Mechanisms of echolocation in bats – comments on the neuroethology of the biosonar system of ‘CF-FM’ bats

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The 'somatotopic' distribution across the sensory cortex of the brain describing the position of the sensory input from the different parts of the body has been well established for a number of years. In this paper we discover how the bat analyses the reflections of its own vocalizations (biosonar) through 'tonotopic' and 'amplitopic' representations of specific areas of its auditory cortex. We also gain an insight into how the animal uses its cortical processing to obtain information concerning the importance of a specified 'target' so that it may alter its behavioural strategy appropriately.

The major goal of auditory neurophysiology is to understand the mechanisms for neural processing of biologically meaningful sound used by animals. Since the auditory system has evolved in parallel with the vocalization system to receive and process the sounds produced by a species, it is appropriate to investigate the auditory system with acoustic stimuli which are designed to mimic the sounds important for survival of the animals in nature. The power of such a neuroethological approach in exploring neural mechanisms in hearing has been shown by our recent series of studies on the auditory system of the Panamanian moustache bat, *Pteronotus parnellii rubiginosus* (Fig. 1A). Here we shall describe how the auditory system of this insectivorous bat is specialized for receiving and processing biosonar signals called orientation sounds, and, more generally, how the use of biologically meaningful stimuli is beginning to clarify the functional organization of the auditory system.

**Echolocation**

For echolocation, the moustache bat produces biosonar signals, each consisting of a long constant-frequency (CF) component followed by a short frequency-modulated (FM) component (Fig. 1B). Each component is composed of 3-4 harmonics. In the 2nd harmonic, which is the most intense in the biosonar signal, the frequency remains at about 61 kHz for 5-30 msec, then sweeps down to about 50 kHz within 2-4 msec. Since the reflected sound energy is highly concentrated at a single wavelength, the long constant-frequency tone is ideal for target detection and measurement of relative target velocity. The frequency-modulated component, on the other hand, is more appropriate for ranging, localization, and characterization of a target, because of the wide distribution of sound energy over many different frequencies. The properties of the biosonar signal and the mode of action...
signal processing performed by the species are related to the particular behavioural strategies employed for echolocation.

The moustach bat, like the horseshoe bat Rhinolophus ferrumequinum, performs a fascinating acoustic behaviour called 'Doppler-shift compensation' during echolocation. When an object is stationary relative to the bat, it will reflect sounds with the 2nd harmonic CF at about 61 kHz. If the bat receives a Doppler-shifted echo, say at 63 kHz, from an object which it is approaching, the bat retains this frequency information and reduces the frequency of the subsequent biosonar signals so as to stabilize the 2nd harmonic CF of the Doppler-shifted echo at about 61 kHz (Fig. 1C). Clearly, the bat is extraordinarily sensitive to echoes from moving targets. This vocal behaviour has apparently evolved together with the specialization of the auditory system for detection and processing echoes from moving targets, as will be described subsequently.

Specialization of the peripheral auditory system of the moustach bat
In the moustach bat, the threshold curve of the cochlear microphonic (CM) response (i.e. receptor potential) is sharply tuned at about 61 kHz. This sharp tuning is apparently due to some mechanical specialization in the cochlea which acts as a sharply tuned local resonator, because for a 61 kHz sound, the amplitude of the cochlear microphonic response shows prominent damped oscillation. It increases exponentially with a time constant of 1.1±0.3 msec to a certain level at the beginning, and then exponentially declines to zero at the cessation of the stimulus. The resonance frequency of this sharply tuned local resonator is 61.1±0.43 kHz. The Q (a quality factor expressing the sharpness of a resonator) of this resonator, which is affected only slightly by the removal of the osiccular chain of the middle ear, is 204±57. When the frequency of a tone burst is slightly different from the resonance frequency, the cochlear microphonic response due to the stimulus and the cochlear microphonic response due to the local resonator overlap, and produce beats. This means that the 61 kHz tuned area of the basilar membrane is weakly coupled to the areas tuned at neighbouring frequencies. The cochlear microphonic response thus represents a unique feature of the cochlea of this species. In mammals, frequency analysis is based upon the properties of a travelling wave moving along the basilar membrane. This is also undoubtedly true in the moustach bat, except for that part of the membrane tuned at around 61 kHz. Frequency analysis here is strongly influenced by local resonators.

Velocity perception
To extract accurate velocity information from an echo, fine frequency resolution is required. Resolution at frequencies higher than 5 kHz is directly related to the sharpness of tuning curves (i.e. frequency-threshold curves) of auditory neurones. In the moustach bat, single auditory nerve fibres sensitive to a 61 kHz sound show extremely sharp tuning. The biosonar signal of this bat contains not only the 2nd harmonic at about 61 kHz, but also the 1st and 3rd harmonics to some extent. Tuning of neurones at either 30.5 or 91.5 kHz (the 1st and 3rd harmonics) is also sharp (Fig. 2C). The cochlea of the moustach bat is apparently specialized not only for target detection, but also for fine frequency analysis of the CF component of the biosonar signal. The horseshoe bat also performs Doppler-shift compensation. The constant-frequency component of its biosonar signal is at 83 kHz, and the tuning of its peripheral neurones is also extremely sharp at this frequency. Unlike the preceding examples, the little brown bat, Myotis lucifugus, emits only frequency-modulated sounds for echolocation. Its peripheral neurones do not show extremely sharp tuning at any frequency (Fig. 2A).

By incorporating Doppler-shift compensation with a group of extremely sharply tuned neurones, the moustach bat can reduce the masking effect of loud emitted sounds (and also non-Doppler-shifted echoes) on weak Doppler-shifted echoes. Sharply tuned neurones are directly related not only to effective target detection, but also to accurate measurement of the relative target velocity. Furthermore, these neurones are exquisitely sensitive to minor fluctuations in frequency.

When the target is a flying insect, the constant-frequency echo from it may be modulated in amplitude and frequency by its wing beat. Sharply tuned neurones can code frequency modulation as low as

![Fig. 2. Sound spectrograms (upper figures) and distribution of Q-10 dB values of peripheral neurones (lower graphs) of M. lucifugus (A), R. ferrumequinum (B) and P. parnellii rubiginosus (C). The distribution of Q-10 dB values (expressing the sharpness of neural tuning curves) as a function of best frequency shows a clear peak in R. ferrumequinum and P. parnellii. Note that the peak(s) appear at the frequency of the predominant components of the echolocation signal. The curves in the lower graphs represent the hearing threshold curves (or audiograms) of these bats.](image_url)
amplitude is the result of both the target cross-sectional area and the inverse 4th power of the target distance. Poorly directional neurones specialized for echo detection (E-E neurones) are mainly found in the unshaded area, while directionally sensitive neurones specialized for target localization (I-E neurones) are mainly found in the unshaded area.

\[ \pm 0.01\% \text{ by changing their discharge rate synchronously with the modulation. A} \]
\[ 0.01\% \text{ frequency modulation corresponds with a 6.1 Hz frequency shift at 61 kHz.} \]
Since the Doppler-shift from the beating wing of a moth can be as high as 300 Hz, it is quite possible that peripheral auditory neurones code the wing beat of an insect by synchronous neural discharges and also by synchronous change in excitation from one group of neurones to another differing in best frequency. The moustache bat may use wing beat information to discriminate not only insect prey from other objects, but also different insect species.

**Functional organization of the central auditory system of the moustache bat**

The primary auditory cortex reflects the remarkable specialization of the peripheral auditory system (Fig. 3). There is a clear tendency for high-frequency sensitive neurones to be located anteriorly and low-frequency sensitive neurones to be located posteriorly (Fig. 3B), as in the primary auditory cortex of other mammals. However, in two respects this tonotopic organization is unique: (1) 50-60 kHz sensitive neurones, i.e. those processing the main frequency-modulated component for ranging, localization, and characterization of a target, are not on the main tonotopic axis, but are displaced anterodorsally. This FM processing area is large and the tonotopic representation in this area is vague and complex; (2) 61-63 kHz sensitive neurones, i.e. those processing the main constant-frequency component for measurements of relative velocity and subtended angle of a target, occupy about 30°, of the primary auditory cortex, even though the animal can probably hear sounds from several to 150 kHz. Since the biosonar signals are quite distinct from this species' communication sounds, the 61-63 kHz tuned area is undoubtedly specialized for processing the constant-frequency component of Doppler-shifted echoes from moving targets. Accordingly, this area (2.3 mm²) is called the Doppler-shifted-CF processing area. We have found that these two areas are functionally organized in an extremely interesting way.

**Constant frequency signal processing**

In the Doppler-shifted-CF processing area, each orthogonal microelectrode penetration is characterized by neurones with nearly identical best frequencies (BF's), excitatory tuning curves, and impulse-count functions. The peak of the impulse-count function in response to a tone burst at the BF uniquely defines the best stimulus amplitude (BA) for maximum excitation. Since each orthogonal penetration is characterized not only by a BF, but also by a BA, it is clear that for the above properties, the auditory cortex shows columnar organization.

In the Doppler-shifted-CF processing area, the BF and BA systematically vary with the location of the neurones in the cortical plane, so that there are tonotopic and amplitopic representations: (1) 0.01 kHz sensitive neurones are located at the centre and 63.0 kHz sensitive neurones at the circumference, while neurones tuned to weak sounds of 30-40 dB SPL are located ventrally, and neurones tuned to strong sounds of 80-90 dB SPL are located dorsally (Fig. 3C). Thus, the amplitude spectrum of a signal is expressed in amplitude vs. frequency coordinates parallel to the cortical surface. This amplitude spectrum representation is, however, apportioned so that acoustic signals of 61 62 kHz and 30-50 dB SPL are projected onto a much larger area than any other signal. This disproportionate representation is correlated with the biological importance of these signals for echolocation. The functional significance of this tonotopic and amplitopic representation is that the frequency of an echo, i.e. the relative velocity of a target, is represented in the radial axis, while the amplitude of an echo, which is related to the target cross-sectional area and range, is expressed along the circular axis (Fig. 3F).

Almost all neurones in the Doppler-shifted-CF processing area are excited by contralateral stimuli, and are either excited or inhibited by ipsilateral stimuli. The latter are called E-E and I-E neurones, respectively. Each orthogonal microelectrode penetration is characterized not only by BF and BA, but also by either E-E neurones, I-E neurones, or neurones exhibiting binural interaction which varies with depth. Thus this area consists of at least three types of columns. E-E neurones are positionally directed, while E-E neurones are more sensitive to weaker echoes and integrable (or even multiply) signals from both ears for effective detection of a target. On the other hand, I-E neurones

*SPL = sound pressure level; dB SPL: a unit relating the 'pressure' of a sound to the weakest sound detectable by man, i.e. 0.0002 dyn/cm² r.m.s.*
are directionally sensitive and respond mainly to stronger echoes. These types of neurones form two functional subdivisions, each suited for either target detection or target localization (Fig. 3D).

Frequency modulated processing

The functional organization of the FM processing area is quite different from that of the Doppler-shifted-CF processing area. Tonotopic organization is vague and amplitopic representation has not been found. This area receives signals related to not only the 2nd harmonic, but also other harmonics to some extent, and contains clusters of neurones which are sensitive to a particular combination or combinations of information-bearing elements of emitted biosonar signals and Doppler-shifted echoes. Neurones in the biggest cluster show facilitation of response to a frequency-modulated sound of either the 2nd or 3rd harmonic when it is preceded by the constant-frequency and/or frequency-modulated components of the 1st harmonic. Some neurones in the cluster are not excited at all by any single component delivered alone, but are strongly activated by two sounds in particular combinations of frequency, amplitude, and timing.

Target tracking capabilities

In a target-orientated flight, the moustache bat systematically changes the rate of sound emission from 5 to 100 signals per second. The duration of the signal decreases from 40 to 7 msec when the rate of emission increases. When acoustic stimuli are delivered mimicking the biosonar signals and echoes in a target-orientated flight, some neurones in the FM processing area are found to be 'tuned' to a particular delay. One neurone, for instance, responded to neither biosonar signals nor echoes delivered alone, but to a combination of these with a certain echo-delay. The best response to the echo occurred at a 5 msec delay when the repetition rate of paired sounds was 10/sec. 4.5 msec delay at 40/sec, and 2.6 msec delay at 100/sec. (The duration of each CF-FM sound was 34, 18, and 7 msec, respectively, for the above repetition rates.) At these best delays, the neurone responded to very weak echoes following strong biosonar signals. Interestingly, the 'delay-tuning' curve becomes narrower with higher repetition rates and shorter biosonar signals. Thus these neurones are not only capable of responding to a weak echo from a target at a certain short range (a 2.6 msec echo delay corresponds to a 45 cm target distance) but, remarkably, also appear to track the target with increasing rejection of echoes from other objects as the bat increases the rate of sound emission during the approach to it. In general, lower-order neurones respond both to emitted biosonar signals and to echoes, regardless of delay. These neurones are not encoding range information. A certain population of higher-order neurones, on the other hand, responds best to an echo with a particular delay, i.e. a target at a particular distance. They are concerned with encoding of range information. Since neurones with different response properties are found in different clusters in this FM processing area, this area may be organized in a fascinating way to process echoes for ranging, localization, and characterization of a target.

Conclusions

As we have shown, the auditory cortex of the moustache bat consists of functional divisions which are devoted to processing information in different ways depending upon the biological significance in each of the frequency bands of important acoustic signals. The clear tonotopic and amplitopic representations in the Doppler-shifted-CF processing area are related to the importance of the CF signal in obtaining information about the relative velocity and subtended angle of a target. The functional organization of this area is probably exceptional because of its high degree of specialization for processing CF signals in the moustache bat, so that such clear organization may not be found in the auditory cortex of animals which use only broadband signals. The FM processing area is, according to studies made thus far, apparently organized for processing one signal (echo) in relation to the other (emitted biosonar signal). We believe, therefore, that there is a clear advantage in using biologically meaningful stimuli in the study of the functional organization of the auditory system, and that there is justification for a trend towards the neuroethological approach in the study of sensory processes in general.

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Reading List

Ralph Lewin

Bats-eye view

I can hear the narrow echoes
From the wires along the street.
I can hear the brittle beetle
And the muffled moth-wings beat.
I have but to click and listen
To the echoes that I make
And I hear the waters glisten
On the surface of the lake.
From the branches and the belfry
To the solid earth below,
These are objects without question;
They are things of which we know.
Though you talk of clouds and moonshine
And of subtle starry beams,
There is only light and darkness;
All the rest are human dreams.