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Frequency-specific, location-nonspecific adaptation of interaural time difference sensitivity^{a)}

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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.

Keywords

Sound localization; binaural sensitivity; psychophysical adaptation; ITD discrimination

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Author Contributions

MSK and WJS conceived of the hypothesis. All authors contributed to the design of the experiment. ADB and MSK performed the experiments and analyzed the data. ADB wrote the initial draft. All authors revised the paper.

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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 $<10\ \mu\text{s}$ 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 (Haftner 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 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 et al. (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 Figure 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 presented at 74 dB SPL. All adapter and test ITD were imposed by advancing the signal to one ear by half the total ITD and delaying the signal to the other ear by an equal amount. Stimuli were programmed in MATLAB, (Mathworks, Natick, NJ) synthesized at 48.848 kHz (Tucker-Davis Technologies RP2.1, Alachua FL) and presented under STAX model 4070 closed-back electrostatic headphones (STAX LTD., Saitama, Japan).

The subject's task on each trial was to indicate whether the target tone burst was to the left or right of the diotic reference burst. A 4-button response box (TDT RBOX) recorded subject responses. Feedback was given via LED display after every trial. Target ITD were adjusted trial-to-trial according to a 2-down 1-up rule to estimate the 71% correct discrimination threshold (Levitt, 1971). The starting value of the adaptive track was either 250 μ s or 125 μ s, depending on listener preference (both values were demonstrated to be well above threshold and led to strong adaptive track convergence for all subjects). Logarithmic step sizes of 0.2 ($ITD_{new} = ITD_{old} * 10^{\pm 0.2}$) were employed up to the fourth reversal in each track, then decreased to 0.05 ($ITD_{new} = ITD_{old} * 10^{\pm 0.05}$) for the duration of the run. Each run terminated after 8 track reversals. The threshold was taken as the geometric mean ITD of the final 4 reversals. Ten threshold estimates were obtained for each condition, for a total of 40 runs for each subject. Subjects completed at least 3 hours of training prior to data collection. Testing sessions lasted a maximum of 2 hours, with most subjects completing at least 5 sessions. In a follow-up experiment designed to assess the effectiveness of an adapter *higher* in frequency than the test stimulus, an additional 1400 Hz Adapter condition was tested in a subset of subjects (0502 and 0601). Thus, subjects 0502 and 0601 each completed three additional sessions (several practice runs and 10 test runs in the 1400 Hz Adapter condition). All testing was completed in a double-walled sound booth (IAC, Bronx, NY).

2.3 Statistical Analysis

Significant variability in sensitivity to ITD has been noted among the normal-hearing population (e.g., McFadden et al., 1973). Such variability was both anticipated and observed in the present dataset (note vertical spread of individual subject traces in Figure 2). Thus, while a repeated-measures ANOVA was conducted using data from the original 4 conditions (No Adapter, 200 Hz, 665 Hz, and 1000 Hz Adapter) to assess the main effect of condition across subjects, subsequent pair-wise testing was conducted *within subjects* using a 10,000-repeat permutation test (e.g., Moore and McCabe, 2005). For a given contrast for a given subject (e.g., 1000 Hz Adapter vs. No Adapter, subject 0601), condition labels were randomly permuted across the 20 runs completed by each subject in the contrast (10 per condition), a mean computed for each randomly determined set of 10, and the new mean difference computed. The obtained *p*-values give the proportion of repeats (out of 10,000) on which permuted mean differences equaled or exceeded the experimentally observed mean differences (determined separately for each contrast and subject).

3. Results

Figure 2 displays ITD discrimination thresholds (in μ s ITD, note logarithmic ordinate) as a function of Adapter condition. Dashed lines and symbols plot individual subjects' mean thresholds based on 10 threshold estimates for each condition, with error bars giving ± 1 standard error of the mean across runs. The solid line and symbols plot the cross-subject mean thresholds for each condition with error bars giving ± 1 standard error of the mean across subjects.

Although clear differences in overall sensitivity were observed between subjects, thresholds followed a similar pattern across conditions for all subjects. The mean threshold was lowest

in the baseline “No Adapter” condition at just over 10 μ s, a value consistent with previously published data (e.g., Zwislocki and Feldman, 1956). In the “Adapter” conditions, thresholds were monotonically elevated relative to baseline with increasing adapter frequency. Thresholds were comparable to “No Adapter” thresholds in the “200 Hz Adapter” condition (mean 12.6 μ s), highest for all subjects in the “1000 Hz Adapter” condition (mean 20.1 μ s), and of an intermediate value (mean 16.3 μ s) in the “665 Hz Adapter” condition. Threshold data were submitted to a one-way repeated-measures ANOVA. The main effect of adapter condition was significant, accounting for over 70% of the total variance in thresholds ($F(3,3)=7.21$, $p<0.01$, $\text{partial } \eta^2=0.71$). Within-subject follow-up pair-wise contrasts (see section 2.3) generally supported the trends evident in Fig. 2, with clear differences between the 1000 Hz Adapter condition and other conditions, most especially the No Adapter and 200 Hz Adapter conditions (see Table 1).

These data suggest that several seconds of exposure to a spectrally invariant, binaurally diffuse “adapter” stimulus produced a frequency-specific decrement in ITD sensitivity that was maximal when the adapter and test frequencies coincided. An alternative explanation is that adapter effects need not be tuned to the target frequency but might instead increase monotonically with increasing adapter frequency. In order to address this concern, an additional two datasets were obtained in a “1400 Hz Adapter” condition for subjects 0502 and 0601. These data are plotted at the right edge of Fig. 2. For both subjects, thresholds in the 1400 Hz Adapter condition were similar to those for the 200 Hz Adapter condition. Values obtained by pair-wise comparison of the 1000 Hz Adapter and 1400 Hz Adapter conditions are given in Table 1. These data demonstrate adaptation of ITD sensitivity that is indeed frequency-specific, but that, unlike the localization aftereffect (cf. Kashino and Nishida, 1998; Getzmann, 2004; Phillips and Hall, 2005; Maier et al., 2010), is *not* location-specific.

4. Discussion

Sensory systems adapt to constant input. Although adaptation is typically associated with a *reduction* in responses (e.g., reduced neuronal firing rate, Adrian and Zotterman, 1926; Abolafia et al., 2011), it may be more generally understood as a *change* in responses (e.g., Fairhall et al., 2001). Recently, Kuznetsova et al. (2008) described a novel type of adaptation in the magnocellular neurons of the avian cochlear nucleus characterized by degraded spike-timing precision resulting from injection of a multi-second adapter stimulus (see section 1). This adaptation, attributable to slow inactivation of Kv1 low-threshold potassium channels, was subsequently shown to degrade the simulated ITD sensitivity of downstream coincidence detector neurons in nucleus laminaris (Kuznetsova et al., 2009). Although the precise mechanisms of ITD processing in birds and mammals differ in important ways (Schnupp and Carr, 2009; Grothe et al., 2010), both require temporally precise firing of pre-binaural neurons known to possess Kv1 potassium channels (e.g., Rothman and Manis, 2003). This observation led Kuznetsova and colleagues (2008) Kuznetsova and colleagues (2009) to predict that similar adaptation would be observed in the mammalian ITD system, and moreover that behavioral sensitivity to ITD in mammals (including humans) would be degraded following exposure to multiple seconds of repeated tonal stimulation.

Here, we have demonstrated that human listeners exhibit a frequency-specific decrement in ITD sensitivity following presentation of a multi-second “adapter” stimulus carrying random ITD. Although any link between *in vitro* avian physiology and human behavior is assuredly tenuous and the mechanisms underlying the behavioral result may not be identified on the basis of psychophysical experiments alone, the present data are *consistent* with the type of pre-binaural mechanism described by Kuznetsova and colleagues (2008, 2009). Unlike the

localization aftereffect (Kashino and Nishida, 1998, Phillips and Hall, 2005), wherein a binaurally static multi-second “adapter” stimulus presented from a given location augments the lateralization of a target stimulus away from that location (see section 1), the present effect apparently does not depend on the specific binaural attributes of the conditioning stimulus (i.e., is *not* location-specific), as it was demonstrated using binaurally random tone bursts drawn from a broad range of ITD. Although we cannot rule out the contribution of “higher-level” (i.e., post-binaural) effects on discrimination performance, such as confusion of the adapter and test stimuli (which we tried to minimize by providing several hours of training and by inserting a brief silent gap between adapter and test intervals), and the potential contributions of other physiological mechanisms discussed in section 1 (e.g., synaptic inhibition) should also be considered, the tuning characteristic of the present effect (Fig. 2) is consistent with a relatively low-level origin (e.g., see psychophysical tuning curves of Moore and Glasberg, 1987). We additionally note that this form of location-nonspecific adaptation could and might indeed be expected to contribute to location-specific adaptation (e.g. the localization aftereffect).

Physiological details of the present effect notwithstanding, it is interesting to consider whether location adaptation of ITD sensitivity may have an adaptive value, such as to reduce the influence of spectrally static and spatially diffuse sound (i.e. background noise) on the localization of spectrally discrete target stimuli. Further studies are required to address this issue.

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Abbreviations

ITD	interaural time difference
ILD	interaural level difference
NM	nucleus magnocellularis

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Highlights

- Listeners' ITD sensitivity was degraded by exposure to a multi-second "adapter" stimulus
- The effect was frequency-specific but did not depend on specific ITD cues in the adapter
- The effect is *consistent* with a pre-binaural site of adaptation

Figure 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.

Figure 2.

ITD discrimination thresholds as a function of adapter condition. Dashed lines and symbols plot individual subjects mean thresholds based on 10 threshold estimates for each condition, with error bars giving ± 1 standard error of the mean across runs. The solid line and symbols plot the cross-subject mean thresholds for each condition with error bars giving ± 1 standard error of the mean across subjects. Individual subject data are offset along the abscissa for clarity. Only subjects 0502 and 0601 completed the 1400 Hz Adapter condition; thus a mean is not displayed for that condition.

Table 1

P-values for within-subject pair-wise contrasts conducted as a series of 10,000-repeat permutation tests (see text). Note that only subjects 0502 and 0601 completed the 1400 Hz Adapter condition.

	1000 Hz v. NA	200 Hz v. NA	1000 v. 200 Hz	1000 v. 1400 Hz
<u>0502</u>	0.0187	0.5436	0.0096	0.0501
<u>0601</u>	0.0001	0.0373	0.0022	0.0001
<u>0804</u>	0.0334	0.5248	0.0323	-
<u>0923</u>	0.0064	0.0820	0.1254	-