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EDITORIAL

Neuroethology of auditory systems: contributions in memory of Albert S. Feng

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Abstract
Albert (Al) S. Feng (1944 – 1921) was a pioneer in the area of neuroethology of auditory systems. This special issue of the *Journal of Comparative Physiology A* commemorates his life and work by presenting 15 articles written by friends, students, and colleagues, many of whom have become leading experts themselves in this field. Their contributions not only provide a comprehensive overview of bioacoustics in amphibians and mammals (including bats), but also are intended to inspire a new generation of scientists to advance our understanding of brain mechanisms of acoustic perception.

Keywords Anuran amphibians · Bats · Binaural processing · Bioacoustics · Sound localization

The *Journal of Comparative Physiology A*: a tradition in celebrating the life and work of pioneers

Ninety-nine years ago, in March 1924, the first issue of the *Zeitschrift für Vergleichende Physiologie*—the predecessor of the *Journal of Comparative Physiology A*— was published. Founded by Karl von Frisch and Alfred Kühn, it was the first scientific journal specifically devoted to the publication of articles in comparative physiology (for a historical review, see Zupanc 2022). Since then, the *Journal* has provided a prominent platform for communicating research in this discipline. The long list of articles published includes numerous classical studies, many of which have become textbook knowledge.

What began as the *Zeitschrift für Vergleichende Physiologie* and is now in its 100th year has gradually evolved from a journal publishing articles in German by the authors predominantly affiliated with German academic institutions into an international journal, with English as the lingua franca, and with contributions from all over the world. Reflecting the increasing specialization, it branched into two sister journals, the *Journal of Comparative Physiology A* (with focus on sensory physiology, neurophysiology, and neuroethology) and the *Journal of Comparative Physiology B* (covering biochemical, systemic, and environmental physiology), in 1984.

As part of this continued evolution, 20 years ago, one of us (GKHZ) proposed to the then Editor-in-Chief, Friedrich G. Barth, to add, as a new feature of the *Journal of Comparative Physiology A*, the sporadic publication of special issues, each dedicated to a topic of interest to a broad readership. Barth enthusiastically accepted this proposal, and 3 years later, the first special issue titled 'Electric Fish: Model Systems for Neurobiology—A Tribute to Walter Heiligenberg' (J Comp Physiol A 192 (6), 2006) appeared. In commemorating the life and work of one of the pioneers of neuroethology, it contained an obituary authored by the Guest Editor, who had been one of his graduate students and postdocs, and by Theodore 'Ted' H. Bullock, a close colleague of Heiligenberg at the Scripps Institution of

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Oceanography of the University of California, San Diego (Zupanc and Bullock 2006).

Sadly, 1 year before the obituary came out, Ted Bullock passed away. His death motivated GKHZ to edit another special issue, now in celebration of Bullock's extraordinary life and his tremendous scientific achievements (J Comp Physiol A 194 (2), 2008). When he invited Al Feng (who was a former postdoc of Ted Bullock) to contribute to this special issue, Al (as he was known to many of us) replied on the same day: "It's my pleasure to accept your invitation to contribute a review article on sound communication (in frogs) to this special issue of JCP-A as a tribute to Ted. Ted influenced so many of us in our pursuit of science, and my recent work with the Chinese ultrasonic frogs is no exception—his fingerprints are all over it. I may ask Peter Narins to co-author it, but I will present a personal recollection of Ted's influence on me." In their article, Al and Peter reviewed research on ultrasonic communication in concave-eared torrent frogs (*Amolops tormotus*) and reflected, as he had promised, on how much Ted's wisdom had guided their own work (Feng and Narins 2008).

With the current special issue, we continue the tradition of the *Journal of Comparative Physiology A* as a forum for honoring great past leaders in our field. Now, in remembrance of Al Feng, who was taken from us in 2021, Peter M. Narins and Daniel A. Llano have brought together some of the finest scientists in the field of bioacoustics — many of them friends and collaborators of Al—to pay homage to the life and the scientific achievements of this great person and scholar (see obituary by Narins and Feng (2023) in this issue). Like in the special issues in memory of Walter Heiligenberg and Ted Bullock, the contributions are not only showcases of excellence in research, but they also reflect on how Feng has influenced the way their authors do science. Perhaps, it is this impact on others that will define Al's legacy more than anything else. Or to paraphrase him, his fingerprints are all over the life and work of so many of us.

Contributions in memory of Al Feng

This special issue is organized into three major parts according to the organisms studied: frogs, mammals (excluding bats), and bats. In the following, we summarize the core messages conveyed by the authors of each of the individual contributions and place their papers in a broader context of the neuroethology of auditory systems and of the work of Al Feng.

Frogs

In "Are frog calls relatively difficult to locate by mammalian predators?," Jones and Ratnam (2023) suggest that there are several features of frog calls that reduce their localizability by mammalian predators. These features include using highly periodic vocalizations, narrowband calls, short-pulsed calls and often calling in dense choruses using various means for controlling synchrony, maintaining chorus tenure, and abruptly switching off calling, all of which serve to confound localization by predators. They illustrate these strategies with call analyses for three different frog species. This work demonstrates that not only do frogs have sophisticated mechanisms for sound localization (many of which were first described by Al Feng), but also employ clever approaches to limit the localizability of their own calls to avoid predation.

In "Female preferences for the spectral content of advertisement calls in Cope's gray treefrog (*Hyla chrysoscelis*)," Gupta and Bee (2023) investigate the amplitude dependence of female preferences for the spectral content of male advertisement calls, which have a "bimodal" spectrum with separate low-frequency (1.25 kHz) and high-frequency (2.5 kHz) components. With few exceptions, preferences are largely independent of amplitude across both a 30-dB range of overall signal amplitude suggesting an "essential nonlinearity" (sensu Goldstein 1967), and an 11-dB range in the relative amplitudes of the two spectral components. Their data speak to the difficulty of blind acceptance of the matched filter hypothesis across all species. These findings also give strong impetus for future comparative neuroethological studies of spectral processing, an approach pioneered and promoted by Al Feng throughout his career.

In "Behind the mask(ing): How frogs cope with noise," Lee et al. (2023) review the literature on release from auditory masking with a focus on frog auditory communication in noisy environments, such as during chorusing. They address many of the mechanisms to which Al Feng's work made a major contribution, such as matched filtering, dip listening, using temporal patterns of sound such as comodulation or spatial separation to facilitate extracting an acoustic signal from a noisy environment. They then look forward, proposing additional mechanisms and approaches to test these mechanisms.

In "Male antiphonal calls and phonotaxis evoked by female courtship calls in the large odorous frog (*Odorrana graminea*)," Shen et al. (2023) examine the acoustic behaviors of males from the species *Odorrana graminea*, a close relative of well-studied concave-eared torrent frog (*Odorrana tormota*). This work, done with Al Feng's longtime collaborator Peter Narins, showed that *Odorrana graminea*, like the sympatric *Odorrana tormota*, display bidirectional courtship-related acoustic communication between males and females. These data suggest that similar environmental pressures between these two species may have produced similar acoustic specializations.

In "DPOAEs and tympanal membrane vibrations reveal adaptations of the sexually dimorphic ear of the concave-eared torrent frog, *Odorrana tormota*," Cobo-Cuan et al. (2023) continue their studies of the remarkable Chinese frog which has an auditory system that can respond to both audible and ultrasonic frequencies. They measured tympanal vibrations using laser Doppler vibrometry and found that Eustachian tube closing in these frogs increases the sensitivity of the ear to frequencies matching that of the opposite sex. This study also includes Al Feng as a co-author.

In "Diversity of temporal response patterns in midbrain auditory neurons of frogs *Batrachyla* and its relevance for male vocal responses," longtime Feng collaborator Mario Penna and colleagues examine responses of neurons in the torus semicircularis (inferior colliculus) of two species of *Batrachyla* to temporally patterned sounds (Penna et al. 2023). They uncovered a diversity of temporal transfer function response types in these neurons. When coupled with previous work in a different species of *Batrachyla*, this work suggests that multiple strategies may exist to extract temporal characteristics of sound within this genus.

De Luca et al. (2023) test the reactions of male midwife toads to the randomized playback of a vibrational crescendo stimulus train in their paper entitled: "Effect of natural abiotic soil vibrations, rainfall and wind on anuran calling behavior: A test with captive-bred midwife toads (*Alytes obstetricans*)." They found that *A. obstetricans* is highly sensitive to very low frequencies, which could explain their sensitivity to vibrational stimuli. This work corroborates the earlier use of playback of a random crescendo stimulus train (Caorsi et al. 2019) and validates it to be a compelling approach for addressing behavioral questions.

In their article entitled "Neuroethology of sound localization in anurans," Gerhardt et al. (2023) review the literature on behavioral and neurophysiological studies of sound localization by frogs and toads. It becomes immediately obvious that Al Feng's contributions to this field are seminal. Moreover, his classical neuroethological approach to understanding the mechanisms underlying this critical behavior in the amphibia has yielded great insights into the neural processes underlying both the encoding of sound direction and binaural processing in these animals.

Mammals (excluding bats)

In their paper "Descending projections to the auditory midbrain: Evolutionary considerations," (Macias and Llano 2023) compare the structure and function of the mammalian inferior colliculus with the analogous structure in the frog—the torus semicircularis. They reflect on whether thalamotectal projections in mammals and amphibians are homologous and whether they interact with evolutionarily more newly derived projections from the cerebral cortex. They also consider the behavioral significance of these descending pathways, given the anurans' ability to navigate complex acoustic landscapes without the benefit of a corticocollicular projection.

William P. Shofner's contribution to this special issue is titled "Cochlear tuning and the peripheral representation of harmonic sound in mammals." In this article, he compares the spectral and temporal representations of stochastic, complex sounds which underlie the perception of pitch strength in humans and chinchillas (Shofner 2023). Specifically, the pitch strengths of these stochastic sounds differ between humans and chinchillas. Shofner's studies with auditory filterbank models and comparisons between summary correlograms and excitation patterns with corresponding behavioral data on pitch strength suggest that the dominant cue for pitch strength in humans is spectral (i.e., harmonic) structure, whereas the dominant cue for chinchillas is temporal (i.e., envelope) structure.

Extending auditory processing work to humans, in "Long-term changes in cortical representation through perceptual learning of spectrally degraded speech," Murai and Riquimaroux (2023) examined neural changes in response to acoustic perceptual training. They found that as humans learned to improve the accuracy of their perception of noise-vocoded speech, responses in the left posterior superior temporal sulcus showed parallel changes. These data point to the posterior temporal sulcus as a candidate region to facilitate the learning of noise-degraded speech sounds in humans.

Bats

In "Oscillatory discharges in the auditory midbrain of the big brown bat contribute to coding of echo delay," Simmons and Simmons (2023) examine a potential mechanism for delay tuning in the bat inferior colliculus. They report that big brown bat inferior colliculus neurons respond with oscillatory discharges at a broad range of latencies in response to pulse-echo pairs. Oscillations to pulse and echo extensively overlap, creating interference patterns that can be used for pulse-echo delay encoding. This work extends Al Feng's early pioneering work that first showed the presence of pulse-echo delay-tuned neurons and his later work on neural oscillations in the inferior colliculus (Feng et al. 1978).

In "Transmitter and receiver of the low frequency horseshoe bat *Rhinolophus paradoxolophus* are functionally matched for fluttering target detection," Schoeppler et al. (2023) show that *Rhinolophus paradoxolophus*, which emits a pulse that is an octave lower than expected for its body size, demonstrates the same Doppler-shift compensation to allow echoes to remain within its foveal frequencies, similar to other species that hunt fluttering insects.

In "Echo feedback mediates noise-induced vocal modifications in flying bats," Luo et al. (2023) examined noise-induced vocal modifications (NIVMs) in flying bats. The authors exposed freely-flying bats to broadcast noise while recording their sonar calls. They found that unlike non-echolocating animals, NIVMs in bats rely on echo feedback rather than vocal feedback.

Outlook

We trust that this collection of 15 articles will serve as a fitting tribute to our friend, colleague and mentor, Al Feng, and will inspire a new generation of scientists to advance our understanding of brain mechanisms of acoustic perception.

Declarations

Conflict of interest The authors declare no conflict of interest.

References

Caorsi V, Guerra V, Furtado R, Llusia D, Miron LR, Borges-Martins M, Both C, Narins PM, Meenderink SWF, Márquez R (2019) Anthropogenic substrate-borne vibrations impact anuran calling. Sci Rep 9:19456. https://doi.org/10.1038/s41598-019-55639-0

Cobo-Cuan A, Feng AS, Zhang F, Narins PM (2023) DPOAEs and tympanal membrane vibrations reveal adaptations of the sexually dimorphic ear of the concave-eared torrent frog, *Odorrana tormota*. J Comp Physiol A. https://doi.org/10.1007/s00359-022-01569-8

De Luca J, Zaffaroni-Caorsi V, Bosch J, Llusia Diego, Francisco Beltrán J, Márquez R (2023) Effect of natural abiotic soil vibrations, rainfall and wind on anuran calling behavior: a test with captive-bred midwife toads (*Alytes obstetricans*). J Comp Physiol A. https://doi.org/10.1007/s00359-022-01596-5

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

Feng AS, Simmons JA, Kick SA (1978) Echo detection and target-ranging neurons in the auditory system of the bat *Eptesicus fuscus*. Science 202:645–648. https://doi.org/10.1126/science.705350

Gerhardt HC, Bee MA, Christensen-Dalsgaard J (2023) Neuroethology of sound localization in anurans. J Comp Physiol A. https://doi.org/10.1007/s00359-022-01576-9

Goldstein JL (1967) Auditory nonlinearity. J Acoust Soc Am 41:676–689. https://doi.org/10.1121/1.1910396

Gupta S, Bee MA (2023) Female preferences for the spectral content of advertisement calls in Cope's gray treefrog (*Hyla chrysoscelis*). J Comp Physiol A. https://doi.org/10.1007/s00359-022-01575-w

Jones DL, Ratnam R (2023) Are frog calls relatively difficult to locate by mammalian predators? J Comp Physiol A. https://doi.org/10.1007/s00359-022-01594-7

Lee N, Vélez A, Bee M (2023) Behind the mask(ing): how frogs cope with noise. J Comp Physiol A. https://doi.org/10.1007/s00359-022-01586-7

Luo J, Lu M, Luo J, Moss CF (2023) Echo feedback mediates noise-induced vocal modifications in flying bats. J Comp Physiol A. https://doi.org/10.1007/s00359-022-01585-8

Macias S, Llano DA (2023) Descending projections to the auditory midbrain: evolutionary considerations. J Comp Physiol A. https://doi.org/10.1007/s00359-022-01588-5

Murai SA, Riquimaroux H (2023) Long-term changes in cortical representation through perceptual learning of spectrally degraded speech. J Comp Physiol A. https://doi.org/10.1007/s00359-022-01593-8

Narins PM, Feng J (2023) Albert Feng: father, friend, scientist, innovator (1944–2021). J Comp Physiol A. https://doi.org/10.1007/s00359-022-01568-9

Penna M, Araya C, Canete M (2023) Diversity of temporal response patterns in midbrain auditory neurons of frogs *Batrachyla* and its relevance for male vocal responses. J Comp Physiol A. https://doi.org/10.1007/s00359-022-01572-z

Schoeppler D, Kost K, Schnitzler HU, Denzinger A (2023) Transmitter and receiver of the low frequency horseshoe bat *Rhinolophus paradoxolophus* are functionally matched for fluttering target detection. J Comp Physiol A. https://doi.org/10.1007/s00359-022-01571-0

Shen JX, Xu ZM, Narins PM (2023) Male antiphonal calls and phonotaxis evoked by female courtship calls in the large odorous frog (*Odorrana graminea*). J Comp Physiol A. https://doi.org/10.1007/s00359-022-01561-2

Shofner WP (2023) Cochlear tuning and the peripheral representation of harmonic sounds in mammals. J Comp Physiol A. https://doi.org/10.1007/s00359-022-01560-3

Simmons JA, Simmons AM(2023) Oscillatory discharges in the auditory midbrain of the big brown bat contribute to coding of echo delay. J Comp Physiol A. https://doi.org/10.1007/s00359-022-01590-x

Zupanc GKH (2022) The Journal of comparative physiology A: rooted in great tradition, committed to innovation and discovery. J Comp Physiol A 208:213–223. https://doi.org/10.1007/s00359-021-01526-x

Zupanc GKH, Bullock TH (2006) Walter Heiligenberg: the jamming avoidance response and beyond. J Comp Physiol A 192:561–572. https://doi.org/10.1007/s00359-006-0098-5