Neural Responses in the Inferior Colliculus to Binaural Masking Level Differences Created by Inverting the Noise in One Ear

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Palmer, Alan R., Dan Jiang, and David McAlpine. Neural responses in the inferior colliculus to binaural masking level differences created by inverting the noise in one ear. J Neurophysiol 84: 844–852, 2000. We have measured the responses of inferior colliculus neurons in the anesthetized guinea pig to signals which in human psychophysical experiments reveal a release of masking as a result of binaural processing (the binaural masking level difference: BMLD). More specifically we have used diotic tones at 500 Hz (So) masked by noise that is either identical at the two ears (No) or inverted in one ear (Np). This combination of signals and noise maskers produces a prominent masking release in humans such that the So signal is about 6–12 dB more detectable in the presence of the Np noise than the No noise. Low-frequency inferior colliculus neurons are sensitive to the interaural delay of the masking noise and generally respond most to the components nearest their best frequency. Since most inferior colliculus neurons have peaks in their delay functions close to zero interaural time delay this means that while No noise is effective in driving the unit, Np noise is much less effective. As the level of an So tone was progressively increased in the presence of No and Np noises, the first response could be either an increase or a decrease in the activity due to the noise. However, because Np generated little or no activity itself, the predominant response to the So tone was an increase in discharge in this condition. Masked thresholds were defined as the point at which the standard separation \( D \) (related to the \( d' \) of signal detection theory) = 1 in either direction. BMLDs were measured in single neurons and in the majority of units were in a direction consistent with the psychophysical observations irrespective of the direction of the discharge rate change that occurred at threshold. The lowest masked thresholds always occurred at or near the signal frequency of 500 Hz. An average value of the single unit BMLD around 500 Hz was 3.6 dB (NoSo vs. NpSo) compared with 6.5 dB for the NoSo versus NoStr BMLD we had previously reported. This lower magnitude is consistent with the hierarchy of human psycho-physical BMLDs.

INTRODUCTION

The binaural detectability of a tonal signal in a wideband masking noise is not only determined by the spectral and temporal characteristics of the signal and noise but also by any differences between the signals or maskers in one ear and those in the other. Thus an identical tonal signal of (say) 500 Hz at both ears (signal condition, So), which is just masked by identical noises in the two ears (noise condition, No), can be made considerably more detectable (by 12–15 dB) simply by inverting the 500-Hz signal in one ear (creating the signal condition Sp). This difference in threshold, discovered by Licklider (1948), is termed the binaural masking level difference (BMLD). Soon after its discovery, Hirsch (1948a,b) investigated many of the signal dependencies of the BMLD and provided a hierarchy of masked thresholds which depended on the binaural configuration increasing in magnitude as follows: Nm-Sm (both noise and signal presented monaurally), Np-Sp (both signal and noise inverted in one ear), No-So (both signal and noise identical), Np-Sm (noise inverted at one ear and signal presented monaurally), No-Sm (noise in phase at the ears and the signal presented monaurally), Np-So (noise inverted in one ear and the signal identical at both ears), and No-Sp (signal inverted in one ear and the noise identical).

The largest BMLD is obtained by subtracting the masked thresholds for NoStr from that for NoSo. Another large, entirely binaural, BMLD is obtained by subtracting the masked thresholds for NpSo from that for NoSo.

In several previous studies, we have described the neural mechanisms underlying the NoSo versus NoStr BMLD (Jiang et al. 1997a,b). By using a method for determining the masked threshold, derived from signal detection theory (Sakitt 1973), we were able to demonstrate that both single neurons and populations of neurons in the inferior colliculus showed lower masked thresholds to NoStr than to NoSo. We suggested that different populations of neurons were responsible for the detection of the tone in these two conditions and that So signals were mostly detected by an increase in the discharge rate while Sp signals were detected by a decrease in discharge. The responses of single neurons to the binaural unmasking signals were consistent with their sensitivity to the interaural delay of the tones and noises. We further provided empirical validity for prevailing computational models of the BMLD, which suggested that the decrease in discharge rate that indicated the presence of Sp signals was caused by a desynchronization of the activity due to the masking noise at the brain stem coincidence detectors (Palmer et al. 1999).

Here we extend these earlier studies to the NoSo versus NpSo BMLD. Because the noise condition against which the signal is to be detected is no longer constant, the possibility exists for different strategies to be employed to detect the tones at masked threshold for this BMLD condition compared with that we have shown for NoSo versus NoSp. For the NoSo versus NoSp condition, the noise provided a constant...
baseline activity level against which the effects of the So and S\(\pi\) tones could be measured. For NoSo versus N\(\pi\)So, the No noise generally drove the neurons well, whereas the N\(\pi\) noise was often ineffective in driving the neurons. Additionally So tones always produce more synchronized activity at the coincidence detector. This meant that the majority of neurons signaled So tones against both No and N\(\pi\) noise by an increase in discharge. Nevertheless both individual neurons and populations of neurons still showed masked threshold differences that were consistent with the direction of the BMLD shown psychophysically and with their sensitivities to interaural delay.

METHODS

The detailed methods have been described previously (Jiang et al. 1997a,b) and will only be described briefly here.

Anesthesia and surgical preparation

Single-unit recordings were made from the inferior colliculi of 28 pigmented guinea pigs weighing between 300 and 450 g, most of which were also used to gather data reported in other publications (Jiang et al. 1997a,b; McAlpine et al. 1996a,b; Palmer et al. 1999). The animals were premedicated with atropine sulfate (0.06 mg sc) and anesthetized with a combination of urethan (1.3 g/kg in 20% solution ip) and phenoperidine (1 mg/kg im) as described in our previous publications. All animals were tracheostomized, and core temperature was maintained at 37°C with a heating blanket. In some cases, the animal was artificially ventilated with 95% oxygen and 5% \(\text{CO}_2\), and end-tidal \(\text{CO}_2\) was monitored. The animal was placed inside a sound-attenuating room, and sounds were presented in closed field. Pressure equalization within the middle ear was achieved by a narrow poly-thene tube (0.5 mm OD) sealed into a small hole in the bulla on each side. The cochlear condition was assessed by monitoring the cochlear tympanic membrane using a calibrated 1-mm probe tube. The sound system response on each side was measured at each recording site) was always 1 Hz greater than that delivered to the right (ipsilateral) ear. The duration of the stimulus was 3,000 ms, which included three complete cycles of the entire range of possible IPDs. The stimulus was repeated 10 times with an interstimulus interval of 6.5 s. Best delays and vector strengths were calculated from a period histogram locked to the IPD cycles constructed from the middle two seconds of the response (0.5–2.5 s).

NOISE DELAY FUNCTIONS (NDFs). NDFs were measured by presenting frozen noise with interaural time disparities over a range equal to three times the period of the neuron’s BF, in 52 equal delay steps, starting from ipsilateral leading. The duration of the stimulus was either 50 or 333 ms, with 20 or 3 repetitions, respectively, giving a total of 1-s stimulation time at each delay.

MASKED RATE-LEVEL FUNCTIONS (MRLFs). MRLFs were obtained by measuring tone rate-level functions in the presence of a noise masker at a fixed level. Tone rate-level functions were generated by presenting tones from the HP 3325A with rolling phase (50-ms duration; rise-fall time, 1 ms) and the frozen noise (5 kHz bandwidth) simultaneously gated and varying the level of the tone pseudorandomly over a maximum range of 100 dB in 1-dB steps. For the first experimental series, the noise level was arbitrarily chosen at 10–20 dB above the No noise threshold, a level at which a reasonable No driven response and a well-tuned noise delay function was obtained. This meant that different noise levels were used in the analysis of different units. In the second experimental series, we used only a single fixed noise level (33 dB SPL/Hz\(^{1/2}\)) that was the same for all units analyzed. Possible order effects were minimized by ensuring that each stimulus was never more than 50 dB weaker than the one preceding it. The number of spikes elicited by each tone was counted and the average MRLF was computed from 10 presentations at each level. The frequency of the tone used was 500 Hz and was always interaurally in phase (So).

DETERMINING THE MASKED THRESHOLD FROM THE MRLFS. To determine the masked threshold for a tone from the MRLF, we used an analysis technique derived from signal detection theory (Green and Swets 1966). However, the classic detectability index \((d')\) metric assumes that the responses of the neurons are normally distributed with equal variances, an assumption that does not necessarily hold for...
neurons in the auditory pathway. Accordingly, we employed a modified version of \( d \), the Standard Separation (\( D \)), described by Sakitt (1973), which allows a simple interpretation that is independent of any assumptions about the underlying distributions:

\[
D_{n,n+s} = \frac{R(n+n) - R(n)}{\sqrt{SD(n)SD(n+s)}}
\]

(1)

where \( R(n+n) \) and \( R(n) \) are, respectively, means for the distribution of the response to the signal-plus-noise and to the noise-masker alone, and \( SD(n) \) and \( SD(n+s) \) are the standard deviations of the respective response distributions. \( R(n) \) and \( SD(n) \) were estimated from the sub-threshold values in the MRLF (see Jiang et al. 1997a for more detail). Random rating would produce \( D = 0 \), and perfect discrimination would produce an infinite \( D \). For our purposes, the masked threshold for a tone in noise was defined as the lowest level at which \( D \) had an absolute value of 1.0, and a positive BMLD is defined where the masked threshold for So tones is lower in No \( \pi \) noise than in No noise. Some neurons gave almost no response to one of the noise configurations and \( D \) could not be calculated because of the poor estimates of the variances, so we estimated their masked threshold as the lowest level of the So tone that produced an increase in the discharge rate.

We chose the value of \( \pm 1 \) for \( D \) following a common usage in psychophysics in which a value of \( d' = 1 \) is taken as threshold. This is close to 71% correct in a two-alternative forced-choice experiment. This seemed an appropriate value since we were assessing the threshold for detectability of the tone. An additional, pragmatic reason for choosing \( D = \pm 1 \) was that many neurons in our sample did not give high discharge rates to the tones even when well above threshold and their D values exceeded \( \pm 1 \) but not \( \pm 2 \). Taking the first instance of \( D \) exceeding \( \pm 1 \) could lead to poor threshold estimates when the MRLF is noisy. To assess the effect of this rigid criterion on the measured thresholds, we examined all 338 MRLFs (both NoSo and N\( \pi \)So for 169 neurons) that constitute the data for this paper. Ten of these MRLFs (3% of our total sample) were noisy as a result of such factors as low discharge rates. In these cases, the choice of only the first instance may have led to some inaccuracy in determination of masked threshold, but this was likely to be of only a few decibels.

RESULTS

Data were obtained from 169 units (BFs ranged from 125 to 2,090 Hz) in 28 guinea pigs. In the first series of 22 animals, we were mainly concerned with measuring the full response profile to provide explanatory leverage, and the yield was consequently modest. We maximized the number of positive BMLD responses by positioning the noise level at 10–20 dB above the No noise threshold for a particular unit. Because this meant that the noise was at different levels for different units, we have labeled these data “variable noise level” in summary histograms. In the second series of six guinea pigs, we were more concerned with summarizing the response of a population of inferior colliculus neurons to the BMLD stimulus, and we obtained higher yields with less analysis of each unit using a single noise level: these data we have labeled as “fixed noise level” in summary histograms. In general, the results from both parts of the study were compatible.

Responses to No and N\( \pi \) noise alone

The baseline from which the tonal responses arise depends on the level of activity evoked by the background noise stimulus. In our previous work describing only the responses to So and S\( \pi \) signals in No noise, the majority of units were well driven by the No noise because most had peak responses at or near zero interaural time delay (ITD). For the same reason, the majority of units are poorly driven by N\( \pi \) noise. In some units, the difference in response to No and N\( \pi \) noise was negligible, and in a small proportion the No noise gave a smaller response than the N\( \pi \) noise representing units that had a trough at zero ITD and a peak at or near a delay of half the BF period.

Shapes of individual rate-level functions to So tones in No and N\( \pi \) noise

In Fig. 1 we show the different shapes of the MRLFs in response to the So tone in the presence of the No and N\( \pi \) noise. Two examples are given for each of the main response types, and the second column shows the conversion to \( D \) values. The most common type of response [73% (38/52) of the variable noise data and 38% (45/117) of the fixed noise data, see Fig. 3] is shown in Fig. 1A. The nomenclature reflects the sign of the \( D \) value at the masked threshold as we have used previously (Jiang et al. 1997a,b). Thus positive-positive (PP) units achieved masked threshold by an increase in discharge rate above the noise-evoked baseline for both No and N\( \pi \) noise, generating a positive \( D \) in each case. For the two PP examples shown, the No noise (●) drives the unit better than the N\( \pi \) noise (○), and the BMLD to the 500-Hz tones is positive (in the same direction as psychophysical data) for the first and negative for the second.

The second most common type [10% (5/52) of the variable noise data and 21% (25/117) of the fixed noise data] is negative-negative (NN), i.e., the masked threshold was achieved by a decrease in discharge rate for both No and N\( \pi \) noise, resulting in a negative \( D \). In Fig. 1B, we again show examples in which the BMLD that resulted was negative in one case and positive in the other and the effectiveness of the two noises were different: N\( \pi \) was more effective in the first and No in the second. Differences in the effectiveness of the noise reflects the noise delay sensitivities as we have described in the preceding text. At higher levels of the So 500-Hz tone the first unit in Fig. 1B shows an increasing discharge. Previously we attributed this either to monaural effects of the tone or simply that the So tone completely dominates the response. The second NN example shows a decrease to reach the D threshold but continues to decrease possibly suggestive of an inhibitory effect similar to that described previously (Palmer et al. 1999, Fig. 8F).

Negative-positive (NP) responses in which \( D \) was achieved by a discharge rate decrease in No and an increase in N\( \pi \) made up 8% (4/52) of the variable noise data and 11% (13/117) of the fixed noise data. The two examples of NP responses that we show in Fig. 1C illustrate a problem with the \( D \) approach when applied to physiological data without due regard to the initial response of the neuron to N\( \pi \) noise. In both units, the N\( \pi \) noise appeared to be strongly suppressive, so much so that the unit was completely silenced. This means that the SD of the discharge was zero and No could be calculated. Equally clear is the fact that at some level the So tone did activate the units. We therefore simply took the point at which the discharge rose above zero as the masked threshold.

Finally in Fig. 1D, we show positive-negative (PN) responses [6% (3/52) of the variable noise data and 3% (3/117) of the fixed noise data] in which No gave positive \( D \) and N\( \pi \) gave negative \( D \), but both BMLDs were positive. Again, at
higher levels in the second unit the So 500-Hz tone dominated the response.

As in our previous studies, the most common response corresponds to those units that show a peak in the delay functions to noise and tones located near zero ITD (see later detailed comments).

For some units, only one configuration actually yielded a masked threshold estimate. Examples are shown in Fig. 2. Here, despite the fact that No drove two of the units well (Fig. 2, A and C), the 500-Hz So tone was ineffective in altering the activity due to the No noise by sufficient amounts to reach $D = 1$. In these cases, the So tone achieved masked threshold in Nπ noise by an increase (Fig. 2A) or by a decrease in discharge (Fig. 2B). Even restricting our sampling to delay-sensitive

**FIG. 1.** Examples of 4 different masked rate-level function (MRLF) types as described in the text for both signal and noise identical (NoSo) and noise inverted in 1 ear and the signal identical at both ears (NπSo). Left: MRLFs. Middle: D functions for each MRLF. Masked thresholds and BMLDs for NoSo and NπSo derived from D are shown to the right. A: 2 PP type units. best frequencies, (BFs), 0.87 and 1.085 kHz; best delays, 120 and 0 μs, respectively. B: 2 NN type units. BFs, 0.241 and 0.814 kHz; best delays 960 and −80 μs respectively. C: Two type NP units. BFs 0.239 and 0.364 kHz, best delays, 520 and 320 μs respectively. D: 2 type PN units. BFs, 0.765 and 0.627 kHz; best delays, −960 and 600 μs, respectively. In this and all other figures, 1 spike/stimulus = 20 spikes/s for a 50-ms stimulus and arrows show masked threshold.
low-frequency units we did encounter some units for which the 500-Hz tone was ineffective in altering the discharge rate, as shown in Fig. 2C. The relative proportions of the various response types that we encountered both in the first (variable noise at +20 dB re threshold) and second series (fixed noise level) are shown in Fig. 3, where “undefined” is used to designate those units where we only obtained one masked threshold.

**BMLD measured in individual neurons**

The magnitude of the BMLD in individual neurons is shown in Fig. 4. As in our previous NoSo versus NoS\(\pi\) data the majority of neurons (64% for the variable noise data and 67% of the fixed noise data after exclusion of single-threshold data) have positive BMLDs with magnitudes above 3 dB. For those units for which the tone only provided a masked threshold in one condition, the BMLD is at least equal to the difference between this masked threshold and the maximum output of the sound system. In the majority, it was the N\(\pi\)So condition that yielded the single masked threshold resulting in large positive BMLDs (Fig. 4B). The bin Fig. 4B, left, indicates those units for which the 500-Hz tone was completely ineffective in changing the discharge rate due to the noise (as in Fig. 2C).

**Relationship of MRLF shape to delay sensitivities**

Our main aim was to examine the magnitude of the BMLD using NoSo versus N\(\pi\)So, but in many instances, we obtained other data that allowed us to suggest the mechanisms that underlie the observed BMLD responses. Figure 5 shows two representative examples of the PP response type (which were in the majority in these data). In Fig. 5, A–C, we show the most typical result. Here both the noise delay function (Fig. 5B) and the binaural-beat response show a peak close to zero interaural phase difference (see lower abscissa in Fig. 5C). The No noise therefore is more effective in driving the unit than the N\(\pi\) noise (Fig. 5A), which completely suppresses the unit. The coincident activity evoked by the So tone raises the discharge rate in response to both No and N\(\pi\) noise. This effect we have described in some detail previously (Palmer et al. 1999).

A second PP unit is shown in Fig. 5, D–F. At first sight this appears to be a paradoxical result since both No noise (Fig. 5E) and the So tone (Fig. 5F) occur at a trough in the discharge rate and one might therefore expect the discharge rate to the noise to be reduced by adding the So tone. However, this unit is not a simple trough unit [a unit in which the major feature of the delay function is a trough at or near zero ITD probably generated by inhibition in the brain stem (Batra et al. 1997)] and may represent either a unit with a long best delay or a mixed unit in which both trough and peak features are present (see

**FIG. 2.** Undefined MRLFs. Format as for Fig. 1. A: MRLF for which it was not possible to derive a masked threshold by \(D\) for NoSo. BF, 0.638 kHz; best delay, not available. B: another MRLF for which it was not possible to derive a masked threshold by \(D\) for NoSo. BF, 0.343 kHz; best delay, 1.301 ms. C: MRLF for which it was not possible to derive a masked threshold by \(D\) for either NoSo or N\(\pi\)So. BF, 1.61 kHz; best delay, not available.

**FIG. 3.** Percentage of our sample of units showing different MRLF types for NoSo and N\(\pi\)So using variable noise levels (●) or a fixed noise level (○) as described in the text. Note an increased number of units with undefined types for the fixed noise level (see RESULTS for details).

**FIG. 4.** A: histogram of magnitude and direction of NoSo vs. N\(\pi\)So binaural masking level differences (BMLDs) among the units tested using variable noise levels or using a fixed noise level. B: histogram of magnitude and direction of BMLD for NoSo vs. N\(\pi\)So among the units with undefined MRLFs using a fixed noise level.
McAlpine et al. 1998). This is evident when the monaural responses to noise are considered (marked as C for contralateral and I for ipsilateral on Fig. 5E). The peaks in the delay function are a result of facilitation above the contralateral response while the troughs are relatively shallow not reaching down to the response to the ipsilateral ear. If the trough is due to coincidence between excitation from one ear and inhibition from the other, the relatively shallow trough represents a lack of perfect coincidence; i.e., every excitatory spike is not cancelled by a corresponding inhibitory input. The MRLF (Fig. 5D) indicates that No is slightly less effective in driving the unit than Nπ, but that the So tone produces an increase for both No and Nπ.

For the other, less common, response types a single unifying explanation based on their other response properties was more difficult. For the NN type units, the only common factor seemed to be that both No and Nπ noise fell at positions on their noise delay function that evoked a reasonably strong response and thus decreases in discharge rate were possible. While in all of the NN units there was a trough of some kind near zero ITD, it was generally not down to zero spikes/stimulus. Assuming this trough is the result of coincidences at the brain stem due to the No noise and therefore presumably inhibitory, adding an So tone could further reduce the activity in the trough. The activity at Nπ on this basis would represent lack of coincidence and might even represent activity mainly due to contralateral input alone: under such conditions adding So tones will also reduce the activity to the Nπ noise since its coincident activation of the brain stem generates inhibition.

Both PN units showed a trough close to zero IPD in the noise delay function, but neither this fact nor other data using tonal stimuli gave any plausible explanation linking their delay sensitivities with the direction and magnitude of their individual BMLDs.

Finally, for one NP unit we also measured the effect on its sensitivity to interaurally delayed noise of either desynchronizing the noise at the two ears or adding So tones to the noise (see Palmer et al. 1999 for details of these paradigms). The effect of the So tone was to desynchronize the activity due to the No noise, as demonstrated by a flattening of the noise interaural delay function (similar to that which we have previously described for 51 and 56 dB SPL So tones in Fig. 8F of Palmer et al. 1999). This desynchronization has the effect of decreasing the activity to No and increasing the activity to Nπ. Further increases in the level for this NP unit resulted in strong excitation, possibly as a result of a monaural response to the So. It is notable that the BMLD in this unit was large and in the opposite direction to the psychophysics.

Responses of populations of inferior colliculus neurons to a single signal-to-noise ratio

In Fig. 6A, the masked threshold for 117 units from six animals are plotted separately for the NoSo (●) and NπSo (○) conditions with the noise level fixed at 33 dB SPL/Hz 0.5. Unsurprisingly, consistent with our previous NoSo versus NoSπ data, the lowest masked thresholds are measured in units with BFs at the signal frequency (in this case 500 Hz). All measured masked thresholds are shown in this figure including those when only one condition yielded a value. Also just discernible in this figure is the fact that the NoSo thresholds (●) are generally higher than the NπSo thresholds (○) reflecting the preponderance of positive BMLDs in individual units (Fig. 4). To emphasize this point, we have plotted in Fig. 6B the average masked threshold for NoSo and NπSo computed from those units with BFs around the signal frequency (300–800 Hz, dotted vertical lines in Fig. 6A). The average value for NoSo is higher than that for NπSo, yielding an average BMLD of 3.6 dB. This value is smaller than that we calculated in a previous study for NoSo versus NoSπ (Jiang et al. 1997b), a result consistent with the ordering of psychophysical magnitudes. The average BMLD value for the whole BF population shown in Fig. 6 is 3.4 dB.

In Fig. 7 we show the D values for the NoSo and NπSo at the levels of the 500-Hz tone shown by the horizontal dashed lines in Fig. 6A. At 58 dB SPL, the presence of the tone is signaled by increases in the discharge rate of units near 500 Hz for both No and Nπ noise (Fig. 7, A and B) with larger changes occurring for Nπ noise. When the level of the tone is reduced by 6 dB to near the lowest NπSo thresholds at 52 dB SPL (Fig. 7, C and D) only sporadic units reach a D of 1 for No noise but a population of units near 500 Hz still shows highly statistically significant (D > 2) increases in discharge for the Nπ noise.

Discussion

The results of the present study may be summarized as follows: when masked by either No or Nπ noise, 500-Hz tones...
identical at the two ears are detected at the lowest signal-to-noise ratio by neurons with best frequencies at or near the signal frequency; $N\pi$ noise is generally less effective in activating inferior colliculus neurons than $N\sigma$ noise because the majority of neurons have peaks in their interaural delay functions near zero ITD (see also Yin et al. 1983, 1986); for the majority of neurons, the first detectable response to So 500-Hz tones masked by $N\pi$ noise is an increase in discharge rate above that due to the $N\pi$ noise alone; in the majority of neurons, the BMLD is in a direction consistent with psychophysical observations; So tones are more detectable in $N\pi$ noise than in $N\sigma$ noise; and the average BMLD in neurons around 500 Hz is smaller for $N\pi$So versus $N\pi$So than for $N\sigma$So versus NoSo. This is consistent with psychophysical observations.

To allow comparison of the masked thresholds in this paper (which are given in dB SPL) with equivalent human values requires a conversion to signal-to-noise ratio (S/N). Because the neural bandwidth is frequency dependent, the within-channel S/N will vary. However, the main channel of interest is at 500 Hz (the signal frequency) because this is where the lowest masked thresholds are obtained. The bandwidths of guinea pig auditory filters are wider than those in humans by 2–2.5 times, thus at 500 Hz the equivalent rectangular bandwidth is about 220 Hz (Evans et al. 1992). Integration of the noise within this bandwidth represents an increase of 23.4 dB over the noise spectral density of 33 dB giving 56.4 dB of noise energy within the 500-Hz channel. The lowest masked thresholds (i.e., those most likely responsible for detection; Fig. 6) within the band at 500 Hz excluding one outlier (2% of the sample) in each case are about 48 dB for $N\pi$So and 52 dB for NoSo, giving within-channel S/N ratios at masked threshold of $-8.4$ and $-4.4$, respectively. These are somewhat higher than typically reported human values. To be more specific: a recent report gave S/N ratios for 19 human subjects for 500-Hz tones in wideband maskers for NoSo and $N\sigma\sigma$ conditions (Bernstein et al. 1998). Their S/N ratios were quoted as E/No: a measure that includes signal duration. Calculating E/No for our data with a duration of 0.05 s gives $48 + 10 \log (0.05) - 33 = 2$ dB for $N\pi$So and 6 dB for NoSo. The NoSo value here is 3.8 dB less than Bernstein’s 19 subjects (mean = 9.8 dB), and the $N\pi$So value is almost 6 dB less (mean = $-3.9$ dB) than the NoSo. We would expect NoSo to be slightly lower than $N\pi$So (see INTRODUCTION), but another likely contribution to these discrepancies is the relatively low level of the masking noise that we have employed in this study compared with that of Bernstein et al., who used 50-dB spectrum level. The relatively low level was chosen to ensure that the signals remained within the dynamic range of the 500-Hz neurons. The BMLD increases with noise level above threshold by as much as 10 dB (e.g., Hirsh 1948a; McFadden 1968) and is almost maximal at 50 dB spectrum level. We have also observed similar increases in neural BMLDs with noise level (McAlpine et al. 1996a, Fig. 12). As the BMLD gets larger, the difference between the NoSo and $N\pi$So conditions increases as a result of larger

**FIG. 6.** Masked thresholds for So 500-Hz tones in No and $N\pi$ noise as a function of the neuron BF. A: masked threshold across a population of low-frequency inferior colliculus neurons pooled from 6 guinea pigs for 500-Hz tones in the fixed level (33 dB SPL/Hz$^{1/2}$) No and $N\pi$ configurations. **---**, the region from 300 to 800 Hz centred around the tone frequency of 500 Hz, which is marked by **---**, masked threshold levels used in calculations in the text. B: the average of the masked thresholds from units with BFs from 300 to 800 Hz for NoSo and $N\pi$So. Only units for which both thresholds were obtained were used to compute the averages.

**FIG. 7.** Population profiles of detectability for signal-to-noise ratios, which have been chosen to provide an indication of the activity in the inferior colliculus when signals are close to the detection threshold. The standard separation $D$ is plotted against BF for 116 units for NoSo and $N\pi$So.
versus NoSo is sensitive to ITDs at or near zero ITD. The BMLD for NoSo is greatest activity in a population of neurons which are most sensitive at 500 Hz. Thus in Fig. 8, we compare the output of such a model for NoSo versus NoS\( \pi \) to those predicted from a generic cross-correlation model of binaural hearing based on that originally developed by Colburn (1973, 1977, 1996) and found that the physiological results were in good agreement with such a model. These models include the assumption that the auditory system uses internal delays to compensate for delays in the waveforms reaching the ears. In Fig. 8, we compare the output of such a model for NoSo versus NoS\( \pi \) with that for NoSo versus N\( \pi \)So. Figure 8A is a recomputation of the figure we showed previously (Fig. 12 in Jiang et al. 1997a). The ordinate represents the level of activity within a single frequency channel centered at the signal frequency; the abcissa represents the most effective or best delays of a population of delay-sensitive neurons. The curve is the result of a computation of the interaural cross-correlation using simulated spike train probabilities after peripheral filtering at 500 Hz. Thus in Fig. 8A, the No noise alone produces greatest activity in a population of neurons which are most sensitive to ITDs at or near zero ITD. The BMLD for NoSo versus NoS\( \pi \) results from an asymmetry in the modifications to the responses to the No noise as a result of the So or S\( \pi \) tones. The No noise generates a peak of activation in neurons with best delays close to zero ITD, and the So tone at masked threshold produces only a small increase in the amplitude of this peak. In contrast, at the same S/N ratio the S\( \pi \) signal produces a larger decrease in the peak amplitude. Assuming increases and decreases in discharge are equally detectable, to achieve the same detectability the S\( \pi \) noise can be reduced in level giving a substantial BMLD. We subsequently demonstrated that the reduction in the activity caused by the S\( \pi \) signal is consistent with a desynchronizing effect of that signal on the responses to the No noise (Palmer et al. 1999).

In Fig. 8B we show a similar treatment for the N\( \pi \)So condition. Of particular note here is the fact that N\( \pi \) noise produces a minimum or trough in activation centered on zero ITD. This corresponds to the relatively poorer activation to N\( \pi \) noise of neurons with peaks in their delay functions near zero. The addition of So signal at zero ITD raises the discharge rate of neurons with best delays near zero ITD (i.e., in the majority of neurons). This represents a desynchronizing effect of the So noise. Addition of identical tones to the filtered noise waveforms from each ear should produces a shift of the instantaneous phase in opposite directions by the same amount and thus reduces the negative cross-correlation due to the noise and hence increases the number of coincident spikes delivered to the coincidence detector. Again assuming equal changes in the curves represent equal detectability changes, it is noteworthy that the So signal produces a larger change to the N\( \pi \) noise response than it does to the No noise response shown in Fig. 8A, but that this is a smaller change than that due to the S\( \pi \) signal on the No noise. This is consistent with a smaller BMLD for NoSo versus N\( \pi \)So than that for NoSo versus N\( \pi \)So. Note that detection of So signals in N\( \pi \) noise in neurons with very long best delays is equivalent to detection of So in No noise in neurons with short best delays. However, at least in our data, neurons with characteristics of simple coincidence detectors, but with very long best delays have not been found (McAlpine et al. 1996b, Fig. 6).

We conclude from comparison of Fig. 8 with the results presented in this paper that there is good agreement between the empirically measured physiological data and those predicted from the cross-correlation model of binaural interaction. Intuitively, one might expect that the lower the firing rate of a cell to the noise masker alone, the lower the detection threshold for a tone because a smaller amount of signal energy would be required to produce a given change in firing rate. In which case, one would expect that the So and S\( \pi \) thresholds would be lowest for the N\( \pi \) masker. However, while this is true for So tones, the lowest detection thresholds for S\( \pi \) tones are with an No masker, which produces a larger firing rate than N\( \pi \). This is not a paradox because the argument misses two important features of the situation. First, the masked firing rate is not determined solely by the energy in the stimulus, it depends mostly on the interaction between the phases of the signal and masker. Second, in determining detectability it is the magnitude of the change in firing rate compared with the variability of the firing rate, as embodied in the statistic \( D \), which is important. When the signal interaural phase is different from the noise interaural phase (i.e., NoS\( \pi \) and N\( \pi \)So), the addition of a low-level signal causes the noise masker to become desynchronized and hence, in the majority of neurons,

**FIG. 8.** Output of a binaural cross-correlation model in which the waveforms are filtered by a gamma-tone filter at 500 Hz set to an equivalent rectangular bandwidth of 200 Hz (Patterson et al. 1995), passed through a hair-cell model (Meddis 1986) and then cross-correlated with matching input from the other ear. The ordinate should be thought of as the best delay value of a population of neurons with 500-Hz best frequency.

**FIG. 8A.** (A) Activity level (%) vs. delay (ms) for No, NoSo, and NoS\( \pi \) with rectangular bandwidth of 200 Hz (Patterson et al. 1995). (B) Activity level (%) vs. delay (ms) for No, NoSo, and NoS\( \pi \) with rectangular bandwidth of 200 Hz (Patterson et al. 1995).
causes the No firing rate to decrease significantly and the Nπ rate to increase significantly. These firing rate changes are often larger than the firing rate change caused by the additional energy added by the signal, which is the only detection cue available in the NoSo and NπSπ cases where the interaural phases of signal and noise are the same.

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