

## Cortical Mechanisms for Auditory Spatial Illusions

LI XU, SHIGETO FURUKAWA and JOHN C. MIDDLEBROOKS

*From the Kresge Hearing Research Institute, Department of Otolaryngology, University of Michigan, Ann Arbor, Michigan, USA*

**Xu L, Furukawa S, Middlebrooks JC.** *Cortical mechanisms for auditory spatial illusions.* Acta Oto-Laryngologica 2000; 120: 263–266.

Frequency transformation by the external ears provides the spectral cues for localization of broadband sounds in the vertical plane. When human subjects listen to spectrally-impooverished narrowband sounds presented in a free field, the perceived locations vary with the centre frequency and are largely independent of the actual source locations. The present study explored the substrate of spatial illusion by examining the responses of cortical neurons to narrowband stimuli. Single-unit responses were recorded in area A2 of anaesthetized cats. Broadband noise bursts were presented at 14 locations in the vertical median plane, from 60° below the front horizon, up and over the head, to 20° below the rear horizon. Narrowband (1/6-oct) noise bursts were presented at +80° elevation. An artificial neural network was trained to recognize the spike patterns elicited by broadband noise and, thereby, to register the spike patterns with sound-source elevation. When the trained network was presented with neural responses elicited by narrowband noise, the elevation estimated by the neural network varied with the centre frequency of the narrowband stimuli. Consistent with psychophysical results in human, the locations associated with a given centre frequency could be predicted by comparing the stimulus spectrum with the directional transfer functions of the cat's external ear. The results support the hypothesis that full spike patterns (including spike counts and spike timing) of cortical neurons code information about sound location and that the auditory cortical neurons play a pivotal role in localization behaviour. *Key words: auditory cortex, cat, neural network, sound localization, spatial hearing, spectral-shape cues, vertical plane.*

### INTRODUCTION

The auditory cortex is essential for sound localization behaviour. Human patients with unilateral temporal lobe lesions have difficulties in localizing sounds from the side contralateral to the lesion (1–4). Experimental ablations of cat's auditory cortex also result in behaviour deficits in localization of sound sources presented on the side contralateral to the lesion (5). How sound location is represented in the auditory cortex is, however, a puzzling question. We have proposed that a distributed code exists for sound localization in the auditory cortex (6). The essence of the distributed code for sound localization is that the activity of individual neuron carries information about broad ranges of location and that accurate sound localization is derived from information that is distributed across large populations of neuron. Previous studies confirm that spike patterns (spike counts and spike timing) of the auditory cortical neurons carry information about sound-source location in both horizontal and vertical dimensions (6–8).

In order to localize sound accurately in the horizontal plane, a subject utilizes binaural cues of the incoming signal, i.e., the interaural time differences and interaural level differences. In the vertical plane, however, accurate localization relies on so-called "spectral-shape cues" that are provided by the differential filter properties of the external ears (see (9) for review). The spectra that result from filtering by the external ears vary according to the direction of incidence of a sound. Behavioural studies in both human and cat have shown that in order for the subjects to

utilize the spectral-shape cues to accurately localize sounds in the vertical plane and front/back dimension, the source spectra must be fairly broad in frequency (10–12). When source spectra are limited in bandwidth, localization based on spectral-shape cues is confounded and subjects make systematic errors in the vertical dimension (13, 14). Middlebrooks (14) has developed an acoustical model based on measurements of the filter characteristics of each subject's ears to predict successfully the subject's location judgements.

In the present study, we examined in cats the cortical neuronal responses to narrowband sounds that produce spatial illusions. We compared the erroneous locations signalled by the neural responses to narrowband sounds with those simulated with the acoustical model based on measurements of the filter functions of each cat's external ears.

### MATERIALS AND METHODS

Single-unit responses were recorded in the right auditory cortex area A2 of 8 adult cats under chloralose anaesthesia. Details of anaesthesia procedures and surgical preparation have been published previously (7). We used silicon-substrate thin-film multichannel recording probes to record unit activity. Each probe had 16 recording sites spaced at intervals of 100  $\mu\text{m}$  along a one-dimensional shank. Unit activity could be recorded simultaneously from up to 16 sites (15). Broadband noise of 80-ms duration were presented from 14 vertical midline loudspeakers spaced by 20°

ranged from 60° below the frontal horizon (−60°), up and over the top, to 20° below the rear horizon (+200°). All loudspeakers were 1.2 m from the animal's head at the centre of the chamber. The stimulus levels were 20 through 40 dB above each unit's threshold in 5-dB steps. A total of 40 trials was delivered for each combination of stimulus location and stimulus level; locations and levels were varied in a pseudo-random order. Narrowband stimuli were presented at +80° elevation. The narrowband noise had a flat centre 1/6-oct wide and skirts that fell off at 128 dB per octave. The centre frequencies of the narrowband noise stimuli varied from 5 to 18 kHz in 1-kHz steps. A total of 20 trials was delivered for each combination of centre frequency and stimulus level. Signals from the recording probe were amplified with a custom 16-channel amplifier, digitized and then stored on a PC hard disk. Off-line, we isolated unit activities from the digitized signal using custom spike-sorting software. Spike times were stored for further analysis.

Measurement of directional transfer functions (DTFs) of the external ears was carried out in each cat after the physiological experiment. A 0.5-inch probe microphone was inserted into the ear canal through an incision at the posterior base of the pinna. Recordings from the microphone in response to broadband noise were amplified, digitized and then subject to fast-Fourier-transformation analysis. Details of the procedure and characteristics of cat DTFs and inter-cat differences in DTFs are detailed in (16).

An artificial neural network algorithm was employed to map the cortical neuronal responses onto source elevations, as in our previous studies (6–8). The architecture of the network consisted of a 4-unit hidden layer with sigmoid transfer functions and a 2-unit linear output layer. The inputs to the neural network were spike density functions expressed in 1-ms time bins. Spike density functions or spike patterns were formed by averaging multiple samples of 8 responses to each stimulus; samples were drawn with replacement. Typically, we formed 20 such spike patterns from the odd-numbered trials of the neural responses to the broadband noise stimuli and used them to train the neural network. The trained network was then used to analyse 100 test spike patterns derived from either the even-numbered trials of the neural responses to broadband noise or the entire set of neural responses to narrowband noise. The two output units of the neural network produced the sine and cosine of the stimulus elevation, and the arctangent of the two

outputs gave a continuously varying output in elevation, i.e., the angle around the interaural axis.

## RESULTS

A total of 389 single units or unit clusters were recorded with 33 multichannel probe placements in auditory area A2 in 8 cats. All of the A2 units showed relatively broad frequency tuning, demonstrated by frequency tuning curves that were at least one octave wide at 40 dB above threshold. In response to broadband noise, A2 neurons typically fired one or a few spikes (action potentials) locked to the stimulus onset with latencies  $\geq 15$  ms. Their responses were not sharply selective for particular source elevations, that is, they showed broad elevation tuning. Nevertheless, units showed changes in the numbers and distribution of spikes and in the latencies of the spike patterns from one elevation to another. An example of the spike patterns of one representative unit (9808B05) in response to broadband noise is represented by a raster plot in Fig. 1A.

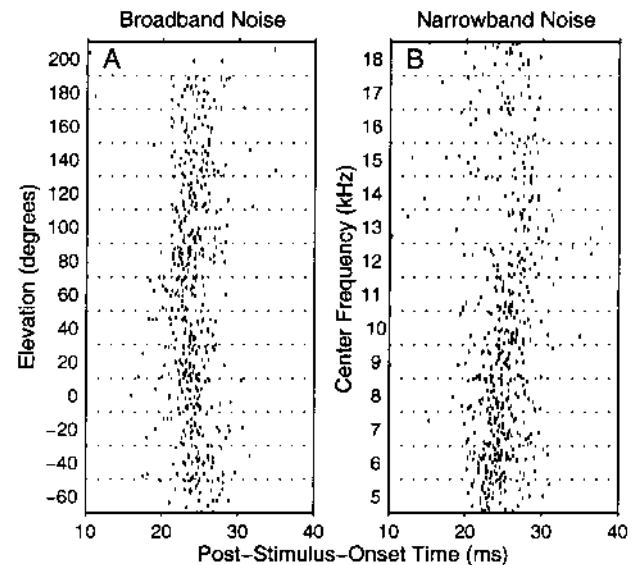


Fig. 1. Unit responses elicited by broadband and narrowband noise (unit 9808B05). (A) Raster plot of responses to broadband sounds presented from 14 locations in the median plane. Each vertical bar represents one spike from the unit. Each row of vertical bars represents the spike pattern recorded from one presentation of the stimulus at the location in elevation indicated along the vertical axis. Only 20 trials recorded at each elevation are plotted. Stimuli were 80 ms in duration starting at 0 ms and 40 dB above threshold. (B) Raster plot of responses to 1/6-oct narrowband noise with centre frequencies varying from 5 to 18 kHz. The narrowband centre frequencies are indicated along the vertical axis. Stimuli were 40 dB above threshold. A total of 20 trials recorded for each centre frequency are plotted.

As in our previous report (8), the elevations of broadband sound sources could be identified by artificial neural network recognition of unit spike patterns. In effect, the spike patterns could signal the elevations of sounds. The accuracy of elevation signalling varied among A2 units. A median error (median of unsigned error) of the neural-network estimates was used as a global measure of network performance. The network analysis of the spike patterns of the unit shown in Fig. 1A yielded a median error of  $30.1^\circ$ , which means that elevations signalled by half of the spike patterns of this neuron were within  $30^\circ$  of the actual targets. We selected the half of our sample of units with the lowest median errors for analysis of responses to narrowband sounds (194 units; median errors  $< 50.4^\circ$ ).

Responses to narrowband noise of A2 neurons varied considerably with the centre frequencies of narrowband sounds. Fig. 1B shows responses of the same unit (9808B05) to a narrowband source fixed at  $+80^\circ$  elevation and varying in centre frequency from 5 to 18 kHz. Note that both the magnitude and timing of spike patterns varied with stimulus centre frequency.

Fig. 2 shows the network estimate of elevation based on responses of unit 9808B05 to narrowband sounds that varied in centre frequency. The network was trained initially with spike patterns elicited by broadband noise and was then tested with spike patterns elicited by narrowband sounds. The grey-scale contour in Fig. 2 represents prediction of an acoustical model adapted from (14). In that model, stimulus spectra were compared quantitatively with the directional transfer functions (DTFs) of listener's external ears. In the present study, we adapted that model to the cat as a means of simulating individual cats' judgements of locations of narrowband sounds. The acoustical model was based on a metric (i.e., "spectral difference") that quantifies the difference between the narrowband noise spectra and the DTFs (17). White and light grey in Fig. 2 represent small spectral differences whereas dark grey and black represent large spectral differences. The model predicted that animal's judgement of a narrowband sound source would be biased towards elevations at which the spectral differences are small. Despite poor correspondence at 5 kHz, there was a clear tendency for the network estimates of elevation to fall at elevations in which small spectral differences were found. Across the sample of 194 A2 units, we identified that the correspondence of elevations signalled by neural responses to the model prediction was better for centre frequencies in the mid-frequency region (i.e., 11–16 kHz) that has been shown to be most important for vertical localization in cats (13, 17).

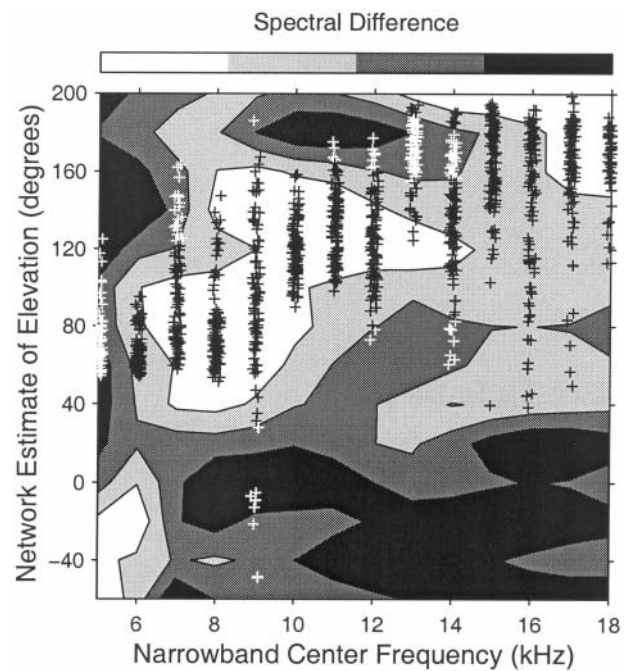


Fig. 2. Neural-network analysis of spike patterns elicited by narrowband noise. Data were from the same unit (9808B05) as is shown in Fig. 1. All narrowband stimuli were delivered at  $+80^\circ$  elevation. The abscissa represents the centre frequency of the narrowband noise and the ordinate represents the elevation in location. The grey-scale contour represents the magnitude of spectral differences between the external-ear transfer functions of this cat and the stimulus spectra. White and light grey represent small spectral difference and dark grey and black represent large spectral differences. Each plus sign (+) represents the network estimation of elevation for one spike patterns elicited by a narrowband sound. There are 100 network estimates for each narrowband centre frequency. Symbols that fall in regions with small spectral differences are plotted in black whereas those that fall in regions with large spectral differences are plotted in white. The network estimates of elevations for the narrowband noise data tended to fall to locations at which spectral differences were small.

## DISCUSSION

Our results confirm previous observations that the spike patterns of units in cortical area A2 can signal accurately the elevations of sound sources under conditions in which human subjects localize accurately, i.e., when source spectra are fairly broad and flat (8). The present study extended such observations into conditions in which accurate localization breaks down and human listeners make systematic errors.

In the procedure of neural network estimation, the neural network was trained to learn to recognize the spike patterns of broadband stimulation according to sound-source elevation. Then the network was used to classify the neural responses to narrowband noise stimulation of varying centre frequencies. We regard this procedure as a physiological analogue of a psy-

chophysical task requiring a listener to report the apparent location of a narrowband sound. By taking advantage of the acoustical model that successfully predicts human localization judgements of narrowband sounds (14), we could simulate the localization behaviour of cats based on spectral differences between the source spectra and the external-ear transfer functions of individual cats. Therefore, if the responses of cortical neurons are influenced by the narrowband stimulus in the same way as is the behaviour of the animal, the spike patterns elicited by narrowband noise of a particular centre frequency should resemble the spike patterns elicited by broadband noise at source elevations at which the spectral differences are small.

Under the condition of narrowband noise stimulation at fixed elevation, elevations signalled by the cortical neurons tend to show systematic errors. Those errors are predicted well by the acoustical model based on a comparison between the stimulus spectra and a template of the external-ear transfer functions. Therefore, the neurons' firing patterns might arise from a similar comparison. The results suggest that the neural mechanisms that lead to cortical responses in the cat's area A2 follow computational principles similar to those followed by the mechanisms that lead to human localization judgements.

#### ACKNOWLEDGMENTS

L. X. thanks Professor C. R. Pfaltz for guidance and support throughout the years. This research was funded by grants from NIH/NIDCD.

#### REFERENCES

- Greene TC. The ability to localize sound: a study of binaural hearing in patients with tumour of the brain. *Arch Surg* 1929; 18: 1825–41.
- Sanchez-Longo LP, Forster FM. Clinical significance of impairment of sound localization. *Neurol* 1958; 8: 119–25.
- Wortis SB, Pfeiffer AZ. Unilateral auditory-spatial agnosia. *J Nerv Ment Dis* 1948; 108: 181–6.
- Klingon GH, Bontecou DC. Localization in auditory space. *Neurol* 1966; 16: 879–86.
- Jenkins WM, Masterton RB. Sound localization: Effects of unilateral lesions in central auditory system. *J Neurophysiol* 1982; 47: 987–1016.
- Middlebrooks JC, Clock AE, Xu L, Green DM. A panoramic code for sound location by cortical neurons. *Science* 1994; 264: 842–4.
- Middlebrooks JC, Xu L, Eddins AC, Green DM. Codes for sound-source location in non-tonotopic auditory cortex. *J Neurophysiol* 1998; 80: 863–81.
- Xu L, Furukawa S, Middlebrooks JC. Sensitivity to sound-source elevation in non-tonotopic auditory cortex. *J Neurophysiol* 1998; 80: 882–94.
- Middlebrooks JC, Green DM. Sound localization by human listeners. *Ann Rev Psychol* 1991; 42: 135–59.
- Hebrank J, Wright D. Spectral cues used in the localization of sound sources on the median plane. *J Acoust Soc Am* 1974; 56: 1829–34.
- Makous JC, Middlebrooks JC. Two-dimensional sound localization by human listeners. *J Acoust Soc Am* 1990; 87: 2188–200.
- May BJ, Huang AY. Sound orientation behavior in cats. I. Localization of broadband noise. *J Acoust Soc Am* 1996; 100: 1059–69.
- Huang AY, May B. Sound orientation behavior in cats. II. Mid-frequency spectral cues for sound localization. *J Acoust Soc Am* 1996; 100: 1070–80.
- Middlebrooks JC. Narrow-band sound localization related to external ear acoustics. *J Acoust Soc Am* 1992; 92: 2607–24.
- Drake KL, Wise KD, Farraye J, Anderson DJ, Bement SL. Performance of planar multisite microprobes in recording extracellular single-unit intracortical activity. *IEEE Trans Biomed Engin* 1988; BME-35: 719–732.
- Xu L, Middlebrooks JC. Individual differences in external-ear transfer functions of cats. *J Acoust Soc Am* (in press).
- Xu L, Furukawa S, Middlebrooks JC. Auditory cortical responses in the cat to sounds that produce spatial illusions. *Nature* 1999; 399: 688–91.

Address for correspondence:

Li Xu, MD, PhD  
Kresge Hearing Research Institute  
Department of Otolaryngology  
University of Michigan  
1301 E. Ann St.  
Ann Arbor, MI 48109-0506  
USA  
Tel: +1 734 763 5159  
Fax: +1 734 764 0014  
E-mail: leehsu@umich.edu