Spatial Receptive Fields of Primary Auditory Cortical Neurons in Quiet and in the Presence of Continuous Background Noise

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Brugge, John F., Richard A. Reale, and Joseph E. Hind. Spatial receptive fields of primary auditory cortical neurons in quiet and in the presence of continuous background noise. J. Neurophysiol. 80: 2417–2432, 1998. Spatial receptive fields of primary auditory (AI) neurons were studied by delivering, binaurally, synthesized virtual-space signals via earphones to cats under barbiturate anesthesia. Signals were broadband or narrowband transients presented in quiet anechoic space or in acoustic space filled with uncorrelated continuous broadband noise. In the absence of background noise, AI virtual space receptive fields (VSRFs) are typically large, representing a quadrant or more of acoustic space. Within the receptive field, onset latency and firing strength form functional gradients. We hypothesized earlier that functional gradients in the receptive field provide information about sound-source direction. Previous studies indicated that spatial gradients could remain relatively constant across changes in signal intensity. In the current experiments we tested the hypothesis that directional sensitivity to a transient signal, as reflected in the gradient structure of VSRFs of AI neurons, is also retained in the presence of a continuous background noise. When background noise was introduced three major affects on VSRFs were observed. 1) The size of the VSRF was reduced, accompanied by a reduction of firing strength and lengthening of response latency for signals at an acoustic axis and on-lines of constant azimuth and elevation passing through the acoustic axis. These effects were monotonically related to the intensity of the background noise over a noise intensity range of ~30 dB. 2) The noise intensity-dependent changes in VSRFs were mirrored by the changes that occurred when the signal intensity was changed in signal-alone conditions. Thus adding background noise was equivalent to a shift in the threshold of a directional signal, and this shift was seen across the receptive field. 3) The spatial gradients of response strength and latency remained evident over the range of background noise intensity that reduced spike count and lengthened onset latency. Those gradients along the azimuth that spanned the frontal midline tended to remain constant in slope and position in the face of increasing intensity of background noise. These findings are consistent with our hypothesis that, under background noise conditions, information that underlies directional acuity and accuracy is retained within the spatial receptive fields of an ensemble of AI neurons.

INTRODUCTION

Under natural conditions a listener often must use acoustic cues to detect, identify, and locate particular sounds in environments filled with competing background noise. For the listener to accomplish these feats, the auditory system had to develop mechanisms not only to minimize the interference that one sound inflicts on another but to do so over a wide range of intensity of both signal and noise. There has been a long history of psychophysical studies of auditory masking, and indeed the auditory system does employ different processing modes depending on the temporal relationships and interaural configurations of signal and masker (for reviews see McFadden 1975; Moore 1993). Most psychophysical and physiological studies of binaural masking have been designed with the idea that signal extraction by the central auditory system is used by the listener to achieve maximal detection performance rather than to derive information about the signal’s spatial location. There have been few reported psychophysical studies of masking of sound-source location or direction under continuous masking conditions. Good et al. (1997) and Good and Gilkey (1996) explored how in the free field the presence of continuous background noise influences a listener’s ability to make an absolute judgment on the true location of a sound. Their results indicate that, whereas accuracy of localization judgments is clearly affected by the presence of masking noise, relatively good localization performance can be observed even where signals are near detection threshold. This implies that the neural mechanisms underlying localization of a sound source are relatively tolerant of competing background sound. We showed previously that, when mapped with transient broadband signals in an otherwise quiet anechoic virtual acoustic space (VAS), neurons in primary auditory cortex (AI) exhibit large virtual space receptive fields (VSRFs) (Brugge et al. 1994, 1996, 1997a,b; Reale et al. 1996, 1998). For many AI neurons, there exists within the spatial receptive field a gradient of response latency or strength, or both, with latency shortest and discharge strength greatest at or near an acoustic axis. We postulated that such gradients in the receptive field could serve to encode sound-source direction in the output of an ensemble of AI neurons whose receptive fields were organized this way, and a quantitative model was proposed that upholds these predictions (Jenison 1998). If our hypothesis is correct that the direction of acoustic transients is encoded in the internal structure of AI spatial receptive fields, then one would predict that this structure would remain relatively intact with wide swings in the levels of both the signal and the background sound. Previous studies indicated that for a single AI cell spatial gradients could remain relatively constant across changes in signal intensity (Brugge et al. 1996). We might therefore expect that a similar structural constancy would obtain when a background noise is introduced into the acoustic environment. To test this we have begun to study AI spatial receptive fields in noisy environments, taking advantage of our ability to generate sounds in VAS. The experiments presented in...
this paper address the issue of whether and to what extent directional sensitivity to a transient signal, as reflected in the VSRF of AI neurons, is retained in the presence of a continuous background noise. This binaurally uncorrelated noise corresponds to a diffuse sound field that might represent a highly reverberant environment or an environment containing many independent sound sources.

**Methods**

Detailed descriptions of the methods of animal preparation, synthesis of virtual space signals, extracellular single-neuron recording, and data collection are found in previous publications (Bruggé et al. 1994, 1996; Reale et al. 1996, 1998). Briefly, cats were anesthetized with sodium pentobarbital (40 mg/kg ip), and a venous catheter was inserted for supplemental administration of the drug (8 mg/kg iv) to maintain a surgical plane of anesthesia. Fluid replacement was maintained with a continuous infusion (3 ml kg⁻¹ h⁻¹) of 5% dextrose in 0.9% sodium chloride. Additional medications included atropine sulfate (0.1 mg/kg sc), dexamethasone sodium (0.2 mg/kg iv), and procaine penicillin (300K units im). Body temperature was maintained at 38°C by a thermostatically controlled DC heating blanket. A tracheal cannula was inserted, and the pinnae and other soft tissue removed from the head. Hollow earpieces for sound delivery were inserted into the ear canals, sealed in place, and connected to specially designed earphones (Chan et al. 1993). The transfer characteristics of the left and right ear sound delivery systems were measured in vivo near the tympanic membrane. A chamber was cemented to the skull over the left auditory cortex, filled with warm silicone oil and hydraulically sealed with a glass plate on which a Davies-type microphone was mounted.

Action potentials were recorded extracellularly from single neurons in cortical area AI with tungsten-in-glass microelectrodes. An effective VAS signal evokes from a single AI neuron one spike or a burst of a few action potentials time locked to the stimulus onset. The times of occurrence of action potentials were recorded with a resolution of 1 μs. Area AI was confirmed by the partial tonotopic map that emerged from repeated electrode penetrations made over the course of the experiment, which typically extended over several days.

**Acoustic stimulus generation**

Acoustic stimuli were tone pips (50-ms duration, 5 ms rise-fall time), continuous broadband noise, and impulsive transients (6.4 ms duration); the latter mimicked in their spectrum and time waveform sounds arriving from a source in free space. Tone pips delivered monaurally or binaurally were used to estimate the characteristic frequency (CF; that frequency for which threshold is lowest) of a neuron. We did not examine systematically other tone-evoked response properties of these cells, as the main goal of the experiment was to study parameterically their directional responses to acoustic transients. Continuous broadband noise by itself did not evoke responses (other than at onset) from any AI neuron in this study, although in all cats studied it modified the responses to directional transient signals. The directional signal was a broadband (3-dB corner frequencies at 800 Hz and 40 kHz) or narrowband (3-dB bandwidth = 2 kHz) impulsive transient waveform originally generated by a sound source in free space and realized as the impulse response of a linear-phase finite-impulse-response (FIR) filter (Chen et al. 1994). The latter had its center frequency set equal to the CF of the neuron and was employed for those neurons where broadband transients did not evoke consistent responses. Digitally synthesized signals (i.e., tone pips and impulsive transients) were compensated for the transmission characteristics of the earphones and sound delivery pathways (Bruggé et al. 1994; Chen et al. 1994) before D/A conversion with a digital stimulus system (DSS). Separate DSS attenuators controlled the intensity of signals delivered to each ear, which in these experiments were set to equal values.

Sound produced by a free-field source and recorded near the tympanic membrane of the cat is transformed in a direction-dependent manner by the pinna, head, and upper body structures (Musican et al. 1990; Rice et al. 1992). The simulation of these directional sounds constitutes a VAS. Improvements in the synthesis and applications of VAS for neurophysiological studies is an ongoing process in our laboratory. Only a brief description and chronology of the relevant work is given here, as the details are found in the published articles (for review see Reale et al. 1996, 1998). First, we obtained an accurate approximation, by using FIR filters (Chen et al. 1994), of the free field to eardrum transformation for each sound-source direction with empirical free-field measurements obtained by Musican and colleagues (1990). Second, we designed a closed field sound delivery/measurement system that did not modify the spectrum of signals delivered to the eardrums (Chan et al. 1993). Third, we designed and acoustically validated a frequency-domain general mathematical model of VAS that used as input the FIR-filter-approximated transformations and provided as output a veridical interpolation of VAS (Chen et al. 1995). Last, the VAS model was enhanced to be used as an interactive tool in binaural electrophysiological studies and was implemented in the time domain by a quasi-real-time algorithm (Reale et al. 1996; Wu et al. 1997). With this tool, any number of simulated signals can be synthesized for selected sound-source directions positioned in a spherical coordinate system [0°–360° azimuth, -90° to +90° elevation] and centered on the cat’s head. For each individually modeled cat and a particular sound source (e.g., broadband transient), there is a unique relationship between sound-source direction and the peak-to-peak amplitudes of synthesized VAS signals.

**Spatial receptive field measurements**

VSRF properties were studied with a protocol that contained three stimulus paradigms. Each paradigm was executed both with-
RESULTS

Results were obtained from seven cats drawn from a larger population of experiments in which we studied the VSRFs of several hundred neurons under various VAS conditions. Thirty of these neurons responded to directional transients and remained in contact with the electrode long enough to be studied parametrically and quantitatively for the effects of background noise on their spatial receptive field properties. The majority of VSRFs were categorized as falling predominantly in the contralateral (56%) or ipsilateral (19%) acoustic hemifield. The remainder were considered frontal (7%), omnidirectional (15%), or complex (3%). These proportions are close to those reported earlier (Brugge et al. 1994). The CFs of these neurons ranged from 7.3 to 28.6 kHz.

Effects of noise on the size of the VSRF

The effects of continuous background noise on the spatial extent of a VSRF are introduced in Fig. 2 with data from two neurons. Each black square on a VSRF map denotes an effective stimulus. The left hemisphere of each connected pair of hemispheres represents frontal acoustic space as seen by the cat. The front right acoustic quadrant is always contralateral with respect to the left AI under study. The right hemisphere of the pair represents the rear acoustic hemifield, with the right rear quadrant adjoining the right front quadrant at +90°.

The VSRF at the top of each of the two columns in Fig. 2 is the signal-alone condition for that neuron obtained with the signal intensity ~20–30 dB above threshold and with background noise held at 110 dBA. Noise intensity (dBA NOISE) is shown above each VSRF in a series. The signal-alone VSRF in the left column occupies essentially all of auditory space, whereas the one in the right is confined mainly to the contralateral front acoustic quadrant. The effects on the VSRF of adding background noise with different noise intensities are illustrated below each of the signal-alone receptive fields. As intensity of the background noise was raised, the VSRF remained intact but was systematically reduced in size. For all cell categories the degree to which the field was reduced in size was a function of the intensity of the noise. A noticeable effect generally required ~10 dB of dynamic range to achieve (see also Figs. 5 and 7). With the possible exception of the few neurons in our sample exhibiting frontal VSRFs, the relatively small VSRF remaining was located in the region of the acoustic axis. The data were not adequate to ascertain more precisely a relationship between the location of the reduced VSRF and the direction of the acoustic axis. Frontal VSRFs tended to remain on or near the midline.

We analyzed further the effects of noise on the size of the spatial receptive field by computing the spherical area (SA) of the VSRF (see Brugge et al. 1997). In Figs. 2 and 7 the SA is shown to the left of its corresponding VSRF. SA is expressed in spherical degrees; one spherical degree is that portion of a sphere enclosed by a spherical
FIG. 2. Virtual space receptive fields (VSRFs) from 2 AI neurons under conditions of signal alone (top, 110 dBA NOISE) and signal in the presence of continuous background noise. Noise intensity shown above each VSRF.

triangle with two sides each having arcs of 90° and a third side having an arc of 1°. Figure 3 summarizes the results of this analysis. In Fig. 3A, SA is plotted as a function of noise intensity for four neurons, including one of those shown in Fig. 2. The size of the VSRF obtained with the signal alone varied among the four neurons as shown here by the range of SA between ~150 and 400°. When background noise was introduced and its intensity raised systematically, the SA fell abruptly and in a nearly linear fashion, reflecting the changes seen in the VSRF maps. We fit a straight line to the linear segment of the SA versus noise-intensity function for each of the 22 neurons in our
suppression index is defined as the change of noise intensity (in dB) required to reduce the size of the VSRF by 50%. Figure 3C illustrates the distribution of the noise-suppression index, including mean (14.7 dB) and SD (5.6 dB), for the entire sample. Thus, on average, a VSRF was reduced to one-half its size when a background noise-

![Graph A: spherical area (SA) of the VSRF plotted as a function of intensity of the continuous background noise for 4 AI neurons.](image1)

![Graph B: normalized SA plotted as a function of the intensity of continuous background noise for those noise intensities that reduced the size of the VSRF. Dashed lines are linear fits to the data.](image2)

![Graph C: distribution of the noise suppression index. See text for details.](image3)

The correlation coefficients ranged from 0.854 to 0.995, although the slopes and intercepts of the functions varied among neurons, as can be seen in the three examples plotted in Fig. 3B. We derived from the slopes of these linear functions a measure that we call the "noise-suppression index." The noise-

![Graph A: number of spikes evoked (filled symbol) and mean onset latency (open symbol) to signal alone at the acoustic axis (110 dBA noise) and in the presence of continuous background noise at increasing intensity. B and C: same as (A) for 13 AI neurons, with spike count normalized to maximum.](image4)
was raised by ~15 dB above noise threshold and was completely obliterated when the noise was raised by 30 dB.

**AA functions**

Changes in the spatial extent of an AI neuron’s VSRF consequent to the addition of continuous background noise reveal nothing about the effects such addition might have on the possible information bearing response properties within the VSRF. To study this question, we first examined the changes in a cell’s discharge properties that took place at the acoustic axis as a function of noise intensity (AA functions). Thus, for AI cells with measurable frequency tuning and CF, VAS transient signals positioned on or near the acoustic axis typically have the lowest detection thresh-

![Graphs showing effects of noise on VSRFs and azimuth (AZ) and elevation (EL) functions for a single AI neuron. Dots on the top left globe indicate directions from which a signal was presented. Trajectories pass through the acoustic axis. VSRFs plotted as in Fig. 2. Spike count, normalized spike count, mean 1st spike latency, and change in mean 1st spike latency as a function of AZ (A–D) or EL (E–H). Noise intensity given in the inset. See text for details.](image-url)
old. Illustrative data from one AI neuron are presented in Fig. 4A. Here the AA functions are plotted for both spike count (filled symbol) and mean first spike latency (open symbol). Plotted data were obtained when the intensity of the signal was held constant and that of the background noise was raised in steps of 5 dB. As is typical for AI neurons under the conditions of this experiment, the response to each of the effective VAS transient signals was a single action potential tightly time locked to stimulus onset. The neuron responded to almost every signal of the 40 presented with a mean response latency of 16.5 ms. The dynamic range, from maximal to minimal response, required only a 15- to 20-dB change in noise intensity. The fall in response strength was accompanied by a concomitant rise in response latency of ~4 ms. We encountered no exceptions to these forms of AA functions, 13 of which are plotted in Fig. 4, B and C, to illustrate the generality of the findings. Here response strength was normalized to the maximum count.

**AZ and EL functions**

We examined the changes in a cell’s discharge properties as a function of noise intensity that took place at multiple directions in the VSRF. A set of directions with constant elevation (AZ function) or constant azimuth (EL function) were chosen to pass through the acoustic axis and thereby cross regions in the VSRF where, for many AI neurons, response gradients tend to be steepest (see Brugge et al. 1996). Figure 5 presents results from one neuron that illustrate response features exhibited by all neurons in the series save those few exhibiting frontal VSRFs. In Fig. 5 VSRFs are illustrated along with AZ and EL functions obtained when transient signals were presented alone and when the same signals were delivered in the presence of continuous background noise. The trajectories of the AZ and EL functions are shown as dotted lines (left column, top) intersecting at the acoustic axis for this cell (CF = 15.8 kHz). The dots along the trajectories represent the signal directions from which data were obtained in both azimuth and elevation. For these data both absolute and relative values of spike count and latency are plotted in the AZ and EL functions. We do this because from our previous studies there was evidence that directional information might be preserved in the relative changes in these response parameters (Brugge et al. 1996). Thus the ordinates are total spike count (Fig. 5, A and E), spike count normalized to the maximal count (Fig. 5, B and F), mean latency (Fig. 5, C and G), and changes in mean latency relative to the minimum (Fig. 5, D and H). The dashed vertical line on each graph represents the frontal midline and the arrow the acoustic axis.

We note first that the VSRF under the signal-alone condition occupied most of the contralateral acoustic hemifield and a substantial portion of the ipsilateral field. The shape of the corresponding AZ and EL functions obtained under this signal-alone condition (Fig. 5, A and B, open symbol) reflect the size, shape, and location of the VSRF. As shown in Fig. 5A, spike count remained near maximum for azimuthal directions across the contralateral frontal quadrant. Spike count fell rather abruptly for directions spanning the midline, between about +18° and −18°. For directions behind the animal the count gradually declined. The EL functions (Fig. 5, E and F) show that the neuron fired maximally around the acoustic axis and maintained near-maximal firing at all other elevations studied. Under these quiet background conditions, onset latency tended to mirror the spike count (Fig. 5, C, G, D, and H, open symbols). Latency was shortest and spike count was highest for signals around azimuth +27° and elevation +18°, which is close to the direction of this acoustic axis. Latency increased and count decreased systematically for directions on either side of the acoustic axis, with steepest gradients occurring along the azimuth across the frontal midline.

The VSRF and the AZ and EL functions underwent demonstrable changes when continuous background noise was introduced and its intensity raised in steps of 5 dB. Four observations can be made of these data. First, the shapes of both AZ and EL functions tended to become narrower as background noise intensity was increased, consonant with the decreasing size of the VSRF. Second, the narrowing in the AZ function shapes was not symmetrical around the peak of the function, and there was a slight displacement of maximal count and minimal latency toward the frontal midline. Near the frontal midline the functional gradients remained steep and relatively closely aligned, whereas segments of AZ functions located behind the animal (e.g., +90° to +180°) exhibited shallower gradients that shifted markedly in position with changes in noise intensity. Third, the narrowing of the EL function shapes tended to be symmetrical around the maximal count and minimal latency. Fourth, normalizing the curves tended to bring the functions into greater alignment (Fig. 5, B, F, D, and H), particularly those segments of AZ functions that cross the frontal midline.

All neurons studied this way exhibited a similar reduction in the size of the VSRF and narrowing in shape of the AZ and EL functions with increasing intensity of background noise. Figures 6 and 10 show AZ functions from three additional neurons that illustrate the variability in these relationships seen among cells in our sample. Additional EL functions are shown in Fig. 11. Again data were plotted as a function of both absolute and relative count and latency. For the first of these cells, except at the highest noise level studied (40 dBA) the AZ functions showed that for signals delivered in the contralateral acoustic hemifield spike count remained at a maximum and latency at a minimum in the signal-alone condition and over a wide range of background noise levels (Fig. 6, A–D). For the second cell (Fig. 6, E–H) the AZ functions exhibited broad spatial tuning only for signal-alone conditions or when the noise was at its lowest intensity. In both cases, steep spatial gradients of count and latency were again evident, spanning azimuthal directions between 0° and 90°. The data shown in Figs. 10 and 11 exhibit AZ and EL functions that resemble even more closely the ones illustrated in Fig. 5. For those neurons having ipsilateral VSRFs the AZ and EL functions tend to mirror those associated with contralateral VSRFs, as described previously. For neurons with frontal VSRFs functional gradients are also exhibited, although the AZ functions tend to remain symmetrical around a peak at the midline, and the EL functions tend to exhibit a broad maximum over a
FIG. 6. Same as Fig. 5, A–D.
FIG. 7. VSRFs obtained under conditions in which the transient signal was presented in the presence of background noise (left column) and when the VSRFs were obtained with the signal alone (right column). VSRF shown at top middle obtained with signal alone at 26 dBA. Intensity of the signal or noise shown above each VSRF. SA: spherical angle (degrees).
wide range of background noise levels. We do not have sufficient data on complex VSRFs for comparison.

**Background noise results in a change in signal threshold**

During the course of this study and from our earlier findings (Brugge et al. 1996) it became evident that the presence of a steady background noise influenced VSRF properties in ways that were similar to those associated with changing signal level under listening conditions in which no background noise was present. To examine more closely this possible relationship we compared directly, in the same neuron, the VSRF properties obtained in the presence of increasingly intense background noise to those same properties recorded when no noise was present but the signal intensity was decreased.

Figure 7 shows the results of such a comparison for one AI neuron, which are illustrative of results obtained for all neurons in this study. The top-middle panel shows the VSRF when no noise was present. The left column shows signal-in-noise conditions where background noise intensity was increased in steps of 5 dB, from top to bottom. The progressive increase in noise intensity systematically decreased the SA and restricted the VSRF to a small region around the plotted as a function of change in ... the background noiseAA, as shown previously in Figs. 2 and 5. The VSRFs in with the signal at a constant intensity (S + N closed symbol) or the intensity of the signal when presented alone in quiet (S open symbol) at the acoustic axis. The abscissa was adjusted to align the curves.

FIG. 9. Normalized spike count (A and C) and mean 1st spike latency plotted as a function of change in intensity of either the background noise with the signal at a constant intensity (S + N closed symbol) or the intensity of the signal when presented alone in quiet (S open symbol) at the acoustic axis. The abscissa was adjusted to align the curves.

FIG. 8. SA plotted, for 4 AI neurons, as a function of change in the intensity of either the background noise with the signal at a constant intensity (S + N closed symbol) or the intensity of the signal when presented alone in quiet (S open symbol). The abscissa was adjusted to align the curves.
FIG. 10. AZ functions obtained under conditions of background noise (A–D) or signal alone (E–H). Inset indicates the intensity of noise and signal associated with these functions.
FIG. 11. Elevational functions obtained under conditions of background noise (A–D) or signal alone (E–H). Inset indicates the intensity of noise and signal associated with these functions. Same neuron as illustrated in Fig. 10.
was presented at different signal intensities (Figs. 10, $E-H$, and 11, $E-H$) are essentially identical to the families of AZ and EL functions (Figs. 10, $A-D$, and 11, $A-D$) with which they are paired.

**DISCUSSION**

There are three major findings in the work presented. First, the presence of continuous wideband background noise reduced the size of the spatial receptive fields of AI neurons and simultaneously reduced firing strength and lengthened response latency throughout the VSRF. Detailed data were obtained for signals at the acoustic axis and on-lines of constant azimuth and elevation that passed through the acoustic axis. These effects were monotonically related to the intensity of the background noise over a noise intensity range of $\sim 30$ dB. At the highest noise intensities studied, the discharge of the cell could be suppressed entirely at all signal directions studied. Second, the changes in these spatial receptive field properties as a consequence of increasing noise intensity were mirrored by the changes that occurred when the signal intensity was reduced in signal-alone conditions. Thus for these response parameters the addition of background noise was equivalent to a shift in the threshold of a directional signal, and this shift was seen across the spatial receptive field. Third, the spatial gradients of response strength and latency remained evident over the range of background noise intensity that reduced spike count and lengthened onset latency. In particular, those gradients along the azimuth that spanned the frontal midline tended to remain relatively steep and fixed in azimuthal position in the face of increasing intensity of background noise.

The first studies of the neural mechanisms of signal masking were carried out at the auditory periphery (Davis 1935; Derbyshire and Davis 1935). These experiments showed that the amplitude of the N1 potential recorded from the round window of the anesthetized cat in response to a click or noise stimulus was reduced when that signal was mixed with a background of continuous broadband noise. Three decades later Kiang and colleagues (1965) went on to demonstrate that for a single auditory nerve fiber the presence of continuous broadband noise reduced the amplitude, but not the latency, of peaks in the poststimulus time histogram obtained with click stimuli. They suggested that the effect of increasing the level of noise “may be compared with the effect of decreasing click level.” Rosenblith (1950) and Goldstein and Kiang (1958) studied the effects of noise on the click-evoked potential from auditory cortex and on the N1 potential at the round window in anesthetized cats, repeating and extending the earlier experiments of Davis and Derbyshire. They found that the response of both auditory nerve and cortex to clicks was affected “in proportion to the amount of noise masking,” although constant noise alone seemed to evoke no measurable response from either site. Erulkar and colleagues (1956) clearly demonstrated, in recordings from single AI neurons in the anesthetized cat, that a tonal background increased markedly the latency of the click response and diminished the average number of spikes per click stimulus. In other words, an intense click when delivered against a certain tonal background caused a unit to discharge “as if the clicks delivered were weak.” Similar observations were made by Phillips and Cynader (1985) and Phillips and Hall (1986), who studied the responses of AI neurons to contralateral CF tones in the presence of continuous wideband noise (see also Phillips 1985, 1990). In our experiments, none of their cells responded in a sustained fashion to continuous noise. The main consequence of continuous noise background was to elevate tone threshold. This general decrease in sensitivity was reflected in a simple linear shift in the input-output function along the signal-intensity axis. The magnitude of the shift was equal to the change in noise level in decibels. Our results are in accord with these findings, namely, the magnitude of change in receptive field properties was a monotonic function of the magnitude of change in the background noise intensity. Phillips and colleagues also noted that noise-induced threshold shifts were the same for cells exhibiting monotonic or nonmonotonic rate-level functions. Imig et al. (1990) on the other hand reported that for AI neurons there was a high correlation between the azimuthal tuning and the growth of spike count with stimulus level; neurons narrowly tuned to azimuth tended to exhibit nonmonotonic spike count-versus-level functions. We did not study rate level functions over a range sufficient to address this issue directly, although it seems clear from our results that functional gradients in VSRF will remain intact over a relatively wide range of signal or noise level (see also Brugge et al. 1996).

Gibson et al. (1985) reported that in decerebrate cats the noise masking of tone-burst responses of neurons in the ventral cochlear nucleus was qualitatively similar to that recorded in auditory nerve fibers. Hence, under our conditions of a continuous diffuse noise background, the output of the two cochleas and ventral cochlear nuclei might be expected to be equivalently masked by the noise, as the spectra and overall level of the noises were kept constant at the two ears. We might infer then that in the lower brain stem, where high-frequency binaural interactions take place, changes in background noise intensity would alter equivalently the absolute strength of left and right ear excitation and inhibition, thereby maintaining a balance among the magnitudes of these bilateral inputs. If this assertion is correct it suggests that, in the steady state, diffuse noise exerts its binaural effects at levels below the auditory cortex, which is also consistent with the observation that AI neurons exhibit no demonstrable response to the steady-state component of the background noise.

The findings of ours and of others that introducing a continuous background noise is equivalent to elevating acoustic threshold places the mechanism for this form of masking mainly, if not entirely, at the level of the cochlea. Thus these results address the issue of detectability of a signal in the presence of a masking sound. They do not, however, address the question of how the direction of a sound is judged correctly in the face of competing background noise, other than that a signal probably needs to be detected to be located (e.g., see Good et al. 1997). Our results imply that, under natural free-field listening conditions in which a signal and the background noise are fluctuating in intensity, the spatial receptive fields of active AI neurons are continuously expanding and contracting. Yet, for a listener in such an environment, sound localization ability can be unexpectedly good even near detection threshold and therefore over some
range of signal-to-noise ratio (see Good and Gilkey 1996; Good et al. 1997). Thus, if AI neurons are normally engaged in determining signal direction, then some information-bearing property or properties of their spatial receptive fields, other than size, must remain relatively tolerant of the intensity of the signal, of the background noise, or of both.

In addition to altering the size of an AI spatial receptive field, continuous diffuse background noise was found to influence the onset latency and strength of the evoked discharge for all onset signal directions in the receptive field. This is a robust phenomenon and was exhibited to a great or lesser extent by all neurons in our study regardless of their class. For sound sources positioned across the frontal midline in particular, however, the relatively steep gradients of response strength and latency expressed by most AI cells in a quiet anechoic environment were maintained over a wide range of signal-to-noise level.

The structure of the VSRF when studied in quiet anechoic space appears to be governed mainly by two mechanisms, pinna filtering and binaural interactions (Brugge et al. 1994, 1996). Functional gradients of spike rate within a peripheral VSRF are established mainly by the spectral filtering properties of the pinna (Poon and Brugge 1993). This monaural spectral information may be retained to a greater or lesser extent within VSRFs of AI neurons (Brugge et al. 1996). Samson et al. (1993, 1994) reported that AZ tuning in some AI neurons survives plugging one ear, which suggests that these cells derive AZ sensitivity, in part at least, from monaural spectral cues. The structure of other VSRFs may be modified substantially by the spectral and temporal filtering properties of neuronal circuits that intervene between the cochlear nuclei and AI cortex. These complex relationships between pinna filtering and the structure of AI spatial receptive fields are poorly understood and remain under study. Binaural interactions are commonly observed in the VSRF of AI neurons (Brugge et al. 1994). In a substantial proportion of recorded AI neurons and at signal levels that exceed the acoustic attenuation created by the head, signals falling in one acoustic hemifield suppress neuronal firing. For these neurons the response is lateralized to the opposite hemifield, and the receptive field boundary at or near the frontal midline becomes sharply defined. Rajan et al. (1990) found that the most common response to variations in CF-tone intensity was maintenance of the shape and frontal midline border of the AZ function, although the proportions of constant AZ functions varied among cell classes. Imig et al. (1990), by using noise-burst signals, also observed that for a high proportion of cells the slope of the AZ function around the midline was relatively constant across level. For other classes of neurons as signal intensity is raised the receptive field may expand to engulf most or all of acoustic space, either because for all directions the signals to both ears are excitatory or because only one ear contributes to the response; yet these fields may retain directional information in their functional gradients. Thus, while binaural interactions no doubt play a role in directional sensitivity of AI neurons, the mechanisms by which spectral information extracted by each cochlea is transmitted to and through monaural and binaural channels to eventually reach AI cortex are poorly understood.

In our previous studies (Brugge et al. 1996, 1997a,b) we emphasized that onset latency was a major direction-dependent response metric of AI neurons. Direction-dependent firing strength mirrors to a large extent that recorded in single auditory nerve fibers under the same stimulus conditions (Poon and Brugge 1993). Because onset latency and firing strength are often highly correlated, firing strength could serve as well as onset latency in encoding sound direction. On the other hand, direction-dependent onset latency is an emerging property of central auditory neurons because in discharges of auditory nerve fibers latency changes little with sound-source direction (Poon and Brugge 1993) or intensity (Kiang et al. 1965). The central auditory system devised strategies at the cellular and molecular levels that faithfully preserve time information (e.g., see Trussell 1997). We favor the proposition that discharge timing as well as rate and firing probability are an important metric in the coding of directional signals at the level of AI, especially the transient sound used in this study (see also Middlebrooks 1998; Middlebrooks et al. 1994). Although onset latency is but a scalar estimate of such time information, Jenison (1998) has shown that the gradients of response latency measured in VSRFs for an ensemble of AI neurons are sufficient for an ideal observer to achieve the level of spatial acuity exhibited by human (Makous and Middlebrooks 1990) and cat (May and Huang 1996) listeners.

Good and Gilkey (1996) and Good et al. (1997) have the only reported human psychophysical data on noise masking of sound direction in the free field. In their experiments, signals and noise maskers were presented from the same or different loud speakers arrayed in a three-pole coordinate system within an anechoic chamber. Subjects were required to report the direction of the source in the presence or absence of background noise. It was found that localization judgments were clearly compromised by the presence of background noise and that the impact of the noise was complex, depending on the signal-to-noise ratio, on the target position, and on the position of the masker with respect to that of the subject. Of particular interest is the target angle and dynamic range. They showed (e.g., their Fig. 7, Good et al. 1997) that the major effects on average performance across subjects occurred when signal-to-noise ratio spanned a range of ~20 dB. Our results depicted by the dynamic range of AA functions (e.g., Fig. 9) are in very good agreement with this observation. They also reported that, although the ability to determine the direction of a signal in noise decreased nearly monotonically with lowered signal-to-noise ratio in all three dimensions, at any signal-to-noise level there were fewer errors made for signals on the frontal horizontal plane (left-to-right) than for signals distributed horizontally front-to-back or vertically (up–down). Furthermore, relatively good localization performance was observed in the frontal (left-to-right) dimension compared with the other dimensions even at low signal-to-noise ratio. This observation is in accord with our finding of steep functional gradients being maintained across the frontal midline of AI spatial receptive fields.

Listeners often find themselves in a sound field where the sound streams at the two ears exhibit various degrees of correlation. For example, uncorrelated streams might be produced in an environment that permits reflections from
multiple surfaces. Here a listener may receive a sound directly from one source and, simultaneously, other sounds that are a mixture of reflections of previously generated sounds and sounds from different sources. A diffuse field may also be produced when the number of primary sources is large and widely distributed spatially as might occur, for example, during a driving rain. In such diffuse field settings, a psychophysical phenomenon referred to as dereverberation provides a listener significant isolation from the competing background noise (Hartmann 1997). Dereverberation is lost when the sound streams arriving at the left and right ear become perfectly correlated. In this study signal direction was detected by AI neurons in the presence of steady, nondirectional, uncorrelated background noise. Under these conditions AI neurons were found to be relatively tolerant of wide changes in the signal-to-noise ratio, as would be required if these neurons are to serve directional sensitivity under certain natural conditions. The extent to which such directional information might be maintained under other competing sound conditions is presently under study.

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