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Binaural masking and sensitivity to interaural delay in the inferior colliculus

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SUMMARY

The binaural masking level difference (BMLD) is a psychophysical effect whereby signals masked by a noise at one ear become unmasked by sounds reaching the other. BMLD effects are largest at low frequencies where they depend on signal phase, suggesting that part of the physiological mechanism responsible for the BMLD resides in cells that are sensitive to interaural time disparities.

We have investigated a physiological basis for unmasking in the responses of delay-sensitive cells in the central nucleus of the inferior colliculus in anaesthetized guinea pigs. The masking effects of a binaurally presented noise, as a function of the masker delay, were quantified by measuring the number of discharges synchronized to the signal, and by measuring the masked threshold. The noise level for masking was lowest at the best delay for the noise. The mean magnitude of the unmasking across our neural population was similar to the human psychophysical BMLD under the same signal and masker conditions.

1. INTRODUCTION

Most low-frequency cells in the cat inferior colliculus are sensitive to interaural time differences. In effect, these cells respond to interaural phase differences (IPDs) in low-frequency components of the signal (Kuwada & Yin 1983). A plot of spike-rate against interaural time delay is a cyclical function whose period is either the reciprocal of the stimulation frequency or, for noise stimulation, a frequency close to the cell's best frequency (Kuwada & Yin 1983; Yin *et al.* 1986). The delay producing the main peak in a plot of the spike rate versus the interaural delay for broadband signals is termed the best delay and it usually corresponds to a sound source position in the contralateral hemifield.

Human psychophysical studies show that the masking of binaural signals by broadband noise depends on the interaural phase relationship of signal and masker. This was first demonstrated in 1948 (Licklider 1948; Hirsh 1948) and has since been extensively studied (see Durlach & Colburn 1978). If identical low-frequency tones and noises are presented to both ears in human subjects, improved detectability of the tone can be achieved by varying the phase of either the tone or noise in one ear. These unmasking effects, which have also been demonstrated in animals (Wakeford & Robinson 1974; Cranford 1975), are termed the binaural masking level difference (BMLD). The association of some of these BMLD effects with lateralization (Jeffress & McFadden 1971), the restriction of large BMLD effects to low frequencies, and the dependency of the BMLD on parameters such as the phase of the signal (Jeffress *et al.* 1962), together suggest that part of the physiological mechanism responsible for the BMLD resides in cells with similar properties to IPD cells.

There were two aims in the present study, first to quantify delay sensitivity in the guinea pig and second to investigate its relation to the BMLD. First we measured the best delays of a large sample of neurons in the guinea pig to allow a detailed comparison of the cat data with those from another mammal with a smaller head. Second, unlike earlier studies (Langford 1984; Caird *et al.* 1989) where the signals replicated the simple psychophysical BMLD test, we optimized our signals for the delay sensitivity of individual cells by measuring the masking effect of the noise on a signal at its best delay. We also investigated noise masking effects on the cells' synchronization to the fundamental frequency of a vowel sound. This experimental design, in which speech sounds are presented with one delay and noise maskers with other delays, has elements in common with the use of binaural cues in the 'cocktail party' effect: the separation of two or more spatially segregated sound sources. More detailed accounts of the data described here may be found elsewhere (Palmer *et al.* 1990; Caird *et al.* 1991).

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2. METHODS

The methods are described in detail elsewhere (Palmer *et al.* 1990; Caird *et al.* 1991) and are only summarized here. The experiments were performed on mature, pigmented guinea-pigs under anaesthesia.

The stimuli were delivered dichotically through sealed acoustic systems. The three stimuli used were, pure tones, broadband noise and synthetic vowel sounds. The onsets and offsets of the tone and noise stimuli were shaped with 5 ms rise-fall times. The speech signal was a segment of a steady-state approximation to the vowel /a/, with a fundamental frequency (F_0) of 100 Hz (see Palmer *et al.* (1986) for details). A pair of two-channel delay lines enabled the interaural delays of the signals and a noise masker to be varied independently between the two ears with a resolution of 1 μs.

The activity of single units in the inferior colliculus was recorded with tungsten microelectrodes positioned stereotaxically. A micro-computer recorded the time of occurrence of the extracellularly recorded action potentials. Histological reconstructions confirmed that the neurones were isolated in the central nucleus of the inferior colliculus.

The delay sensitivity of neurons with best frequencies (BFs) below 4.0 kHz was measured in response to 50 ms bursts of BF tone, noise, and vowel, presented with a repetition rate of 5 per second. The best delays were estimated visually or, when at least one cycle of response was available, using a single cycle vector strength analysis (see Kuwada & Yin 1983).

In the first masking test, the signal (a 50 ms burst of best-frequency tone or vowel) was set at its best delay and level and the masked threshold was measured as a function of the delay of a continuous noise masker. The masking was assessed either (i) subjectively using audio-visual criteria, or (ii) objectively using a computer-controlled adaptive procedure (Taylor & Creelman 1967) in which the discharge rate in the noise-alone interval was compared with that in the signal plus noise interval and the noise level was adjusted until a criterion difference (one spike more in the signal interval) was achieved on 75% of presentations.

In the second masking test we examined the effects of the interaural delay of a continuous noise masker on the response to a 500 ms segment of the synthetic vowel. The vowel was set at its best delay and level and presented at a repetition rate of 1 Hz. The level of masking noise was adjusted so that it just masked the response to the vowel when at the same delay. The delay of the noise was then varied in 100 μs steps over the range ±2000 μs. The cell's mean firing rate during the signal plus noise and noise-alone intervals were calculated as was the discharge rate synchronized to the F_0 of the vowel.

Human psychophysical masking was measured in three subjects listening over headphones to the signals used in the physiological experiments. The synthetic vowel /a/ was presented at 62 dB SPL with a 300 μs right ear lead and a continuous wideband noise was used to mask the vowel. A method of adjustment was used to estimate the masked theshold as a function of the interaural delay of the noise masker.

3. RESULTS

(*a*) *Response as a function of the interaural delay of best frequency tones and noise*

Delay sensitivity was measured in 171 neurons with best frequencies from 120 to 1800 Hz. Twenty-eight percent of these cells (48 out of 171) and all 72 cells tested with BFs between 1800 and 4000 Hz were not sensitive to the interaural delay of the BF tone.

We first measured the response to a single presentation of a stimulus (noise or tone) as a function of both delay and mean binaural intensity level. Having established the level which gave the greatest variation in response as a function of interaural time delay, we then measured the delay function at that optimal intensity with repeated presentations of each delay in random order.

As in other species, the discharge of most units to low-frequency tones fluctuates as the delay is varied. This is illustrated for a single unit in figure 1 (open circles). The period of the cycling in figure 1 is 1350 μs which is close to the reciprocal of the stimulation frequency (1/760 Hz = 1315 μs), which in this case was at the unit BF.

The filled squares in figure 1 show the delay function in response to wideband noise. For this cell, the best delays for noise and tones are the same (300 μs). However, unlike the responses to pure tones, the fluctuations in the noise delay functions become less pronounced at larger delay values. Indeed, in the example shown there is only one peak in the noise delay function.

There was a wide variation in the shapes of the noise delay curves from different cells. Generally, the peak of the delay curve was flanked by one or two

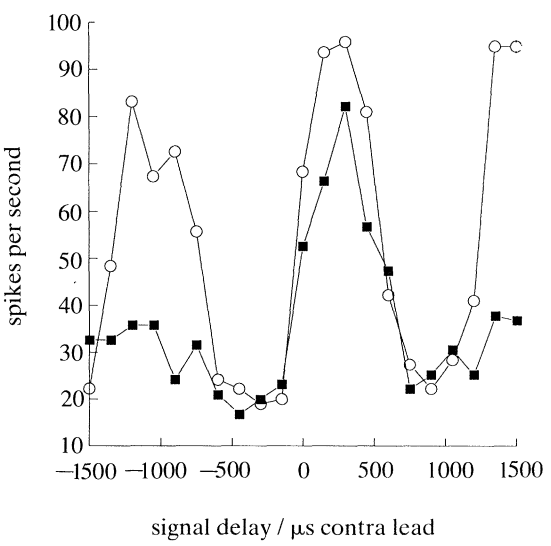

Figure 1. Response as a function of the interaural delay of best frequency tones (open circles: 760 Hz 55 dB SPL) and wideband noise (filled squares: 28 dB SPL spectrum level). (Replotted from figure 4*a* of Palmer *et al.* (1990).)

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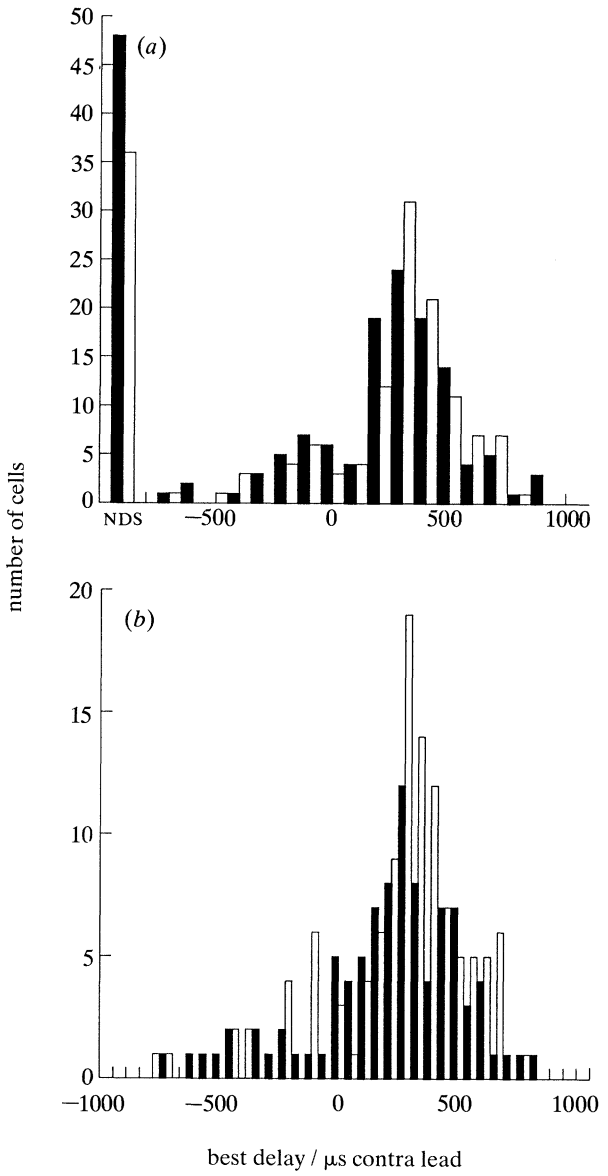

Figure 2. (*a*) Histogram of the number of neurons with different best delays. The filled bars are data obtained with best frequency tones and the unfilled bars are with wide-band noise. Only cells with best frequencies below 1.8 kHz are included in the data obtained with pure tones. NDS indicates neurons not delay sensitive. (Replotted from figure 6, Palmer *et al* (1990).) (*b*) Comparison of the best delays to noise stimulation between the cat (filled bars: replotted from Yin *et al.* (1986)) and the guinea pig (unfilled bars).

troughs. However, although some cells showed sustained cycling, in others only a single peak was present and in yet others only a trough (see figure 5 in Palmer *et al.* (1990)). For these latter neurons the major effect of delaying the noise was to produce a reduction of the output near zero delay, without facilitation at other delays. For these cells (4%, 10 out of 237) we have used the position of the minimum in the delay function as our estimate of the best delay.

The range of best delays in our sample of neurons is shown as a histogram in figure 2*a*, for both BF tone and noise signals. Most of the neurons responded best when the stimulus at the contralateral ear occurred 100–400 μs before that to the ipsilateral ear, corresponding to sound sources in the contralateral hemifield. Figure 2*b* shows a direct comparison of our range of best delays (for noise stimulation) with data from the cat (replotted from Yin *et al.* (1986)). The distributions clearly overlap and are not statistically different ($t = 1.07$, $p > 0.05$; $F = 1.19$, $p > 0.05$).

(*b*) *Measurement of masking by comparisons of responses to signal plus masker with that to masker alone*

Masking in individual cells was quantified by comparing the response to signal plus noise with that to noise alone to determine the masked threshold. This method yields a measure that is directly analogous to the BMLD. We have completed these analyses on 76 single neurons (five audio-visually and 71 objectively), of which 43 gave a variation in masked threshold with the masker delay. Twenty eight units showed no delay dependent masking despite sensitivity to the interaural delay of the masking noise. These 28 units had no best frequency or delay sensitivity characteristics that set them apart from the other cells in our sample.

The level of noise required for masked threshold was lowest when the noise was at its best delay, and highest at the minimum of the noise delay function for 38 of the 43 cells showing delay dependent masking. Two examples are shown in figure 3. For each cell, the responses to the noise and signal presented alone are shown as a function of interaural delay in the upper panel, with the level of the masking noise required to achieve the masked threshold, at each noise delay, immediately below. The delay functions were used to select a delay which resulted in a strong response to the signal (shown by the arrows in figure 3); in most instances this was the best delay. The shapes of the masking functions are approximately the inverse of the noise delay functions (filled squares); the delay sensitivity to the signal or the nature of the signal are not relevant, since the signal merely establishes a level of driven activity against which the masking can be demonstrated. This can be seen in figure 3*b* where both the noise delay function and the masking function with a tone signal, cycle at 625 Hz, whereas the delay function to the tone alone cycles at the best frequency of 820 Hz (see Yin *et al.* (1987) for a description of this phenomenon).

Some IPD cells are characterized by delay-dependent inhibition rather than a peak due to facilitation, and the best delay of such cells is defined as the delay producing the strongest inhibition (see Palmer *et al.* 1990). For these cells, the response to the signal was inhibited by the noise and the lowest levels of noise required for masking were at delays corresponding to the minimum in the noise delay functions.

The correlation between the best delay to the noise and the minimum in the masking function is shown in figure 4. The deviation of the minimum in the masking function from the the noise best delay is plotted as a fraction of the noise response period. In most of the cells the minimum masked threshold

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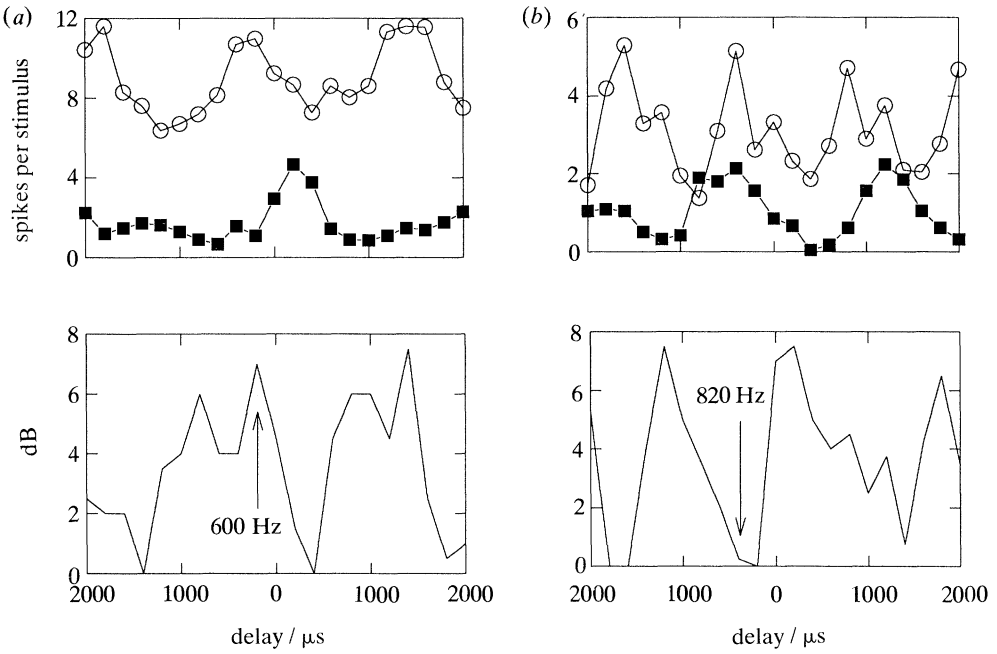

Figure 3. The upper panels show the delay functions from two different cells for noise (filled squares) and tone (open circles) stimuli. These delay functions were determined at the optimal sound level for each stimulus. The lower panels show the masked thresholds as a function of the interaural delay of the noise masker for the same cells. The labelled arrows indicate the signal interaural delay. (*a*) Data from a cell with BF of 600 Hz. The signal was a BF tone signal at 60 dB SPL. The zero reference level for the masked thresholds was 22 dB SPL spectrum level. (*b*) Data from a cell with BF of 820 Hz. The tone signal was presented at the best delay at 62 dB SPL. The zero reference level for the masked thresholds was 30 dB SPL spectrum level. (Replotted from figure 1, Caird *et al.* (1991).)

occurred when the noise was at or near (± 10%) its best delay.

For the cells that showed delay-dependent masking, the difference in noise level between the minimum and maximum masked thresholds varied between 5 and 36 dB as shown in figure 5. To emphasize the similarities in cell responses we have eliminated the differences in best frequency and best delay by scaling the delays to fractions of the period of the noise delay function (± 100%) and shifting the functions to coincide at the noise best delay (0%). The noise level at which the masking curves are at the minimum is redefined as 0 dB. A small number of cells exhibited large variations in masked threshold and for these (dotted lines) the second ordinate has been used. The mean population responses were calculated at each 10% normalized delay inteval and are shown to the right (figure 5*b*, *d*). The peak-to-trough masking level differences in these mean curves are 6.9 dB and 6.8 dB for vowel and tone respectively. The maximum levels of noise to achieve masking are reached at approximately ± 50% and only a suggestion of cycling can be seen in the mean functions (figure 5*b*, *d*); cycling is seen in the masking functions of some individual neurons (figure 5*a*, *c* and figure 3*a*, *b*). The open symbols in figures 5*b*, *d* show psychophysical measures of binaural masking obtained under conditions comparable to those used to obtain the physiological data. The psychophysical data have been scaled to a single period of the stimulus (or of the first formant for the vowel) and shifted to coincide with the physiological data at the curve minimum.

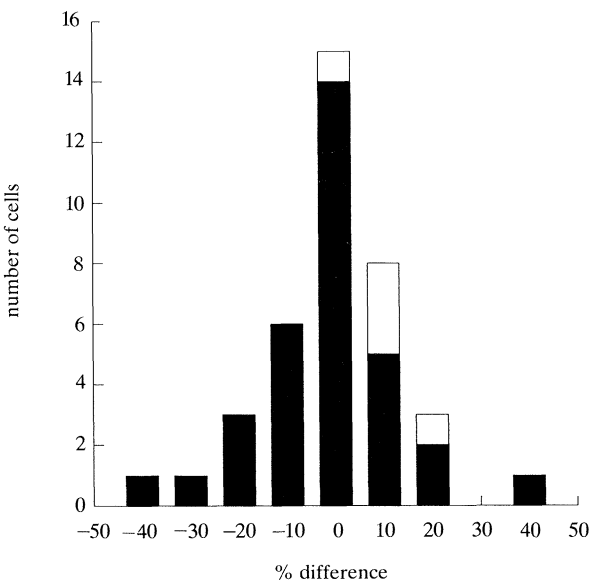

Figure 4. Histogram of the differences between the best delay of the cell to the masking noise and the noise delay producing the minimum masked threshold level. These differences have been expressed in terms of percent of the response period to the noise. The cells with inhibitory best delays are shown separately (clear bars). (Replotted from figure 5*b*, Caird *et al.* (1991).)

(*c*) *Measurements of masking within the signal interval*

The measurements of masking described above do not provide information about the mechanisms under-

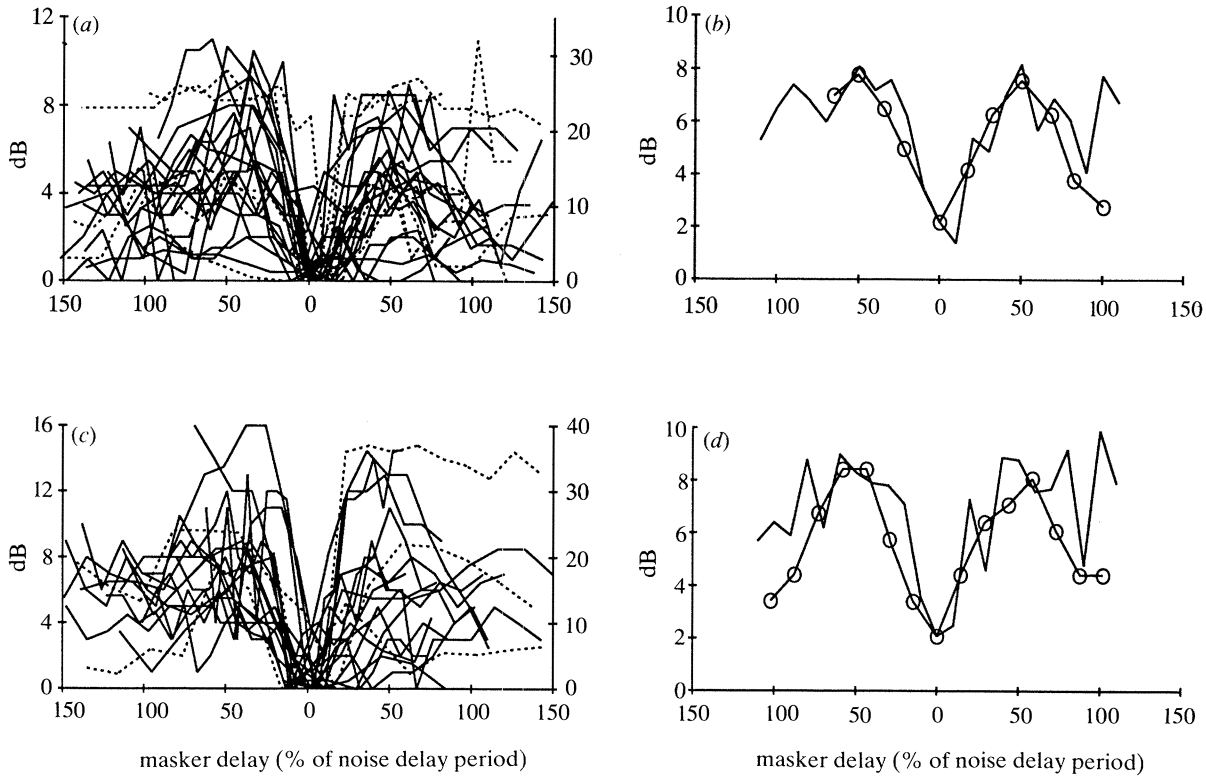

Figure 5. (*a*) The masked thresholds as a function of the masking noise delay for all the cells tested with BF tones ($n=25$); (*c*) shows similar data for those tested with the vowel stimulus ($n=19$). The second ordinate refers to the few cells which showed large variations in the masked thresholds (shown as the dotted lines). (*b*) and (*d*) show the average curves obtained from the data in (*a*) and (*c*) respectively computed at intervals of 10% along the abscissa. The open symbols in (*b*) and (*d*) show the psychophysical measures of BMLD (our own vowel data and tone data from Rabiner *et al.* (1966)) under similar conditions which have been scaled and shifted in the same way as the physiological data. (Replotted from figure 6, Caird *et al.* (1991).)

lying the masking, to do this we used a second paradigm. This paradigm is more akin to that which is naturally encountered, in that the level of the noise is constant as its delay is varied; equivalent to the masking of a signal by the same noise at progressively different azimuthal positions. The mean spike rate in the signal plus noise interval, may be a result of excitation by the masking noise and will not necessarily, therefore, be a reliable indicator of the degree to which the noise masker has disrupted the responses to the signal. By using a synthetic vowel we were able to use a single signal irrespective of the best frequency and exploit the ability of collicular neurons to phase-lock to the fundamental of such complex sounds (see Palmer *et al.* 1990) to distinguish the responses to masker and signal.

We have completed the analysis of spike rate and synchronization to a vowel signal on 18 neurons. In nearly all cases, when the masking noise was present, irrespective of its delay, the response to the vowel was reduced, whether assessed in terms of the mean or the synchronized discharge rate. In figure 6 we plot both the mean and the synchronized rates for two cells. For the analyses shown in figure 6*a* the signal (indicated by the arrow) was presented at best delay and the delay of the noise masker varied. For the cell in figure 6*a*, the rate synchronized to the F_0 (triangles) is lowest for noise delay values close to the noise best delay. As the noise delay is moved away from its best delay, the synchronized rate first increased and then decreases. The synchronized rate function thus approximates a mirror image of the noise delay function (dashes and squares in figure 6). For this cell, therefore, masking, assessed from the synchronized rate, changes in the same direction as the masked thresholds described above.

The data shown in figure 6*b* are from a cell characterized by delay-dependent inhibition. For this cell the signal was located (as shown by the arrow) to evoke activity against which masking could be evaluated. The cell response is so strongly inhibited when the noise is presented at its 'best delay' that both the mean discharge rate and the synchronized rate are lowest at the minimum in the noise delay function. This is consistent with the cell shown in figure 6*a*, but now the most effective masking of the signal does not occur when the noise and signal have the same interaural delay. The change in the cell response is in the opposite sense to the BMLD.

Data from all the cells that we tested with this second paradigm are shown in figure 7. As in figure 5, to emphasize the similarities in the responses, we have eliminated the variation due to differences in the cells' best delay and response frequency. The degree to which the discharge rate was altered by the noise masker varied between neurons (23–100%), on

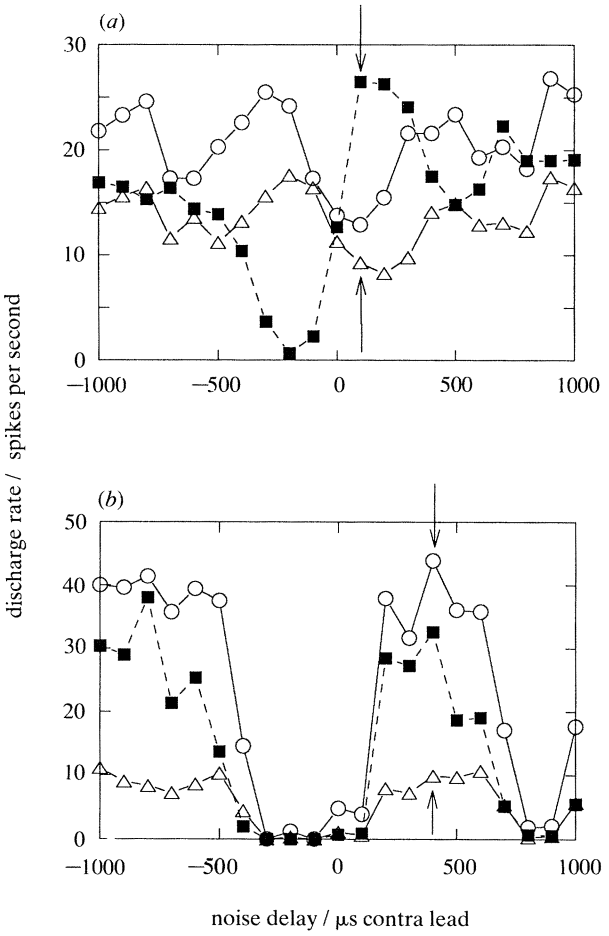

Figure 6. The continuous curves in (*a*) and (*b*) show the mean discharge rate (open circles) and discharge rate synchronized to the fundamental (100 Hz) of the vowel /a/ (open triangles) as a function of the interaural delay of a continuous wideband masking noise. The dashed curve shows the mean discharge to the noise alone. The BFs of the cells were 1500 Hz (*a*) and 990 Hz (*b*). The vowel signal was positioned as indicated by the arrow and at 64 and 54 dB SPL in (*a*) and (*b*) respectively. The level of the noise was adjusted to just completely mask (by audio-visual assessment) the response to the vowel when it was at the best delay (28 dB SPL spectrum level in both cases). (Replotted from figure 7, Caird *et al.* (1991).)

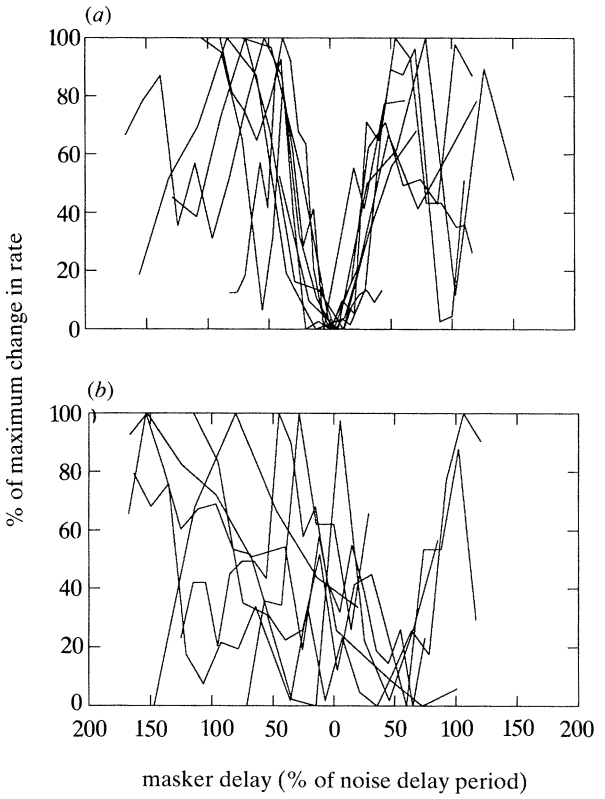

Figure 7. (*a*) Discharge rate synchronized to the F_0 of the vowel versus masker delay for nine cells showing responses like those in figure 6*a*. These data have been normalized for differences in (i) the degree of discharge rate modulation; (ii) the period of the cyclic delay sensitivity, and (iii) the best delay. (*b*) The rate synchronized to F_0 as a function of the masker delay for the remaining seven cells which did not show minima in this response measure at the best delay of the masking noise. (Replotted from figure 9, Caird *et al.* (1991).)

average the response measures changed by 50%. In figure 7, the changes in the synchronized discharge rate as the noise delay is varied are plotted for 16 cells. In figure 7*a* we have grouped together those responses which showed maximum reduction in the synchronized rate when the noise was at its best delay. The responses of the cells in figure 7*a* have maxima near ±50%. In other words, the synchronous discharge is maximally reduced when the masker is at its best delay and least reduced when the masker is separated by one half cycle of the noise delay functions; an effect that corresponds to the majority of the masked threshold measurements described above. The functions from the rest of our sample are shown in figure 7*b*. The only feature common to these functions is the minimum near the half cycle; the maxima of these curves are widely distributed and appear to bear no obvious relation to the noise delay function.

4. DISCUSSION

(*a*) *Delay sensitivity*

The shapes of the interaural delay functions in the guinea pig, and the positions of their peaks, are very similar to those in the cat (Kuwada & Yin 1983; Yin *et al.* 1986). Indeed, a comparison between our data and those available for other animals shows no significant species differences (rabbit: Aitkin *et al.* 1972; Kuwada *et al.* 1987; kangaroo rat: Moushegian *et al.* 1971; Stillman 1971; barn owl: Moiseff & Konishi 1981). This remarkable similarity of IPD interactions, even across vertebrate classes, strongly suggests that these effects are general rather than species-specific and are a reflection of the physiology of a binaural processing system common to all animals, as has been suggested by other authors (Phillips & Brugge 1985).

(*b*) *Comparison of single unit masking with human* BMLD *measurements*

In any detection task the decision will be made using those neurones which provide the most advan-

tageous signal-to-noise ratio. We have deliberately optimized the BMLD configuration for each cell by using signals placed at the best delay and at a sound level evoking a good response. For any specific BMLD condition there should be a population of cells whose binaural characteristics are optimal for the sound level and interaural delay of the signal. Thus the pooled data in figure 5 may be taken as an indication of the average masking effects which can be detected in the population of cells which have binaural properties matched to the signal.

If we are assessing the responses of a population that is involved in encoding the BMLD, the masking level differences in our study should show a dependence on the stimulus parameters similar to that in the equivalent psychophysical data. Large BMLDs for sinusoids are limited to below 1.5 kHz in humans (see Durlach & Colburn 1978, figure 50). The delay sensitivity of collicular neurons is similarly limited in the guinea pig and other animals, although in the cat behavioural BMLD measures remain large up to 1.5 kHz (Wakeford & Robinson 1974). In human psychophysics, when single sinusoids are masked by wideband noise with different interaural delays, the maximum magnitude of the BMLD is frequency-dependent, with a value of approximately 10 dB at 500 Hz, falling to about 5 dB below 200 Hz and above 1000 Hz (Durlach & Colburn 1978, figure 57). The mean value in our pooled data (figure 5*b*) is 6.8 dB which falls within the range of values found in humans. Our single cell measures of the masking level difference did not, however, correlate with the frequency of the tone signal. Our own psychophysical data gave a BMLD magnitude for the vowel masked by noise of 7.3 dB. This compares with a value of 6.9 dB in the pooled neuronal data which we obtained using the vowel as the signal (figure 5*d*).

In psychophysical data the masked threshold cycles as the noise delay is varied. Although such cycling was sometimes evident in the masked thresholds obtained from single neurons (figure 3) it is notably absent from the pooled data obtained with either tone or vowel signals. This is because the masking reflects the noise delay function, which for most neurons is not cyclic (Yin *et al.* 1986; Palmer *et al.* 1990).

Many cells (32%) failed to show delay-dependent masked thresholds, despite being sensitive to the interaural delay of the noise. Carney & Yin (1989) have demonstrated that individual cells, among those sensitive to interaural time delay, fall on a continuum in respect of the strength of the excitatory and inhibitory inputs that they receive from each ear. The cells in the present study that were sensitive to interaural delay and yet showed no BMLD effects, may have levels of excitation and inhibition that are a variable function of delay. The combined effect of these two processes may result in a masked threshold independent of masker delay.

BMLDs can be demonstrated using continuous signals and maskers. Under such masking conditions a comparison between masker alone and masker plus signal is not available within the activity of a single neuron. Our use of a synthetic vowel has allowed the study of information which relates specifically to the signal and not the noise. The data obtained using this measure show that the degree to which the synchronized response to the vowel is disrupted depends upon the delay sensitivity to the noise. We have shown that both mean rate and temporal patterning of the discharge of a unit are affected by the interaural delay of the masking noise. Although we cannot quantify these changes to allow direct comparisons with psychophysical data, in most of our sample they are in a direction consistent with the BMLD.

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