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Research paper

Frequency-specific, location-nonspecific adaptation of interaural time difference sensitivity☆

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ABSTRACT

Human listeners' sensitivity to interaural time differences (ITD) was assessed for 1000 Hz tone bursts (500 ms duration) preceded by trains of 500-ms "adapter" tone bursts (7 s total adapter duration, frequencies of 200, 665, 1000, or 1400 Hz) carrying random ITD, or by an equal-duration period of silence. Presentation of the adapter burst train reduced ITD sensitivity in a frequency-specific manner. The observed effect differs from previously described forms of location-*specific* psychophysical adaptation, as it was produced using a binaurally diffuse sequence of tone bursts (i.e., a location-*nonspecific* adapter stimulus). Results are discussed in the context of pre-binaural adaptation.

1. Introduction

Microsecond differences in the arrival time of sound at the two ears (interaural time differences [ITD]) provide the major cue to sound source location in land vertebrates with low-frequency hearing (for recent reviews, see Schnupp and Carr, 2009; Grothe et al., 2010). Normal-hearing human listeners are exquisitely sensitive to ITD carried by low-frequency tones. Discrimination thresholds for ITD carried by pure tones of sufficient duration and intensity in the range 700–1000 Hz may be <10 μs for some listeners under optimal conditions (Zwislocki and Feldman, 1956). The usual task of the binaural system, however, is to extract ITD and other spatial cues (i.e., interaural level differences [ILD]) from complex signals under non-optimal conditions – in listening environments featuring background noise, signal reflections, and diffuse reverberation. While it is certainly impossible to simulate in the laboratory the variety of auditory experience modulating binaural sensitivity on multiple time scales, many psychophysical studies have evaluated the effects of the recent stimulus context on binaural thresholds. Studies of the precedence effect (Wallach et al., 1949), onset dominance in lateralization (Freyman et al., 1997), and binaural adaptation (Hafter et al., 1988) have offered a common conclusion: Many types of binaural stimuli produce frequency-specific attenuation of binaural sensitivity after stimulus onset. Such attenuation is generally construed to be adaptive biologically, because it should serve to reduce the influence of potentially redundant or spurious binaural information. In the precedence effect, for example, binaural sensitivity is reduced during the later part of a signal, such that localization relies to a greater extent on information carried by the early-arriving direct signal rather than later-arriving reflections and reverberation (Wallach et al., 1949).

Although dynamic changes in binaural sensitivity evident in the precedence effect and related phenomena (e.g., binaural adaptation) have most typically been studied over tens or hundreds of milliseconds, changes have also been demonstrated over longer time scales. Kashino and Nishida (1998), for example, demonstrated that presentation of a long (60 s) low-frequency tone carrying a right- or left-lateralized ITD could produce a leftward or rightward shift, respectively, in listeners' lateralization of a target ITD presented subsequently. Phillips and Hall (2005) examined this same "localization aftereffect" using shorter-duration (5–35 s) interleaved tones of different frequencies carrying static ITD or ILD and demonstrated that a shift in target lateralization could be induced for both cues. Similarly, Getzmann (2004) and Maier et al. (2010) demonstrated using still shorter-duration (1–3 s) adapter stimuli carrying 0 ITD and 0 ILD that lateralization of target stimuli could also be augmented around the frontal midline. Whether the

Abbreviations: ITD, interaural time difference; ILD, interaural level difference; NM, nucleus magnocellularis.

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localization aftereffect (i.e., location-specific adaptation) has a biologically adaptive function, such as to enhance the spatial contrast between "old" and "new" target signals, or is rather a benign side effect of binaural processing fatigue (Kashino and Nishida, 1998; Phillips and Hall, 2005) is an interesting matter that has not been systematically investigated.

Nonetheless, that psychophysical sensitivity to binaural information is dynamic over multiple time scales suggests that multiple physiological mechanisms are involved in modulating sensitivity. Indeed, several candidate mechanisms have been identified that may contribute to post-onset attenuation of binaural sensitivity. Such mechanisms include post-onset resonance of low-frequency cochlear filters (Tollin and Henning, 1999; Hartung and Trahiotis, 2001), delayed recurrent inhibition in the cochlear nucleus (e.g., Wickesburg and Oertel, 1990), and synaptic inhibition in the inferior colliculus via the dorsal nucleus of the lateral lemniscus (e.g., Pecka et al., 2007). Dynamic regulation of inhibitory GABAergic (Grothe and Koch, 2011) and glycinergic (Kapfer et al., 2002) inputs to the nuclei of the superior olivary complex may be additionally important for context-dependent control of binaural sensitivity, as may be corticofugal systems such as cortico-collicular inputs to the central nucleus of the inferior colliculus (see Nakamoto et al., 2008). The aforementioned localization aftereffect has been attributed to fatigue of cross-correlating binaural neurons (Kashino and Nishida, 1998) or opponent populations of neurons with broad (e.g., contralateral hemispheric) spatial tuning (Phillips and Hall, 2005).

Recently, Kuznetsova et al. (2008) described a novel type of adaptation in the magnocellular neurons of the avian cochlear nucleus (nucleus magnocellularis [NM]). NM neurons are highly analogous to the spherical bushy cells of the mammalian cochlear nucleus, in that they relay input from primary auditory nerve fibers to downstream binaural neurons with extraordinary temporal fidelity. Such fidelity is critical for the accurate encoding of ITD in downstream "coincidence detector" neurons. Kuznetsova et al. (2008) demonstrated that multi-second (7–10 s) electrical stimulation of NM neurons (with simulated auditory nerve input given a 1000 Hz pure tone stimulus) caused a significant decrease in the temporal precision (vector strength) of their firing. The authors demonstrated that this effect was specifically due to slow inactivation of Kv1 low-threshold potassium channels, which regulate the excitability and thus the firing selectivity of NM neurons, and which are also ubiquitous in the mammalian auditory system, including the spherical bushy cells of the cochlear nucleus (e.g., Rothman and Manis, 2003). Critically, Kuznetsova and Spain (2009) further demonstrated that the changes in NM firing led to a frequency-specific reduction in the simulated ITD sensitivity of downstream coincidence detector neurons in nucleus laminaris, a structure analogous to the mammalian medial superior olive (for review, see Grothe et al., 2010). This finding led the authors to hypothesize that a similar form of adaptation might occur in the mammalian ITD system, which also depends on the temporally precise firing of pre-binaural neurons (e.g., Grothe et al., 2010). The present study probed this hypothesis by measuring ITD discrimination performance in human listeners following presentation of a multi-second tonal "adapter" stimulus or an equal duration period of silence. Presentation of the adapter degraded ITD discrimination performance in a frequency-specific, location-nonspecific manner, consistent with – though not necessarily attributable to – a pre-binaural mechanism (e.g., Kuznetsova et al., 2008).

2. Methods

2.1. Subjects

Four normal-hearing subjects (0502, 0601, 0804, 0923) aged 21–36 participated in this experiment. Subjects 0601 and 0923 were naive to the purposes of the experiment and were compensated for their participation. Subjects 0502 and 0804 were the first two authors. All subjects reported normal hearing and demonstrated pure-tone detection thresholds <20 dB HL at octave frequencies over the range 250–8000 kHz.

2.2. Stimuli and procedure

Stimuli consisted of an adapter interval followed by a reference interval and a test interval (see Fig. 1). Adapter and reference intervals were separated by a 500 ms silent period; reference and test intervals were separated by a 100 ms silent period. In "Adapter" conditions, the adapter interval was comprised of 14 tone bursts presented at 74 dB SPL, each 500 ms in duration (20 ms cos^2 rise/fall), for a total adapter-interval duration of 7 s. Adapter burst frequencies were 200 Hz, 665 Hz, or 1000 Hz, selected to stimulate auditory filters distant from, on the edge of, or identical to the 1000 Hz auditory filter stimulated during the test interval (e.g., Moore and Glasberg, 1987). Each adapter burst carried a random ITD, drawn from a uniform distribution spanning $\pm 1/4$ cycle of the burst frequency. In a baseline "No Adapter" condition, adapter tone bursts were replaced by an equal-duration (7 s) silent period. The reference interval always consisted of a 500 ms, 1000 Hz diotic tone burst, while the test interval consisted of a 500 ms, 1000 Hz tone burst carrying a left- or right-leading ITD (varied adaptively trial-to-trial, see below). Both reference and test intervals were

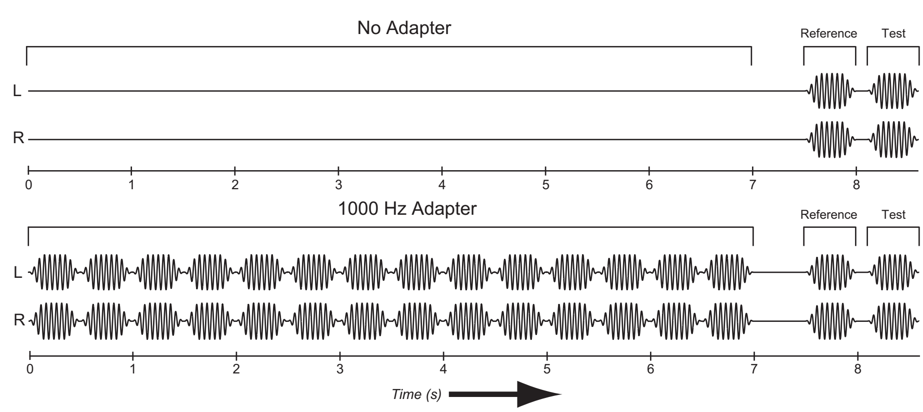

Fig. 1. Schematic illustration of example stimuli. Each trial consisted of a 7 s adapter interval followed by a 500 ms pause and a 1.1 s test interval (see text). Here, "No Adapter" and "1000 Hz Adapter" conditions are illustrated. The subject's task was to indicate whether the final 1000 Hz tone burst was shifted to the left or right of the preceding 1000 Hz diotic reference tone burst.