Neurobiology of Neocortex
eds. P. Rakic and W. Singer, pp. 331–349
John Wiley & Sons Limited

What Does Single-Unit Analysis in the Auditory Cortex Tell Us About Information Processing in the Auditory System?

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Abstract. In both the auditory periphery and in the central auditory system, an acoustic signal is expressed by a spatiotemporal pattern of neural activity. At the periphery, the spatiotemporal pattern appears along a single frequency axis which has an anatomical basis on the sensory epithelium. On the other hand, in the auditory cortex the spatiotemporal pattern is much more complex than that at the periphery because of multiple tonotopic representation and variation/complexity in the response properties of cortical neurons. Single-unit analysis of cortical neurons, performed in reference to auditory behavior and peripheral neurons, has explored several important principles of information processing in the central auditory system. The most important principles found in auditorily specialized animals are that the central auditory system produces neurons tuned to information-bearing parameters (IBPs), which characterize biologically important sounds; that biologically important complex sounds are eventually processed by combination-sensitive neurons; and that different types of auditory information are systematically represented in separate auditory areas.

INTRODUCTION

In this background paper to facilitate discussion on single-unit physiology of the auditory cortex, I shall focus only on the data directly related to two major auditory functions: neural mechanisms for complex-sound processing and sound localization.

NEUROETHOLOGICAL VIEW OF THE AUDITORY SYSTEM

Since the auditory system has evolved for communication and also detection of preys and predators, it has become specialized for receiving and processing those acoustic signals most important for the survival of a species. This neuroethological view of the auditory system suggests that auditory neurophysiology must be performed in relation to the processing of acoustic signals which are produced or heard by the species in nature, and which are important for the species. If such biologically important signals are physically unique and evoke unique auditory behavior, the physiological mechanisms for processing these signals can be more easily explored than those for processing biologically less important signals.

The coding of acoustic signals by peripheral auditory neurons may be basically the same across almost all species of mammals. This coding has been successfully studied by examining the responses of these neurons to pure tones and clicks without considering biologically important sounds. In certain species of mammals, peripheral mechanisms shared by many different species have been modified to permit finer frequency analysis. The biological significance of such specialization becomes clear only by reference to biologically important signals, because these occur to fulfill species-specific requirements.

The processing of acoustic signals by the central auditory system can vary across different species of mammals, because central auditory mechanisms shared by the different species are expected to be modified in various ways for processing biologically important signals. Therefore, the examination of the responses of central auditory neurons, cortical auditory neurons in particular, *only* to pure tones and clicks has not been and will not be successful in exploring central auditory mechanisms for acoustic pattern recognition. To explore the central auditory mechanisms, the neurophysiology of the central auditory system must be performed first in order to understand how biologically important sounds and the *information-bearing parameters (IBPs)* of these are processed, and how the emitters of these sounds are localized. An IBP is the limited part of a continuum that carries information for the species. IBPs include not only parameters characterizing information-bearing elements of a complex sound, such as frequency, FM rate, FM depth, amplitude, AM rate, AM depth, duration, etc., but also interaural time and amplitude differences, intervals between signals (e.g., echo delay) and other parameters related to combinations of information-bearing elements. IBPs for acoustic pattern recognition can be different among species, and the same IBPs can carry different information for different species. Therefore, for auditory physiology, IBPs must first be identified. Then, the filter properties of neurons should be systematically studied by changing values of individual IBPs. Since acoustic communication and detection of preys and predators take place over different distances, the level-tolerance of neural response must be examined by varying the amplitude of acoustic stimuli. Almost none of the experiments on the mammalian auditory system have been performed with this neuroethological view.

Neurophysiological studies of acoustic pattern recognition performed without the neuroethological view have hardly explored functional organization beyond cochleotopic or tonotopic representation, and have not explained the biological significance of various shapes of frequency-tuning curves and various types of response patterns. However, research performed with the neuroethological view has gone further, demonstrating that the central auditory system contains neurons tuned to IBPs, and that it has a functional organization extending tonotopy.

In neurophysiological research on sound localization, interaural time difference (ITD) and/or interaural amplitude difference (IAD)* have been systematically varied over ranges important for human sound localization, but not over ranges important for sound localization by the animal under investigation. Nonetheless, the major IBPs for sound localization in all species are ITD and/or IAD, and thus such research has unintentionally been performed with a neuroethological approach. Consequently, this research has revealed interesting response properties of binaural neurons, and a functional organization which is probably related to sound localization in several other species.

To write this background paper on "What does single-unit analysis in the auditory areas tell us about cortical processing?", I have considered first what response properties of cat cortical auditory neurons are uniquely cortical because the cat has been most extensively used for auditory physiology. Various response properties of neurons, including binaurality, are already produced in the pontine auditory nuclei. These neurons, together with neurons in the dorsal cochlear nucleus, project to the nucleus of the lateral lemniscus and/or the inferior colliculus, which in turn projects to the medial geniculate body. As a result, some thalamic neurons are already as complex as cortical auditory neurons. Therefore, it is not clear what response properties of neurons are uniquely cortical. Research on the thalamus and the auditory cortex of the mustached bat, on the other hand, suggests that the difference in response properties between these two regions are quantitative rather than qualitative.

Since the response properties of cortical auditory neurons depend greatly upon those of peripheral neurons and upon subcortical neural interactions, differences in response properties between cortical auditory and peripheral neurons have revealed important mechanisms operating within the auditory system for signal processing. Therefore, I shall first enumerate these mechanisms, and then summarize the neural mechanisms for complex-sound processing found in the mustached bat. I will then describe problems related especially to the cortical auditory areas.

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* In auditory physiology, n dB always represents a pressure (amplitude) ratio, not a power (intensity) ratio.

IMPORTANT MECHANISMS FOR THE PROCESSING OF IBPs

A comparison of the data obtained from the mustached bat with that obtained from other species illustrates the specialization of the bat's auditory system for echolocation and also general neural mechanisms probably shared by several different species. These mechanisms are listed below. The data indicating the existence of each mechanism were obtained mainly from the animals listed in parentheses. Data from the owl (e.g., Konishi et al. 1988) are related to sound localization, and those obtained from the other species are related to sound reception, frequency analysis and/or complex-sound processing (e.g., Suga 1984, 1988; Margoliash 1983; Mudry et al. 1977).

1) The peripheral auditory system has evolved not only for the reception of biologically important sounds, but also for frequency analysis of sounds that fulfill species-specific requirements. The sharpness of a frequency-tuning curve, sensitivity, and/or population can be higher for peripheral neurons tuned to frequencies of sounds that are most important to the species (bats, mice, and frogs).

2) The frequency tuning of some central neurons is sharpened by lateral inhibition, which eliminates the "skirt" of a frequency-tuning curve (bats, cats, and frogs). The more important the frequency analysis of particular components of sounds, the more pronounced is the neural sharpening for neurons tuned to thse components (bats).

3) The frequency tuning of some other central neurons is broadened by "excitatory" convergence. Broadly-tuned neurons are separately clustered from sharply-tuned neurons in different portions of the auditory system (cats and bats).

4) A phase-locked or stimulus-locked response is commonly strong and observed up to 3 kHz at the periphery, but is weak and observed only up to 0.3 kHz in the auditory cortex. The population of "phase-locking" neurons is smaller and the degree of phase-locking is progressively lower at higher levels of the auditory system (cats). A temporal code at the periphery can be changed into a place code at higher levels of the auditory system (bats and frogs).

5) The cochlea or a part of it is projected in parallel to different subdivisions of a nucleus or nuclear complex at each level of the ascending auditory system (bats, cats, and monkeys). These multiple cochleotopic or tonotopic representations result from the divergence of axons. This divergence is usually associated with a convergence of axons for sorting out different types of auditory information. This combined divergence-convergence occurs repeatedly in the central auditory system and is the anatomical basis of a parallel-hierarchical processing of information for both acoustic pattern recognition and sound localization. By this divergence-convergence, neural filters are created which are tuned to various IBPs other than frequency

(bats, owls, and frogs). These IBP-tuned neurons (hereafter IBP neurons or filters) act as cross-correlators, which correlate incoming signals with their filter properties, i.e., with neurally stored information. It should be noted that complex sounds are processed by combination-sensitive neurons, i.e., IBP filters tuned to different combinations of signal elements (bats, song birds, and frogs).

6) IBP filters can be sharpened by lateral inhibition (owls, frogs, and bats).

7) Different types of IBP filters are clustered separately at particular locations of the central auditory system. In other words, the system contains functional subdivisions or areas specialized for processing particular types of auditory information important to a species (bats, owls, and frogs).

8) In each subdivision or area, IBP filters are systematically arranged so that they form an axis or axes representing the IBP or IBPs (bats and owls). If small differences in IBP values are not biologically important, the IBP axis may not be formed within a cluster of IBP filters (frogs). It should be noted that with the exception of frequency, there is no peripheral anatomical basis for IBP axes: they are created centrally from neural interactions. That is, they are computational axes or maps.

9) The axis or population of neurons representing an IBP is apportioned according to the species-specific importance of the IBP (bats and owls).

10) Normal development of an IBP map is due not only to the genetic code, but also to postnatal experience. Plasticity of the map is larger for younger animals (owls).

11) The bandwidth of IBP filters is not so narrow as to express a particular value of an IBP by the excitation of only a few neurons located at a single location along the IBP axis. Even after sharpening of the tuning of IBP filters by lateral inhibition, it is expressed by a spatiotemporal pattern of excitation of many neurons distributed along the IBP axis (bats and owls).

12) The functional organization of the auditory system can be different among different species, reflecting differences in species-specific auditory behavior and/or the properties of the acoustic signals used by them. The organization can also be different among individuals or between sexes within the same species when the properties of their biologically important acoustic signals are different among conspecifics (bats and frogs).

13) For protection of information processing during and immediately after vocalization, vocal self-stimulation is reduced not only by the middle ear muscles, but also by inhibition occurring in the central auditory system (bats, monkeys, and song birds).

14) Cortical representation of certain types of auditory information by combination-sensitive neurons is protected from masking by their unique response properties (bats).

It is worth listing the functional organizations beyond tonotopy thus far found in the auditory system of different species of animals: amplitopic representation (Suga 1977; Suga and Manabe 1982); odotopic or echo-delay representation (Suga and O'Neill 1979; O'Neill and Suga 1982; Suga and Horikawa 1986); Doppler-shift representation or frequency-versus-frequency coordinates (Suga et al. 1981; Suga, Niwa et al. 1983); azimuth representation (Kujirai and Suga 1983) and binaural bands (Manabe et al. 1978) found in the auditory cortex of the mustached bat; binaural bands (Imig and Adrian 1977) and representation of AM rate (Schreiner 1988) found in the auditory cortex of the cat; auditory space map found in the midbrain of the barn owl (Knudsen and Konishi 1978; Konishi et al. 1988), the guinea pig (King and Palmer 1983) and the cat (Middlebrooks and Knudsen 1984); and clusters of thalamic neurons sensitive to either combinations of two signal elements, or AM rate and duration in frogs (Hall and Feng 1986, 1987; Fuzessery and Feng 1983; Rose and Capranica 1985).

AN EXAMPLE OF RESEARCH CENTERED AT THE AUDITORY CORTEX: THE NEUROETHOLOGY OF THE BAT AUDITORY CORTEX

Biosonar Signals

For capture of preys (flying insects) and orientation, the mustached bat (*Pteronotus parnellii*) emits orientation sounds (biosonar signals or pulses), each of which consists of a long constant-frequency (CF) component followed by a short frequency-modulated (FM) component. Since each orientation sound contains four harmonics (H_{1-4}), there are eight components that can be defined (CF_{1-4}; FM_{1-4}). In the emitted sound, the second harmonic (H_2) is always predominant and the frequency of CF_2 is about 61 kHz (Fig. 1A). The frequency of the CF component is different among subspecies and also to some extent among individuals of the same subspecies. It is also different between males and females. In FM_2, the frequency sweeps down from 61 kHz to about 49 kHz. H_3 is 6–12 dB weaker than H_2, while H_1 and H_4 are 18–36 and 12–24 dB weaker than H_2, respectively.

Echoes eliciting behavioral responses in the mustached bat always overlap temporarily with the emitted sound. As a result, biosonar information must be extracted from a complex sound potentially containing up to 16 components. The CF component is an ideal signal for target detection and the measurement of target velocity (relative movements and wing beats), because the reflected sound energy is highly concentrated at a particular frequency. The mustached bat uses the CF component for this purpose and performs a unique behavior called Doppler-shift compensation. The short FM component, on the other hand, is suited for ranging, localizing, and characterizing a target because of the distribution of its energy over many frequencies. Different parameters of echoes received by the bat carry different types of information about a target (Fig. 1D).

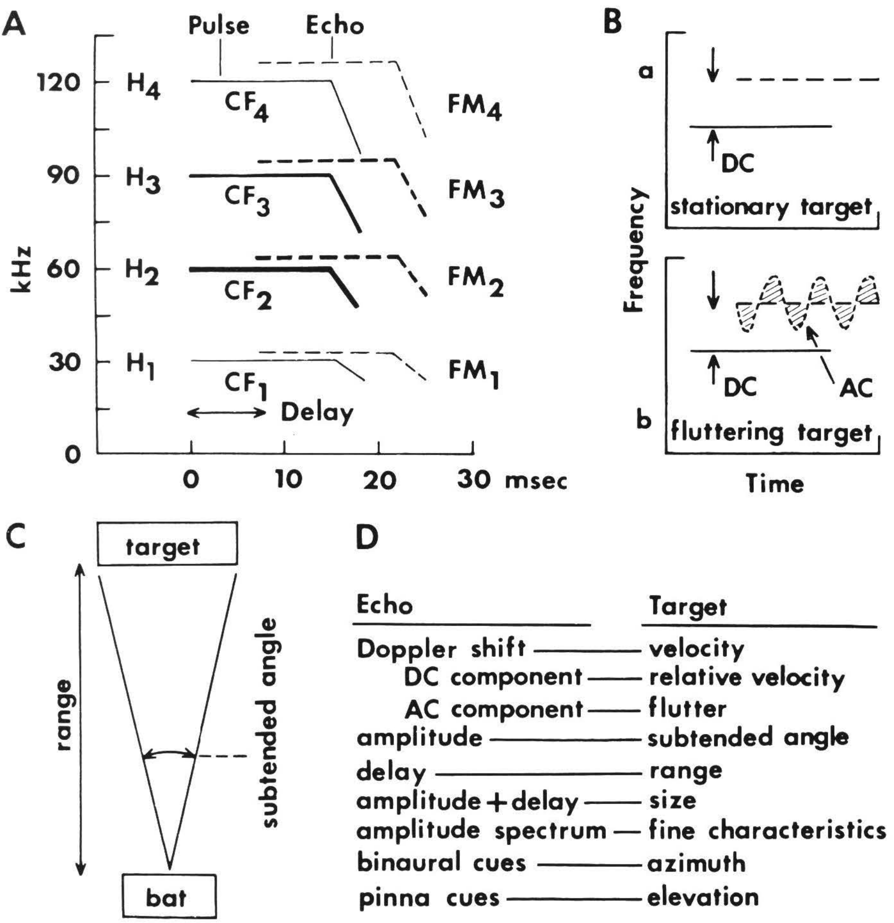


Fig. 1—Biosonar signals (orientation sounds) of the mustached bat, *Pteronotus parnellii*, and the information carried by its signals. A: Schematized sonagram of the orientation sound (solid lines) and the Doppler-shifted echo (dashed lines). The orientation sound is also called a *pulse*. The four harmonics (H_{1-4}) of both the orientation sound and the echo each contain a long CF component (CF_{1-4}) and a short FM component (FM_{1-4}). Thickness of the lines indicates the relative amplitude of each harmonic in the orientation sound. H_2 is the strongest, followed by H_3, H_4, and H_1. B: When the mustached bat flies toward or near a stationary object, the frequency of the echo becomes higher than the emitted sound due to the Doppler effect (graph a). This steady shift is called the DC component of the Doppler shift. When the bat flies toward a flying insect the Doppler shift of the echo consists of a DC component proportional to relative velocity and the periodic frequency modulation (FM) proportional to the speed of wing beat (graph b). This periodic FM is called the AC component of the Doppler shift. The AC component is complicated because the insect's four wings are moving in complex patterns and in different phase relationships relative to the bat. The echo from the flying insect is also modulated in amplitude. C: Target size is determined from both target range and subtended angle. D: Relationship between echo properties and target properties (Suga, O'Neill et al. 1983).

Parallel-hierarchical Processing of Complex Sounds and the Functional Organization of the Auditory Cortex

The eight components (CF_{1-4} and FM_{1-4}) of the orientation sound of the mustached bat are all different from each other in frequency, so that they are analyzed in parallel at different regions of the basilar membrane (Fig. 2, bottom). The signals are then coded and sent into the brain by peripheral neurons. In the brain, the signals are sent up to the auditory cortex through many auditory nuclei. For simplicity, we may consider that there are 8 channels for the processing of these signal elements: CF_1 channel, CF_2 channel, and so on. The CF_2 channel is very big compared with any other channel and is associated wtih an extraordinarily sharply tuned local resonator in the cochlea for fine frequency analysis (Fig. 2).

In the CF_1, CF_2 and CF_3 channels (Fig. 2), frequency selectivity is increased and amplitude selectivity is added by lateral inhibition to some neurons in the cochlear nucleus and also to many neurons at higher levels. In a certain region of the medial geniculate body, a part of the CF_1 channel and a part of CF_2 or CF_3 channel are integrated, so that neurons in this region poorly respond to CF_1, CF_2, and CF_3 tones when delivered alone, but respond strongly when the CF_1 tone is delivered together with the CF_2 or CF_3 tone. A deviation of the CF_2 or CF_3 frequency from the exact harmonic relationship with the CF_1 frequency, i.e., an amount of Doppler shift, is a critical parameter for their excitation. These CF/CF combination-sensitive neurons project to the CF/CF area of the auditory cortex. In the CF/CF area, two types of CF/CF neurons, CF_1/CF_2 and CF_1/CF_3, are separately clustered and form the frequency-versus-frequency coordinates in each cluster for the representation of Doppler shifts, i.e., target velocity information (Fig. 3). CF/CF neurons show sharp "level-tolerant" frequency-tuning curves and are remarkably specialized to respond to particular frequency relationships of two CF tones. The signal processing in the CF channels is thus "parallel-hierarchical."

In the FM_1, FM_2, FM_3, and FM_4 channels (Fig. 2), frequency selectivity is increased and amplitude selectivity is added by lateral inhibition to some neurons. Interestingly, FM selectivity is also added to some neurons by disinhibition, so that these "FM specialized" neurons respond to FM sounds, but not to CF tones and noise bursts. In a certain region of the medial geniculate body, a part of the FM_1 channel and a part of the FM_2 or FM_3 or FM_4 channel are integrated, so that neurons in this region respond poorly to these FM sounds when delivered alone, but respond strongly to the FM_1 sound combined with the FM_2, FM_3, or FM_4 sound. The delay of the FM_2, FM_3, or FM_4 from the FM_1 sound, i.e., echo delay, is a critical parameter for their facilitative responses. These FM-FM combination-sensitive neurons project to the FM-FM area of the auditory cortex. In the FM-FM area, three types of FM-FM neurons, i.e., FM_1-FM_2, FM_1-FM_3 and FM_1-FM_4, are separately clustered and form a time (echo-delay) axis in each cluster for the representation of target-range information (Fig. 3). Therefore, the signal processing in the FM channels is also parallel-hierarchical.

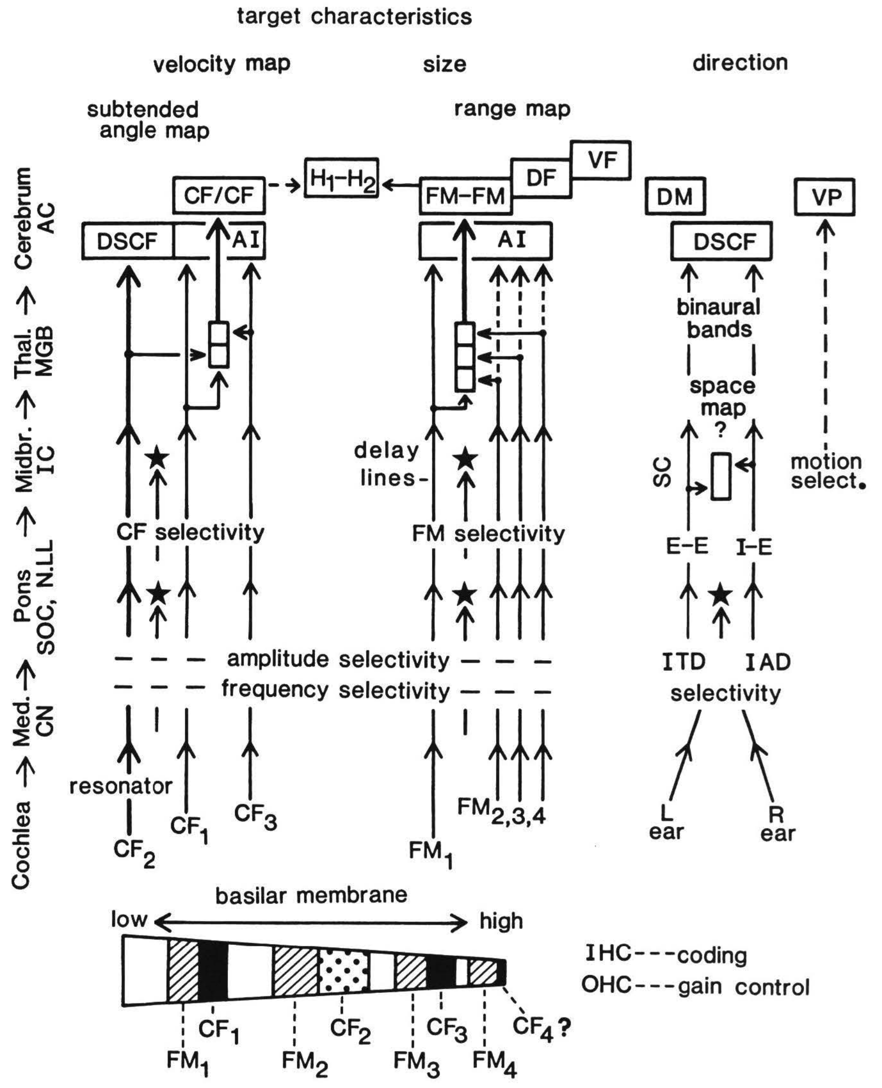
As described above, a part of one channel is integrated with a part of the other channel in the medial geniculate body. The remaining parts of these channels project to the auditory cortex which is not described above. For instance, a part of the CF_2 channel projects to the DSCF (Doppler-shifted CF processing) area of the auditory cortex which has the frequency-versus-amplitude coordinates to represent target-velocity information and subtended-target-angle information. The DSCF area overrepresents frequencies beween the CF_2 resting frequency (about 61 kHz) of the bat's own sound and 1.0 kHz above it. The DSCF area can be divided into two subdivisions which predominantly contain either I-E or E-E neurons (Figs. 2 and 3). Fig. 2 is only to explain the parallel-hierarchical processing of biosonar information which has thus far been explored.

Almost all frequencies found in the biosonar signals are projected not only to the areas which appear to be important for echolocation, but also to the other areas which appear not to be important for echolocation. These areas are probably important for processing communication sounds. Except for the CF_2 channel which is specialized for processing biosonar information from the periphery through the auditory cortex, clear separation of biosonar-signal processing from nonbiosonar-signal processing appears to first take place in the medial geniculate body.

The auditory cortex of the mustached bat shows multiple cochleotopic (tonotopic) representation, which is directly related to representation of different types of biosonar information. Fig. 3 shows several functional areas explored electrophysiologically. In these areas, certain response properties of single neurons arranged orthogonally to the cortical surface are identical. In this sense, there is a columnar organization. Along the cortical surface, however, the response properties vary systematically and, as shown in Fig. 3, form axes for representation of particular types of biosonar information. Among the several functional areas, the CF/CF, FM-FM, DF, VF, and VA areas consist of combination-sensitive neurons, so that these areas are particularly interesting in terms of neural mechanisms for processing complex sounds. [For further information on the auditory cortex of the mustached bat, see Suga (1984).]

The FM-FM area, representing target ranges from 7 cm to 310 cm, projects to the DF and VA areas of the cerebrum as well as other regions of the brain (Fig. 3). The DF area consists of three clusters of FM-FM neurons. In each cluster, target ranges from 7 cm to 140 cm are systematically represented. The DF area projects to the VF area, as well as to other areas in the cerebrum to which the FM-FM area does not project. The VF area

Parallel-Hierarchical Signal Processing (Tentative Scheme)

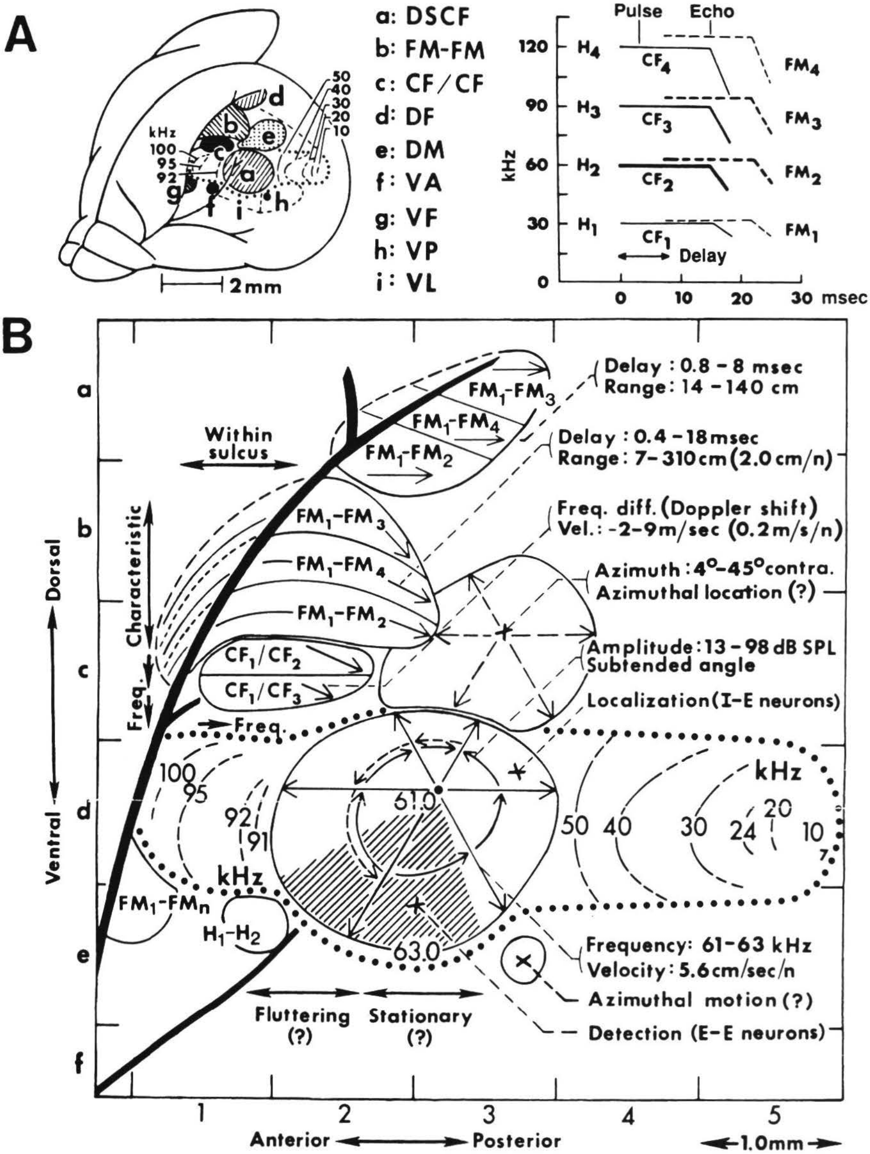


also consists of three clusters of FM-FM neurons and appears to represent target ranges between 7 and 80 cm. We do not yet know the functional significance of these multiple range (echo-delay) axes. One may hypothesize that these three different areas are related to echolocation behavior at different distances to targets. The H_1-H_2 area, a part of the VA area, contains combination-sensitive neurons which are different from FM-FM and CF/CF neurons. They show facilitative responses to the CF_2 and/or FM_2 of an echo when these are combined with the CF_1 and/or FM_1 of the orientation sound.

Auditory information is sent not only to the association cortex from the auditory cortex, but also to the motor system. Both the FM-FM and CF/CF areas project to the pontine motor nuclei, which in turn project to the cerebellum. In the cerebellar vermis, there are tiny clusters of FM-FM and CF/CF neurons. Biosonar information is also sent to the vocal system. Some neurons in the periaqueductal gray and midbrain reticular formation, for instance, become active prior to vocalization and respond to acoustic stimuli delivered from a loudspeaker.

The projections of the CF/CF area thus far studied do not overlap with those of the FM-FM area. If the overlap exists, however, it may be in the H_1-H_2 area. *All data thus far obtained indicates that complex-acoustic signals are processed in a parallel-hierarchical way in the ascending auditory system and beyond the auditory cortex.*

Fig. 2—Parallel-hierarchical processing of different types of biosonar information carried by complex biosonar signals. The CF_{1-4} and FM_{1-4} of the orientation sound and echo are analyzed at different portions of the basilar membrane in the cochlea (bottom). Inner and outer hair cells (IHC and OHC) on the membrane are respectively related to stimulus coding and gain control. The signal elements are separately sent up to the auditory cortex (AC) through several auditory nuclei (left margin): cochlear nucleus (CN), superior olivary complex (SOC), nucleus of lateral lemniscus (N.LL), inferior colliculus (IC), and medial geniculate body (MGB). During the ascent of the signals, frequency, amplitude, CF, and FM selectivities are added to some neurons (arrows with a star). Each star indicates that the addition of selectivity also takes place in the auditory nuclei and cortex as well as in the nucleus where the arrow starts. The CF_2 channel is disproportionately large and projects to the DSCF (Doppler-shifted CF processing) area of the auditory cortex. In certain portions of the MGB, two channels processing different signal elements (e.g., CF_1 and CF_2 or FM_1 and FM_2 channels) are integrated to produce "combination-sensitive" neurons. CF/CF and FM-FM combination-sensitive neurons respectively project to the CF/CF and FM-FM areas of the auditory cortex, where target velocity or range information is systematically represented. Because of corticocortical connections, DF, VF, and VA areas also consist of combination-sensitive neurons (center top). Target velocity and range information is thus processed in a parallel-hierarchical manner. The DSCF area has the frequency-versus-amplitude coordinates to represent velocity and subtended angle information of a target. The DSCF area consists of two subdivisions mainly containing I-E or E-E neurons (right column). Motion-sensitive neurons appear to be in the ventroposterior (VP) area of the auditory cortex.


A
kHz
100
95
92
50
40
30
20
10
a b c d e f g h i
2mm
a: DSCF
b: FM-FM
c: CF/CF
d: DF
e: DM
f: VA
g: VF
h: VP
i: VL
Pulse
Echo
kHz
120
90
60
30
0
H4
H3
H2
H1
CF4
CF3
CF2
CF1
FM4
FM3
FM2
FM1
Delay
0
10
20
30 msec
B
a
b
c
d
e
f
Dorsal
Ventral
Within sulcus
Characteristic Freq.
→Freq.
FM1-FM3
FM1-FM4
FM1-FM2
CF1/CF2
CF1/CF3
Delay : 0.8 - 8 msec
Range: 14 - 140 cm
Delay : 0.4 - 18msec
Range: 7- 310cm (2.0cm/n)
Freq. diff. (Doppler shift)
Vel.: -2-9m/sec (0.2m/s/n)
Azimuth : 4°-45° contra.
Azimuthal location (?)
Amplitude: 13 - 98 dB SPL
Subtended angle
Localization (I-E neurons)
100
95
92
91
61.0
63.0
kHz
50
40
30
24
20
10
7
kHz
FM1-FMn
H1-H2
Frequency: 61-63 kHz
Velocity: 5.6cm/sec/n
Azimuthal motion (?)
Detection (E-E neurons)
Fluttering (?)
Stationary (?)
1
2
3
4
5
Anterior
Posterior
1.0mm

QUESTIONS AND SPECULATIONS ABOUT THE FUNCTIONAL ORGANIZATION OF CORTICAL AUDITORY AREAS

In both the auditory periphery and cortex, an acoustic signal is expressed by a spatiotemporal pattern of neural activity. Since response properties of individual neurons contributing to the pattern are quite different between the periphery and cortex, the spatiotemporal pattern between them is also quite different. At the periphery, neurons show a "tonic-on" response to any acoustic signal whenever its energy or component falls into their frequency-tuning curves (excitatory areas), and a spatiotemporal pattern of neural activity is formed along a frequency axis which has an anatomical basis. On the other hand, response patterns of cortical neurons are diverse, and the cortex shows multiple cochleotopic representations. In the primary auditory cortex, tonotopic representation is systematic and neurons usually respond well to pure tones. In the non-primary auditory cortices, on the other hand, tonotopic representation is poor or even vague, and responses to pure tones are usually weak and variable (cats, monkeys, and bats). This suggests that different auditory cortices are each involved in processing

Fig. 3—Functional organization of the auditory cortex of the mustached bat. A: Dorsolateral view of the left cerebral hemisphere. The auditory cortex consists of several areas (a–i). DSCF, FM-FM, CF/CF, DF, and DM areas (a,b,c,d, and e, respectively) are specialized for the systematic representation of biosonar information. The branches of the median cerebral artery are shown by the branching lines. The longest branch is on the sulcus. B: Graphic summary of the functional organization of the auditory cortex. The tonotopic representation of the primary auditory cortex and the functional organization of the DSCF, FM-FM, CF/CF, DF, and DM areas are indicated by lines and arrows. The DSCF area has axes representing either target velocity (echo frequency: 61–63 kHz) or subtended target angle (echo amplitude: 13–98 dBSPL) and is divided into two subdivisions suitable for either target detection (shaded) or target localization (unshaded). These subdivisions are occupied mainly by excitatory-excitatory (E-E) or inhibitory-excitatory (I-E) neurons, respectively. The FM-FM area consists of three major types of FM-FM combination-sensitive neurons (FM_1-FM_2, FM_1-FM_3, and FM_1-FM_4), which form separate clusters. Each cluster has an axis representing target ranges from 7 to 310 cm (echo delay: 0.4–18 msec). The dorsoventral axis of the FM-FM area probably represents fine target characteristics. The CF/CF area consists of two major types of CF/CF combination-sensitive neurons (CF_1/CF_2 and CF_1/CF_3), which aggregate in independent clusters. Each cluster has two frequency axes and represents target velocities from -2 to $+9$ m/sec (echo Doppler shift: -0.7 to $+3.2$ kHz for CF_2 and -1.1 to $+4.8$ kHz for CF_3). The DF area and a posterior part of the VA area are projected from the FM-FM area. The DF area consists of the three types of FM-FM neurons, but the VA area contains only H_1-H_2 combination-sensitive neurons. The DF area projects to the VF area, which consists of the three types of FM-FM neurons. The DM area appears to have an azimuthal axis representing the azimuthal location of a target. In the VP area, motion-sensitive neurons have been found. The functional organization of the VF, VA, and VP areas remains to be studied further.

different types of auditory information or different attributes of acoustic signals. As a matter of fact, different auditory areas *are* devoted to processing different types of IBPs (bats) or have functional organization beyond tonotopy (cats and bats). Therefore, the spatiotemporal pattern of neural activity formed in the auditory cortex is much more complex than that formed at the periphery.

There are several important questions about the responses of single cortical neurons, the functional organization of the auditory cortex, and recognition of spatiotemporal patterns of neural activity. In the following, I shall enumerate some of these questions and shall present my speculative answers to them.

Question 1: Why does the auditory cortex have different clusters of neurons tuned to IBPs or combinations of IBPs?
Peripheral neurons are excited by any acoustic stimulus whenever its energy falls into their excitatory areas. Therefore, they are excited almost all the time by both signals and noise. This is apparently an inappropriate situation for cortical neurons which are more or less directly related to perception. They should be circuited to be excited only by biologically important sounds or potentially important ones. As a matter of fact, the bat's auditory cortex contains a large number of neurons tuned to IBPs. They either do not respond or respond poorly to biologically irrelevant sounds. Interestingly, different types of IBP neurons are separately clustered in certain auditory areas, presumably for easy reading of a spatiotemporal pattern of neural activity (a value of an IBP) and/or for mediating different behavioral outputs.

Question 2: Why does the primary auditory cortex (AI) contain neurons somewhat like peripheral ones?
In the AI, a significant number of neurons show tonic-on responses and frequency tunings somewhat similar to those of peripheral ones, although they are clearly different from these in binaurality and phase-locking (cats, monkeys, and bats). In the mustached bat, the tonotopically organized AI and the specialized auditory areas with the IBP maps receive projections independently from different portions of the medial geniculate body, so that the tonotopically organized AI is not simply an intermediate stage between the medial geniculate body and the specialized auditory areas. There must be a reason to have neurons and organization in the AI which are somewhat similar to those in the periphery.

One may speculate that IBP neurons in the specialized auditory areas perform quickly the processing of information carried by biologically important sounds, while avoiding excitation by biologically less significant sounds. If all cortical auditory neurons were tuned to IBPs, the auditory cortex would not be able to process information except for that extracted by IBP neurons. For processing acoustic signals less familiar or unfamiliar to the animal, it may be desirable for the auditory cortex to contain some primary-like auditory neurons and organizations so that it can maintain "raw data" coded by primary auditory neurons intact. Decoding, based upon the spatiotemporal pattern of activity of these neurons, may be slower than that based upon the pattern of activity of IBP neurons.

Neurons in the tonotopically organized AI are excited, of course, by biologically important sounds as well as by biologically irrelevant sounds. What functional role does their activity play relative to the activity occurring in the specialized areas? Does it act as a backup and/or supplement to the information processing in the specialized areas? Research to answer these questions has not yet been performed.

Question 3: How reliable are cortical IBP neurons in stimulus encoding?
Threshold for excitation has been defined as the smallest amplitude of a sound that evokes, e.g., 0.1 impulse per stimulus on the average, or a just noticeable increase in discharge rate beyond a background. The threshold (tuning) curves of IBP neurons based upon the above definition are sometimes very sharp, but not so sharp that they are excited only by a particular value of an IBP. The ambiguity in stimulus encoding by each IBP neuron is not small enough to relate its excitation directly to behavior. We have to consider stimulus encoding by a population of IBP neurons which are tuned to slightly different values of the IBP.

Responses of cortical IBP neurons often periodically change in magnitude and threshold. In an extreme case, the response completely disappears for several seconds, then reappears. Such a change is probably due to attention mechanisms, wakefulness, drowsiness, non-auditory sensory inputs, etc. Dynamic properties of cortical auditory neurons have not yet been well studied.

Question 4: What kinds of advantages are obtained from IBP maps? Can acoustical signals be processed without IBP maps?
There are four possible reasons why the auditory system creates an IBP map: (a) variation in an IBP is biologically important so that it is systematically represented for easy "reading"; (b) a mechanism to produce an array of neurons tuned to different values of the IBP operates systematically according to anatomical locations; (c) lateral inhibition for the sharpening of neural tuning to the IBP can be easily circuited; and (d) the IBP map makes the sensorimotor interface easier. Possibilities (a), (c) and (d) indicate obvious advantages resulting from such maps.

Any parameter characterizing an acoustic signal shows some variation. If the variation is biologically very important, the auditory system may develop a subdivision for systematic representation of the variation, i.e., an IBP map. If it is not biologically important there may be no map, even if there are neurons tuned to different values of the IBP. The best example related to this problem is amplitopic representation thus far found only in the DSCF area of the auditory cortex of the mustached bat (Fig. 3). In the mustached bat, the echo amplitude carries the information about the subtended angle of a target, so that a variation in amplitude is itself biologically important. In cats and monkeys, neurons tuned to particular amplitudes of tone bursts have been found, but amplitopic representation has not yet been found. In these animals, a variation in amplitude itself is not an IBP for communication, so that there is no necessity to express it separately from other acoustic parameters.

Question 5: How is a cortical IBP map read?
IBP maps found in the auditory cortex are quite interesting, and one may interpret that a particular value of an IBP is perceived by a location of optimally excited neurons within the map. This is a reasonable hypothesis, but there is a problem in determining the kind of mechanism that operates to identify this location. Since tuning of cortical IBP neurons is not so sharp that only neurons in a single column (or slab) are excited by an acoustic signal, many neurons in different columns would be excited by it (Fig. 4, A and B). For simplicity, we may consider that 50 neurons are contained within a 20 μm-diameter, 1,000 μm-tall cortical column. Then, there are 2,500 neurons within a 1,000 μm-long isoIBP slab. These neurons are optimally excited by a given stimulus. If we assume that neurons within, say, a 500 μm distance from the optimally excited slab are also excited, the total number of excited neurons would be 125,000. This number would be a rough estimate for a bat's brain, but it would be an underestimate for a cat's brain. How is the optimally excited slab identified? When several locations within the map are simultaneously excited by multiple stimuli, the spatial distribution of neural activity becomes multimodal. How is a multimodal distribution processed?

One may consider that the location of the optimally excited column (or slab) becomes much more discrete by lateral inhibition when the IBP map is projected to some other area of the cortex (Fig. 4B). Sharpening of IBP filters by lateral inhibition takes place in the CF/CF area of the bat's auditory cortex, so that the optimally excited column is expected to be surrounded by inhibited columns. However, many neurons in several columns are still excited to a considerable extent. The above is also true within the auditory space map found in the midbrain of the barn owl. It is unlikely that there is an area where only the neurons in a single column respond to a particular value of an IBP. We have to consider that in a cortical auditory area, there is an intrinsic mechanism for the evaluation of the spatiotemporal pattern of neural activity. For the evaluation, neural activities at different columns

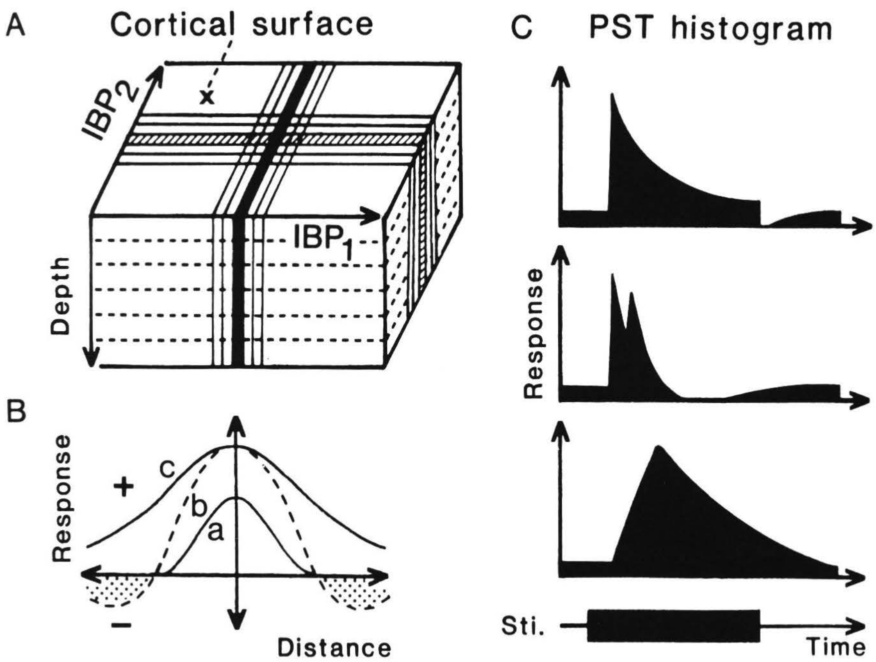


Fig. 4—Spatiotemporal pattern of neural activity in a cortical auditory area. A: There are two IBP axes along the cortical surface, IBP_1 and IBP_2. For a particular value of IBP_1 or IBP_2, an iso-IBP slab (filled or shaded) is maximally excited, and slabs nearby are submaximally excited. B: A spatial distribution of magnitudes of neural responses along the IBP_1 axis: curve "a" for a weak stimulus, curve "b" for a strong stimulus when lateral inhibition operates, and curve "c" for a strong stimulus when lateral inhibition does not operate. A lateral spread of excitatory response by the strong stimulus is minimized by lateral inhibition. As a result, the excited slabs are sandwiched between inhibited slabs (dotted areas). "+" = excitation, "−" = inhibition, C: PST histograms show a large variation in envelope and latency for different neurons and different stimulus parameters. What parameter of response is mainly utilized for cross-correlation analysis to identify the maximally excited slab, highest instantaneous discharge rate, highest total number of impulses/stimulus, or other measures?

must be cross-correlated. How are neural activities cross-correlated? What portion of neural responses are cross-correlated?

The response patterns of cat auditory neurons have been classified into several types. What kind of functional significance do they have? In the bat's auditory cortex, for example, some neurons show very phasic on-responses, while others show long-lasting on-responses. The envelope of a PST histogram and the response latency are different among neurons (Fig. 4C). Which is more directly related to determining the optimally excited column: the maximum instantaneous discharge rate, or the total number of impulses per stimulus, or some other measures?

Along an IBP axis, an IBP value changes at a particular intercolumn step. Is this step the same as a just-noticeable IBP difference (behavioral data)? If the former is much larger than the latter, one must consider how the behavioral acuity emerges from the IBP map. In this case, the behavioral acuity is probably based upon some combinations of intercolumn step, the bandwidth of tuning curves of IBP neurons, and the size of the population of the IBP neurons.

Question 6: How high is the upper limit of complexity of single neurons? Are there "super" maps, "categorizers", and "grandmother" neurons for processing auditory information?
A tonotopic map is an "epithelial" map, while all other maps in the auditory system are "computational" maps. The tonotopic map is not an IBP map except for special cases, while the computational maps are. One hypothesis on acoustic pattern recognition says that the spatiotemporal patterns of neural activity occurring in the different IBP maps somehow are directly related to recognition of overall acoustic signals. Another hypothesis says that these IBP maps are integrated to create a "super" map. The spatiotemporal pattern of activity in the super map somehow is directly related to overall signal recognition. Another hypothesis says that there is no super map, but there are groups of detectors for biologically important sounds.

In the barn owl, the ITD and IAD maps are separately formed in the subcollicular nuclei. Then, these are integrated in the anterior division of the inferior colliculus to form an ITD-versus-IAD map, i.e., an auditory space map. This is a "lower order" super map which represents combinations of two IBPs. In the auditory cortex of the mustached bat, velocity, range, and subtended angle of a target are separately mapped. The frequency-versus-amplitude map in the DSCF area may be considered to be a lower order super map. It is not yet known whether all the maps in the DSCF, FM-FM, and CF/CF areas are eventually integrated in another area of the cerebral cortex. A lower order super map for complex-sound processing may exist, but a "higher order" super map representing combinations of more than 3 IBPs is hardly conceivable. Complex sounds each characterized by more than 3 IBPs may not be expressed by a location in a map, but may be expressed by a group of neurons which may be called "categorizers."

Acknowledgement. The work on the auditory system of the mustached bat has been supported by a research grant from the U.S. Public Health Service, RO1-NS17333 Javits Neurosci. Invest. Award. I thank S. J. Gaioni and D. R. Humphrey for their comments on this article.

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