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Neural Axis Representing Target Range in the Auditory Cortex of the Mustache Bat

Abstract. *In echolocating bats, the primary cue for determining distance to a target is the interval between an emitted orientation sound and its echo. Whereas frequency is represented by place in the bat cochlea, no anatomical location represents target range. Target range is coded by the time interval between grouped discharges of primary auditory neurons in response to both the emitted sound and its echo. In the frequency-modulated-signal processing area of the auditory cortex of the mustache bat (*Pteronotus parnellii rubiginosus*), neurons respond poorly or not at all to synthesized orientation sounds or echoes alone but respond vigorously to echoes following the emitted sound with a specific delay from targets at a specific range. These range-tuned neurons are systematically arranged along the rostrocaudal axis of the frequency-modulated-signal processing area according to the delays to which they best respond, and thus represent target range in terms of cortical organization. The frequency-modulated-signal processing area therefore shows odotopic representation.*

In the mustache bat (*Pteronotus parnellii rubiginosus*), the auditory cortex has been found to have at least three specialized areas for processing different types of biosonar information: the Doppler-shifted constant-frequency (DSCF), frequency modulated (FM), and CF/CF processing areas (Fig. 1A) (*1*-*6*). Neurons of the DSCF processing area are arranged along two axes, one representing echo amplitude (target subtended angle), the other representing echo frequency (target velocity information) (*2*). The DSCF processing area consists of two functional subdivisions adapted for target detection or localization (*3*). The FM and CF/CF areas process information carried by different combinations of information-bearing elements in the emitted biosonar signal and its echo (*4*-*6*). We report that the FM processing area represents target-range information along an anatomical axis without a corresponding anatomical dimension at the periphery.

The mustache bat emits biosonar signals (orientation sounds), each of which contains four harmonics. Each harmonic consists of a CF component and an FM component. Therefore, there are eight components (CF_{1-4}, FM_{1-4}) in each emitted signal (*1*, *5*, *7*). Echoes that elicit behavioral responses in the mustache bat always overlap with the emitted signal (inset, Fig. 1C). As a result, biosonar information must be extracted from a complex sound with up to 16 components.

Neurons in the FM processing area are maximally excited only when an echo from an orientation sound arrives after a particular delay. The essential elements in such paired stimuli are the first harmonic FM component (FM_1) in the orientation sound and one or more higher harmonic FM components (FM_{2-4}) in the echo. Therefore, these neurons are called FM_1-FM_n facilitation neurons (*4*, *5*).

One of the most important aspects of echolocation is ranging. The primary cue for ranging is the delay of the echo from the emitted sound. The FM_1-FM_n facilitation neurons are sensitive to this delay and are therefore range-sensitive. Range-sensitive neurons can be classified into two categories, tracking and range-tuned. The best delays (BD's) (*8*) of tracking neurons shorten and their delay-tuning curves become narrower as the bat changes the signal repetition rate and duration as it approaches a target. These neurons zero in on the target, rejecting echoes from more distant objects (*4*, *5*). Range-tuned neurons, on the other hand, are tuned to particular echo delays, regardless of repetition rate and duration of paired stimuli. They respond to the target only when it is within a certain narrow range (*5*). The obvious question is whether range-tuned neurons with different BD's (that is, best ranges) are systematically arranged along an axis in the FM processing area to represent target range information.

Experiments were performed with 12 mustache bats collected in Panama. The activity of single neurons was recorded in unanesthetized bats with a tungsten-wire electrode (5- to 10-μm tip) during the period from 4 days to 4 weeks after surgery to expose the skull. When necessary, local anesthetic (Xylocaine) and tranquilizer (droperidol) were administered. Acoustic stimuli were pure (CF) tones, FM sounds, and combinations of them that mimicked the biosonar signal-echo pair in the search, approach, and terminal phases of echolocation in this species (*9*). The stimuli were delivered from a loudspeaker 73 cm in front of the animal in a soundproof, echo-suppressed room. For details of the surgery and the stimulation and recording systems, see (*4*) and (*5*).

In the first stage of our experiment, we inserted an electrode orthogonal to the surface of the FM processing area and recorded single-unit activity at various depths to determine whether there was columnar organization for response parameters, such as best frequency, minimum threshold, and frequency bandwidth, with pure tones, FM sounds, and pairs of sounds used to elicit facilitation. We also measured BD, threshold at BD, and width of the delay-tuning curves with pairs of sounds eliciting the strongest facilitation. Neurons at depths between 200 and 1000 μm had nearly identical response characteristics, including BD's. (At depths less than 200 μm, the signal-to-noise ratio was usually small and responses to acoustic stimuli were poor.)

Confirmation of the columnar organization of BD's simplified our study of cortical representation of target range, because we could rely on the uniformity of activity at different depths in the cortex. To gather data from many locations in the cortical plane, we inserted the electrode at a 30° angle into the FM processing area; neuronal responses were studied at 200-μm intervals. We plotted BD's of range-tuned neurons only on a surface map of the cerebral cortex that was drawn prior to the recordings.

The FM processing area consists of three major clusters: FM_1-FM_3, FM_1-FM_4, and FM_1-FM_2 facilitation neurons (*4*), which are usually arranged dorsal to ventral in that order (Fig. 1B). For each electrode penetration through those clusters in the rostrocaudal direction, BD systematically varied. Figure 1B gives a schematic representation of the iso-BD contour lines that comprise a target-range axis. Neurons with extremely short BD's were recorded only at the

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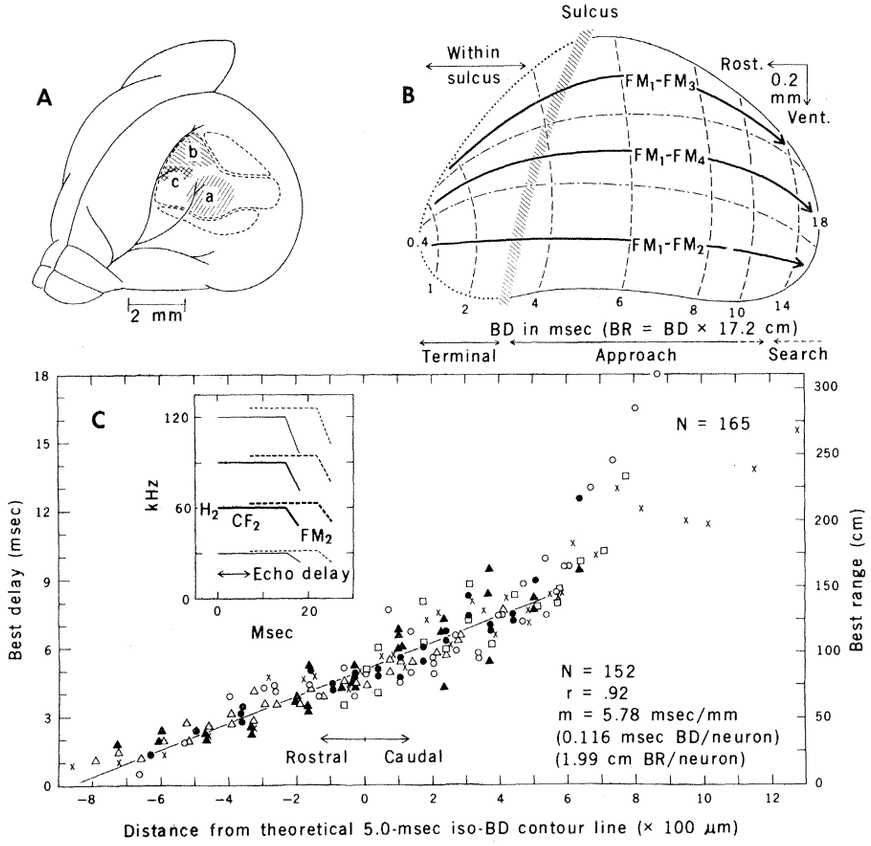
rostroventral part of the FM processing area. The shortest BD of a range-tuned neuron was 0.4 msec, corresponding to a target range of 6.9 cm. Neurons with very short BD's responded strongly to each paired stimulus even at a rate of 100 repetitions per second (the terminal phase). When BD was shorter than 2.0 msec, the FM component (2.0 msec) of the echo in the terminal phase overlapped that of the orientation sound. The delay-tuning curve for such a short BD is very sharp but nevertheless may cross the 0-msec delay line at 60 to 80 dB SPL. In that case, when the orientation sound is louder than 60 dB SPL, facilitation is evoked by the combination of different harmonics in the sound per se and is further augmented by an echo with a very short delay. Response latencies of range-tuned neurons to the echo FM are short—7 to 10 msec. Thus, the auditory cortex seems to be involved in information processing even in the terminal phase of echolocation.

Neurons with long BD's were recorded at the caudal part of the FM processing area (Fig. 1B). The longest BD obtained was 18 msec, corresponding to a target range of 310 cm. The delay-tuning curves of such neurons are broad, and they responded strongly to each paired stimulus only when delivered at the lower repetition rates characteristic of the search phase. The response was very poor at a rate of 40 repetitions per second and completely disappeared at 100 per second.

The role of such neurons in range discrimination may be limited because of their broad delay-tuning curves. The population of neurons with best delay longer than 10 msec is small. The central part of the FM processing area is occupied by neurons with BD's between 4 and 7 msec. Their delay-tuning curves are sharp and their responses are strong and clearly locked to each paired stimulus even at a rate of 100 repetitions per second. Neurons with BD's from 3 to 8 msec are distributed over a disproportionately large area. This suggests that processing of echoes from targets 50 to 140 cm away (the approach phase) is particularly important to the mustache bat.

Best delays were plotted as a function of distance from the 5.0-msec iso-BD contour line (Fig. 1C) (*10*). The correlation coefficient (r) for the BD's between 0 and 10 msec is .92 (N = 152). The slope (m) of the regression line is 5.78 msec BD per millimeter of cortical surface. Since the average interneuronal distance in the cortical plane of frozen sections of the brain is about 20 μm, adjacent neurons could express target range in 1.99-cm increments.

There is an interesting correspondence between these results and certain behav-



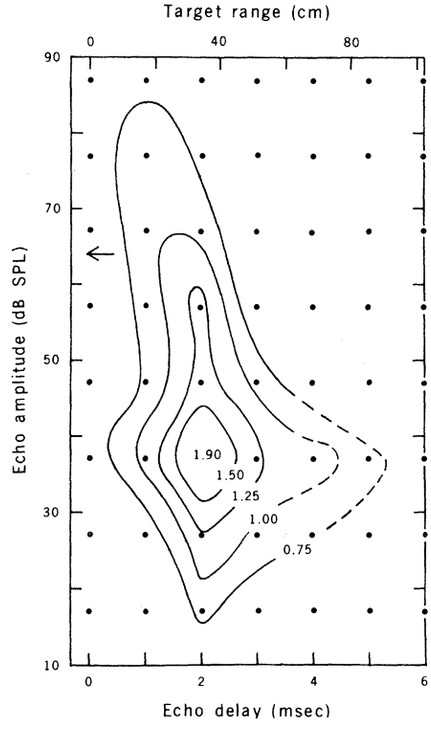


Fig. 1 (left). (A) The left cerebral hemisphere of the mustache bat showing (a) Doppler-shifted CF, (b) FM, and (c) CF/CF processing areas. (B) The FM processing area consists of three major clusters of delay-sensitive neurons: FM_1-FM_2, FM_1-FM_3, and FM_1-FM_4 facilitation neurons. Each cluster shows odotopic representation. Iso-BD contours and range axes are schematically shown by dashed lines and solid arrows, respectively. Best delays of 0.4 and 18 msec correspond to best ranges (BR's) of 7 and 310 cm. Range information in the search, approach, and terminal phases of echolocation is represented by activity at different loci in the cerebral hemisphere. (C) The relationship between BD (or BR) and distance along the cortical surface. The data were obtained from six cerebral hemispheres and are indicated by six different symbols. The regression line represents the average change in BD with distance. Since the 5-msec iso-BD contour line always crossed the central part of the FM processing area along the exposed surface of the cortex, the 5-msec BD on the regression line is used as a reference point to express distance (*10*). The inset is a schematized sonagram of an orientation sound and a Doppler-shifted echo in the approach phase of echolocation. Fig. 2 (right). Iso-impulse-count contours representing the response magnitude of range-tuned neuron plotted on the coordinates of echo amplitude against delay (or target range). Since the neuron was tuned to targets at a short distance, the orientation sound-echo pair for this plot was delivered at a repetition rate of 100 per second (terminal phase). Dots indicate where an average number of impulses per paired stimulus was obtained by presenting the identical paired stimulus 200 times. The contour lines are drawn on the basis of these data points. The dashed parts of the contour lines indicate where the responses were inflated by background noise associated with animal movement; *SPL*, sound pressure level.

ioral data. The little brown bat (*Myotes lucifugus*) begins the approach phase for wire obstacles 0.3 cm in diameter at an average distance of 225 cm (*11*), and the horseshoe bat (*Rhinolophus ferrumequinum*) compensates for Doppler-shifted echoes only when delayed less than an average of 17.5 msec (301 cm) (*12*). The finding that bats react when targets are closer than 301 cm corresponds to our finding that the range axis ends at about 310 cm. *Eptescius fuscus, Phyllostomus hastatus, Pteronotus suapurensis*, and *R. ferrumequinum* are all able to discriminate range differences of 1.2 to 2.5 cm at an absolute distance of 30 to 60 cm (*13*). This also corresponds to our finding if we assume that the rate of change in best range (1.99 cm per neuron) is the theoretical limit of just-noticeable difference in distance.

Delay-tuning curves themselves are sometimes insufficient to express the properties of range-tuned neurons and may even be misleading. Their responses are more appropriately expressed by iso-impulse-count contours plotted on coordinates of echo amplitude against delay. In Fig. 2, for instance, the neuron is clearly tuned to an echo of 37 dB SPL delayed by 2.1 msec. Range information is apparently processed by a series of such neural filters in both the time and amplitude domains, and as such they may be considered cross-correlators (*14*).

Odotopic representation is the term we use to describe the representation of target range by the location of neurons tuned to different BD's. This representation is the same regardless of wide variations in repetition rate (10 to 100 per second) and signal duration (7 to 34 msec). In the auditory system, the synthesis of a range axis, which has no corresponding anatomical precursor in the periphery, is suggestive of the methods by which sensory information may be extracted and displayed in the brain.

When many conspecific bats echolocate in a confined space, their many orientation sounds and echoes would impair odotopic representation unless some mechanism protected the system from jamming. The fundamental harmonic (H_1, particularly FM_1) of the orientation sound is always critical to the response of range-tuned neurons in spite of the fact that H_1 is always much weaker than the other harmonics and is sometimes barely detectable in laboratory recordings. This means that range-tuned neurons are probably not excited by combinations of orientation sounds and echoes produced by bats flying nearby. To excite range-tuned neurons, H_1 must stimulate the ears prior to an echo in spite of its weakness in the emitted sound. This implies that H_1 produced by the vocal cords stimulates the animal's own ears by bone conduction but is not emitted at a significant amplitude, possibly because of suppression by vocal-tract antiresonance. In nature, range-tuned neurons would be selectively excited only when the animal itself emits orientation sounds and echoes return after particular short delays. Jamming is thereby avoided in most situations.

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8. The best delay is the echo delay at which the minimum threshold for facilitation is obtained. Best delay corresponds to the best range of a neuron.
9. For mimicking orientation sounds and echoes (inset, Fig. 1C) (*4, 5*) in the three phases of echolocation, the repetition rate of paired stimuli and the durations of the CF and FM components of the signal were, respectively, 10 per second, 30 msec, and 4 msec (search phase); 40 per second, 15 msec, and 3 msec (approach phase); and 100 per second, 5 msec, and 2 msec (terminal phase). Synthesized echoes were independently varied in frequency, amplitude, and delay from the synthesized orientation sounds. To identify which combination of signal components was essential for excitation of neurons, both the synthesized orientation sounds and echoes were independently simplified by eliminating individual signal components.
10. The sulcus cannot be used as an anatomical reference line since iso-BD contour lines are neither straight nor parallel to it. In each oblique electrode penetration, BD's between 4 and 6 msec were recorded. Therefore, the data for each entire penetration were shifted to be in register with those values. The relative distances between individual data points within each penetration are not affected by this technique.
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Laser-EXAFS: Fast Extended X-ray Absorption Fine Structure Spectroscopy with a Single Pulse of Laser-Produced X-rays

Abstract. *The extended x-ray absorption fine structure (EXAFS) spectrum of aluminum has been measured with a nanosecond pulse of soft x-rays generated by a laser-produced plasma. This technique provides a practical alternative to synchrotron radiation for the acquisition of EXAFS data. It also provides a unique capability for the analysis of molecular structure in highly transient chemical species.*

Determining the identities and exact spatial arrangement of the atoms surrounding any particular atom in a molecule is fundamental to understanding the properties of any type of liquid, gas, or solid. In the case of materials with long-range order, such as perfect crystals, this information can often be obtained with x-ray or particle beam diffraction techniques. Such diffraction techniques rely on the fact that all of the atoms in a perfect lattice reside at fixed, periodic distances from any given atom, and that this periodicity is retained regardless of how far one moves within the lattice from the atom in question.

For materials without long-range order, the diffraction techniques are far less useful; one can determine local configurations in this way only for relatively simple molecules composed of a single element. For more complicated molecules, considerable insight can often be gained from optical spectroscopy and magnetic resonance techniques. However, these techniques have the drawback of providing only indirect evidence, from which the structural parameters of interest for a molecule must be inferred.

Many of these limitations can be overcome with the recently developed technique of extended x-ray absorption fine structure (EXAFS) spectroscopy (*1, 2*). In EXAFS spectroscopy, the x-ray absorption coefficient of a material is measured as a function of energy from the *K* edge or *L* edge of a specific element in the material to as far as 1000 eV above the edge. The absorption of x-rays by the element is accompanied by the ejection of photoelectrons, which can be scattered from neighboring atoms. Backscattering of these photoelectrons from atoms in the immediate vicinity of the absorbing atom gives rise to a periodic "wiggle" structure in the x-ray absorption spectrum (*1, 3, 4*). By analyzing this wiggle structure above the absorption

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