

Temporal characteristics of neural sensitivities to the interaural phase difference in the inferior colliculus

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1. Introduction

The interaural phase difference (IPD) derives from the difference in the time taken for a sound to reach the left and right ears, and is an important acoustical cue for sound localization. If we are to understand auditory space perception, it is essential to investigate the neural mechanisms used for IPD-information processing. It is known that the inferior colliculus (IC), a major neural structure in the mammalian auditory pathway, contains neurons that are sensitive to the IPD in terms of the firing rate of action potentials or spikes. Previous studies (e.g., [1]) have involved extensive analyses of spike rate versus IPD functions, on the basis of spike rates computed by using relatively long temporal windows (> several tens of milliseconds). However, as far as we aware, there has been no quantitative analysis of the temporal characteristics of neural sensitivities to the IPD. In this report, we present an example of IC neurons for which the temporal firing patterns of the spikes were sensitive to a stimulus IPD, and discuss the implications of the temporal aspects of the response patterns for the neural representation of IPD information.

2. Experimental methods

Figure 1a is a diagram of our experimental apparatus. We conducted our experiments in an electrically-shielded sound-attenuating chamber. We used Mongolian gerbils (*Meriones unguiculatus*), which were anesthetized with an intramuscular injection consisting of a mixture of ketamine and xylazine. We employed an extracellular technique to record the neural activity. This technique involved the use of enamel-coated elgiloy electrodes that we inserted dorso-ventrally through several holes (about 0.5 mm diameter) made in the posterior region of the skull. The responses were amplified with a pre-amplifier (WIP, DAM80), and stored at a sampling rate of 44.1 kHz in the hard disk of a PC. On-line, recorded responses were bandpass-filtered (passband 0.3–3 kHz), and the spike waveforms of single-units or multi-unit clusters

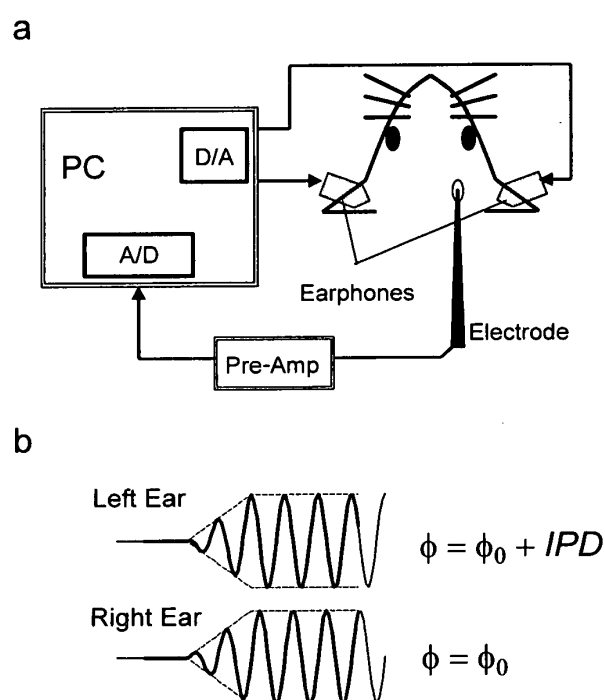


Fig. 1 Experimental apparatus and stimuli. **a.** Diagram of the experimental apparatus. **b.** An example of the binaural stimuli. Stimuli presented to the two ears had identical envelopes, and their IPD varied between $-\pi$ and $+\pi$. A positive IPD indicates an advanced phase of the sinusoid in the left ear, and vice versa.

(simply referred to as “units” in this report) were isolated. We used this information to determine the best frequencies of neurons and threshold sound pressure levels (SPLs). Off-line, we also isolated the spike waveforms in a similar way. The neural IPD sensitivity data we obtained were based on the results of the off-line spike sorting.

Stimuli were generated by a PC at a sampling rate of 44.1 kHz, and were FIR-filtered to correct the earphone responses so that the stimulus spectrum was flat near the tympanic membrane. Two-channel stimuli were generated by a sound card (SEK'D, Siena) on the PC, and presented

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through earphones (Sony, MDR-EX70SL) that were fixed over the animals' ear canals.

The signals we used were tone bursts with a duration of 50 ms. The signal frequencies were the units' best frequencies (377–2,000 Hz), and the SPLs were 20 dB above the threshold SPLs of the units (49–94 dB SPL). Signals were gated synchronously between the ears with 5-ms raised-cosine ramps. We varied the IPD from $-\pi$ to $+\pi$, divided in equal steps (Fig. 1b). A positive IPD indicates that the phase of the left ear was in advance of that of the right ear. Stimuli were presented once per second in a random order.

3. Results

Here we report the results of unit G010704.5 as an example of our data set. The unit was recorded from the right IC. The stimulus level was 79 dB SPL, and the frequency was 755 Hz. Figure 2a represents spike firing times for various IPDs relative to the stimulus onset. The figure indicates that for a post-onset time of around 27 ms, the unit responded

rather selectively to stimuli with an IPD of around $-\pi/3$ radians. After that, it can be seen that the unit generally responded to a broad IPD range. Figure 2b shows the normalized spike-firing rate (i.e., the number of spikes per unit time) as a function of the stimulus IPD. The three lines represent spike rates based on different time windows. For the time window centered at 27 ms (circles in Figs. 2a, b), the IPD function showed sharp tuning in the stimulus IPD. For the time window centered at 37 ms (triangles in Figs. 2a, b), however, no obvious IPD tuning was observed. These results indicate that the IPD selectivity of the unit varied over time after the stimulus onset. When a broad time window was used (thick lines; Figs. 2a, b), we observed a shallow tuning function.

We performed an analysis of variance to evaluate the IPD selectivity of the units at different time points after stimulus onset. At each time point, we counted the number of spikes within a 5-ms wide rectangular time window centered at that time point. We then computed the ratio of the sum of squares

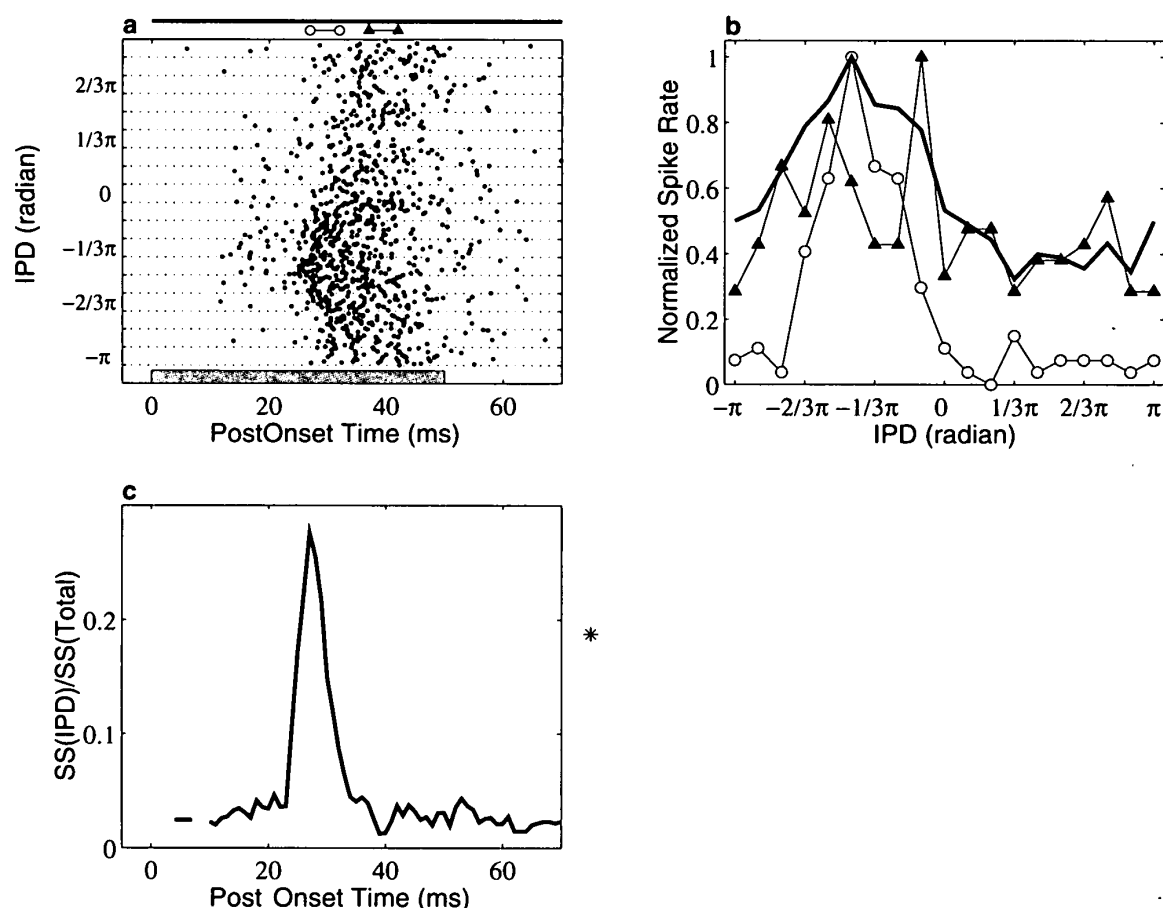


Fig. 2 Results for unit G010704.5. **a.** Raster representation of responses to tone burst with various IPD. Each dot represents one spike, and each row of dots represents a spike train elicited by one presentation of a stimulus. The vertical dimension plots the stimulus IPD, with 39 spike patterns at each IPD. The horizontal bar at the bottom indicates the length of the stimulus. **b.** Spike-rate-versus-IPD profiles of the unit. Each profile is normalized to the maximum spike rate. The thick line and lines with symbols respectively represent spike rates calculated based on time windows as indicated by the corresponding horizontal lines above Fig. 2a. **c.** Result of ANOVA on the time course of IPD sensitivity of spike count. The abscissa represents the center time of the 5-ms rectangular time window. The ordinate represents the ratio of variance accounted for by the IPD, relative to the total variance. The asterisk on the right represents the variance ratio for spike rate calculated with a broad (70 ms) time window.

(SS) of the spike-count variation caused by the variation to the SS of the total variation of the spike count (i.e., the variation caused by the IPD plus the variation within each IPD). A larger SS ratio indicates the greater IPD selectivity of the unit, and thus reveals that a greater amount of IPD information is carried by the spike count within the time window. The result of our analyses of unit G010704_5 is shown in Fig. 2c. The plot has a peak at about 27 ms followed by a rapid decrease until about 35 ms. This indicates that about 35 ms after the stimulus onset, the spike-firing rate carried no appreciable amount of IPD-related information, despite the generally large spike rate. The SS ratio (asterisk in Fig. 2c) based on a broad time window (indicated by the thick line above Fig. 2a) was smaller than the SS ratio based on the "best" 5-ms window, i.e., the peak value in Fig. 2c. This relatively poor SS ratio for the broad time window resulted from the fact that the window included responses after the 35-ms post-onset time, which added "noise" when representing the IPD information.

The significance of the temporal information as shown for the example above was generally true for our data set. Of a total of 22 units tested, 9 units were somewhat sensitive to the stimulus IPD. For 7 of those 9 units, the analysis of variance indicated that the SS ratio for the best 5-ms window was greater than the SS ratio for the broad, 70-ms, time window.

4. Conclusion

The present results suggest that neural sensitivities to the IPD could be underestimated if only broad time windows are employed, as used in earlier studies. We believe that the temporal aspects of the response characteristics deserve more attention. A recent report [2] provided an example that demonstrated the importance of the temporal aspects of IC responses, and showed that the IPD selectivity of the IC neurons is sensitive to the temporal context of the stimuli. We expect that systematic analyses of the temporal characteristics of neural responses will help us fully to understand IPD-information processing in the inferior colliculus.

Acknowledgements

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