Relative importance of different acoustic cues to the directional sensitivity of inferior-colliculus neurons

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1 Introduction

Sound localization is based on multiple acoustic cues such as interaural differences in time and level, spectral cues, and changes in these cues resulting from head movements (Blauert, 1983; Searle et al., 1976). Physiological studies done in the free field have shown that many cells in the inferior colliculus (IC) are sensitive to the direction of sound sources (Aitkin et al., 1985; Calford et al., 1986; Aitkin and Martin, 1987, 1990). These directionally-sensitive cells are likely to play an important role in sound localization. However, free-field studies cannot determine which of the many possible acoustic cues are responsible for this directional sensitivity because they do not allow independent control over each cue.

Control over individual acoustic cues is achieved in dichotic studies that deliver stimuli through closed acoustic systems. Many studies have demonstrated that cells in the IC and the superior olive are sensitive to interaural time (ITD) and level (ILD) differences (Rose et al., 1966; Goldberg and Brown, 1969; reviewed by Irvine, 1986). However, with few exceptions (e.g. Caird and Klinke, 1987), most of these studies varied a single cue without consideration of possible interactions between cues. Furthermore, most studies have focused on pure tone stimuli, which do not include the spectral cues provided by directionally-dependent filtering of acoustic stimuli by the head and the pinnae.

Recent advances in digital technology have made it possible to simulate the sound pressure waveforms produced in the ear canals by free-field sound sources through closed acoustic systems (Blauert, 1983; Wightman and Kistler, 1989; Poon and Brugge, 1993). Such "virtual-space" (VS) techniques provide stimuli with multiple, realistic localization cues, and also give precise control over individual localization cues. They are beginning to provide information about which cues are most important for sound localization by human listeners (Wightman and Kistler, 1992). In this paper, we used VS techniques for identifying which acoustic cues are most important for the directional sensitivity of single units in the central nucleus of the IC of anesthetized cats. We used head-related transfer functions (HRTF's) measured in the cat by Musicant et al. (1990) to synthesize VS stimuli possessing realistic ITD's, ILD's, and spectral shape. Although this approach ignores other important cues such as echoes and head and pinna movements, it provides a first

important cues such as echoes and head and pinna movements, it provides a first approximation applicable to an animal at rest in an anechoic environment. This brief report focuses on VS stimuli located in the horizontal plane, although our experiments were also concerned with stimuli in the median vertical plane.

2 Method

Methods for recording from single units in the IC of barbiturate-anesthetized cats are essentially the same as described by Yin et al. (1986). The only significant difference with the earlier studies is that we focused on units with high characteristic frequencies (CF > 2-4 kHz), for which spectral cues might be important.
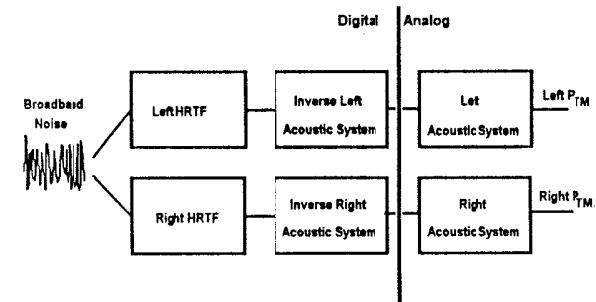

Figure 1. Block diagram of the signal processing used for synthesizing virtual-space stimuli.

The method for synthesizing virtual-space stimuli (Fig. 1) is similar to that used in the human psychophysical experiments of Wightman and Kistler (1989) and the physiological study of Poon and Brugge (1993). The input signal is a sample of pseudo-random broadband noise, 200 msec in duration, with significant energy between 2 and 35 kHz, the range in which the measurements of Musicant et al. (1990) were most reliable. This signal is first processed through digital filters constructed from acoustic measurements made in one "standard" cat by Musicant et al. (1990). These filters (one for each ear) represent the directionally-dependent transformation of sound pressure from the free field to the ear canal. Stimuli in each ear were then processed through another digital filter that compensated for the transfer function of the closed acoustic system measured with a calibrated probe-tube microphone. With compensation, the sound pressures (magnitude and phase) produced in both ear canals by our closed systems are the same as those that would occur for free-field stimuli originating from a particular direction in the standard cat.

The VS stimuli described above include three cues to sound localization (ITD, ILD, and spectral shape), and referred to as 'full-cue". We have also generated modified VS stimuli in which one or more of these cues was set to a constant for every azimuth. Table I

lists some of these "partial-cue" stimuli. "0-ITD" stimuli were generated by delaying the waveforms of the full-cue stimuli at the two ears so as bring the ITD to zero for every azimuth. ITD was measured by picking the maximum of the crosscorrelation function between the waveforms in the left and right ear. "Δ-ITD" stimuli were generated by taking the full-cue waveforms for zero azimuth, where the ITD is 0, then introducing the appropriate ITD for each azimuth. These stimuli are similar to those used by Yin et al. (1986) for studying ITD sensitivity for broadband noise, except that there is a known mapping between ITD and azimuth. The manipulation of ILD cues was necessarily more complicated because of the difficulty in defining ILD for a broadband stimulus. The sound pressure level (SPL) was measured for each ear and each azimuth in either of two ways: broadband, or narrowband. The broadband SPL is the r.m.s. amplitude of the stimulus waveform. The narrowband SPL was measured using a third-octave Gaussian bandpass filter whose center frequency was at the CF of the neuron. After measuring SPL's, "0-ILD" stimuli were generated by adjusting the gains of the full-cue stimuli so as to make their SPL's at both ears coincide with those of the stimulus at zero azimuth. Thus, SPL's in both ears did not vary with azimuth for these stimuli, and the ILD was always equal to the ILD at zero azimuth, which is approximately zero. Finally, we generated "Δ-ILD" stimuli by taking the full-cue waveforms for zero azimuth, and then introducing gains so as create the appropriate SPL in each ear for each azimuth, and therefore the appropriate ILD.

Table 1: Cue manipulations for the virtual-space stimuli.

	ITD	ILD	Spectral Shape
Full Cue	+	+	+
0-ITD	-	+	+
Δ-ITD	+	-	-
0-ILD	+	-	+
Δ-ILD	-	+	-

3 Results

Our results are based on data from 60 well-characterized single units in 10 cats. Two questions are of particular interest: how binaural interactions shape the directional responses to VS stimuli, and which localization cues are most important for this directional sensitivity.

3.1 Binaural interactions in responses to VS stimuli

A majority of units in our sample showed directional sensitivity for VS stimuli at moderate stimulus levels. Figure 2 shows data for a single unit with a CF of 9 kHz. The top panel shows the average discharge rate in response to the VS stimuli as a function of azimuth. The stimulus level was approximately 20 dB above threshold for 0 azimuth. In this figure

as in all others, positive azimuths correspond to VS stimuli located contralaterally to the recording site. When the VS stimuli were presented binaurally (as would naturally occur in the free-field), the response was clearly directional: there was little response for azimuths on the ipsilateral side, a steep rise in response for azimuths near zero, and a broad maximum on the contralateral side. In order to examine the role of binaural interactions, VS stimuli were also presented to the contralateral ear only. This condition corresponds to plugging one ear in free-field experiments. The monaural response was much less directional than the binaural response. Thus, binaural interactions are important for the directional sensitivity of this unit.
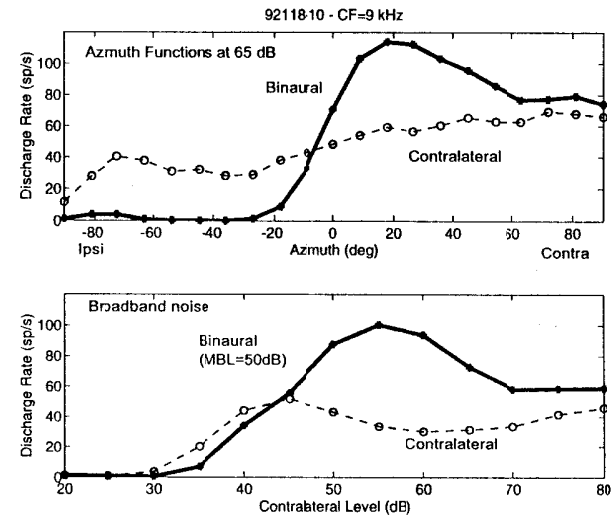

Figure 2. Binaural interactions in the response of a single IC unit for VS stimuli (Top) and broadband noise (Bottom).

An advantage of VS techniques over free-field stimulation is that they provide independent control over the inputs to each ear, making it possible to study binaural interactions. The dashed line in the bottom panel of Fig. 2 shows the response to a 200-msec broadband noise presented to the contralateral ear as a function of stimulus level. The solid line shows responses for a binaural condition used for studying ILD sensitivity (Irvine and Gago, 1990): As the stimulus level was increased in the contralateral ear, the level in the ipsilateral ear was correspondingly decreased so as to keep the mean binaural level (MBL) constant at 50 dB. This condition crudely mimics the changes in level that occur when a free-field stimulus moves from the ipsilateral to the contralateral side. For ILD's favoring the contralateral ear (contra levels > 50 dB), the binaural response is

greater than the monaural response obtained with contralateral stimulation, meaning that the ipsilateral ear has a facilitatory influence. On the other hand, for ILD's favoring the ipsilateral side, the binaural response is smaller than the contralateral response, meaning that the ipsilateral ear is inhibitory. Such mixed facilitatory and inhibitory binaural interactions, which are commonly seen in the IC (Semple and Kitzes, 1987; Irvine and Gago, 1990), are also apparent for the VS stimuli in the top panel. The binaural response is greater than the monaural response for contralateral azimuths, but smaller than the monaural response for ipsilateral azimuths. Thus, the binaural interactions found with VS stimuli are consistent with those found for broadband noise using the stimulus paradigms of traditional dichotic studies.
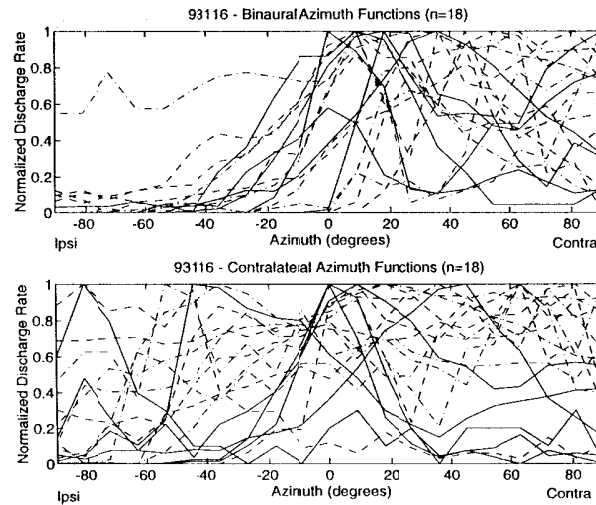

93116 - Binaural Azimuth Functions (n=18)

93116 - Contralateral Azimuth Functions (n=18)

Figure 3. Azimuth functions for 18 units from the same cat measured with VS stimuli presented binaurally (Top) and contralaterally (Bottom).

The importance of binaural interactions for the directional sensitivity of IC neurons is a general finding. The top panel of Fig. 3 shows binaural azimuth functions for 18 units from one cat. Unit CF's ranged between 4 and 30 kHz. With one exception, all units show little response for ipsilateral azimuths, and strong response for a range of contralateral azimuths. Most units also show a steep rise in response which occurs at different azimuths for different units. The bottom panel shows responses of the same units to VS stimuli presented to the contralateral ear alone. Again, this condition corresponds to plugging one ear in the free field. The contralateral azimuth functions do not show the orderly

pattern seen for the binaural condition, and many of them are less directional. Thus, binaural interactions are important for the directional sensitivity of this population of units.

3.2 Effect of selective cue manipulations on responses to VS stimuli

All the binaural data shown so far were for "full-cue" VS stimuli, which include all 3 localization cues. A major advantage of VS techniques is their ability to selectively manipulate each cue. Fig. 4 shows results for a contralaterally-excited, ipsilaterally-inhibited unit with a CF of 14 kHz. The top panel shows the effects of manipulating ITD. The azimuth function for the full-cue condition showed a typical directional sensitivity for our sample of units. When ITD was set to zero for every azimuth (dashed line), the response was largely similar to the full-cue response. This suggests that ITD is not the primary determinant of the directional sensitivity of this unit. When ITD only was varied with azimuth (dot-dash line), the response was not very directional, confirming that this unit is not very sensitive to ITD.
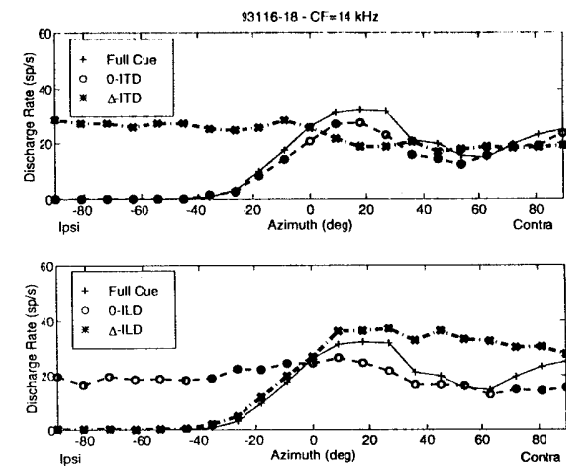

93116-18 - CF=14 kHz

Figure 4. Azimuth functions for a single unit in response to modified VS stimuli. Top: Cue manipulations involving ITD. Bottom: Manipulations involving ILD. The stimulus level was 15 dB above threshold for zero azimuth for all conditions.

The bottom panel of Fig. 4 illustrates the effect of manipulating ILD. In this case, the ILD was measured in a 1/3-octave band centered at the unit CF. The solid line is the same full-cue response as on top. When ILD was fixed to its value at 0 azimuth, the response became almost flat, suggesting that ILD is very important for the directional sensitivity of this unit. The response for the Δ-ILD condition showed the same rapid rise

in response seen for the full-cue condition for azimuths near zero, but failed to show the broad dip seen for azimuths near 40-60 degrees Thus, while ILD is important, level cues alone do not fully predict the directional response of this unit, suggesting that there may also be sensitivity to spectral cues. In fact, for the full-cue and Δ-ILD conditions, the SPL's in a third octave band centered are the CF are the same in each ear, yet the responses are different. This behavior suggests that this unit performs a more complex form of spectral integration than a third-octave filter.

Figure 5 summarizes the effects of cue manipulations for a population of IC units from 10 cats. For each partial-cue condition, we computed the correlation coefficient between the azimuth function for that condition and the function for the full-cue condition. This gives a measure of similarity between the shapes of the two curves. For the 0-ITD condition, the correlation coefficients are near one for the vast majority of units. Thus, setting ITD to zero has little effect on the directional response of this population of units. For the Δ-ITD condition, correlation coefficients never approach one, and are even negative in some cases, confirming that ITD is not the major determinant of directional sensitivity for these high-CF units. Results of ILD manipulations are clearly
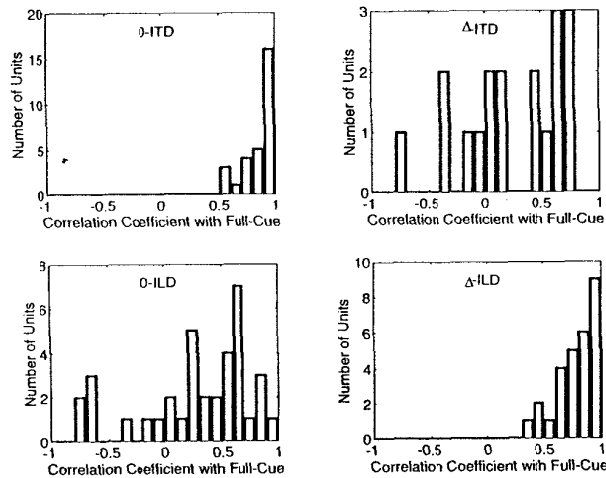

Figure 5. Histograms of the correlation coefficients between the azimuth functions for each partial-cue condition and the function for the full-cue VS stimuli.

different. For the 0-ILD condition, the vast majority of correlation coefficients are well below one, suggesting that ILD is important for the directional sensitivity of this population. For the Δ-ILD condition, some of the correlation coefficients are near one, while others are significantly smaller. Thus, while level cues are important, they do not

entirely determine the directional sensitivity of these units. Again, this suggests that spectral cues may be important for some units.

4 Discussion

Our results demonstrate how virtual-space techniques can address questions about neural mechanisms for sound localization that cannot be directly answered through either free-field or traditional dichotic studies alone. Our principal finding is that ILD is the most potent cue for the directional sensitivity of high-CF inferior-colliculus neurons. Another important finding is that binaural interactions studied with VS stimuli are consistent with those found using traditional dichotic paradigms. This result confirms that information obtained in detailed parametric studies of binaural interactions can be applied to the more complex situation found in the free field.

A limitation of our study is that we used acoustic data from one standard cat of Musicant et al. (1990) for generating VS stimuli in all of our experiments. Thus, the sound pressure waveforms of VS stimuli in the ear canal did not exactly match those that would occur in the free field for each individual animal. Several arguments suggest that this limitation may not be severe for the questions that we are addressing in this paper. The most prominent features of HRTF's, and in particular the spectral notches in the 8-20 kHz region appear to be stable across animals (Musicant et al., 1990; Rice et al., 1992). Psychophysical data from human listeners show that localization, particularly in the horizontal plane, can be quite accurate and comparable to free-field localization for naive subjects listening to VS stimuli synthesized using someone else's HRTF's. The general shapes of azimuth functions measured with VS stimuli are similar to those obtained in free-field studies for IC units in the same range of CF's (Aitkin and Martin, 1986; Calford et al., 1985), suggesting that the most important cues for directional sensitivity were present in our VS stimuli. Further, binaural interactions for VS stimuli were generally consistent with those for broadband noise, suggesting that the underlying neural mechanisms may not depend on the exact shape of the stimulus spectrum.

As a whole, our sample of high-CF units showed little sensitivity to ITD for VS stimuli. This result contrasts with physiological studies demonstrating that many high-CF neurons in the IC and the lateral superior olive are sensitive to the ITD of amplitude modulated (AM) tones (Yin et al., 1984; Joris and Yin, 1992; Batra et al., 1993). ITD sensitivity of high-CF units has not been studied for long-duration broadband stimuli such as our VS stimuli. For such stimuli, effective AM frequencies are primarily determined by the bandwidths of the cochlear filters, and are likely to be higher than the low modulation frequencies (< 600 Hz) of the AM tones used in studies of ITD sensitivity. Many natural stimuli such as speech, animal vocalizations, and sounds produced by animals in motion show more pronounced low-frequency AM than do our VS stimuli. Thus, our results may somewhat underestimate the importance of ITD cues for the directional sensitivity of IC units with natural stimuli. This issue could be investigated using VS techniques by replacing the broadband noise input in Fig. 1 by waveforms showing more pronounced AM.

It is difficult to make a firm distinction between ILD and spectral cues because ILD depends on frequency (Musicant et al., 1990). Nevertheless we feel that such a distinction is useful for relating our results with those of studies of binaural interactions which manipulate ILD without changing the spectrum (Rose et al., 1966; Semple and Kitzes, 1987; Irvine and Gago, 1990). In our experiments, ILD was defined either by integrating intensity over the entire 40 kHz bandwidth of our stimuli, or by measuring intensity in a 1/3-octave band centered at the CF of each unit. The latter definition seems to be the most appropriate because most units in the central nucleus of the IC are sharply tuned, and the effective bandwidths of auditory-nerve fibers are approximately 1/3-octave (Evans and Wilson, 1973). Some units such as that of Fig. 4 had clearly different directional responses for the full-cue and Δ-ILD conditions, although these stimuli have the same intensities in the 1/3-octave band centered at the CF. These units behave very differently from auditory-nerve fibers, for which the response to broadband stimuli is primarily determined by the intensity in a 1/3-octave band centered at the CF (Evans and Wilson, 1973). Thus, these units may perform a more complex form of spectral integration than that of auditory-nerve fibers. This conclusion is consistent with findings of complex response areas with prominent lateral inhibition for many IC neurons (Ehret and Merzenich, 1988). Complex spectral integration may also arise at more peripheral levels of the auditory system: for example it has been demonstrated for Type IV neurons in the dorsal cochlear nucleus using stimuli with sharp spectral notches similar to those occurring with free-field stimulation (Young et al., 1992). The IC may differ from more peripheral levels in that many neurons show both powerful binaural interactions and complex spectral integration. Understanding neural mechanisms of spectral integration is important not only for sound localization, but also for the recognition of speech and animal vocalizations.

Our physiological results are generally in harmony with psychophysical data on sound localization. The most directly comparable psychophysical experiments are those of Wightman and Kistler (1992), who used VS stimuli very similar to our broadband noise. Wightman and Kistler showed that ITD is the dominant cue for localizing noise possessing frequency components below 1-2 kHz. However, when their stimuli were highpass-filtered at 2 kHz, ILD cues became dominant. Because localization of highpass noise is likely to be based primarily on high-CF neurons such as those we studied, the Wightman and Kistler results are consistent with our finding that ILD is the most potent cue for the directionality of high-CF neurons.

Our results may also be related to psychophysical experiments conducted in the free field. In both cats and humans, the minimum audible angle (MAA) is smaller for azimuths near zero than for more lateral azimuths (Mills, 1958; Heffner and Heffner, 1988). Figure 3 shows that a majority of our directional neurons show a steep rise in response for azimuths near zero. If sound localization were based on the pattern of activity in a neural population such as that of Fig. 3, one would expect changes in this pattern resulting from a small change in azimuth to be most pronounced for azimuths near the midline, consistent with the MAA data.

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Comment by D. Green

First let me congratulate the authors on a very interesting paper. The use of head-related transfer functions (HRTF) has provided new information for the study of sound location.

I am concerned about one point. As I understand it, the HRTF used in the experiments were obtained from cat, measured in other experiments. Thus, we may assume that the HRTFs used for the animals in this experiment have at least some error component in the spectra used to represent the different sound locations. First, how large do you think this error component is? Second, will this error, whatever its size, degrade some cues more than others? For example, perhaps the interaural level cue is less affected by the exact shape of the HRTF than is the interaural time cue and hence the level appears to be more robust when you modify the cues as you did in table I?

Reply

The issue you raise has been of concern to us, and some general arguments suggesting that variability in HRTF may not be a severe limitation are in the written discussion. Concerning specifically your point that different localization cues (e.g. ITD and ILD) might be differentially affected by inaccuracies in the HRTF, both ITD and ILD, when measured over a 1/3 octave band, are smooth functions of azimuth and frequency, so that they are likely to be stable across animals. The major irregularity in these functions are due to a prominent spectral notch in the 8 - 18 kHz region, which is also stable across animals (Musicant et al., 1990; Rice et al., 1992). A possible direction for future studies that would settle the issue would be to examine how cats trained to localize sounds respond to VS stimuli.

At a more general level, the neural mechanisms that we are studying appear to be similar for VS stimuli and broad band noise, so that models for the behaviour of IC cells constructed from responses to VS stimuli are likely to be generally applicable, including the free-field situation.