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Disproportionate Tonotopic Representation for Processing CF-FM Sonar Signals in the Mustache Bat Auditory Cortex

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Abstract. *The extent of cortical representation of the peripheral sensory field depends on its importance for species behavior. The orientation sound of the mustache bat (*Pteronotus parnellii rubiginosus*) invariably consists of long constant-frequency and short frequency-modulated components and is indispensable for its survival. A disproportionately large part of the auditory cortex of this bat is occupied by neurons processing the predominant components in the orientation signal and Doppler-shifted echoes. This disproportionate cortical representation related to features of biologically significant signals is comparable to that in the somatosensory and visual systems in many mammals, but it has not previously been observed in the auditory system.*

In both the sensory and motor areas of the cerebral cortex of mammals, the size of the population of neurons concerned with particular sensory signals or movements greatly varies, depending on their functional importance and the demand for fine analysis of the signals or for delicate performance of movements. Fine analysis of a visual image is performed at the fovea centralis, which contains a high density of sensory cells, but which is very small compared with the total retinal area. The visual cortex, however, is occupied predominantly by neurons concerned with signals coming through the fovea centralis. Such a disproportionate projection of a sensory field to the cortex has also been demonstrated in the somatosensory system of many species, and comparable disproportionate organization of the motor cortex has also been seen. For example, a monkey uses its hand with dexterity in the performance of delicate manipulative tasks. Consequently, sensory signals coming from the hand are important. "Hand" areas in the somatosensory and motor cortices are therefore disproportionately large in comparison with the representation of the remainder of the body surface (*1*).

In the auditory system, such a dramatically disproportionate projection has not been found. The rather proportionate tonotopic representation is probably due to the fact that the acoustic signals used by most mammals have a broad frequency band and their sound energy is commonly not concentrated at a particular frequency. Cat's cries, for example, contain many harmonics or consist of broadband noise. In the cerebral cortex of the cat, nine separate auditory areas have been found, and tonotopic organization has been demonstrated in at least five of these (*2*). Among them, the primary auditory cortex (area AI) has been most frequently studied (*3*–*5*). The most recent and reliable single unit data obtained indicate that high-frequency-sensitive neurons are located anteriorly and low-frequency-sensitive neurons are located posteriorly, with neurons sensitive to intermediate frequencies lying between. The AI shows orderly tonotopic organization (*4*, *5*). The single unit data further demonstrate that neurons tuned to very similar best frequencies are organized in columns and that the cortical surface area per octave is somewhat larger for higher frequencies (*4*). In a dog's AI treated with 3 percent strychnine sulfate solution, there is no such tendency toward disproportionate representation; the cortical area per octave is the same for all frequencies (*6*). In monkeys, the AI is apparently tonotopically organized (*7*), and it appears that there is no clear disproportionate representation.

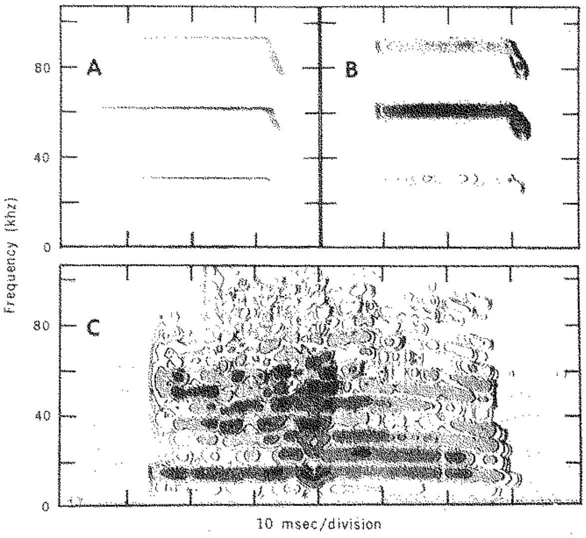

Fig. 1. Sonagrams of orientation sounds (A, B) and squeak (C). The signals tape-recorded at 60 inches (1 inch = 2.54 cm) per second with an Ampex tape recorder (FR-100) were played back at 7½ inches per second and were analyzed with a Kay sonograph (model 7030A and 6070A). The bandwidth of the analyzer was 45 × 8 hz for (A) and 300 × 8 hz for (B) and (C), in which contour line spacing is 6 db.

In *Myotis lucifugus* (little brown bat), which uses frequency-modulated (FM) orientation sounds with about an octave band, the AI is also tonotopically organized—that is, high-frequency-sensitive and low-frequency-sensitive neurons are located along the anteroposterior axis, as in the AI area of the cat and dog (*8*). There is no noticeable disproportionate projection. Another insectivorous bat *Pteronotus parnellii rubiginosus* (mustache bat), from Panama, emits a different type of orientation sound, and we have found that this is associated with a remarkable elaboration of the part of the auditory cortex involved in the processing of this sound and its echoes. Each orientation sound of the mustache bat consists of a long constant-frequency (CF) component followed by a short FM component, in which frequency sweeps downward. The CF component is sometimes preceded by a short, faint, upward-sweeping FM component (Fig. 1A). In the orientation sounds, the second harmonic is always predominant. The first and third harmonics are often about 18 and 12 db weaker than the second, respectively (Fig. 1B). The frequency of the CF component is about 30.5, 61.0, and 91.5 khz for these three harmonics. The frequency of the FM component following the CF sweeps down either from 30.5 to 25 khz or 61.0 to 50 khz or 91.5 to 74 khz, depending on the harmonic. There are, of course, minor variations in the frequency of the CF and the range of the frequency sweep. The duration of the CF component ranges from 5 to 30 msec, while that of the FM component ranges from 2 to 3 msec. Since the CF component is much longer than the FM, the 61-khz component in particular is far more intense in total energy than the other components of the orientation sound. The long CF component is an ideal signal for echo detection and velocity (or Doppler shift) measurement. Schnitzler (*9*) first demonstrated that the mustache bat adjusts the frequency of the emitted CF to receive a Doppler-shifted echo CF at a certain preferred frequency. This interesting acoustic behavior is called "Doppler-shift compensation." In terms of the energy distribution in the orientation sound, the audiogram of the animal (*10*–

12), and the behavioral responses to tonal stimuli (*11*), the 61-khz CF component is an essential signal for the Doppler-shift compensation. Communication sounds of the mustache bat have not yet been studied. When the bat is handled, it often squeaks. The energy in a squeak scatters in a wide range from below 10 khz to above 100 khz, and is most intense between 20 and 60 khz (Fig. 1C).

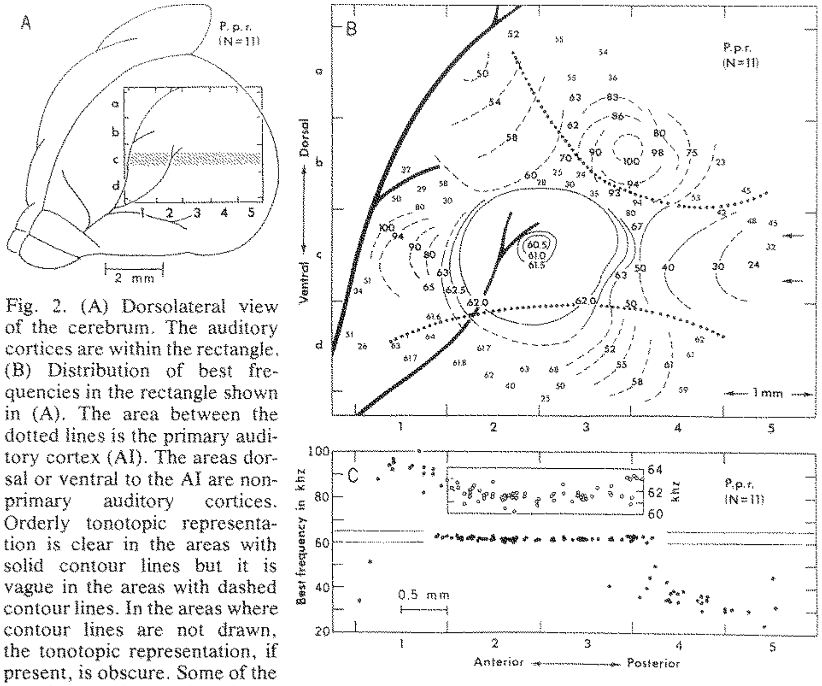

Fig. 2. (A) Dorsolateral view of the cerebrum. The auditory cortices are within the rectangle. (B) Distribution of best frequencies in the rectangle shown in (A). The area between the dotted lines is the primary auditory cortex (AI). The areas dorsal or ventral to the AI are nonprimary auditory cortices. Orderly tonotopic representation is clear in the areas with solid contour lines but it is vague in the areas with dashed contour lines. In the areas where contour lines are not drawn, the tonotopic representation, if present, is obscure. Some of the best frequencies obtained in the obscure areas are shown by small letters. (C) Distribution of the best frequencies along the anteroposterior axis in the shaded area in (A). Since the minor differences among the best frequencies in areas 2 and 3 cannot clearly be shown in (C), the distribution of the best frequencies in this area is shown by the inset with a larger frequency scale and using open circles. *P.p.r.*, *Pteronotus parnellii rubiginosus*.

The peripheral auditory system of the mustache bat is unusually sharply tuned to a sound of 61 khz, which is the predominant component in its orientation sound and Doppler shift compensated echoes (*10–12*). Peripheral auditory neurons with best frequencies at about either 30 or 61 or 92 khz show very sharp tuning curves. In particular, the curves of those tuned at 60.5 to 62.0 khz are extraordinarily sharp. Their Q values, which are the best frequency divided by the width of the tuning curve at 3 db above the minimum threshold, are 210 on the average and are as large as 900 (*12, 13*). A group of these sharply tuned neurons is apparently specialized for detecting and analyzing the CF component in echoes which would be Doppler-shifted by targets moving relative to the bat or by the wingbeats of flying insects, or both. These sharply tuned neurons can code a frequency shift as small as ± 0.01 percent, but these are comparable to any other neurons in coding of amplitude modulation which would be evoked by the wingbeats (*13*).

As described above, the mustache bat uses a 61-khz sound predominantly for echolocation, which is indispensable for its survival, and its peripheral auditory system is specialized for the detection and analysis of this sound. Therefore, if it is true in the auditory system that the extent of the cortical representation of the sensory field depends on its importance for species behavior, one could expect that dramatically disproportionate tonotopic representation would be found in area AI. To test this prediction, we mapped the auditory cortices in 11 specimens (20 to 26 g) of *P. p. rubiginosus*. Under light anesthesia with sodium pentobarbital (23 mg per kilogram of body weight) and ether, if necessary, the flat head of a nail 1.8 cm long was mounted on the posterior part of the bat's skull with glue and cement. To immobilize the head, the shank of the nail was locked onto a metal rod with a set screw. The skull covering the cerebral hemisphere was widely opened. A tungsten wire electrode with a tip diameter of 20 to 30 μm was inserted into the cerebral cortex perpendicular to the cortical surface, and single or multiunit activity was recorded at depths not greater than 0.6 mm. Tone bursts with a rise-decay time of 0.5 msec and a duration of 4 msec were delivered at a rate of 1.5 per second from a condenser loudspeaker placed 60 cm in front of the animal.

Multiunit activity evoked by a tonal stimulus was easily recorded from area AI. The activity was strong at a depth of 400 to 500 μm. In the first three animals, the best frequencies of some single neurons were measured at a few different depths in a single penetration. The best frequencies of all neurons encountered in a single penetration were found to be the same. For convenience, in the remaining eight animals, measurements were concentrated on units found at a depth of 400 to 500 μm unless single unit activity was poor. With this change in sampling method, it became possible to measure the best frequencies at many cortical locations (up to 90) in a single bat. The cortical surface, including fine blood vessels, was sketched with the aid of an ocular micrometer. A composite sketch of a dorsolateral view of the cerebrums of the 11 animals is shown in Fig. 2A. The position of the blood vessels showed significant variations, but the main branches of the artery were rather constant. The best frequency obtained at each recording site was indicated on the sketch for each animal. When multiunit activity showed multiple peaks in sensitivity, these were listed as the primary best frequency, secondary best frequency, and so on. All these peaks were measured, but only the primary best frequency, where the threshold was the lowest, was used for mapping. What first surprised us in the early experiments was that neurons tuned at 61 to 63 khz occupy an exceptionally large area in the auditory cortex. It was difficult to find neurons tuned at 64 to 79 khz. These were the consistent observations in the subsequent experiments.

Since the arteries were not entirely reliable as a reference for superimposition, the data obtained from 11 bats were superimposed by adjusting the location maps so that a conspicuous area tuned at 60.5 to 62.0 khz fell in register. It was difficult to put all the data together so as to draw an equal best-frequency contour map, because the area tuned at a certain frequency is not necessarily the same in size, although there was an orderly tonotopic representation in the AI area of each of the bats studied. Therefore, the best-frequency contour map (Fig. 2B) was drawn on the basis of both the superimposed map and individual maps. The central area between the two dotted lines (Fig. 2B) is the AI area, because of the short latency of tonal responses, 4.4 to 5.2 msec, and reliable strong responses (*14*). The areas dorsal or ventral to area AI are the nonprimary auditory areas, where the response latency was usually longer than in AI (6 to 10 msec), and the response was not necessarily as strong as in AI. In the part of AI indicated as zone c in Fig. 2B, there is a clear tendency for high-frequency-sensitive neurons to be located anteriorly and low-frequency-sensitive ones to be located posteriorly, exactly as in the AI of other mammals. However, in three respects this tonotopic representation is quite unique in the mid-frequency range. (i) Neurons tuned between 50 and 60 khz or between 64 and 79 khz were not found along this anteroposterior axis, that is, neurons concerned with main components in the FM signals are not on the main tonotopic axis. (ii) The areas concerned with the CF components in the orientation sounds and Doppler-shifted echoes occupy most of the auditory cortex. In particular, the 61- to 63-khz sensitive area is represented with considerable magnification. (iii) The 60.5- to 63-khz sensitive area is concentrically organized. These three significant points are shown by the distribution of best frequencies in a narrow strip along the anteroposterior axis of area AI (Fig. 2, A and C). There is a tendency for a progressive change in best frequency between 80 and 100 khz in the area lying anterior to the 60.5- to 63.0-khz area (dashed lines in Fig. 2B). But areas concerned with 50 to 60 khz and 64 to 79 khz were not on the anteroposterior axis. The area concerned with 64 to 79 khz was obscure in area AI, but the area processing 50- to 60-khz sounds is large and is located in the anterodorsal part of the AI. Thus, the area processing the FM component in the predominant harmonic is isolated from the others and appears to be specialized. The tonotopic representation in this area appears to be orderly. Independent processing of the FM component is essential. Otherwise, the information carried by the FM component would be disturbed by the overwhelmingly intense CF component.

In the nonprimary auditory cortex, the tonotopic representation is not easily defined. Neurons sensitive to 20 to 70 khz are found on both sides of the AI. However, most of the ventral nonprimary auditory cortex is devoted to 50- to 63-khz sounds, and neurons tuned above 70 khz were not found in this area. The dorsal nonprimary auditory cortex contains mostly neurons tuned between 75 to 100 khz. These neurons appear to show a coiled tonotopic representation. Although not shown in Fig. 2, the nonprimary auditory cortex has another intriguing feature—that is, multiunit activity often showed multiple peaks in sensitivity, and these peaks were roughly harmonically related in most cases (*15*).

As is described above, the auditory cortex of the mustache bat shows a highly disproportionate frequency representation. Since squeaks, which may be termed "distress calls," are broadband noise (Fig. 1C) and since other communication sounds also differ from the orientation sound, the disproportionate frequency representation is due to the specialization of the auditory system for processing the stereotyped species-specific echolocation signals (*16*). As one would expect, afferent fibers innervating cochlear hair cells show some regional variations in innervation density (*17*). Within an area on the basilar membrane between 5.5 and 7.0 mm from the round window, the densities of sensory hair cells and dendrites of primary auditory neurons are higher than those at other areas, while these densities are lower between 3.8 and 5.0 mm from the round window (*13*). We suspect that the high-density area is tuned at 60.5- to 63.0-khz sounds and the low-density one is for the reception of 64- to 79-khz sounds. The general rule, that the disproportionate cortical representation reflects a corresponding distribution of sensory cells or peripheral nerve fibers (or both), is therefore also applicable to the auditory system of the mustache bat.

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13. N. Suga and P. H.-S. Jen, in preparation. A Q value is the best frequency divided by the bandwidth of a tuning curve at 3 db above the minimum threshold. This Q value is about 2.6 times larger than a Q value at 10 db.
14. The 4.4- to 5.2-msec latency of responses is too short to be those of cortical neurons. Tonal responses with such short latencies were probably recorded from nerve fibers from the medial geniculate body. In a study of the single unit in AI (unpublished), the majority of neurons sampled showed a response latency of 7 to 10 msec, and a few of them showed a latency of 5 to 6 msec. In our experiments the best frequencies of neurons were measured in terms of their responses, mainly appearing after 7 msec. In other words, the best-frequency contour map in Fig. 2 was for cortical neurons.
15. Some of the single neurons studied in such an area showed two peaks, which were approximately harmonically related. Since no neurons with a double peaked tuning curve were found at the periphery (*12, 13*), it is evident that harmonically related components in acoustic signals are converging on some single neurons in higher levels of the auditory system.
16. N. Suga [*J. Physiol. (London)* **203**, 729 (1969)] studied the effect of the ablation of the auditory cortex on a wire-avoidance performance in *Myotis lucifugus* and suggested that the auditory cortex was less important for sound localization in bats than in cats, because the bat can avoid wires without the auditory cortex on both sides. This does not mean at all that the auditory cortex plays no role in echolocation. In *Myotis*, the auditory cortex contains specialized neurons at a higher percentage than the inferior colliculus does [see (*8*)]. Our results show that the AI receives ascending impulses with a very short latency. The auditory cortex is probably important in the performance of echolocation tasks which are more complex than the simple wire avoidance.
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Mustache bat (*Pteronotus parnellii rubiginosus*). Each of its orientation sounds consists of a long constant-frequency component for echo detection and velocity measurement, and a short frequency-modulated component for echo localization, target characteristics, and ranging. This bat has an auditory system remarkably specialized for processing echolocation signals. See page 542. [James H. Jaeger, Washington University, St. Louis, Missouri 63130]