

Cortical representation of real and illusory sound sources

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Unilateral lesions of the auditory cortex lead to contralateral deficits in the accuracy of sound localization. Such observations have motivated several searches for a point-to-point cortical representation of auditory space. The generally broad spatial tuning of neurons has frustrated such searches. At moderate sound levels, spatial receptive fields often encompass the entire sound field, impeding efforts to assign preferred locations to particular neurons. As an alternative, we have examined systematic changes in neural response patterns within broad spatial receptive fields. We find that single neurons can signal the locations of sound sources throughout as much as 360° of auditory space (Middlebrooks et al., 1994; 1998; Xu et al., 1998) and that the accuracy of location signaling by small ensembles of neurons approaches that of behaving animals (Furukawa et al., 2000). This presentation will consider the cortical signaling of the locations of broadband sounds, which human listeners localize accurately, as well as the signaling of locations of sounds that, in humans, produce localization illusions.

We record unit activity in auditory cortical area A2 in anesthetized cats. We use multi-channel recording probes that permit simultaneous recordings of single- or multiple-unit spike activity at 16 sites. The probe contains recording sites spaced at $100\text{-}\mu\text{m}$ intervals along a line passing through the middle cortical layers. Noise-burst stimuli are presented from multiple loudspeakers, one loudspeaker at a time, positioned in the horizontal and vertical-midline planes, 1.2 m from the cat.

Figure 1 shows the responses of a single unit to broadband noise bursts presented from various locations in the horizontal plane. The three raster plots show spike patterns elicited by sounds at 20, 30, and 40 dB about the unit's threshold. At the lowest level, responses were elicited only by sources in the hemifield contralateral to the recording site, but the spatial receptive field expanded with increasing sound level to cover 360° of azimuth. The spike patterns of the unit varied in spike rate, latency, and temporal dispersion of latency as a function of sound-source level.

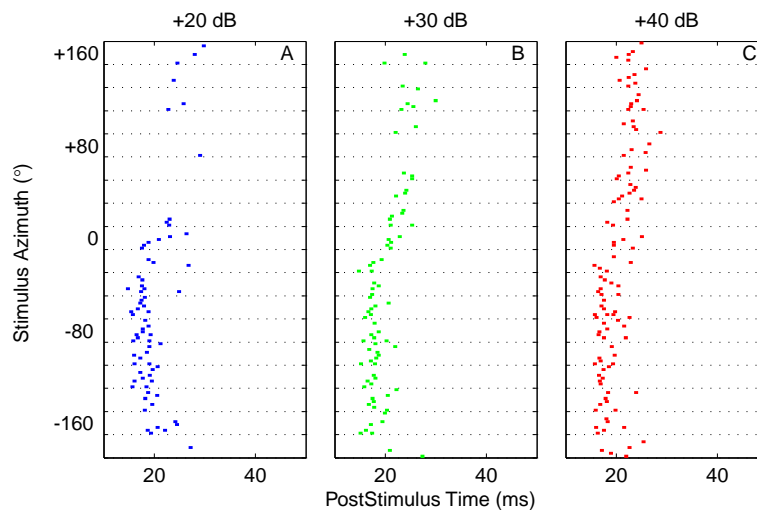


Figure 1

We have used artificial neural networks to recognize sound-location-specific spike patterns and, thereby, to estimate sound-source locations. We train a network with one set of spike patterns from a cortical neuron, then use the trained network to classify an independent set of spike patterns from the same neuron. In one study (Middlebrooks et al., 1998), location estimates were obtained under conditions in which sound-source locations varied throughout 360° of azimuth in 20° steps and sound levels varied from 20 to 40 dB above threshold. The median error for signaling of sound-source azimuth averaged around 45° , and all units showed median errors substantially smaller than the chance-performance level of 90° . Information about sound-source location is carried both by spike rates and by the timing of spikes. We computed the stimulus-related information transmitted by various uni-dimensional features of spike patterns (i.e., spike rates, first-spike latencies, and the dispersion of spike latencies) and by spike patterns that were manipulated to isolate selected features of neural responses (Furukawa and Middlebrooks, unpublished observations). Of the features that we tested, first-spike latencies typically transmitted more stimulus-related information than did spike rates. Moreover, in many cases, spike patterns showed no loss in stimulus-related information under conditions in which the patterns were truncated after the first spike.

Under several classes of experimental conditions, human subjects will report hearing a sound at a location at which there is no actual sound source. We have argued that a complete model of cortical sound representation should account for correct localization of sounds that subjects localize accurately (such as broadband noise bursts) and should account equally well for sound localization illusions. One such illusion is the phenomenon of summing localization, which is one of a class of phenomena known collectively as the precedence effect (Litovsky et al., 1999). When two brief sounds are presented in quick succession (typically <1 ms) from two locations, subjects report hearing a sound at the intermediate location. We recorded the responses of cortical neurons to similar paired stimuli. We trained an artificial neural network with spike patterns elicited by single sounds at various locations, then used the trained network to classify responses to the paired stimuli. The cortical responses closely followed the behavior of human subjects in that the location judgement was of an intermediate location that varied according to the inter-stimulus interval (Mickey and Middlebrooks, 2000).

A second class of localization illusions that we have examined pertains to spectral-shape cues for localization in the vertical and front/back dimension. The head and external ears filter a sound as it travels from the source to the ear canal. The filter functions vary with the angle of incidence of the sound, so the spectrum of the sound arriving at the tympanic membrane carries information about sound-source location. Such spectral-shape cues permit accurate vertical localization under conditions in which the sound source has a broad flat spectrum, but application of certain filters to the source results in systematic localization errors. When presented with $1/6$ octave noise bursts, human listeners reported well defined auditory images that varied in elevation according to the center frequency of the spectrum but were independent of the actual source location (Middlebrooks, 1992) (Fig. 2, upper panels). A computational model that incorporated the source spectra and the direction-dependent filter functions of listeners' ears accurately predicted those erroneous location judgements; in the figure, light colors indicate the model predictions and the symbols indicate actual location judgements. We tested the responses of cat cortical neurons to similar narrow-band sounds (Xu et al., 1999). An artificial neural network was trained with response patterns elicited by broadband sounds at various locations, then the trained network was used to classify responses to narrow-band sounds

(Fig. 2, lower panels). The computational model that predicted human location judgments was modified only by substituting the filter functions from the feline subjects. That model successfully predicted the elevations that were signaled by the cat cortical neurons in response to the narrow-band sounds.

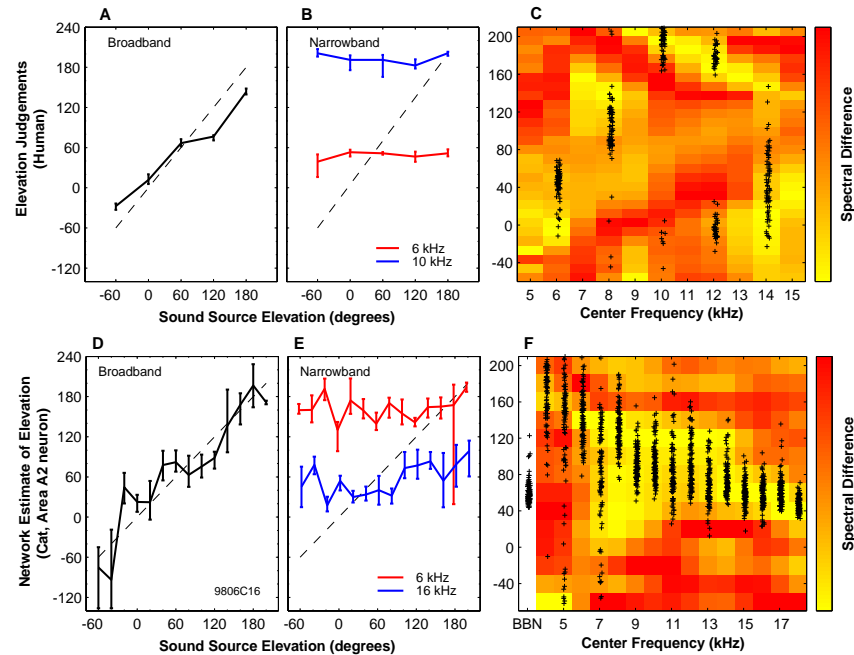


Figure 2

The results of these studies suggest that locations of sound sources are written in the auditory cortex in a syntax that incorporates both the magnitudes and temporal features of neural spike patterns. The accuracy of location coding succeeds and fails under conditions similar to those that in humans produce accurate or illusory location sensations.

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