Detection of Auditory Signals by Frog Inferior Collicular Neurons in the Presence of Spatially Separated Noise

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Ratnam, R. and A. S. Feng. Detection of auditory signals by frog inferior collicular neurons in the presence of spatially separated noise. J. Neurophysiol. 80: 2848–2859, 1998. Psychophysical studies have shown that the ability to detect auditory signals embedded in noise improves when signal and noise sources are widely separated in space; this allows humans to analyze complex auditory scenes, as in the cocktail-part effect. Although these studies established that improvements in detection threshold (DT) are due to binaural hearing, few physiological studies were undertaken, and very little is known about the response of single neurons to spatially paired signal and noise sources. To address this issue we examined the responses of neurons in the frog inferior colliculus (IC) to a probe stimulus embedded in a spatially separated masker. Frogs perform auditory scene analysis because females select mates in dense choruses by means of auditory cues. Results of the extracellular single-unit recordings demonstrate that 22% of neurons (A-type) exhibited improvements in signal DTs when probe and masker sources were progressively separated in azimuth. In contrast, 24% of neurons (V-type) showed the opposite pattern, namely, signal DTs were lowest when probe and masker were colocalized (in many instances lower than the DT to probe alone) and increased when the two sound sources were separated. The remaining neurons demonstrated a mix of these two types of patterns. An intriguing finding was the strong correlation between A-type masking release patterns and phasic neurons and a weaker correlation between V-type patterns and tonic neurons. Although not decisive, these results suggest that phasic units may play a role in release from masking observed psychophysically. Analysis of the data also revealed a strong and nonlinear interaction among probe, masker, and masker azimuth and that signal DTs were influenced by two factors: 1) the unit’s sensitivity to probe in the presence of masker and 2) the criterion level for estimating DT. For some units, it was possible to examine the interaction between these two factors and gain insights into the variation of DTs with masker azimuth. The implications of these findings are discussed in relation to signal detection in the auditory system.

INTRODUCTION

The ability to extract a signal from complex auditory environments is a focus of interest for auditory psychophysicists and physiologists. In real-world situations, a signal of interest is usually masked by noise originating from spatially discrete sources. Therefore the central question is how the auditory system extracts the signal and how its performance is affected by maskers. In humans, the analysis of complex auditory scenes is due to the ability to attend one talker in an acoustically cluttered environment (so-called cocktail-party effect) (Cherry 1953). This task, in numerous guises, is common to other animals such as frogs, which must select mates calling in dense choruses. Results from psychophysical experiments suggest that the cocktail-party effect requires listening with two ears (binaural hearing) and is severely degraded when one ear is blocked or otherwise impaired (Cherry 1953; Hirsh 1950; Kock 1950; for review see Zurek 1992).

Binaural hearing offers advantages over monaural hearing in terms of sound localization because minute differences in intensity and time between the two ears can be computed (for reviews see Blauert 1983; Durlach and Colburn 1978; Mills 1972; Moore 1982). Additionally, binaural hearing confers improved detection thresholds (DTs), loudness detection, speech intelligibility, and a reduction in difference limens for both intensity and frequency discrimination at all frequencies (Ebata et al. 1968; Flanagan and Watson 1966; Gatehouse 1986; Jesteadt and Wier 1977; Kidd et al. 1995; Levitt and Rabiner 1967; Plomp and Mimpen 1981; Reynolds and Stevens 1960; Scharf 1969). The importance of binaural hearing in the cocktail-party effect was demonstrated by psychophysical experiments in humans (Festen and Plomp 1986; Hirsh 1950, 1971; Kock 1950; Plomp and Mimpen 1981; Saberi et al. 1991; Santon 1986, 1987; Terhune and Turnbull 1989). A listener’s sound DT was highest when a noise and sound source were colocalized but decreased when the angular separation between the two sources was increased. Separation of the two sounds in space allowed a decomposition of the auditory scene into its component sound sources, thus improving signal detection. In humans, the improvement in DTs (release from masking) was as much as 15–18 dB for click sounds (Saberi et al. 1991) or 11–14 dB for tone bursts (Gatehouse 1987). In the budgerigar (Dent et al. 1997) and ferret (Hine et al. 1994) release from masking was ~9–10 dB. The only results for frogs indicate that masking release may be between 3 and 6 dB (Schwartz and Gerhardt 1989), but this result cannot be compared directly with results obtained from other species because the behavioral task was discrimination, rather than detection, of species vocalizations.

The frog auditory system is well suited for the study of auditory scene analysis because females perform mate selection based strictly on auditory information (Blair 1958; Feng et al. 1976; Gerhardt 1982; Rheinlaender et al. 1979). In a typical breeding pond, numerous individuals from as many...
as 15 to 25 different species may chorus simultaneously. Females must recognize conspecific calls in the chorus, localize a conspecific male, and then move toward him. For males participating in the chorus, conspecific calling males must be located so as to ward off competitors. This requires good localization ability and the ability to discriminate conspecific from heterospecific sounds. Although this ability was investigated in a number of behavioral studies (Ehret et al. 1990; Narins 1982; Schwartz 1994; Schwartz and Gerhardt 1989, 1995; Schwartz and Wells 1983a,b; Simmons 1988), most physiological studies employed a closed acoustic system where both the signal and masker are presented to the frog via a single headphone (Freedman et al. 1988; Megela and Capranica 1982; Michelsen et al. 1986; Moss and Simmons 1986; Narins 1983, 1987; Narins and Wagner 1988, 1989; Narins and Zelick 1988; Simmons et al. 1992; Wang and Narins 1996). Only a few studies (Schwartz and Gerhardt 1989, 1995; Wang and Narins 1996) directly investigated the importance of sound direction on signal detection in the presence of noise in the free field.

The goal of this study was to advance our understanding of the neural mechanisms that underlie release from masking mediated by increasing the angular separation between signal and noise sources (i.e., spatially mediated release from masking). To this end, single neurons in the frog inferior colliculus (IC) were tested to determine their ability to detect a probe stimulus in the presence of spatially segregated noise. The frog IC is a prominent central auditory processing center and is presumed to play an important role in directional hearing (Epping and Eggermont 1985; Gooler et al. 1993, 1996; Melssen and Epping 1990; Xu et al. 1994) and in the encoding of spectral and temporal features of complex sounds (Eggermont and Epping 1986; Epping and Eggermont 1986a,b; Feng et al. 1990, 1991; Fuzessery and Feng 1983b; Gooler and Feng 1992; Walkowiak 1980).

METH ODS

Experiments were performed on 34 adult male northern leopard frogs (Rana pipiens pipiens) having a mean weight of 19.8 g. The frogs were obtained from animal suppliers and kept in terrariums with running deionized water and fed with live meal worms twice a week. The terrariums were maintained on a 12 h day/night cycle at 18°C.

Surgery

Frogs were anesthetized by means of hypothermia (Kaplan 1969) and immobilized with an intramuscular injection of d-tubocurarine chloride (10 μg/g body weight). The animal was placed dorsal side up on a styrofoam board with its mouth closed and wrapped in moist gauze to facilitate cutaneous respiration. A flap of skin was cut away to expose the dorsal surface of the skull, and a small hole (2-mm diam) was made above the optic tectum with a dental drill. The dura mater was dissected away to expose the dorsal surface of the brain. After surgery, the animal was placed in a sound-attenuated room (IAC No. 404, with walls and ceiling covered with 6-in. anechoic foam wedges) and allowed to warm to room temperature for ~1 h. During the experiment, which usually lasted from 8 to 17 h, immobilization was maintained with periodical injections of d-tubocurarine chloride. Surgical procedures were reviewed and approved by the Laboratory Animal Care Committee of the University of Illinois at Urbana-Champaign.

Acoustic calibration and stimulation

Responses of single auditory neurons were evaluated when a probe stimulus was presented through a loudspeaker in the free field, with and without a masker (wideband noise) presented from another loudspeaker positioned at various azimuths. The signal generation system was a modification of the system described previously for a single sound source (Gooler et al. 1993, 1996; Xu et al. 1994); here stimuli for the two sound sources could be controlled independently. The frog was placed at the geometric center of two semicircular hoops each holding a free-field loudspeaker (ADS-L200E) located at the same elevation as the frog and driven by a pulley system controlled from outside the sound-attenuated chamber. The two loudspeakers could be positioned around the animal, while maintaining a constant distance, for a range of 180° (±90° on either side of the frog's midsagittal plane). The probe stimulus was delivered through loudspeaker P, and the masker was delivered through loudspeaker M, except when P and M were colocated. In this case, because loudspeaker M was obscured by loudspeaker P, the two sounds were mixed and presented through loudspeaker P.

Following the convention employed in earlier studies (Gooler et al. 1996; Xu et al. 1994), the midline of the frontal field of the frog was considered to be 0°. Angular positions were measured from the midline and prefixed with the letters c (contralateral) and i (ipsilateral) to indicate the side of the IC from which units were studied (e.g., i45° was 45° from the midline in the ipsilateral field). Loudspeaker P was fixed at 0°, whereas loudspeaker M could originate from any of five azimuths θ in (90°, i45°, 0°, c45°, or c90°). Loudspeaker positions will be referred to as M,Pθ when both sounds are presented. The subscript indicates the angular position of the corresponding sound source.

Probe and masker stimuli were sound bursts with trapezoidal shaped envelope, 400 ms in total duration having a 1 ms rise/fall time. Both signals were presented simultaneously with an interburst interval of 2.5 s for a total of 20 presentations. The masker was broadband noise with a flat power spectrum that encompassed the leopard frog’s audible range (100–3,000 Hz). The probe was a sinusoidal amplitude-modulated (SAM) tone burst; the carrier was a tone at the neuron’s characteristic frequency (CF), and this was modulated at a modulation frequency of 20 Hz. Modulation depth was 100%, and the phases of both the amplitude-modulated (AM) component and carrier were fixed at zero relative to stimulus onset. This eliminated onset transients and phase errors. Because frogs communicate in a dense chorus where the background noise is often very high, the masker level (ML) was normally maintained at 6 dB over probe alone threshold. Signals were generated with two programmable D/A signal generators (RC-200 system, RC Electronics) and independently attenuated to required levels with two programmable attenuators (PA4 System, Tucker Davies Technologies); these were amplified by separate amplifiers (Sony GX59ES and Yamaha AX490) before being presented to loudspeakers P and M. Both the probe and the masker were equalized to ±1.5 dB (RMS) at the midpoint of the frog’s interaural axis (Brew & Kjaer, Type 2606, RMS fast). Representative waveforms (SNR: ~6 dB) and power spectral densities of the masker are shown in Fig. 1, A and B, and those of the probe plus masker are shown in Fig. 1, C and D (peak intensity in the masker spectrum was normalized to 0 dB).

Recording procedure

Extracellular single-unit recordings were made with glass micropipettes (1- to 2-μm tip diam) and filled with a solution of 0.05 M potassium acetate in 0.05 M Tris buffer. The electrode was lowered to the dorsal surface of the brain above the IC by means of a precision micromanipulator and advanced ventrally into the
were also used to determine the unit’s directional response (DR). The RLFs for probe alone (P): waveform of probe plus masker (P + M); the masker was as in B, and the probe signal was a sinusoidal amplitude-modulated SAM waveform with carrier frequency of 350 Hz and a modulation frequency of 20 Hz. The envelope of the probe is not visible because the SNR was ~6 dB. D: power spectral density of P + M for the probe described. The power spectral density of the probe alone is also shown (labeled P in D). For calibration details, see text.

The brain was prepped by a remote-controlled hydraulic microdrive. Action potentials were amplified (Dagan 2400 extracellular preamplifier) and filtered (Krohn-hite, model 3700). The filtered signal was monitored audiovisually. Action potentials were acquired by an A/D converter (RC Electronics) at a sampling rate of 10 kHz, discriminated on-line by software from RC Electronics and stored as event times on the hard disk of a personal computer. These were further analyzed off-line to generate peristimulus time histograms, raster displays, and spike counts. All recordings were performed in the principal nucleus of the left IC (Feng and Lin 1991).

**Experimental protocol**

A unit’s rate-level function (RLF) was derived under the following conditions: 1) P alone at 0°, 2) M alone at 0°, and 3) P + M at a fixed ML and varying probe levels (this was obtained with P at 0° and M at each of the 5 azimuths). The RLFs for P alone and M alone served as controls. The RLFs for P + M (at each of the 5 masker azimuths) were used to determine the threshold for detection by using the unit’s response to M alone as a reference at each of the five azimuths (see Data analysis). These responses were also used to determine the unit’s directional response (DR) to masker. Further, because all previous work on the DR for frog IC neurons was carried out with pure tones at CF, it was of interest to compare a unit’s DR with broadband sounds (masker) with its DR to narrowband sounds (probe). Thus the DR to P alone was also estimated at each of the five azimuths and served as a control for making this comparison.

**Data analysis**

Spike counts were measured in a 400-ms window coinciding with the duration of stimulation, after correcting for the unit’s response latency to P alone at 0°. Because the focus of the study was to characterize the response to the probe in the presence of a masker, this window was the most important interval for such a characterization. Furthermore, units produced few spikes, if any, to M alone and with greater variability in latency. Thus selecting a time window with respect to P alone latency allowed a more consistent and reliable characterization of a unit’s masking response. Spike counts were averaged over the total number of stimulus presentations. RLFs were presented as average spike count versus the probe sound level (for P alone and for P + M) or the masker sound level (for M alone). DRs were presented as spike count versus azimuth of probe or masker.

The DTs for P and P + M were estimated from the RLFs with the procedure of McAlpine et al. (1996). The DT for P alone at 0° was defined as the probe level at which the unit responded with an average of 0.75 spikes/trial over spontaneous firing rate (if any). The DT for P + M (also called signal DT in the presence of masker at θ) was defined as the probe level at which the unit achieved a threshold criterion response of 0.75 spikes/trial over the M alone response at θ (see Experimental protocol). Statistical tests comparing populations of cells were performed with either the χ² test or the Kolmogorov-Smirnov test (Siegel 1956). Wherever possible, the maximum of the distance between the cumulative distribution functions (D), degrees of freedom (df), and exact probabilities (p) is reported.

**RESULTS**

**Basic response properties**

Data were obtained from 74 single units in the IC of 34 leopard frogs. The temporal discharge patterns and distributions of CFs, MTs, latencies, and Q₁₀ dB values of the units were similar to those reported earlier (Eggermont 1989; Feng 1981; Fuzessery and Feng 1983b; Gooler and Feng 1992). Two general discharge patterns were discernible, tonic (57%, n = 42) and phasic (43%, n = 32). Tonic units generally showed an initial onset response that decayed to a sustained plateau for the remainder of the stimulus. Phasic units produced one to four spikes at the stimulus onset in a relatively narrow time window. A unit’s temporal discharge pattern was in general independent of the source azimuth and remained unchanged over the range of sound pressure levels tested (20–30 dB over threshold).

CFs ranged from 150 to 1,800 Hz and encompassed the spectral band of vocal signals in this species. The thresholds at CF ranged from 6 to 72 dB SPL (mean, 31.98 dB SPL). The average threshold for phasic units (37.27 dB) was higher than that for tonic units (26.37 dB). Q₁₀ values ranged from 0.6 to 3.7 (n = 29) and agree with values reported previously (Feng 1981; Gooler and Feng 1992).

**RLFs**

The RLFs for probe alone (n = 64) and masker alone (n = 32) could be classified as monotonic or nonmonotonic based on the shape of the response function. Monotonic RLFs demonstrated spike counts that increased progressively with increasing stimulus intensity. If the spike count increased at first and then decreased to 50% or less of the maximum spike count, the RLF was classified as nonmonotonic. Most cells demonstrated monotonic RLFs to both probe (77%) and masker (59%). Although some units showed a change in the shape of the RLF when stimulated...
with masker (19%), the majority of IC units exhibited the same shape of RLF for both P and M (Ratnam 1998). When stimulated with P alone, 73% of phasic units and 80% of tonic units exhibited monotonic RLFs, and the remaining exhibited nonmonotonic RLFs. However, when stimulated with M alone, 33% of phasic units and 75% of tonic units exhibited monotonic RLFs. Further, a number of phasic units (34%) and one tonic unit failed to respond to M for the range of MLs tested. The remaining units exhibited nonmonotonic RLFs.

**DR properties**

DRs of 74 IC units were obtained for masker. Because of time constraints DRs to probe stimuli were obtained for only 44 of these 74 units. Representative examples of DRs are shown in Fig. 2. When stimulated with P alone, majority of IC units (phasic and tonic) gave strong responses at contralateral probe azimuths and showed poor responses at ipsilateral azimuths (Fig. 2, ○). The greatest change in response with a change in azimuth was usually observed at ~0° (Fig. 2A). The distribution of best and worst response azimuths is shown in Fig. 3, A (phasic) and B (tonic). The two populations of cells did not show any significant differences in the distributions of best (2-tailed $\chi^2$ test, $df = 4$, $\chi^2 = 0.5624$, $P = 0.905$) or worst response azimuths ($\chi^2 = 5.0649$, $P = 0.1671$). When stimulated with M alone, the DRs demonstrated three distinct features. 1) A unit’s response to M (Fig. 2, ■ and □) was significantly less than its response to P. Although the masker, in most cases, was 4 dB less intense than the probe, the response to M rarely exceeded the response to P even when the masker was more intense (Fig. 2A, □). 2) Best and worst response azimuths for M (Fig. 3, C and D) were distributed over all azimuths to a greater extent as compared with P. 3) Many units, particularly phasic cells, did not respond to noise at some or all azimuths (category marked NR, Fig. 3, C and D). Some phasic cells also showed a preference for masker originating from 0° (Fig. 3C) but never demonstrated best response azimuths in the ipsilateral hemifield. Thus DRs for phasic cells were significantly different from DRs for tonic cells, both in the distribution of best (2-tailed $\chi^2$ test, $df = 5$, $\chi^2 = 17.1142$, $P = 0.0022$) and worst response azimuths ($\chi^2 = 21.432$, $P = 0.00067$).

**Probe DTs**

The probe RLF was significantly altered when a masker at a fixed sound level was presented from different azimuths. As such, a unit’s DT was modified by the masker azimuth as shown for two representative neurons (Figs. 4 and 5). The masking data for one phasic unit (Fig. 4) illustrate a case where the DTs were lowered by increasing the angular separation between probe and masker sources. The DT to probe alone at 0° was 32 dB SPL. When a masker (6 dB over probe threshold) was added at the same azimuth (Fig. 4, top row, middle panel) the DT for probe was elevated to 38.2 dB SPL. The change in DT in the presence of a masker at 0° over that of probe alone was defined as the reference threshold shift (RTS). For the unit shown, the RTS was 6.2 dB. When the angular separation between probe and masker sources was progressively increased to 45° and 90° on the ipsilateral side (Fig. 4, panels marked i45° and i90°), the DT was reduced to 32.9 and 31.3 dB SPL, an improvement of 5.3 and 6.9 dB, respectively. On the contralateral side, however, when the masker was presented from c45° (Fig. 4, top row, right panel), the DT was almost unchanged (38 dB SPL) but lowered to 35.1 dB SPL when the masker was presented from c90° (Fig. 4, bottom row, right panel). Thus, for this unit, complete release from masking was evident in the ipsilateral side within 45° of the midline position. The change in DTs with masker azimuth is summarized in the panel marked DT in Fig. 4. Units demonstrating this type of DT function were classified as A-type.

Two features of interaction between probe and the masker

**FIG. 2.** Representative directional responses (DRs) of inferior colliculus units showing how the response to probe alone (P, ●) or masker alone (M, ■ and □) at a fixed sound level is affected by sound azimuth. Sound levels (in dB) are indicated in the panels relative to probe alone threshold.

**FIG. 3.** Distributions of best and worst response azimuths for phasic and tonic units to probe alone (A and B) and masker alone (C and D). Abscissa indicates azimuthal position of sound source, and ordinate indicates the relative proportion of units having best (black bars) or worst (gray bars) response at that azimuth. In C and D the category NR indicates no response.

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FIG. 4. Example of how a masker changes a unit’s response in terms of the unit’s rate-level function (RLF) (i.e., the masking effect), and how masker direction influences release from masking for a phasic neuron (R493). Shown here are the RLFS for probe alone at 0° (P) and for probe plus masker (P + M) at various masker azimuths (labeled at the top left corner of each panel) and the unit’s detection threshold (DT) as a function of masker azimuth. At masker azimuth of 0°, probe and masker were colocalized (top center panel), whereas at c90° and i90° masker and probe were separated by 90° (bottom row, right and left panels, respectively). RLFS (filled squares) were obtained by varying the probe sound level (abscissa) at fixed masker level (ML). Ordinate is spikes/trial. The response to masker alone (M, horizontal dotted line) was used as a reference for estimating the DT (filled arrow). Each of the 5 panels also shows the RLF to probe alone at 0° (P, thin line) and the threshold for probe alone (open arrow in top middle panel). These are shown only for reference.

are evident: 1) a change in the sensitivity to the probe as seen by the shift in the RLFS to P + M (re: P _0° RLF) at c45° and c90° (Fig. 4, right panels). A rightward shift indicated a reduction in sensitivity to probe in the presence of a masker, whereas a leftward shift indicated an increase in sensitivity. 2) A change in the threshold criterion resulting from the unit’s response to M alone (see Data analysis). The stronger the masker response, the higher was the criterion response (as observed, for instance, at 0° in Fig. 4). At ipsilateral azimuths the unit had low threshold criteria (Fig. 4, left panels), and the unit’s sensitivity to probe in the presence of masker at these azimuths was nearly the same as its sensitivity to P alone at 0°. Thus the DTs were similar to the DT to P alone at 0°. For masker in the contralateral sound field, however, although criterion levels were lower compared with 0°, the unit showed a marked reduction in sensitivity to probe in the presence of the masker (Fig. 4, right panels). As a result, the DTs did not improve as much as for masker in the ipsilateral field.

In contrast, a number of IC neurons (24%, n = 18) exhibited a different type of DT function, which was classified as V-type (Fig. 5 from a tonic unit). This unit exhibited changes in DT that were opposite those observed previously. The DT to P alone was 28 dB SPL. When masker was presented at 0°, i45°, or c45° (Fig. 5, top row), the unit demonstrated lower DTs (i45°: 26.4 dB SPL, 0°: 24.6 dB SPL, c45°: 25.3 dB SPL) caused by improved sensitivity to probe in the presence of masker (as evident from the leftward shift in the RLFS), although threshold criteria were larger than the criterion for P alone. With masker at i90°, the unit

FIG. 5. Example of how a masker changes a unit’s response in terms of the unit’s RLF (i.e., the masking effect), and how masker direction influences release from masking for a tonic neuron (R561). Shown here are the RLFS for probe plus masker (P + M) and the DT function. Explanation follows Fig. 6.
was less sensitive to the probe, but the threshold criterion was comparable with P alone. This resulted in an increase in DT (29.9 dB SPL). Conversely, at c90°, the threshold criterion was highest, although the sensitivity to P + M was greater than sensitivity to P alone (Fig. 5, c90°; SPLs <32 dB). This increased the DT (30.9 dB SPL). Thus masking was more prominent in the lateral auditory fields.

To test the effect of ML on signal detection, DTs were obtained at 2 different MLs for 14 units. Figure 6 illustrates results from two neurons. Unit R483 was tested at a ML of 10 dB (Fig. 6A) and 14 dB (Fig. 6B) above the P-alone threshold. At the lower ML, the unit demonstrated release from masking when the masker was positioned in the contralateral field, including improvement of the probe DT by as much as 7 dB for masker at c90°. On increasing the ML to 14 dB, the unit DT was elevated at all azimuths with the exception of i45° where the DT was comparable with P alone. For this unit, the shape of the DT function changed with an increase in ML. On the other hand, for one-half the units tested at two different MLs, a 4-dB difference in ML did not affect the shape of the DT function. For example, unit R471 (Fig. 6B) was masked at all azimuths at a ML of 6 dB, but when the ML was increased to 10 dB the DT function was displaced almost linearly by approximately +5 dB.

As a whole, we found that the DTs at any given ML were broadly distributed and resembled the distribution of thresholds at CF (Ratnam 1998). The effect of masker at a given ML on DT was not uniform across the population. Some neurons were strongly masked, i.e., their DTs were greatly elevated (as in Fig. 6B), whereas other neurons exhibited improvements in DTs (as in Fig. 5). Analysis of the data also did not reveal any correlations between a unit’s CF and its 1) best response azimuth to P alone or M alone, 2) RTS, 3) maximum change in DT (P alone), or 4) DT function (A- or V-type).

**DT functions**

The DT function differed somewhat among IC neurons. On the basis of its shape, units could be divided into four broad categories. The most commonly observed patterns were the V-type (Fig. 7A; 24%) and A-type (Fig. 7B; 22%). Psychophysical experiments on humans and animals show that release from masking is typically stronger with increasing angular separation between P and M sources. Thus A-type units appear to be the physiological correlates of such observations. On the other hand, V-type units demonstrate an opposite response pattern to the psychophysical observations.

Two other types of DT functions were also observed. These showed both peaks and troughs and had a mixture of A- and V-type characteristics. They were classified as complex–symmetrical (C-S, Fig. 7C; 27%) if the shape exhibited a symmetry about the midline or complex–asymmetrical (C-A, Fig. 7, D and E; 27%) if there was no symmetry. There were two types of C-S DT functions, and the most common pattern was the W-type (65%; Fig. 7C). W-type units demonstrated elevated DTs at i90°, 0°, and c90° with low DTs at i45° and c45°. The remaining C-S units showed the opposite DT function, i.e., M-shaped instead of W-shaped. Among the C-A type units, 53% followed an A-type response at all azimuths except at c90°, where the DT was sharply elevated (Fig. 7D). A mirror image of this type of response, with a sharp increase in DT at i90°, was also observed in 30% of C-A neurons (not shown). Another C-A type, although rarely encountered (only 3 units were observed), is shown in Fig. 7E.

**Correlations between unit discharge patterns and DTs**

The temporal discharge pattern of a unit was correlated with changes in DT function in three ways: 1) changes in unit sensitivity to the probe in the presence of masker, 2) direction of the shift in DT, and 3) modification of the shape of the DT function.

**Effect on Unit Sensitivity.** As shown earlier, the presence of a masker could shift the RLF to P + M to the right or left with reference to the RLF for P alone (Figs. 4 and 5). When the proportion of units exhibiting a shift in a given direction were pooled for phasic (Fig. 8A) and tonic units (Fig. 8B), we found that most phasic units exhibited a rightward shift at all masker azimuths, indicating that they were less responsive to the probe in the presence of a masker. On the other hand, most tonic units exhibited a leftward shift at all masker azimuths except at i90°, indicating that they were generally more responsive to the probe in the presence of a masker. At i90° tonic units showed roughly equal preference for leftward and rightward shifts. Although the shift in the direction of the RLF to P + M is an important indicator of a unit’s susceptibility to masking, this information alone is insufficient to predict DTs as the threshold criterion is also an important factor.

**Effect of Masker Azimuth on DTs.** This could be quantified by the change in DT (ΔDT) as the masker was progressively moved from the colocalized position (i.e., 0°) to more lateral positions. Because we employed five masker azimuths, four such ΔDTs could be calculated for c45° – 0°, i45° – 0°, i90° – i45°, and c90° – c45°. Population averages of ΔDT are shown in Fig. 9A for phasic units (left panel) and tonic units (right panel). Phasic units as a group showed
a mean reduction in DTs when the angular separation between the probe and the masker was increased in the ipsilateral field and when the masker was moved from 0° to c45° in the contralateral field. They showed a mean increase in DT when the masker was moved from c45° to c90°, as indicated by the positive value of ΔDT in Fig. 9A, left panel. This increase was largely caused by C-A type phasic units, which tended to exhibit a marked increase in DT when the masker was presented from c90° (e.g., Fig. 7D). Tonic units,

![Figure 7](image-url)

**FIG. 7.** Types of DT functions. Neurons demonstrated diverse DT functions. Four broad classes of functions were observed: A: V-type pattern, where DT was lowest when probe and masker were colocalized at 0° but increased with increasing angular separation; B: A-type pattern, where DT was highest when probe and masker were colocalized but decreased with increasing angular separation; C: complex-symmetrical (C-S) pattern, where the DT function demonstrated a symmetry around 0°; D: complex-asymmetrical (C-A) pattern, where the DT function was a mix of A- and V-types (left panel) or monotonic (right panel).

mean change in DT with a change in azimuth for IC units. Mean change in DT was calculated for a 45° change in masker source location. For instance, i90°–i45° (black bar) was the mean change in DT for a population of neurons obtained by subtracting the DT at i45° from the DT at i90°. A: phasic units (left panel) showed a mean decrease in DT with an increase in angular separation except for c90°–c45°, where the change was positive. Tonic units (right panel) showed a mean increase in DT with an increase in angular separation. B: average changes in DT for units with A- and V-type DT functions. A-type DT function was characterized by a mean reduction in DTs with an increase in angular separation, and V-type DT function was characterized by a mean increase in DTs with an increase in angular separation.

![Figure 8](image-url)

**FIG. 8.** Change in sensitivity of RLF for P + M for phasic and tonic neurons. Sensitivity was defined as the relative position of the RLF for P + M around criterion (see text) with respect to the P alone. The RLF for P + M could be shifted to the right (black bars) or to the left (gray bars) of the RLF to P alone. A rightward shift indicates that for a given probe sound level the neuron responded with fewer spikes in the presence of a masker than in its absence. The converse was true with a leftward shift. Most phasic units demonstrated a rightward shift at all masker azimuths, whereas most tonic units demonstrated a leftward shift at all azimuths except at 90°, where leftward and rightward shifts were present equally.
A phasic (79%, Fig. 10A, B), although cells that demonstrated negative RTS were when stimulated with probe. Azimuthal receptive fields were between positive RTS (54%) and negative RTS (46%), whereas cells that demonstrated negative RTS were mostly tonic (Fig. 10B). Finally, most A-type units were phasic (79%, Fig. 10A), whereas most V-type units were tonic (69%, Fig. 10A).

As a group A-type units typically demonstrated negative ΔDTs, i.e., lowering of DTs, with increasing angular separation between probe and masker sources (Fig. 9B, right panel), whereas V-type units showed positive ΔDTs (Fig. 9B, right panel). Taken together with Fig. 9A, these figures indicate that phasic units were largely associated with A-type units (11/14 units), whereas tonic units were largely associated with V-type units (11/16 units).

**Discussion**

**Basic response properties**

The information processing ability of tonic and phasic units was widely discussed in both mammals (see reviews in Popper and Fay 1992) and frogs (Condon et al. 1991; Feng and Lin 1994; Gooler and Feng 1992; Xu et al. 1994). The results from this study indicate that phasic and tonic units also exhibit different signal detection abilities.

In the frog, a noteworthy feature of this division into tonic and phasic types is the increase in the number of phasic units along the ascending auditory pathway; they comprise ~10% of the population in the dorsal cochlear nucleus (Fuzessery and Feng 1983a), ~25% in the superior olivary nucleus (Condon et al. 1991); and 33% in the IC (Feng 1981; Gooler and Feng 1992). In this study, 43% of units encountered were phasic. Because phasic units respond to transients in the envelope of the signal, it is likely that at higher auditory centers large numbers of such units will respond to the onset of behaviorally relevant sounds superimposed on background noise. Tonic units, which have a greater ability to encode temporal characteristics, may serve a different function such as discriminating between two different sounds.

**RLFs**

When units were stimulated with broadband noise, RLFs for IC units differed from those to probe alone in two ways. First, all except two units were less responsive to noise than to probe because the RLFs to M alone were shifted to the right of the RLF to P alone. Second, a small but sizable number of units (16%) failed to respond to noise over the range tested. The poor response of IC units to noise presumably results from two factors, 1) Suppression in the auditory periphery originating from the motion of the basilar membrane (Feng et al. 1975; Gilbert and Pickles 1980; Patuzzi et al. 1984; Ruggero 1973; Schalk and Sachs 1980) and 2) neural inhibition in brain stem auditory pathways (Ehret and Merzenich 1988; Ehret and Moffat 1985; Fuzessery and Feng 1982, 1983a; Xu et al. 1994; Zhang and Feng 1998). Thus the presence of energy in the inhibitory sidebands flanking the excitatory response area may result in improved noise tolerance on ascending the auditory pathway and have a direct impact on detecting signals in noise.

**DR characteristics**

When stimulated with probe, azimuthal receptive fields were usually broad and located largely in the contralateral field for probe stimuli. These results are in agreement with previous studies in the frog (Feng 1981) and mammalian IC (Aitkin and Martin 1987; Aitkin et al. 1985; Calford et al. 1986; Geisler et al. 1969). However, when stimulated with noise, neurons responded strongly in a narrow range.
of azimuths in the frontal field (Fig. 3C), a result similar to that reported in the cat IC (Aitkin and Martin 1987). Additionally, we found that there were significant differences between noise DRs of phasic and tonic cells (Fig. 3, C and D), although both populations had similar DRs to probe (Fig. 3, A and B). Thus the neural processing of broadband noise differs markedly from the processing of sounds at units CFs, with the differences between phasic and tonic units becoming most apparent in their azimuthal response to noise. These findings have a direct impact on detection of signal in noise because noise DRs form the threshold criterion from which DTs are estimated.

Factors influencing DTs for probe in the presence of masker

SENSITIVITY AND THRESHOLD CRITERION. A unit’s DT is determined by its sensitivity to P (in the presence of M) and by the threshold criterion (Figs. 4 and 5). Adding a masker to P alters both the sensitivity and threshold criterion in a complex manner that is nonlinear and not easily predicted from the control data. Thus, although some general statements can be made about the DT for probe in noise (e.g., a larger threshold criterion and reduced sensitivity always result in an increase in DT), the factors appear to constitute two independent degrees of freedom. This is clearly seen in instances where improvements in DT may be due to a trade-off in sensitivity and threshold criterion. In some cases, even if the sensitivity is improved, a sufficiently high-threshold criterion may elevate the DT, and likewise, if the sensitivity is reduced, a reduction in criterion level may improve the DT. Both cases were observed in this study. The difficulty in predicting unit sensitivity and threshold criterion may be due to two factors, 1) nonlinear interactions between P and M resulting from the presence of energy across a wide range of the frequency spectrum (nonlinear frequency processing) and 2) inputs from channels tuned to different frequencies converging via binaural pathways (cross-channel interactions). Although some understanding exists of the former (Gilbert and Pickles 1980; Ruggero 1973; Schalk and Sachs 1980), very little is known of the latter.

Tonic and phasic populations differ in two respects. 1) In the presence of masker, phasic units were generally less sensitive, and tonic units more sensitive, to probe (Fig. 8). 2) The threshold criterion was more variable for tonic units than for phasic units. Thus variability in DTs (which are constrained by the variability in threshold criterion and unit discharge rates) were more predictable for phasic than tonic units. Phasic units typically showed an elevation in DT whenever the RLF to $M_0P_0$ shifted to the right and a reduction in DT whenever the RLF shifted to the left (Ratnam 1998). The correlation was not so strong for tonic units. Therefore the two factors determining DTs appear to differ in their relative importance for phasic and tonic units.

DIRECTION OF MASKING SOURCE. Most IC neurons showed elevation of DTs to varying degrees when probe and masker sources were colocalized (Fig. 7). From a behavioral point of view, when P and M sources are colocalized, the expected threshold shift is both upward and larger than the shift experienced at other masker azimuths. However, responses of single neurons were not always consistent with the behavioral observations; 75% of neurons had maximum threshold shifts at masker azimuths other than $0^\circ$, indicating that maximum masking was not limited to the situation where P and M were colocalized (Fig. 7, A and C–E). Most phasic units exhibited maximum threshold shifts with M in the contralateral field and at $0^\circ$, whereas for tonic units maximum threshold shifts typically occurred when M was in lateral azimuths, and only infrequently at $0^\circ$. Consequently, release from masking whenever it was observed occurred at different regions of the auditory field for phasic and tonic units (in the lateral field for phasic units and in the frontal field for tonic units). The two populations were thus complementary to one another.

The paucity of data on free-field unmasking for central auditory units makes it difficult to provide comparisons with other studies. The only comparable data are results for single-unit studies of binaural masking level differences (BMLD) obtained from neurons in the guinea pig IC under closed-field conditions (Jiang et al. 1997; McAlpine et al. 1996). These investigators show that BMLD for IC units is also variable across the population. The most interesting result obtained by Jiang et al. (1997) while comparing the response to $N_0S_0$ versus that to $N_0S_0$ ($N$: masker; $S$: probe) was that, for some units, detectability was greater for $S_0$ than for $S_0$ tones. This is also incompatible with psychophysical results because $N_0S_0$ corresponds to colocalization, and $N_0S_0$ corresponds to spatial separation of N and S sources. Their result is similar to the V-type units in this study, which also exhibit an improvement in DT at $M_0P_0$ and elevated DTs when probe and masker are separated. In general, both the current and the BMLD studies provide an indication that signal detection by auditory neurons is more complex than the behavioral observation.

At present we may only speculate on how the direction of masker influences a unit’s sensitivity to probe. Recent studies on the influence of sound direction on a unit’s frequency tuning demonstrated that there was a narrowing of

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2 Because of the method of data analysis employed in this study, criterion levels were no smaller than 0.75 spikes/trial (corresponding to no spike output in the presence of the masker alone). On the other hand, it was possible for criterion levels to increase over a much larger range, being limited only by the maximal discharge rate of the unit. Phasic units that usually produced fewer spikes demonstrated criterion levels that were modest (between 0.75 and 2 spikes/trial) and thus exhibited much less variability in spike count with azimuth, whereas tonic units that produced more spikes usually demonstrated higher criterion levels (as much as 8–12 spikes/trial) with correspondingly greater variability in spike count on changing masker azimuth.
the excitatory response area (Gooler et al. 1993; Xu et al. 1994) with a concomitant increase in the unit’s inhibitory response areas (Zhang and Feng 1998) when the sound was presented from 90° compared with 0°. These studies suggest that there is an interplay between excitatory and inhibitory inputs arising from sounds in the free field, which are in part due to binaural mechanisms and which are likely to play an important role in free-field responses to masking noise.

**Effect of ML**. Changing the masker level altered the DT function of many neurons in a predictable manner, i.e., there was a parallel and upward shift in the DT function whenever the ML was increased (Fig. 6B). However, for nearly one-half of the IC neurons, shifts in DTs were direction dependent (e.g., Fig. 6A), with regions in the azimuthal space where the unit was less sensitive to ML (at 45° in Fig. 6A) and regions where it was more so (at 90° in Fig. 6A), that is, there was a direction dependent level tolerance (or robustness) to noise. Because of the limited numbers of neurons studied at more than one ML (n = 14), more extensive evaluations are necessary.

**DT functions**

A-type units, whose DT functions support spatially mediated release from masking, had an average of 5.85-dB improvement for angular separations of 90° in the ipsilateral field and 4.04-dB improvement for a 90° separation in the contralateral field (Fig. 9B, left panel). However, changes in DT for 4 of 15 A-type units was as high as 6 dB for separations of just 45° (e.g., see Fig. 7B). In many A-type units, a separation of 90° on either side was sufficient to obtain complete release from masking. For some units, the change in DT with azimuth (ΔDT/Δθ) was so steep that a 45° separation produced complete release from masking (Fig. 7B). Thus A-type units appear to correlate well with psychophysical observations, although masking release (in dB) in some units was greater in one or the other auditory hemifields (e.g., Fig. 4). Asymmetry in physiology can presumably be resolved by A-type units on both sides of the IC. The majority of V-type units (75%) showed lower DTs when probe and masker were colocalized (Fig. 10). Increasing the angular separation of sound sources by 90° in either direction produced an increase in DTs averaging 4.5 (ipsilateral) and 5.4 dB (contralateral; Fig. 9B, right panel). Some of these units (5/21) also demonstrated ΔDT/Δθ of 6 dB or more over a 45° separation.

**Comparison with masking in auditory nerve fibers**

Data obtained from auditory nerve fibers in the leopard frog, with probe positioned at 90°, indicate that the DT is slowly but progressively lowered with increasing sound source separation (Lin and Feng, unpublished observation). This improvement resembles the release from masking obtained with A-type units and supports the hypothesis of spatially mediated release from masking. Further, their results suggest that ΔDT/Δθ for auditory fibers is much smaller than the ΔDT/Δθ observed for the IC. Complete release from masking in most auditory fibers was not guaranteed even with a 180° separation of probe and masker sources.

When there was complete release, it was obtained mostly with angular separations of 90° – 180° (in contrast to 45° – 90° for the IC). These results suggest that, although A-type units may originate in the periphery (i.e., they are a consequence of the directional characteristics of a frog’s acoustic receiver), central mechanisms may be responsible for sharpening the DT function of IC neurons. Further, auditory fibers rarely demonstrated an improvement in DTs when probe and masker were colocalized (e.g., as seen in V-type IC units) nor did they demonstrate the complex DT functions observed in the IC. These observations suggest that central auditory pathways play a role in improving the direction-dependent signal detection, presumably via binaural interactions. A point that proves puzzling is the strong correlation between A-type DT functions and phasic units. Some studies suggest that there is an interplay between excitatory and inhibitory inputs arising from sounds in the free field, which are in part due to binaural mechanisms and which are likely to play an important role in free-field responses to masking noise.

**Implications for signal detection**

The diversity of neural DT functions is not so surprising considering the known diversity of neuronal selectivities to AM, duration, intensity, etc. Indeed, population coding of stimulus features benefits from such diversity and explains the vastly improved acuity exhibited in diverse behaviors. For instance, at the fixed levels of masker employed in this study (6 dB, re: DT to probe alone at 0°), DTs of IC neurons spanned a range of ~50 dB (not shown); this may serve to function in essentially the same way as the distribution of minimum thresholds given the restricted dynamic range of IC neurons (20–30 dB), that is, it serves to increase the range of signal intensities detectable in noise (Ratnam 1998). However, at high noise levels (ML of 10 dB or more, re: DT to probe alone at 0°), unit DTs appear to increase rapidly at all masker azimuths, possibly reducing the population’s range of DTs. This may contribute to the reduced ability to detect signal at low SNRs and thus have an impact on both the callers and receivers in a chorus.

The data from the present study also point to the possibility that A- and V-type units may be better suited for different listening conditions, e.g., for detecting signals when sound sources are separated in space and when sound sources are colocalized, respectively. Hence the two types may complement one another. The presence of other types, particularly the C-A type, indicates more sharply tuned DT functions that are likely to be useful for signal detection when the masker originates from restricted regions in the azimuthal space. Taken together, the azimuthal distribution of best DTs suggests that different populations may contribute to signal detection under different listening conditions.

An altogether different possibility is that only one class of neurons is particularly important for signal detection, namely, phasic neurons. This may be likely because, on ascending the auditory pathway, there are increasingly more phasic than tonic cells (phasic units, may however, serve other tasks as well). Further, there are indications that the cocktail-party effect involves perceptual processing such as the use of attentional mechanisms to attend to a given sound. Because these are likely to involve higher centers in the
brain, it is probable that phasic units play a greater role in subverting this function. Supporting this hypothesis is the observation that phonotaxis begins with an orienting response that centers the sound source in the frontal field (Feng et al. 1976; Rheinlaender et al. 1979). Phasic units can detect senders in the lateral sound field and initiate an orienting response, after which tonic units with their greater SNR in the frontal field can contribute to a better perception of sound parameters.

An important, albeit unresolved issue is the degree to which unit sensitivity and threshold criterion shape the DT function. A significant obstacle that stands in the way toward resolving this is the nonlinear nature of the response to P + M (i.e., presentation of P and M together did not result in a response corresponding to the linear sum of the unit’s responses to the individual sounds). As a consequence, the sensitivity of a unit to P + M is also related nonlinearly to its sensitivity to P alone and M alone. Although qualitative features of this interaction were reported here, it appears crucial to bring in more quantitative methods, such as a suitable model of signal detection based on unit discharge patterns, to fully explore and characterize this interaction.

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