Hemmen JL, Christensen-Dalsgaard J, Carr CE, Narins PM (2016) Animals and ICE: Meaning, origin, and diversity. Biol Cybern 110 (4-5):237-246. doi:https://doi.org/10.1007/s00422-016-0702-x

Vélez A, Bee MA (2010) Signal recognition by frogs in the presence of temporally fluctuating chorus-shaped noise. Behav Ecol Sociobiol 64:1695-1709. doi:https://doi.org/10.1007/s00265-010-0983-3

Vélez A, Bee MA (2011) Dip listening and the cocktail party problem in grey treefrogs: Signal recognition in temporally fluctuating noise. Anim Behav 82 (1319-1327):1319-1327. doi:https://doi.org/10.1016/j.anbehav.2011.09.015

Vélez A, Gordon NM, Bee MA (2017) The signal in noise: Acoustic information for soundscape orientation in two North American tree frogs. Behav Ecol 28 (3):844-853. doi:https://doi.org/10.1093/beheco/arx044

Verhey JL, Pressnitzer D, Winter IM (2003) The psychophysics and physiology of comodulation masking release. Exp Brain Res 153 (4):405-417. doi:https://doi.org/10.1007/s00221-003-1607-1

Vlaming MSMG, Aertsen AMHJ, Epping WJM (1984) Directional hearing in the grass frog (*Rana temporaria* L.): I. Mechanical vibrations of tympanic membrane. Hear Res 14 (2):191-201. doi:10.1016/0378-5955(86)90043-2

Wang J, Ludwig TA, Narins PM (1996) Spatial and spectral dependence of the auditory periphery in the northern leopard frog. J Comp Physiol A 178 (2):159-172. doi:https://doi.org/10.1007/BF00188159

Ward JL, Buerkle NP, Bee MA (2013) Spatial release from masking improves sound pattern discrimination along a biologically relevant pulse-rate continuum in gray treefrogs. Hear Res 306:63-75. doi:https://doi.org/10.1016/j.heares.2013.09.006

Wilczynski W, Resler C, Capranica RR (1987) Tympanic and extratympanic sound transmission in the leopard frog. J Comp Physiol A 161 (5):659-669. doi:https://doi.org/10.1007/bf00605007

Wiley RH, Richards DG (1978) Physical constraints on acoustic communication in the atmosphere: Implications for the evolution of animal vocalizations. Behav Ecol Sociobiol 3 (1):69-94. doi:https://doi.org/10.1007/BF00300047

Xu J, Gooler DM, Feng AS (1996) Effects of sound direction on the processing of amplitude modulated signals in the frog inferior colliculus. J Comp Physiol A 178 (4):435-445. doi:https://doi.org/10.1007/BF00190174

Zhang F, Zhao J, Feng AS (2017) Vocalizations of female frogs contain nonlinear characteristics and individual signatures. PLoS ONE 12 (3). doi:https://doi.org/10.1371/journal.pone.0174815

Zhang H, Xu J, Feng AS (1999) Effects of GABA mediated inhibition on direction-dependent frequency tuning in the frog inferior colliculus. J Comp Physiol A 184 (1):85-98. doi:https://doi.org/10.1007/s003590050308

Figure legends

Fig. 1 Orientation behavior of a female green treefrog (*Hyla cinerea*) in response to playback of advertisement calls. **a** In a control trial in which both eardrums were untouched, the female exhibits a zig-zag pattern of hopping directly toward the speaker. **b** When vibration of the animal's right eardrum was attenuated by coating with a thin layer of silicone grease, the animal consistently turned toward the left and was unsuccessful in localizing the sound source. **c** When vibration of the animal's left eardrum was attenuated by coating with a thin layer of silicone grease, the animal consistently turned toward the right and was unsuccessful in localizing the sound source. Frogs and speakers not drawn to scale. Modified from Feng et al. (1976)

Fig. 2 Activity of two EI neurons in the dorsal medullary nucleus (DMN) as a function of interaural level differences (ILD), depicted as the level differences between ipsilateral (IL) and contralateral (CL) stimulation. For both neurons, CL stimuli are presented 10 dB above threshold. Response to monaural CL stimulation is shown by the dotted line. **a** Neuron with a best frequency of 435 Hz and a threshold of 25 dB SPL. **b** Neuron with a best frequency of 575 Hz and a threshold of 23 dB SPL. Modified from Feng and Capranica (1976)

Fig. 3 A measurement of acoustical crosstalk in 27 auditory nerve fibers in *Lithobates pipiens* with a cubic polynomial fitted curve (line). The crosstalk was measured as the dB difference in sound level eliciting the same spike rate with monaural dichotic stimulation (closed couplers). Negative values show lower sensitivity for contralateral than ipsilateral stimulation. Modified from Feng (1980), Fig. 6, Copyright 1980, Acoustical Society of America

Fig. 4 Directional characteristics of two auditory nerve fibers in the northern leopard frog (*Lithobates pipiens*), measured in the frontal horizontal plane. The figures show equivalent dBs relative to threshold. The fibers are stimulated by sound from frontal horizontal directions a constant intensity (10 dB above threshold with 90˚ stimulation). The firing rates at each direction are converted to equivalent dBs using the fibers rate-intensity curve, measured at 90˚ sound incidence. **a** Directional characteristic of a low-frequency unit (BF 170 Hz). Modified from Feng (1980), Fig. 2, used by permission. Copyright 1980, Acoustical Society of America. **b** Directional characteristic of a high-frequency unit (BF 1900 Hz). Modified from Feng (1980), Fig. 4, used by permission. Copyright 1980, Acoustical Society of America

Fig. 5 Directionality of the tympanum in the eastern gray treefrog (*Hyla versicolor*). The plot shows vibration amplitude as a function of source incidence angle in azimuth in 30° steps (relative to the snout at 0°). The center of the plot corresponds to a vibration amplitude of 10 nm; distance between the concentric reference circles is 10 dB. Data are shown for three frequencies: 1080 Hz (blue circles), 1520 Hz (red squares), and 2200 Hz (green triangles). The tympanum's frequency response is shown at each angle (solid black lines), and the response from 60° is re-plotted as a gray area behind each spectrum. Note that the greatest directionality is generally seen at frequencies intermediate between the two peaks of the bimodal frequency response of the tympanum (e.g., 1520 Hz) and that the two peaks correspond approximately to the lower peak (e.g. 1080 Hz) and upper peak (e.g. 2200 Hz) of conspecific advertisement calls. Modified from Jørgensen (1991)

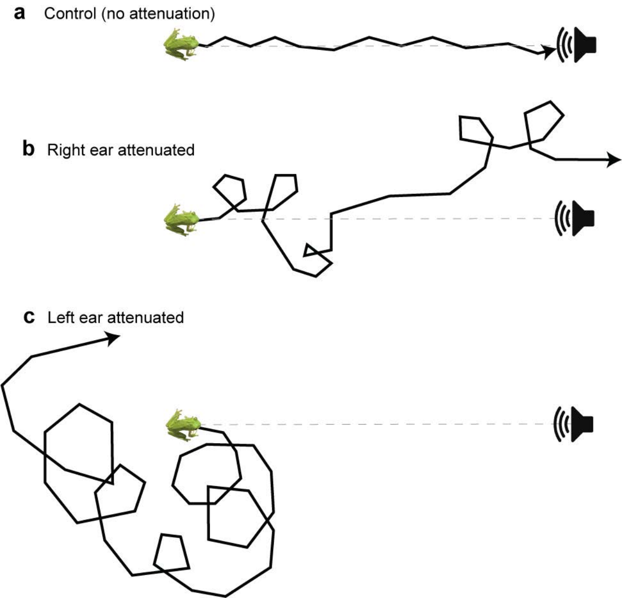
Fig. 6 Sensitivity to interaural time differences (ITDs) and interaural level differences (ILDs) in an EI neuron in the dorsal medullary nucleus (DMN). The neuron was stimulated with dichotic clicks with the same level for contralateral (CL) and ipsilateral (IL) stimulation (filled symbols) and with IL clicks at 10 dB higher level (open symbols). Negative time differences are IL stimuli leading, positive differences are CL stimuli leading. Firing probability in response to monaural CL stimulation is shown by the dotted line. Modified from Feng and Capranica (1976)

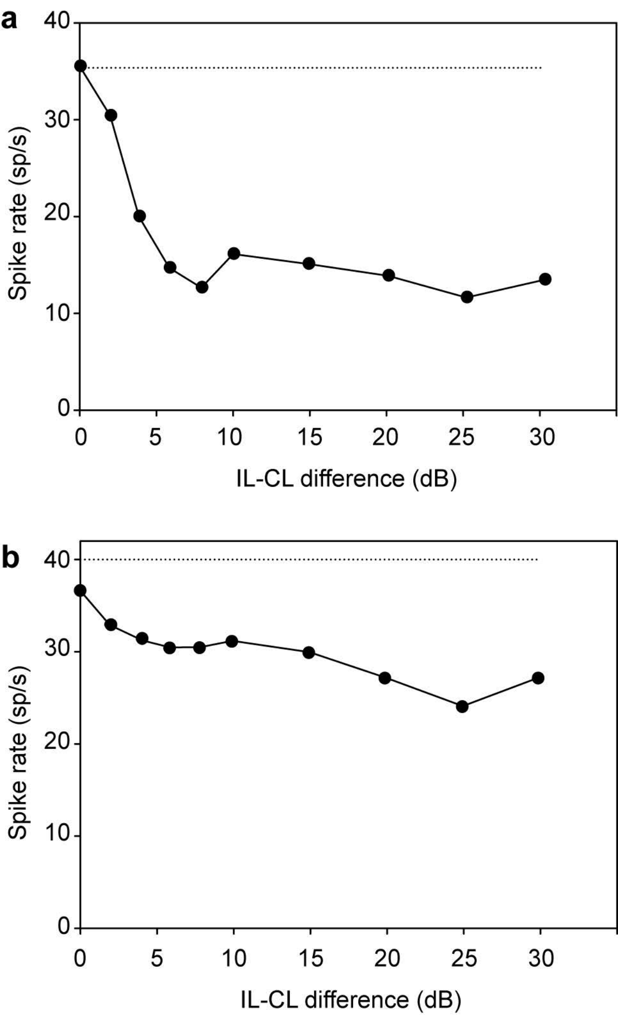
Fig. 7 Measures of behavioral performance in closed loop phonotaxis tests of source localization in azimuth in green treefrogs (*Hyla cinerea*). Histogram showing distributions of head orientation angles (α) and jump error angles (γ) when females engaged in head scanning behavior. Insets show how head orientation angle and jump error angle were computed. Data from Rheinlaender et al. (1979); figure modified from Bee and Christensen-Dalsgaard (2016)

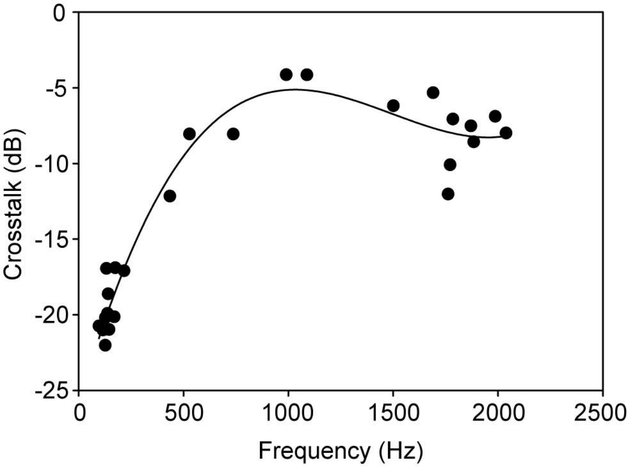
Fig. 8 Measures of behavioral performance in open loop phonotaxis tests of source localization in azimuth in barking treefrogs (*Hyla gratiosa*) and Cope's gray treefrog (*Hyla chrysoscelis*). Shown here are the mean orientation angles of subjects after making a translational or rotational movement relative to the position of a source of advertisement calls at sound incident angles in the frontal hemifield between -45° (left) and +45° (right) of the animal's midline. Redrawn from data in Klump and Gerhardt (1989) and Caldwell and Bee (2014) and modified from Bee and Christensen-Dalsgaard (2016)

Fig. 9 Diagrams of the grid over which female tree frogs moved during approaches to a speaker broadcasting synthetic mating calls. To provide for vertical movements of the animals, thin aluminum stakes (diameter, 10 mm; height, 1 m) were arranged on the grid area (1 m by 1 m); each stake position is indicated by a fine cross or other junction of fine lines in the figure. The grid of vertical 1-m stakes was stabilized by a series of crossbars at 25, 50, and 75 cm. These crossbars also served as reference points for estimating the vertical positions of the animals. Thus, a spatial arrangement of many possible positions within 1 m^3 was provided. The speaker suspension plane (vertical) is indicated by the dashed line. The speaker and its support system were physically isolated from the grid so that there were no vibrational cues. **a** Diagram of a typical approach when the elevated speaker was active. The course of the frog is indicated by the heavy line, the numbers representing the frog's positions (1 to 12). The lengths of vertical lines below a number indicate the elevations to which the frog jumped or climbed at each position. **b** Diagram of a typical approach when the ground-level speaker was active, the numbers representing the frog's positions (1 to 8). Modified from Gerhardt and Rheinlaender (1982)

Fig. 10 Phonotaxis scores (black circles and error bars represent medians ±95% CI; gray circles and error bars represent mean values ±95% CI) for the **a** synthetic *H. versicolor* call, **b** 1 m chorus. The data were pooled for all chorus exemplar/SPL pairs. The data were pooled for all chorus exemplar/SPL pairs. Phonotaxis scores were calculated using the time to reach the loudspeaker. Horizonal bars and asterisks indicate significant differences with Dunn's multiple comparison tests (*$p \leq 0.05$; ****$p \leq 0.0001$) after Kruskal-Wallis one-way ANOVA on the speaker-derived scores. Modified from Christie et al. (2019)

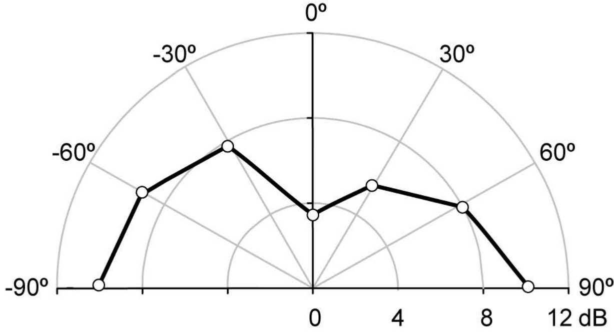

a Control (no attenuation)
b Right ear attenuated
c Left ear attenuated


a
b
Spike rate (sp/s)
IL-CL difference (dB)
0
10
20
30
40
0
5
10
15
20
25
30

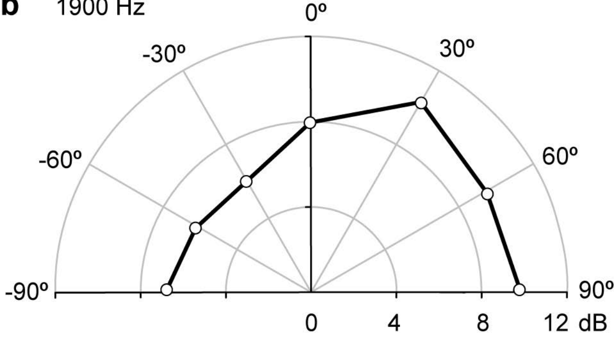


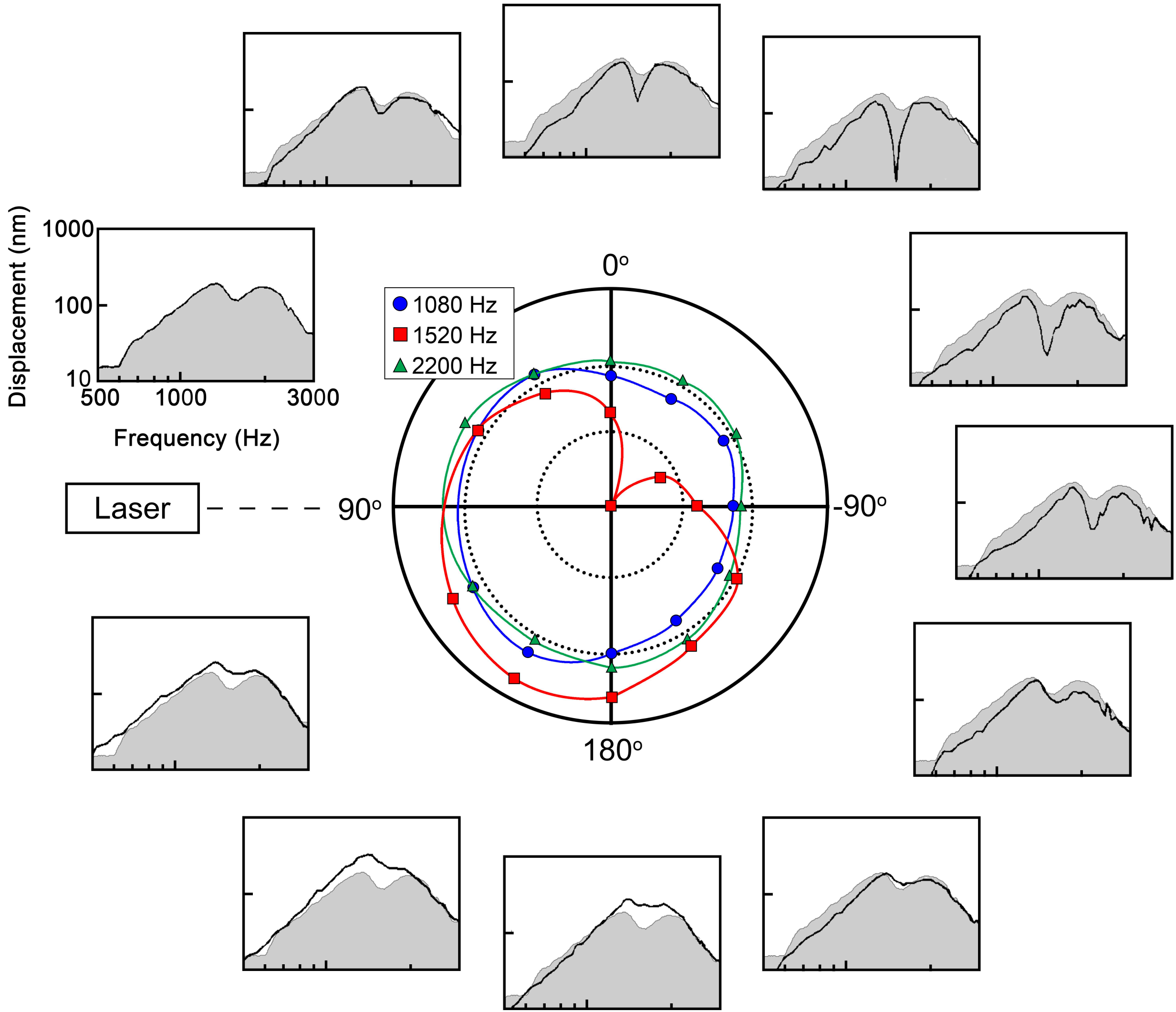
0
-5
-10
-15
-20
-25
Crosstalk (dB)
0
500
1000
1500
2000
2500
Frequency (Hz)

a 170 Hz

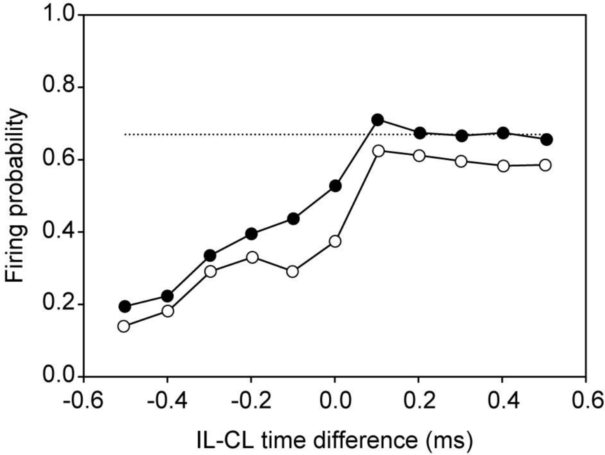


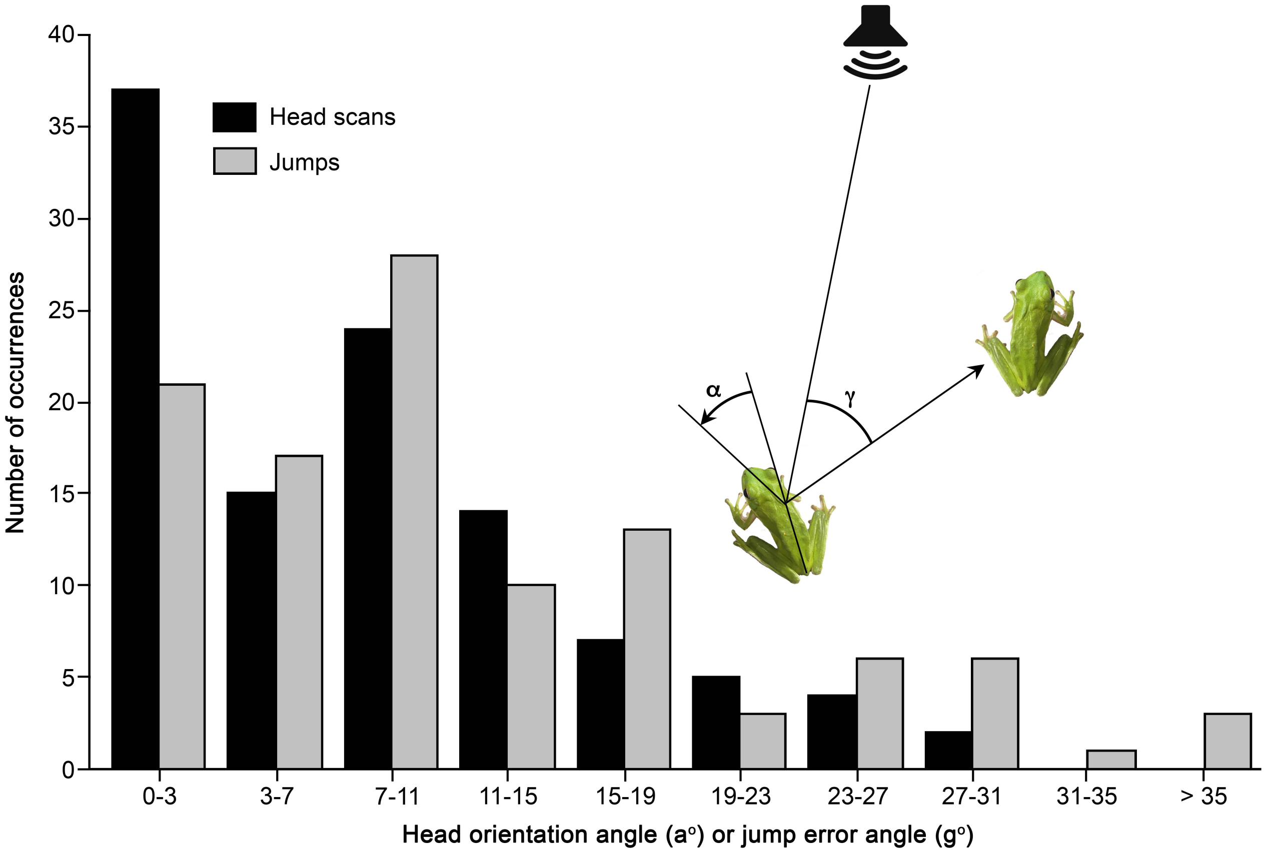
b 1900 Hz



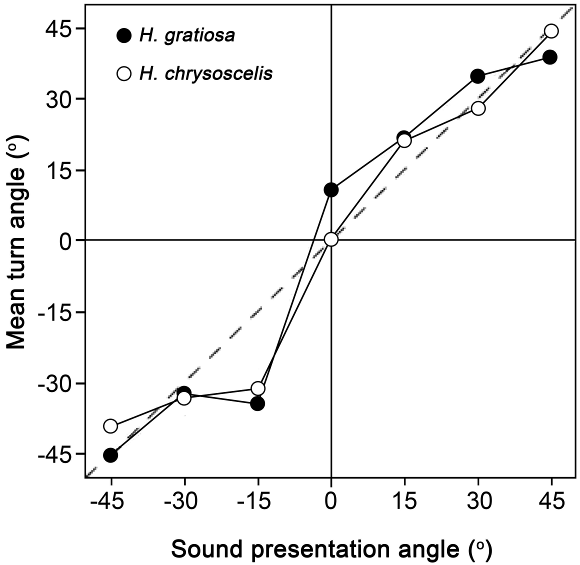


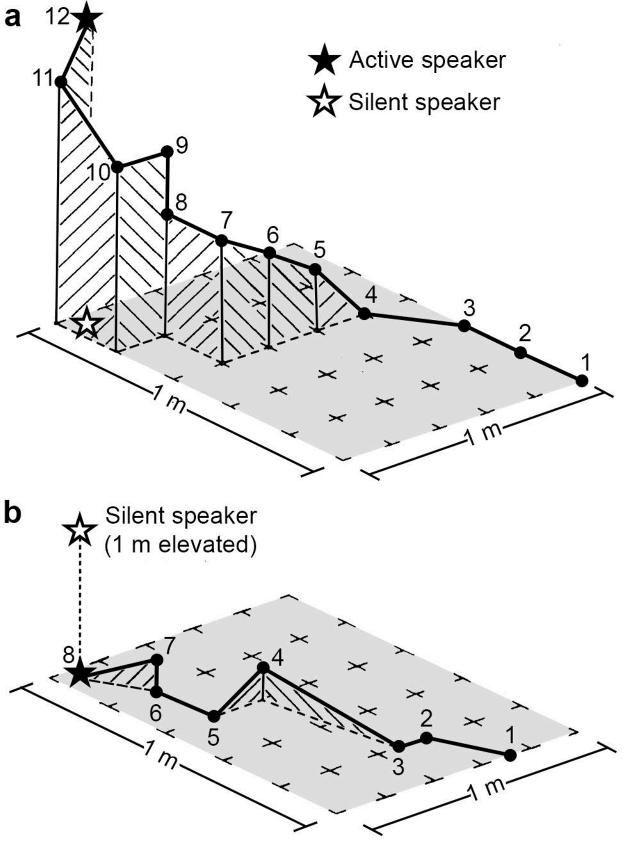
Displacement (nm)
1000
100
10
500
1000
3000
Frequency (Hz)
Laser
0°
90°
-90°
180°
1080 Hz
1520 Hz
2200 Hz

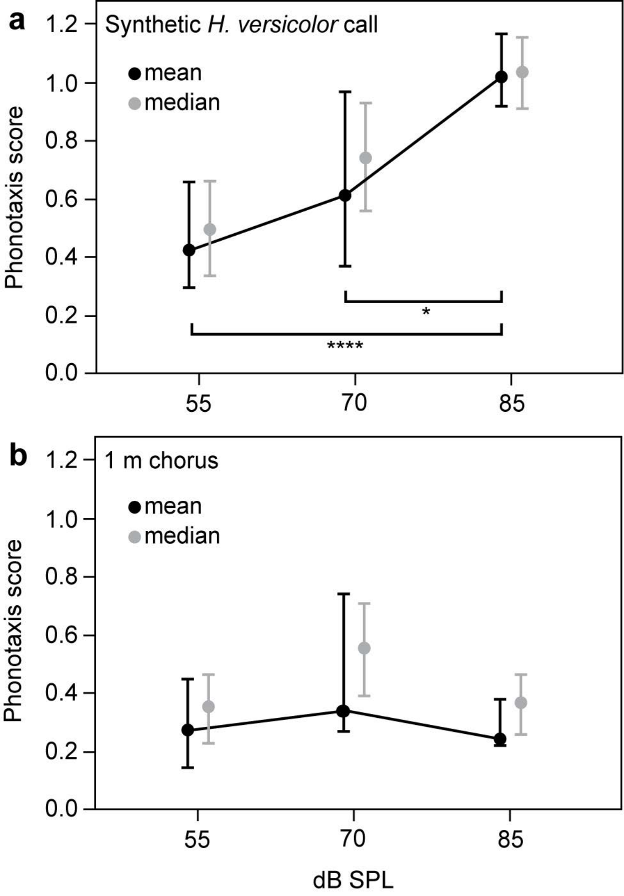

1.0
0.8
0.6
0.4
0.2
0.0
-0.6
-0.4
-0.2
0.0
0.2
0.4
0.6
Firing probability
IL-CL time difference (ms)



Head scans
Jumps
Number of occurrences
0
5
10
15
20
25
30
35
40
0-3
3-7
7-11
11-15
15-19
19-23
23-27
27-31
31-35
> 35
Head orientation angle (a°) or jump error angle (g°)
α
γ


H. gratiosa
H. chrysoscelis
Mean turn angle (°)
Sound presentation angle (°)
45
30
15
0
-15
-30
-45
-45
-30
-15
0
15
30
45


a
Active speaker
Silent speaker
12
11
10
9
8
7
6
5
4
3
2
1
1 m
1 m
b
Silent speaker
(1 m elevated)
8
7
6
5
4
3
2
1
1 m
1 m


a
Synthetic H. versicolor call
mean
median
Phonotaxis score
1.2
1.0
0.8
0.6
0.4
0.2
0.0
*
****
55
70
85
b
1 m chorus
mean
median
Phonotaxis score
1.2
1.0
0.8
0.6
0.4
0.2
0.0
55
70
85
dB SPL