Directionality Derived From Differential Sensitivity to Monaural and Binaural Cues in the Cat’s Medial Geniculate Body

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Samson, Frank K., Pascal Barone, W. Andrew Irons, Janine C. Clarey, Pierre Poirier, and Thomas J. Imig. Directionality derived from differential sensitivity to monaural and binaural cues in the cat’s medial geniculate body. J Neurophysiol 84: 1330–1345, 2000. Azimuth tuning of high-frequency neurons in the primary auditory cortex (AI) is known to depend on binaural disparity and monaural spectral (pinna) cues present in broadband noise bursts. Single-unit response patterns differ according to binaural interactions, strength of monaural excitatory input from each ear, and azimuth sensitivity to monaural stimulation. The latter characteristic has been used as a gauge of neural sensitivity to monaural spectral directional cues. Azimuth sensitivity may depend predominantly on binaural disparity cues, exclusively on monaural spectral cues, or on both. The primary goal of this study was to determine whether each cortical response pattern corresponds to a similar pattern in the medial geniculate body (MGB) or whether some patterns are unique to the cortex. Single-unit responses were recorded from the ventral nucleus (Vn) and lateral part of the posterior group of thalamic nuclei (Po), tonotopic subdivisions of the MGB. Responses to free-field presentation of noise bursts that varied in azimuth and sound pressure level were obtained using methods identical to those used previously in field AI. Many units were azimuth sensitive, i.e., they responded well at some azimuths, and poorly, if at all, at others. These were studied further by obtaining responses to monaural noise stimulation, approximated by reversible plugging of one ear. Monaural directional (MD) cells were sensitive to the azimuth of monaural noise stimulation, whereas binaural directional (BD) cells were either insensitive to its azimuth or monaurally unresponsive. Thus BD and MD cells show differential sensitivity to monaural spectral cues. Monaural azimuth sensitivity could not be used to interpret the spectral sensitivity of predominantly binaural cells that exhibited strong binaural facilitation because they were either unresponsive or poorly responsive to monaural stimulation. The available evidence suggests that some such cells are sensitive to spectral cues. The results do not indicate the presence of any response types in AI that are not present in the MGB. Vn and Po contain similar classes of MD and BD cells. Because Po neurons project to the anterior auditory field, neurons in this cortical area also are likely to exhibit differential sensitivity to binaural disparity and monaural spectral cues. Comparison of these MGB data with a published report of cochlear nucleus (CN) single-unit azimuth tuning shows that MGB sensitivity to spectral cues is considerably stronger than CN sensitivity.

INTRODUCTION

Sound localization is important for survival, and neural mechanisms have evolved that utilize two available acoustic cues for location. Binaural time and level disparities are available to the brain as a consequence of the separation of the two ears on either side of the head, and they are most important for left-right (azimuth) localization. Spectral (pinna) cues derive from diffraction of high-frequency broadband sounds primarily with the pinna and are most important for up-down (vertical, elevation) and front-back localization (Middlebrooks and Green 1991).

Many neurons in the cat’s central auditory system are sensitive to the azimuthal direction of noise bursts. They respond well to some sound directions and poorly to others over a broad range of sound pressure level (SPL) (Aitkin and Martin 1987; Barone et al. 1996; Clarey et al. 1992, 1995; Imig et al. 1990; Rajan et al. 1990). Single-unit azimuth tuning in the primary auditory cortex (AI) has been shown to depend on binaural disparity and monaural spectral cues (Samson et al. 1993, 1994). Whether cortical neurons’ response patterns reflect input from medial geniculate body (MGB) neurons with similar response patterns or are unique to the cortex is not completely understood. A major goal of this report is to analyze mechanisms underlying azimuth sensitivity in the MGB. This will allow comparison of neural response properties at these two levels of the auditory forebrain.

Cortical field AI receives ascending input from several subdivisions of the MGB, including two tonotopic regions, the ventral nucleus (Vn) and the lateral part of the posterior group of thalamic nuclei (Po) (Imig and Morel 1985a,b). These are major and minor sources of input to AI, respectively, judging from the number of neurons in each structure that is labeled by cortical injections of horseradish peroxidase (Andersen et al. 1980; Morel and Imig 1987). A large proportion of high (>4 kHz) best-frequency (BF) neurons in Vn and Po is azimuth sensitive (Barone et al. 1996), and in some cases this has been shown to derive from monaural spectral inhibition (Clarey et al. 1995; Imig et al. 1997). In other cases azimuth sensitivity depends on binaural mechanisms (Clarey et al. 1995), consistent with results of dichotic stimulation studies (Adrian et al. 1966; Aitkin 1973; Aitkin and Dunlop 1968; Aitkin and Webster 1972; Altman et al. 1970; Ivarsson et al. 1988). Nevertheless monaural and binaural response patterns of azimuth-sensitive MGB neurons have not been described in detail so the extent to which they differ from those in field AI is unknown.

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Neurons in Vn and Po provide a massive source of ascending input not only to cortical field AI but also to the anterior auditory field (AAF). AI receives input predominantly from the rostral part of Vn, and AAF receives input predominantly from Po (Andersen et al. 1980; Morel and Imig 1987). Consequently, information regarding directional mechanisms in Vn and Po neurons provides important clues regarding directional mechanisms in these two cortical fields. Finally, monaural spectral inhibition contributes to azimuth sensitivity of CN neurons, especially those in the dorsal cochlear nucleus (DCN) (Imig et al. 2000). We shall compare the effect of monaural spectral inhibition on the azimuth sensitivity and tuning of DCN and MGB neurons to determine how spectral inhibition changes between the DCN and the MGB. Some of these results have been published in preliminary form (Samson et al. 1996).

**METHODS**

Single-unit recordings were obtained from the left MGB of 18 cats with clean external ears and normal thresholds estimated from unit responses. All husbandry and experimental procedures were carried out according to National Institutes of Health guidelines and using protocols approved by the Institutional Animal Care and Use Committee of the Kansas University Medical Center. Chronic recording procedures were used in 14 cats and acute recording procedures for the remainder. Acute recording procedures have been described in detail elsewhere (Barone et al. 1996).

Surgical implant of a chronic recording chamber was carried out using inhalation anesthesia (0.8–1.5% isoflurane in O2) and standard aseptic procedures under veterinary supervision. Postoperative discomfort was ameliorated with analgesics. A stainless steel recording chamber was stereotaxically positioned over a craniotomy and fastened to the skull with dental acrylic and stainless steel screws. A stainless steel tube, used to secure the animal’s head to a support rod during recording sessions, was attached to the chamber. The chamber was sealed with a stainless steel cap at times other than during recording sessions to prevent movements. Anesthesia was induced with isoflurane in O2 and atropine (0.1 mg/kg im) was injected. Isoflurane was replaced with pentobarbital sodium, which was maintained throughout the recording session with an intravenous infusion pump at a rate sufficient to eliminate pinna reflexes and spontaneous movements (~8.5 mg·kg⁻¹·h⁻¹). Dexamethasone (2 mg/kg iv) was injected to reduce the possibility of cerebral edema. Application of ophthalmic ointment prevented corneal drying. Tracheal intubation ensured a patent airway. Breathing and heart rates were monitored during the recording session, and temperature was maintained at 38°C using a thermostatically controlled heating pad. Following the record-

**FIG. 1.** A BD-EL unit (9408-20) that received excitatory input from the contralateral ear and inhibitory input from the ipsilateral ear. The recording site was located in posterior group of thalamic nuclei (Po). A: azimuth-level response area (ALRA) for binaural noise stimulation. B: ALRA for contralateral monaural noise stimulation. An ALRA displays normalized response magnitude (% of maximum) as a joint function of azimuth and sound pressure level (SPL). Azimuth representation: 0°, median plane in front of the head; ±180°, median plane behind the head; ±90°, contralateral (right) pole; −90°, ipsilateral (left) pole. Small squares indicate azimuths and SPLs of the stimuli used during data collection. Lightest to darkest shaded areas represent responses that are ≥5, ≥25, ≥50, and ≥75% of maximum response, respectively. Diamonds indicate maximum (100%) response. Maximum responses in A and B were 1.2 and 1.3 spikes/stimulus, respectively. C: gross responses for binaural (B-stim) and contralateral monaural stimulation (C-stim) are plotted as a function of azimuth. Gross responses were obtained by averaging over SPL, and identical SPLs were used for each function. Numbers indicate the sequential order of data collection. ANOVA revealed significant overall ($P_{F} = 0.0001$) and azimuth-dependent ($P_{TA} = 0.0001$) differences between binaural and contralateral monaural responses. Post hoc Fisher exact probability tests revealed that binaural responses were significantly smaller than contralateral monaural responses at azimuth-SPL combinations indicated by circled minus signs in A ($P = 0.0001$; corrected $\alpha = 0.05/48 = 0.001$).

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Cats were allowed to recover fully from the surgery before the first recording session, and thereafter recording sessions were scheduled at 2-wk or longer intervals. Animals were anesthetized during chronic recording sessions to prevent movements. Anesthesia was induced with isoflurane in O2 and atropine (0.1 mg/kg im) was injected. Isoflurane was replaced with pentobarbital sodium, which was maintained throughout the recording session with an intravenous infusion pump at a rate sufficient to eliminate pinna reflexes and spontaneous movements (~8.5 mg·kg⁻¹·h⁻¹). Dexamethasone (2 mg/kg iv) was injected to reduce the possibility of cerebral edema. Application of ophthalmic ointment prevented corneal drying. Tracheal intubation ensured a patent airway. Breathing and heart rates were monitored during the recording session, and temperature was maintained at 38°C using a thermostatically controlled heating pad. Following the record-

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**FIG. 2.** Normalized gross response (GR) as a function of azimuth, showing measures of azimuth sensitivity (modulation), width of tuning (PAR, preferred azimuth range), and azimuth preference (BA, best azimuth). Azimuth function modulation is the difference between the maximum and minimum azimuth function values. The PAR is the azimuth range measured at 75% of maximum response using linear interpolation. The BA is the azimuth of the PAR's midpoint.
During the recording session, animals were kept warm until they awakened from the anesthesia. Marking lesions were placed during terminal recording sessions for histological localization of recording sites. Each animal was given a lethal dose of anesthetic at the end of the terminal recording session and perfused through the heart with a 10% solution of formol saline. Brain sections 50-μm thick were cut frozen in the transverse plane and were stained with cresyl violet.

Recordings were carried out in an electrically shielded, quasi-anechoic, sound-isolation chamber (Imig et al. 1990; Samson et al. 1993, 1994). The anesthetized cat rested in a sling with its head rigidly fixed. The head was positioned with the horizontal Horsley-Clarke plane tilting forward and down at an angle of ~18° from horizontal, which approximates the head position of an alert cat looking forward. The ears were pulled to an upright position using strings that were glued to the outer surfaces of each pinna. Sterility was maintained within the recording chamber throughout the procedure. Paralene-insulated tungsten microelectrodes (Frederick Haer) with nominal impedance between 1 and 4 MΩ (measured in the brain) were advanced by a hydraulic micromanipulator controlled from outside the sound chamber. Electrode penetrations were oriented perpendicular to the Horsley-Clarke horizontal plane.

Single-unit waveforms were isolated using an amplitude-window discriminator. Times of occurrence of action potentials were stored in computer disk files, with a resolution of 10 μs, for later analysis. A time window was used to reduce the effect of spontaneous discharge on the response of some neurons.

A semicircular array of 13 loudspeakers (Radio Shack 40-1310B) with similar frequency response characteristics provided free-field sound stimulation (Imig et al. 1997). These were spaced at 15° intervals in the horizontal plane that intersected the interaural axis. Loudspeakers had a usable frequency range between 4 and 40 kHz. Sound direction could be varied by presenting sound from different loudspeakers or by rotating the array. Stimulus generation, loudspeaker switching, stimulus sequencing, and data collection were controlled by a PDP 11/73 computer (Imig et al. 1997; Samson et al. 1993, 1994). The noise waveform was an electrical signal with a flat...

**FIG. 3.** Examples of binaural directional cells showing binaural facilitation and inhibition (BD-FI) with lateral and midline azimuth preferences. Left column. This unit (9504-06) received excitatory input from the contralateral ear, and was recorded in Po. A: ALRA for binaural noise stimulation (maximum response was 5.7 spikes/stimulus). B: ALRA for contralateral monaural noise stimulation (maximum response was 3.7 spikes/stimulus). C: azimuth functions for binaural (B-stim) and contralateral monaural (C-stim) noise stimulation. ANOVA revealed significant azimuth-dependent differences between binaural and contralateral monaural responses ($P_T < 0.05$). Post hoc Fisher exact probability tests revealed that binaural responses were significantly smaller than contralateral monaural responses at some azimuth-level combinations (A, −) and significantly larger at others (A, +; $P < 0.0005$, corrected $\alpha = 0.05/28 = 0.0018$). Right: this unit (9317-08) received excitatory input from the contralateral ear and was recorded in ventral nucleus (Vn). D: ALRA for binaural noise stimulation (maximum response was 5.5 spikes/stimulus). E: ALRA for contralateral monaural noise stimulation (maximum response was 2.1 spikes/stimulus). F: azimuth functions for binaural (B-stim), contralateral monaural (C-stim), and ipsilateral monaural (I-stim) noise stimulation. ANOVA revealed significant overall and azimuth-dependent differences between binaural and contralateral monaural responses ($P_T < 0.02$, $P_{TA} < 0.0001$). Post hoc Fisher exact probability tests and $\chi^2$ tests revealed that binaural responses were significantly smaller than contralateral monaural responses at some azimuth-level combinations (D, −) and significantly larger at others (D, +; $P < 0.0016$, corrected $\alpha = 0.05/28 = 0.0018$).
MECHANISMS OF DIRECTIONAL SENSITIVITY IN THE MGB

RESULTS

The MGB sample consisted of 98 well-isolated, azimuth-sensitive (defined in the following text), single-unit waveforms (equivalently referred to as units, cells, or neurons) with BF's between 5 and 37 kHz. Units responded to noise bursts with one or a few spikes (a burst of spikes in a few cases), and at minimal latencies of 4.7–32.7 ms [10.2 ± 3.7 (SD) ms]. Five units also exhibited long latency responses in the range of 43–200 ms, but these long-latency responses are not included in this analysis. Once a unit was isolated, noise bursts were presented from one of seven equally spaced azimuths in the frontal hemifield (±90, ±60, ±30, and 0°) and occasionally at 15° intervals or behind the head. At each azimuth, stimulus level was typically varied between 0–80 dB SPL in 10- or 20-dB steps. Spike counts for 10 or 20 stimulus repetitions were normalized and displayed as an azimuth-level response function (ALRA, e.g., Fig. 1A). The actual spectrum of the noise delivered to the animal was shaped by the sound-generation system (mainly the loudspeaker). Noise bursts were presented at a repetition rate of 3 Hz and at 30° intervals across the frontal hemifield. At each azimuth, noise bursts were presented that ranged from 0 to 80 dB sound pressure level (SPL) in 20-dB steps. Single- and multi-unit BF's (the midpoint of the frequency range that excited units at 10–20 dB above lowest threshold) were assessed regularly to ensure that the electrode was located in a high-frequency representation. Tone- and noise-bursts had a duration of 50 ms with 5-ms linear rise-fall times. Frequency response areas were obtained for most units using 10 stimulus repetitions at each frequency-SPL combination. Tone bursts were presented that varied in frequency (one-quarter or one-eighth octave steps between 4 and 40 kHz) and level (10- to 20-dB steps from near threshold to 80 dB SPL).

Monaural stimulation was approximated by using an ear plug (ear mold impression material, All American Lab.) to attenuate sound reaching one ear. Attenuation varied between 32 and 70 dB in the range of 4–32 kHz, between 35 and 55 dB at 2 kHz and 25 dB at 1 kHz (Samson et al. 1993, 1994).

Single-unit spike counts were compared statistically to determine whether ear plugging had a significant effect. Differences across all azimuth-SPL combinations between binaural and monaural responses were detected by ANOVA on the ranks, in which the total number of spikes obtained after 10 (occasionally 20) stimulus presentations at each azimuth-SPL combination was entered as one response. If ANOVA revealed significant differences, a post hoc χ² or a Fisher exact probability test was applied to determine the azimuth-SPL combinations at which differences existed. For each azimuth-SPL combination, these tests compared the number of stimulus presentations to which the cell was unresponsive, responded with one spike, or responded with more than one spike. A Bonferroni correction of the significance level (α) was used to control the error rate for multiple comparisons (corrected α = uncorrected α/number of comparisons). If no duplicated data sets were available (i.e., ANOVA was inapplicable), χ² or Fisher exact probability tests were directly applied in the same fashion of the post hoc tests. Details about statistical analysis can be found elsewhere (Samson et al. 1993, 1994).

Some of this work represents part of the PhD research conducted by W. A. Irons.

FIG. 4. A BD-FI unit (9408-59) exhibited binaural facilitation at the midline and flanking binaural inhibition. The recording site was located in Vm A: ALRA for binaural noise stimulation (maximum response was 2.0 spikes/stimulus). B: ALRA for contralateral monaural noise stimulation (maximum response was 2.2 spikes/stimulus). C: azimuth functions for binaural (B-stim) and contralateral monaural (C-stim) noise stimulation. ANOVA revealed significant overall differences between B-stim and C-stim responses and significant interaction terms (P< 0.04, P< 0.0001, P< 0.01, P< 0.0001). Post hoc tests revealed that binaural responses were significantly larger than contralateral responses at 0° (χ² test, P< 0.0001; corrected α = 0.05/42 = 0.0012) and significantly smaller than contralateral monaural responses at −60 and +60° (Fisher exact probability test, P< 0.0011; corrected α = 0.05/42 = 0.0012) as indicated by circled plus and minus signs, respectively, in A.

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In searching for single-unit responses, azimuth and SPL were systematically varied to increase the chance of exciting cells that might be selective to narrow ranges of azimuth and/or level. Sounds were sequentially presented at a repetition rate of 3 Hz and at 30° intervals across the frontal hemifield. At each azimuth, noise bursts were presented that ranged from 0 to 80 dB sound pressure level (SPL) in 20-dB steps. Single- and multi-unit BF's (the midpoints of the frequency range that excited units at 10–20 dB above lowest threshold) were assessed regularly to ensure that the electrode was located in a high-frequency representation. Tone- and noise-bursts had a duration of 50 ms with 5-ms linear rise-fall times. Frequency response areas were obtained for most units using 10 stimulus repetitions at each frequency-SPL combination.
monaural and binaural stimulation revealed the presence of binaural interactions, monaural excitatory inputs, and whether azimuth tuning (azimuth sensitivity and azimuth function shape) was dependent on monaural stimulation, binaural stimulation, or both.

Azimuth tuning of binaural directional (BD) cells depended predominantly on binaural stimulation. The vast majority was either insensitive to the azimuth of monaural noise bursts, i.e., responded well at each direction, or failed to respond to monaural stimulation. Three BD response classes were distinguished depending on whether cells exhibited inhibitory, facilitatory, or mixed binaural interactions. One class was composed of BD-EI cells \( n = 33 \) that received excitatory input from one ear (usually the contralateral) and inhibitory input from the other, i.e., they exhibited binaural inhibition. Their responses to noise bursts were confined mainly to one lateral hemifield, as is the case for the example shown in Fig. 1. This unit was contralateral preferring, i.e., it exhibited lowest thresholds and highest discharge rates to contralateral sound directions (B-stim, A and C). It responded well to monaural contralateral noise bursts at each azimuth (C-stim, B and C). Greater monaural than binaural responsiveness at ipsilateral
locations indicated that stimulation of the ipsilateral ear had an inhibitory effect. Azimuth-SPL combinations at which binaural responses were significantly smaller than monaural responses are indicated by circled minus signs in A. Eighteen of 33 BD-EI cells were studied using monaural stimulation of each ear, and they were excited only by stimulation of the ear on the preferred side. For the remainder, monaural responses were obtained only to stimulation of the ear on the preferred side.

A second response class was composed of BD-FI cells (n = 18) that exhibited both binaural facilitation and inhibition. They varied in azimuth preference, and examples of lateral and midline preferring cells are shown in Fig. 3. The left column shows the binaural response of a contralateral preferring cell (A) with a contralateral monaural response that was insensitive to azimuth (B). The cell was more responsive to binaural than to monaural stimulation throughout the contralateral quadrant, revealing the presence of binaural facilitation, and was less responsive to binaural than to monaural stimulation throughout the ipsilateral quadrant, revealing the presence of binaural inhibition (C). Circled plus and minus signs (A) indicate azimuth-SPL combinations for which binaural responses were significantly larger or smaller than monaural responses, respectively. The cell in the Fig. 3, right, was most responsive to binaural noise stimulation presented from the frontal midline (D). Contralateral monaural noise stimulation produced a weak, azimuth-insensitive response (E and F). The unit was unresponsive to ipsilateral monaural stimulation (F). ANOVA revealed overall and azimuth-dependent significant differences between binaural and ipsilateral monaural responses (P<0.0001, P<0.0001, P<0.0002). Circled plus signs in A show azimuth-SPL combinations that exhibited statistically significant binaural facilitation (Fisher exact probability test, P<0.0017, corrected α = 0.05/28 = 0.0018).

Most BD-FI cells (14/18) exhibited inhibition only on one side of the midline (e.g., Fig. 3), but a few (4/18) exhibited inhibition on both sides. The example in Fig. 4A showed greatest responsiveness and lowest thresholds to binaural stimulation at the midline. The cell was insensitive (<75% modulation) to the azimuth of contralateral monaural stimulation (B and C), and exhibited high-threshold responses to monaural...
ipsilateral stimulation (C). High-threshold responses to monaural stimulation were not uncommon, and we assume that they were usually, if not always, a result of leakage of sound through the ear plug. The midline response peak in this cell was created by a combination of facilitation and flanking inhibition (A and C).

Ten of the 18 BD-FI units were tested with monaural stimulation of each ear, and in each stimulation of the ear on the preferred side was excitatory. Stimulation of the other ear produced little or no excitation; no response in 6/10 cases, high-threshold responses in 3/10 cases, and a weak low-threshold response in 1 case. Monaural responses were obtained only to stimulation of the ear on the preferred side for the remainder of the sample.

A third response class was composed of BD-F cells (n = 14) that exhibited binaural facilitation in the absence of inhibition. This group included nine predominantly binaural cells (Kitzes et al. 1980) that were unresponsive to monaural stimulation or exhibited high-threshold monaural responses and five cells that exhibited low-threshold, weak monaural responses to stimulation of each ear (n = 3), only the ipsilateral ear (n = 1), or only the contralateral ear (n = 1). Predominantly binaural (PB) cells varied in azimuth preference and selectivity. Two of them were responsive only at near midline locations, one of which is shown in Fig. 5 (A and B). Other PB cells exhibited lowest thresholds at or near the midline but also responded at more lateral directions (e.g., C–F). Monaurally responsive BD-F cells also varied in azimuth preference. Figure 6A shows the binaural response of one cell that was most responsive and had lowest thresholds near the midline and was responsive to monaural stimulation of each ear (B and C). The cell was considerably less responsive to monaural than to binaural stimulation (D). An example of a monaurally responsive, midline-prefering cell is shown in the Fig. 6, right. The cell’s binaural response was somewhat variable as seen by comparison of two ALRAs that were collected before (E) and after ear plugging (F). In both cases, the gross response was maximal at the midline and decreased in magnitude toward each lateral pole (B-stim, H). There was a weak response to monaural ipsilateral stimulation but not to contralateral monaural stimulation. The ipsilateral monaural response occurred at a low threshold and showed a central field azimuth preference somewhat similar to that of the binaural response.

The monaural responses of the two units illustrated in Fig. 6 exhibit azimuth sensitivity that may derive from monaural spectral cues. The ipsilateral monaural response of the lateral-prefering unit (C) would have met the 75% criterion for azimuth sensitivity if the high-threshold response, which presumably reflects leakage through the contralateral ear plug, were eliminated from the GR average. The ipsilateral monaural response of the midline preferring unit (I-stim, Fig. 6, G and H) clearly meets the 75% criterion for azimuthal sensitivity. In both cases, there is a similarity between the azimuth preference of the monaural and binaural responses, suggesting that sensitivity to monaural spectral cues may play a role in shaping these responses. Arguably, these should have been classified as monaural directional (MD) rather than BD cells as discussed later.

The directions at which a cell’s binaural responses were largest and occurred at lowest thresholds define its azimuth preference. Azimuth preferences of BD cells differed among response classes. The azimuth at which lowest threshold response occurred (e.g., 0°, Fig. 5A) was measured for each cell. Lowest thresholds for BD-EI cells were located furthest from the midline, those for BD-F cells were closest to the midline,
and those for BD-FI cells were in between (Fig. 7, left). Azimuth preferences for ipsilateral preferring cells were left/right reversed so that positive angles represent locations on the preferred side. The mean lowest threshold azimuth for the BD-EI class was significantly different from that for the BD-FI and BD-F classes (Fig. 7, legend). A second measure of azimuth preference was the best azimuth (BA, Fig. 2) which is based on response magnitude. The mean BA for BD-EI cells was located furthest from the midline, that for BD-F cells was closest to the midline, and that for BD-FI cells was in between (Fig. 7, right). Means for the three groups were significantly different from each other (Fig. 7, legend). The BA distributions are similar to lowest threshold azimuth distributions.

MD cells were distinguished from BD cells by their greater sensitivity to the azimuth of monaural noise bursts and composed about one-third of the azimuth-sensitive sample (30/98). These cells responded well to monaural stimulation at some azimuths and poorly or not at all at others. The largest MD response class was composed of MD-E0 cells (n = 18) that were strictly monaural in the sense that their monaural and binaural responses were statistically indistinguishable. An example of such a cell is shown in Fig. 8. The unit was most responsive at 60° and least responsive at 30°. Differences between monaural and binaural responses were not significant, suggesting that azimuth tuning depended exclusively on stimulation of the contralateral ear. Responsiveness to stimulation of the other ear was not tested as was the case for most MD-E0 cells. However, four MD-E0 cells were tested using monaural stimulation of each ear, and each cell was found to be strictly monaural.

A second MD response class was composed of MD-EI cells (n = 10) that exhibited binaural inhibition. Figure 9A shows an example whose binaural response was centered in the contralateral rear quadrant. It also exhibited a contralateral monaural response restricted to the same location (B). Nevertheless ipsilateral ear plugging caused an increase in responsiveness throughout the ipsilateral hemifield indicating that stimulation of the ipsilateral ear was inhibitory (C). One MD-EI cell was studied using monaural stimulation of each ear, and it was excited only by stimulation of the contralateral ear. All others were studied using monaural stimulation of only one ear.

The role of binaural inhibition in shaping azimuth tuning varied among MD-EI cells. The shape of the response peak of the MD-EI cell shown in Fig. 9, left, depended only on monaural directional cues. Response peaks of other MD-EI cells depended on both monaural and binaural cues. The right border of the response peak in Fig. 9, right, was nearly identical under monaural and binaural conditions, indicating that it depended only on monaural cues. On the other hand, an increase in ipsilateral responsiveness under monaural conditions caused a decrease in the slope of the left border (C-stim, F), indicating that it was shaped by both monaural and binaural cues.

A third MD response class was composed of two MD-F cells that exhibited binaural facilitation, and one is shown in Fig. 10. This cell exhibited a response peak in the contralateral frontal quadrant (A), and the pattern of its contralateral monaural response (B) was indistinguishable from that of its binaural response, indicating that the cell derived azimuth tuning from monaural cues at the contralateral ear. However, the response peak was over twice as large to binaural than to contralateral monaural stimulation (C), showing that stimulation of the ipsilateral ear facilitated the response. The hemifield azimuth tuning of this cell to binaural tonal stimulation (not shown) suggested that it received inhibitory input from the ipsilateral ear. Nevertheless contralateral monaural responses were not recorded in the ipsilateral frontal field, so it is unclear whether or not this cell would exhibit binaural inhibition to noise stimulation.

A MD-F cell with different characteristics is shown in Fig. 11. Unlike any BD cell but like a few MD-E0 cells, this cell was most responsive to sound directions on the side of the head contralateral to the ear that provided monaural excitatory drive (A). Its contralateral monaural azimuth tuning was similar to its binaural azimuth tuning (B). This showed that the cell derived azimuth sensitivity from monaural cues at the contralateral ear. The cell exhibited high-threshold responses to monaural stimulation of the ipsilateral ear (C). It was considerably more responsive to binaural than to monaural stimulation of either ear (A and D), revealing binaural facilitation.
Patterns of azimuth tuning dependent on monaural spectral cues varied greatly among MD cells. This variety can be appreciated in the monaural responses of MD-EI and MD-F cells and in the monaural or binaural (equivalent to monaural) responses of MD-E0 cells. Many cells exhibited focal responses. Response peaks for contralaterally excited cells could be appreciated in the monaural responses of MD-EI and MD-F cells and in the monaural or binaural (equivalent to monaural) responses of MD-E0 cells. Many cells exhibited focal response peaks. These examples show that spectral inhibition, which shapes the azimuth modulation, reflects not only azimuth-dependent differences in NTR but also function profiles for the two data sets are quite different, suggesting that random fluctuation in excitability, not sound shadowing, is a major contributor to modulation. In contrast to this example, many MD cells were completely unresponsive at some azimuths (Fig. 12A).

MD/BD classification of many cells was based on monaural GR azimuth function modulation. An advantage of using GR modulation is that it allows straightforward comparison of the present MGB results with previous work in cortical field AI where GR modulation was also used to distinguish MD and BD responses (Samson et al. 1993, 1994). On the other hand, GR modulation reflects not only azimuth-dependent differences in unit responsiveness due to spectral inhibition but also azimuth-dependent differences in threshold produced by head shadow. For example, the contralateral monaural responses of some units show a decrease in GR magnitude in the ipsilateral quadrant relative to the contralateral quadrant (e.g., C-stim Figs. 1C, 3C, and 4C). This is likely the result of sound shadowing by the head that causes threshold increases in the ipsilateral quadrant and consequently a decrease in GR magnitude at these locations. To assess the effect of azimuth-threshold dependency on classification of MD and BD responses, we used a second measure of unit responsiveness that is unaffected by sound shadow (see Imig et al. 2000). Figure 13 shows the method for calculation, using the monaural contralateral responses of the BD-EI cell shown in Fig. 1. ALRA data are plotted as a family of level response functions, one for each azimuth (Fig. 13A). Thresholds differ for the functions, but in each discharge rate increases from threshold to about the same plateau, showing that unit responsiveness is similar at each azimuth. In B the level response functions are aligned with respect to threshold. A measure of responsiveness was obtained for each function by averaging the interpolated values at 1-dB intervals over a 10-dB range, usually 20–30 dB re: threshold. In the case of strongly nonmonotonic responses, ranges of 10–20 or 15–25 dB re: threshold were used to capture the peak of the level function. These values were normalized (normalized threshold response, NTR) and are plotted as a function of azimuth in C, together with another monaural NTR data set for the same unit. Some azimuth-dependent differences in NTR are apparent, but function profiles for the two data sets are quite different, suggesting that random fluctuation in excitability, not sound shadowing, is a major contributor to modulation. In contrast to this example, many MD cells were completely unresponsive at some azi-
NTR measures, a wide range of modulation was exhibited by cells with BFs between 5 and 37 kHz, showing that differential sensitivity to monaural spectral cues extends over a wide range of high-frequency BFs. These results demonstrate that the minor contribution of azimuth-dependent threshold differences to GR modulation did not significantly affect classification of MD and BD responses.

Comparison of MGB and AI responses

The MGB sample (n = 95) was compared with a previously described AI sample (n = 98) (Samson et al. 1993, 1994) to identify response types that might be unique to the cortex. Both data samples were obtained using identical methods and categorized using the same criteria.

The results of the comparison revealed only minor differences between AI and MGB samples except that AI units exhibited stronger nonmonotonic level tuning than MGB units. The original AI sample was re-examined to ensure uniformity of criteria, and a few new units were added. There were no significant differences in the proportions of MD and BD units in the two samples (Fig. 15). Approximately 70% of the sample was classified as BD and 30% as MD in each location.

For the purpose of comparing azimuth tuning, each cell was classified as contralateral, ipsilateral, or midline. Cells with BAs (Fig. 2) located >15° from the midline were classified as either contralateral or ipsilateral. Cells were classified as midline if the BA was located within 15° of the midline and function values were ≤25% on both sides of the midline (e.g., Fig. 5B). Cells with midline BAs that did not meet the bilateral response reduction criterion were classified as contra- or ipsilateral depending on whether the cell was more responsive to contra- or ipsilateral locations, respectively. For example, responses in Figs. 3, D and F, and 6, A and D, showed prominent midline peaks but were classified as contralateral because function values at contralateral azimuths were >25%. Contralateral cells predominated in both the MGB and AI samples with smaller proportions of ipsilateral and midline cells (Fig. 16). Considering MD and BD cells as a single group, there is no significant difference in the distribution of contralateral, ipsilateral, and midline responses in the MGB and AI samples. However, some differences are apparent within certain BD and MD response classes. There is a higher proportion of ipsilateral BD-FI and BD-F cells in AI than in the MGB (A). Midline cells in AI were exclusively of the PB type, but in the MGB they comprised BD-FI and BD-F types, the latter including both PB and monaurally excitable cells. Within the MD samples, there was a higher proportion of ipsilateral dominant cells in MGB than in AI (B).

Cells were classified as contralateral or ipsilateral ear dominant if they received excitatory input predominantly from one ear or as neither ear dominant if they were unresponsive or responded to monaural stimulation of each ear (Fig. 17). For the majority of units both in the MGB and AI, the contralateral ear was dominant with smaller percentages of ipsilateral dominant and neither-ear dominant cells. The AI and MGB ear dominance distributions were not significantly different. Some differences are apparent if one considers the MD and BD samples separately. There was a higher proportion of ipsilateral dominant BD-FI and BD-F cells in AI than in the MGB, (A), and there was a higher
The proportion of ipsilateral dominant MD cells in MGB than in AI (B). Although not identical, the distribution of ear dominance is quite similar to the distribution of contralateral, ipsilateral, and midline cells.

The preferred azimuth range (PAR, Fig. 2) in the frontal hemifield was used as an index of breadth of azimuth tuning. In the case of cells with multiple PARs, PAR width was equal to the sum of the PARs. Mean PAR in the MGB (49.3 ± 23.6°, n = 93) was slightly broader but not significantly different from that in AI (45.0 ± 24.9°, n = 98). Neither were there any significant differences between mean PARs in MGB and AI for any individual response class. However, MD cells were more narrowly tuned than BD cells in the MGB (MD: n = 30, 33.9 ± 19.2°; BD: n = 65, 56.2 ± 22.1°, t-test, P = 0.0001).
and in AI (MD: \( n = 28, 30.6 \pm 21.4\% \); BD: \( n = 70, 50.8 \pm 24.0\% \); \( P = 0.0002 \)).

Shapes of level-response functions for binaural noise stimulation varied from monotonic to nonmonotonic. Shapes of binaural and dominant-ear monaural level response functions were similar for all but five MGB units. NM strength was defined as the greatest response reduction (in percent) that occurred with increasing SPL and could vary between 0 and 100%. Level functions were obtained from ALRA data at azimuths within the PAR (Fig. 2), and NM strength was measured at the azimuth with the lowest threshold response. In most cases, this was also the azimuth at which the maximum response occurred. If a unit exhibited similar thresholds (difference \( <5 \) dB) at two or more contiguous azimuths, responses were averaged to obtain a single level function. Averaging was also used when replicated data sets were available. For the MGB sample, the mean NM strength of MD-E0 (69.7 \( \pm \) 37.0%) and MD-EI (89.4 \( \pm \) 17.1%) groups was greater than that of BD-EI (48.3 \( \pm \) 35.9%), BD-FI (27.3 \( \pm \) 35.0%), and BD-F (38.2 \( \pm \) 33.0%) groups. Analysis of variance showed a statistically significant difference between groups (\( P = 0.0001 \)). A Tukey Kramer post hoc test showed that mean NM strength for MD-EI cells was significantly greater than that of all BD cell classes, and mean NM strength for MD-E0 cells was significantly greater than that of BD-F cells. NM strength values for MD and BD cells in AI and the MGB were compared in a two-factor ANOVA in which one factor was cell location (i.e., AI or the MGB) and the other factor was response class (i.e., MD or BD). The test indicated that NM
The strength of AI cells (66.4 ± 35.3%, n = 93) was significantly greater than that of MGB cells (51.3 ± 38.7%, n = 92, P = 0.005). Additionally, NM strength of MD cells (82.7 ± 27.8%, n = 57) was significantly greater than that of BD cells (48.3 ± 36.7%, n = 128, P = 0.0001). Post hoc tests (unpaired, 2-tail t-test; corrected α = 0.05/4 = 0.0125) revealed that NM strength of MD cells was significantly greater than that of BD cells at each site (i.e., AI and the MGB; P = 0.0001). No significant difference in the distribution of ear dominance was observed between Vn and Po units.

Vn and Po units exhibit similar response properties

Histological reconstruction of electrode tracks allowed localization of 86/95 units to either Vn (n = 38) or Po (n = 48). Each response class was represented in Vn and Po with the exception of the two MD-F cells that were found only in Po. There was no significant difference in the distribution of the response classes in Po and Vn (χ² test without the MD-F cells). Neither was there any significant difference between Vn and Po units with respect to the distribution of contralateral, ipsilateral, and midline cells or the distribution of ear dominance. Regardless of whether the entire sample of azimuth-sensitive cells was compared or whether MD and BD groups were compared separately, neither mean breadth of azimuth tuning nor NM strength showed significant differences between Vn and Po.

Discussion

These results show that azimuth tuning of single units in the cat’s MGB is derived from sensitivity to monaural-spectral and binaural-disparity directional cues. Comparison of monaural and binaural responses to free-field noise stimulation allowed identification of the presence of monaural excitatory inputs, the presence of inhibitory and facilitatory binaural interactions, and a unit’s differential sensitivity to monaural spectral and binaural disparity directional cues. Single units in cortical field AI (Samson et al. 1993, 1994) and in the cochlear nucleus (Imig et al., 2000) have been characterized using identical methods, thus allowing detailed comparison with the MGB sample.

MGB neurons exhibit differential sensitivity to monaural spectral and binaural disparity directional cues

Many MGB neurons are sensitive to the azimuth of binaural noise bursts, meaning that they respond well at some azimuths, and poorly or not at all at others (Barone et al. 1996; Clarey et al. 1995). Neuron responses to monaural stimulation revealed differential sensitivity to monaural spectral and binaural disparity cues. MD cells are more sensitive to the azimuth of monaural noise bursts than monaurally excitable BD cells (i.e., BD-EI and BD-FI cells). Azimuth sensitivity of BD cells strongly depends on binaural stimulation. Such differential sensitivity occurs in neurons with BFIs that span a broad high-frequency range.

We identified six azimuth-sensitive response classes based on differences in monaural and binaural azimuth sensitivity, monaural excitatory inputs, and binaural interactions. The azimuth tuning of neurons in each of these classes reflects varying contributions of sensitivity to monaural and binaural directional cues. The azimuth sensitivity of MD-E0 cells depends exclusively on monaural spectral cues as MD-E0 responses reflect exclusively monaural input. We didn’t use ear plugging to study the responses of MGB neurons that were insensitive to the azimuth of monaural noise stimulation, but the presence of such cells in cortical field AI (Samson et al. 1993) strongly suggested their existence in the MGB. Presumably monaural
MGB cells vary greatly in sensitivity to monaural spectral directional cues. Both MD-EI and BD-EI cells exhibited binaural inhibition, indicating that the azimuth tuning of both response classes depended in part on binaural cues. MD-EI cells were distinguished from BD-EI cells by their greater monaural spectral sensitivity. And, although we divided EI cells into two classes, this does not mean that BD-EI cells were devoid of monaural spectral sensitivity. It is possible that monaural spectral sensitivity is continuously distributed among EI cells; however, the MD-BD division serves to distinguish those that exhibited greater and lesser spectral sensitivity.

Two MD cells exhibited binaural facilitation. Azimuth tuning and modulation under monaural and binaural conditions appeared similar suggesting that sensitivity to monaural spectral cues was the main contributor to azimuth tuning. Binaural facilitation appeared to amplify the magnitude of the monaurally shaped response in these cells.

BD-FI and BD-F cells represent a more challenging group regarding interpretation of the relative contribution of monaural-spectral and binaural-disparity sensitivity to azimuth tuning. Some BD-FI cells are quite similar to BD-EI cells in that their monaural responses to noise stimulation are relatively insensitive to azimuth (e.g., Fig. 3 A). It seems that the azimuth tuning of these responses reflects sensitivity mainly to binaural disparity cues. On the other hand, the responses of a BD-FI midline-prefering cell (e.g., Fig. 3D) additionally appears to reflect sensitivity to spectral cues. This cell responded in front of the head but not behind it. The high-frequency binaural-disparity cue for a midline response is 0 dB interaural level difference (ILD), and this ILD should result from sounds presented on the midline, whether in front or behind the head. This cell’s lack of a response behind the head strongly suggests that ILD alone is insufficient to account for the restricted frontal midline response and that spectral cues do play a role. On the other hand, the mechanism by which spectral cues affect the response is unknown.

The role of monaural spectral sensitivity in the azimuth tuning of BD-F cells is difficult to assess. In a few cases (e.g., Fig. 6), there is a similarity between monaural and binaural azimuth tuning, suggesting that sensitivity to spectral cues played a role. On the other hand, many BD-F cells are unresponsive (PB cells) or poorly responsive to monaural stimulation, so their monaural azimuth tuning cannot be used to assess spectral sensitivity.

Comparison of azimuth tuning to noise and tonal stimulation is one means of assessing spectral contributions to azimuth tuning. Clarey et al. (1995) recorded single neuron responses in AI and the MGB and noted that MD cells exhibited much broader azimuth tuning and less function modulation to BF-tones than to noise as expected because tones do not cause spectral inhibition that strongly shapes MD directional responses. In contrast, BD-EI and BD-FI hemifield responses showed no significant noise/tone differences in breadth of azimuth tuning or modulation, consistent with their lesser sensitivity to monaural spectral cues. Interestingly, tonal stimulation of BD-F cells with midline preference resulted in significantly broader tuning and less modulation than did noise stimulation, although the difference was smaller than for MD cells. These observations suggest that spectral sensitivity contributes to the azimuth tuning of some BD-F cells.

Binaural interactions and azimuth preference

Binaural interactions have previously been shown to be a major determinant of azimuth preference. ILD-sensitive neurons in the cat’s superior colliculus (Hirsch et al. 1985; Wise and Irvine 1985) exhibit binaural inhibition, binaural facilitation, and mixed interactions. Cells exhibiting binaural inhibition exhibit maximal responsiveness at ILDs corresponding to lateral azimuths, cells exhibiting facilitation have maximal responsiveness corresponding to near midline azimuths, and cells exhibiting mixed interactions have maximal responsiveness corresponding to intermediate locations. A similar relationship has been reported in high-BF neurons in the cat IC (Delgutte et al. 1999) and in 60-kHz BF neurons in the mustache bat IC (Fusezzery et al. 1990; Wenstrup et al. 1988a,b). Ivarsson et al. (1988) reported similar results in the cat MGB except that the mixed interaction class was not specifically identified.

Our results are consistent with the previous findings. Of the three binaural interaction classes, mean azimuth preferences (lowest thresholds and maximum responses) of BD-EI cells were most lateral, those of BD-F cells were closest to the midline, and those of BD-FI cells were in between. Nevertheless there was considerable overlap of azimuth preferences between groups, and the overlap within the BD-F and BD-FI groups is particularly noteworthy. Cells with midline azimuth preference could exhibit PB (Fig. 5A), BD-FI (Fig. 3D), or monaurally excitable BD-F responses (Fig. 11A). BD-FI cells often exhibited lateral azimuth preferences but some PB cells did as well (Fig. 5D) as previously reported in AI (Samson et al. 1994).

The distinction between BD-F and BD-FI responses appears to be somewhat artificial. Detection of binaural inhibition requires a monaural excitatory response, and since this does not exist in PB cells, binaural inhibition is not demonstrable even if it exists. Ivarsson et al. (1988) recorded PB neurons with 0 dB ILD preference in the MGB in nitrous oxide anesthetized cats and found in some cases that inhibition of spontaneous activity occurred at ILDs corresponding to lateral azimuths. Consequently mixed facilitation and inhibition contributed to these responses. Thus binaural inhibition may contribute to azimuth tuning of some PB cells although it is not detectable in barbiturate anesthetized cats.

Neural excitability may account for one difference that was noted between AI and the MGB. All midline preferring cells in AI were of the PB type, while those in the MGB included PB, BD-FI, and monaurally excitable BD-F responses. In barbiturate-anesthetized cats, AI neurons are less responsive than Vn and Po neurons (Barone et al. 1996). If cortical responsiveness was increased, some PB cells might become monaurally excitable and binaural inhibition might become detectable.

A sizable proportion of MGB MD cells receive EI input, and the inhibitory input typically completely suppresses responses at azimuths throughout the quadrant on the side of the inhibitory ear. This is similar to MD-EI cells that have been described in cortical field AI (Samson et al. 1993). MD-EI cells are also found in the IC (Poirier et al. 1996), suggesting that this type of response is synthesized below the level of the MGB. Many DCN neurons also receive EI input, but the inhibition is much weaker and never completely abolishes the excitatory input in barbiturate anesthetized cats (Imig et al.
ral interactions have previously been described in Vn (Aitkin et al. 1996) and exhibit quite similar response properties. High-BF single-unit Neurons in Vn and Po exhibit similar response properties with an increase in nonmonotonic strength that occurs in both cases. Nevertheless, these results indicate that the cortical linkage of these units neither case does the difference reach statistical significance. AI than in the MGB for both BD and MD groups, although in

AI neurons and additionally failed to find a statistically significant relationship between nonmonotonic level tuning and azimuth sensitivity in the MGB. This suggests that the linkage of MD and BD cells in AI reflect inputs from corresponding response types in rostral Vn. The finding of similar MD and BD response classes in Vn and Po suggests that MD and BD responses are likely to be found in AAF as well.

Mechanisms of MD sensitivity

Spectral-directional cues are represented by the head-related transfer function (HRTF) that describes the free-field to tympanic-membrane spectral transformation caused by diffraction of high-frequency sounds by the pinna and head (e.g., in cat, Musicant et al. 1990; Rice et al. 1992). There is a unique HRTF pattern associated with each sound direction. MD cells’ frequency response areas consist of excitatory and inhibitory frequency domains, and azimuth sensitivity is derived from the HRTF by antagonistic comparison of sound energy in these domains (Imig et al. 1997). Spectral notches are salient features of the HRTF from which MD cells presumably derive azimuth sensitivity. A spectral notch centered at BF will reduce sound energy in excitatory relative to inhibitory frequency domains, and thus inhibit neural discharge (Imig et al. 1997). Spectral notch inhibition has been described in the dorsal cochlear nucleus (DCN) (Joris 1998; Nelken and Young 1994; Spirou and Young 1991; Young et al. 1992a,b), and neurons there exhibit greater spectral-dependent directional sensitivity than ventral cochlear nucleus (VCN) neurons (Imig et al. 2000).

The extent to which MGB MD responses reflect neural activity processed in the DCN is unknown, but there are clear differences in the pattern and strength of spectral sensitivity in the two structures. The most common pattern of azimuth tuning of DCN neurons is characterized by a response null, a decrease in responsiveness over a narrow range of azimuth (Imig et al. 2000). Commonly, MGB MD neurons had azimuth functions characterized by narrow response peaks. The null pattern was relatively uncommon, but it did occur in a few MD cells (e.g., Figs. 8B, 9B, and 12E). This shows that spectral inhibition suppresses responses over a wider range of azimuth in the MGB than in the DCN. Azimuth function modulation of
the monaural response to noise reflects magnitude of spectral inhibition. GR azimuth-function modulation was $\approx 75\%$ for 18% of MGB neurons and 2% (1/61) of DCN neurons. These modulation differences show that spectral inhibition is considerably stronger in the MGB than in the DCN.

The MGB estimate is based on the finding in this study that MD cells composed 31% (31/99) of the azimuth-sensitive cells in Vn and Po, and that 57% (124/217) of a sample of cells in these subdivisions was azimuth sensitive (Barone et al. 1996). The DCN estimate is based on unpublished GR modulation values for the DCN sample described elsewhere (Imig et al. 2000).

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