Sensitivity of Auditory Cortical Neurons to Locations of Signals and Competing Noise Sources

SHIGETO FURUKAWA AND JOHN C. MIDDLEBROOKS
Kresge Hearing Research Institute, University of Michigan, Ann Arbor, Michigan 48109-0506

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Furukawa, Shigeto and John C. Middlebrooks. Sensitivity of auditory cortical neurons to locations of signals and competing noise sources. J Neurophysiol 86: 226–240, 2001. The present study examined cortical parallels to psychophysical signal detection and sound localization in the presence of background noise. The activity of single units or of small clusters of units was recorded in cortical area A2 of chloralose-anesthetized cats. Signals were 80-ms click trains that varied in location in the horizontal plane around the animal. Maskers were continuous broadband noises. In the focal masker condition, a single masker source was tested at various azimuths. In the diffuse masker condition, uncorrelated noise was presented from two speakers at ±90° lateral to the animal. For about 2/3 of units (“type A”), the presence of the masker generally reduced neural sensitivity to signals, and the effects of the masker depended on the relative locations of signal and masker sources. For the remaining 1/3 of units (“type B”), the masker reduced spike rates at low signal levels but often augmented spike rates at higher signal levels. Increases in spike rates of type B units were most common for signal sources in front of the ear contralateral to the recording site but tended to be independent of masker source location. For type A units, masker effects could be modeled as a shift toward higher levels of spike-rate- and spike-latency-versus-level functions. For a focal masker, the shift size decreased with increasing separation of signal and masker. That result resembled psychophysical spatial unmasking, i.e., improved signal detection by spatial separation of the signal from the noise source. For the diffuse masker condition, the shift size generally was constant across signal locations. For type A units, we examined the effects of maskers on cortical signaling of sound-source location, using an artificial-neural-network (ANN) algorithm. First, an ANN was trained to estimate the signal location in the quiet condition by recognizing the spike patterns of single units. Then we tested ANN responses for spike patterns recorded under various masker conditions. Addition of a masker generally altered spike patterns and disrupted ANN identification of signal location. That disruption was smaller, however, for signal and masker configurations in which the masker did not severely reduce units’ spike rates. That result compared well with the psychophysical observation that listeners maintain good localization performance as long as signals are clearly audible.

INTRODUCTION

The auditory system has evolved to process behaviorally relevant sounds in a background of competing sounds. Nevertheless, most studies of spatial hearing and of its neural substrates have employed acoustic stimuli presented in a silent background. The present study examined the responses of auditory cortical neurons to signals in the presence of continuous noise presented from various locations. The results of this study bear on two important aspects of hearing: spatial unmasking and sound localization.

Spatial unmasking refers to improved detection or identification of a signal by increasing separation of signal and competing noise sources. Spatial unmasking has been demonstrated psychophysically in humans (detection: Saberi et al. 1991; Terhune and Turnbull 1989; identification: Bronkhorst and Plomp 1988, 1989, 1992; Kidd et al. 1998; Plomp and Mimpen 1981) and in animals (ferrets: Hine et al. 1994; birds: Dent et al. 1997). Stimulus conditions used by Saberi and colleagues (1991) were most comparable to those used in the present study. They measured listeners’ detection thresholds for a click-train signal in the presence of a continuous-noise masker, varying signal, and masker locations on the horizontal plane. The elevation of detection thresholds by the masker tended to be greatest when the masker and the signal sources coincided in location, and masking tended to decrease with increasing spatial separation of the masker and the signal sources (Saberi et al. 1991).

Two groups have studied sound localization in the presence of a masking noise. Good and colleagues (Good and Gilkey 1996; Good et al. 1997) and Lorenzi and colleagues (1999) measured human listeners’ location judgements of click-train signals in a free field in the presence of a masker presented from a single source. Those studies agreed that listeners maintained relatively accurate location judgements in the presence of a masker as long as the signal was clearly audible (i.e., signal-to-noise ratio more than ~10 dB). That result implies that neural mechanisms for sound localization are fairly resistant to competing sounds.

Previous studies of neurons in the auditory cortex have examined the impact of continuous noise on neuronal responses (Brugge et al. 1998; Phillips 1985; Phillips and Cynader 1985; Phillips and Hall 1986). In those studies, neurons showed little or no sustained response to a continuous noise, and the presence of continuous noise tended to decrease spike rates and to increase spike latencies in response to an added stimulus. An increase in the level of a background noise was largely equivalent to a decrease in the level of the signal. Brugge and colleagues (1998) recorded the responses of neurons in the cat primary auditory cortex to broadband signals.
that simulated sources at various locations in virtual auditory space. A spatially diffuse masker was simulated by adding binaurally uncorrelated noise to the signals at the two ears. Analysis of virtual spatial receptive fields, spike rates, and first-spike latencies indicated that the size of the masker-induced shift in neural sensitivity was largely independent of virtual signal-source location.

The present study further examined the effects of continuous background noise on the responses of cortical neurons to click trains that varied in location in a free field. We refer to the click-train stimulus as the signal and to the continuous background noise as the masker. Click trains were used as signals because they were also used in psychophysical studies reviewed above (Good et al. 1996, 1997; Lorenzi et al. 1999; Saberi et al. 1991) and because they were somewhat comparable to the single-impulse stimuli used in the physiological study by Brugge and colleagues (1998). We focused on the effects of focal maskers presented from single loudspeakers and examined the influences of masker and signal source locations on responses of cortical neurons in the cat’s auditory cortical area A2. Neurons in area A2 have several response properties that invite study of sound-location coding. Those properties include broad frequency tuning (Schreiner and Cynader 1984), sensitivity to sound location in both horizontal and vertical planes (Middlebrooks et al. 1998; Xu et al. 1998), and spatial sensitivity that parallels psychophysical responses to sounds that produce spatial illusions (Xu et al. 1999).

Consistent with previous studies, we found that the presence of a masker reduced neural sensitivity to signals for the majority of units. The size of the reduction in sensitivity varied with the relative locations of the signal and masker sources: the effect of the masker decreased with increasing separation of signal and the masker. That result resembled psychophysical spatial unmasking found by Saberi and colleagues (1991). We obtained an unexpected result for a sizeable minority of units: the masker reduced spike rates at low signal-to-noise ratios but augmented spike rates at higher signal-to-noise ratios. We used an artificial neural network (ANN) algorithm to evaluate the accuracy with which neural spike patterns signaled the locations of signal sources in the absence and presence of the masker. For many configurations of signal and masker, addition of a masker altered spike patterns and profoundly disrupted ANN identification of signal location. That disruption, however, was less severe for configurations of signal and masker in which the masker did not severely reduce the unit’s spike rate. That result resembled the psychophysical observations by Good and colleagues (Good and Gilkey 1996; Good et al. 1997) and by Lorenzi and colleagues (1999) that listeners localized signals accurately under conditions in which the signals were clearly audible and showed degraded performance when the signals were near or below audibility.

**Methods**

**Experimental apparatus, stimulus generation, and data acquisition**

Stimuli were click trains (250-s⁻¹ rate, 80-ms duration) presented in quiet or in the presence of a continuous broadband background noise. Throughout the present paper, we refer to the click trains as the signals and to the background noise as the masker. Additional stimuli were 80-ms noise bursts used as search stimuli and 80-ms tone bursts used for measuring units’ frequency sensitivities. The experimental apparatus for stimulus generation was identical to that detailed previously (Middlebrooks et al. 1998) except for the addition of background noise. Briefly, experiments were controlled with an Intel-based personal computer. Maskers were generated with analog devices (described later). All stimuli other than the masker were synthesized digitally at a sampling rate of 100 kHz, using equipment from Tucker-Davis Technologies (Gainesville, FL). Experiments were conducted in a sound-attenuating chamber that was lined with acoustical foam (Illbruck, Minneapolis, MN) to suppress reflections of sounds at frequencies <500 Hz.

Signals were presented from multiple loudspeakers, one loudspeaker at a time. A circular hoop held the loudspeakers in the horizontal plane at a distance of 1.2 m from the animal’s head. The speaker location directly in front of the animal was labeled 0°, and positive azimuths indicated speakers on the right side of the animal, which was ipsilateral to the recorded cortical hemisphere. Signal source locations varied between −160° and +160° in 40° steps. Speakers were calibrated using a precision microphone (ACO Pacific) with Golay codes as probe sounds (Golay 1961; Zhou et al. 1992). An inverse filter response for each loudspeaker was stored on computer disk. The click signal presented to a loudspeaker was the time-domain waveform of the inverse transfer function of the particular loudspeaker, windowed to a 3-ms duration. Clicks emitted from the loudspeakers had 80% of the power restricted to an 80-μs compressive peak and had flat spectra between 0.5 and 30 kHz. Noise and tone bursts were 80 ms in duration, ramped on and off with 5-ms rise/fall times. Signals and tone bursts were presented once per second.

Continuous maskers were generated by a custom broadband random noise generator, spectrally flattened by a two-channel graphic equalizer (Rane, Mukilteo, WA), and presented through a single loudspeaker placed at various azimuths. The amplitude spectrum of the masker sound field measured at the center of the chamber was low-passed <30 kHz and showed root-mean-squared fluctuation of 3 dB from 0.5 to 30 kHz. The center of the masker loudspeaker was positioned 5° below the circular hoop that held the signal loudspeakers. Masker source locations varied between −120° and +120° in 40° steps. We refer to the maskers presented from single loudspeakers as focal maskers. An additional, diffuse, masker condition used two uncorrelated noise sources. In that condition, noises were generated by the two independent random noise sources, shaped with the two channels of the graphic equalizer, and presented through two loudspeakers at azimuths of −90° and +90°. The resulting signals in the two ears were largely uncorrelated. Such uncorrelated signals at two ears produce a sensation of a spatially diffuse sound (Blauert 1997). The diffuse masker condition was the condition that was most similar to the masker used in the study by Brugge and colleagues (1998). All units, except 13 units recorded in a supplementary experiment (described later), were tested with focal-masker locations of −40, 0, and +40° and masker levels of 35 dB SPL (re: 20 μPa). A subset of units was tested with additional focal masker locations, the diffuse masker, and/or masker levels of 15 and 25 dB SPL. In a supplementary experiment, units were tested with the 0° focal masker and with the diffuse masker levels of 15, 25, and 35 dB SPL.

Procedures for unit recording and for spike sorting were identical to those detailed by Furukawa et al. (2000). Briefly, unit activity was recorded extracellularly with silicon-substrate multi-channel probes (Anderson et al. 1989). Each probe had one shank along which 16 recording sites were located in 100- or 150-μm intervals. The activity at each site was amplified with custom hardware, digitized at a rate of 25 kHz, sharply low-pass filtered <6 kHz, resampled at 12.5 kHz, and stored on computer disk for off-line spike sorting (described later). For monitoring purposes, spikes were discriminated on-line with a simple peak-detection algorithm. On-line monitoring was used to estimate units’ threshold SPLs and frequency tuning.
Animal preparation

This report presents data from six purpose-bred adult cats of both sexes. One additional cat was used for the supplementary experiment. The animal preparation was identical to that detailed previously (Middlebrooks et al. 1998). In brief, isoflurane anesthesia was used during surgery, and α-chloralose was used for unit recording. All recordings were made from the right cortical hemisphere. A skull opening was made to reveal the middle ecstosylvan gyrus, and a plastic chamber was cemented around the ventral margin of the opening to contain a pool of silicone oil. The scalp was sutured closed around the plastic chamber. The animal was positioned in the center of the sound-attenuating chamber, with its body supported in a sling that also held a heating pad. Its head was supported from behind by a bar attached to a skull fixture. Thin wire supports were used to push the external ears into a forward position (Middlebrooks and Knudsen 1987). The position of the ears was constant throughout each experiment.

At the end of each experiment, the animal was killed. The cortex was immersed in buffered formalin and later inspected to confirm the gyrus recorded from.

Experimental procedure

Recordings were made from cortical area A2. Electrode penetrations passed dorsoventrally, oblique to the cortical surface near the crest of the middle ecstosylvan gyrus, ventral to area A1. Area A2 was distinguished from area A1 by the absence of tonotopic organization and by response bands that were ≥1 octave wide at signal levels 40 dB above threshold (Reale and Imig 1980; Schreiner and Cynader 1984). Search stimuli consisted of broadband noise bursts, presented at 0° or contralateral 40° azimuth. The depth of the recording probe was adjusted so as to observe unit responses at as many recording sites as possible. Typically, unit spike responses were observed at ~10 of 16 recording sites in each probe penetration.

Study of units in each electrode penetration began by identifying units’ frequency sensitivities with a sound source fixed at a location from which a noise burst produced a strong response, usually 0° or contralateral 40° azimuth. Tone frequencies were varied in 1/3-octave steps from 1.18 to 30 kHz. Next, responses to click trains presented from the same location were recorded for a range of SPLs in 5-dB steps. Units’ thresholds were estimated to the nearest 5 dB by inspection of on-line poststimulus time histograms and spike-rate-versus-level plots. When units’ thresholds differed among the multiple recording sites at one probe position, we adopted the modal threshold of SPLs of units as the representative threshold for that probe position. Usually, units’ thresholds differed by ≥10 dB at each probe position.

The units’ spatial sensitivities were measured using a stimulus set that consisted of signals presented from nine azimuths in the horizontal plane (−160° to +160° in 40° steps). When signals were presented in quiet, tested signals ranged between 0 and 40 dB above the units’ threshold in 5-dB steps. When presented with masker, tested signal levels ranged in 5- or 10-dB steps between 20 and 40 dB above the units’ threshold in quiet. Each series of trials consisted of every combination of signal location and level presented once in pseudorandom order, and each block consisted of 10 or 20 series of trials. Blocks of trials in quiet and masker conditions were interleaved to monitor the stability of recording throughout the recording session. For the quiet condition, two to four blocks were presented, interleaved with masker conditions, yielding a total of 20–40 repetitions of each stimulus. For each masker condition, one or two blocks were presented, yielding a total of 10–20 repetitions for each signal-masker combination. The order of blocks of masker conditions was randomized to reduce systematic bias due to any potential slow drift in units’ response characteristics. Before starting each block of trials, we waited ≥30 s to permit units to adapt to the continuous masker or quiet. Study at each probe placement typically lasted ~2–5 h, depending on the number of masker conditions tested. Outside of the 2- to 5-h period, additional stimuli often were tested at each probe placement to provide data for other studies. Experiments typically lasted 3–5 days and yielded recordings from 2 to 7 electrode penetrations.

Data analysis

Spikes were discriminated off-line using custom software that employed a template-matching algorithm. Well-isolated single units were encountered in only ~7% of recordings, so the majority of recordings were from clusters of two or more unresolved units; examples of single units and cluster recordings are illustrated in Furukawa et al. (2000). We observed no systematic difference in masker effects between well-isolated units and multi-unit clusters, so we do not distinguish types of unit isolation in the presentation of the results. For simplicity of presentation, we refer to both the multi-unit clusters and the well-isolated units as “units.”

Units were screened for responsiveness and stability based on responses obtained in quiet. Responsiveness of each unit was evaluated by the mean spike rate for the stimulus that elicited the maximum number of spikes. If the mean spike rate for the best stimulus was <1 spike per trial, the unit was excluded from further analysis. Stability of a unit was determined by spike rates for the quiet condition, using a two-way ANOVA, with factors being stimulus condition (i.e., combinations of signal SPL and location) and block number. We excluded units for which the variance accounted for by series number plus the variance accounted for by interaction of block number and stimulus condition exceeded 7% of the total variance. The screen by block number eliminated units for which there was a change in unit responsiveness or in the number of neurons included in a multi-unit cluster. The screen by block number and stimulus condition eliminated units for which sensitivity to SPL or location changed. The final data set that satisfied all criteria included 117 recording sites at 21 probe placements.

Spike times were stored as latencies relative to the onset of sound at a loudspeaker. The arrival of sound at the cat’s head was delayed by ~3.5 ms because of the acoustical travel time. Cortical neurons’ spike latencies were >10 ms after the stimulus onset, and robust responses after 60 ms were rare. To reduce any influence of occasional unreliable late spikes, we restricted analysis to the range of spike times from 10 to 60 ms after the stimulus onset. Mean spike rates (spikes per trial) were computed within that 50-ms time window. The distribution of first spike latencies was generally highly skewed, having a long tail toward longer latencies, and the standard deviations of first-spike latencies tended to be larger for longer latencies. For that reason, mean first-spike latencies were represented by the geometric means.

Mean spike rates and first-spike latencies were sensitive to signal levels. For the majority of units, addition of continuous background noise tended to shift that sensitivity along the level axis. The following procedure was used to compute the rate-versus-level-function (RLF) shift and latency-versus-level-function (LLF) shift. First, RLFs for the quiet condition and for each masker condition were linearly interpolated in 1-dB steps. Second, the RLF for the quiet condition was shifted along the level axis in successive 1-dB steps. For each shift, we computed the root-mean-square (RMS) of the difference in spike rate between the shifted RLF for the quiet condition and the RLF for masker condition over the range of levels for which the two functions overlapped. The RLF shift due to the masker was defined as the dB shift that minimized the RMS difference in spike rate. A positive shift indicated that the masker reduced a unit’s sensitivity, shifting the RLF toward higher signal levels. Generally, shifts ranged between 0 and 20 dB, but sometimes were allowed to range between 10 and 30 dB if that reduced the RMS difference significantly (1-tailed t-test, P < 0.01) relative to the minimum RMS for shift ranging between 0 and 20 dB. LLF shifts were computed in a similar manner.
fashion to RLF shifts but on a logarithmic latency scale. Poststimulus times of the first spikes were first converted to a logarithmic scale, and the mean of first-spike latencies at each SPL was computed based on all the trials with any spikes. Note that there were SPLs at which mean latencies were not computed because of the absence of spikes on any trials. The LLF for each signal location was constructed by interpolating among all the SPLs at which mean latencies were computed. The LLF shift was defined as the dB shift that minimized the RMS difference in logarithmic latency.

We examined the effects of maskers on location coding by cortical neurons. The procedure employed an ANN algorithm that associated neuronal spike patterns with particular signal locations. Neural responses recorded on odd- and even-numbered trials were divided into training and test sets, respectively. The training set was used to train the ANN, then the trained network was used to estimate sound-source locations by recognizing spike patterns in the test set. The procedure for computing averaged spike patterns, the network architecture, and the procedures for training and testing were identical to those detailed previously (Middlebrooks et al. 1998). Twenty and 50 spike patterns were formed for training and testing, respectively. The ANN analysis in the present study consisted of two stages. In the first stage, the ANN was trained and tested with spike patterns recorded in the quiet condition. In the second stage, the trained ANN was tested with spike patterns recorded in each masker condition. The ANN estimates of signal locations in the quiet and masker conditions at each signal location were compared in terms of the circular centroid and the quartiles below and above the centroid. The centroid was formed by treating each network location estimate as a unit vector, then computing the direction of the vector sum of the unit vectors (Fisher 1993; Furukawa et al. 2000).

An additional measure of location coding was given by the best azimuth. The spatial tuning of most units broadened at high sound levels, so best azimuths were computed for the lowest tested signal level at which the maximum spike rate was >20% of the maximum across all levels. Best azimuths were computed only for units that showed >50% modulation of spike rate by signal azimuth at that sound level. The spike-rate-versus-azimuth function was interpolated linearly in 1° steps. From that interpolated function, the response peak was identified as the set of contiguous points at which spike rates were >75% of the maximum, and a vector sum was formed from all the points within the peak. The best azimuth was the direction of the resultant.

RESULTS

The database consisted of 117 single units or unit clusters recorded from cortical area A2 of six cats. An additional 13 units from one additional cat were tested in a supplementary experiment. Units responded to broad ranges of pure-tone frequencies (typically >2 octave) and favored high frequencies: ~90% of units responded robustly to frequencies >6 kHz, whereas only ~30% of units responded robustly to frequencies <2 kHz. Azimuth sensitivities of the units were similar to those found in our previous studies (Furukawa et al. 2000; Middlebrooks et al. 1998). The spike rates of the majority of units were broadly tuned to contralateral signal-source azimuths, and units’ azimuth selectivity broadened with increasing signal level. Only ~27% of units showed RLFs that were nonmonotonic in that the spike rate at the highest tested sound level was <75% of that measured at a lower sound level. There was no systematic qualitative difference in masker effects among units that differed in frequency tuning, sharpness of azimuth sensitivity, or monotonicity of RLF.

No unit showed appreciable steady-state firing in quiet or in the presence of a continuous masker. Units typically responded to the signal with a few spikes locked to the signal onset both in quiet and in the presence of a continuous masker.

Response patterns and spatial tuning in backgrounds of quiet and of masking noise

Figure 1 represents the responses of one unit. Each raster plot shows responses to click trains at a range of signal locations. Each column of raster plots represents one signal level (labeled relative to the threshold in the quiet condition). Each row of raster plots represents the quiet condition (top), one of three focal masker locations (rows 2–4) or the diffuse masker condition (row 5). The rightmost column shows plots of spike rate versus signal location; each plot shows three to five signal levels.

In the quiet condition (top), signal levels within 20 dB of threshold produced maximum spike rates and minimum latencies when signal sources were located around −40° (i.e., contralateral to the recording site). The azimuth sensitivity flattened as the signal level was increased to 40 dB above threshold. The addition of a continuous masker (rows 2–5) tended to decrease spike rates at all but the highest signal levels. In the masker conditions, the raster plots at each signal level generally resembled the plots for the quiet condition at signal levels that were 10–20 dB lower. The focal maskers tended to show the greatest effect on responses to signal sources located near the masker. The +40° masker, for instance, tended to reduce spike rates and increase latencies in response to signals on the ipsilateral side; responses to the contralateral 160° signal also were reduced. The −40° masker, in turn, tended to reduce responses to contralateral signals while preserving most of the response to targets around ipsilateral 40 and 80°. The reduction of signal sensitivity due to the 0° focal masker (row 3) and the diffuse masker (row 5) was rather uniform across signal locations (although the masker effect was least for signals around −40°). That is, each of the rate profiles for the 0° or diffuse masker condition somewhat resembled a profile for the quiet condition at a lower signal level.

The unit represented in Fig. 1 was typical of the majority of units in that maskers reduced units’ sensitivities to signals and in that focal maskers had the greatest influence on signal sources located near the masker location. For descriptive purposes, we refer to units that showed that characteristic as type A. The remainder of units, type B, showed less sensitivity to the location of a focal masker. The type B unit represented in Fig. 2 showed a preference for contralateral signals at lower SPLs and a broad range of azimuths at higher SPLs, like the unit represented in Fig. 1. All of the masker conditions reduced responses to signals at the lowest SPL, with relative sparing of responses to signals away from the masker location. At the highest signal levels, however, this unit and other type B units showed enhancement of the response to signals, particularly at −80 and −40°, regardless of masker location. This is particularly clear in the spike-rate plots in Fig. 2, which show that the maximum spike rate elicited by signals at −40° in the +40°-masker condition was nearly three times that obtained in the quiet condition.

We distinguished types A and B because, as shown in a later section, masker effects on type A units could be quantified conveniently in terms of shifts in RLFs whereas that analysis proved to be invalid for type B units. Details about the differences between those two types of units will be described in later sections in which we examine rate- or latency-versus-
level functions for various conditions. Before then, the following sections describe effects of maskers on spatial tuning and on the size of the population of active units; those sections pertain to both type A and type B units.

**Masker effects on spatial tuning**

The magnitude of masker effects tended to vary with signal locations, as illustrated in Figs. 1 and 2. For that reason, addition of a focal masker could change the apparent azimuth preference of a unit. In Fig. 1, for example, a masker presented at −40° selectively reduced responses to signal sources at −40° while preserving responses to signal sources at +40° and +80°. The effect was to shift the unit’s best azimuth from −40° to +40°. Note that the masker did not create a response to a signal that would not have elicited a response in quiet. Instead, the effect of the focal masker was to carve a response peak out of an otherwise-flat azimuth function. Figure 3 summarizes the effects of maskers on the best azimuths of all units that showed azimuth tuning (including unit types A and B); the procedure for computation of best azimuths is given in METHODS. Each panel represents one masker condition and plots units’ best azimuths in the presence of a masker against best azimuths in quiet. Each circle represents one unit, and asterisks represent the locations of focal maskers. In the quiet condition, the majority of units preferred contralateral signal locations. The contralateral maskers tended to displace the best azimuth away from the masker location toward the ipsilateral side.

**Masker effects on the size of the population of active units**

The effects of maskers on the size of the population of active units was summarized by plotting the percentage of units that were activated above a criterion level in various signal and masker conditions. Figure 4, left, shows the percentages of the unit population that were activated by the 20-dB SPL signal at various locations. In this analysis, we defined a unit as active when its average spike rate was $50\%$ of that unit’s maximum rate measured across all signal locations in the quiet condition. Each panel represents one masker condition. The — and – $F$ – represent the active population in the quiet and masked conditions, respectively. Slight differences among the panels in the plots for the quiet condition reflect differences in the numbers of units that were tested in each masker condition.

The plots for the quiet condition in Fig. 4 show that a signal source at any location activated a large percentage of the unit population and that the greatest percentage was activated by frontal contralateral signals. A masker from any location tended to suppress strongly the size of the population activated by rear and ipsilateral signals. Figure 4, right, shows, of the population that was active in quiet, the percentage that was suppressed by the various maskers. Maskers tended to have the greatest impact on the units activated by signal sources near the masker source, particularly for ipsilateral (+40 and +80°) maskers.
**Masker effects on rate- and latency-versus-level functions**

Mean spike rates tended to increase, and mean latencies tended to decrease, with increasing signal levels. Addition of a masker tended to shift the RLFs and LLFs of units to higher signal levels. This finding was consistent with previous studies (Brugge et al. 1998; Phillips 1985; Phillips and Cynader 1985; Phillips and Hall 1986). As stated in the preceding text, ~27% of units showed nonmonotonic RLFs. Nonmonotonic units tended to preserve the nonmonotonic characteristic of their RLFs in the presence of masking noise. Figure 5, left, shows examples of RLFs and LLFs for one unit for the 0° signal. The –●– represent RLF (top) and LLF (bottom) for the quiet condition. The –△– and –□– represent corresponding plots for the −40° and +40° maskers, respectively. One can see that the RLF and LLF in the masker conditions resembled the quiet-condition functions shifted to the right. In the majority of cases, masker effects could be characterized by the shift sizes of the RLF or LLF functions.

There were, however, cases in which masker effects could not be characterized by shifts in RLFs. Specifically, addition of a masker sometimes increased the spike rate, so that masker-induced RLF changes could not be accounted for by a simple shift of the RLF. Figure 5, right, shows examples of such cases for one unit. Although the presence of the −40° (△) or 0° (○) masker appeared to elevate signal thresholds, the spike rate for the masker condition increased rapidly with signal SPL, reaching greater rates than the highest rate for the quiet condition (top). One concern was that instability of unit responses might have produced the observed changes of RLFs for the masker conditions. In the course of studying this unit, however, we divided the recording for the quiet condition into four blocks of trials and interleaved those blocks with recordings for the masker conditions. The - - - in the top right panel show the range of the RLFs in quiet computed for the individual blocks of trials. One can see that the RLFs for the masker conditions generally fell out of the range of the RLFs in quiet, indicating that changes in RLFs could not be accounted for by unit instability.

The LLF for the same cases (bottom right) showed little or no indication of facilitation (i.e., shorter spike latencies). In general, first-spike latency was bounded by a minimum post-stimulus time, which was probably determined by specific axonal conduction velocity and synaptic delays.
For cases of facilitation like that shown in Fig. 5, right, it was not appropriate to represent masker effects by RLF and LLF shifts. Thus we excluded a group of units (the type B units) for which the masker-induced facilitation was particularly robust and applied analyses of RLF and LLF shifts to the rest of the unit sample (the type A units). Types A and B were distinguished in the following way. For each unit in each of signal-masker configurations including the quiet condition, we found the maximum spike rate across all signal levels tested. Then, at each signal location, we computed the ratio of the maximum spike rates for the masker condition versus the quiet condition. Ratios appreciably greater than unity indicated increased maximum spike rate by the presence of the masker. A somewhat distinct population of units showed increased rates in several signal-masker configurations. We classified a unit sensitivity for a signal-masker configuration as "facilitated" when the ratio of maximum spike rates was $>1.2$. Across all 117 units and nine signal locations ($-160–160^\circ$ in $40^\circ$ steps), 7.2, 6.9, and 15.4% of signal-masker configurations showed facilitation for the $-40, 0$, and $40^\circ$ maskers, respectively. For the diffuse masker, 11.9% of signal-masker configurations (41 units by 9 signal locations) showed facilitation. We defined as type B a population of units that showed facilitation in units in $\geq$4 of the 27 signal-masker configurations for which all the units were tested (9 signal locations; 3 masker locations: $-40, 0$, and $+40^\circ$; 1 masker SPL: 35 dB). The remainder of units were classed as type A. Of the total of 117 units, 79 and 38

units were classified as types A and B, respectively. The proportion of units classified as type B was fairly insensitive to the choice of the criterion for facilitation. That is, when the criterion was varied between 1.0 and 1.4, 26 units were consistently included among the 38 units with the highest ranks in the number of configurations with facilitation. Type B units were recorded in 12 of 21 electrode penetrations in five of six cats; in 6 of those 12 penetrations, $\geq50\%$ of units recorded were type B. Penetrations in which both types were found did not show any significant clustering of unit types along recording sites. We were able to apply "runs tests" for randomness of sequence (Sokal and Rohlf 1995) to three of the penetrations, none of which showed significant nonrandom sequences of unit types ($P > 0.05$). Type A and B units were similar in that the majority of units showed contralateral or broad azimuth sensitivities, and the average best azimuths showed no significant difference (type A: $-50.0^\circ$, type B: $-65.1^\circ$; 2-tailed $t$-test, $P \geq 0.0728$). Also, there was no significant association of unit type with monotonicity of the RLFs (as defined earlier in RESULTS, $\chi^2$ test $P \geq 0.2286$). The only reliable difference between types A and B was the absence or presence of increases in maximum spike rate by the masker. We focus on type A units in the following paragraphs, then return to type B units at the end of RESULTS.

RLF and LLF shifts in type A units provided single values to represent masker effects across a range of signal levels and provided a consistent unit (i.e., dB) for comparing masker effects between two aspects of neural responses: spike rate and latency. Also, the RLF shift permits a comparison of the present results with psychophysical studies of spatial unmasking (e.g., Saberi et al. 1991) and with other physiological studies that represented masker effects with threshold shifts (Jiang et al. 1997; Ramachandran et al. 2000; Ratnam and Feng 1998). The RLF shift adopted in the present study was con-
Effects of signal and masker locations on RLF and LLF shifts

Figure 6 shows RLF and LLF shifts for the type A unit that was represented in Fig. 1. That unit had broad spatial sensitivity, a broad frequency response area, and monotonic RLFs, as was typical of our sample of units. The three panels of the figure show plots for three masker-source locations: $-40^\circ$, 0, and $+40^\circ$. RLF and LLF shifts showed similar sensitivity to signal- and masker-source locations. Masker sources located at $-40^\circ$ and $+40^\circ$ had the strongest effects on responses to signal sources located near the maskers. The effects of a masker at 0° were less sensitive to signal-source location. Note that the negative LLF shift obtained for the $-40^\circ$ signal and the $+40^\circ$ masker likely was a result of imprecise shift estimation due to our sampling from shallow parts of the unmasked and masked LLFs around the shorter extreme of the dynamic range.

Figure 7 shows RLF and LLF shifts averaged across the type A population as a function of signal-source locations. The mean data confirm the impression given by individual examples. Both RLF and LLF shifts generally were greatest when signal and masker sources coincided in location, with LLF shifts showing somewhat greater modulation by signal location than RLF shifts, particularly for ipsilateral maskers. The modulation of the profile for the $0^\circ$ focal masker was relatively small: the difference between the maximum and minimum of the shift profile was $\approx 5$ dB for the $0^\circ$ masker for both RLF and LLF shifts, whereas the differences for the $-80^\circ$ masker were $\approx 10$ and 14 dB for RLF and LLF shifts, respectively. The shift...
profile for the diffuse masker was quite flat for the RLF shift and was somewhat irregular for the LLF shift.

The cat’s external ear has the greatest gain for sound sources in front of the ear, along the “acoustic axis” (e.g., Middlebrooks and Pettigrew 1981). Thus we considered the possibility that the directional dependence of the masker effects in Fig. 7 might be determined simply by the signal-to-noise ratio (SNR) in a single ear. Here, we consider the SNR in power integrated across a broad frequency range, and do not regard the detailed frequency-by-frequency SNR due to the location-dependent transfer functions of the external ears (Musican et al. 1990; Rice et al. 1992; Xu and Middlebrooks 2000). In each panel of Fig. 7, the masker was fixed in location and in level, so in each panel the decrease in SNR within each ear relative to the quiet condition was constant across signal locations (here, “noise” in the quiet condition refers to the internal noise). If masker effects were due exclusively to changes in SNR at only one ear, one would predict that RLF and LLF shifts would be insensitive to signal-source location. The plots in Fig. 7 clearly contradict that prediction, and thus we conclude that the SNR in a single ear could not account for the signal-location dependence of the masker effects.

Cortical neurons in the present study, as in previous reports, tended to be most sensitive to sound sources located near the acoustic axis of the contralateral ear. Thus we expected the masker effect to be greatest when the masker source was located on the contralateral side. This expectation was tested by averaging RLF and LLF shifts across signal locations and then plotting the averages as a function of masker location (Fig. 8). The figure also shows the directional gain of the contralateral ear (---), represented by the pressure gain averaged over frequencies from 3 to 30 kHz. That range of frequency covered frequency response areas of the majority of units in our sample. The physiological data roughly paralleled the acoustical data; this suggests a dominance of contralateral ear inputs in determining the overall reduction in sensitivity induced by maskers. The shift sizes for the diffuse masker were as great as the shift sizes for the most effective focal maskers.

**Effects of masker level**

So far, we have described the results for a masker fixed at 35 dB SPL. We tested two additional masker levels (15 and 25 dB SPL) at masker locations of −40, 0, and +40°, for 29 type A units. Figure 9 represents average RLF or LLF shifts (left and right, respectively) at three masker levels as a function of signal location. Each row of panels represents one masker SPL, 15, 25, and 35 dB, respectively. Each row of panels represents one masker location (---). The data represent 29 type A units for which masker level was varied.

![Figure 9](http://jn.physiology.org/
"Downloaded from http://jn.physiology.org/"
by 10.20.33.4 on October 26, 2016)
level depends on the relative locations of signal and masker sources.

For 13 units obtained in a supplementary experiment, we compared the effects of masker level between the focal 0° and the diffuse masker (data not shown). The effect of masker level was similar between the two masker conditions. The average increase of RLF shift by a 10-dB increment of masker SPL was 6.5 and 6.6 dB for the 0° and the diffuse masker, respectively (P = 0.44; paired t-test; df = 226). Similarly, the average increase of LLF shift was 6.6 and 5.5 dB for the 0° and the diffuse maskers, respectively (P = 0.037; paired t-test; df = 226).

Masker effects on accuracy of location coding

We examined the effects of a continuous masker on the coding of sound-source location by cortical units. As detailed in Methods, the approach was to train an ANN to recognize the spike patterns associated with particular signal-source locations in the quiet condition and then to test the trained network with spike patterns recorded in various masker conditions. Results presented in previous sections have indicated that addition of a masker was somewhat like reducing the signal level, so it seemed obvious that maskers would influence spike patterns and thus influence the ANN estimate of signal-source location. Nevertheless our previous studies have demonstrated that estimation of source location by this ANN procedure is fairly robust to changes in stimulus level as long as the ANN is trained with cortical responses to stimuli that varied in level (e.g., Middlebrooks et al. 1998). For that reason, we anticipated that an ANN that was trained with spike patterns obtained for multiple signal levels in the quiet condition could estimate signal-source locations based on spike patterns obtained in a masked condition. In the present analysis, we trained and tested the ANN for signal levels between 20 and 40 dB above the unit thresholds obtained in the quiet condition.

Figure 10 represents ANN results for one unit for the quiet condition and in the presence of focal maskers at −40°, 0°, and +40°. The distribution of ANN estimates of signal-source location is represented by lines that show the centroids and the ranges of second and third quartiles. The results for the quiet condition (the leftmost plot) are repeated by gray shading in all the other plots. The top row of plots shows data for all the tested signal-source locations and levels. Location accuracy was markedly degraded in the masker condition compared with the quiet condition. In the −40° masker condition, for example, most cortical responses to signal sources in front of the animal were incorrectly assigned to rear locations. In that case, spike rates elicited by frontal targets were strongly reduced by the masker, thereby causing them to resemble spike rates that were elicited by rear targets in the quiet condition.

The degradation of location estimates in Fig. 10, top, could have been due at least in part to large RLF and LLF shifts. That is, the masked signal levels at some signal locations fell below the “operating range” of the ANN. That would be analogous to the localization errors shown by human listeners when masked signal are near the limits of audibility (Good and Gilkey 1996; Good et al. 1997; Lorenzi et al. 1999). We addressed this problem by expressing masked signal levels as the signal level relative to threshold in quiet shifted by the mean of the RLF and LLF shifts computed for each signal- and masker-source location; these shifted levels are referred to as “effective signal levels.” The ANN analysis was repeated using only the conditions for which effective signal levels fell in the range of 20–40 dB above the unit threshold in quiet. The results are shown in Fig. 10, bottom. Signal locations with missing points are locations at which the RLF and LLF shifts were so large that no data were available for computing the statistics, which was often the case for locations around the masker. Compared with the results in the top panels, the ANN estimates of locations in the masker conditions were closer to the estimates in the quiet condition. There were, however, configurations for which ANN estimates for the masker condition deviated greatly from those for the quiet condition, even after the adjustment by the effective signal level; that was most apparent.

FIG. 10. Sound-location estimates by an artificial neural network (ANN) trained with spike patterns for the quiet condition. The abscissa shows the actual signal location, and the ordinate shows the network responses. From left to right: the quiet condition and masker locations of −40°, 0°, and +40° (dashed vertical lines), respectively. The lines connecting filled circles and the solid lines (top) are the response centroids and the upper and lower quartiles, respectively, of the ANN responses for spike patterns in the presence of the focal maskers. The lines and the symbols in the bottom panels are the same as in the top panels but were computed after excluding the data for stimuli with effective signal level falling out of the range of 20–40 dB relative to the unit threshold. The upper and lower quartiles for the quiet condition are repeated in panels for the masker conditions, indicated by shaded areas. See text for details.
for the 0° masker. This indicates that the masker had effects on features in the spike patterns that could not be accounted for by the RLF or LLF shifts and that the trained ANN was somewhat sensitive to those features.

The illustrated results were generally representative of the population of type A units. The accuracy of location coding was characterized for each unit by the centroid error (defined in METHODS). Centroid errors were computed for all available units, signal locations, and masker locations. The average centroid error for the quiet conditions was 42.8°. The error increased to 80.1° averaged across the three masker conditions ($P < 0.001$; $t$-test of mean; df = 1,700). The error was significantly reduced to 62.9° by removing responses for stimuli with out-of-range effective signal levels ($P < 0.001$; $t$-test of means 62.9 vs. 80.1°; df = 1,762).

Units exhibiting facilitation by maskers (type B units)

In this section, we briefly consider the cases in which a masker produced facilitation of unit responses. Here, we limit our analyses to type B units, which exhibited facilitation of their responses in the presence of a masker for a greater number of signal-masker configurations than did type A units. Most type A and B units were similar to each other in that they tended to show contralateral or broad spatial preference in the quiet condition: examples of A and B units were shown in Figs. 1 and 2, respectively.

We noted that facilitation, as defined earlier, was most often observed for signals around $\pm 80$ and $\pm 40°$, regardless of masker location. Figure 11 plots the number of type B units that exhibited facilitation by $>20\%$ as a function of signal location for masker locations of $-40$, 0, and $+40°$. Generally facilitation occurred most often for the $+40°$ masker, but within all masker conditions, facilitation was most common for a signal location of $-40°$.

Maskers generally had two effects on RLFs of type B units: elevation of response threshold and increased maximum spike rate. These effects resulted in a steepening of the slope of the RLF. The influence of the masker on threshold and maximum spike rate varied across signal-masker configurations and across units, so we were not able to draw general conclusions. Figure 12 shows examples of RLFs for three units, each of which was tested with three masker levels. In the top panel, a masker with increasing level gradually elevated the response threshold and increased the maximum spike rate. In the middle panel, a masker at the two lowest levels substantially increased the maximum spike rate, while the threshold level was relatively unaffected. Threshold elevation was observed only for the highest masker level. In contrast, the unit represented in the bottom panel showed an elevation of threshold without an increase in the maximum spike rate for the lowest masker levels; an increased maximum spike rate occurred only for the highest masker SPL.

DISCUSSION

In the present study, we examined the responses of cortical neurons to signals at various source locations in the presence of continuous diffuse maskers or of focal maskers at various locations. Consistent with previous physiological results, the continuous masker elicited no sustained cortical spike activity and generally reduced responses to signals, although a sizeable minority of units showed facilitated spike rates in some masker conditions. The principal new finding of the study was that masker effects were sensitive to the locations of signal and masker sources. The majority of units showed greatest masker effects when signal and masker sources coincided in location, and the effects decreased with increased separation of signal and masker sources. Masking noise tended to degrade the accuracy of cortical coding of signal-source location, at least in the range of signal and masker sound levels that were tested in this study. Location-coding accuracy improved when the analysis was restricted to conditions in which signal levels were well above masked thresholds.

Comparison with previous studies

We are aware of two groups of researchers that have examined the effects of a continuous masker on unit responses in the
auditory cortex. Phillips and Cynader (1985), Phillips (1985), and Phillips and Hall (1986) tested characteristic-frequency tone bursts presented against continuous broadband maskers with both signal and the masker presented monaurally to the ear contralateral to the recorded cortical hemisphere. Brugge and colleagues (1998) used single-impulse signals presented from various locations in a “virtual acoustic space.” The masker in that study was diffuse, produced by presenting binaurally uncorrelated noise to the two ears. Both groups studied neurons in cortical area A1 of anesthetized cats.

Consistent with both those groups, the present study showed that the presence of a masker tended to elevate units’ thresholds. The previous studies showed an overall reduction of responses. That was also the case for type A units in the present study, although type B units showed spike-rate facilitation under some masker conditions. The Brugge group demonstrated that the magnitude of the sensitivity shift induced by a diffuse masker was relatively uniform across signal locations. Similar results were shown in the present study for the comparable, diffuse-masker condition: RLF shifts (and LLF shifts to a lesser degree) were relatively constant across signal locations (Fig. 7). Another finding common to both those groups was that the presence of a masker decreased units’ signal sensitivity such that an increase in the level of the masker was roughly equivalent to an equal-magnitude decrease in the level of the signal. That reciprocal trading of masker and signal levels was seen in RLFs and LLFs in both studies and in the structure of virtual-space receptive fields in the Brugge study. For the focal 0° masker condition in the present study, the increase in RLF and LLF shift resulting from a 10-dB increment of masker level was about 6–12 dB, which was not far from the decibel-for-decibel trading of signal and masker levels reported previously. Note that the focal 0° condition was similar to the diffuse masker condition in the Brugge study and in the present study in that the diffuse and focal 0° maskers produced nearly equal spectra and equal overall sound levels at the two ears. The maskers differed mainly in temporal fine structure, which probably had little influence on the high-frequency neurons that we studied, and in short-term interaural level differences. In fact, the supplementary experiment showed little difference between the focal 0° and the diffuse conditions in shift increase per 10-dB increment of masker level.

The novel findings of our study derived from presentation of focal maskers from locations off the midline. For the majority of units, RLF and LLF shifts by a focal masker located away from the midline were greatest when signal and masker sources coincided in location. Conversely, the strength of masking could be decreased by separating signal and masker sources. That observation has a counterpart in psychophysical studies that have demonstrated that the detectability of a signal improves if it is separated in location from a continuous noise source (Saberi et al. 1991). Furthermore we observed a signal-location dependence of the reciprocal trading between signal and masker sound levels. When signal sources were located near masker sources, a 10-dB increase in masker level tended to produce a nearly 10-dB increase in the masker-induced shift in RLFs or LLFs. That is consistent with the previous study by Brugge and colleagues (1998) and with our results for the focal 0° and the diffuse maskers. In contrast, signal sources located contralateral to off-midline masker sources showed a much smaller growth of masking, as low as 2–3 dB per 10-dB masker increase. This small growth of masking could be explained by a floor effect for some conditions, e.g., contralateral signals for the +40° masker (Fig. 9). There were, however, instances of very small growth rates for signal-masker conditions that produced sufficiently large RLF and LLF shifts even for the lowest masker level (ipsilateral signals for the −40° masker). This result suggests that a near-reciprocal relationship between masker and signal level holds only for a limited set of conditions.

A facilitative effect of the masker like that found in the present study was not formally reported in studies by Phillip’s or Brugge’s groups, who studied units in area A1. Thus it is possible that masker-induced facilitation was a phenomenon that is true for units in area A2 but not in area A1. An example of RLFs by Phillips and Hall (1986, Fig. 2b), however, did demonstrate increased maximum spike rate accompanied by elevated response thresholds in the presence of masker, as often found in the facilitation cases in the present study (cf. Figs. 5 and 12). Thus it is possible that previous studies have overlooked a population of A1 neurons that show facilitation by background noise. Clearly, more extensive studies are required to understand masker-induced facilitation across the cortex.

**Significance of multi-unit cluster recording**

We used multi-channel recording probes that permitted us to record from as many as 16 cortical sites simultaneously. That made it possible to test a sizeable sample of units with a large number of signal and masker conditions. The disadvantage of the multi-channel probe was that it generally did not permit reliable isolation of single units. It is a concern that the multi-unit clusters that were studied might have contained neurons that differed from each other in their detailed response properties. Any averaging of differing response characteristics that resulted from multi-unit cluster recording would have blunted differences among various unit types. That is, we might have failed to detect rare response types that could only be seen by recording from individual neurons. Moreover, the two response types that we defined, types A and B, might have demonstrated quantitatively greater differences if single units had been isolated. Perhaps finer differences among neurons will be discovered in later studies. Nevertheless the major conclusions in the present study about effects of signal and masker locations on the responses of unit populations are based on data averaged over multiple recording sites and are unlikely to reflect an artifact of multi-unit cluster recording.

One serious concern about the interpretation of multi-unit cluster recordings is that it is not possible to guarantee that a cluster studied over 2–5 h contained the same units. For that reason, one must be concerned that apparent masker-related changes in responses might be confounded by changes in the recorded population. We guarded against this in two ways. First, we tested the various masker conditions in blocks that differed in order among animals and probe placements. That prevented the association of particular masker condition with the beginning, middle, or end of study at each recording site. Second, we repeated measures of sensitivity to azimuth and signal level in the quiet condition in two to four repeated blocks of trials distributed among the blocks of masker trials.
As detailed in Methods, any systematic change in the sensitivity of units at a particular recording site to azimuth or signal level led to rejection of data from that site. It is possible that data were included in cases in which the members of a unit cluster changed during a lengthy recording session. If so, however, units that left the cluster were replaced by units with similar responsiveness and similar azimuth and level specificity.

**Underlying mechanisms for the masker effects**

Ramachandran and colleagues (2000) reported the effects of continuous background noise on neurons in the cat inferior colliculus (IC) that generally paralleled the effects on cortical neurons: the dynamic range of the RLF shifted to higher signal SPLs, and 1-dB increases in noise level tended to result in near 1-dB increases in the shift size. Thus it is possible that the reduced signal sensitivity of cortical neurons due to continuous background noise can be attributed in part to the reduced excitatory inputs from brain stem pathways. In the IC, however, the presence of a background noise generally resulted in the compression of the dynamic range of spike rate due to elevated background spike rate and reduced maximum signal-driven spike rate for neurons with monotonically RLFs (Ramachandran et al. 2000). Such a compression effect was not observed in the cortex. Cortical neurons do not respond to a continuous background noise in a sustained fashion (Brugge et al. 1998; Phillips and Hall 1986; present results), and generally there is no indication of reduced maximum signal-driven spike rate (Phillips and Hall 1986). In certain conditions, the maximum rate even was increased by the presence of the masker, as found for the type B units in the present study. Short-term adaptation in cortical neurons might play a role in the reduction of the masker-driven background spike rate (Volkov and Galazyuk 1992). The maintenance or facilitation of the maximum spike rate might be explained in terms of the balance of excitatory and inhibitory inputs from ascending pathways that converge on single cortical neurons. The maximum spike rate could be maintained in the presence of masker if a reduction of excitatory inputs is accompanied by reduced inhibitory inputs. Similarly facilitation would occur if the attenuation of inhibitory inputs exceeds that of excitatory inputs.

A major finding of the present study was the dependence of RLF and LLF shifts on the locations of signal and masker in the free field. Previous studies have demonstrated both binaural and monaural processes that might contribute to the masker effects. As an example of a binaural process, Jiang and colleagues (1997) found a population of neurons in the guinea pig IC that showed differential sensitivities between in-phase and anti-phase signals between the ears in the presence of anti-phase noise masker. Also, Ramachandran and colleagues (2000) studied the effects of interaural level difference of signal and masker in the cat IC neurons. The sensitivity of their type I units to a signal with contralaterally dominant interaural level difference (ILD) (i.e., level in the contralateral ear higher than in the ipsilateral ear) was greater when presented against a masker with ipsilaterally dominant ILD than when presented against a masker with contralaterally dominant ILD. Thus it is possible that the binaural processes found in those IC studies contribute to cortical sensitivity to relative locations of signal and masker. We also note a demonstration in an amphibian IC of neurons that showed effects of signal and masker locations equivalent to spatial unmasking, i.e., decreased response thresholds for signals by increasing spatial separation of a masker from the signal (Ratnam and Feng 1998).

Regarding monaural processes, the responses of individual cortical neurons are influenced by location-dependent spectral details of the acoustical inputs to each eardrum (Samson et al. 1993; Xu et al. 1999). The transfer function of each external ear varies with the angle of incidence of sound, so the spectral envelope of a sound at each eardrum varies with the sound-source location (Musicant et al. 1990; Rice et al. 1992; Xu and Middlebrooks 2000). For that reason, the frequency-by-frequency SNR is determined by an interaction of the signal and masker locations. A single neuron’s responses could be determined by a further interaction of the frequency-dependent SNR and the neuron’s frequency sensitivity. Thus the across-neuron and -subject variances of the masker-signal interaction in masker effect may be partly accounted for by the fact that frequency sensitivities varied somewhat across neurons and that the directional transfer functions varied among cats (Xu and Middlebrooks 2000).

**Relationship to psychophysical spatial unmasking**

Saberi and colleagues (1991) demonstrated spatial unmasking in human listeners, using stimulus configurations comparable to the present study. That study showed the highest detection threshold for signals around the masker location and decreasing threshold for increasing separation of signal and masker. The present results in cortical physiology (Fig. 7) mirrored the results of Saberi et al.: the RLF and LLF shifts tended to be largest when the signal location coincided with the masker location and became smaller for increasing separation between the signal and the masker. This effect can be seen clearly for the lateral maskers and to a lesser degree for the 0° masker. The present findings differed in two ways from those of the Saberi study. First, we found smaller overall spatial-unmasking effects than in the previous study. For example, the RLF shifts and LLF shifts in the present study were no more than 10 and 14 dB, respectively, for the −80° masker, whereas Saberi and colleagues observed threshold shifts as large as 17 dB for a 90° masker (Fig. 4 of Saberi et al. 1991). Second, compared with the lateral maskers, the 0° masker showed only a small spatial unmasking, only ≈ 5 dB. The Saberi study, on the other hand, demonstrated threshold shifts of as much as 15 dB for the 0° masker. The generally smaller modulation size in the present study was partly due to our procedure for computation of RLF and LLF shifts, which forces shifts to take a limited range (−10−+30 dB), resulting in compressed profiles of average shifts. The relatively small modulation size for the 0° masker in the present study might be accounted for by the insensitivity of A2 neurons to low frequencies. Unlike neurons in cat A2, human listeners integrate information across a broad range of frequencies. For human listeners, the magnitude of spatial-unmasking effect is greater for frontal maskers than for lateral maskers when the signal is restricted to low frequencies (<1 kHz); but the reverse is true when the signal is restricted to mid (1−5 kHz) or high (>5 kHz) frequencies (Good et al. 1997). Quantitative differences between the two studies might also reflect spatial attention effects that could have been present in the human listeners but not in the anesthetized cats.
Listeners can improve signal detection by attending to the ear at which the SNR is greater. This “better-ear” listening is a process that accounts at least partly for spatial unmasking (Bronkhorst and Plomp 1988, 1989, 1992; Kidd et al. 1998; Terhune and Turnbull 1989). In the presence of a lateral focal masker, the noise level is greater in the ear ipsilateral to the masker than in the contralateral ear, because of shadowing by the head. Separating the signal from the masker location would increase the SNR in the ear contralateral to the masker, and thus attention to that ear would improve detection. Although the better-ear listening is feasible for psychophysical listeners, who in principle could base their judgements on populations of neurons in both cortical hemispheres, such a strategy could not account entirely for the signal-masker interaction found in the present study. This is because the two ears have asymmetrical influences on each cortical hemisphere. Most neurons in area A2 are excited by stimulation of the contralateral ear, but a smaller proportion of neurons (~40%) are excited by ipsilateral stimulation (Schreiner and Cynder 1984). Thus according to the better-ear listening hypothesis, we would expect weaker unmasking of ipsilateral signals (smaller modulation of shift-vs.-signal-location function) with a contralateral (~80 and ~40%) masker than of contralateral signals with an ipsilateral (+40 and +80°) masker. The results in Fig. 7 conflict with this expectation. Furthermore the noise levels in the two ears were nearly equal for the 0° masker condition, so the hypothesis of better-ear listening would predict no spatial unmasking by separation of signal and masker. In fact, the 0° masker condition in Fig. 7 showed a slight dependence of RLF and LLF shifts on signal location, the greatest shift being found for signals near 0°. Therefore other mechanisms are needed to explain the signal-masker interaction found in the present study.

**Implications for sound localization**

The results of the present study and of the study by Brugge and colleagues (1996) suggest that the masker effects on spike rates and first-spike latencies are in many cases equivalent to the effects of a reduction in signal level. This implies that the perturbation by maskers of the neural coding of sound location would be equivalent to the perturbation by varying signal level. It is known that cortical neurons can signal location-related information by their spike patterns and that this signaling is robust to variation in stimulus levels (Brugge et al. 1996; Middlebrooks et al. 1998). Therefore we predicted that location signaling by cortical neurons would also be fairly robust to the presence of masker. In the present study, location estimates by an ANN trained with spike patterns recorded in the absence of a masker were severely disrupted when presented with spike patterns in the presence of a masker. That disruption, however, was reduced significantly under conditions in which the effective levels of signals remained within the operating range of the ANN. This result was comparable to the psychophysical result that a continuous masker has relatively little impact on the accuracy of localization judgement by human listeners at least when the signal level is above a modest (~10 dB) sensation level (Good et al. 1996, 1997; Lorenzi et al. 1999). Nevertheless considerable errors in ANN location estimates under masker condition remained even after adjustment by the effective signal level (see, for example, the panel for the 0° masker in Fig. 10). This indicates that some features of spike patterns are sensitive to signal locations in quiet (thus captured by the ANN as information-bearing features) but are disrupted by the presence of a masker. Further studies will be necessary to identify information-bearing features in spike patterns that are robust to perturbations by maskers.

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