

Cortical Neurons Sensitive to Combinations of Information-Bearing Elements of Biosonar Signals in the Mustache Bat

Abstract. *The auditory cortex of the mustache bat, Pteronotus parnellii rubiginosus, is composed of functional divisions which are differently organized to be suited for processing the elements of its biosonar signal according to their biological significance. Unlike the Doppler-shifted-CF (constant frequency) processing area, the area processing the frequency-modulated components does not show clear tonotopic and amplitopic representations, but consists of several clusters of neurons, each of which is sensitive to a particular combination (or combinations) of information-bearing elements of the biosonar signal and echoes. The response properties of neurons in the major clusters indicate that processing of information carried by the frequency-modulated components of echoes is facilitated by the first harmonic of the emitted biosonar signal. The properties of some of these neurons suggest that they are tuned to a target which has a particular cross-sectional area and which is located at a particular distance.*

One of the most important problems in auditory physiology is the neural basis of acoustic pattern recognition. A possible neurophysiological approach to this problem is to study the functional organization of the central auditory system. In such studies, biologically significant sounds and their information-bearing elements should be used to determine (i) the degree of neuronal specialization for these sounds and (ii) the way the system expresses acoustic signals by the topographic arrangement of neural activity. Since the auditory system has evolved to process biologically significant sounds, the central auditory system is probably organized to process these signals. If so, and if the biological significance of these sounds differs depending on their frequencies, the functional organization may be expected to be different among areas devoted to different frequencies of the signals. Our first aim in this report is to show that the auditory cortex of the mustache bat, *Pteronotus parnellii rubiginosus*, consists of divisions which are differently organized for processing acoustic signals according to differences in their biological significance.

For echolocation, the mustache bat emits orientation sounds (that is, biosonar signals) which always consist of a long constant-frequency (CF) portion followed by a short frequency-modulated (FM) portion (1, 2). Since each portion contains four harmonics, H_1 , H_2 , H_3 , and H_4 , there are eight components in total: CF_1 , CF_2 , CF_3 , CF_4 , FM_1 , FM_2 , FM_3 , and FM_4 (see Fig. 1A). Components CF_2 and FM_2 are always predominant in the orientation sounds. The CF_2 ranges between 60 and 62 kHz in the resting state, when the bat is not compensating for a Doppler shift (2). The FM_2 sweeps from the CF_2 frequency to about 49 kHz. The long CF sound is an ideal signal for a Doppler measure-

ment—that is, for detecting the relative velocity of a target. When the size of the target is comparable to or larger than the wavelength of the signal, the CF sound is also suited for target detection, because the energy of the reflected sound is highly concentrated at a particular frequency. However, the CF sound is not suited for ranging, localization, and characterization of the target. For these, the short FM sound is more appropriate, because of the wide distribution of sound energy over many frequencies (3). Our second aim in this report is to describe the properties of neurons sensitive to a particular combination of CF and FM components in the orientation sound and echoes, in relation to echolocation.

When the mustache bat receives Doppler-shifted echoes of a higher frequency than its orientation sound, it reduces the frequency of subsequent orientation sounds so as to stabilize the CF_2 of the echoes at a particular frequency, 61 to 62 kHz (2). This interesting acoustic behavior, called Doppler-shift compensation, clearly indicates that the bat is sensitive to a target moving relative to it. The cochlear microphonic of this bat is very sharply tuned at about 61 kHz (4–6) and its cochlear nerve fibers tuned to 60 to 63 kHz have unusually sharp tuning curves (5, 6). The sharp filter characteristics of the cochlea increase the signal-to-noise ratio for effective target detection and also the capability of fine frequency analysis for detection of target movement, including the wingbeat of an insect (4–7).

The organization of the primary auditory cortex of the mustache bat reflects the peripheral specialization. About 30 percent is primarily devoted to processing the CF_2 in Doppler-shifted echoes (Fig. 1B, 61- to 63-kHz area) (8). This area, called the Doppler-shifted-CF processing area, has two coordinates which express either the relative velocity

(Doppler shift) or the subtended angle (echo amplitude) of a target. Thus, the amplitude spectrum of an acoustic signal is expressed by a spatiotemporal pattern of activity of neurons within these frequency-amplitude coordinates. The selectivity of neurons to acoustic signals differs from neuron to neuron. Some of them are “CF-specialized neurons,” which selectively respond to a CF signal but not to an FM sound or noise burst (9, 10). Interestingly, the CF processing area consists of two subdivisions which are suited for either target detection or target localization (11).

Anterodorsal to the Doppler-shifted-CF processing area is the FM processing area. We have studied its functional organization with techniques that have already been described (9, 10). The experiments were performed on 34 specimens of *P. p. rubiginosus* from Panama. Most bats were used once a week for 3 to 5 weeks. A bat was lightly anesthetized with sodium pentobarbital (12), and the flat head of a 1.8-cm-long nail was mounted onto the dorsal part of its skull with glue and cement. In weeks following surgery, some of the experiments were performed only with local anesthesia (12). To immobilize the head, the shank of the nail was locked onto a metal rod with a setscrew. A tiny hole or holes were made in the skull covering the FM processing area. Through the hole a tungsten wire electrode (7- to 15- μ m tip) was inserted orthogonally or obliquely into the cortex, and the activity of either a single neuron or a few neurons was recorded at depths between 100 and 1000 μ m. Unless otherwise stated, 30-msec-long CF tones, 4.0-msec-long FM sounds, or both were delivered at a rate of 2.5 per second from a condenser loudspeaker 66 cm in front of the head. Nerve impulses evoked by identical acoustic stimuli were sampled 50 or 100 times and expressed in the form of peristimulus-time (PST) or cumulative histograms, or both, by a Nicolet computer (for example, see Fig. 1, C and D). All experiments were performed in a sound-proof room, which was heated to 33° to 35°C.

In the FM processing area, tonotopic and amplitopic representations are very vague, and not only the second harmonic but also the first, third, and fourth harmonics are projected. Thus neurons in this area show response properties quite different from those in the Doppler-shifted-CF processing area. Neurons recorded in each orthogonal penetration showed nearly identical response properties. Most importantly, the majority of

neurons studied in this area showed a facilitation of response to an FM sound in one harmonic when it was preceded by a CF or FM component, or both, from another harmonic. To date, we have found 11 types of combinations of two sounds for facilitation: H_1 - FM_2 , H_1 - FM_3 , H_1 - FM_4 , H_1 - $FM_{2,3}$, H_1 - $FM_{2,4}$, H_1 - $FM_{3,4}$, H_1 - $FM_{2,3,4}$, FM_1 - FM_2 , CF_2 - FM_2 , CF_1 - CF_2 , and CF_1 - $CF_{2,3}$. That is, there were 11 types of facilitation neurons (13). Each type of neuron was found in a cluster occupying a certain area. Within each area, facilitation was faint at the margin and stronger at the center. There was a continuous spectrum in the degree of facilitation. This was clearly demonstrated when oblique penetrations were made across such an area. The H_1 -FM neurons showing weak facilitation, for instance, responded to pure tones near CF_1 , FM_1 , and FM of some higher harmonic delivered alone, but responded somewhat better to particular combinations. The response to the CF_1 (at the amplitude for best facilitation) was inhibitory and usually followed by rebound off-discharges. An on-discharge, if any, was phasic. Thus the mechanism for the facilitation of the response to the subsequent FM sound was the rebound off-response to the CF_1 . In the extreme case, on the other hand, a neuron showed no excitatory response at all to either a CF tone or an FM sound, but responded when the two were combined in a certain way. This type, an H_1 -FM-specialized neuron, was often inhibited during the H_1 , so that the neural mechanism for its excitation was probably the same as that for the excitation of the H_1 -FM-facilitation units. Among the 11 types of neurons, H_1 - FM_2 -facilitation neurons were most widely distributed in the FM processing area (Fig. 1B). This may mean that the H_1 - FM_2 combination is somehow more important than the other combinations in echolocation. Consequently, the properties of H_1 - FM_2 -facilitation and H_1 - FM_2 -specialized neurons are described in detail.

Figures 1, C and D, and 2 show the response properties of a single H_1 - FM_2 -specialized neuron. This neuron produced irregular background discharges at about 0.04 per second and no response to any CF tone, FM sound, or noise burst presented alone. However, it responded strongly to a combination of CF_1 and downward-sweeping FM_2 ($FM_2 \downarrow$), discharging 1.7 impulses per stimulus. When an upward-sweeping FM_2 ($FM_2 \uparrow$) or a noise burst (NB) followed the CF_1 , however, the response was very poor, at most 0.2 impulse per

stimulus (Fig. 1, C and D). The response to CF_1 followed by CF_2 was also very poor. The response of the neuron to either CF_1 - $FM_2 \uparrow$, CF_1 -NB, or CF_1 - CF_2 was barely above the criterion of threshold regardless of stimulus level, although a broad range of $FM_2 \uparrow$, NB, and CF_2 could excite the neuron when these were combined with CF_1 (Fig. 2B). For the excitation of this neuron, the best component following the CF_1 was obviously $FM_2 \downarrow$, as in the natural sound. Other combinations of signals (such as H_1 - H_1 or H_2 - H_2) had no effect on this neuron.

The ranges of CF_1 and $FM_2 \downarrow$ to be

combined for facilitation are comparable to or wider than the tuning curves of neurons in the Doppler-shifted-CF processing area (Fig. 2A). If the number of impulses per stimulus at the threshold was defined to be 0.5 instead of 0.1, however, the ranges would be much narrower. The neuron was maximally excited when CF_1 was 27.80 kHz and FM_2 swept from 61.74 to 49.74 kHz. The neuron was apparently "tuned" to a certain combination of a CF_1 and an FM_2 . This was a typical best combination for most of the H_1 - FM_2 -specialized and H_1 - FM_2 -facilitation neurons. Interestingly, the best frequen-

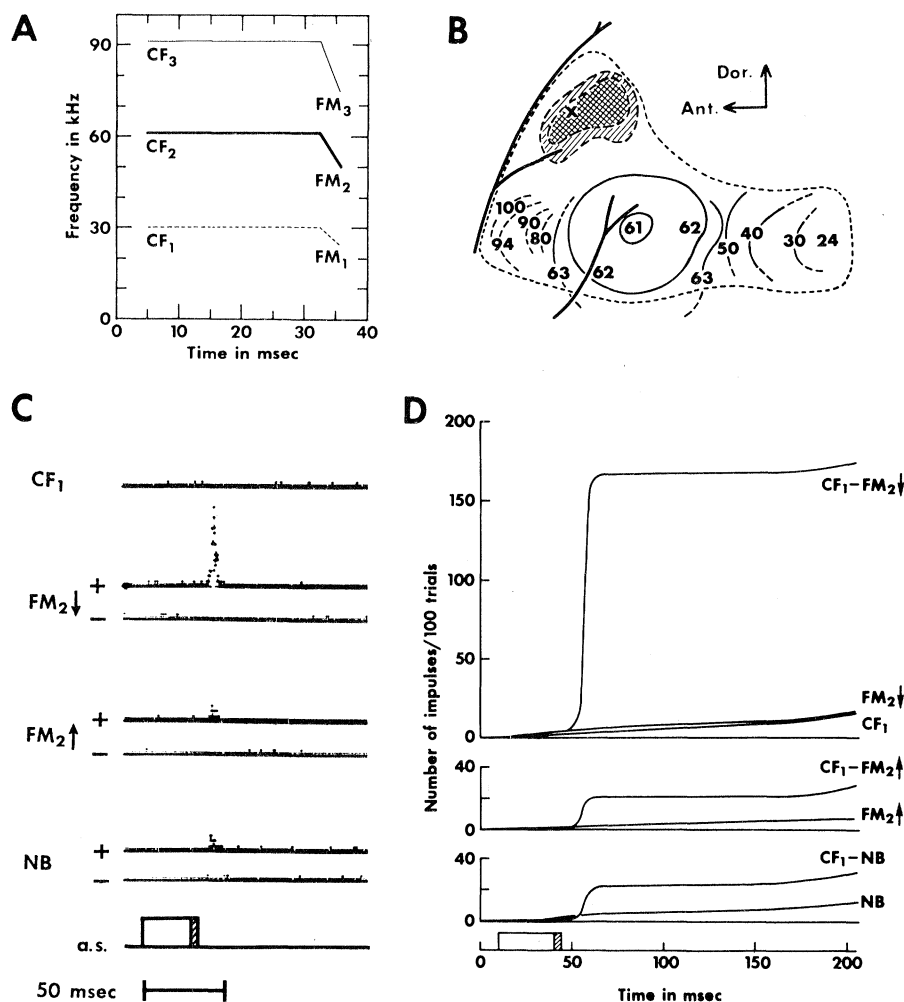


Fig. 1. (A) Sonogram of an orientation sound. Each of the four harmonics (H_1 , H_2 , H_3 , and H_4) consists of constant-frequency (CF) and frequency-modulated (FM) components, so that there are eight components in total, CF_1 , CF_2 , CF_3 , CF_4 , FM_1 , FM_2 , FM_3 , and FM_4 (the fourth harmonic is not shown). (B) Primary auditory cortex of the left cerebral hemisphere. Numbers and lines show the distribution of best frequencies (in kilohertz) of single neurons—that is, a tonotopic representation. Anterodorsal to the Doppler-shifted-CF processing area (61 to 63 kHz) is an FM processing area which contains a large cluster of H_1 - FM_2 -facilitation neurons (shaded area) and also some H_1 - FM_2 -specialized neurons (X). The facilitation is weak in the lightly shaded area, but it is strong in the heavily shaded area. (C) PST histograms of responses of a single H_1 - FM_2 -specialized neuron. The acoustic stimulus (a.s.) is either a 30-msec-long CF_1 alone (open rectangle) or a 4-msec-long sound alone (shaded rectangle), which is a downward-sweeping FM_2 ($FM_2 \downarrow$, -), an upward-sweeping FM_2 ($FM_2 \uparrow$, -), or a noise burst (NB, -), or one of the 4-msec sounds preceded by the CF_1 (+). The CF_1 is 27.8 kHz and 56 dB SPL. The $FM_2 \downarrow$ and $FM_2 \uparrow$ are 56 dB SPL and sweep in the range 61.5 to 49.5 kHz. The NB is 56 dB SPL with a bandwidth of 51.5 to 59.5 kHz. Each PST histogram consists of neural activity for 100 presentations of an identical sound or sounds. (D) Cumulative histograms of the responses and background discharges. Each histogram is the average of two samples of 100 presentations.

cy of the CF₁ for the excitation of these types of neurons is 27.23 ± 1.03 kHz ($N = 151$), slightly lower than that of the CF₁ of the orientation sound when the animal is at rest. The CF₁ bandwidth at the best amplitude for facilitation is 4.51 ± 2.13 kHz ($N = 24$). In all these

neurons, facilitation is thus mainly evoked by FM₁ sweeping from 30.5 to 24.5 kHz on the average. In the neurons with the CF₁ best frequency higher than 28.0 kHz, the facilitation is further enhanced by CF₁ during Doppler-shift compensation. The combination of CF₁

and FM₁ never evoked facilitation.

The relationship between the number of impulses per stimulus and stimulus amplitude indicates that the best amplitudes of the CF₁ and FM₂ for the excitation of this H₁-FM₂-specialized neuron were 71 and 43 dB SPL (sound pressure level), well below the largest amplitudes available (Fig. 2C). The best amplitude of the CF₁ for maximum facilitation and facilitation neurons was 70.6 ± 7.4 dB SPL ($N = 113$), while the best amplitudes for FM₂ were highly variable (81.5 ± 13.3 dB SPL, $N = 84$) and the impulse-count functions were often relatively flat over a wide amplitude range. Since the ear of the animal might be stimulated by the H₁ of the self-vocalized orientation sound at about 70 dB SPL (14), the emitted H₁ probably conditions these neurons to respond better to the echo FM₂, which carries important information for echolocation. An alternative possible mechanism is that an echo H₁ facilitates responses to an echo FM because the H₁ suffers less transmission loss than the other harmonics, although it is weak in the emitted signal. The validity of these explanations may be examined by studying the responses of these neurons to the H₂ following the H₁ with various delays.

In a target-oriented flight, the mustache bat changes the rate of sound emission from 5 to 100 per second. The duration of the signal decreases from 40 to 7 msec when the rate of emission increases (1, 2). We therefore delivered pairs of H₁ and H₂ at various rates and durations mimicking the natural situation, and measured the threshold of H₁-FM₂-specialized and -facilitation neurons as a function of the delay of H₂ from H₁ (15).

One of the H₁-FM₂-specialized neurons recorded from lightly anesthetized bats did not respond to either H₁ or H₂ alone, but optimally responded to H₁-H₂ when the H₂ was delayed 5 msec at a repetition rate of 10 per second, 4.5 msec at 40 per second, and 3 msec at 100 per second. The neuron was apparently tuned to a target at a certain range. At the best delays, the signals overlapped considerably.

Comparable data were also obtained from unanesthetized animals. Figure 2D

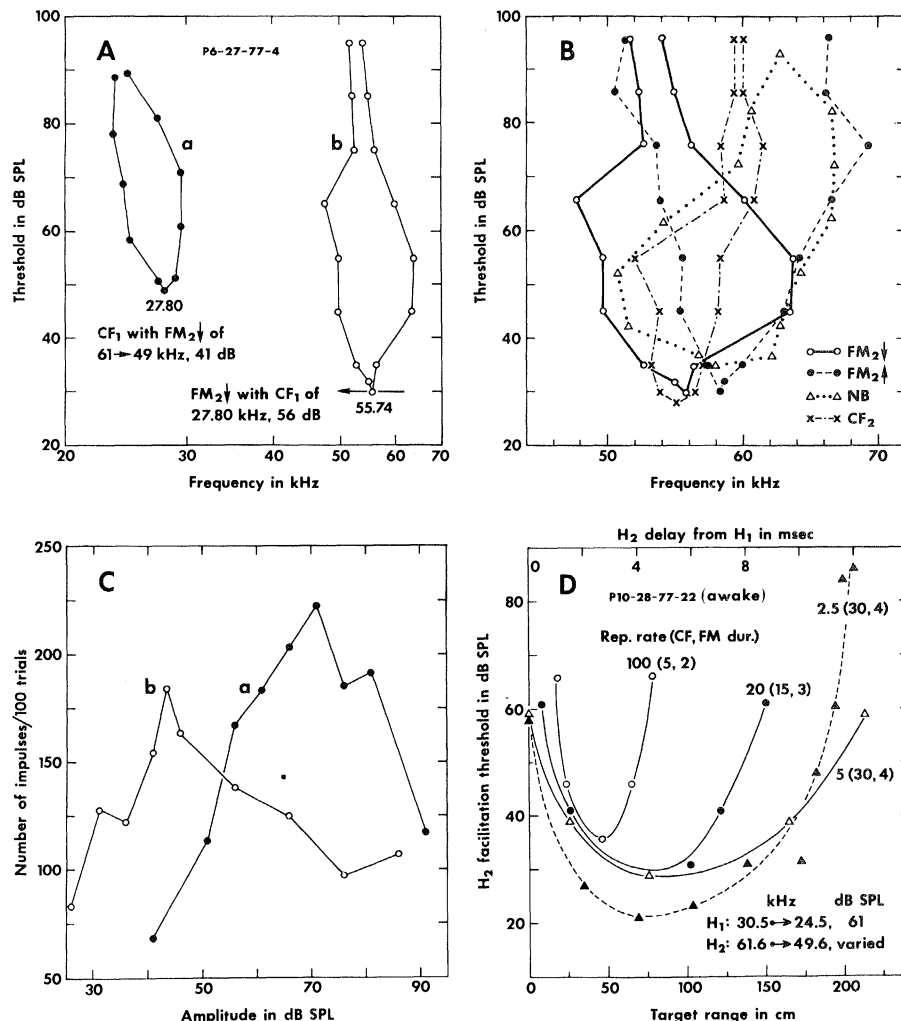


Fig. 2. Graphs representing the response properties of an H₁-FM₂-specialized neuron. (A) Curves a and b, respectively, represent the CF₁ and FM₂ facilitation areas. To measure the range of the 30-msec-long CF₁ to be combined with the FM₂ for facilitation of the neuron, the latter was fixed near the parameters for best facilitation and the amplitude range of the former was measured as a function of frequency. The threshold of the response was defined to be the stimulus amplitude which evoked 0.1 impulse per stimulus on the average. The range of the 4-msec-long FM₂ to be combined with the CF₁ for facilitation was measured by varying the amplitude and initial and terminal frequencies of a 12-kHz frequency sweep (the center frequency of the sweep is plotted). The parameters of the CF₁ were set near those for the best facilitation. (B) The FM₂ ↓, FM₂ ↑, NB, and CF₂ facilitation areas. To examine the importance of the structure of a sound following the CF₁ for the facilitation of the neuron, the downward-sweeping FM₂ (FM₂ ↓) was replaced with an upward-sweeping FM₂ (FM₂ ↑), a noise burst (NB), or CF₂, and the facilitation area was measured for each of these. The response of the neuron to CF₁-FM₂ ↑, CF₁-NB, or CF₁-CF₂ was very poor regardless of stimulus level, so that the facilitation areas for them were very difficult to measure. (C) Impulse-count function measured as a function of either the CF₁ (curve a) or the FM₂ (curve b). One of them was fixed in amplitude, and the number of impulses per stimulus was measured as a function of the amplitude of the other. (D) The H₂ threshold for facilitation as a function of the delay of H₂ from H₁ (target range) at different repetition rates of an H₁-H₂ paired stimulus. The H₁ and H₂ consisted of CF and FM components. In H₁, the CF₁ was 30.5 kHz and FM₁ swept from 30.5 to 24.5 kHz. Its amplitude was 61 dB SPL. In H₂, the CF₂ was 61.6 kHz and FM₂ swept from 61.6 to 49.6 kHz. The H₂ amplitude was varied to measure the facilitation threshold. The repetition rate of the paired stimulus is indicated by the number near each curve without parentheses, and the durations of the CF and FM components (milliseconds) are respectively shown by the numbers in parentheses. Note that as repetition rate increases, the delay (or range)-tuning curves become narrower, and the best delay (best range) becomes shorter. The data in (D) were obtained with an unanesthetized bat.

tion rate was 2.5, 5, or 20 per second, as in the search and approach phases of echolocation. The H_2 threshold for facilitation ranged between 20 and 30 dB SPL. At a repetition rate of 100 per second, as in the terminal phase of echolocation, the best delay became shorter (2.6 msec), the threshold for facilitation was 36 dB SPL, and the "delay (or range)-tuning" curve became much narrower. At these best delays, this neuron showed clear discharges to each paired stimulus. In contrast, the response to either H_1 or H_2 (or FM_2) alone was barely above the criterion of threshold at low rates (2.5 to 20 per second) and completely disappeared at higher rates, regardless of amplitude. Other combinations of signals, such as H_2 - H_2 , had no effect on these neurons. These data indicate that the facilitation is not evoked by the emitted (or echo) H_1/H_2 , but by that of the emitted H_1 and delayed echo H_2 from a target at a certain range. [Of course, the emitted H_1 and echo H_2 always overlapped at these delays, as is true of pulses and echoes during a target-oriented flight by "CF-FM" bats (1, 2).]

These H_1 - FM_2 -facilitation neurons are not only capable of responding to weak FM echoes (30 to 40 dB SPL in Fig. 2D) from a target at a certain range (20 to 167 cm in Fig. 2D), but remarkably, because of shorter best delays and narrower range tuning, they also appear to track the target with increasing rejection of echoes from objects at other distances as the bat increases the rate of sound emission during the approach to it. In general, higher-order neurons show a broader spectrum of recovery cycles and some of them respond better to an echo from a certain range (16). Furthermore, a few neurons sensitive to a pulse-echo combination with a particular time relationship have recently been found (17). The H_1 - FM_2 -specialized and -facilitation neurons are fascinating in that they are able to track an echo source or are tuned to respond best to an echo from a certain range (18). Furthermore, these neurons showed a response latency of 7 to 10 msec to the FM_2 component of H_2 following H_1 . Thus the auditory cortex may be involved in echolocation even during the terminal phase of prey capture. The next obvious step is to study the response properties of these neurons with the complete orientation sounds and echoes.

The response properties of H_1 - FM_2 -specialized and -facilitation neurons, explained above, indicate that for their maximum excitation there is an optimum combination of two signal elements with respect to their amplitude spectra, over-

all intensities, and time relationship. Since vocal self-stimulation always exists and may be assumed to be relatively constant (14), one may conclude that these neurons are tuned to a target which has a particular cross-sectional area in terms of FM_2 and which is located at a particular distance. The response properties of the other seven types of H_1 -FM facilitation neurons are less well studied than those of H_1 - FM_2 -specialized and -facilitation neurons. Our data, however, indicate that these neurons have comparable properties.

The H_1 -FM-specialized neurons that have been studied were not so specialized as to respond only to a combination of H_1 at a particular frequency and intensity and an FM sound of a particular amplitude spectrum. Both the H_1 and the FM sound could vary over a certain range, although there was a certain optimum combination. Thus the amplitude spectrum of an acoustic stimulus, which would vary with time, is expressed not only by the activity of specialized neurons in a single column, but also by the activity of those in several columns, and furthermore by that of less specialized or unspecialized neurons in the area surrounding these columns. The FM processing area thus expresses biosonar echoes by the spatiotemporal pattern of neural activity. But the method of expression is quite different from that of the Doppler-shifted-CF processing area. 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 relative velocity and subtended angle of a target (9). The functional organization of this area is probably exceptional because of its high degree of specialization for processing CF signals in the mustache bat. The FM processing area is organized quite differently, probably reflecting the difference in the nature of the information processed in this area. Our series of experiments clearly indicate that each functional division of the auditory cortex is organized differently for processing acoustic signals according to their biological significance.

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12. Single-unit activity was recorded 3 to 15 hours after the initial injection of 30 mg of sodium pentobarbital per kilogram of body weight. When the animals moved too much for PST and cumulative histograms to be plotted, a 10 mg/kg dose of sodium pentobarbital was injected. In this case, single-unit study was continued 10 minutes after the injection. The response pattern, magnitude of facilitation, and threshold of a single unit or a few neurons were not noticeably different before and after the injection. Furthermore, when an electrode was inserted at nearly the same place in the auditory cortex of an unanesthetized animal a few days or a week later, the data obtained were nearly the same as those obtained with the lightly anesthetized bat. We therefore believe that our data are not significantly affected by light anesthesia.
13. The hyphen and the slash mean successive and simultaneous deliveries of two sounds, respectively. For instance, H_1 - FM_2 means that FM_2 should be delivered after H_1 for best facilitation, and CF_1/CF_2 means that CF_1 and CF_2 should be delivered simultaneously. A multiple suffix, such as $FM_{2,3}$ in H_1 - $FM_{2,3}$, means that FM_2 and FM_3 effect the same or similar facilitation when delivered after H_1 . The H_1 -FM-facilitation (or specialized) neurons are those whose response to FM is facilitated by H_1 , so that this category includes all H_1 - FM_2 , H_1 - FM_3 , H_1 - FM_4 , H_1 - $FM_{2,3}$, H_1 - $FM_{2,4}$, H_1 - $FM_{3,4}$, H_1 - $FM_{2,3,4}$, and FM_1 - FM_2 facilitation (or specialized) units. In the H_1 -FM-facilitation neurons, either CF_1 , FM_1 , or H_1 evokes facilitation of the response to the FM of another harmonic following it. However, eight neurons were found which showed facilitation for H_1 - FM_2 , but not for CF_1 - FM_2 . In these neurons, the essential part of the combined signals for the facilitation was FM_1 - FM_2 .
14. The amount of vocal self-stimulation remains to be measured by analyzing the cochlear microphonic evoked by self-vocalization.
15. Delay is measured as the interval between the onsets of the CF (or FM) components in a stimulus pair. This delay corresponds to the echo delay due to the bat-target distance.
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18. To our knowledge, our experiments are the first to explore the properties of neurons specialized for responding to complex acoustic signals by manipulating their individual parameters. A detailed investigation of tuning in echo delay in relation to target detection and ranging will be reported separately (W. E. O'Neill and N. Suga, in preparation).
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