Rate-Limited, But Accurate, Central Processing of Interaural Time Differences in Modulated High-Frequency Sounds. Focus on: "Neural Sensitivity to Interaural Envelope Delays in the Inferior Colliculus of the Guinea Pig"

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Editorial Focus

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Rate-Limited, But Accurate, Central Processing of Interaural Time Differences in Modulated High-Frequency Sounds. Focus on: "Neural Sensitivity to Interaural Envelope Delays in the Inferior Colliculus of the Guinea Pig"

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Interaural time difference (ITD; the delay between arrival of sound at the 2 ears) is one of the primary cues for localization of sound in the azimuthal (left-right) dimension. Its use, however, is limited to tone frequencies below ~1,500 Hz in part due to the ambiguity of leading and lagging high-frequency waveforms and the reduced ability of peripheral auditory neurons to phase-lock at high frequencies. For this reason—among others—localization of tonal stimuli follows Rayleigh's "duplex theory" (Macpherson and Middlebrooks 2002; Strutt 1907): low-frequency stimuli are localized on the basis of ITD, whereas high-frequency stimuli are localized on the basis of interaural level differences (ILDs). An important exception to the duplex theory, on the other hand, is localization based on ITDs of envelope fluctuations in modulated high-frequency sounds. In this issue of the *Journal of Neurophysiology* (p. 3463–3478), Griffin and colleagues demonstrate that sensitivity to these envelope ITDs among high-frequency neurons in the inferior colliculus (IC) can be equivalent to that of low-frequency IC neurons—given the appropriate stimulus—helping to resolve a significant discrepancy in our understanding of ITD processing at low and high frequencies.

ITD sensitivity at high frequencies appears to be strongly stimulus-dependent. Numerous behavioral studies using high-frequency sinusoidally amplitude-modulated (SAM) tones suggest that sensitivity to envelope delays at high frequencies is inferior to pure tone ITD sensitivity at low frequencies. This difference suggests that neural mechanisms for low- and high-frequency processing are differently specialized. For instance, high-frequency envelope-ITD sensitivity could be an epiphenomenon of ILD processing (Joris and Yin 1995, 1998, Tollin 2003). In contrast, some authors have suggested that the limitation lies in the different effects of peripheral processing on low-frequency tones and high-frequency SAM tones (Bernstein and Trahiotis 2002; Colburn and Equissad 1976; van de Par and Kohlraush 1997), and indeed localization on the basis of high-frequency stimuli with pulsatile modulation (i.e., possessing steep slopes and well-defined "off periods" in the envelope) produce ITD discrimination that is comparable to low-frequency pure-tone performance (Bernstein and Trahiotis 2002; Hafter and Dye 1983). One such stimulus used by Griffin et al. (2005) is the "transposed tone" (van de Par and Kohlrausch 1997), which was designed to produce auditory-nerve responses equivalent to those produced by low-frequency pure tones—given current models of the auditory periphery. By equating the input to central processing across frequency, the transposed tone can be used to identify similarities in central processing that are masked by differences in peripheral processing.

The degree to which limitations in high-frequency ITD sensitivity reflect peripheral or central processing is an important issue in spatial hearing. Griffin et al. (2005) address it at the single-neuron level by comparing IC responses to envelope ITDs carried by transposed and SAM tones. In every regard, they report better sensitivity to transposed than to SAM tones. Compared with SAM tones, transposed tones produced stronger modulation of neural firing rate and tighter phase-locking of responses, consistent with the more impulsive characteristic and pronounced "off periods" of the transposed modulator. As a result, responses to transposed tones better preserved the temporal characteristics of stimulus envelopes and provided greater sensitivity to envelope ITD than did the responses to SAM tones. Moreover, Griffin et al. (2005) computed neural ITD-discrimination functions based on single-neuron firing rates and found lower ITD thresholds for transposed than for SAM tones. In fact, the lowest ITD thresholds were comparable to thresholds for ITDs of low-frequency pure tones obtained from low-frequency IC neurons (Shackleton and Palmer 2004).

The similar sensitivity to ITDs carried by low-frequency pure tones and high-frequency transposed tones suggests equivalent or similar mechanisms for ITD processing in different frequency ranges. The similarity, however, holds only for transposed modulation rates below ~250 Hz. Whereas the ITD sensitivity of low-frequency IC neurons improves with increasing tone frequency up to 500–1,000 Hz, Griffin et al. (2005) observed a conspicuous failure of ITD sensitivity at high modulation rates due to a limitation in the ability of IC neurons to follow rapid modulations. The limitation applies to both transposed and SAM modulators and is consistent with previous reports of rate-limited phase-locking occurring at or below the level of the IC (Joris and Yin 1998). A similar limitation has been reported in human psychophysical studies, notably those of Hafter and colleagues (e.g., Buell and Hafter 1988; Hafter and Dye 1983) and Bernstein and Trahiotis (2002). Both groups employed high-frequency stimuli with pulsatile modulators (transposed tones or trains of filtered impulses) and observed limited sensitivity above ~100–200 Hz. Both have accounted for the limitation by proposing a (monaural) rate-limiting mechanism at the level of input to the binaural system; a 150-Hz low-pass filter in the case of Bernstein and Trahiotis (2002) and a rate-sensitive "binaural adap-

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tation" affecting modulations above ~100 Hz in the case of Hafter and Dye (1983). Subsequent studies estimating the time course of binaural adaptation (Buell and Hafter 1988; Saberi 1994; Stecker and Hafter 2002) have suggested that localization of stimuli modulated above the limiting rate depends increasingly on interaural cues contained in the stimulus onset (cf. Freyman et al. 1997). This latter effect might pertain to the observation by Griffin et al. (2005) that measurements of neural response that included the onset suffered a reduction in phase locking but maintained similar ITD sensitivity to measurements of only the middle portion of the response. The degree to which the onset responses of IC neurons help to compensate for limited phase-locking at high modulation rates would be an interesting question for future research.

By demonstrating similar ITD sensitivity in the responses of IC neurons to low- and high-frequency stimulation, Griffin et al. (2005) lend further support to the view that central mechanisms of ITD processing are similar, if not equivalent, across frequency—at least for relatively slow envelope fluctuations. The results of this study are thus important for our understanding of auditory spatial processing, not just in the IC but also in the cortex. The auditory cortex plays a necessary role in sound localization (as evidenced by lesion studies) yet appears to contain a preponderance of neurons responsive mainly to high-frequency stimulation, especially in nonprimary fields involved in spatial coding (e.g., Loftus and Sutter 2001; Stecker et al. 2003). Based on the duplex theory, one would therefore expect the majority of spatially sensitive neurons in the cortex to exhibit tuning primarily to ILD, but the results of Griffin et al. (2005) highlight the role that high-frequency ITD sensitivity might play in spatial processing throughout the auditory system.

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