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Khaleel A. Razak and Zoltan M. Fuzessery
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Single Cortical Neurons Serve Both Echolocation and Passive Sound Localization

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Razak, K. A., Z. M. Fuzessery, and T. D. Lohuis. Single cortical neurons serve both echolocation and passive sound localization. *J. Neurophysiol.* 81: 1438–1442, 1999. The pallid bat uses passive listening at low frequencies to detect and locate terrestrial prey and reserves its high-frequency echolocation for general orientation. While hunting, this bat must attend to both streams of information. These streams are processed through two parallel, functionally specialized pathways that are segregated at the level of the inferior colliculus. This report describes functionally bimodal neurons in auditory cortex that receive converging input from these two pathways. Each brain stem pathway imposes its own suite of response properties on these cortical neurons. Consequently, the neurons are bimodally tuned to low and high frequencies, and respond selectively to both noise transients used in prey detection, and downward frequency modulation (FM) sweeps used in echolocation. A novel finding is that the monaural and binaural response properties of these neurons can change as a function of the sound presented. The majority of neurons appeared binaurally inhibited when presented with noise but monaural or binaurally facilitated when presented with the echolocation pulse. Consequently, their spatial sensitivity will change, depending on whether the bat is engaged in echolocation or passive listening. These results demonstrate that the response properties of single cortical neurons can change with behavioral context and suggest that they are capable of supporting more than one behavior.

INTRODUCTION

The functional organization of sensory cortices was approached largely from the perspective of understanding the different, complementary roles of its subdivisions (Brugge 1982; Kowalski et al. 1995; Phillips et al. 1995; Suga 1984). In auditory cortex, the clearest structure/function relationships have come from studies of the more auditorily specialized species that use stereotypic sounds to mediate well-defined behaviors. In the mustached bat, for example, the different forms of response selectivity in several cortical regions suggest that they serve to extract different information from a biosonar echo (O'Neill and Suga 1982; Suga 1984; Suga et al. 1983). This suggests a division of labor among specialized regions, with each contributing to a unified target image. However, a recent reevaluation of the mustached bat's FM–FM region suggests that this region may play a role in both echolocation and intraspecific communication (Ohlemiller et al. 1996). This finding suggested a multifunction theory of cortical processing; a single region or neuron may have a primary function but is capable of serving one or more secondary functions (Suga 1994).

This report provides clear evidence that single cortical neurons can indeed exhibit multiple forms of selectivity for sounds associated with different behaviors. The pallid bat is a "gleaner" that feeds on terrestrial prey (Bell 1982; Fuzessery et al. 1993). It uses passive listening in the lower one-half of its audible range (1–35 kHz) to detect and locate noise transients produced by prey and reserves its high-frequency (30–80 kHz) biosonar for general orientation and obstacle avoidance. While hunting, it attends to both streams of auditory information. These streams are processed through two parallel pathways that are anatomically and physiologically segregated at the level of the inferior colliculus (IC). Biosonar information is processed through the ventral division of the IC (Fuzessery 1994; Fuzessery and Hall 1996). This division is tuned to biosonar frequencies (30–80 kHz), and >50% of neurons tested responded selectively to the downward FM sweep direction of the bat's biosonar pulse (60–30 kHz) (Brown 1976; Fuzessery et al. 1993). Approximately 30% of these neurons respond exclusively to this signal and are suppressed by tones, noise, or spectrally equivalent upward sweeps. In contrast, the response properties of neurons in the lateral division of the IC suggest that they serve the detection and localization of prey-generated noise transients (Fuzessery 1997). They are tuned to the lower end of the audible range (4–35 kHz), all respond to noise transients used in prey detection, and 13% respond exclusively to noise transients. They are extremely sensitive to behaviorally relevant interaural intensity and time differences (Fuzessery 1997), making them well suited for localizing prey-generated sounds.

This study of the pallid bat auditory cortex provides physiological evidence that single neurons receive converging input from these two brain stem pathways. They are bimodally tuned to low and high frequencies and exhibit a dual selectivity for sounds associated with echolocation and prey detection, endowing them with the potential to serve either behavior.

METHODS

Bats were anesthetized by Metofane inhalation, followed by an intraperitoneal injection of sodium pentobarbital (Nembutal, 30 μg/g BW) and acepromazine (2 μg/g BW). A midline incision was made in the scalp, and the muscles over the skull were reflected. A large lateral blood vessel and the rostrocaudal extent of neocortex, both visible through the transluscent skull, were used as landmarks to make a small 200-μm diameter hole over auditory cortex. A small, hollow aluminum rod (2 × 10 mm) was cemented to the front of the skull, and the bat was placed in a restraining device, with the rod secured to a crossbar. The bat was kept in a sedated state during neural recordings with additional sodium pentobarbital/acepromazine injections of 50% of the presurgical dosage. All experiments were conducted in a

heated, soundproofed room. Sounds were presented through dichotic, closed-field speakers (Infinity emit-K ribbon tweeters) fitted with cotton-lined funnels. Recording were made with glass micropipettes (tip resistance 4–12 MΩ, 1 M NaCl) that were advanced tangentially into the neocortex with a remote-controlled hydraulic microdrive.

On isolating a single neuron or sampling a multiunit cluster, frequency tuning curves were obtained, followed by a determination of response thresholds for pure tones at best frequencies, 1- to 30-kHz band-pass filtered noise transients of 1–10 ms, and upward and downward FM sweeps of 30–50 kHz over 2–6 ms. Response thresholds served as an index of selectivity for the different sounds. Monaural and binaural response properties were then tested with tones, noise, and FM sweeps, each at several SPLs. Interaural intensity differences (IIDs) were created by holding the SPL constant at the contralateral ear and varying the ipsilateral intensity in 5-dB steps. A binaural interaction was considered inhibitory if the response magnitude decreased ≥30% relative to excitatory monaural stimulation and facilitatory if it increased ≥30%. Otherwise the response was considered monaural. Response magnitudes represent the number of spikes obtained over 30 stimulus presentations, presented at a rate of 1 stimulus/s. All neurons were recorded in a region of auditory cortex that preliminary studies (Fuzessery et al. 1996) revealed to contain a high proportional of neurons with bimodal frequency tuning curves.

RESULTS

Data are based on 16 single unit and 27 multiunit recordings that had bimodal frequency tuning. Multiunit cluster recordings were estimated to comprise the activity of three to eight neurons and are therefore are not useful in supporting the contention that single neurons can have bimodal frequency tuning and exhibit selectivities for more than one behaviorally relevant sound. They are used only to support observations from single-neuron recording that different sounds cause neurons to express different monaural and binaural response properties. Multiunit recordings also provide evidence that low and high frequencies and selectivity for sounds associated with both echolocation and passive sound localization can be represented at a single cortical recording site.

Neurons were first tested with pure tones to determine their frequency tuning curves. They were then presented with sounds used by the bat in echolocation and prey detection, which are known to be effective stimuli for IC neurons that process these sounds. Lower response thresholds for the downward 50- to >30-kHz FM sweep used in echolocation, relative to a spectrally equivalent upward FM sweep or a pure tone within these sweeps, was taken as evidence of response selectivity for echolocation signals. Similarly, lower response thresholds for low-frequency noise transients relative to single low-frequency tones was taken as evidence of response selectivity sounds use in prey detection.

The 16 single neurons with bimodal frequency tuning curves had best frequencies located in two bands of 8–20 and 35–45 kHz (Fig. 1, A and C). Although the majority of neurons responded to pure tones in both frequency bands, tones were typically not the most effective stimuli. In 12 (75%) neurons, thresholds for downward FM sweeps and low-frequency noise bursts were lower than for pure tones within the spectra of these sounds. An example of this is shown in Fig. 1A, where the response threshold for noise is 4 dB lower than the threshold for a 10-kHz pure tone. Likewise, the threshold for a 50-to >30-kHz downward FM sweep is 10 dB lower than the thresh-

old for a 40-kHz pure tone and 15 dB lower than the threshold for a spectrally equivalent upward FM sweep.

A novel feature of these bimodally tuned neurons was that, in 12 of 16 (75%) neurons, binaural response properties changed as a function of the sound presented (Fig. 1, B and D). This change persisted when binaural properties were tested at several SPLs (Fig. 1B). Moreover, the direction of these changes was remarkably consistent. All 12 of these neurons appeared binaurally inhibited when presented with noise, but when presented with downward FM sweeps 7 were monaural and 5 were binaurally facilitated. For example, the neuron in Fig. 1, A and B, was excited at similar response magnitudes by monaural contralateral (CL) stimulation with noise or downward FM sweeps at 50 and 60 dB SPL. Neither stimulus evoked a response when presented ipsilaterally (IL). However, when stimulated binaurally with the CL intensities fixed at 50 and 60 dB and the IL intensity level varied to produce a range of IIDs, the neuron was completely binaurally inhibited at an IID of −5 dB (CL intensity level) when tested with noise but not when tested with downward FM sweeps. This indicates that IL stimulation with noise evokes an inhibitory input, but IL stimulation with an FM sweep does not.

The frequency of pure tones could also influence binaural properties. For example, the neuron in Fig. 1, C and D, was excited at similar response magnitudes by monaural CL stimulation with single tones at the best frequencies of the two tuning curves (10 and 37 kHz) and with noise and a downward FM sweep. IL monaural stimulation with these sounds did not excited the neuron. When stimulated binaurally with low-frequency noise and a 10-kHz tone located within the noise band, the neuron was completely binaurally inhibited at IIDs of −5 to −10 dB. No binaural inhibition was observed in response to the downward FM sweep or a 37-kHz tone within this FM sweep.

Single neurons that did not change binaural properties were binaurally inhibited in response to all sounds tested. The same trend was observed in recordings from multiunit clusters. Of 27 clusters that were bimodally tuned, 22 (73%) showed stimulus-dependent changes in binaural properties. All 22 were binaurally inhibited in response to noise, and all appeared monaural or binaurally facilitated in response to downward FM sweeps.

The monaural rate-level functions of single neurons could also change with the stimulus, although this change was less common. Eleven of 16 maintained monotonic (plateaued or increasing response) or nonmonotonic (peaked) functions, regardless of the stimulus. The remainder showed stimulus-dependent changes in their monaural rate functions. Similar changes were observed in 30 multiunit clusters. Nine (30%) exhibited changes in the shapes of their monaural rate functions.

DISCUSSION

We intepret bimodal frequency tuning, dual forms of response selectivity, and context-dependent changes in monaural and binaural response properties as physiological evidence that parallel pathways serving echolocation and passive hearing converge at some point in the system, allowing each pathway to impart its own suite of response properties on single cortical neurons. Exactly where this convergence first occurs remains to be determined, but the result is that single cortical neurons
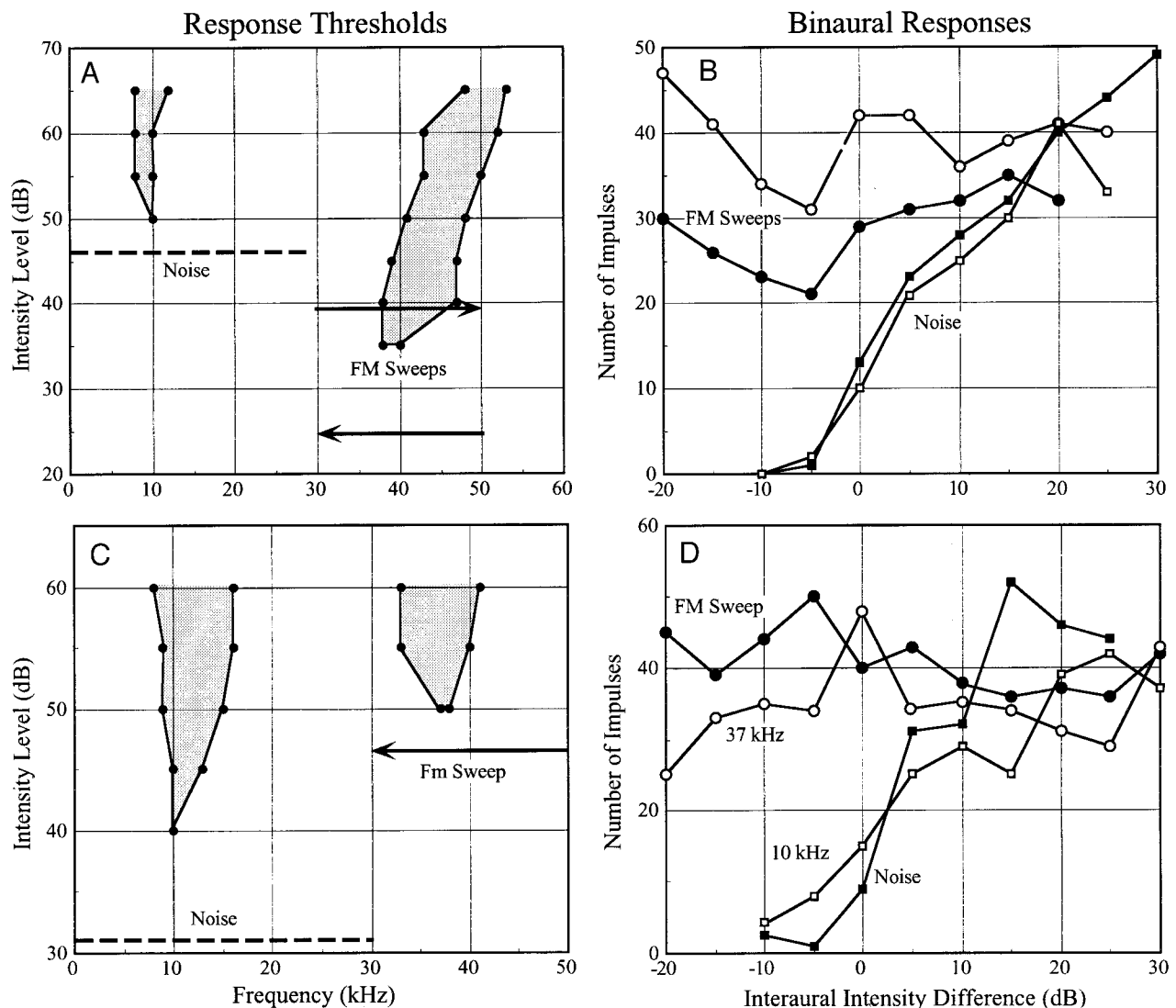
FIG. 1. The response properties of 2 functionally bimodal cortical neurons. *A* and *C*: bimodal frequency tuning curves (gray areas) and response thresholds for noise (dashed line) and 5-ms FM sweeps (arrows) of 30–50 kHz. FM sweep direction is indicated by arrow direction. *B* and *D*: responses to changes in interaural intensity differences (IIDs). Both neurons had lower thresholds for low-frequency noise and the downward FM sweeps than for individual tones within these frequency ranges. Both neurons were binaurally inhibited when presented with noise but not when presented with FM sweeps. *B*: when presented with noise at two fixed contralateral (CL) intensity levels (filled squares, CL 50 dB; open squares, CL 60 dB), this neuron was binaurally inhibited at increasing ipsilateral (IL) intensity levels. When presented with downward FM sweeps of 50–30 kHz (open circles, CL 30 dB; filled circles, CL 40 dB), the neuron appeared to be monaural or slightly binaurally facilitated at IIDs favoring the IL ear. *D*: this neuron was binaurally inhibited when presented with noise (filled squares) or a low-frequency, 10-kHz tone (open squares) but appeared monaural when presented with a downward FM sweep (filled circles) or a high-frequency, 37-kHz tone (open circles). Thus its binaural properties changed both with the type of sound and tone frequency.

can apparently be recruited to serve more than one behavior, and their response properties will change depending on whether the bat is engaged in echolocation or the passive sound localization of prey.

The multimodal frequency tuning observed in this study is not unique, but it does have unusual functional implications. Bimodally tuned neurons were described in several vertebrate groups (e.g., Fuzessery and Feng 1983; Langner et al. 1981; Margoliash and Fortune 1992; Sutter and Schreiner 1991) and were suggested to serve one of two functions, the detection of behaviorally important, complex sounds or the extraction of specific information from a sound. An example of the latter is seen in the mustached bat. The multiharmonic tuning of neu-

rons in the FM–FM region serves to resolve pulse–echo delay and hence target distance (O'Neill and Suga 1982; Suga et al. 1983). Bimodal tuning in the pallid bat cortex represents a third functional category because it indicates the convergence of information used for two distinct behaviors, echolocation and passive listening.

The stimulus-dependent changes in binaural properties have interesting implications in terms of spatial attention. Pronounced frequency-dependent changes in the directionality of the pallid bat ears (Fig. 2) (from Fuzessery 1996) coupled with stimulus-dependent changes in binaural properties suggest that functionally bimodal neurons will be sensitive to different points in space when processing biosonar or prey-detection
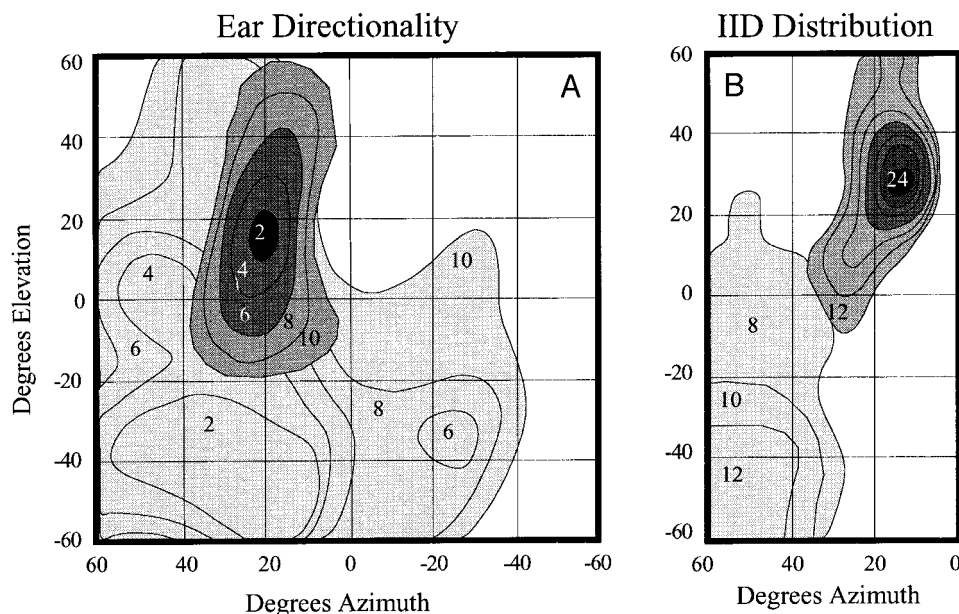
Ear Directionality

IID Distribution

FIG. 2. The frontal sound field of the pallid bat, showing the ear directionality and the distribution of interaural intensity differences (IIDs) at two frequencies, one in the passive listening range (10 kHz) and the other in the echolocation range (35 kHz). The darker gray contours at 35 kHz are overlain on top to the uniformly light gray contours at 10 kHz. *A*: ear directionality is shown by isointensity threshold contours (2-dB steps). The ear is most sensitivity to sounds where the intensity values are lowest (2 dB). At 10 kHz, the ear is broadly directional and most sensitive to sounds in the lower, lateral part of the sound field. At 35 kHz, directionality is much sharper, and the ear is most sensitive to a small area centered at 20° azimuth and elevation. *B*: distribution of IIDs were calculated by subtracting mirror-image intensity threshold values (from *A*) in each one-half of the sound field. At 10 kHz, IIDs of only ≤12 dB are created, and they are greatest in the lower, lateral part of the sound field. At 35 kHz, much larger IIDs are created (≤24 dB), and they are maximum in the upper part of the sound field. Data from Fuzessery 1996.

information. At low frequencies (10 kHz), the bat's ears are broadly directional, and large IID are created only in the lateral, lower part of the sound field. The binaural inhibition typically generated by low-frequency noise would make neurons most sensitive to sound locations where intensities are greater at the excitatory ear. These occur below the bat, where the sounds of terrestrial prey would originate. In contrast, at high frequencies (35 kHz), the ears are sharply directional for sounds emanating near the center of the upper one-half of the frontal sound field. Monaural or binaurally facilitated response properties at higher frequencies would make neurons most sensitive to sounds originating at the center of the upper sound field, the expected origin of the echoes of biosonar pulses emitted along the bat's flight path.

If these neurons receive input from pathways dedicated to both echolocation and passive listening, how does the rest of the auditory system decipher which input triggered their responses? The answer may be quite simple. The initiation of echolocation can be signaled by corollary discharge or direct sensory input triggered at pulse emission (Kawasaki et al. 1988; Kick and Simmons 1984; Roverud and Grinnell 1985; Suga and Schlegel 1972). The only time that a functionally bimodal neuron will be operating in echolocation mode is within a ~5- to 20-ms time window after the emission, when an echo is expected. The neuron will be serving passive listening at all other times.

A more profound issue is why the pallid bat auditory system routes two functionally distinct pathways onto single neurons, as opposed to processing this information in different parts of cortex. There are several possible explanations for this convergence, and they are not mutually exclusive. One is a conser-

vation of computational power, with the same neurons to perform two functions. The pallid bat is equally dependent on echolocation and passive listening while hunting. Sharing cortical tissue may serve to increase the neural representation of both functions. Echolocation and passive listening may "time-share" functionally bimodal neurons. Auditory scene analysis (Bregman 1990; Cherry 1953) suggests that we can attend to only one stream at a time, identified by its coherence in spectrum, temporal organization, and spatial origin, but that attention can be rapidly switched between two coherent streams. The hunting pallid bat is dealing with two streams that indeed differ in all of these attributes, and in addition one stream (echolocation) is voluntarily instigated. These features would facilitate the rapid switching of attention, allowing single neurons to serve two functions.

Another possibility is that convergence of input is a binding mechanism that provides a unification of perception. The hunting pallid bat requires echolocation for global imaging of its environment and passive detection and localization to place its prey within that environment. The routing of both pathways onto single neurons suggests that a single, unified representation of external space, derived from two streams of information, may be best served by overlain cortical representations.

In summary, studies of two bat species (Ohlemiller et al. 1996; this study) now provide evidence that single auditory cortex neurons are capable of serving more than one function. Although both examples demonstrate the potential recruitment of neurons for processing either active (echolocation) or passive hearing, we emphasize that this phenomenon may represent a general principle of cortical function and not a peculiarity of auditorily specialized species.

REFERENCES

BELL, G. P. Behavioral and ecological aspects of gleaning by the desert insectivorous bat, *Antrozous pallidus* (Chiroptera: Vespertilionidae). *Behav. Ecol. Sociobiol.* 10: 217–223, 1982.

BREGMAN, A. S. *Auditory Scene Analysis.* Cambridge, MA: MIT Press, 1990.

BROWN, P. Vocal communication in the pallid bat, *Antrozous pallidus. Z. Tierpsychol.* 41: 34–54, 1976.

BRUGGE, J. F. Auditory cortical maps in primates. In: *Cortical Sensory Organization,* edited by C. N. Woolsey. Clifton, NJ: Humana, 1982.

CHERRY, E. C. Some experiments on the recognition of speech with one and two ears. *J. Acoust. Soc. Am.* 25: 975–979, 1953.

FUZESSERY, Z. M. Response selectivity for multiple dimensions of frequency sweeps in the pallid bat inferior colliculus. *J. Neurophysiol.* 72: 1061–1079, 1994.

FUZESSERY, Z. M. Monaural and binaural spectral cues created by the external ears of the pallid bat. *Hear. Res.* 95: 1–17, 1996.

FUZESSERY, Z. M. Acute sensitivity to interaural time differences in the inferior colliculus of a bat that relies on passive sound localization. *Hear. Res.* 109: 46–62, 1997.

FUZESSERY, Z. M., BUTTENHOFF, P., ANDREWS, B., AND KENNEDY, J. M. Passive sound localization of prey by the pallid bat (*Antrozous p. pallidus*). *J. Comp. Physiol.* 171: 767–777, 1993.

FUZESSERY, Z. M. AND FENG, A. S. Mating call selectivity in the thalamus and midbrain of the leopard frog (*Rana p. pipiens*). *J. Comp. Physiol.* 150: 333–344, 1983.

FUZESSERY, Z. M. AND HALL, J. C. The role of GABA in shaping frequency tuning and selectivity for FM sweep direction in the inferior colliculus. *J. Neurophysiol.* 76: 1059–1073, 1996.

FUZESSERY, Z. M., LOHUIS, T., AND WEIMING, S. *Functional Organization of Pallid Bat Auditory Cortex: Processing Active and Passive Hearing.* Association for Research in Otolaryngology, 1996.

KAWASAKI, M., MARGOLIASH, D., AND SUGA, N. Delay-tuned combination-sensitive neurons in the auditory cortex of the vocalizing mustached bat. *J. Neurophysiol.* 59: 623–635, 1988.

KICK, S. A., AND SIMMONS, J. A. Automatic gain control in the bat's sonar receiver and the neuroethology of echolocation. *J. Neurosci.* 4: 2725–2737, 1984.

KOWALSKI, N., VERSNEL, H., AND SHAMMA, S. A. Comparison of responses in the anterior and primary auditory fields of the ferret. *J. Neurophysiol.* 73: 1513–1523, 1995.

LANGNER, G., BONKE, D., AND SCHEICH, H. Neuronal discrimination of natural and synthetic vowels in field L of trained mynah birds. *Exp. Brain Res.* 43: 11–24, 1981.

MARGOLIASH, D. AND FORTUNE, E. S. Temporal and harmonic combination-sensitive neurons in the zebra finch's HVc. *J. Neurosci.* 12: 4309–4326, 1992.

OHLEMILLER, K. K., KANWAL, J. S., AND SUGA, N. Facilitative responses to species-specific calls in cortical FM-FM neurons in the mustached bat. *NeuroReport* 7: 1749–1755, 1996.

O'NEILL, W. E. AND SUGA, N. Encoding of target-range information and its representation in the auditory cortex of the mustached bat. *J. Neurosci.* 2: 17–31, 1982.

PHILLIPS, D. P., SEMPLE, M. N., AND KITZES, L. M. Factors shaping the tone level sensitivity of single neurons in the posterior field of cat auditory cortex. *J. Neurophysiol.* 73: 674–686, 1995.

ROVERUD, R. C. AND GRINNELL, A. D. Echolocation sound features processed for distance information in the CF/FM bat, *Noctilio albiventris*: evidence for a gated window utilizing both CF and FM components. *J. Comp. Physiol.* 156: 457–469, 1985.

SUGA, N. The extent to which biosonar information is represented in the bat auditory cortex. In: *Dynamic Aspects of Neocortical Function,* edited by G. M. Edelman, W. E Gall, and W. M. Cowan. New York: Wiley, 1984.

SUGA, N. Multi-function theory of cortical processing of auditory information: implication of single-unit and lesion data for future research. *J. Comp. Physiol.* 175: 135–144, 1994.

SUGA, N., O'NEILL, W. E., AND MANABE, T. Cortical neurons sensitive to combinations of information-bearing elements of biosonar signals in the mustached bat. *J. Neurophysiol.* 49: 1573–1626, 1983.

SUGA, N. AND SCHLEGEL, P. Neural attenuation of responses to emitted sounds in echolocating bats. *Science* 177: 82–84, 1972.

SUTTER, M. L. AND SCHREINER, C. E. Physiology and topography of neurons with multipeaked tuning curves in cat primary auditory cortex. *J. Neurophysiol.* 65: 1207–1226, 1991.