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# Receptive Fields and Binaural Interactions for Virtual-Space Stimuli in the Cat Inferior Colliculus

BERTRAND DELGUTTE,<sup>1,2</sup> PHILIP X. JORIS,<sup>3</sup> RUTH Y. LITOVSKY,<sup>1,3</sup> AND TOM C. T. YIN<sup>3</sup>

<sup>1</sup>Eaton-Peabody Laboratory, Massachusetts Eye and Ear Infirmary, Boston 02114; <sup>2</sup>Research Laboratory of Electronics, Massachusetts Institute of Technology, Cambridge, Massachusetts 02139; and <sup>3</sup>Department of Physiology, University of Wisconsin, Madison, Wisconsin 53706

**Delgutte, Bertrand, Philip X. Joris, Ruth Y. Litovsky, and Tom C. T. Yin.** Receptive fields and binaural interactions for virtual-space stimuli in the cat inferior colliculus. *J. Neurophysiol.* 81: 2833–2851, 1999. Sound localization depends on multiple acoustic cues such as interaural differences in time (ITD) and level (ILD) and spectral features introduced by the pinnae. Although many neurons in the inferior colliculus (IC) are sensitive to the direction of sound sources in free field, the acoustic cues underlying this sensitivity are unknown. To approach this question, we recorded the responses of IC cells in anesthetized cats to virtual space (VS) stimuli synthesized by filtering noise through head-related transfer functions measured in one cat. These stimuli not only possess natural combinations of ITD, ILD, and spectral cues as in free field but also allow precise control over each cue. VS receptive fields were measured in the horizontal and median vertical planes. The vast majority of cells were sensitive to the azimuth of VS stimuli in the horizontal plane for low to moderate stimulus levels. Two-thirds showed a “contra-preference” receptive field, with a vigorous response on the contralateral side of an edge azimuth. The other third of receptive fields were tuned around a best azimuth. Although edge azimuths of contra-preference cells had a broad distribution, best azimuths of tuned cells were near the midline. About half the cells tested were sensitive to the elevation of VS stimuli along the median sagittal plane by showing either a peak or a trough at a particular elevation. In general receptive fields for VS stimuli were similar to those found in free-field studies of IC neurons, suggesting that VS stimulation provided the essential cues for sound localization. Binaural interactions for VS stimuli were studied by comparing responses to binaural stimulation with responses to monaural stimulation of the contralateral ear. A majority of cells showed either purely inhibitory (BI) or mixed facilitatory/inhibitory (BF&I) interactions. Others showed purely facilitatory (BF) or no interactions (monaural). Binaural interactions were correlated with azimuth sensitivity: most contra-preference cells had either BI or BF&I interactions, whereas tuned cells were usually BF. These correlations demonstrate the importance of binaural interactions for azimuth sensitivity. Nevertheless most monaural cells were azimuth-sensitive, suggesting that monaural cues also play a role. These results suggest that the azimuth of a high-frequency sound source is coded primarily by edges in azimuth receptive fields of a population of ILD-sensitive cells.

## INTRODUCTION

Sound localization is a complex process that integrates sensory information with cognitive influences. Three main acoustic cues contribute to sound localization: interaural disparities

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in time (ITD) and level (ILD) and spectral cues (Blauert 1983; Searle et al. 1976). Physiological studies under free-field stimulation have shown that many cells in the auditory midbrain are sensitive to the direction of sound sources (King and Palmer 1983; Knudsen 1982; Knudsen and Konishi 1978; Semple et al. 1983; see Irvine 1992 for review). However, free-field studies alone cannot determine which acoustic cues are responsible for this directional sensitivity because they do not allow independent control over each cue.

Such control can be achieved in dichotic studies that deliver stimuli through closed acoustic systems. Many studies have shown that cells in the auditory brain stem and midbrain are sensitive to ITD and ILD (Goldberg and Brown 1969; Rose et al. 1966; reviewed by Irvine 1986, 1992). With few exceptions (e.g., Caird and Klinke 1987), these studies varied a single cue without consideration of possible interactions between cues. Furthermore most studies have focused on pure tone stimuli, which do not contain the spectral cues provided through directionally dependent filtering by the pinnae.

It is possible to simulate the sound-pressure waveforms produced in the ear canals by free-field sound sources through closed acoustic systems. Pioneered in the 1970s (Blauert 1983), these “virtual-space” (VS) techniques now are used widely in human psychophysics (Blauert and Hartung 1997; Bronkhorst 1995; Wightman and Kistler 1989, 1992, 1997) and also are being applied to physiological studies of sound localization in animals (Brugge et al. 1994; Delgutte et al. 1995; Keller et al. 1998; Nelken et al. 1997; Poon and Brugge 1993; Rice et al. 1995). VS techniques provide stimuli with multiple, realistic localization cues and also give precise control over individual cues. In the present study, VS techniques were used for studying how sensitivity to various localization cues contributes to spatial sensitivity in the cat inferior colliculus. We used head-related transfer functions (HRTFs) measured in one cat by Musicant et al. (1990) to synthesize VS stimuli possessing realistic ITDs, ILDs, and spectral cues.

One reason for choosing the inferior colliculus (IC) as the site for applying VS techniques is its rich pattern of inputs from brain stem auditory nuclei (Adams 1979; Oliver and Huerta 1992; Oliver and Shneiderman 1991). The IC receives inputs from nuclei specialized for processing interaural time and level disparities such as the medial superior olive and the lateral superior olive (LSO) (Boudreau and Tsuchitani 1968; Joris and Yin 1995; Yin and Chan 1990). It also receives inputs from the contralateral dorsal cochlear nucleus, which has been implicated in the processing of monaural spectral cues for sound

localization (Young et al. 1992). Such convergence of inputs suggests that the IC may play an important role in cue integration, a phenomenon ideally suited to VS techniques. Another reason for applying VS techniques to the IC is that a large body of data are available on responses of IC neurons to both free-field stimulation (Aitkin and Martin 1987, 1990; Aitkin et al. 1984, 1985; Calford et al. 1986; Moore et al. 1984a,b; Semple et al. 1983) and dichotic stimuli varying in ITD and ILD (see Irvine 1986, 1992; Yin and Chan 1988 for reviews). These data can help in verifying the validity of VS stimulation and in understanding neural mechanisms underlying sensitivity to individual cues in VS stimuli.

A traditional technique for assessing the relative importance of monaural spectral cues and interaural disparity cues for sound localization is monaural ear occlusion. This technique is popular in human psychophysics (see Wightman and Kistler 1997 for review) and also has been applied to single-unit studies in animals (Knudsen and Konishi 1980; Middlebrooks 1987; Samson et al. 1993 1994). While seemingly straightforward, monaural ear occlusion experiments actually are fraught with difficulties. A major issue is the interaural attenuation provided by ear plugs. Wightman and Kistler (1997) showed that even a strongly attenuated ( $>30$  dB) input from the plugged ear still produces interaural disparities that contribute to sound localization. The same difficulty arises in single-unit studies, where an additional issue is reproducibility of the multiple plug insertions that are required to record responses of each neuron to both monaural and binaural stimulation. VS stimuli offer the advantage that monaural stimulation can be obtained by simply turning off the acoustic input to one ear, providing much better interaural attenuation than typical ear plugs.

The present report focuses on a quantitative description of spatial receptive fields in the horizontal and median vertical planes of the frontal hemifield for cells in the inferior colliculus of anesthetized cats using VS stimuli. Responses to VS stimuli are described for both binaural and monaural stimulation to assess the role of binaural interactions in shaping receptive fields. We also compare responses to VS stimuli with responses to broadband noise stimuli that have been used traditionally in dichotic studies. In a subsequent paper, we use VS techniques for identifying which acoustic cues are most important for the directional sensitivity of IC cells. A preliminary report of these findings has appeared (Delgutte et al. 1995).

## METHODS

The results presented in this paper are based on two separate series of experiments: six experiments were carried out at the University of Wisconsin in Madison, whereas eight others were carried out at the Massachusetts Eye and Ear Infirmary in Boston. Unless otherwise noted, techniques for both series of experiments were very similar and examination of their results revealed no substantial differences so that both sets of data were pooled.

### *Recording techniques*

Methods for recording from single units in the IC of barbiturate-anesthetized cats are essentially the same as described by Yin et al. (1986) and Carney and Yin (1989). In the Madison experiments, healthy adult cats free of middle-ear infection were anesthetized by intraperitoneal injection of pentobarbital sodium (35 mg/kg). A ve-

nous canula was used for injecting additional doses of anesthetic to maintain a surgical level of anesthesia throughout the experiment. The cat's temperature was monitored by a rectal thermometer and maintained at 37°C with a heating pad. A tracheal canula was inserted, both pinnae were dissected away, and the ear canals severed to allow insertion of acoustic assemblies. A small hole was drilled into each bulla, and a 60-cm plastic tube (0.9 mm ID) was inserted to prevent static pressure build-up in the middle ear.

The animal was placed in a double-walled, electrically shielded, sound-proof room. The dorsal surface of the IC was exposed on the left side by a craniotomy anterior to the tentorium and aspiration of the overlying cerebral cortex. Parylene-insulated tungsten microelectrodes (Microprobe, Clarksburg, MD) with exposed tips of 8–12  $\mu\text{m}$  were mounted on a remote-controlled hydraulic microdrive and aimed at the IC. Spikes from single units were amplified and isolated. The times of detected spikes were measured by a custom-built timer with a resolution of 1  $\mu\text{s}$  and stored in a computer file for analysis and display.

Cells encountered in the dorsal-most millimeter of an electrode penetration were broadly tuned to high frequencies. Further ventrally, characteristic frequencies (CFs) rapidly dropped to low frequencies, after which a regularly increasing sequence of CFs was encountered. The rapid drop in CF was taken as the dorsal boundary of the central nucleus of the inferior colliculus (ICC), and all units encountered as the CFs increased were assumed to be in the ICC.

Recording techniques for the Boston experiments were essentially the same as those of the Madison experiments with two exceptions. First, dial-in urethan (75 mg/kg ip) rather than pentobarbital sodium was used for anesthesia. Second, the posterior surface of the IC rather than its dorsal surface was exposed via a posterior-fossa craniotomy and aspiration of the overlying cerebellum. The electrode was oriented nearly horizontally in a parasagittal plane, approximately parallel to iso-frequency laminae (Merzenich and Reid 1974). In these horizontal penetrations, sparse, poorly responsive units were encountered in the posterior 500–800  $\mu\text{m}$  as described by Semple and Aitkin (1979), after which there was a noticeable increase in background activity and a higher density of sharply tuned single units.

### *Histology*

Histological processing for reconstruction of the electrode tracks was performed for nine cats. At the end of the experiment, the brain was fixed by either perfusion or immersion in aldehyde fixatives, and the brain stem processed for either paraffin-embedded or frozen sections stained with cresyl violet. The vast majority of tracks clearly traversed the ICC. Because the dorsal border of the ICC is hard to determine in Nissl sections, some electrode tracks from the dorsal-most horizontal penetrations may have encompassed the pericentral nucleus. There were no obvious physiological differences between these tracks and those that were unambiguously in the ICC so that it seems appropriate to treat our entire sample of cells as being from the ICC.

### *Stimuli*

Acoustic stimuli consisted of tone bursts, broadband noise, and VS stimuli presented either binaurally or monaurally. All stimuli were generated digitally (16 bits), then converted to analogue signals using sampling rates of either 80 or 100 kHz and antialiasing filters. Stimulus levels in each ear were set by custom-built programmable attenuators having resolutions of either 1 (Madison) or 0.1 dB (Boston).

The attenuated output of the D/A converter was sent to an acoustic assembly comprising an electrodynamic speaker (Realistic 40–1377) and a calibrated probe-tube microphone (Larson-Davis 2530 or Brüel and Kjaer 1/2-in). The assembly was inserted into the cut end of the ear canal to form a closed system. The sound pressure near the tympanic membrane was measured as a function of frequency from 50 Hz to 40 kHz, and these measurements were used to synthesize digital

filters that equalized the response of the acoustic system. This equalization technique gave a flat frequency response within  $\pm 2$  dB for frequencies  $< 25$  kHz.

Bursts of broadband, Gaussian noise were synthesized by a random number generator. Noise bursts were 200 or 250 ms in duration and had rise-fall times of either 4 or 20 ms. The same sample of pseudorandom noise was used throughout an experiment and, when stimuli were delivered binaurally, the same waveform was applied to both ears. These broadband noise bursts were equalized digitally, then either directly delivered to the acoustic systems or preprocessed by digital filters to generate VS stimuli. In either case, the stimulus repetition rate was normally two per second, although slower rates occasionally were used for units that showed fatigue.

The method for synthesizing virtual-space stimuli was similar to that used in the human psychophysical experiments of Wightman and Kistler (1989) and the physiological studies of Poon and Brugge (1993) and Brugge et al. (1994). The equalized, pseudorandom broadband noise was processed through digital filters constructed from HRTFs measured in one "standard" cat by Musicant et al. (1990). These HRTFs (1 for each spatial position and each ear) represent the directionally dependent transformation of sound pressure from free field to the ear canal. Thus the sound-pressure waveforms produced in both ear canals by the closed systems were the same as for free-field stimuli originating from a particular direction in the standard cat. VS stimuli were synthesized for azimuths varying from  $-90$  to  $+90^\circ$  in the horizontal plane and for elevations ranging from  $-36$  to  $+90^\circ$  in the median vertical plane. Positive azimuths and elevations correspond to virtual sound sources contralateral to the recording site and above the ears, respectively.

Digital filters for equalization and synthesis of VS stimuli were implemented in the frequency domain using fast Fourier algorithms (Oppenheim and Schaffer 1989). Two points required special care. First, an additional band-pass filter was introduced to restrict stimulus components between 2 and 35 kHz, the range where the HRTFs of Musicant et al. (1990) are the most reliable. Thus the VS stimuli contained no energy  $< 2$  kHz where ITDs are most useful. Second, in some animals the frequency response of the acoustic system showed a rapid roll-off at high frequencies. Attempts to digitally equalize this roll-off yielded very poor signal-to-noise ratios because virtually the entire amplitude range of the D/A converter was occupied by boosted high-frequency components. To avoid this problem, the upper cutoff frequency of the band-pass filter was lowered to 25 kHz for these animals.

Figure 1 shows waveforms and power spectra of the VS stimuli for two azimuths along the horizontal plane ( $0$  and  $18^\circ$  to the right, respectively). Only the first 3 ms of each noise waveform are plotted. For  $0^\circ$  azimuth, the waveforms and spectra are similar in both ears, as expected for a sound source located in the median plane. The power spectra (measured with a resolution of 1/6 octave) show prominent notches at 11.5 and 23 kHz. For  $+18^\circ$  azimuth, the waveform in the right ear has both a higher amplitude and a shorter latency than that in the left ear. These are the expected ILDs and ITDs. ILDs are even more apparent in the power spectra, where the magnitude in the right ear exceeds that in the left ear by 15–20 dB over most of the frequency range. The power spectra show prominent notches for  $18^\circ$  as they do at  $0^\circ$ , but first-notch frequencies differ somewhat for the two azimuths. Thus the VS stimuli possess three different cues to the azimuth of the sound source: ITD, ILD, and spectral notches.

### Procedure

Either broadband noise bursts or tone bursts of varying frequency were used as search stimuli. Once a single unit was isolated, its frequency tuning curve was measured using an automatic tracking procedure (Kiang and Moxon 1974) to determine the CF. In rare cases when the tracking procedure failed (e.g., for units with closed response areas), the CF was estimated by audiovisual criteria.

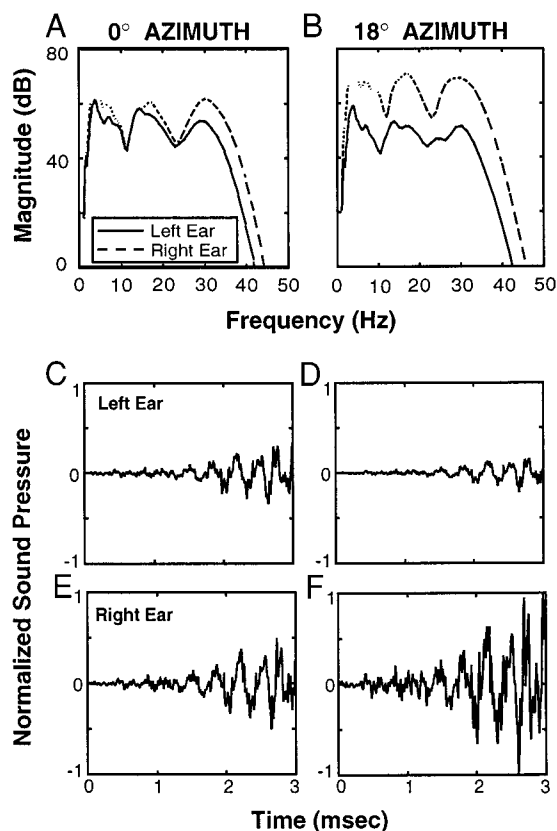


FIG. 1. Examples of virtual-space (VS) stimuli for 2 source positions along the horizontal plane:  $0^\circ$  azimuth (left) and  $18^\circ$  toward the right (right). Stimuli were obtained by filtering a burst of random noise. A and B: power spectra of the sound pressures at the tympanic membranes in each ear. Spectra were analyzed through a 1/6-octave Gaussian filter bank. C–E: sound-pressure waveforms at the tympanic membranes. Only the first 3 ms of the 200-ms noise bursts are shown.

After determining the CF, a rate-level function was measured for the VS stimulus located directly in front ( $0^\circ$  azimuth,  $0^\circ$  elevation), from which a sound level was chosen (usually 15–20 dB above threshold) for subsequent stimuli. Responses to VS stimuli were then studied as a function of azimuth or elevation, using 20 stimulus presentations for each location. Azimuths were presented from  $-90$  to  $+90^\circ$  in  $9^\circ$  steps and elevations from  $-36$  to  $+90^\circ$ , in ascending (Madison) or randomized (Boston) sequences. VS stimuli were presented both binaurally and monaurally to characterize binaural interactions, and in some units, at more than one stimulus level.

Specification of stimulus level for VS stimuli requires special care because the gains of the HRTFs, and therefore sound pressures at the tympanic membranes, depend on the location of the sound source. In the Boston experiments, we specify the SPL that a free-field stimulus would have at the center of the cat's head in the absence of the animal. Responses to VS stimuli were studied for free-field SPLs ranging from 20 to 60 dB in these experiments, with 65% of the measurements made at SPLs of  $\geq 40$  dB. In the Madison experiments, we could not always calculate free-field SPLs, so instead we specify a "nominal SPL" such that 127 dB corresponds to the unattenuated output of the D/A converter. Free-field SPLs typically would be 30–50 dB lower than nominal SPLs, depending on the experiment.

To compare azimuth sensitivity for VS stimuli with ILD sensitivity for stimuli devoid of spectral features, responses to broadband noise were studied as a function of ILD. Typically, ILD was varied over a  $\pm 30$  dB range by increasing the SPL at one ear while decreasing the SPL at the other ear so as to keep the mean binaural level (MBL, the arithmetic mean of the SPLs in dB at both ears) constant. This



“MBL-constant method” roughly mimics the changes in SPL that occur when a sound source is moved in the horizontal plane (Irvine 1987b). For some cells, ILD also was varied by changing the SPL in the ipsilateral ear while keeping the contralateral SPL constant (“contra-constant method”). Although less realistic than the MBL-constant method, this simpler method is useful for characterizing mechanisms of binaural interactions (Irvine 1987a). Positive numbers denote ILDs favoring the contralateral ear, consistent with the convention for azimuth.

**DATA ANALYSIS.** Discharge rate was averaged over the entire stimulus duration (200 or 250 ms), and rate-level, rate-ILD, rate-azimuth, and rate-elevation functions were smoothed by three-point triangular filters. Summary statistics derived from these basic data are introduced in RESULTS.

## RESULTS

### *Azimuth receptive fields for VS stimuli*

Our results are based on recordings from 173 single units in 14 cats. We selected cells with CFs  $>4$  kHz because the VS stimuli had little energy  $<2$  kHz and the spectral features such as notches are only found in HRTFs for frequencies  $>8$  kHz (Musicant et al. 1990). The data presented here are from a subset of 96 units for which we obtained responses to VS stimuli presented both binaurally and monaurally. Virtually all

the cells encountered responded to VS stimuli and, among these, a vast majority showed directional sensitivity for azimuth at moderate stimulus levels.

Figure 2 shows both temporal patterns and average rates of discharge as a function of azimuth for two cells from the same cat. Temporal discharge patterns in *A* and *B* are shown as dot rasters based on 20 stimulus presentations for each of 21 azimuths. For the cell in Fig. 2, *left*, the average rate was clearly directional: it was low for ipsilateral (negative) azimuths, then rose to a maximum at  $+9^\circ$  azimuth before settling to a broad plateau on the contralateral side. The dot raster shows that discharges occurred in brief bursts at specific times during the 200-ms stimulus. Although these bursts tended to occur at the same times for wide ranges of azimuths, the temporal discharge patterns did provide some additional directional information over that available in the average rate. In interpreting these temporal patterns, it is important to keep in mind that stimulus waveforms were synthesized by filtering the same sample of pseudorandom noise through different HRTFs. Thus the preferred times of discharge are likely to reflect features of the envelope of this specific noise waveform, as seen through the frequency selectivity of the neuron.

For the cell in Fig. 2, *right*, the rate response was poorly directional but the temporal discharge pattern still contained

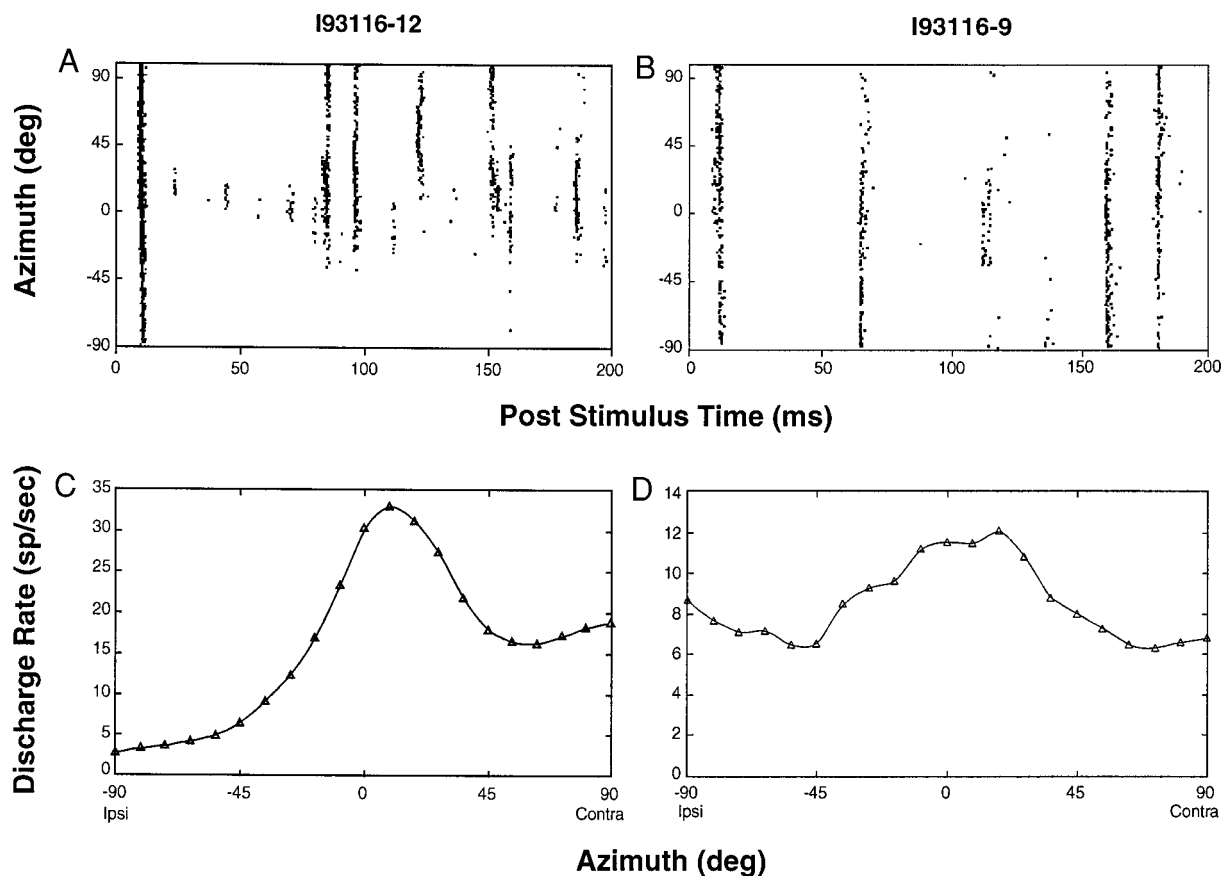


FIG. 2. Temporal discharge patterns and average discharge rate as a function of the azimuth of VS stimuli for 2 inferior colliculus (IC) neurons from the same cat. Unit characteristic frequencies (CFs) are 12 (*left*) and 13.5 kHz (*right*). *A* and *B*: temporal discharge patterns are shown as dot rasters based on 20 stimulus presentations for each of 21 azimuths. Each dot represents 1 spike. Positive azimuths refer to virtual sound sources located contralateral to the recording site. *C* and *D*: discharge rate averaged over the 200-ms stimulus duration plotted against azimuth. Curves are cubic splines fit to the data points. Nominal sound-pressure levels of 80 (*left*) and 90 dB (*right*) both correspond to 20 dB above threshold for  $0^\circ$  azimuth.

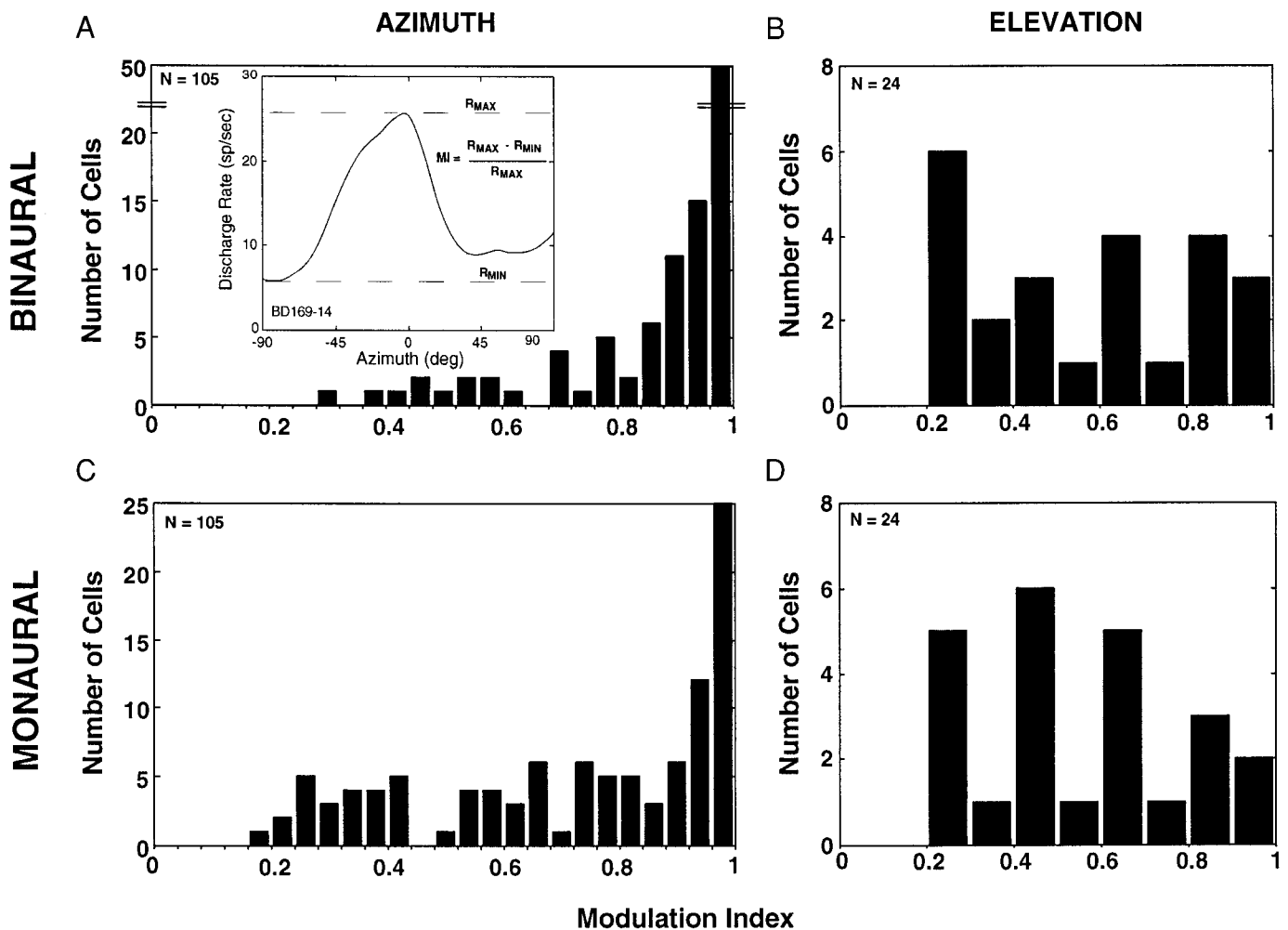


FIG. 3. Distribution of azimuth (*left*) and elevation (*right*) modulation index for binaural (*A* and *B*) and monaural (*C* and *D*) stimulation of the more effective ear. *Inset*: method for computing the modulation index (MI).

information about azimuth. Examples such as these are unusual, in part because most cells in our sample had more directional rate responses than this one. Furthermore both cells in Fig. 2 were selected because their temporal discharge patterns showed particularly prominent directional information. About 1/3 of the cells tested only responded at the onset of the VS stimuli. For these cells, the only directional information available in the temporal discharge pattern was a variation in latency with azimuth. Nevertheless, Fig. 2 suggests that at least some IC neurons may code sound-source location in their temporal discharge patterns as well as their averages rates (Middlebrooks et al. 1994). In the remainder of RESULTS, we focus on how azimuth and elevation are coded in the average rates of discharge of IC neurons.

#### Types of azimuth receptive fields

Cells were initially classified based on whether they were sensitive to changes in azimuth using the *modulation index*  $MI = (R_{MAX} - R_{MIN})/R_{MAX}$ , where  $R_{MAX}$  and  $R_{MIN}$  are, respectively, the maximum and minimum discharge rates over the entire range of azimuths (Fig. 3A, *inset*). Figure 3A shows the distribution of azimuth modulation indices for our sample of cells. The distribution is highly skewed toward large mod-

ulation indices, with nearly half the responses (50/105) being 100% modulated. Although cells with CFs between 6 and 15 kHz had, on the average, the highest modulation indices, fully modulated units were found in all CF regions. Thus sensitivity to azimuth of VS stimuli is a robust feature of the IC cell population at moderate stimulus levels.

Cells then were classified into four groups based on their azimuth receptive field for VS stimuli. This classification scheme is similar to those used in free-field studies of auditory neurons (Aitkin and Martin 1987; Imig et al. 1984; Rajan et al. 1990). Examples of each type of receptive field are shown in Fig. 4.

**CONTRA-PREFERENCE UNITS.** One key element in classifying directional units is the “best azimuth,” the location where the response is maximal. Contra-preference units (Fig. 4A) are those for which the response falls <50% of maximum on the ipsilateral side of the best azimuth but remains >50% on the contralateral side. These units formed the majority (63/105, 60%) of our sample. For these units, a characteristic feature (CF) is the half-maximal azimuth, the location where the response reaches 50% of maximum (Fig. 5A, *inset*). Figure 5B shows that the distribution of half-maximal azimuths for all contra-preference cells is bimodal, with a major mode near  $-9^\circ$ , and a much smaller mode at  $+54^\circ$ . There was no obvious

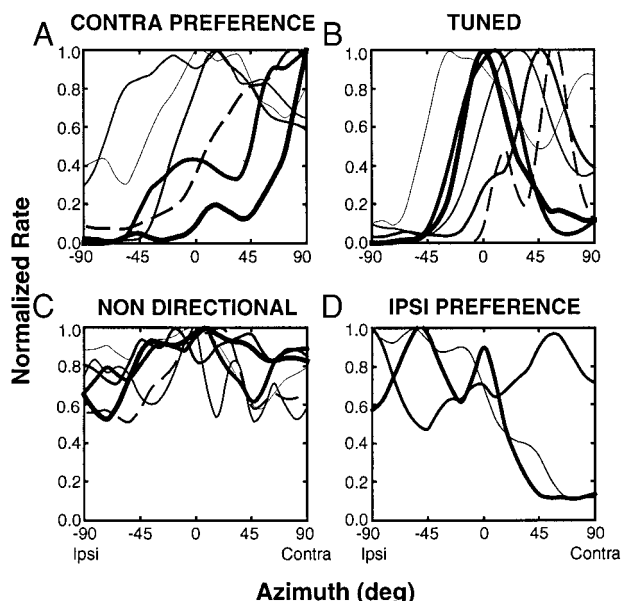


FIG. 4. Examples of the 4 types of azimuth receptive fields found for VS stimuli. Each trace shows the average discharge rate (normalized to the maximum response) as a function of azimuth for 1 unit. See text for definition of the 4 types of receptive fields.

correlation between CF and half-maximal azimuth, except that 2/3 of the cells with half-maximal azimuths lying in the small mode centered at  $+54^\circ$  had CFs near 10–15 kHz.

A contra-preference unit with a steep rate-azimuth function may provide precise information for azimuth discrimination in the vicinity of the half-maximal azimuth. On the other hand, a unit with a gradual azimuth function may encode changes in azimuth over a broad range. We define the *half rise* as the range of azimuths between 25 and 75% of the maximum response (Fig. 5A, inset). Figure 5A shows the half rises for all contra-preference cells. Each cell is represented by a horizontal bar extending over the half rise with the symbol placed at the half-maximal azimuth. Cells are arranged from low to high in order of increasing half-maximal azimuth. Although some cells have narrow ( $<20^\circ$ ) half rises, the median half rise is  $33^\circ$ , and the cell population as a whole can represent increments in azimuth by increases in discharge rate over most of the frontal hemifield.

**TUNED UNITS.** Tuned units (Fig. 4B), those with responses that fall  $<50\%$  of maximum on both sides of the best azimuth, represent the second most common type (33/105) of azimuth receptive field in our sample. Most (20/33) had CFs between 6 and 15 kHz. Figure 6B shows the distribution of best azimuths for all tuned units. Most best azimuths were between 0 and  $+54^\circ$  with a pronounced maximum near the midline ( $+9^\circ$ ). A measure of tuning around the best azimuth is the half-width, the range of azimuths over which the response exceeds 50% of maximum (Fig. 6B, inset). Figure 6A shows the half-widths for all tuned units. Most units are broadly tuned, with half-widths exceeding  $45^\circ$ ; the median half-width is  $64^\circ$ . Unlike contra-preference units, which, together, can encode a wide range of azimuths, tuned units seem most suitable for encoding azimuths near the midline.

**Nondirectional units** (Fig. 4C) have modulation indices less than 50%, i.e., their response never falls  $<50\%$  of maximum for any azimuth. Although nondirectional units were rare in our

sample (6/105), their actual proportion may be somewhat greater because cells with poor azimuth sensitivity were not always studied.

**Ipsi-preference units** (Fig. 4D) are symmetrical to contra-preference units with respect to the midline: their azimuth functions fall  $<50\%$  of maximum on the contralateral side of the best azimuth but not on the ipsilateral side. Only three ipsi-preference units were found in our sample. For one of these, the azimuth function showed two maxima at  $-90$  and  $+63^\circ$ , respectively, with a trough in between. This unit could alternatively be classified as “multi-peaked” (Rajan et al. 1990).

#### Binaural interactions for VS stimuli and broadband noise

Responses to VS stimuli were obtained both for binaural stimulation (as naturally occurs in the free field) and for monaural stimulation of the more effective ear (usually the contralateral ear). This monaural condition is approximated by occlusion of the less effective ear in free-field experiments (Knudsen and Konishi 1980; Middlebrooks 1987; Samson et al. 1993, 1994). In some units, we also examined binaural interactions for broadband noise lacking spectral features.

The importance of binaural interactions for the azimuth sensitivity of IC neurons is shown by the differences between azimuth modulation indices for binaural and monaural stimu-

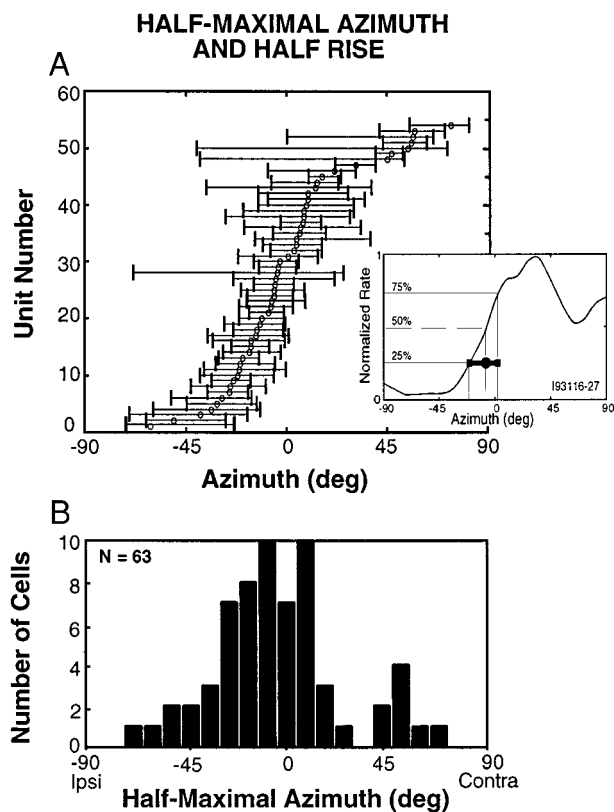


FIG. 5. Distribution of half-maximal azimuths and half rises for all IC units that showed a contra-preference pattern in response to VS stimuli (see examples in Fig. 4A). A: each unit is represented by a horizontal bar extending over the half rise with the circle at the half-maximal azimuth. Units are arranged in order of increasing half-maximal azimuths. For 9 cells, the half-width could not be determined because the response did not fall  $<25\%$  of maximum. These cells are included in B but not in A.

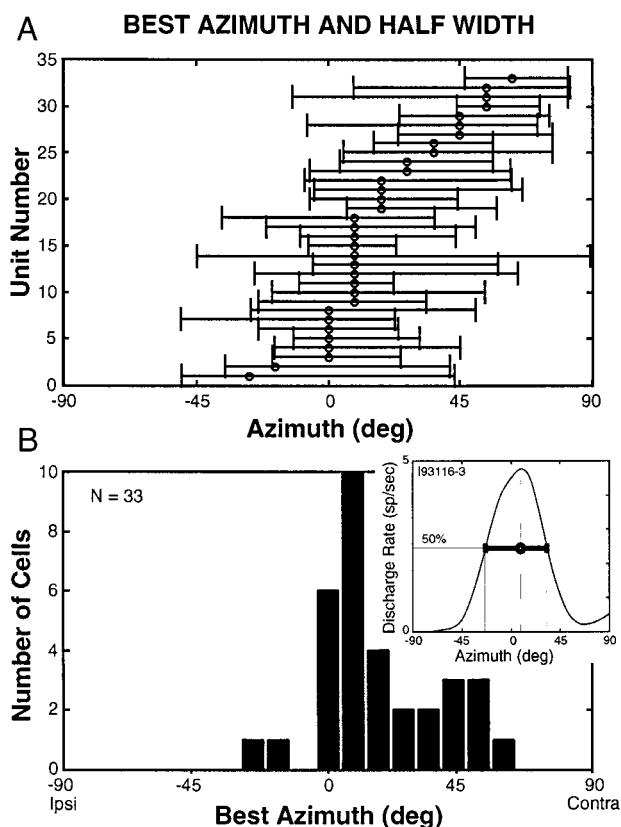


FIG. 6. Distribution of best azimuths and half-widths for all IC units that showed a tuned pattern in response to VS stimuli (see examples in Fig. 4B). A: each unit is represented by a horizontal bar extending over the half-width with the circle at the best azimuth. Units are arranged in order of increasing best azimuths.

lation (Fig. 3, A and C). On the average, modulation indices were lower for monaural stimulation than for binaural stimulation. A greater fraction of units had modulation indices <50% in the monaural condition than in the binaural condition (24 vs. 6%), and a smaller fraction of units were 100% modulated in the monaural condition (24 vs. 49%). Statistical analysis confirms that differences in distributions of modulation indices for the two conditions are highly significant [ $\chi^2(12) = 37.8, P < 0.001$ ]. Thus although responses to monaural stimulation can be directional at these moderate stimulus levels, binaural interactions do play an important role in enhancing the azimuth sensitivity of IC neurons. Azimuth sensitivity in the monaural condition may reflect directionally dependent changes in the gains of the HRTFs at the contralateral ear as well as sensitivity to spectral features of the HRTFs.

**MIXED FACILITATORY/INHIBITORY INTERACTION.** Figure 7 shows detailed results from a single unit that exemplifies a frequently observed type of binaural interaction. Figure 7A shows responses to binaural and contralateral stimulation with VS stimuli. When the VS stimuli were presented binaurally, the response was clearly directional: there was little response for azimuths on the ipsilateral side, a steep rise for azimuths near 0°, and a broad plateau on the contralateral side. In contrast, the monaural response was hardly directional. Thus binaural interactions were critical for the azimuth sensitivity of this unit. Specifically, for positive azimuths, the binaural response was greater than the monaural response obtained with contralateral

stimulation, meaning that the ipsilateral ear had a facilitatory influence. On the other hand, for negative azimuths, the binaural response was smaller than the contralateral response, meaning that ipsilateral stimulation had an inhibitory effect. Such mixed facilitatory and inhibitory binaural interactions are commonly seen in the IC (Brückner and Rübsamen 1995; Fuzessery et al. 1990; Irvine and Gago 1990; Park and Pollak 1993; Semple and Kitzes 1987).

Mixed binaural interactions are also apparent in Fig. 7B, which shows responses to broadband noise lacking spectral features for the same unit as in Fig. 7A. We compare responses to increasing stimulus level for noise presented to the contralateral ear with the cell's sensitivity to ILD measured by the MBL-constant method (Irvine 1987a; Semple and Kitzes 1987). For the MBL-constant stimuli, stimulus level was increased in the contralateral ear while the level in the ipsilateral ear was correspondingly decreased so as to keep the MBL constant at 50 dB. Thus ILD varied from -60 to +60 dB, reaching zero when the contralateral and ipsilateral SPLs were both at 50 dB. As in Fig. 7A, the binaural response was greater than the monaural response for ILDs favoring the contralateral

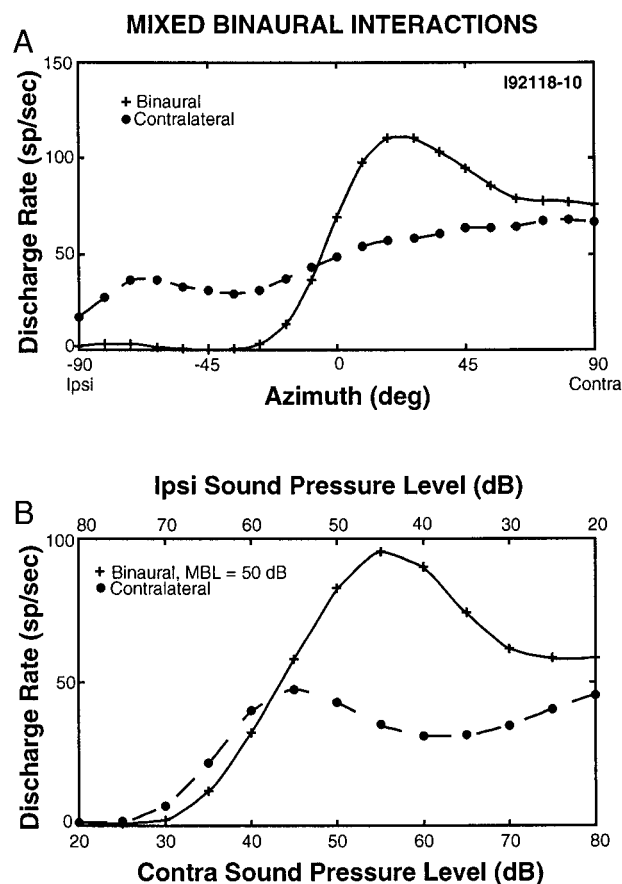


FIG. 7. Binaural interactions for VS stimuli (A) and broadband noise (B) for an IC unit with CF of 9.5 kHz that showed mixed facilitatory/inhibitory interactions. A: average neural response as a function of the azimuth for normal binaural stimulation (+) and monaural stimulation of the contralateral ear (●). Nominal SPL: 65 dB. B: rate-level function for broadband noise presented to the contralateral ear (●) and interaural level difference (ILD) sensitivity for broadband noise measured by the mean binaural level (MBL)-constant method (+). As the contralateral SPL was increased from 20 to 80 dB (bottom), the ipsilateral SPL was decreased from 80 to 20 dB (top) so as to keep the MBL constant at 50 dB. Thus ILD varied from -60 to +60 dB.



ear but smaller than the monaural response for ILDs favoring the ipsilateral ear. For this cell then, the mixed binaural interactions found with VS stimuli are consistent with those found for broadband noise using the MBL-constant method.

**INHIBITORY INTERACTION.** Figure 8A shows results for a cell showing another frequently observed type of binaural interaction. In this case, both binaural and monaural responses to VS stimuli were sensitive to azimuth. The binaural response was smaller than the monaural response to contralateral stimuli over the entire range of azimuths, indicating that stimulation of the ipsilateral ear had a purely inhibitory effect. Cells showing this type of binaural interaction are formally classified as EO/I (Irvine 1986) and commonly referred to as EI. This type of binaural interaction also predominates for broadband noise, as shown in Fig. 8B: the response to contralateral noise exceeds the binaural response measured at a constant MBL of 60 dB over a wide range of contralateral SPLs. Only at the lowest ipsilateral level (30 dB) is the binaural response clearly greater than the contralateral response, indicating weak facilitation.

Although the MBL-constant method for measuring ILD sensitivity roughly mimics the changes in stimulus level resulting from changes in azimuth in free field, a simpler method for varying ILD, called the "contra-constant method," is to vary the ipsilateral level while keeping the contralateral level

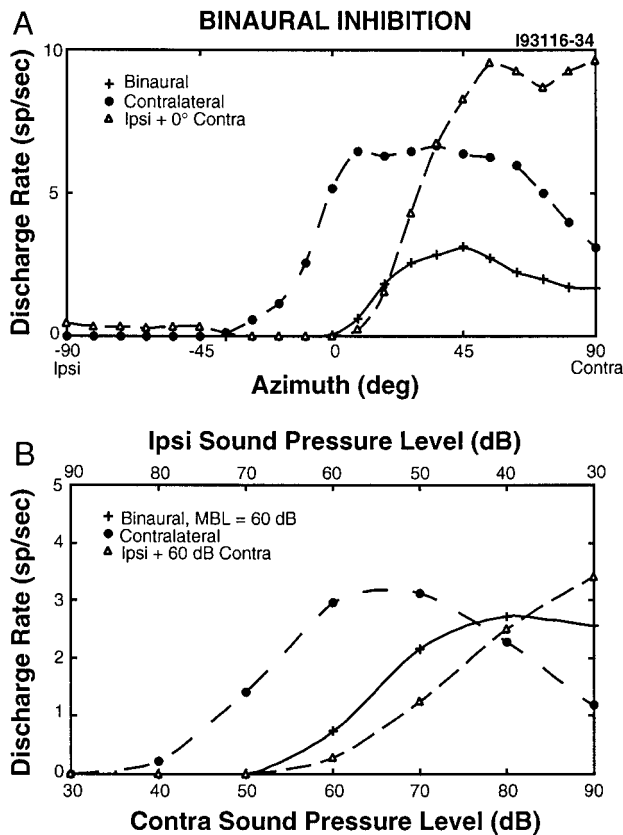


FIG. 8. Binaural interactions for VS stimuli (A) and broadband noise (B) for an IC unit with CF of 15 kHz that showed inhibitory binaural interactions. + and ●, as in Fig. 7. A: △, responses for a binaural condition in which azimuth was varied in the ipsilateral ear while the azimuth in the contralateral ear was held constant at 0°. B: △, ILD sensitivity measured by the contra-constant method: ipsilateral SPL varied from 80 to 20 dB (top) while the contralateral SPL was held constant at 60 dB. Nominal SPL was 80 dB in A; MBL was 60 dB in B.

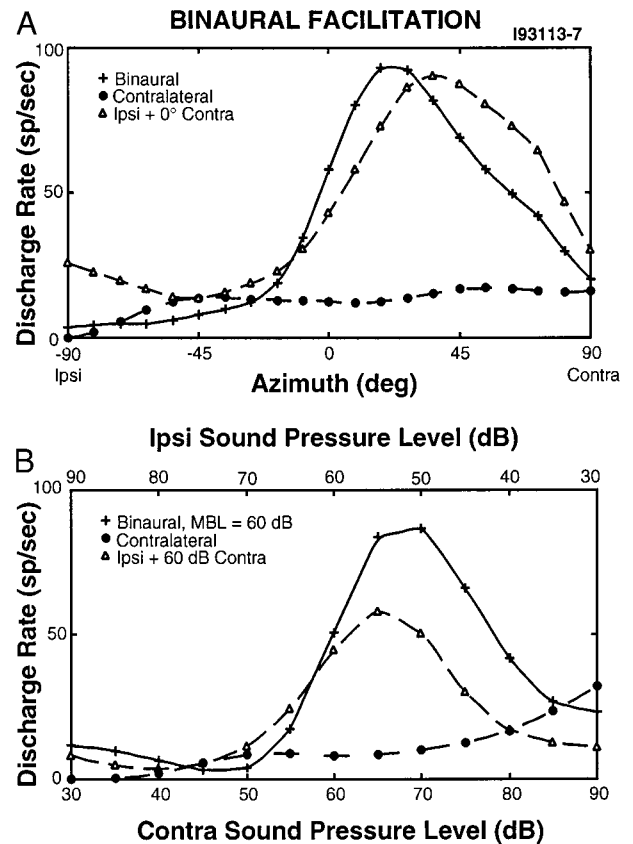


FIG. 9. Binaural interactions for VS stimuli (A) and broadband noise (B) for an IC unit with a CF of 8 kHz that showed binaural facilitation. Symbols as in Fig. 8. Nominal SPL for VS stimuli: 70 dB.

constant, here at 60 dB (Fig. 8B, △). The response increases monotonically as the ipsilateral level is decreased from 90 to 30 dB (Fig. 8B, top), indicating, again, an EI type of binaural interaction. An analogue of the contra-constant method for VS stimuli is to vary the azimuth in the ipsilateral ear while keeping the azimuth for the contralateral ear constant at 0° (Fig. 8A, △). The response increases monotonically as the azimuth in the ipsilateral ear is increased from 0 to 45°, then saturates. Because moving the azimuth toward the contralateral side results in a decreased SPL at the ipsilateral ear, the increase in response is also consistent with an EI binaural interaction. The saturation for azimuths >45° might result from the ipsilateral level falling below threshold, so that it can no longer influence the cell response. Overall, results for two different stimuli (VS and broadband noise) and two different methods for varying ILD (contra-constant and MBL-constant) concur in showing that binaural interactions for this cell are primarily EI.

**FACILITATORY INTERACTION.** While most cells in our sample showed either purely inhibitory or mixed inhibitory/facilitatory binaural interactions, some showed prominent facilitatory interactions. An example of such a cell is shown in Fig. 9. The cell did not respond to stimulation of the ipsilateral ear alone (not shown) and was weakly responsive to contralateral stimulation with VS stimuli. In contrast, the response to VS stimuli presented binaurally showed a prominent maximum for azimuths near +18° (Fig. 9A). This maximum resulted from powerful binaural facilitation because the binaural response

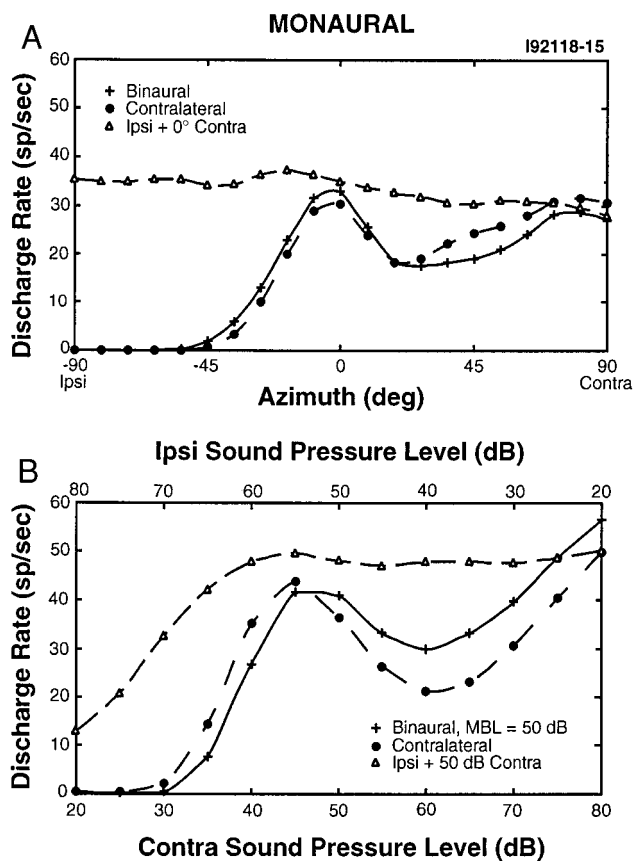


FIG. 10. Binaural interactions for VS stimuli (A) and broadband noise (B) for a monaural IC unit with a CF of 22 kHz. Symbols as in Fig. 8. Nominal SPL for VS stimuli: 50 dB.

exceeded the response to contralaterally presented VS stimuli over a broad range of azimuths. While facilitation was the dominant binaural interaction for this cell, there was also weak inhibition for azimuths between  $-63$  and  $-36^\circ$ . Facilitation is also apparent for responses measured when varying the azimuth for the ipsilateral ear while holding the contralateral ear at an azimuth of  $0^\circ$ : these responses exceeded the monaural response to the contralateral,  $0^\circ$ -azimuth stimulus for virtually all azimuths.

Responses to binaural broadband noise with an MBL of 60 dB (Fig. 9B) are similar to responses to VS stimuli in that they show a prominent maximum for ILDs favoring the contralateral ear by 5–10 dB. Again, this maximum results from binaural facilitation because the binaural response greatly exceeds the response to contralateral noise over a wide range of ILDs. There is also a narrow range of negative ILDs where the binaural response is slightly smaller than the contralateral response, consistent with the weak inhibition found with VS stimuli for negative azimuths. Thus for this cell as for those of Figs. 7 and 8, binaural interactions for VS stimuli are consistent with those for broadband noise.

**MONAURAL CELL.** Not all cells sensitive to azimuth showed binaural interactions. An example of a primarily monaural cell with a CF of 22 kHz is shown in Fig. 10. The responses to VS stimuli presented binaurally and contralaterally were very similar (Fig. 10A). Moreover, when azimuth in the ipsilateral ear was varied while holding the azimuth in the contralateral ear constant at  $0^\circ$ , the cell response remained nearly constant,

confirming that ipsilateral stimulation has a minimal effect. A similar pattern of results is apparent for broadband noise (Fig. 10B), where varying ILD by the MBL-constant method gives a response similar to the rate-level function for contralateral noise. However, when ILD sensitivity was assessed by the contra-constant method, the response dropped for ILDs more negative than  $-15$  dB, indicating an inhibitory effect of intense ipsilateral stimulation. This inhibition was not apparent for VS stimuli, possibly because the effective range of ILDs achieved by varying azimuth did not extend below  $-15$  dB. Nevertheless the overall pattern of responses was similar for VS stimuli and broadband noise for this primarily monaural cell.

*Quantification of binaural interactions*

To summarize results such as those of Figs. 7–10 for the entire unit population, two quantitative measures of binaural interactions were derived from responses to VS stimuli (Fig. 11A). When the binaural and monaural responses are plotted together as a function of azimuth on the same coordinates, the two curves define three regions: an area of facilitation AF where the binaural response is greater than the monaural response; an area of suppression AS where the binaural response is smaller than the monaural response; a common area A0 located below both curves. From these three areas, two dimensionless measures of binaural interactions were defined, the binaural interaction strength,  $BIS = (AF + AS)/(A0 + AF +$

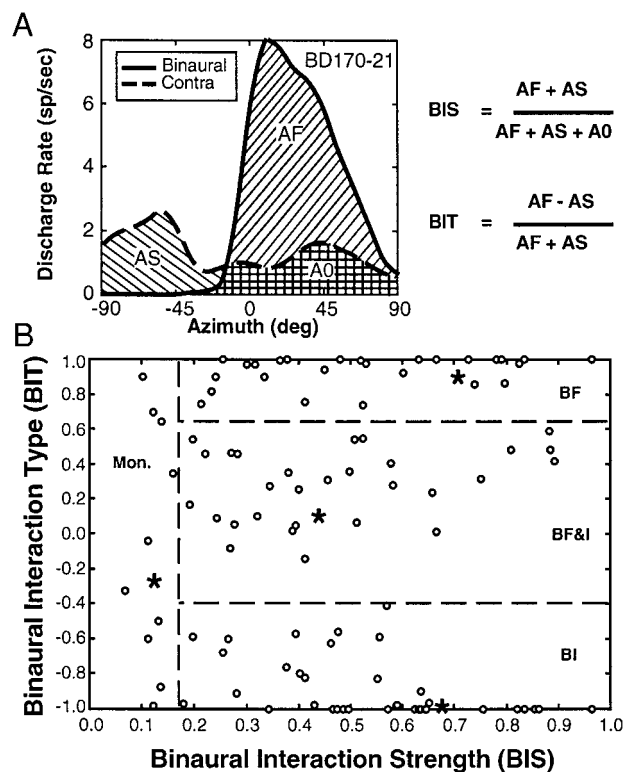


FIG. 11. Quantitative characterization of binaural interactions for VS stimuli. A; method for computing the binaural interaction strength (BIS) and the binaural interaction type (BIT) from responses to VS stimuli presented binaurally (—) and monaurally to the contralateral ear (- - -). B; scatter plot of BIT against BIS for all IC units. \*, cells corresponding to those shown in Fig. 7–10. - - -, boundaries used to separate units into 4 categories of binaural interactions: monaural, binaural facilitation (BF), binaural inhibition (BI), and mixed facilitatory/inhibitory interactions (BF&I).

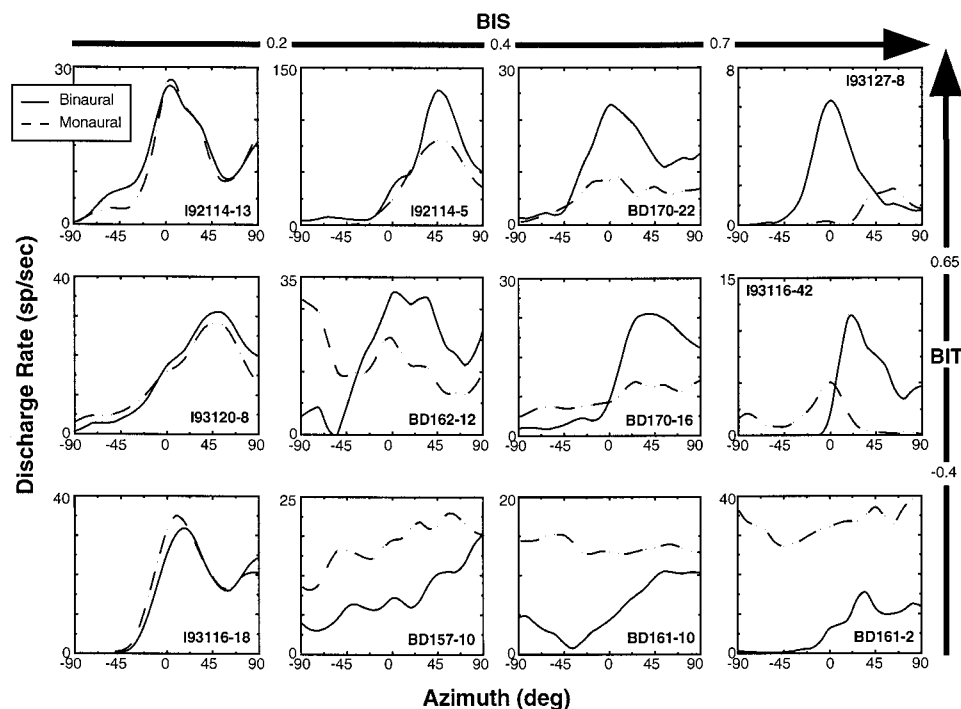


FIG. 12. Binaural interaction for VS stimuli in 12 IC units. Each panel shows the azimuth sensitivity of one unit for stimuli presented binaurally (—) and monaurally to the most effective ear (---). Units are arranged in a matrix so that going from *left to right* corresponds to increasing values of BIS, whereas going from *bottom to top* corresponds to increasing values of BIT. *Left*: monaural units. *Right 3 columns*: *top*, BF units; *middle*, BF&I units; *bottom*, BI units.

AS), and the binaural interaction type,  $BIT = (AF - AS) / (AF + AS)$ . BIS is a number between 0 and 1 characterizing how much the monaural and binaural responses differ regardless of how they differ. Thus a zero BIS means that the monaural and binaural responses are identical for all azimuths (implying a monaural cell), whereas a BIS near 1 means that either the binaural or the monaural response is large compared with the other one for all azimuths, implying strong binaural interactions. BIT, on the other hand, is a number between  $-1$  and  $+1$  expressing whether binaural interactions are primarily inhibitory or facilitatory regardless of their strength. A positive BIT means that, on the average, the binaural response exceeds the monaural response, implying a facilitatory interaction, whereas a negative BIT means the opposite, as occurs for an EI cell. A large BIS with a BIT near 0 implies mixed facilitatory and inhibitory interactions.

To help interpret these measures, Fig. 12 shows further examples of binaural interactions for VS stimuli. Each panel shows the response of one cell as a function of azimuth for both binaural and contralateral stimulation. The cells are arranged in a matrix so that the horizontal position along each row corresponds to the value of BIS and the vertical position along each column to the value of BIT. Cells in the *leftmost column* have BISs  $< 0.2$  and are therefore primarily monaural. Moving toward the *right* (increasing BIS), monaural and binaural responses increasingly differ. Units in the *top row* have strongly positive BITs ( $> 0.7$ ) and show predominantly facilitatory interactions. In contrast, units in the *bottom row* have strongly negative BITs (less than  $-0.4$ ) and show predominantly inhibitory interactions. Finally, units in the *middle row* have BITs near 0 and show a mix of facilitation and inhibition.

Figure 11B shows BIT plotted against BIS for the entire sample of cells in which VS responses were studied both binaurally and monaurally. This display was used to classify cells into four broad categories of binaural interactions (separated by ---). These boundaries were drawn to encompass

clear instances of each category, and attempts were made to place boundaries at troughs in the distributions of BIT and BIS. Monaural units are defined as having BISs  $< 0.18$ . Among the other (binaural) units, facilitatory (BF) units have BITs  $> 0.65$ , inhibitory (BI) units have BITs less than  $-0.30$ , and mixed (BF&I) units have BITs between  $-0.30$  and  $0.65$ . Although these divisions are largely arbitrary, there does seem to be a firm distinction between BI and BF&I units in that very few units have BITs between  $-0.40$  and  $-0.15$ . There is also a high density of units with BITs near  $-1$  and  $+1$ , providing some justification for the BI and BF categories. Units from all four categories were found throughout the range of CFs.

Table 1 gives a cross-classification of our IC cells according to azimuth sensitivity and binaural interactions for VS stimuli.<sup>1</sup> To a large extent, the type of azimuth receptive field can be predicted from binaural interactions. With few exceptions, contra-preference units have either BI (25/63) or BF&I (23/63) interactions, consistent with their weak response for ipsilateral azimuths where ILD is negative. Tuned units are most frequently BF (15/33). These cells respond maximally near the midline and, correspondingly, show the greatest facilitation for ILDs near 0 dB. Nevertheless, monaural factors also play a role in azimuth sensitivity. A high proportion (10/11) of monaural units were azimuth-sensitive at these relatively low sound levels. Even for binaural units, variations in SPL at the contralateral ear seem to contribute to tuning around a best azimuth. Specifically, a significant fraction (9/33) of tuned units showed EI interactions. For these units, the decrease in response for azimuths farther contralateral than the best azimuth cannot be due to inhibition from the ipsilateral ear, which is minimum at these azimuths. Instead, this decrease in response

<sup>1</sup> Binaural interactions for two of three ipsi-preference cells were not quantitatively characterized (and are excluded from the table) because a full azimuth function for ipsilateral stimulation was not measured. In the one ipsi-preference cell for which an ipsilateral azimuth function was measured, binaural interactions were of the IE type.

TABLE 1. Cross-classification of IC cells according to binaural interactions and type of azimuth receptive field for VS stimuli

	Mon	BF	BI	BF&I	Total
Nondirectional	1	4	1	0	6
Contra-preference	8	7	25	23	63
Tuned	2	15	9	7	33
Total	11	26	35	30	102

IC, inferior colliculus; VS, virtual space; Mon, monaural; BF, binaural facilitation; BI, binaural inhibition; BF&I, mixed facilitation/inhibition.

may reflect the decrease in the gain of the HRTFs at the contralateral ear for azimuths more contralateral than the pinna axis at  $+45^\circ$  (Calford et al. 1986; Musicant et al. 1990) or nonmonotonicities in the contralateral rate-level function.

### Effect of overall SPL

To examine the stability of azimuth receptive fields with respect to changes in stimulus level, responses to VS stimuli were measured at two or more sound levels in a few cells. Figure 13 shows results from one unit where VS responses were measured at three different levels in both monaural and binaural conditions. At the lowest sound level (60 dB), the unit had a tuned response with a best azimuth at  $+36^\circ$  in both conditions. Because this level was very close to threshold, these responses probably reflect the directional sensitivity of the contralateral pinna, which has its acoustic axis near the best azimuth (Calford et al. 1986). At 80 and 100 dB, responses in the binaural condition changed to a contra-preference pattern with a half-maximal azimuth near the midline. The half-maximal azimuth moved only slightly when the level was increased from 80 to 100 dB. This relative stability contrasts with responses to monaural stimulation of the contralateral ear, which progressively invaded the ipsilateral hemifield as stimulus level was increased. Thus for this unit, although responses are directional for both binaural and monaural stimulation at stimulus levels near threshold, inhibitory binaural interactions play an important role in creating a level-tolerant azimuth receptive field at suprathreshold levels.

Among 20 units for which responses were studied at two or more stimulus levels, half had only relatively small ( $<1.5^\circ/\text{dB}$ ) changes in half-maximal azimuth with stimulus level. For most (7/10) of the remaining units, half-maximal azimuths moved toward the ipsilateral side at a rate  $>1.5^\circ/\text{dB}$  with increases in stimulus level. Only three units showed large movements toward the contralateral side. Thus on the basis of this small sample, there is a trend for receptive fields to expand toward the ipsilateral side when stimulus level is increased, but some units have relatively level-tolerant sensitivity.

### Sensitivity to elevation

Neural representation of sound sources located in the median vertical plane are interesting because interaural disparity cues are minimal for these stimuli so that their localization must be based primarily on spectral features. In 49 neurons, we studied responses to VS stimuli varying in elevation in the median vertical plane. Here, we report results for a subset of 24 neurons for which elevation sensitivity was studied in both monaural and binaural conditions.

Figure 3, B and D, shows the distribution of modulation indices for elevation for both binaural stimulation and monaural stimulation of the more effective ear. In the binaural condition (Fig. 3B), modulation indices for elevation were, on the average, lower than those for azimuth (Fig. 3A). Some neurons that were strongly sensitive to azimuth were much less so to elevation. Unlike the situation for azimuth, modulation indices for elevation were similar in the monaural and binaural conditions. Indeed, differences in the distributions of elevation modulation indices for monaural and binaural stimulation were not statistically significant [ $\chi^2(6) = 3.15, P = 0.79$ ]. Thus as expected binaural interactions are less important for the elevation sensitivity of IC neurons than they are for azimuth sensitivity.

Figure 14 shows examples of monaural and binaural elevation sensitivities for VS stimuli in three units. One (Fig. 14A) was classified as monaural based on its azimuth sensitivity shown in Fig. 10. Consistent with this classification, the elevation sensitivity for VS stimuli was similar for binaural and monaural stimulation, with prominent tuning to elevations near  $+27^\circ$ . Figure 14B shows elevation sensitivity for the BF&I unit, for which azimuth sensitivity is shown in Fig. 7. This unit was poorly sensitive to elevation in the binaural condition and somewhat more sensitive for contralateral stimulation. The binaural response exceeded the monaural response for all elevations, consistent with the slight binaural facilitation seen for VS stimuli at  $0^\circ$  azimuth in Fig. 7A and for broadband noise at 0 dB ILD in Fig. 7B. Figure 14C shows elevation sensitivity for the BF unit, for which azimuth sensitivity is shown in Fig. 9A. In the binaural condition, the unit showed broad tuning to

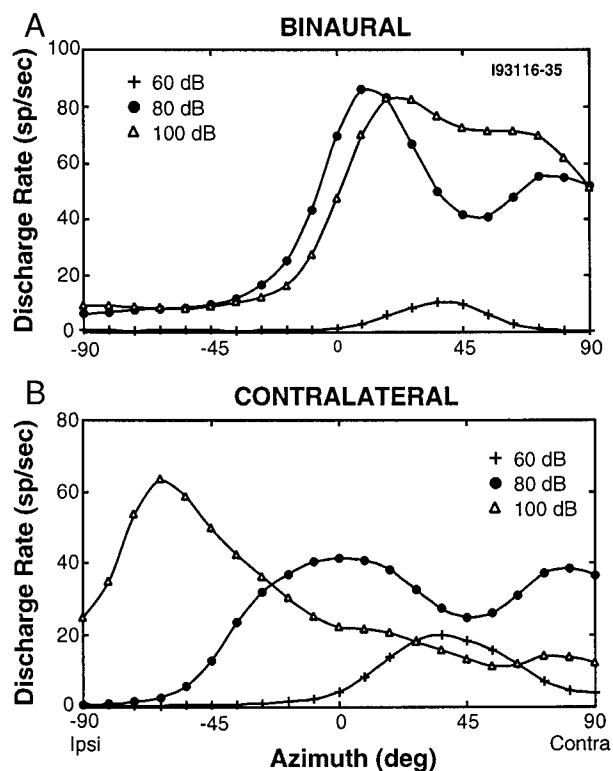


FIG. 13. Azimuth receptive fields of 1 IC unit for 3 different sound levels and for both binaural stimulation (A) and monaural stimulation of the contralateral ear (B). Unit CF: 12 kHz. Legend gives nominal SPLs. Note different vertical scales in A and B.



elevation around a maximum at  $0^\circ$ . Responsiveness to stimuli varying in elevation was markedly lower when these stimuli were delivered to the contralateral ear only. This observation is consistent with the powerful binaural facilitation exhibited by this unit in response to VS stimuli varying in azimuth. Thus for all three units in Fig. 14, binaural interactions measured with VS stimuli varying in elevation are consistent with those for VS stimuli varying in azimuth.

Units were classified into four categories based on their receptive field for elevation (Fig. 15). Two of these categories, nondirectional units (Fig. 15A) and tuned units (Fig. 15B), are defined in the same manner as the homonymous types of azimuth receptive fields. The fraction of units classified as nondirectional was considerably higher for elevation (11/24) than for azimuth (6/105). Best elevations of the four tuned

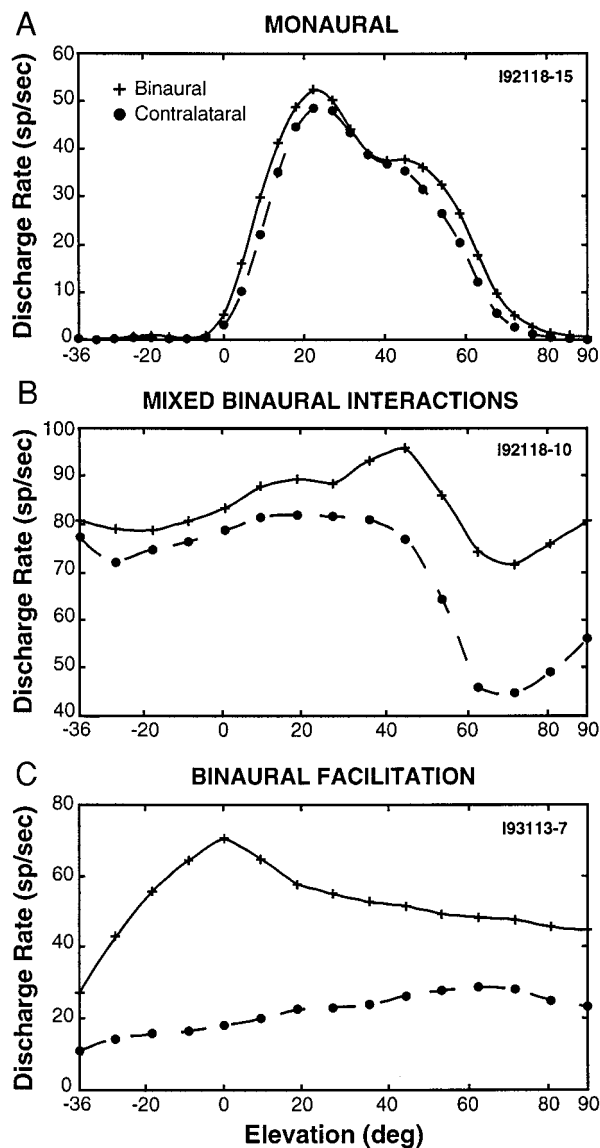


FIG. 14. A: elevation sensitivity for VS stimuli of the monaural unit, for which azimuth sensitivity is shown in Fig. 10A. Responses are shown for both binaural (+) and monaural (●) stimulation of the contralateral ear. Nominal SPL: 50 dB. B: elevation sensitivity of the BF&I unit, for which azimuth sensitivity is shown in Fig. 7A. Nominal SPL: 65 dB. C: elevation sensitivity of the BF unit, for which azimuth sensitivity is shown in Fig. 9A. Nominal SPL: 70 dB.

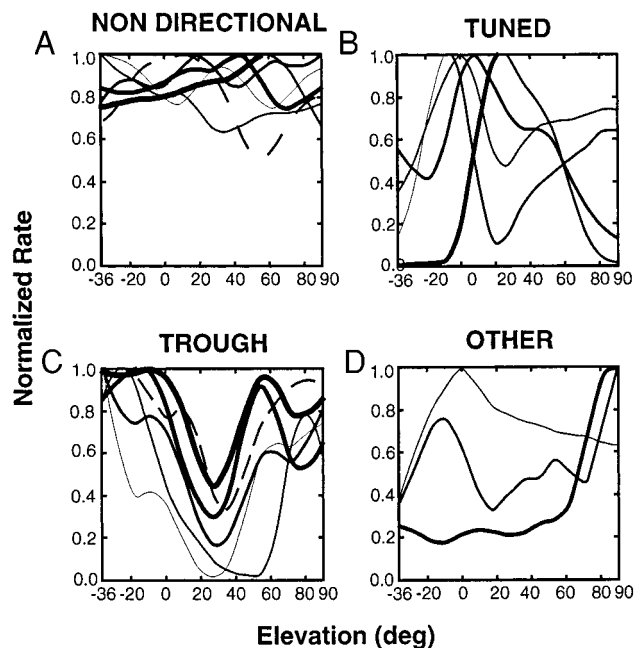


FIG. 15. Examples of the 4 types of elevation sensitivity found for VS stimuli. Each trace shows the average discharge rate (normalized to the maximum response) as a function of elevation for 1 unit. See text for definition of the 4 types of sensitivity.

units ranged between  $-9$  and  $+27^\circ$ . A third type of elevation sensitivity was trough units (Fig. 15C), for which elevation functions showed a pronounced minimum, with the response rising to  $\geq 50\%$  of maximum on both sides of the minimum. Trough units formed 25% (6/24) of our sample, and their troughs were restricted to elevations between  $+27$  and  $+54^\circ$ . One of the tuned units also showed a trough so that it could fit into either category (Fig. 15B). Finally three elevation-sensitive units showed neither a simple peak nor a trough and were left unclassified (Fig. 15D).

There was no obvious relationship between the elevation and azimuth exhibited by a given unit. For example, among the most numerous class of units that showed a contra-preference pattern for azimuth, 9 were classified as nondirectional for elevation, whereas the other 10 were distributed among trough, tuned, and other units. Interestingly, two of three units that were classified as nondirectional for azimuth were sensitive to elevation. On the other hand, 9 of 10 units nondirectional for elevation had contra-preference patterns for azimuth. No systematic correlations between elevation sensitivity and binaural interactions were apparent either. This general lack of correlation is consistent with the view that azimuth and elevation sensitivities largely depend on separate localization cues and neural mechanisms.

RELATION TO SPECTRAL FEATURES IN HRTFs. Most (10/13) elevation-sensitive units had CFs in the  $>8$  kHz frequency region where HRTFs show prominent spectral features. One hypothesis is that troughs in neural elevation functions for VS stimuli are due to the prominent spectral notches found in HRTFs for sound sources located in the frontal hemifield (Musicant et al. 1990; Rice et al. 1992). However, not every HRTF spectral notch necessarily will be reflected in neural responses, depending on how the notch frequency varies with elevation. When seen through 1/6-octave filters, HRTFs in the

median plane typically show two prominent spectral notches (Fig. 1). The first notch frequency increases systematically from 8 kHz at  $-36^\circ$  to 19 kHz at  $+54^\circ$ . Thus neurons tuned to frequencies in the first-notch region are expected to show a trough in their rate-elevation function at the elevation for which the notch frequency is near the cell's CF. In contrast, because the second notch frequency stays nearly constant at 22–24 kHz regardless of elevation, neurons having CFs near the second notch frequency are not expected to show a trough as elevation is varied. Instead they might show a broad maximum near  $+20$ – $30^\circ$  elevation, reflecting the slight upward tilt of the pinna axis (Calford et al. 1986; Musicant et al. 1990).

The situation is complicated further when we consider that many IC neurons have nonmonotonic rate-level functions. For these neurons, troughs in neural elevation functions might correspond to peaks in HRTF iso-frequency contours, providing that the effective SPL at the peak elevation exceeds the reversal point of the rate-level function.

Neural data are broadly, but not entirely, consistent with these predictions. There were 10 neurons<sup>2</sup> for which the rate-elevation function showed a trough that exceeded 25% of the maximum response. For four of these, the neural trough elevation coincided with a trough in the HRTF at the CF. All four of these neurons had CFs in the first notch region (8–19 kHz) as predicted. For three other neurons, the trough elevation coincided with a peak in the HRTF at the CF. All three had nonmonotonic rate-level functions. Finally, three neurons had a trough in their elevation function that occurred neither at a peak nor at a trough in the HRTF at CF. Thus on the basis of this small sample, there is a tendency for troughs in neural elevations to correspond to features (peaks or troughs) in HRTF iso-frequency contours, but some neurons may exhibit highly nonlinear spectral processing that is not easily related to HRTFs.

## DISCUSSION

### *Spatial receptive fields of IC neurons in free field and VS*

We have studied the directional sensitivity of IC cells for VS stimuli synthesized by filtering broadband noise through HRTFs from a standard cat. For a vast majority of cells, average discharge rates varied appreciably with the azimuth of VS stimuli along the horizontal plane for moderate stimulus levels. About 2/3 of azimuth-sensitive cells showed a contra-preference receptive field with a pronounced edge near their half-maximal azimuth. The other third showed a tuned receptive field around a best azimuth. Although half-maximal azimuths of contra-preference units had a broad distribution, best azimuths of tuned units were restricted to positions near the midline. About half the cells tested were sensitive to the elevation of VS stimuli placed in the median vertical plane. Most elevation-sensitive cells showed either a peak or a trough at a particular elevation that could be related to features of the HRTFs.

Two obvious limitations of the study are the synthesis of VS stimuli from nonindividualized HRTFs and the use of low to moderate stimulus levels (usually 15–20 dB above neural thresholds). Discussion of these issues is deferred until our

results have been compared with those of both free-field studies of directional sensitivity and dichotic studies of ILD sensitivity in the IC.

Most free-field studies of IC neurons in the cat (Aitkin et al. 1984, 1985; Calford et al. 1986; Moore et al. 1984a,b; Semple et al. 1983) were concerned primarily with mapping the entire spatial receptive field for tonal stimuli and did not give detailed characterizations of neural responses in the horizontal and median vertical planes. The two studies most comparable with ours are those of Aitkin and Martin (1987, 1990) because they focus on high-CF ( $>3$  kHz) neurons, give detailed characterizations of azimuth and elevation sensitivity, and describe responses to broadband noise as well as CF tones.

Aitkin and Martin (1987) report that 44% of IC units in their sample were “azimuth selective” for broadband noise. At first sight, this seems to be a much lower proportion than the 94% azimuth-sensitive units that we found. However, to be called azimuth selective, the units studied by Aitkin and Martin (1987) not only had to meet our 50% response modulation criterion, but in addition their half-maximal azimuth had to change by  $<0.5^\circ/\text{dB}$  when overall intensity was varied. Among the units the responses to VS stimuli of which were studied at more than one stimulus level, most showed changes in half-maximal azimuth  $>0.5^\circ/\text{dB}$ , so that they would not be considered “azimuth selective” according to the criteria of Aitkin and Martin (1987). Moreover, our sample is biased toward azimuth-sensitive units because insensitive units sometimes were skipped with no further study. These differences in sampling techniques and criteria for azimuth selectivity may account for differences in the proportion of sensitive units between the Aitkin and Martin (1987) study and our own.

As in our study, a majority of azimuth-sensitive units studied by Aitkin and Martin (1987) showed a contra-preference receptive field, whereas a smaller fraction of units were tuned around a best azimuth. From their Fig. 6, half-maximal azimuths of most contra-preference cells were between  $-20$  and  $+20^\circ$  with a skew toward ipsilateral (negative) azimuths. This result is consistent with our own distribution, which is somewhat broader (Fig. 5B). Best azimuths of tuned units studied by Aitkin and Martin (1987) were centered at  $+20^\circ$ , again consistent with our results (Fig. 6B). Thus azimuth receptive fields for high-CF IC neurons shows striking similarities between the free field and our virtual acoustic space. This result suggests that our VS stimuli contained the essential cues for the azimuth sensitivity of IC neurons.

The situation is less clear for elevation sensitivity. Aitkin and Martin (1990) estimate that 35% of high-CF IC units are sensitive to the elevation of broadband noise stimuli in free field. Considering the small sample sizes, this proportion is consistent with our 54% for VS stimuli. Most elevation-sensitive units studied by Aitkin and Martin (1990) were tuned around a best elevation. Best elevations ranged from 0 to  $+40^\circ$  (their Fig. 4), consistent with our findings in tuned units (Fig. 15B). However, an obvious difference between the two studies is that trough units were at least as common as tuned units in our sample, whereas Aitkin and Martin (1990) did not report observing trough units. A majority of troughs in neural responses to VS stimuli coincided with either a trough or, for nonmonotonic units, a peak in the pattern of HRTF gain against elevation at the CF. Although the Aitkin and Martin (1990) data included neurons having CFs in the first-notch

<sup>2</sup> These 10 neurons include the 6 trough neurons of Fig. 15 as well as 4 others that had smaller troughs.

region of HRTFs (8–18 kHz), where trough responses would be expected, none of the examples shown in their figures are from this CF region. One methodological difference between the two studies is that Aitkin and Martin (1990) measured elevation sensitivity of neurons at their best azimuth, whereas we always varied elevation for VS stimuli in the median vertical plane (0° azimuth). However, because HRTFs show similar features for typical best azimuths near +20° as they do at 0°, one would expect to find trough responses at these azimuths as well. Thus both the lack of trough responses in the Aitkin and Martin (1990) study and the minority of our trough responses that did not obviously correspond to HRTF features remain unexplained. Because both studies investigated elevation sensitivity in only small numbers of neurons, the question needs further investigation.

#### *Binaural and monaural factors underlying azimuth sensitivity in the IC*

Because VS stimuli contain multiple sound localization cues, the azimuth sensitivity of IC neurons for VS stimuli might be based on monaural spectral cues, on interaural disparities such as ILD and ITD, or on a combination of binaural and monaural cues. To assess the relative importance of monaural and binaural cues, we measured the azimuth sensitivity of IC neurons to VS stimuli for both normal binaural stimulation and monaural stimulation of the more effective ear (usually contralateral). This monaural technique offers substantial advantages over monaural ear occlusion in free-field experiments.

Four broad types of binaural interactions were defined based on a quantitative comparison of responses to VS stimuli presented binaurally and monaurally. A majority of cells showed either purely inhibitory (BI) or mixed facilitatory/inhibitory (BF&I) interactions. Some cells showed either purely facilitatory (BF) or no interactions (monaural). Binaural interactions for VS stimuli were generally consistent with those for broadband noise lacking spectral features. Binaural interactions also were correlated with azimuth sensitivity. Most contra-preference cells had either BI or BF&I interactions, whereas tuned cells were most often BF (Table 1). These correlations demonstrate the importance of binaural interactions for azimuth sensitivity in most cells. Nevertheless monaural cues also play a role, as shown by the observations that most monaural cells were azimuth sensitive and that 2/3 of binaural cells retained some azimuth sensitivity for monaural stimulation.

Our binaural classification scheme obviously is related to the traditional EO-EE-EI scheme (see Irvine 1986 for review), but differs in that it emphasizes binaural interactions rather than monaural responses to each individual ear. Our scheme represents an effort to define binaural interactions based on quantitative and explicit criteria. Because VS stimuli approximate the free field, it may be more functionally meaningful than the traditional one based on pure-tone stimuli. On the basis of the fairly uniform distribution of the binaural interaction measures BIS and BIT in Fig. 11B, there is no justification for further dividing IC cells into finer categories. In fact, some of the category boundaries are arbitrary, and it would be more accurate to describe the difference between monaural and binaural units as a continuum of BIS and that between BF and BF&I units as a continuum of BIT. Nevertheless the boundary be-

tween BI and BF&I units is less arbitrary because few units had BITs near the border. In any case, discrete categories are convenient for linguistic reference.

Despite these classification issues, all four types of binaural interactions have been reported in previous studies of ILD sensitivity in high-CF IC neurons (cat: Benevento et al. 1970; Caird and Klinke 1987; Geisler et al. 1969; Irvine and Gago 1990; Rose et al. 1966; rat: Stillman 1972; gerbil: Brückner and Rübsamen 1995; Semple and Kitzes 1987; mustache bat: Fuzessery and Pollak 1985; Fuzessery et al. 1990; Wenstrup et al. 1988). In general, our results with VS stimuli show a greater proportion of BF&I neurons and a lower proportion of monaural units than previous studies with tones and noise (with the exception of Semple and Kitzes 1987). The low proportion of BF&I neurons in some studies may be due to a failure to adequately sample the ILD continuum, in the extreme, testing for 0 dB ILD only. Because BF&I cells show different interactions depending on ILD, their identification requires a fine sampling of ILD. Furthermore coarse samplings may miss interactions limited to certain ranges of ILDs and thereby exaggerate the proportion of monaural cells. On the other hand, we may have underestimated the number of monaural cells by focusing on azimuth-sensitive cells.

IC cells showing purely inhibitory interactions resemble cells in the lateral superior olive (LSO). Binaural neurons in LSO are excited by ipsilateral stimulation and inhibited by contralateral stimulation and are classified as IE in the traditional scheme (Boudreau and Tsuchitani 1968; Joris and Yin 1995; Tsuchitani 1988a,b). Thus a simple hypothesis is that EI cells in the IC receive predominant excitatory inputs from the contralateral LSO (Fuzessery and Pollak 1985; Irvine and Gago 1990; Semple and Kitzes 1987). However, evidence from pharmacological studies with neurotransmitter antagonists (Klug et al. 1993), chemical lesion studies (Sally and Kelly 1992), and intracellular recordings from IC neurons (Kuwada et al. 1997) strongly suggest that not all EI cells in the IC result from this simple circuitry and that some inhibitory binaural interactions are formed at supraolivary levels, including the IC and the dorsal nucleus of the lateral lemniscus (DNLL).

Facilitatory interactions require more complex neural circuitry than purely inhibitory interactions because facilitation has not been reported in the LSO. Both BF&I and BF interactions have been reported in the DNLL of the big brown bat (Covey 1993), and BF&I cells have been found in the DNLL of the mustache bat as well (Markovitz and Pollak 1994). However, in the mustache bat, the proportion of facilitated units is considerably smaller in DNLL than in the IC (Markovitz and Pollak 1994). Pollak and his colleagues (Markovitz and Pollak 1994; Park and Pollak 1993) have hypothesized neural circuits consistent with brain stem anatomy and pharmacology that qualitatively account for observed binaural interactions in the IC and DNLL. In their scheme, binaural facilitation in the IC is actually disinhibition from presumed inhibitory interneurons in the DNLL that have different half-maximal ILDs than excitatory inputs from the contralateral LSO.

Our results clearly show that facilitatory binaural interactions play an important role in azimuth sensitivity of high-CF IC neurons. For every BF&I unit in our sample, facilitation always occurred on the contralateral side of the half-maximal azimuth, whereas inhibition always occurred on the ipsilateral side. The net result is that BF&I cells show greater azimuth sensitivity than would be achieved through either monaural



cues or purely inhibitory interactions alone. Similar observations have been made in studies of ILD sensitivity in the IC (Fuzessery et al. 1990; Irvine and Gago 1990; Semple and Kitzes 1987). Binaural facilitation plays an even more important role for BF cells, which often show pronounced tuning around a best azimuth usually (but not always) located near the midline. Such cells, which respond poorly to monaural stimulation, have been referred to as “predominantly binaural” in studies of ILD sensitivity (Fuzessery et al. 1990; Semple and Kitzes 1987).

**ILD SENSITIVITY IN THE CAT IC.** The quantitative data of Irvine and Gago (1990) on ILD sensitivity for tones and noise in the cat IC can be compared in detail with our results for VS stimuli. Using the MBL-constant method for studying ILD sensitivity, Irvine and Gago (1990) found that most cells show a pronounced edge centered at a half-maximal ILD. This pattern is similar to our contra-preference azimuth receptive field. To make the comparison quantitative, we note that, when seen through 1/6-octave filters, the HRTFs of Musicant et al. (1990) show a nearly linear relationship between azimuth and ILD between  $-45$  and  $+45^\circ$ . Using the median rate of change in ILD of  $0.34 \text{ dB}/^\circ$  for frequencies  $>3 \text{ kHz}$ , our median half-maximal azimuth of  $-7^\circ$  translates into an ILD of  $-2.4 \text{ dB}$ , which closely corresponds to the  $-3.4 \text{ dB}$  median half-maximal ILD of Irvine and Gago (1990). Moreover, the 60-dB range of half-maximal ILDs in their Fig. 5 is consistent with our  $90^\circ$  range of half-maximal azimuths (Fig. 5B) providing that rates of change of ILD reach  $0.6 \text{ dB}/^\circ$ . Such high rates indeed occur near 10–20 kHz in the HRTFs of Musicant et al. (1990). Thus the distribution of half-maximal ILDs in the cat IC is consistent with the distribution half-maximal azimuths. In particular, both distributions show a slight but definite skew toward the ipsilateral side. Such a skew also has been observed in a study of ILD sensitivity in the IC of the unanesthetized mustache bat (Wenstrup et al. 1988).

In the Irvine and Gago (1990) study, half-maximal ILDs tended to move toward the ipsilateral side with increases in stimulus level, although some cells were relatively level tolerant, as found in the present study. Specifically, their median rate of change in half-maximal ILD with stimulus level was about  $-0.5 \text{ dB/dB}$ . Using, again, the median rate of change in ILD of  $0.34^\circ/\text{dB}$  from the HRTFs, this value corresponds well with the  $-0.5 \text{ dB/dB}$  predicted from our median rate of change in half-maximal azimuth of  $-1.5^\circ/\text{dB}$ . Thus both qualitatively and quantitatively, effects of stimulus level on ILD and azimuth sensitivities in the cat IC are similar.

In summary, many different lines of evidence show a strong similarity between azimuth sensitivity for VS stimuli and ILD sensitivity for tones and noise. First, we found that binaural interactions for VS stimuli are consistent with interactions for broadband noise in individual cells. Second, we found a correlation between patterns of azimuth sensitivity and types of binaural interactions for VS stimuli. Third, the four types of binaural interactions identified for VS stimuli correspond to those observed in studies of ILD sensitivity in several species. Fourth, the distribution of half-maximal azimuths for VS stimuli is consistent with the distribution of half-maximal ILDs in studies of ILD sensitivity. Finally, effects of stimulus level on azimuth and ILD sensitivities are similar. Taken together, these lines of evidence strongly suggest that ILD is the main local-

ization cue underlying azimuth sensitivity of high-CF neurons in the IC. Although this conclusion is consistent with those of previous studies, the present results make the case particularly strong through the use of broadband stimuli that approach natural free-field conditions and through detailed quantitative analyses. In a subsequent paper, we give further evidence that ILD is the main cue by studying responses to VS stimuli in which ILD is selectively manipulated.

#### *Validity of VS stimulation*

Most of our data were collected for relatively low stimulus levels, typically 15–20 dB above threshold for  $0^\circ$  azimuth. When free-field SPLs could be estimated, these ranged from 20 to 60 dB, with two thirds of the neural measurements being made at  $\geq 40 \text{ dB SPL}$ .<sup>3</sup> Thus most of our data were obtained at sound levels typical for psychophysical studies of sound localization. Nevertheless our results on receptive fields and binaural interactions for VS stimuli may only hold over a limited range of levels. On the basis of our small sample of neurons that were studied at two or more levels, as well as the more extensive free-field data of Aitkin and Martin (1987), azimuth receptive fields of most neurons tend to expand with increasing stimulus level, but some neurons are relatively level tolerant and could encode sound location at higher sound levels. In general, the contrast between the stability of psychophysical performance over wide ranges of levels and the tendency for neural receptive fields to expand with stimulus level remains a nagging issue not only for sound localization but for other behavioral tasks such as intensity and spectral-shape discrimination.

Because we used HRTFs from one cat of Musicant et al. (1990) for synthesizing VS stimuli in all of our experiments, the sound-pressure waveforms of our VS stimuli in the ear canals did not exactly match those that would occur in the free field for each individual animal. Acoustic measurements from cats (Musicant et al. 1990; Rice et al. 1992) show that although certain features of HRTFs are stable across individuals, there also can be significant individual differences. Human psychophysical experiments show that although most listeners can accurately localize VS stimuli synthesized using someone else’s HRTFs, front-back confusions and localization errors in the median vertical plane are more common than when using individual HRTFs (Bronkhorst 1995; Møller et al. 1996; Wenzel et al. 1993). Thus it is important to assess the effect of nonindividualized HRTFs on our results. Given the paucity of physiological data directly relevant to the issue in mammals (Blauert and Hartung 1997; Sterbing and Hartung 1998), this assessment must rely on indirect arguments.

Measuring HRTFs in animals with moving pinnae such as cats is not straightforward because the positions of the pinnae are not easily standardized. There may be as much variability in HRTFs due to placement of the pinna in an individual cat as there are individual differences in HRTFs at the same pinna position (Rice et al. 1992). Despite this difficulty, both low-frequency ( $<8 \text{ kHz}$ ) ILD cues and the prominent midfrequency (8–20 kHz) spectral notches in HRTFs are relatively stable across animals, although the exact notch frequency for a given

<sup>3</sup> For frontal sound sources, sound-pressure levels at the tympanic membranes would be even higher due to the amplificatory action of the pinnae.



source location may vary somewhat (Rice et al. 1992). Large individual variations are limited to high frequencies (>20 kHz), where HRTFs show a complicated pattern of spectral peaks and notches. When HRTFs are analyzed through a 1/6-octave filter bank, the most prominent of these high-frequency features is a notch that stays nearly constant at 22–24 kHz throughout the horizontal and median vertical planes. Thus high-frequency HRTFs features appear to be poor candidates for precise encoding of either azimuth or elevation.

Several arguments suggest that the use of nonindividualized HRTFs may not be a severe limitation for studying the azimuth sensitivity of IC neurons. We have shown that azimuth receptive fields of high-CF neurons for our VS stimuli closely resemble those in free-field studies of the cat IC (Aitkin and Martin 1987). This result suggests that our VS stimuli based on nonindividual HRTFs contain the essential acoustic cues for azimuth sensitivity. Moreover we found pervasive similarities between azimuth sensitivity for VS stimuli and ILD sensitivity for tones and noise. These findings suggest that ILD is the primary cue for the azimuth sensitivity of high-CF IC neurons and that neural mechanisms underlying ILD sensitivity may not depend on the exact shape of the stimulus spectrum. Because ILD cues are more stable across animals than high-frequency features of HRTFs (Rice et al. 1992), this further suggests that individual differences in HRTFs may not be a major factor for azimuth sensitivity in the horizontal plane.

The situation is more complex for elevation sensitivity because there were differences in the proportions of tuned and trough units between VS and free-field stimulation (Aitkin and Martin 1990). These differences are based on small data samples and might be accounted for partly by methodological differences. Furthermore it is hard to see how interindividual differences in the frequency of the first notch in HRTFs could transform a tuned unit into a trough unit. Nevertheless it is possible that some of the differences in neural responses to free-field and VS stimuli reflect the use of nonindividualized HRTFs.

In summary, although individualized HRTFs may be important in some cases, nonindividualized HRTFs suffice to address many questions regarding sound localization particularly in the horizontal plane. The use of nonindividualized HRTFs is not the only difference between our experimental model and sound localization in natural conditions. Anesthesia, acoustic reflections (echoes), head and pinna movements, and visual and proprioceptive cues are also likely to affect the directional sensitivity of auditory neurons. As such, the present study should be seen as one of many steps required to understand the neural mechanisms for sound localization in natural environments. This study clearly shows that, for the most part, results of traditional dichotic studies of sensitivity to interaural disparities also apply to neural responses in a situation that better approximates the free field.

#### *Neural codes for sound localization in the IC*

Most IC neurons show either of two prominent features in their azimuth receptive fields for VS stimuli: a peak at the best azimuth or an edge centered at the half-maximal azimuth. Which of these two features is most likely to code the azimuth of a sound source?

Neural codes for sound localization based on neurons tuned

to specific spatial locations have been proposed for the external nucleus of the IC of the barn owl (Knudsen and Konishi 1978; Konishi 1986) and for the superior colliculus (SC) of both birds (Knudsen 1982) and mammals (King and Hutchings 1987; King and Palmer 1983; Middlebrooks and Knudsen 1984). This type of code is appealing when, as in the case of these nuclei, best locations are arranged topographically to form a map of auditory space because, in principle, the location of the sound source can be identified from the place of maximum activity in the map. Unlike the SC and the barn owl IC, however, there is no compelling evidence for a map of azimuths in the mammalian IC. On the other hand, codes such as the population vector (Fitzpatrick et al. 1997; Georgopoulos et al. 1986) can provide accurate directional information based on best azimuths without requiring topographic maps. For either neural maps or population-vector codes to be effective, the distribution of best azimuths must encompass the behaviorally relevant range. This requirement is not met for tuned neurons in the mammalian IC where best azimuths are rarely more contralateral than  $+18^\circ$  (Fig. 6). Thus the class of high-CF IC cells that show a tuned response to azimuth is not likely to provide a general code for azimuth and seems most suitable for enhancing azimuth acuity near the midline where psychophysical performance is the best (Heffner and Heffner 1988; Huang and May 1996b; May and Huang 1996).

Alternatives to neural codes based on best azimuths are those based on the edge centered at the half-maximal azimuth. Such “edge codes” have been proposed for the mammalian superior colliculus (Wise and Irvine 1985), inferior colliculus (Wenstrup et al. 1986), and auditory cortex (Rajan et al. 1990). One possibility is that edge azimuths are organized topographically so that the azimuth of the sound source can be determined by detecting the location of a sharp increase in neural activity along a neural map. Evidence for such edge maps is available for both the cat superior colliculus (Middlebrooks and Knudsen 1984; Wise and Irvine 1985) and the expanded 60-kHz CF region of the mustache bat IC (Wenstrup et al. 1986) but is lacking for the cat IC. Alternatively one can conceive of schemes similar to the population vector that would provide accurate directional information based on edges without requiring neural maps.

As we mentioned for codes based on tuned neurons, a requirement for both edge-map or population-edge codes is that edges encompass the behaviorally relevant range of azimuths. Figure 5 shows that this condition is approximately met in the IC in that the distribution of half-maximal azimuths extends from  $-54$  to  $+54^\circ$  with a small gap near  $+36^\circ$ . Figure 5 only shows data for the IC on one side; the overall distribution of half-maximal azimuths for both ICs would show a broad maximum at the midline. This overrepresentation of central azimuths is consistent with psychophysical observations in both cats (Heffner and Heffner 1988; Huang and May 1996b; May and Huang 1996) and humans (Makous and Middlebrooks 1990; Mills 1958) that sound localization is more accurate near the midline than for lateral positions. This midline advantage is particularly strong in cats, where the direction toward which animals turn their head severely undershoots actual source position for azimuths more lateral than  $\pm 45^\circ$  (May and Huang 1996). If this finding is not a limitation of the head-turning paradigm, this undershoot is consistent

with the paucity of IC cells having half-maximal azimuths more lateral than  $45^\circ$ .

Huang and May (1996a) found that cats more accurately localize noise bands when the noise encompasses the 5–18 kHz region than when it consists entirely of higher frequency components. They interpreted their result as evidence that the sharp spectral notches in HRTFs between 8 and 18 kHz play a key role in sound localization (Musicant et al. 1990; Rice et al. 1992). Although their interpretation seems appropriate for elevation, the first notch in the HRTFs of Musicant et al. (1990) remains nearly constant at 11–13 kHz throughout the horizontal plane so that it is not likely to provide a robust cue for azimuth. Indeed azimuth receptive fields for VS stimuli never showed a trough that could be unambiguously accounted for by the first notch. A more likely explanation for the Huang and May (1996a) result lies in the frequency dependence of ILDs. Azimuth modulation indices of IC neurons were maximal for units with CFs between 6 and 15 kHz. This frequency region is that where the rate of change of ILD with azimuth is maximal and where localization is the most accurate. Thus edge codes are consistent with the frequency dependence as well as the azimuth dependence of sound localization in the horizontal plane.

One difficulty with edge codes is the ipsilateral bias in the distribution of half-maximal azimuths (Fig. 5). This bias is not unique to VS stimuli in anesthetized cats but also is found for free-field stimuli in the cat IC (Aitkin and Martin 1987) and in the IC of the unanesthetized mustache bat (Wenstrup et al. 1988). Thus it seems to be a robust result. This ipsilateral bias seems inconsistent with observations that unilateral ablation of the IC causes severe deficits in sound localization on the contralateral side (Casseday and Neff 1975; Jenkins and Masterton 1982). Two hypotheses might explain this inconsistency. The first one is that contralateral sound-localization deficits induced by unilateral ablation primarily reflect a loss of sensitivity to ITD, which only plays a weak role with our high-frequency VS stimuli. Consistent with this hypothesis, best ITDs of IC neurons do show a contralateral bias (Fitzpatrick et al. 1997; Yin and Chan 1988). A second hypothesis is that IC cells with ipsilateral half-maximal azimuths may not play a primary role in sound localization. Because the IC is essentially an obligatory way station in the auditory pathway, the population of IC neurons must support all forms of auditory behaviors in addition to sound localization. Cells with ipsilateral half-maximal azimuths give a robust response for azimuths near the midline, so that they are well suited for representing stimulus properties (such as spectral features) that are not primarily directional in the natural situation when the listener is facing the sound source.

Our results on neural responses to monaural stimulation of the contralateral ear are relevant to psychophysical studies of “monaural” sound localization achieved by ear occlusion. Despite some inconsistencies attributable to incomplete occlusion (Wightman and Kistler 1997), most studies conducted with low-level, broadband, free-field stimuli report a severe reduction in azimuth acuity, with only minor impairments in elevation discrimination (Butler et al. 1990; Oldfield and Parker 1986; Slattery and Middlebrooks 1994). These findings are consistent with our observation that IC neurons show significantly less response modulation as a function of azimuth for monaural stimulation than for binaural stimulation, whereas

modulation indices for elevation are similar in the two conditions (Fig. 3). Psychophysical studies with monaural ear occlusion consistently report a strong bias in azimuth judgments toward the side of the unoccluded ear. This behavior is also consistent with a neural code based on edge azimuths because a vast majority of our contra-preference units responded vigorously to monaural stimuli located near the midline, as would occur for a binaural stimulus located well on the contralateral side.

Although the preceding discussion focused on edges and peaks in receptive fields, azimuth might be coded by the overall pattern of activation in the neural population without an explicit dependence on peaks or edges. One such “population-pattern” code was proposed by Wise and Irvine (1985) for the cat superior colliculus SC. In their scheme, ILD (and, by implication, azimuth) is coded by the relative proportions of activated neurons in three groups corresponding roughly to our BF, BI, and BF&I neurons. Although this exact scheme may not work for the IC because differences in best azimuths among the three groups are not as clear-cut as they are in the SC, other similar schemes might be workable. A general issue with population-pattern codes is the potential complexity of the neural circuitry needed to decode stimulus information.

Yet another alternative are codes based on temporal discharge patterns. Figure 2 suggests that temporal discharge patterns of IC cells may contain directional information that is not available in the average rates of discharge. In this respect, the situation in the IC resembles that found by Middlebrooks et al. (1994) in the anterior ectosylvian sulcus of the cat auditory cortex. However, one important difference between the two studies is that Middlebrooks et al. (1994) used random noise stimuli, whereas our VS stimuli were synthesized by filtering the same exactly reproducible waveform through every HRTF. Thus temporal discharge patterns for VS stimuli may reflect fluctuations in the envelope of this particular noise waveform as well as a code for sound localization. On the other hand, many IC cells have sustained response patterns and therefore a richer opportunity for encoding directional information in their temporal discharge pattern than cortical cells that only respond to stimulus onset. A systematic study of directional information available in temporal patterns for various stimulus waveforms is needed.

In summary, we have discussed four classes of neural codes for localization of high-frequency stimuli in the horizontal plane: edge codes based on half-maximal azimuths of contra-preference cells, codes based on best azimuths of tuned neurons, population pattern codes, and codes based on temporal discharge patterns. Although none of these codes can be ruled out and all may play a role in certain conditions, edge codes seem to be the most promising for representing azimuth in high-CF IC neurons. Edge codes can account for both the frequency and azimuth dependence of sound localization in the horizontal plane and for the effects of monaural ear occlusion but have difficulties accounting for the effects of unilateral ablation of the IC. Although our results favor edge codes for localization of high-frequency stimuli in the horizontal plane, localization of low-frequency stimuli and localization in the median vertical plane probably rely on different codes. How these codes are integrated to subsume the wide range of sound localization behavior is a key question for future research.

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Present addresses: P. X. Joris, Division of Neurophysiology, University of Leuven Medical School, B-3000 Leuven, Belgium; R. Y. Litovsky, Dept. of Biomedical Engineering, Boston University, Boston, MA 02215.

Address for reprint requests: B. Delgutte, Eaton-Peabody Laboratory, Massachusetts Eye and Ear Infirmary, 243 Charles St., Boston, MA 02114.

E-mail: bard@epl.meei.harvard.edu

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