Temporal Damping in Response to Broadband Noise. I. Inferior Colliculus

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Submitted 15 September 2004; accepted in final form 30 November 2004

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Temporal damping in response to broadband noise. I. Inferior colliculus. J Neurophysiol 93: 1857–1870, 2005. First published December 8, 2004; doi:10.1152/jn.00962.2004. Many cells in the inferior colliculus (IC) are sensitive to interaural time differences (ITDs), in the form of an oscillatory dependency of average firing rate on ITD. We studied the degree of damping in such binaural responses, recording from neurons in the inferior colliculus of pentobarbital-anesthetized cats to binaural broadband noise and tones. Noise-delay (ND) functions and composite curves were characterized by computing the difference between responses to correlated and anticorrelated stimuli. We use a new metric, based on the envelope of this difference, to quantify damping. There is a clear relationship between damping and characteristic frequency (CF), but even neurons of the same CF can differ in their damping. For individual cells, damping can be stronger to tones or to noise; at the population level the two are positively correlated and are scarcely affected by SPL. The frequencies that dominate ITD sensitivity are near the CF in response to noise, but are often below CF in response to tones. These findings qualify conclusions from earlier reports but overall they support the conclusion that, at a population level, basic aspects of binaural responses to wideband noise are consistent with summed responses to pure tones.

INTRODUCTION

Despite the oft-stated fact that mammalian auditory systems did not evolve to deal with pure tones, these stimuli are still pervasive in auditory research. Binaural physiology is no exception: characterizations of binaural temporal processing make extensive use of pure tones, following the lead of pioneering studies by Goldberg and Brown (1969) and Rose et al. (1966). This is somewhat of an anomaly for several reasons. First, in various ways, binaural performance is poorer with pure tones than with broadband signals (Blauert 1983). Second, complex stimuli may allow a better dissection of the binaural system, as demonstrated by psychophysical studies (Kohlrusch 1988; van der Heijden and Trahiotis 1999). Third, it is to be expected that nonlinearities in the cochlea, and in the subsequent processing of the cochlear output by the CNS, preclude simple predictions of responses to nontonal stimuli from tonal responses. Thus there are several reasons to suspect there is much to be gained from binaural studies with broadband stimuli.

The first systematic study of responses of low-frequency binaural cells to broadband noise was the elegant series of experiments by Yin and colleagues (Chan et al. 1987; Yin et al. 1986, 1987). As first shown by Geisler et al. (1969), the noise-delay (ND) functions of such cells [i.e., graphs of average response rate as a function of interaural time delay (ITD)] typically have a damped oscillatory shape and Yin and colleagues argued that this basic shape is consistent with the known cochlear properties of band-pass filtering, phase-locking, and rectification, followed by a stage of coincidence detection or cross-correlation. In those and subsequent studies, the focus has generally been on the features of the ND function near the central peak or trough. Little effort has been directed toward a quantification of the damping of ND functions; this is the first goal of the present series of experiments. Our motivation to look into damping is partly the observation that cells with the same characteristic frequency (CF: frequency of lowest threshold) can differ in the number of cycles visible in their ND function. Moreover, Yin et al. (1986) reported a lack of correlation between damping and spectral bandwidth. These observations suggest that other factors than the damping of the monaural inputs are reflected in the damping of binaural responses and that the study of damping may thus provide insights in the process of binaural integration.

A second issue relates to the important observation of Yin et al. (1986) that key features of the ND functions could be surprisingly well predicted from a linear summation of responses to pure tones, the so-called composite curves, which agreed well with ND functions in the location and width of the central peak. However, the behavior away from this central peak was often rather different between composite curves and ND functions, resulting in different degrees of damping and depth in their oscillation. On average the ND functions appeared less damped than the composite curves, but the opposite also occurred and there was little correlation at the population level in the damping to tones and to noise. There are reasons (see RESULTS) to suspect that the damping metric used by Yin et al. is affected by several factors unrelated to damping. In short, the relationship between tonal and noise responses merits reevaluation and a proper evaluation of this relationship requires a closer comparison with properties of the monaural stages preceding binaural interaction.

Our goal in this paper is thus two-fold: to quantify temporal damping in binaural responses, and to compare damping in responses to tones and to noise. In a subsequent report we will compare our results with measurements on the auditory nerve.

METHODS

Recording

Our methods for single-unit recording in the IC have been described before (Joris 2003). All procedures were approved by the University of Wisconsin Animal Care Committee and the K.U. The costs of publication of this article were defrayed in part by the payment of page charges. The article must therefore be hereby marked “advertisement” in accordance with 18 U.S.C. Section 1734 solely to indicate this fact.
Leuven Ethics Committee for Animal Experiments and were in accordance with the National Institutes of Health Guide for the Care and Use of Laboratory Animals.

Anesthesia was induced with a 1:3 mixture of acepromazine and ketamine and maintained for surgical preparation and recording with pentobarbital infused through a femoral vein. The animals were placed on a heating pad in a double-walled sound-attenuated chamber. The bullae were vented with a polyethylene tube. The IC was exposed anterior to the tentorium; some tentorium was removed in cases where it severely limited access to the IC. Sound stimuli were delivered dichotically with dynamic speakers (Supertweeter, Radio Shack, Arlington, TX) coupled to earbars that were tightly inserted into the cut ear canals. The stimuli were generated digitally with custom-built or commercial (Tucker-Davis Technologies, Alachua, FL) hardware and were compensated for the acoustic transfer function measured with a probe tube near the eardrum and a 12.7-mm condenser microphone (Brüel & Kjær, Nærum, Denmark). IC neurons were isolated with parylene- or glass-insulated tungsten electrodes. The neural signal was amplified, filtered, timed (1-μs resolution), and digitized with standard techniques. The dorsal border of the central nucleus of the IC was defined physiologically by the presence of background discharges phase-locked to binaural beats of low-frequency pure tones (Kuwada et al. 1979), and the IC was histologically processed to confirm the site of recording to the central nucleus.

**Stimuli**

CF was determined with a threshold tracking algorithm: this involved contralateral, ipsilateral, and/or binaural stimulation. Binaural, long-duration (typically 1 or 5 s, repeated every 1.5 or 6 s) tones bracketing CF were then sequentially presented at increasing frequency in linear steps. The range of frequencies was chosen to bracket the limits of the response area at the chosen sound pressure level (SPL); the step increment was chosen between 25 and 200 Hz to ensure adequate sampling. The tones to the two ears had a small (1 or 2 Hz) difference, forming a binaural beat (Kuwada et al. 1979). Typically the contralateral ear was at the higher frequency (positive beat) but the opposite (negative beat) was also often tested. The number of repetitions was typically between 1 and 10, and the SPL was 60 dB but occasionally other SPLs were tested as well. In initial experiments, only beat-sensitive neurons were further studied, but in later experiments all neurons whose response rate was modulated by ITDs of broadband noise were included, even if no phase sensitivity to pure tones was present (Joris 2003).

Independently generated pseudorandom noise tokens (lower cutoff 50 or 100 Hz; upper cutoff between 4 and 32 kHz, chosen to be well above CF) were presented in several pairwise combinations of the original and polarity-inverted waveforms (e.g., A/A, A/–A, A/B, etc., where A and B are independent noise tokens and where a minus sign indicates inversion of polarity) (see Joris 2003). These combinations result in ND functions to correlated, anticorrelated, and uncorrelated noise. Typical stimulus parameters (duration/repetition interval × number of presentations) were 1/1.5 s × 10 or 20, or 5/6 s × 3. The range of ITDs and step increment were chosen to appropriately characterize the shape of the ND functions. As illustrated by several examples in RESULTS, the range extended to ITDs where the average rates of responses to correlated, anticorrelated, and uncorrelated stimuli converged and were independent of ITD; the increment was sufficiently small to clearly outline the “fine structure” within the functions. To estimate these ITD parameters, a preliminary run with few stimulus repetitions was often obtained first. The stimuli were usually presented at a fixed attenuator setting throughout the experiment, equal for the two ears, which was on average 31 dB above threshold (measured in 89 neurons with a rate-level function to noise). If time allowed, data collection was repeated at several settings. We express the noise sound level as “effective SPL,” which is the power in a 1/3-octave frequency band geometrically centered at the CF of the cell, averaged for the two ears, and expressed in dB re 20 μPa. Effective SPL was calculated using the actual noise waveforms and calibration curves used during data collection.

**Analysis**

The analysis of binaural beat responses and construction of composite curves follows established methods (Kuwada et al. 1987a; Yin and Kuwada 1983b; Yin et al. 1986) and is briefly illustrated in RESULTS (Fig. 1). If a strong onset component was present, this part of the response, or the response to the entire first beat cycle, was discarded. Besides the conventional composite curve, we also constructed an anticorrelated composite curve, as illustrated in RESULTS. We use the generic term “ITD functions” to refer to both ND functions and composite curves.

To quantify damping, it is necessary to trace the dependency of the response on ITD. Yin et al. (1986) measured the amplitude of the peaks that straddled 0 ITD and defined the primary peak as the one closest to 0, i.e., the primary peak being the secondary peak. They then computed the ratio between the amplitude of the secondary to the primary peak, which we refer to as the peak ratio. In ND functions with little damping the two peaks tend to have equal amplitude, resulting in a peak ratio near 1. Unequal amplitudes lead to peak ratios less than or greater than 1 and indicate stronger damping. The peak ratio does not give a measure in the time domain, and makes use of only a few data points in each data set; it has several other disadvantages (see RESULTS), but we nevertheless used it on our data for comparison to the data of Yin et al.

Note that we use the term “damping” in a loose way as a descriptor of the spindle shape of ITD functions. This damping should not be equated with the more exact term referring to the decay in the step or impulse response of physical or even cochlear filters (e.g., Carney and Yin 1988), even though the latter decay is likely an important determinant of the damping of ITD functions.

The metric (further described in RESULTS) that we developed to measure damping uses a comparison of responses to correlated and anticorrelated stimuli to define a response envelope as a function of ITD. Because such responses were obtained sequentially rather than interleaved, and because IC neurons in our preparation can show slow drifts in their excitability, the two sets of responses were normalized to their respective overall mean firing rate, and multiplied by the geometric mean of these two averages. Thus in effect firing rates were rescaled as follows

\[ y^p(\text{ITD}) = y^p(y^c) = \frac{y^p_1(\text{ITD}) / y^c_1(\text{ITD})}{y^c_1(\text{ITD})} \]

where \( y^c_1 \) and \( y^p_1 \) are the firing rates at different ITDs in response to correlated and anticorrelated noise; \( y^c_1 \) and \( y^p_1 \) are the corresponding rescaled firing rates; and \( y^c_2 \) and \( y^p_2 \) are the overall mean firing rates averaged over all ITDs in the responses to correlated or anticorrelated noise. After rescaling, \( y^p_2 = y^c_2 = (y^p_0 / y^c_0)^{1/2} \). Finally, at each ITD the response to anticorrelated noise was subtracted from the response to correlated noise (Joris 2003), and we refer to this difference as the “difcor.” Many examples of difcors are shown in subsequent figures.

An important feature of ND functions and composite curves is the frequency of oscillation. We define the dominant frequency (DF) as the maximum in the spectrum of the difcor, calculated with a fast Fourier transform. DF and CF were used for semiautomatic determination of the relevant peaks of an ITD function, required to calculate its peak ratio. First, the local maximum located at ITDs approximately CF−1 or DF−1 (i.e., one period of the characteristic or dominant frequency) above or below the primary peak was identified, keeping the requirement that the peaks straddle 0 ITD. Whether CF or DF was the better choice was determined by visual inspection. For composite curves, use of the DF was adequate in nearly all cases. However, for
ND functions, CF was usually the better choice, especially at mid-CFs of a few kilohertz, where envelope components increasingly dominate the ND functions but not the composite curve.

RESULTS

In the first two sections we report results with an analysis that largely follows that of Yin et al. (1986). We then extend the analysis and develop a new measure of damping for both composite curves and ND functions.

Composite curves and responses to noise in the IC

Figure 1 illustrates the different steps involved in the construction of a composite curve. Figure 1A shows the response rates to binaural beat stimuli at different frequencies, averaged over the entire stimulus duration. The firing rate, averaged over the entire stimulus duration, reaches a maximum at 500 Hz. In phase-sensitive cells, the response to the binaural beat is modulated at the beat frequency, as illustrated for two frequencies in Figure 1, B and C. In these period histograms, the instantaneous firing rate is graphed as a function of the interaural phase difference (IPD; i.e., the phase difference between the tone to contra- and ipsilateral ear). As was extensively documented by Yin and Kuwada (1983a), these period histograms generally agree very well with the responses to tones for which the ITD is changed discretely. Figure 1D again graphs the period histograms but now on an abscissa of ITD, by multiplying IPD by the stimulus period, and periodically extended and superimposed for all stimulus frequencies. Finally, averaging of all curves in Fig. 1D yields the composite curve (Fig. 1E). This curve gives a linear prediction of the response that would be obtained if all frequency components were presented simultaneously, as a function of ITD, and thus a prediction of the ND function. In contrasting the composite curve with the ND function, we will often refer to the composite curve as the “response to tones.” Figure 1F shows the actual ND function. For this neuron there is a good correspondence between the two curves in the location of the central peak (the best delay) and its width, consistent with the observations of Yin et al. (1986) on a large sample of IC neurons. The two curves differ, however, in their damping: the ND function shows several smaller peaks on either side, whereas the composite curve reaches a steady firing rate at ITDs that differ only a few milliseconds from the best delay.

Damping quantified with the peak ratio

Measurement of damping with the peak ratio is illustrated in Fig. 1, E and F (circles joined by solid line). For the cell illustrated, the peak ratio is smaller for the composite curve (E) than for the ND function (F), consistent with the fact that the composite curve is more damped than the ND function. Figure 2A compares the distribution of the peak ratios for ND functions (abscissa) and composite curves (ordinate) for a sample of 108 IC cells, all with CF < 3 kHz, plotted as in Yin et al. (1986). The relationship shows only a weak (r = 0.41) but significant (P < 0.001) trend of correlation with the majority (69%) of data points below the diagonal of equality, indicating the general bias of composite curves being more damped than ND functions. The distribution is very similar to the sample reported by Yin et al. (1986; their Fig. 7C: r = 0.38, n = 72, 65% of data points below diagonal). In our data, the scatter in the vertical dimension is less than that in the horizontal dimension, indicating that the range of peak ratios is more restricted for the tonal responses than for the responses to...
noise; this is somewhat less the case for the data of Yin et al. For some cells Fig. 2A shows two measurements, based on positive beats (open circles) and negative beats (filled circles) and joined with a vertical line, to illustrate the repeatability of the measure.

The low correlation of peak ratios in Fig. 2A suggests large differences in the degree of damping between tones and noise, but there are several reasons to suspect that this is partly a result of the metric used. Several features of ITD sensitivity are expected to affect the size of the peak ratio without affecting damping per se. Figure 3 (heavy lines) shows examples of noise-delay functions (column A) and composite curves (column C) for 3 cells (3 rows). The circles indicate the primary and secondary peaks. Some ITD functions show a prominent central trough rather than peak (e.g., ND function in Fig. 3A, top row; composite curve in Fig. 3C, 2nd row), and in such cases the peak ratio underestimates damping because the trough is usually flanked by peaks of similar amplitude. The tendency of the composite curve to show a central trough or peak can be measured with the characteristic phase (CP), obtained through a phase analysis of the response to binaural beats (Yin and Kuwada 1986). Neurons with a CP near 0 or 1 show central peaks, whereas those with a CP near 0.5 show central troughs. Figure 2B shows the composite curve peak ratio as a function of CP for all available data sets. Indeed, binaural beat responses with a CP near 0.5 tend to have large peak ratios in their composite curves (Fig. 2B), and this is also the case for the ND functions obtained from the same cells (not shown). Note that this relationship is much clearer than the correlation in Fig. 2A.

Another problem in the quantification of damping is that with increasing CF, envelope contributions increasingly dominate ITD sensitivity to noise (Joris 2003), but not to tones, because of the absence of envelope fluctuations in pure tone stimuli. For example, the peak ratio of the ND function of the third cell in Fig. 3 (column A, row 3) is strongly affected by a central mound of activity in both the correlated and anticorrelated functions, which is absent in the composite curves (column C) and results in very different peak ratios. A third problem is that cells also differ in the baseline response rate of their ITD functions. Some ITD functions have a high baseline and the modulation of response rate with ITD is small relative to this baseline (for an example, see Fig. 11, E and H). The presence of a high baseline should not affect the measurement of damping, yet it will increase the peak ratio. Finally, ITD functions are often asymmetrical and the designation of secondary peaks is rather arbitrary (e.g., Fig. 3A, row 2), so that slightly different criteria would result in quite different peak ratios.

The concerns expressed above may be minor to the extent that the analysis addresses comparisons within IC neurons of the response to tones and noise and the sample does not include responses dominated by envelope components (Yin et al. 1986). However, our ultimate goal is to compare IC responses over a wide range of CFs with their monaural inputs, using autocorrelograms (Joris 2003). Such autocorrelograms are always symmetrical around 0 delay and always have central peaks. We therefore developed a damping metric that is less affected by the above factors.

Damping quantified with difcors

The response feature of interest is not so much response rate at different ITDs per se, but rather the extent to which this rate can be influenced by binaural changes in fine structure. We systematically obtained the response to opposite polarities of correlation. Figure 3A illustrates ND functions to correlated (heavy line) and anticorrelated noise (thin line) for 3 cells. As first shown by Yin et al. (1987), the response to anticorrelated noise, obtained by inverting the noise in polarity at one ear, causes an inversion of the ND function. Next, we followed the procedure of Joris (2003) and subtract the two kinds of ND functions from each other point by point (Fig. 3, column B). After subtraction, only the oscillating component, which reflects ITD sensitivity arising from fine structure, remains. We refer to this difference as the “noise difcor.” This procedure removes ITD sensitivity arising from envelope components, which are insensitive to waveform polarity. For example, the

![Figure 2](https://example.com/figure2.png)

**Fig. 2.** A: comparison of peak ratio for ND functions (abscissa) and composite curves (ordinate). Dashed line is the diagonal of equality; solid line is linear regression. n = 126 from 108 IC neurons. Open and closed circles joined by a vertical line are measurements from the same cell to positive and negative beats (symbols and lines often overlap and then appear as a single closed circle). In such cases the peak ratio from the response with the lowest discharge rate (closed circle) was ignored in the calculation of the regression and statistics stated in RESULTS. Included in the statistics but not shown are 7 data points with peak ratios >1.4. Average suprathreshold levels were 38 dB for tones and 34 dB for noise. B: peak ratio of the composite curve as a function of the characteristic phase (CP) of the cell, for all binaural beat data available (n = 338), from a total of 274 IC neurons. Sign of the binaural beat was not taken into account in the CP calculation; 2 points with peak ratio >1.4 are not plotted.
central mound of activity in the ND functions of Fig. 3A (3rd row) is not present in the difcor (Fig. 3B).

The difcors generally show spindle-shaped oscillations that are better fit for calculation of damping than the original ND functions. The envelope of the difcor is calculated from the complex analytical function obtained from the difcor and its Hilbert transform (Hartmann 1997), and is smoothed with a moving Hanning window of width DF/1.0^2. These smoothed envelopes are superimposed on the difcors in Fig. 3B. Finally, the envelope half-width (i.e., width at half-height) is measured, henceforth referred to as HWND.

The same procedure was followed in the analysis of the composite curves, except that construction of the anticorrelated composite curve did not involve the collection of additional data. In the binaural beat stimulus, the tones in the two ears start at the same phase, and responses to an “anticorrelated” condition could have been obtained by collecting responses to a beat in which the tones started in antiphase. Rather, we simply shifted the spiketimes of the responses to binaural beats by half a beat cycle, and then constructed a composite curve in the usual manner. Examples are shown in Fig. 3C. Again, the composite curves for correlated and anticorrelated conditions are then subtracted, yielding the “tone difcor” (Fig. 3D). These difcors also have a spindle-shaped envelope, obtained with the Hilbert transform, from which a half-width (HW_{CC}) is calculated. Note that some noise difcors are asymmetric (Fig. 3, rows 1 and 2), in that the envelope is steeper on one side than on the other.

Examination of the ND functions and noise difcors of the 3 cells illustrated (Fig. 3, A and B) reveals clear differences in damping, HWND being several milliseconds in rows 1 and 2, but <1 ms in row 3 (note the differences in scaling of the abscissa). The composite curves of the same cells also show differences in damping but the ordering in size of HW_{CC} is different. For the cell in row 1, HWND and HW_{CC} are about equal; for the cell in row 2, HWND > HW_{CC}; and for the cell in row 3 HWND < HW_{CC}.

Because we ultimately want to compare binaural responses with autocorrelograms of neurons in the monaural input pathway, the strongest conclusions can be drawn if the IC sample is restricted to responses that show key time-domain resemblances to monaural neurons. Damping was measured only on those difcors that could be characterized as a damped oscillation (i.e., an alternating series of peaks and troughs that wax and wane in amplitude as a function of ITD with a spindle-shaped envelope). Some neurons (about 5%) showed idiosyncratic responses for which damping could not be measured and that were excluded from further analysis. The ND functions of the neurons in Fig. 4 show an oscillatory component that is suppressed over the central range of ITDs, where the largest responses are expected. The resulting difcors are not spindle-shaped and were therefore unfit for our analysis. For some of...
these neurons the tonal data still resulted in spindle-shaped dicsors and were included in the further analyses.

Damping measurements to both noise and tones are compared for 87 measurements on 73 neurons in the scatter plot of Fig. 5. We included only neurons for which the maximal response rate to the ND function or to the binaural beats (as in Fig. 1A) was >10 spikes/s, and for which CF was <3 kHz because at higher CFs the contribution of fine structure becomes negligible. Figure 5 shows a significant correlation, which is higher \((r = 0.65)\) than is the case for the peak ratio (Fig. 2A). Moreover, in contrast to the distribution for the peak ratio, there is no clear bias toward a larger number of data points below the diagonal (52%). The total range of half-widths is larger for ND functions than for composite curves, and the general relationship is tilted relative to the diagonal of equality, as illustrated by the regression line. For cells with larger half-widths the HW tends to be smaller (stronger damping) to tones than to noise, whereas for cells with smaller half-widths the opposite tends to be the case. As in Fig. 2A, for some cells two measurements are shown but only one value (from the response with the highest discharge rate) was used in the calculation of the correlation and regression.

**Relationship of damping to CF**

The half-widths in ND functions vary over roughly one order of magnitude (Fig. 5), and the most straightforward explanation for this is spectral bandwidth. In peripheral neurons, spectral bandwidth tends to increase with CF and SPL. To the extent that binaural properties are determined by monaural input properties, damping of ITD sensitivity would therefore be expected to increase with CF and SPL.

Figure 6 shows dicroit half-widths of responses to noise (A), tones (B), and their ratio (C), as a function of CF. The inverse relationship between half-width and CF in Fig. 6, A and B is qualitatively consistent with peripheral physiology because the bandwidth of cochlear filters increases with CF. Perhaps more surprising is the large range of half-widths at any given CF, particularly in response to noise. To fully appreciate this range, it is illustrated in Fig. 7 with ND functions for a sample of neurons with CF near 500 or 1,000 Hz. Three examples, ordered to increasing half-width from top to bottom, are shown for each CF range [other examples at these CFs are also shown in Fig. 3, top row (590 Hz), and middle row (1,090 Hz)]. The half-widths range from 2.2 to 7.9 ms at CFs near 500 Hz (Fig. 7B), and from 0.8 to 4.4 ms near 1,000 Hz (Fig. 7D).

Damping to the two kinds of stimuli is again compared in Fig. 6C, which shows the ratio between half-widths (HW\text{CC}/HW\text{ND}) as a function of CF. Data points below the horizontal dashed line also fall below the diagonal of equality in Fig. 5. There is a weak tendency for a preponderance of data points below the horizontal at low CFs and above it at mid-CFs. Thus Figs. 5 and 6 can be summarized as follows: half-widths are larger at low CFs than at mid-CFs, and tend to be larger for noise than for tones at low CFs and larger for tones than for noise at mid-CFs.
Dependency on SPL

An increase in damping (decrease in HW) in ITD functions with SPL is expected based on the increase of spectral bandwidth of cochlear filters with SPL. We did not routinely obtain data over an extensive range of SPLs. Figure 8 shows half-width measures for all neurons for which measurements were available at two SPLs or more. The data to noise (Fig. 8A) generally lack a strong SPL dependency. The data for tones (Fig. 8B) are very limited, but seem to indicate a similar lack of SPL dependency in HWCC except possibly at the lowest SPLs tested.

Figure 9 shows examples of ND functions and difcors for the two neurons, identified with filled symbols in Fig. 8, which showed the strongest SPL dependency to noise (columns A and B) and tones (columns C and D). The firing rate in the ND functions on the left is nonmonotonic with SPL, being highest at an effective SPL of 55 dB (45 dB above threshold). With increasing SPL, the peak at the best delay diminishes proportionally less than the other peaks, resulting in a narrower half-width at high SPL. In the tonal responses for the neuron on the right, average rate increases monotonically with SPL, but the composite curves and difcors become increasingly complex and deviate from a spindle shape at the highest SPL (for which a half-width cannot be computed). This complexity was accompanied by phase shifts in the beat responses at individual carrier frequencies, causing nonmonotonic phase–frequency relationships (not shown).

Relationship between CF and DF

So far, we have analyzed the envelope of difcors without paying attention to the fine structure within the temporal envelope, and data as shown in Fig. 9 draw attention to the fact that this fine structure can be complex. Detailed study of the fine structure and a comparison between ND functions and composite curves touches on issues outside the scope of this paper, and we restrict ourselves to a single simple question that is important to interpret the data shown so far: how do the DFs of the difcors to tones and to noise compare with CF?

In Fig. 10, DF population data for difcors obtained from ND functions (Fig. 10A) and from composite curves (Fig. 10B) are compared with CF. The relationship is strikingly different for the two types of stimuli. The CF is reasonably consistent with the DF to noise (Fig. 10A), up to the highest CFs where it can be calculated (i.e., where enough fine structure remains in the difcor), although for CFs above approximately 1,500 Hz DF is systematically lower than CF. In contrast, the DF to tones (Fig. 10B) is strongly biased away from the diagonal of equality, already for CFs <1,000 Hz. This also holds for neurons for which both measures were available (Fig. 10D): DF to tones was smaller than the DF to noise for the vast majority of cells. The DF to noise showed very little dependency on SPL (Fig. 10C): only for 2 cells with CFs >2 kHz, for which the ND function is dominated by envelope, is there a noticeable decrease in DF with SPL.

Figure 11 illustrates the difference in DF for tones and noise for one representative neuron. The tuning curve (A) shows that its CF is 1,900 Hz. However, the response to binaural beats evokes the strongest response at 1,200 Hz, both in terms of rate (B and D) and synchronization (C and D). The composite curves (E) and difcor to tones (F) give a half-width of 1.2 ms, and the power spectrum of the difcor to tones (G) peaks at 1,100 Hz. The ND functions (H) differ from the composite curves in the presence of a central mound of activity in both the response to correlated and to anticorrelated noise, and by the higher-frequency fluctuations in the fine structure. The half-width of the difcor (I) to noise is identical to that of tones (1.2 ms), but its power spectrum peaks at 1,700 Hz (J). Note moreover that the phase of the fine structure within the difcor envelope is very different for tones and noise: the peak of the fine structure coincides with the peak of the envelope in the difcor to noise, but is clearly asymmetrically placed in the difcor to tones.

Discussion

Most physiological binaural studies have focused on the central portion of ITD functions, such as the location of the central peak or trough, the slopes of these features, and so forth. This is of course justified because the features of ITD

FIG. 6. Damping as a function of CF. Half-widths of difcors obtained ND functions (A) and from composite curves to tones (B). C: ratio of half-widths to tones and noise. Values were included only if the maximal discharge rate exceeded 10 spikes/s. Each symbol represents one neuron (n = 126 in A, 167 in B, 65 in C).
functions within the physiological range of ITDs are most important for the response of these neurons in natural environments and thus most relevant behaviorally. Much less attention has been devoted to the damping of these functions. We studied this damping because it may yield information about the binaural integration process. We devised a new metric to measure damping as a function of interaural delay in IC neurons, in responses to tonal stimuli and to broadband noise. The main findings are as follows. IC neurons show a considerable range of damping (Figs. 5–7). This damping depends on CF (Fig. 6), but even neurons of similar CF can differ considerably in their damping (Figs. 6 and 7). At the population level, damping to noise did not show a systematic dependency on SPL (Fig. 8A) and was not systematically biased relative to tones (Figs. 5 and 6C). There is a positive correlation between the damping to tonal stimuli and to noise (Fig. 5). The frequencies dominating ITD sensitivity are near CF in response to noise, but are often much lower than CF in response to tones (Figs. 10 and 11).

What determines damping?

Many factors potentially affect damping. These factors can be grouped as peripheral, olivary, and supraolivary. The damping of ND functions presumably reflects to a large extent the binaural bandwidth, by which we mean the spectral bandwidth over which stimulus fine structure at the two ears is compared. Narrow binaural bandwidths would be expected to generate strongly oscillatory ND functions, whereas broad binaural bandwidths should generate strongly damped ND functions. This binaural bandwidth is in turn presumably mostly determined by the bandwidths of the structures that form the monaural chain supplying the signals to the binaural integrator, i.e., the bandwidths in cochlea, auditory nerve, and bushy cells: these are the peripheral factors.

As discussed more fully below, in the auditory periphery temporal damping or decay increases with CF; likewise, temporal damping increases with CF in IC neurons (Fig. 6), from which we conclude that the damping of peripheral neurons is at least a contributing factor to the damping of binaural neurons. However, several observations in this study show that additional factors must be involved. The range of damping in the IC is large (Figs. 6A and 7), spanning approximately a four-fold change at CFs of 500 and 1,000 Hz. This range is probably larger than can be accounted for by the range of damping in monaural afferents, although this needs to be examined quantitatively in the latter neurons. Also, some ND functions show

FIG. 7. Examples of ND functions and dicros for neurons with CFs near 500 Hz (columns A and B) or 1,000 Hz (columns C and D). From top to bottom: CFs, effective SPLs, and dicro half-widths were (Hz/dB/ms) (A and B): 560/62/2.2, 455/40/3.6, 476/49/7.9; (C and D): 951/60/0.8, 1,045/50/2, 951/74/4.4. For 3 cells, the response to uncorrelated noise is also shown (A and C: thin, nonoscillatory line).
has been proposed that excitatory inputs of different CF con-

vergence on bushy cells without increasing their spectral band-

width because they behave as coincidence detectors (Carney 1990). On the other hand, some onset cells in the cochlear nucleus have wide spectral bandwidths, which has also been attributed to a coincidence-detection mechanism (Palmer et al. 1995). The binaural integrators (MSO neurons), and possibly also their primary excitatory inputs (bushy cells), behave as coincidence detectors, and it is plausible that the ipsi- and contralateral afferents to individual MSO neurons may be asymmetric in some property (numbers, CFs, synaptic strength). Whether and how all these factors may influence damping have not been explored in computational models of MSO cells, which invariably have used matched excitatory and inhibitory and ipsi- and contralateral inputs (e.g., Brughera et al. 1996). Again, availability of MSO recordings would constrain the different possibilities listed above.

An interesting feature of some noise difcors (Fig. 3B, rows 1 and 2; Fig. 9B), which may be related to such olivary factors, is their asymmetry along the ITD dimension so that they are steeper, say, at positive ITDs (contralateral ear leading) than at negative ITDs. A possible explanation for this asymmetry is a difference in decay of the impulse responses of ipsi- and contralateral afferents. If the impulse responses of these afferents have short rise times and slower decay times (see next section), and the decay is longer on the contralateral side than on the ipsilateral side, an asymmetric difcor will result with slow tapering at ITDs where the contralateral ear leads (i.e., at positive ITDs, e.g., Fig. 3B, row 1). A shorter decay on the contralateral side will result in an asymmetry as in Fig. 3B, row 2.

Finally, even though we surmise that binaural bandwidth is a major determinant of the damping measured here, we caution that the present measurements do not constitute a direct measure of binaural bandwidth. We have presented preliminary results (Massie et al. 2003) using a method in which a spectral measure of binaural bandwidth is obtained (Kohlrausch 1988), and from which we also concluded that factors in addition to the bandwidth of monaural afferents can contribute to binaural bandwidth.

Dependency on CF and SPL

Damping in the IC is strongly dependent on CF (Fig. 6), which is to be expected in view of the properties of the monaural neurons in the afferent chain to the binaural integrators. For example, early studies of auditory-nerve responses to clicks indicate that temporal damping increases with CF (Kiang et al. 1965; Pfeiffer and Kim 1972). Low-CF nerve fibers respond with multiple modes of activity of decaying amplitude. With increasing CF, the number of modes increases, consistent with increasing sharpness of tuning (i.e., smaller bandwidth relative to CF). On the other hand, with increasing CF the decay becomes faster (i.e., more damped), consistent with the increasing absolute spectral bandwidth. Similar behavior is revealed by responses to noise, as shown by reverse-correlation studies (Carney and Yin 1988; De Boer and de Jongh 1978; Evans 1977) and autocorrelation analysis (Louage et al. 2004; Ruggero 1973). It is unclear whether there is quantitative agreement in the increase in damping with CF between binaural neurons and their monaural afferents. We will examine this
issue in a subsequent paper by applying the analysis presented here to autocorrelograms of auditory nerve fibers.

Using the reverse-correlation technique, an increase in spectral bandwidth and a decrease in damping have also been reported with increasing SPL in the auditory nerve (Carney and Yin 1988; De Boer and de Jongh 1978; Evans 1977). In contrast, SPL has surprisingly little effect on the overall shape of ITD functions of low-CF neurons (Pen˜a et al. 1996; Yin et al. 1986), and an increase in damping with SPL is not convincingly present in the binaural noise data presented here (Fig. 8A). However, again, before concluding that this is inconsistent with the peripheral changes, the damping metric used here needs to be applied to responses from these monaural inputs.

Comparison of damping to noise and to tones

Using the peak ratio, Yin et al. (1986) found a low correlation between damping to noise and to tones, and the authors emphasized the bias toward stronger damping in composite curves than in ND functions. Using their metric, our observations agree (Fig. 2A), although an improved metric reveals a higher correlation between damping to noise and tones and also makes the overall bias just mentioned disappear (Figs. 5 and 6C). At face value these findings, combined with the lack of systematic change in half-width with SPL, offer even stronger support for the general conclusion of Yin et al.: binaural responses at the level of the IC behave surprisingly linearly; that is, there is a basic consistency in the shape of the response to a broadband stimulus compared with that of the summed responses to sequential tones covering the response area. We concur with that conclusion with the qualifications that at the level of individual cells composite curves can differ markedly from ND functions, not only in their bandwidth but also in their “fine structure” (Figs. 1, 3, 11), and that the “surprisingly” in the preceding statement remains untested (see final section).

To explain the preponderance of larger peak ratios to noise than to tones in their results, Yin et al. (1986) proposed that two-tone suppression at the level of the cochlea restricts the bandwidth in response to noise but not to tones. This preponderance at the population level disappears with our new damps-
ing measure, which reveals a trend between the damping to tones and to noise (Figs. 5 and 6C): half-widths in low-CF fibers are often larger to noise than to tones, whereas half-widths in mid-CF fibers are often larger to tones than to noise. Two-tone suppression is an unlikely explanation for this trend because, in the reasoning of Yin et al., it would need to be stronger in low-CF than in mid-CF fibers, which is not the case (Costalupes et al. 1987; Schmiedt 1982). Rather, this trend, in combination with the systematic deviation of DF with increasing CF (Fig. 10), suggests that the decline in phase-locking with frequency is somehow involved and imposes itself differently on narrowband and wideband stimuli.

Because of the many nonlinearities interposed between the sound stimulus and IC neurons, comparison of responses to tones and noise always remains somewhat of a comparison between oranges and apples. Should responses be compared for equal acoustic power, at equal suprathreshold levels, or for equal response rates? That this choice is not relevant to our conclusions is strongly suggested by the lack of SPL dependency in half-width, except perhaps for tonal responses at low SPLs (Fig. 8).

Dominant frequency

From the difcors to noise and tones, we extracted the DF to capture the dominant periodicity of ND functions and composite curves. The DF to noise is remarkably stable with SPL (Fig. 10B) and generally shows a good correspondence with CF (Fig. 10A), although there are clearly outliers, particularly for CFs >1 kHz. Above 2 kHz, DF is systematically lower than CF. These features are also present in DFs measured on autocorrelograms of auditory nerve fibers (Louage et al. 2004), but the correspondence between CF and DF is tighter in the nerve than in the IC and extends to higher CFs. In contrast to the DFs to noise, the DFs to tones strongly deviate from CF and are below CF for the vast majority of IC cells (Fig. 10C). Thus neurons may have the same damping to tones and noise, but at the same time differ strongly in the fine structure of ND functions and composite curve, as illustrated by the neuron in Fig. 11. Clearly, frequencies are differently weighted whether present as pure tones or as part of a wideband stimulus, and this is increasingly the case for increasing CF. Again, we suspect that the decrease in phase-locking above 1 kHz, in afferents to the binaural nuclei in the superior olivary complex (Blackburn and Sachs 1989; Johnson 1980; Joris et al. 1994), affects responses to tones and noise in different ways.

Comparison with previous studies

To our knowledge, the only previous study reporting a measure of binaural damping was the first extensive study of ND functions by Yin et al. (1986). These authors were particularly interested in comparing responses to noise with responses to tones, obtained to binaural beats and summarized in composite curves. They concluded that composite curves show generally a remarkable similarity to ND functions of the same neuron, particularly in the features near the center of these functions, and less comprehensive comparisons between tonal

FIG. 10. Comparison of CF with the dominant frequency (DF) of difcors obtained from ND functions (A) or from composite curves (B). C: dependency of DF from ND functions on SPL. D: comparison of DF from ND functions (abscissa) with DF from composite curves (ordinate). Number of cells/measurements: (A) 148; (B) 187/222; (C) 22/61; (D) 106/128. Open and closed circles in C and D as in Fig. 2A.
and ND functions in other species and areas have also emphasized general similarity (Fitzpatrick et al. 2000; Palmer et al. 1990). However, in the study of Yin et al. the correlation between damping to noise and to tones was poor, and for the majority of cells the damping to tones was stronger than that to noise.

We applied the peak ratio metric of damping of Yin et al. to our data and obtained a distribution (Fig. 2A) very similar to theirs, but we also find that this metric is strongly influenced by factors separate from damping per se. Indeed, when our metric, based on the envelope of ND functions rather than on individual peaks, is applied to the same data (Fig. 5), the correlation between the damping to tones and to noise is higher and the bias toward stronger damping in the response to tones disappears.

Yin et al. (1986) did not compare the periodicity of composite and ND functions directly but measured a time-domain “response frequency” from the peaks of ND functions and a frequency-domain “median frequency” from the sync-rate function (obtained by multiplication of average rate, as in Fig. 11B, and vector strength to binaural beats, as in Fig. 11C). The relationship between these two values was closer to equality than our corresponding DF measurements (Fig. 10D), but our sample includes more cells with CF >1 kHz, where the discrepancy between tonal and noise ITD sensitivity is particularly large. From their results, Yin et al. (1986) considered the sync-rate and ND functions Fourier transform pairs. We did not systematically study sync-rate functions but it is clear that this description breaks down with increasing CF because ITD sensitivity based on fine structure becomes increasingly dominated by that based on envelope (Joris 2003), which is not reflected in the sync-rate function.

Remaining questions

The view that emerged from early studies of ITD sensitivity (for review see Kuwada and Yin 1987b; Yin and Chan 1988) is largely consistent with the model first proposed by Jeffress (1948), in which binaural coincidence detectors convert temporal information in their afferents to a rate code and spatial map (for review see Joris et al. 1998). Although there is no consensus on the validity of all components of Jeffress’s qualitative model, there is no doubt that the properties of the monaural afferents are important in shaping binaural sensitivity. Yet there has been little effort toward a systematic comparison of peripheral monaural responses with the binaural
responses measured at later synaptic stages. The present study is part of our effort to characterize monaural preprocessing with measures that afford comparison with binaural properties.

In the context of this study, a remaining question is how remarkable the general agreement is between ND functions and the linear prediction based on tonal responses, to which Yin et al. (1986) first drew attention. To judge this agreement as “good” or “poor” requires an expectation based on peripheral physiology, which can be obtained by a similar analysis on peripheral neurons. This is the subject of a subsequent paper.

Another open question is whether the damping of ND functions indeed largely reflects the binaural bandwidth, as suggested above. Direct measurement of this bandwidth (Kohrausch 1988; Massie et al. 2003) should reveal whether this is indeed the case.

Acknowledgments

We thank T.C.T. Yin for support and hospitality and are grateful for the assistance of the staff at the department of physiology (University of Wisconsin, Madison) and Division of Neurophysiology (K.U. Leuven). Thanks also to A. Recio and two reviewers for providing useful feedback on a previous draft.

Grants

This work was supported by the Fund for Scientific Research, Flanders (G.0297.98 and G.0083.02), K.U. Leuven research fund (OT/01/42), and National Institute of Deafness and Other Communications Disorders Grant DC-00116. M. van der Heijden was supported by a K.U. Leuven Fellowship (F/00092).

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