Responses of Neurons in the Inferior Colliculus to Binaural Masking Level Difference Stimuli Measured by Rate-Versus-Level Functions

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Jiang, Dan, David McAlpine, and Alan R. Palmer. Responses of neurons in the inferior colliculus to binaural masking level difference stimuli measured by rate-versus-level functions. J. Neurophysiol. 77: 3085–3106, 1997. The psychophysical detection threshold of a low-frequency tone masked by broadband noise is reduced by $\pm 15$ dB by inversion of the tone in one ear (called the binaural masking level difference: BMLD). The contribution of 120 low-frequency neurons (best frequencies 168–2,990 Hz) in the inferior colliculus (ICC) of the guinea pig to binaural unmasking of 500-Hz tones masked by broadband noise was examined. We measured rate-level functions of the responses to identical signals (So) and noise (No) at the two ears (NoSo) and to identical noise but with the signal inverted at one ear (NoS$\pi$): the noise was 7–15 dB suprathreshold. The masked threshold was estimated by the standard separation, ‘‘D’’. The neural BMLD was estimated as the difference between the masked thresholds for NoSo and NoS$\pi$. The presence of So and S$\pi$ tones was indicated by discharge rate increases in 55.3% of neurons. In 36.4% of neurons, the presence of So tones was indicated by an increase in discharge rate and S$\pi$ tones by a decrease. In 6.8% of neurons, both So and S$\pi$ tones caused a decrease in discharge rate. In only 1.5% of neurons So was indicated by a decrease and S$\pi$ by an increase in discharge rate. Responses to the binaural configurations were consistent with the neuron’s interaural delay sensitivities; 34.4% of neurons showing increases in discharge rate to both So and S$\pi$ tones gave positive BMLDs $\geq 3$ dB (S$\pi$ tones were detected at lower levels than So), whereas 37.3% gave negative BMLDs $\geq 3$ dB. For neurons in which So signals caused an increase in the discharge rate and S$\pi$ a decrease, 72.7% gave positive BMLDs $\geq 3$ dB and only 4.5% gave negative BMLDs $\geq 3$ dB. The results suggest that the responses of single ICC neurons are consistent with the psycho-physical BMLDs for NoSo versus NoS$\pi$ at 500 Hz, and with current binaural interaction models based on coincidence detection. The neurons likely to contribute to the psychophysical BMLD are those with BFs near 500 Hz, but detection of So and S$\pi$ tones may depend on different populations of neurons.

INTRODUCTION

When listening with two ears, the ability to detect a target signal in a background of masking noise depends not only upon the spectral and temporal characteristics of the target and the masker, as it does when listening monaurally, but also upon the interaural differences in the target and the masker. With identical noises and tones at the two ears, simply inverting the waveform of the tone at one ear can reduce the detection threshold for that tone dramatically. The amount of “binaural unmasking”, i.e., the improvement in the detection threshold when the tone at one ear is inverted, can reach 12–15 dB and is referred to as the binaural masking level difference (BMLD). Since this phenomenon was discovered and investigated by Licklider (1948) and Hirsh (1948a,b), it has been the subject of intensive human psychophysical investigation. The magnitude of the BMLD is dependent upon a number of factors, including the signal frequency, the interaural correlation of the noise, the phase relationship of the signal and the masker, the masker level, and the masker bandwidth (see Blauert 1983; Durlach and Colburn 1978; Green 1976). For signal frequencies $> 1,500$ Hz, when either the signal (S$\pi$) or the masker is inverted, the BMLD is $\sim 3$ dB. The BMLD reaches a maximum of $\sim 15$ dB at lower frequencies (500–700 Hz) (e.g., Jeffress et al. 1952; Robinson and Jeffress 1963). BMLDs also have been demonstrated in behavioral studies in the cat and ferret (Cranford 1975; Hine et al. 1994; Wakeford and Robinson 1974), although the magnitude of the BMLD was smaller (6–8 dB) than for human subjects for the same binaural configurations.

The demonstration that large BMLD effects were restricted to low frequencies, where localization depends on interaural phase differences (Rayleigh 1907), and the dependence of the magnitude of the BMLD on parameters such as the phase of the signal (Jeffress et al. 1962), suggest that some part of the physiological mechanism responsible for the BMLD resides in low-level cells sensitive to differences in the interaural timing of the signals. Early this century, Bowler (1908) suggested that a central mechanism may exist to transform interaural time differences (ITDs) into place differences for the purpose of localizing low-frequency sounds. A more detailed model of the same mechanism was proposed by Jeffress (1948), who hypothesized that external interaural delays could be inferred by central units that record coincidences of neural impulses from pairs of peripheral nerve fibers. Each central unit was assumed to compare information from the two ears after a series of internal time delays. A network of coincidence detectors fed by delay lines would enable humans to use microsecond differences in the time of arrival of low-frequency signals at the ears to compute sound position.

Consistent with this hypothesis, physiological studies have suggested that cells exhibiting the properties of interaural coincidence detectors exist in the medial superior olive (MSO) of the mammal. The discharge rate of these neurons varies as a function of the interaural time or phase differences of the stimuli, i.e., neurons appear to be maximally sensitive to signals presented with a specific interaural delay (Crow et al. 1978; Goldberg and Brown 1969; Yin et al. 1990). Furthermore, anatomic studies suggest that differ-
ences in the length of the axonal paths to these neurons, in the MSO, may provide the basis for a delay-line system (Carr and Boudreau 1993; Konishi et al. 1988; Smith et al. 1993). However, it is notoriously difficult to record in this nucleus (e.g., Guinan et al. 1972), and more extensive studies on interaural delay sensitivity have been conducted in the inferior colliculus where the cells receive projections from the coincidence detectors of the MSO. In general, the low-frequency cells in the central nucleus of the inferior colliculus (ICC) act in a similar manner of those in the MSO and exhibit sensitivity to interaural time and phase differences in a manner consistent with binaural coincidence detection (e.g., Hind et al. 1963; Kuwada and Yin 1983; Kuwada et al. 1987; McAlpine et al. 1996b; Palmer et al. 1990; Rose et al. 1966, 1967; Yin et al. 1986, 1987). The delay sensitivity to tones exhibited by both MSO and ICC neurons is limited to low frequencies, a result consistent with the restriction of large BMLDs in humans to frequencies <1,500 Hz.

Given the extensive auditory psychophysical studies of the BMLD in the last 40 yr, it is surprising that the physiological study of its neural basis only started in the mid-1980s, and so far, only a few very papers have been published. Langford (1984) investigated the responses of MSO cells in the chinchilla by using standard BMLD [noise and signals identical at the two ears (NoSo) vs. identical noise but with signal inverted at one ear (NoSπ)] stimulus configurations. Responses of single units to best frequency (BF) tones in noise, when the phase of both were identical at the two ears, were compared with those when the phase of either the tone or noise at one ear was inverted. A similar approach was adopted in a study of cat ICC by Caird et al. (1989). Neither study was able to demonstrate sufficient differences in response patterns between the different stimulus configurations to provide a convincing explanation for the psychophysically observed results.

In contrast, Caird et al. (1991) and McAlpine et al. (1996a) used a different approach in the guinea pig ICC that revealed differences in masked thresholds of single low-frequency neurons consistent with the BMLD. In these studies, the investigators measured responses to tones at the BF of the unit and with an interaural delay at which the discharge rate was maximal (the best delay) as a function of the interaural delay of the masking noise. Apart from using signals and masker optimized for each unit’s delay sensitivity, in both studies, an adaptive threshold tracking procedure (PEST) (Taylor and Creelman 1967) was used to determine masked threshold for the different stimulus configurations employed. Both studies demonstrated that the majority of ICC delay-sensitive neurons showed the lowest masked thresholds for an optimized signal (i.e., signal at best delay) masked by a noise at the least favorable interaural delay.

However, extension of the method to nonoptimized signals (500 Hz in 0 or π) and identical noise (No) regardless of the unit’s BF gave less convincing results (McAlpine et al. 1996a). These authors attributed the poor correspondence with the psychophysics to the consequence of using an increase in the discharge rate as the sole cue for threshold detection. This suggestion is entirely consistent with predictions from the earlier modeling work of Colburn (1973, 1977). Colburn combined Siebert’s (1970) model of peripheral auditory-nerve spike generation with a delay-line and coincidence-detection mechanism (as in Jeffress 1948) to model the pattern of activity across coincidence-detecting units of different characteristic delay and best frequency. He suggested that signal detection in noise depended on those units in the activity pattern that produced the largest changes in activity between the signal and nonsignal noise intervals. The largest changes were decreases in activity for units whose characteristic delays matched that of the noise and whose best frequencies matched that of the signal. Using this cue, the model was highly successful in predicting a wide range of psychophysical data. Thus for the standard binaural configurations at 500 Hz, the first response of a neuron to an increase in the level of SN signals could either be an increase or a decrease in discharge rate, in different units.

To investigate this possibility and to allow generalization of responses to the standard binaural configurations, we have examined rate-versus-level functions of low-frequency ICC neurons to 500-Hz tones (0 or π phase) masked by identical noise at fixed suprathreshold levels. We have used a method that takes into account the discharge variance to determine the masked threshold from these rate-level functions. We also have documented the relationship between the neuron’s delay sensitivity and their response to different binaural masking configurations.

**METHODS**

**Anesthesia and surgical preparation**

The recordings described in this paper were made from the inferior colliculi of 54 pigmented guinea pigs, weighing between 300 and 450 g, most of which were used in experiments with other primary aims. The animals were premedicated with atropine sulphate (0.06 mg sc) and anesthetized with urethane (1.3 g/kg in 20% solution, ip). Further analgesia was obtained with phenoperidine (1 mg/kg im). Supplementary doses of phenoperidine (0.5–1 mg/kg im) were given on indication provided by the pedal withdrawal reflex. All animals were tracheotomized and core temperature was maintained at 37°C with a heating blanket. In some cases, the animal was ventilated artificially with 95% O2–5% CO2, and end-tidal CO2 was monitored. The animal was placed inside a sound-attenuating room in a stereotaxic frame with hollow plasticies, the investigators measured responses to tones at the BF of the unit and with an interaural delay at which the discharge rate was maximal (the best delay) as a function of the interaural delay of the masking noise. Apart from using signals and masker optimized for each unit’s delay sensitivity, in both studies, an adaptive threshold tracking procedure (PEST) (Taylor and Creelman 1967) was used to determine masked threshold for the different stimulus configurations employed. Both studies demonstrated that the majority of ICC delay-sensitive neurons showed the lowest masked thresholds for an optimized signal (i.e., signal at best delay) masked by a noise at the least favorable interaural delay.

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Stimulus presentation

The stimuli were delivered through two sealed acoustic systems identical on each side. Each system consisted of a 12.7-mm condenser earphone (Brüel and Kjaer 4134) coupled to a damped 4-mm diameter probe tube that fitted into the spectum. The output was calibrated a few millimeters from the tympanic membrane using a Brüel and Kjaer 4134 microphone fitted with a calibrated 1-mm probe tube. The sound system response on each side was flat to within ±0.5 dB from 100 to 10,000 Hz, and the left and right systems were matched to within ±2 dB over this range.

Stimuli

The stimuli used in this study were tones and noises presented to the two ears. The noise used was digitally synthesized “frozen” noise with a bandwidth of 50 Hz to 5 kHz, and output at a sampling rate of 50 kHz via a digital-analogue converter (TDT QDA2) and a waveform reconstruction filter (Kemo VBF33, cut-off slope 135 dB/octave from 5 kHz). The level of the noise is expressed as noise spectrum level (NSL). The same frozen noise sample was used for all units. Interaural delays of the noise were introduced during synthesis. Tonal stimuli were either from a Hewlett Packard 3325A waveform synthesizer or digitally synthesized and output from a digital-analogue converter (TDT QDA2) and a waveform reconstruction filter (Kemo VBF33, cut-off slope 135 dB/octave from 5 kHz). A two-channel digital delay line enabled the interaural delays of the tones to be set by computer or manually with a resolution of 1 μs.

Data collection and analysis

Single neurons were isolated using 50-ms tone and/or noise bursts as search stimuli. The extracellularly recorded neural action potentials were amplified (Axoprobe 1A: ×1,000), filtered (155–1,800 Hz), converted to logic pulses by an amplitude discriminator and timed with 10-μs resolution (CED 1401 plus). The lowest binaural threshold to interaurally in-phase tones and the frequency at which it was obtained (BF) were determined audiovisually. The spontaneous rate was measured routinely during a 10-s period in the absence of controlled acoustic stimulus. All the stimuli in this study could be presented monaurally to either side or binaurally.

The following analyses were carried out in the present study.

FREQUENCY-RESPONSE AREA. These were obtained by pseudo-randomly presenting 50-ms tone bursts at 5/s covering a frequency range from 2 octaves above to 4 octaves below the unit’s BF in steps of 0.12 octaves, and over a sound level range of 100 dB in 5-dB steps. The number of spikes elicited by a single frequency and level combination was counted and, after smoothing, displayed as a rectified response. The frequency response area and level were used to construct a continuous and systematic change in the binaural phase disparity at a rate of 1 Hz. In the present study, the beat stimulus was configured such that the frequency of the signal delivered to the left ear (contralateral to the 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. The best IPD, the corresponding mean best delay for the signal (SBD), and the vector strength (r) for each frequency (at least including the BF and 500 Hz) were computed from the binned middle two cycles (during the middle 2 s of the stimulus duration) using the method described by Goldberg and Brown (1969) and Yin and Kuwada (1983a).

NOISE DELAY FUNCTIONS. Noise delay functions (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 1-s stimulation time at each delay. The ITD corresponding to the maximum discharge rate is denoted as the noise best delay (NBD), whereas the ITD corresponding to the minimum discharge is denoted as the noise worst delay (NWD). In some cases, the NDFs had two or more large peaks situated at large positive and negative delays with a trough at zero delay (i.e., the NWD was close to 0 ITD). In these cases, the NBD was designated as the delay of the largest peak close to zero delay, in the range of contralateral leading ITDs.

MASKED RATE-LEVEL FUNCTIONS. Masked rate-level functions (MRLFs) were obtained by running tone rate-level functions in the presence of a noise masker at a fixed level. Tone rate-level functions were generated by presenting digitally synthesized tones (50-ms duration, rise-fall time 1 ms) and 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. The phase of the tone was not fixed with respect to the noise onset on successive sweeps. The fixed noise level was chosen arbitrarily at 7–15 dB above the No noise threshold, a level at which a reasonable No driven response and a well-tuned noise delay function was obtained. Possible order effects were minimized by ensuring that each stimulus was never > 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 either interaurally in phase (So) or out of phase (Sπ). The stimulus presentation consisted of alternating the signal-plus-noise and the noise alone at a rate of 5/s. Only the discharges in the signal plus noise interval were used to construct the MRLFs. The discharges in the noise alone interval were also recorded.

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). This technique already has been used widely in the analysis of the responses of auditory-nerve fibers (e.g., Delgutte 1987; Rice et al. 1995; Viemeister 1988; Winslow and Sachs 1987). However, the classic detectability index (d’) metric assumes that the responses of the neurons are distributed normally with equal variances, an assumption that does not necessarily hold for the discharge characteristic of auditory-nerve fibers (Teich and Khanna 1985; Young and Barta 1986b) or, for that matter, other neurons in the auditory pathway. Accordingly, we employed a modified version of d’, the Standard Separation (D), described by Sakitt (1973), which is independent of any assumptions about the underlying distributions

\[
D_{(n \neq s)} = \frac{R_{(n \neq s)} - R_{(s)}}{SD_{(n \neq s)} \cdot SD_{(s)}}
\]

where \( R_{(n \neq s)} \) and \( R_{(s)} \) are, respectively, means for the distribution of the response to the signal-plus-noise and to the noise-masker alone, and \( SD_{(n \neq s)} \) and \( SD_{(s)} \) are the standard deviations of the respective response distributions. 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 Sπ tones is lower than that for So tones.
RESULTS

A total number of 120 neurons were recorded from the ICC, as judged from their responses to a range of stimuli (see McAlpine et al. 1996b; Yin and Kuwada 1983a,b; Yin et al. 1986, 1987). Recording sites were confirmed by electrolytic lesions made in the last recording track in 27 animals. The BFs of the neurons included in this study ranged from 168 to 2,090 Hz. Throughout this paper, we refer to these neurons as low-frequency ICC neurons. Once a single unit was isolated, the thresholds to binaurally presented BF tones and noise at 0 ITD were determined, and the spontaneous discharge rate was measured.

Determination of masked thresholds using signal detection theory

Figure 1 shows examples of how the D metric was used to estimate masked thresholds from MRLFs in two ICC units. The MRLFs were measured using a 500-Hz binaural tone, in which the phase was inverted at one ear in the presence of a suprathreshold noise masker with identical phase at the two ears. For each unit, the MRLF was measured over a 70 dB range, in 1-dB steps (Fig. 1, A and D), and the means and SD of the responses to 10 repeats were calculated. In both cases in Fig. 1, when the signal level was low, the neuron was driven by the noise alone. However, as the level of the tone increased, the discharge rate increased for the unit in Fig. 1A and decreased for the other (Fig. 1D). To compute D, both the means and SD were first three-point smoothed (Fig. 1, B and E). The mean discharge rate over the lowest 10 dB range of the tone signal, indicated by double arrows in Fig. 1, B and E, then was used as an estimate of \( R_{\text{na}} \), and the standard deviation over the same range was used as an estimate of \( \text{SD}_{\text{na}} \). Using Eq. 1, the detectability (D) of the tone in the noise was computed as a function of tone level (D value-level functions, Fig. 1, C and F). For the example given in Fig. 1, A–C, a D value of 1 was obtained when the tone evoked an increase in the discharge rate above that to the noise alone, whereas for the example in Fig. 1, D–F, a D value of −1 was obtained when the tone produced a reduction in discharge rate below that to the noise alone.

The two examples in Fig. 1 show that for NoS\( \pi \), first, masked thresholds can be reached by either an increase above or a decrease below that evoked by noise alone and, second, at suprathreshold values, rate-level functions may demonstrate nonmonotonicity. Thus the unit in Fig. 1A showed first an increase then a slight decrease in discharge rate at the highest tone levels, whereas the unit in Fig. 1D showed first a decrease then a recovery in discharge rate as tone level was increased. In fact, nonmonotonicity in MRLFs was observed to varying extents for both NoSo and NoS\( \pi \) binaural configurations throughout this study. However, here we are concerned mainly with signal detectability, and the nonmonotonicity will not be discussed further in this paper.

We have divided MRLFs into two groups based on whether increases or decreases in discharge rate were observed as the tone level was increased. Type-P MRLFs showed an increase in discharge rate as the tone level was increased, and gave a positive D value of 1 at masked threshold (as in Fig. 1, A–C). Type-N MRLFs showed a reduction in discharge rate as tone level was increased and gave a negative D value of −1 (as in Fig. 1, D–E). This classification is independent of whether the signal was S\( \pi \) or S\( \pi \).

Responses of neurons in the ICC to binaural configurations in which 500-Hz signals in zero or \( \pi \) phase were masked by zero-phase noise (No)

For the NoSo configuration, the majority of units (91.7%, 110/120) showed Type-P MRLFs, whereas, for the NoS\( \pi \) configuration, 57.5% (69/120) of the units showed Type-P MRLFs and 42.5% (51/120) showed Type-N MRLFs. All four possible combinations of Type-P and N responses at masked threshold were observed. These are: P-P, for which the masked thresholds for both NoSo and NoS\( \pi \) were achieved at \( D = 1 \) (55.5% of units); P-N, for which the masked threshold for NoSo was achieved at \( D = 1 \), whereas that for NoS\( \pi \) was achieved at \( D = -1 \) (36.4% of units); N-N, for which both masked thresholds were at \( D = -1 \) (5.7% of units); and N-P, for which the masked threshold for NoSo was achieved at \( D = 1 \), whereas the masked threshold for NoS\( \pi \) was achieved at \( D = 1 \) (23% of units).

The relationship between the D value at the masked threshold and the BF is shown in Fig. 2. Figure 2A shows a histogram of the distribution of BFs for the 120 neurons for which masked threshold data were obtained. This shows that half of our units (64/120) had BFs within the range 300–699 Hz, near the signal frequency (500 Hz) used in this study. From Fig. 2B, it can be seen that virtually all units with BFs in this range (92.2%, 59/64) showed an increase in discharge rate to So signals (Type-P MRLFs), whereas for NoS\( \pi \) (Fig. 2C), a considerable number of the neurons (34.3%, 22/64) in this frequency range showed Type-N MRLFs. In fact, the increase in the proportion of Type-N responses when NoS\( \pi \) was used is also evident in frequency bands <300 and >700 Hz. Thus the increase in the proportion of Type-N MRLFs observed when the 500-Hz tone was switched from So to S\( \pi \) is independent of best frequency.

Relationship of neural BMLDs for 500-Hz signals (NoSo vs. NoS\( \pi \)) to ITD sensitivity

P-N units. Forty-four units showed P-N type responses at masked threshold using 500 Hz signals and the standard (NoSo and NoS\( \pi \)) configurations. Of these, 32 (72.7%) showed positive BMLDs of ≥3 dB, i.e., the masked threshold for NoS\( \pi \) was lower than that for NoSo. Two units (4.5%) showed negative BMLDs of ≥3 dB, i.e., the masked threshold for NoS\( \pi \) was higher than that for NoSo, and 10 (22.7%) showed BMLDs of <3 dB in either direction.

An example of the responses of a low-frequency ICC neuron to binaural stimuli is shown in Fig. 3. The response area in Fig. 3A, measured with binaural tones presented at 0 ITD, indicates that the neuron had a BF ~600 Hz. The MRLFs to the binaural configurations NoSo and NoS\( \pi \) are shown in Fig. 3B. In response to NoSo, the neuron showed an increase in discharge rate above that evoked by the noise masker, as the level of the So signal was increased, i.e., Type-P response. Increasing the S\( \pi \) signal level, however,
FIG. 1.  A and D: masked rate-level functions (MRLFs) for 2 inferior colliculus (ICC) low-frequency neurons for binaural configuration of noise with signal inverted at one ear (NoSp) with signal at 500 Hz. Increment in signal level is 1 dB/step. Error bars: standard deviation for responses at each stimulus level. Low-sound level part of each curve is neuron’s response to noise fixed at 10 dB above its threshold (±±±). A shows a Type-P response, B shows a Type-N response. B and E: 3-point smoothed versions of MRLFs in A and D. Mean of neuron responses from lowest 10 dB level range (±±±) was used as R_{(n)}, and mean standard deviation from same signal level range was used as SD_{(n)} in Eq. 1. C and F: D value-level functions derived from smoothed MRLFs in B and E using Eq. 1. Masked thresholds, D = 1 for C and D = −1 for F (−−−) are indicated (±±±); corresponding sound levels are shown (±±±) in B and E.
caused a decrease in the discharge rate below the noise evoked discharge rate, i.e., Type-N response, and the neuron’s activity was suppressed almost completely by high levels of the Sπ signal. The D value-level functions computed from the two MRLFs indicates a lower masked threshold for Sπ (49 dB SPL) at D = −1 than for So (59 dB SPL) at D = 1 (Fig. 3C, double arrows, also shown by the double arrows in Fig. 3B and its inset). Thus inverting the signal from So to Sπ has produced a positive BMLD of 10 dB.

The P-N type response pattern of the unit to the binaural masking stimuli was consistent with its interaural delay sensitivity. Figure 3D shows the response of this unit to interaurally delayed noise. Arrows indicating the monaural discharge rates show that the unit was driven by the contralateral ear alone (arrow labeled C) but not driven by the
FIG. 3. Characterization of a typical P-N type unit. A: response area evoked by binaurally presented tones at 0 interaural time difference (ITD). B: MRLFs for NoSo (●) and NoSπ (○). C: D value-level functions derived from MRLFs in B. ■, NoSo; □, NoSπ; ○, D value = ±1. Masked thresholds are indicated (■) in both B and C. B, inset: 2, size of BMLD. D: noise-delay function of unit. Monaural responses are indicated (≈). C, contralateral stimulus alone; I, ipsilateral stimulus alone; −−−−−−, 0 ITD (N0). E: interaural phase difference (IPD)-histogram to a 1-Hz binaural beat presented at 500 Hz. BD, best delay; BP, best phase; r = vector strength. Noise spectrum level (NSL) for MRLFs (B) and noise-delay function (NDF; D) was 23 dB SPL.

Signal Levels (500 Hz dB SPL)

Response Area

IPD histogram

Noise delay function

D value - level functions

Masked rate-level functions
ipsilateral ear alone (arrow labeled 1). Two features of the delay function are prominent. First, there is a single peak in the function at +200 μs (the best delay NBD) and the discharge at 0 ITD, corresponding to the No configuration, is relatively high. Second, ITDs of ±1,000 μs are within the regions of ITDs eliciting the weakest responses. At ITDs of ±1,000 μs, the 500 Hz component within the noise would be in anti-phase.

Figure 3E shows the IPD histogram to a 1-Hz binaural beat presented at 500 Hz. The unit was driven relatively strongly by the 0 IPD signal at this level but showed very weak responses to inverted IPDs (π and −π; equivalent to ±1,000 μs ITD for a 500-Hz signal).

The similarly robust response of the neuron to No noise and So signals suggests that introducing an in-phase So signal to a No noise would cause an increase in discharge rate. In contrast, introducing an unfavorable Sπ signal to No noise would suppress the neuron’s response to the noise masker.

The generality of the description of the unit in Fig. 3 to neurons with BFs remote from 500 Hz and with different monaural response characteristics is illustrated in Fig. 4. In this figure, four P-P type responses to NoSo and NoSπ are shown. Each row of the figure shows the noise delay function (left), IPD histogram to 500 Hz (middle), and D value-level functions of the neurons. The BFs of the four neurons are 180 Hz (Fig. 4, A–C), 505 Hz (Fig. 4, D–F), 950 Hz (Fig. 4, G–I), and 1033 Hz (Fig. 4, J–L). All the noise delay functions are cyclic, with peaks or troughs separated by a period equivalent to the unit’s BF. All four show similar responses to those described in Fig. 3 in three respects. First, all noise delay functions have a maximum discharge rate at ITDs at, or close to, 0. Second, the IPD histograms to 500 Hz show strong driving by the So signal, whereas responses to Sπ were weaker compared with So or even weakest in whole IPD cycle. Third, all four neurons showed positive BMLDs of between 9 and 40 dB.

P-P TYPE UNITS. Of the 66 units that showed P-P type responses for both NoSo and NoSπ, 18 units (27.3%) showed negligible unmasking effects (BMLDs <3 dB), 23 units (34.8%) showed positive BMLDs ≥3 dB, and 25 (37.9%) showed negative BMLDs ≥3 dB.

Figure 5 shows four examples of P-P type responses to NoSo and NoSπ in the same format as Fig. 4. The BFs of the four neurons were 400 Hz (Fig. 5, A–C), 627 Hz (Fig. 5, D–F), 739 Hz (Fig. 5, G–I), and 914 Hz (Fig. 5, J–L). In contrast to the noise-delay functions of P-N types in Fig. 4, the peaks in the noise-delay functions are closer to half the period of the BF of each unit rather than to 0 ITD, whereas the minimum discharge occurs at, or very close to, 0 ITD, i.e., these neurons were driven poorly by No noise. The IPD histograms for binaural beat stimuli at 500 Hz showed that all units responded better to the Sπ signal than to the So signal. In response to NoSo and NoSπ, the plots of D value-level functions (Fig. 5, C, F, I, and L) show that the discharge rate increased with increasing tone level for both So and Sπ signals. In all four cases, consistent with the relative efficacy of the So and Sπ signals, the Sπ signal produced a lower masked threshold than the So signal, as indicated by double arrows. Thus BMLDs for all of these units were positive. In this study, of the 23 P-P type units that showed positive BMLDs ≈3 dB, 19 had responses like those described above.

Unlike the P-N type units, most of which gave positive BMLDs, there was a considerable proportion of P-P type units that either yielded no BMLD or negative BMLDs. Examples of four such neurons are shown in Fig. 6, again in the same format as Fig. 4. The noise-delay and IPD functions of these units (Fig. 6, A, D, G, and J) were intermediate between those shown in Figs. 4 and 5. The peaks of the noise were closer to 0 than the P-P type units shown in Fig. 5, but overall the relative efficacy of noise at zero delay was less than for the P-N units shown in Fig. 4 in terms of the discharge at No as a proportion of the peak discharge. In fact, the driven rates at 0 noise delay for the units in Fig. 6, A and D, are at the mean of the rates at the noise best delay and worst delay; this has implications for the MRLF type and the magnitude and the direction of the BMLD (see DISCUSSION). Similarly, in contrast to those shown in Figs. 4 and 5, the IPD histograms show that neither So nor Sπ were at the most or least favorable IPD for these units. The IPD histograms show an almost equal response to So and Sπ. For the two units shown in Fig. 6, A and D, no BMLD was apparent from their D value-level functions. For the units with negative BMLDs, the D value-level functions demonstrate that the Sπ signal evoked a generally weaker response compared to the So signal, consistent with the IPD histograms. The results suggest that the response at masked threshold for NoSo and NoSπ, whether an increase or a decrease in discharge rate, is a combined result of the neuron’s delay sensitivity to the noise and the signal.

SUMMARY OF P-N AND P-P TYPE UNITS. The relationship between the neuron’s delay sensitivity and its response to NoSo and NoSπ is further explored in Fig. 7. In Fig. 7A, the noise best delay of P-P or P-N type units yielding positive BMLDs are plotted against their BFs. The separation of the noise best delays between P-P and P-N type units is visible, especially at BFs <800 Hz. The P-P type neurons have relatively longer best delays at these BFs than P-N type units. Note that those P-N type units with positive BMLDs invariably had NBDs close to 0 ITD regardless of their BF. In comparison with these two groups of units, in Fig. 7B, the noise best delay of the P-P or P-N type units, but with negative or 0 BMLDs are plotted against their BFs. Note the considerable overlap in the noise best delays not only between P-P and P-N type units in this plot but also with those units yielding positive BMLDs in Fig. 7A. There is some tendency for the best delays in Fig. 7B to lie between the two groups shown in Fig. 7A. The response type, the BMLDs and the delay sensitivities are further explored in Fig. 7C, which shows the BMLDs of units with BFs between 400 and 599 Hz plotted against their NBDs. The positive BMLDs were characteristic of P-P type units, most of which (4 out of 5) had NBDs >800 μs, and of P-N type units, most of which (5 out of 7) had NBDs within ±200 μs. For the units showing negative or 0 BMLDs, the NBDs were scattered between 120 and 600 μs.

A summary of the direction and the magnitude of the BMLDs for NoSo versus NoSπ at 500 Hz for the major response types is shown in Fig. 8, A and C, as a function...
FIG. 4. Shown are noise-delay functions (A, D, G, J); IPD histograms for a binaural beat stimulus at 500 Hz (B, E, H, K); and D value-level functions for NoSo and NoSp for 4 P-N type units with BFs of 180 Hz (A–C); 505 Hz (D–F); 950 Hz (G–I); and 1,033 Hz (J–L). All 4 units showed positive BMLDs. NSL: Noise spectrum level.
FIG. 5. Shown are noise-delay functions (A, D, G, J); IPD histograms for a binaural beat stimulus at 500 Hz (B, E, H, K); and D value-level functions for NoSo and NoSp for 4 P-P type units with BFs of 400 Hz (A–C); 627 Hz (D–F); 739 Hz (G–I), and 914 Hz (J–L). All 4 units showed positive BMLDs.
FIG. 6. Shown are noise-delay functions (A, D, G, J); IPD histograms for a binaural beat stimulus at 500 Hz (B, E, H, K); and D value-level functions for NoSo and NoS for 4 P-P type units with BFs of 443 Hz (A–C); 496 Hz (D–F); 553 Hz (G–I), and 705 Hz (J–L). Two units showed no BMLD, 2 units showed negative BMLDs.
of BF. The distribution of BMLD magnitudes is shown in histogram form in Fig. 8, B and D. Large positive and negative BMLDs were observed irrespective of BF for P-P type units and the largest BMLDs ($\leq 42$ dB) are given by those neurons with BFs relatively close to 500 Hz. In contrast, for P-N type units, the majority of BMLDs are positive (Fig. 8, C and D), although in this case, the largest BMLDs (again $\leq 42$ dB) are given by those neurons with BFs near 1 kHz. In this study, a total of 49.1% of units (including all 4 types responses) showed positive BMLDs, and the grand average BMLD for NoSo versus NoS$\pi$ in this study is 4.3 dB with lower masked thresholds for
NoS\(\pi\). However, it has to be borne in mind that the magnitude of BMLD for both single units and for the grand average gives little indication of the S/N ratio required for signal detection for the whole system (see below for further details).

**OTHER UNIT TYPES.** Three out of seven units with N-N type responses showed positive BMLDs \(\approx 3\) dB, whereas the remaining four units showed no BMLDs. All seven units had BFs remote from 500 Hz; four \(>1,084\) Hz, three \(<363\) Hz. An example of an N-N type response is shown in Fig. 9. The response area (Fig. 9A) indicates that the neuron had an unusually sharp high frequency cut-off so that the neuron was almost unresponsive to 500-Hz signals at 0 IPD, an indication of possible inhibitory effects on this neurone. The N-N type response for both NoSo and NoS\(\pi\) can be seen in the MRLFs (Fig. 9B), and value-level functions indicate a positive BMLD of 6 dB (arrows in Fig. 9, C and B and its inset). Although the noise delay function (Fig. 9D) is periodic and similar to those shown by units with P-N type responses, the IPD histogram to 500-Hz signal in Fig. 9E indicates that the neurone is only sensitive to positive (contralateral leading) IPDs and both 0 and \(\pm \pi\) are unfavorable. Combining the IPD and response area information (Fig. 9A, which was measured at 0 IPD), one possible interpretation is that the unit may be under a strong inhibitory influence from 500-Hz signals at 0 or \(\pi\) phase, as is suggested by the effects of So and S\(\pi\) signals observed in the MRLFs. In this particular case, a positive BMLD indicates that the S\(\pi\) signal had stronger suppressive effects than the So as indicated in the IPD histogram (Fig. 9D).

Only two units showed N-P type response for these binaural configurations. However, a relationship (not shown) between the delay sensitivity and the responses also was demonstrated for this type of response.
FIG. 9. Binaural responses in same format as Fig. 3 for a N-N type unit with a BF of 300 Hz. 

A: response area measured with binaural presentation of tones with 0 IPD. 

B: MRLFs for NoSo (●) and NoSπ (○). 

C: D value-level functions derived from MRLFs in B, NoSo (●), NoSπ (○). 

D: NDF. 

E: IPD histogram for a binaural beat stimulus at 500 Hz.
Signal-to-noise ratios at masked threshold

For a fixed level of masking noise, as used in many psychophysical paradigms, the relative masked thresholds of the units would be indicative of their contribution to the detection of the tonal signal: the units with the lowest masked thresholds presumably mediate the detection of the tone. Here we investigated the BMLD effects in each neuron with a noise level that was ~10 dB suprathreshold. In this case, neither the magnitude and direction of the BMLD (Fig. 8) nor the value of the masked threshold gives an unequivocal indication of the contribution of any single unit to the population response when a fixed level of noise is presented. However, using a 500-Hz tone, the signal-to-noise (S/N) ratio for any unit can be taken as some measure of a unit contribution, if we assume that it is an indication of what the relative signal level at threshold would be for a fixed noise.

The simple approach is to express the S/N ratio as tone level in decibels minus the noise spectrum level. The mean, maximum output tone level of our sound system (in dB SPL) from 150 experiments is shown in Fig. 10A. The maximum spectral level of the 50-5,000 Hz wide noise used was 48 dB below the maximum output level for a single tone at each frequency. Thus for a noise level of 60 dB of attenuation at a BF of 500 Hz, the spectral level of the noise is 101 dB SPL (the maximum level of the 500 Hz tone) minus 48 dB minus 60 = −7 dB SPL. For a masked threshold for the tone of 23 dB SPL, this gives a S/N ratio of 30 dB. In Fig. 10, B and C, the single neuron's S/N ratio at masked threshold for NoSo (●) and NoSπ (○) is plotted as a function of BF for the P-P type (Fig. 10B) and P-N type (Fig. 10C) units. As expected, for both types of responses, the majority of units with low S/N ratios are those with BFs ~500 Hz, although there is some scattering across frequency. Another interesting point is that some units with large positive BMLDs, like those with BFs ~1,000 Hz shown in Fig. 8C, are not among those units with the lowest S/N ratios.

The current results suggest that the units that are most likely to contribute to detection of the tone at masked threshold for both NoSo and NoSπ are those units with BFs ~500 Hz, because these give the smallest S/N ratios at masked threshold. The results suggest that equally low S/N ratios were found for both P-P and P-N units and S/N ratios for NoSπ were generally lower than for NoSo for N-P units as also indicated in Fig. 8.

In the previous section, we demonstrated that the delay sensitivity is an important factor in the determination of a neuron’s response type and thus the direction and the magnitude of the BMLD. This point also can be demonstrated by the relationship between the S/N ratio at masked threshold for each configuration (NoSo or NoSπ) and each neuron’s delay sensitivity. In Figure 11, we have replotted the S/N ratio at masked threshold for NoSo (●) and NoSπ (○) as a function of noise best delay separately for P-P type (Fig. 11A) and P-N type (Fig. 11B) units. For the NoSo, the lowest S/N ratios were given by those units with noise best delays between 0 and 280 μs. For the NoSπ, the lowest S/N ratios among Type-P responses correspond to those neurons with relatively long noise best delays, whereas for Type-N responses, the lowest S/N ratios were among those neurons with relatively short noise best delays.

**FIG. 10.** A: mean maximum output of sound system in dB SPL close to eardrum from 150 experiments (~ ± 1 SD). B and C: signal-to-noise ratios (see text for details) at masked threshold for P-P type units (●) and P-N type units (○) plotted against BF for NoSo (●) and NoSπ (○).
masked threshold, we have been able to demonstrate an analogue of the BMLD in single ICC neurons of the guinea pig to the standard binaural masking configuration of NoSo and NoS\(\pi\) with the signal at 500 Hz. A positive BMLD, i.e., a lower masked threshold for the S\(\pi\) signal, consistent with psychophysical results, was observed in those neurons with noise best delays at or close to 0 (P-N type response units) and also in those with long noise best delays (P-P type response units). The response to the binaural masking stimulus and the direction and magnitude of the BMLD are generally predictable from the delay sensitivity demonstrated by low-frequency neurons in the ICC.

Comparison with previous physiological studies

The consistency of the responses to binaural masking stimuli with the delay sensitivity has been suggested indirectly previously. Thus Langford (1984) reported that MSO neurons showed a decrease in discharge rate when an S\(\pi\) BF signal was added to No noise. Caird et al. (1989) reported that, in ICC units with strong responses to So signals, the changes in the discharge rate when the signal or masker were inverted at one ear, were in the opposite direction to those units with strong responses to the S\(\pi\) signals. In more recent studies, Caird et al. (1991) reported that the noise level required to mask a signal was a periodic function of the interaural delay of the masking noise, with peaks and troughs approximating the inverse of the noise delay function. However, in this paradigm, the delay sensitivity to the signal or the nature of the signal were not relevant, because the signal merely established a level of driven activity against which the masking could be demonstrated. McAlpine et al. (1996a) tracked the masked threshold of optimized signals (BF tones at their BDs) masked by noise with different interaural delays. Consistent with the earlier studies, they found that for noise delays that evoked high discharge rates, signal masked thresholds were relatively high, whereas at noise delays that evoked little activity, signal masked thresholds were lower. Both of these earlier studies found units whose responses to BMLD stimuli were not apparently predicted by their delay sensitivities. When the standard configurations NoSo and NoS\(\pi\) were used, a substantial number of the units showed either no measurable BMLD or negative BMLDs. McAlpine et al. (1996a) argued that because the majority of ICC units were only weakly driven by S\(\pi\) signals, a high S\(\pi\) signal level would be needed to reach masked threshold. However, it was acknowledged that one possible effect of S\(\pi\) signals was to cause a decrease in the discharge rate. This suggestion is supported by the present results in which 42.5% of units produced Type-N responses to the NoS\(\pi\) configuration. The nonmonotonicity of the MRLFs in some units, especially those with Type-N responses to NoS\(\pi\), such that at high S\(\pi\) signal levels the discharge rate exceeded the rate to the No noise, provide an explanation of the negative BMLDs observed by McAlpine et al. (1996a), because the tracking paradigm they used would have produced a high masked threshold for NoS\(\pi\).

Discussion

Using the masked rate-level functions and the standard separation D, based on signal detection theory, to define the

![Fig. 11.](http://jn.physiology.org/Downloadedfrom)
response behavior to binaural masking stimuli, and the direction of the BMLDs. The best delay to noise has been suggested to be the relevant functional measure of a unit’s delay sensitivity (Yin and Kuwada 1984). The characteristic delay (CD) is, however, an estimate of the difference in the time of arrival of spikes from each ear at the binaural coincidence detector and, for the purposes of comparisons with model data, would have been a very useful metric to have determined. The concept of the characteristic delay was introduced by Rose et al. (1966), who discovered that the responses to the interaural delays of different frequencies all gave the same relative discharge rate at some common or “characteristic” delay for the neuron. This common delay in the early studies and certainly in later studies often coincided with peaks or troughs in the tonal delay functions. Rose et al. (1966) proposed that characteristic delays represented a fixed physiological delay between the input from each side that could be compensated by equal and opposite interaural time delays in the sound signal. This concept has been further investigated in other species and in several other auditory nuclei (Aitkin et al. 1972b; Brugge and Merzenich 1973; Brugge et al. 1969, 1970; Geisler et al. 1969; Kuwada and Yin 1983; Kuwada et al. 1984, 1987; Yin and Chan 1990; Yin and Kuwada 1983b; Yin et al. 1986).

In the MSO, the CD occurs at a peak in the delay function, (Spitzer and Semple 1995; Yin and Chan 1990), and hence the CD and the best delay to the noise coincide. However, this is not necessarily true in the ICC. Yin and Kuwada (1983b) found that only a small percentage of ICC units had CDs corresponding to a peak in the delay function, whereas most corresponded to an intermediate point on the delay function, with the majority of CDs being close to 0. In subsequent studies, however, (rabbit: Kuwada et al. 1987; guinea pig: McAlpine et al. 1996b), the majority of delay-sensitive units had CDs close to a peak in the delay functions, with a mean CD ~200–300 μs leading at the contralateral ear. Thus although we have been careful only to describe our data in terms of the relationship of the BMLD to the noise best delay, in many instances, the extension of this observation to the CDs may be justified but needs further investigation.

The data presented in Figs. 4–7 suggest that the neural delay sensitivities to noise and tone determine what the magnitude and direction of the BMLD in each individual neuron will be. However, the wide variation in the shapes of the individual delay functions and the overlap of the best delays for different response categories in Fig. 7 preclude unequivocal predictions of the BMLD simply from a perusal of the delay functions.

Comparison with modeling studies

Since the original descriptions of the BMLD (Hirsh 1948a,b; Licklider 1948) and Jeffress’s (1948) suggestion of a neural coincidence mechanism to detect interaural time differences, many sophisticated computational models have been constructed to account for its properties (see reviews by Colburn 1996; Colburn and Durlach 1978; Stern and Trahiotis 1995). In the 1970s, Colburn (1973, 1977) produced a model quantification of the Jeffress hypothesis that has been used as a specific example of this generic class of model. Colburn’s model compared the information that could be extracted from the response of populations of auditory-nerve fibers with performance in binaural detection and interaural discrimination experiments. It consisted of two parts: a model of auditory-nerve activity (Siebert 1970) and a central processor that analyses the number of coincidences between the spike trains of fibers with similar BF from each ear. In recent years, more computationally oriented and physiologically accurate models for the auditory-nerve firing have been developed (e.g., Carney 1993; Meddis et al. 1990), without substantially affecting the behavior of the models.

A general coincidence detector stage, for a given BF, can be approximated mathematically as a running cross-correlation $[R_{LR}(\tau, t)]$ of the spike trains of fibers from the two ears

$$R_{LR}(\tau, t) = \int_{-\infty}^{\infty} r_L(t')r_R(t' - \tau)w_c(t - t')p(\tau)dt'$$  \hspace{1cm} (2)

Where $r_L(t)$ and $r_R(t)$ are the inputs from auditory-nerve fibers from the two ears at time $t$, and $R_{LR}(\tau, t)$ is the response rate at internal interaural delay $\tau$. $w_c(t)$ is an exponentially decaying integration window emphasizing the most recent cross-correlation event, which is 0 for $t < 0$ and approaches 0 as $t$ approaches infinity (i.e., a “leaky integrator”). Here we used a value of the time constant $w_c(t)$ of the order of 50 ms. $p(\tau)$ is a density function for the internal delays that describes the distribution of fiber pairs as a function of the internal delay. Such models have been used to obtain predictions for BMLD experiments. Figure 12A illustrates how the averaged output of the ensemble of coincidence detectors within a single frequency channel centered at 500 Hz (ERB = 200 Hz) and, in the absence of the weighting function $p(\tau)$, changes with different binaural stimulation configurations. The figure shows the numbers of coincident spikes for No noise (thin solid line), NoSo (dotted line), and NoSπ (thick solid line). The signal frequency is 500 Hz. The S/N ratio for NoSo and NoSπ is −8 dB. It shows that No noise produces a cyclic variation in the number of coincidences with the maximum output at 0 delay and minima at ±1,000-μs delays. The addition of an So tone to the No masker, at a level close to the masked threshold, produces only a small increase in the number of coincidences in the region between ±200-μs internal delay. This is because the within-channel interaural phase differences of the signal and masker are identical so the resultant IPD is unchanged when the signal and masker are combined. The So tone and the No noise thus add vectorially and cause an increase in rate. The addition of a Sπ signal to the No masker, at same S/N ratio, causes a decrease in the number of coincidences within a region between ±500-μs internal delay, and an increase in the number of coincidences from +500 to −1,500 μs and from −500 to −1,500 μs. This effectively causes a slight broadening of the peak. The Sπ signal and No masker have different interaural phase relationships, so the addition of Sπ signal to the noise desynchronizes the resultant phases of the noise-plus-signal complex between the ears, causing a dynamically varying IPD (Webster 1951). Because the tone and noise are no longer in phase, their vector addition is less than in the NoSo case. Note that the largest decrease in the number of coincidences...
occurs at 0 ITD, the largest increase at ±800–1,000 μs, and no change occurs at ±500 μs. The model predicts two important features of the responses of the ensemble of coincidence units. First, the BMLD: addition of a So signal to a No masker produces a smaller change in the pattern of the coincidence events than does adding a Sπ signal. Second, the changes in the response pattern: the increase or decrease in the number of coincidences is delay dependent.

In such models, to take account of the highest acuity for localization at the midline, different weighting functions \( p(\tau) \) have been used to describe the distribution of fiber pairs with different internal delays (e.g., Colburn 1977; Shackleton et al. 1992). Figure 12B shows the model of Fig. 12A implemented with the \( p(\tau) \) function described by Colburn (1977)

\[
p(\tau) = \begin{cases} 
C & \text{for } |\tau| \leq 0.15 \\
Ce^{0.042(\tau - 2.4)} & \text{for } 0.15 < |\tau| \leq 2.2 \\
Ce^{0.031(\tau - 2.2)} & \text{for } |\tau| > 2.2 
\end{cases} 
\]

(3)

where \( C \) is a constant and \( \tau \) is the internal delay in milliseconds. The major effect of this implementation is to replace the cyclic coincidence function in Fig. 12A with a narrower coincidence peak centered at 0 delay. The model including the weighting function still retains the major features of Fig. 12A, with a more prominent reduction in number of coincidences ~0 delay and a less prominent increase at longer delays, when NoSp is presented.

To relate the model to the physiological measurements, the internal delay axis in Fig. 12 should be regarded as an array of binaural delay-sensitive neurons with different best interaural delays, the delay sensitivity of each of which can be approximated by Eq. 2 without the weighting function \( p(\tau) \) (Yin et al. 1987). The increase or decrease in the output of the running cross-correlation is interpreted as the predictor of increase or decrease in the discharge rate, caused by the addition of the signal. The predictions made by the model of the ensemble of coincidence units in Fig. 12, \( A \) and \( B \) are qualitatively consistent with our current data in three respects. First of all, our data show that a large majority of ICC units with BFs between 400 and 599 Hz (48/50) demonstrated a Type-P response at masked threshold for NoSp, equivalent to an increase in the number of coincidences predicted by the model (Fig. 12A). Although Fig. 12, \( A \) and \( B \), shows that the major effects of the addition of So is to increase the number of coincidences in the region of 0 internal delay, it can be assumed that high levels of So will raise the No function at all internal delays by addition...
of coincidences irrespective of the internal delay in the same manner as simply raising the level of No. This would correspond to our finding of Type-P responses for NoS for units at all best delays. Second, our data show that both Type-P and Type-N responses are observed in the 500-Hz region for NoSπ: neurons giving Type-N responses had best delays for the noise close to 0, whereas those giving Type-P responses had relatively long noise best delays (Fig. 7). This is equivalent to the decrease at 0 and the increase at +800 and 1,000 μs for NoSπ, respectively, in the number of coincidences in Fig. 12A. Third, our data show that neurons giving positive BMLDs (especially those with BF s ~ 500 Hz) show either P-N type responses with noise best delays close to 0 or P-P type responses with noise best delays close to the half period of 500-Hz signal (Fig. 7, A and C). In the model, the largest decrease in the number of coincidences for NoSπ occurs at 0, whereas the largest increases occur at ±800–1,000 μs delays, thus these are presumably the regions used in the detection of signals in the BMLD task. Figure 12A shows the potential contribution of each neuron, as a function of its best delay, to the BMLD task. After application of the weighting function shown in Fig. 12B, the contribution to the population response of neurons with best delays away from 0 is much reduced, despite the fact that these individual neurons often give very large BMLDs.

Although there is good qualitative consistency between our data and the model in Fig. 12, A and B, there are obvious discrepancies between our data and the model’s predictions. For example, our data show that more than half of the P-P type units gave no BMLD or negative BMLDs, whereas the model predicts positive BMLDs for all delays apart from those close to ±π/2. Colburn’s p(τ) function implies that there are relatively more coincidence detectors with internal delays of near 0, a result consistent with at least one earlier physiological study of distribution of characteristic delay in the cat ICC (Yin and Kuwada 1983b). This function (Eq. 3) is also in reasonable agreement with the delay sensitivities of ICC neurons in the guinea pig measured either as noise best delay or characteristic delay (McAlpine et al. 1996b; Palmer et al. 1990) when both sides of the brain are taken into account. In a single ICC, neither the noise best delays nor the characteristic delays in the guinea pig ICC are symmetrically distributed ~0 delay, as shown in Fig. 12C, which shows a histogram (of data recently collected in our laboratory) in which the noise best delays of units with BF s between 400 and 599 Hz were binned with a resolution of 120 μs (the same resolutions used to obtain the NBD). It shows that the majority of ICC units had noise best delays corresponding to positions in the contralateral sound field, a result also obtained in the cat ICC (Chan et al. 1983), and consistent with the study of Jenkins and Masterton (1982) on the effects on sound localization after lesions of the ICC. We have computed a weighting function p(τ) based on this distribution

\[ p(\tau) = \begin{cases} 22e^{-0.0003(\tau-240)} & \text{for } \tau \geq 240 \\ 22e^{0.004(\tau-240)} & \text{for } \tau < 240 \end{cases} \] 

(4)

where τ is in microseconds.

To mimic the p(τ) functions used in the psychophysical models, we computed a mirror function of the p(τ) in Eq. 4 and then combined this with the original function. The application of this combined weighting function to the model of Fig. 12A is shown in Fig. 12D. With this weighting function most of the features demonstrated in Fig. 12, A and B, are preserved, whereas Fig. 12D represents a more physiologically based version of the model. The model in Fig. 12D demonstrates for units with best delays close to 0 (±250 μs), BMLDs are represented by a greater decrease in the number of coincidences for Sπ than the increase for So; a region ~250–500 μs (and ~250 to ~500 μs) in which no BMLD is predicted; and at 500–1,000 μs (and ~500 to ~1,000 μs) BMLDs are represented by increases in the number of coincidences for Sπ. These results are similar to those shown in Fig. 7: the averages of the absolute values of the noise best delays for units showing positive BMLDs, with BF s between 400 and 599 Hz, is 780 μs for P-P type units and 85.7 μs for P-N type units. Units showing no BMLDs had an average value of 237 μs.

Possible mechanisms for the Type P and Type N response

The models of binaural detection based on coincidence suggest that the delay-dependent decrease or increase in discharge to Sπ signals represents a desynchronization of the response to the No noise, as a result of within-channel disruption of the interaural phase (Colburn 1977). We specifically have tested this desynchronization hypothesis for the generation of the Type-N responses (Jiang et al. 1996b). Our results, which we will be reporting fully elsewhere, support the hypothesis in many of the Type-N response units but indicate, in others, that neural inhibitory effects generated by Sπ signals also may contribute to the Type-N response. Type P responses for So seem to result from increasing the number of firings arriving from each ear. Type-P responses to Sπ seem to result from more than one process. For units with long and intermediate best delays, for which the response to the No noise is a low discharge rate, desynchronization caused by the Sπ signal causes an initial increase in the discharge rate. At higher levels of the Sπ signal, it evokes increased coincidences because of the increased rate in the input fibers and further increases the discharge rate. When the No response is at the mean of the noise delay function (as occurs for units such as those shown in Fig. 6, A and D) and therefore occupies a position on the steep slope of the noise delay function, disruption of the interaural correlation caused by low-level Sπ signals will produce both increases and decreases in the discharge rate; these cancel out, and no net change in discharge rate is detected. Such responses are predicted at internal delays around ±500 μs by the coincidence detection model. As the Sπ signal is increased, it increases the number of coincidences and the discharge rate rises, resulting in the Type-P response.

Other cues for neural detection of BMLD

The results presented in this paper are based on an assumption that disruption of the interaural correlation of No noise, caused by low-level Sπ signals, would produce increases or decreases in the neuron’s discharge rate from that due to the noise alone. Also, in discussing the binaural modeling, the only output that was considered was the average of the run-
ning cross-correlation function, and this was taken to reflect the S/N ratio. The results have demonstrated that, for considerable number of units, the S/N ratio required for a significant change in the discharge rate is lower for NoSπ than for NoS. However, this takes no account of the variability of the measures of the cross-correlation.

The importance of interaural correlation discrimination on binaural detection has been demonstrated in psychophysical experiments (Koehnke et al. 1986). Later studies (Bernstein and Trahiotis 1992; Jain et al. 1991) confirmed that, in many cases, binaural signal detection can be predicted by performance in interaural correlation discrimination tasks. This implies that the change in interaural correlation is the salient and relevant cue in these binaural detection tasks. It is possible that as well as the change in the discharge rate we have shown here, neurons also may respond to the fluctuation of instantaneous IPD (or interaural correlation) induced by introducing low-level Sπ signals by changes in their temporal discharge pattern. We would have detected any temporal pattern changes that also resulted in a change in discharge rate, but we did not specifically measure the temporal patterns.

One hypothesized effect of the fluctuation of instantaneous IPD on a unit sensitive to a particular IPD, is to change its interspike intervals. It may well be the case that if we had employed temporal measures that BMLDs would have been detected even in those units not showing substantial mean rate BMLDs.

Comparison with human psychophysical studies

In human psychophysical studies, for the binaural signal configurations used in the present study, BMLDs range from 8 to 16 dB (Green 1966; Hirsh 1948b; Hirsh and Burgeat 1958; Jeffress et al. 1952, 1962; Rabiner et al. 1966). It also has been shown that signal detection is possible when the S/N ratio within an auditory filter at the tone frequency is negative (Green 1966; Henning and Wartini 1990; Hirsh 1948b). For example, applying an auditory ERB estimated using Moore and Glasberg’s equation (Moore and Glasberg 1983) to Hirsh’s study (1948b) gives within-channel S/N ratios at masked threshold of -3 dB for NoSo and -14 dB for NoSπ when the signal was 500 Hz and noise level was 59.1 dB SPL/Hz, giving a BMLD of 11 dB. In the current study, we have shown that, for those neurons showing positive BMLDs, the magnitude of the BMLD can be as large as 47 dB, but that such large BMLDs may not necessarily be associated with the lowest S/N ratios. When individual neurons were only sensitive to the signal in one of its configurations, a large BMLD necessarily resulted, but even the threshold to the most sensitive of the configurations could be quite high compared with that at 500 Hz. It is obvious that for a detection task like the BMLD, the nervous system must rely on changes in the responses of single neurons that occur at the lowest possible S/N ratios. Units with very large individual BMLDs may only contribute to the detection of So or Sπ, but not to both. The lowest S/N ratio in these units is obtained for one or other signal and if the threshold for the other signal is, say, 40 dB higher, it will be well above the level at which other units in the population already will have signaled the presence of the tone. Thus the population that contributes to detection of So signals may be different from that contributes to detection of Sπ.

Population averages of the BMLDs obtained in the present study, and the BMLDs of the majority of neurons, are generally smaller than the values obtained with the same signals in human psychophysical studies. It seems highly likely that the guinea pig, like the cat (Wakefield and Robinson 1974), may exhibit smaller behavioral BMLDs than humans.

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