Published in final edited form as:

Hear Res. 2018 December ; 370: 65–73. doi:10.1016/j.heares.2018.10.002.

Spatial variation in signal and sensory precision both constrain auditory acuity at high frequencies

Andrew D. Brown,

University of Washington, Department of Speech and Hearing Sciences, Seattle, WA 98015

Victor Benichoux,

Institut Pasteur/INSERM, Unité de Génétique et Physiologie de l'Audition, 75015 Paris, France

Heath G. Jones,

U.S. Army Aeromedical Research Laboratory, Auditory Protection and Performance Division, Fort Rucker, AL 36362

Kelsey L. Anbuhl, and

New York University, Center for Neural Science, New York, NY 10003

Daniel J. Tollin

University of Colorado School of Medicine, Department of Physiology & Biophysics, Aurora, CO 80045

Abstract

Sensory performance is constrained by the information in the stimulus and the precision of the involved sensory system(s). Auditory spatial acuity is robust across a broad range of sound frequencies and source locations, but declines at eccentric lateral angles. The basis of such variation is not fully understood. Low-frequency auditory spatial acuity is mediated by sensitivity to interaural time difference (ITD) cues. While low-frequency spatial acuity varies across azimuth and some physiological models predict strong medial bias in the precision of ITD sensitivity, human psychophysical ITD sensitivity appears to vary only slightly with reference ITD magnitude. Correspondingly, recent analyses suggest that spatial variation in human low-frequency acuity is well-accounted for by acoustic factors alone. Here we examine the matter of high-frequency auditory acuity, which is mediated by sensitivity to interaural level difference (ILD) cues. Using two different psychophysical tasks in human subjects, we demonstrate decreasing ILD acuity with increasing ILD magnitude. We then demonstrate that the multiplicative combination of spatially variant sensory precision and physical cue information (local slope of the ILD cue) provides improved prediction of classic high-frequency spatial acuity data. Finally, we consider correlates of magnitude dependent acuity in neurons that are sensitive to ILDs.

Corresponding author: Andrew D. Brown, University of Washington, Department of Speech and Hearing Sciences, 1417 NE 42nd St, Box 354875, Seattle, WA 98015, Tel: +1 206-616-5273, Fax: +1 206-543-1093, andrewdb@uw.edu.

Publisher's Disclaimer: This is a PDF file of an unedited manuscript that has been accepted for publication. As a service to our customers we are providing this early version of the manuscript. The manuscript will undergo copyediting, typesetting, and review of the resulting proof before it is published in its final citable form. Please note that during the production process errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.

Keywords

Spatial hearing; sound localization; auditory acuity; interaural level difference; interaural time difference

1. Introduction

Hearing is nearly omnidirectional. Indeed, the ability to perceive and react to peripheral events is a key advantage of the auditory sense (over vision, for example, which is in most species directionally restricted) (e.g., Schone, 1984). However, the precision of sound location perception varies considerably with source position: Sources to the sides, toward $\pm 90^\circ$ azimuth, are harder to tell apart than sources directly in front (near 0° azimuth). This prominent spatial dependence in auditory acuity has been demonstrated in humans (e.g., Mills, 1958) and a wide variety of other species (e.g., macaque, Brown et al., 1982; cat, Heffner and Heffner 1988; ferret, Parsons et al., 1999). Spatial dependencies in other sensory systems (visual, Hubel and Wiesel, 1960; somatosensory, Stevens and Choo, 1996) can be attributed in part to peripheral factors, e.g. variations in receptor density across the intrinsically spatial sensory end organ. The basis of spatial dependence in auditory acuity, which emerges central to the cochlea, is less clear.

Spatial discrimination in azimuth depends on sensitivity to small differences in signal level and timing at the two ears, the interaural level and time difference cues (ILD and ITD). The availability and utility of each cue is frequency dependent, with ILD used by all mammals and many other vertebrates for high-frequency sounds, and ITD dominating performance for low-frequency and broadband sounds in species with sufficient low-frequency hearing (Rayleigh, 1907; Wightman and Kistler, 1992). While ILD and ITD are fundamentally different acoustically and thought to be encoded in at least partially discrete brainstem pathways (Boudreau and Tsuchitani, 1968; Goldberg and Brown, 1969; Grothe et al., 2010), behavioral auditory acuity is strongly azimuth dependent at both low and high frequencies (Mills, 1958), suggesting the possibility of an acuity-limiting factor common to both cues.

Recently, Smith and Price (2014) demonstrated that the azimuth dependence of ITD-mediated low-frequency acuity appears to be fully accounted for by the azimuth dependence of the ITD cue itself (cf. Pavao et al. 2018). At lateral source angles, a given change in source location yields a smaller change in ITD than at the midline; thus, even with spatially invariant ITD sensitivity, performance deteriorates predictably with increasing azimuth (Mills, 1958). While this finding contrasts with some neural data suggesting best ITD acuity near the midline (i.e., around 0 ITD) (e.g., McAlpine et al., 2001) and ITD acuity indeed appears to vary somewhat with ITD magnitude for some stimuli (Haftner and de Maio, 1975; Hancock and Delgutte, 2004) (but see Carlile et al., 2016), incorporating such variation across azimuth does *not* yield a better explanation of human low-frequency spatial acuity data (Smith and Price, 2014). That is, in the case of low-frequency auditory spatial acuity via ITD, the resolution-limiting factor appears to lie in the acoustic signal rather than in the precision of the sensory system.

Previous work has yielded mixed evidence for magnitude dependence in ILD acuity (Hershkowitz and Durlach, 1969; Hafter et al. 1977; Yost and Dye, 1988; Carlile et al., 2016). Hafter et al. (1977), for example, concluded that ILD and ITD acuity were similarly and minimally magnitude dependent, “indicating that, unlike the case for vision, spatial resolution in the auditory system is not concentrated in the center.” In contrast, Carlile et al. (2016) showed a clear divergence in acuity for the two cues, with no magnitude dependence in ITD acuity, but clear magnitude dependence in ILD acuity (see Fig. 3 of that paper). Here, following on the approach of Smith and Price (2014), we revisit this topic to examine whether an acoustic explanation is sufficient to account for the spatial dependence of high-frequency auditory acuity. After generating purely acoustic predictions of classic perceptual acuity data (Mills, 1958) from a database of manikin measurements (Porschmann et al. 2017), we assessed behavioral ILD acuity as a function of ILD magnitude using two different psychophysical tasks. Psychophysical and acoustic factors were then combined, yielding improved prediction of high-frequency acuity data (Mills, 1958) and suggesting that spatial variation in high-frequency acuity is attributable to azimuthal variation of both signal information and sensory (ILD) precision. Lastly, toward comparative insight on the origins of magnitude dependence in ILD sensitivity, we examined neural ILD acuity as a function of ILD magnitude in a population of auditory midbrain neurons (in the chinchilla, a species audiometrically similar to humans).

2. Materials and Methods

2.1. Psychophysical experiments

Nine adult human subjects (3 female) aged 25 to 43 years (mean=30.3 years) participated in psychophysical experiments. All subjects reported normal hearing and demonstrated pure-tone audiometric thresholds <20 dB HL at octave frequencies over the range 0.25 – 8 kHz. Three subjects participated in both experiments. One subject of the second experiment was the last author. All study procedures complied with a protocol approved by the Colorado Multiple Institutional Review Board.

Stimuli were generated using MATLAB, synthesized at a sampling rate of 44.1 kHz at 16-bit resolution using a PCI soundcard (Lynx TWO-A, Lynx Studio Technology), and presented via circumaural headphones (Bose AE2). Stimuli consisted of narrowband noise tokens (bandwidth of 25 Hz, 2nd-order Butterworth filter) 250 ms in duration, presented at an average binaural level of ~65 dB SPL. In terms of their spectral width and associated ILD cues expected in a free field (e.g., Fig. 1), tokens were essentially similar to tone bursts employed in previous studies of acuity, including Mills (1958) and Yost and Dye (1988). Imposed ILDs randomly favored the left or right ear, as described below, and were generated symmetrically by amplifying the signal to the favored ear by half of the total ILD and attenuating the signal to the opposite ear by half of the total ILD. Additionally, as all trials contained two successive stimuli (see below), the average binaural level was randomly varied over a 10-dB range (uniform distribution) between intervals to limit the informativeness of monaural level cues versus the binaural ILD cue.

During testing, subjects faced a large (80-cm diagonal) touch-sensitive display (elo Touchsystems 3200L). In a first psychophysical experiment, subjects performed a

lateralization task. On each trial, a diotic reference stimulus was presented, followed after 500 ms by the target stimulus, which carried a nonzero ILD. Data are presented here for two test frequencies for which ILD was the only usable binaural cue, 4 kHz and 8 kHz. Data were drawn from eight different ILDs intended to be suprathreshold (i.e., readily lateralized), presented in random order (± 2 , ± 4 , ± 8 , ± 16 dB). On each trial, the subject was instructed to indicate the perceived lateral position of the second (target) stimulus using one of two panels displayed on the monitor (“LEFT (how far left?)” and “RIGHT (how far right?)”), displayed at eye level, each spanning half the width of the monitor. Response values ranged from 0 (far left) to 1 (far right; see below).

In the second psychophysical experiment (discrimination), only the 4-kHz stimulus center frequency was tested. Each trial contained two successive stimuli separated by a 500-ms silent period. The first was the reference stimulus, carrying an ILD of 0, 8, 16 or 24 dB, randomly left- or right-favoring. The second was the target stimulus, carrying an ILD with a left- or right-favoring increment of varied magnitude relative to the reference interval. The subject’s task was simply to indicate whether the target was shifted to the left or right of the reference using the corresponding response panel.

Psychophysical data were analyzed offline in MATLAB. Lateralization responses were fitted using a two-parameter logistic function of the form,

$$\Phi(ILD) = \frac{1}{1 + e^{\left(\frac{ILD - b_0}{b_1}\right)}} \quad (\text{Eq.1})$$

where $\Phi(ILD)$ is the lateralization response as a function of the ILD, b_0 is the inflection point of the function (and thus the ILD at which responses switch from left-favoring (<0.5) to right-favoring (>0.5)), and b_1 is a width parameter reflecting the slope of lateralization across ILD. Prior to fitting, lateralization values were centered around 0.5 (midline) to remove any mean shift in responses (generally negligible). After fitting, values for raw and fitted lateralization responses were expanded to cover the range -1 to $+1$ (midline=0). Lateralization-based discrimination thresholds were then computed using lateralization response magnitude and standard deviation,

$$\Delta_{lat}(ILD) = 1 / \left(\frac{\Phi'(ILD)}{\sigma_{\Phi}(ILD)} \right) \quad (\text{Eq.2})$$

where $\Delta_{lat}(ILD)$ is the discrimination threshold as a function of ILD, $\Phi'(ILD)$ is the derivative of fitted lateralization across ILD, and $\sigma_{\Phi}(ILD)$ is the standard deviation in lateralization across ILD (which was set to be ILD-invariant; see Fig. 2A). Here we define threshold at a standard separation of 1. The final threshold curve was taken across absolute values of ILD, i.e., averaging across left- and right-favoring ILDs.

Psychophysical discrimination responses were analyzed using standard methods: Each subject's ILD-versus-percent correct performance was fit using a Weibull function (Wichmann and Hill, 2001) with a lower bound of 50% (random guessing) and an upper bound of 100% (readily attained by all subjects at the larger tested ILDs). The ILD threshold was taken as the fitted ILD yielding 76% correct ($d' = 1$). Performance as a function of ILD was well described by an exponential function $discrim(ILD) = 0.933 \times e^{0.05129ILD}$ ($R^2=0.98$), enabling continuous prediction of the minimum audible angle (as described below). For comparison to other studies of ILD/ILD performance, the relative change in sensitivity across reference ILD was again normalized to performance at the midline (see Fig. 5).

2.2. Predicting human auditory acuity from acoustic ILD and behavioral ILD sensitivity

Acoustic variation of ILD across azimuth was quantified using a publicly available database (Porschmann et al., 2017) of high-resolution (1° increment) binaural manikin impulse response measurements taken at 0.5 m source distance, matching the paradigm of Mills (1958). ITDs were computed from the cross-correlation of lowpass filtered (0.5 kHz cutoff) impulses responses; ILDs were computed from the amplitudes of filtered impulse responses (center frequencies as specified in figures). Computed ITDs and ILDs were then fitted with sinusoids, and the slopes of these sinusoids were used to predict spatial acuity, with midline discrimination thresholds set to $20 \mu s$ (cf. Smith and Price, 2014) and 1 dB (present data; cf. Mills, 1960), respectively. For ILDs, two scenarios were compared – that of constant sensitivity (cf. Smith and Price, 2014), and that of azimuth-dependent sensitivity. For constant-sensitivity predictions, the predicted MAA is simply the inverse of the acoustic ILD slope scaled by the value of the (azimuth-invariant) discrimination threshold. For azimuth-dependent predictions, the effects of worsening sensitivity across reference ILD and of decreasing ILD slope across azimuth are multiplicative,

$$MAA(\theta) = \frac{\Delta_{discrim}(ILD(\theta))}{ILD'(\theta)} \quad (\text{Eq.3})$$

where $MAA(\theta)$ is the minimum audible angle as a function of source azimuth, $discrim(ILD(\theta))$ is the ILD discrimination threshold as a function of the azimuth-dependent acoustic ILD, and $ILD'(\theta)$ is the derivative of acoustic ILD as a function of azimuth. Lastly, the absolute error in prediction was computed for both constant-sensitivity and sensitivity-dependent cases at azimuths from 0° - 60° by computing the absolute differences between predicted and observed values and taking the mean across azimuth. Note that the MAA could not be determined at 75° for most frequencies in Mills (1958), and performance at azimuths $>60^\circ$ is likely to be affected by non-monotonicities in ILD (e.g., Macaulay et al., 2010), which are not well-captured by the fitted $ILD'(\theta)$ function (see Sec. 3.1. and Discussion).

2.3. Neurophysiological experiments

Toward insight on neural correlates of magnitude dependencies in ILD sensitivity, neural ILD acuity was assessed for a population of auditory midbrain neurons. Data were obtained

from 42 (21 female) adult (270-820 g) long-tailed chinchillas (*Chinchilla lanigera*). All experimental procedures were approved by the University of Colorado Health Sciences Center Animal Care and Use Committee. Neurophysiological methods have been described in prior publications (Brown and Tollin, 2016; Benichoux et al., 2017) and are summarized only briefly here. Animals were anesthetized with intramuscular injections of ketamine hydrochloride (KetaVed, 22.5 mg/kg) and xylazine hydrochloride (TranquiVed, 5 mg/kg). Body temperature was maintained at 37° C by use of a heating pad and isothermal probe. A tracheal cannula was implanted, the head was immobilized in a stereotaxic instrument (David Kopf Instruments) and a midline incision was made to expose the skull. The ears were reflected laterally, a cautery was used to expose the bony auditory meati, and custom earphones were placed snugly into each meatus. A craniotomy was made approximately 11 mm caudal and 1.5 mm lateral-right from bregma, and the underlying dura mater was removed to expose cortex overlying the right inferior colliculus (IC, auditory midbrain).

Experiments were completed in a double-walled sound-attenuating chamber. Acoustic stimuli were generated in MATLAB and presented using Tucker-Davis Technologies System 3 hardware. Earphone outputs (TDT CF-1 routed to foam inserts) were calibrated to achieve a virtually flat acoustic response using a 256-tap digital FIR filter (MATLAB) (± 2 dB at frequencies 16 kHz, measured and verified using probe tube microphones). Each experiment began with the presentation of ~40 dB SPL repeating tone bursts of frequencies 0.1 – 16 kHz via the left earphone (excitatory to the right IC). A tungsten microelectrode (2-3 M Ω , Microprobe) was advanced ventrally from the center of the craniotomy via piezoelectric microdrive (Kopf) while the tone sweep stimulus was presented on a continuous loop. The electrode signal was amplified and filtered (0.3-3 kHz) (ISO-80, World Precision Instruments; SRS 560, Stanford Research Systems). Auditory responses were typically first encountered at an electrode depth of ~4 mm. Action potentials (“spikes”) from individual neurons (“units”) were discriminated using an amplitude-time window discriminator (Model DDIS-1, BAK). Unit characteristic frequency (CF) was estimated online from a three-dimensional surface plot (contralateral signal frequency $\times$ intensity $\times$ unit firing rate [spikes/s]). A rate-level function was then measured using either a 50-ms or 200-ms CF-tone bursts presented with varied intensity. The contralateral signal intensity that elicited approximately 50% of maximal firing rate (typically 50-60 dB SPL and ~20-30 dB re: threshold) was used for subsequent binaural testing. During binaural stimulation, ILDs were imposed by holding the amplitude of the left (contralateral, excitatory) ear constant and varying the amplitude of the right (ipsilateral, inhibitory) ear over a 40-60 dB range, resulting in ILDs ranging from ± 20 to ± 30 dB. Each ILD cue value was presented at least 20 (up to 50) times, with cue values presented in random order over the course of a testing block. A total of 146 neurons were characterized using this method; a subset of these neurons was evaluated in the context of frequency-dependence in ILD sensitivity in a previous report (Jones et al., 2015).

Neurophysiological data were processed offline in MATLAB. Responses (spike rate elicited as a function of ILD) were fitted with a four-parameter logistic function of the form,

$$y(ILD) = a + \left(\frac{d - a}{1 + e^{\frac{ILD - c}{b}}} \right) \quad (\text{Eq.4})$$

where $y(ILD)$ is the firing rate (in spikes / s) as a function of ILD, a is the minimum spike rate, d is the maximum spike rate, c is the inflection point (and therefore also the “half-maximal” ILD), and b controls the slope at the inflection point (i.e. a tuning width parameter). Units were classified as ILD-sensitive if the fitted curve was modulated 50% (i.e., the minimum fitted spike rate was no greater than half of the maximum), the R^2 of the fit was at least 0.70, and the transition of the fitted curve from minimum to maximum firing rate occurred over a range of at least 5 dB (generally the smallest ILD increment measured empirically). All units of the present report ($n=146$) met these inclusion criteria. In the interest of deriving a metric more readily comparable to psychophysical acuity metrics, neural ILD discrimination thresholds were estimated using Fisher information (FI),

$$FI(ILD) = \frac{y'(ILD)^2}{y(ILD)} \quad (\text{Eq.5})$$

where $y'(ILD)$ is the derivative of the spike rate-ILD tuning curve (Eq. 4) and it is assumed the data are Poisson distributed such that spike rate variance is equal to the mean spike rate ($y(ILD)$) (empirically demonstrated in previous measurements, see Jones et al., 2015; cf. Seung and Sompolinsky, 1993). Our use of spike rate assumes that the observed spike count for the given stimulus duration (50-200 ms) predicts the spike count that would be elicited for a 1-s stimulus (i.e., spike counts are multiplied by 1/stimulus duration in s), increasing absolute values of FI correspondingly. Since our interest was in relative information across ILD (see below), over- or underestimation of absolute FI for a standard 1-s stimulus is not relevant to the conclusions drawn (see also Benichoux et al. 2017 for further caveats regarding absolute FI). FI is computed from the slope and variance of spiking across stimulus values, and is easily converted to a signal detection theoretic measure by evaluating the change in stimulus value (ILD) necessary to achieve 1 standard separation in spiking distributions, i.e. ILD threshold at $d'=1$ (Green and Swets, 1966),

$$\Delta_{neural}(ILD) = \frac{1}{\sqrt{FI(ILD)}} \quad (\text{Eq.6})$$

where $\Delta_{neural}(ILD)$ gives the neuron's ILD discrimination threshold, and $FI(ILD)$ is the FI as computed in Eq. 5. Population-level analysis was computed using a 10,000-repeat bootstrapping procedure. For this procedure, each studied neuron (in the right IC) was assumed to have a mirror symmetric counterpart in the left IC, with $\Delta_{neural}(ILD)$ computed on the mean of summed measured and mirrored $FI(ILD)$ across the sample (e.g., Tsai et al., 2010; Dahmen et al., 2010). We again note that for our purposes, absolute threshold values (which, like FI, can be affected by the number of neurons or the stimulus duration

considered) are not relevant; rather, we were interested in the *change* in acuity across ILD relative to acuity at the midline, i.e. $neura(ILD) / neura(0)$.

3. Results

3.1. Acoustic predictions do not account for variation of high-frequency spatial acuity

The ITD cue is a sinusoidal function of azimuth with a modest dependence on frequency (e.g. Kuhn, 1977; Benichoux et al., 2016). As discussed in the Introduction, its saturation at extreme azimuths accounts for the decline in low-frequency spatial acuity (Fig. 1A-C, see Mills, 1958; Smith and Price, 2014). The ILD cue is more complex, being strongly dependent on frequency, azimuth, and also source distance (e.g., Brungart and Rabinowitz, 1999). At a given frequency, ILD magnitude increases with azimuth up to a maximum near but generally somewhat medial to $\pm 90^\circ$. ILD is notably non-monotonic at some frequencies, particularly in the region of the “bright spot”, over which the ILD decreases with increasing azimuth (e.g., Macaulay et al. 2010; see Discussion Sec. 4.1.). ILD is thus approximated quite well as a sinusoidal function at moderate azimuths, but less well at extreme azimuths where non-monotonicities emerge (Fig. 1B, cf. Middlebrooks 1992). The high-frequency minimum audible angle (MAA) can be predicted at a given reference azimuth by dividing the ILD discrimination threshold at that azimuth by the local acoustic ILD slope (dB/deg) (Eq. 3). Under the assumption that ILD sensitivity, like low-frequency ITD sensitivity (Smith and Price, 2014), is approximately constant across azimuth, i.e., spatially invariant, the predicted MAA is then simply the inverse of the acoustic ILD slope scaled by the value of the discrimination threshold (here we used a fixed value of 1 dB; present psychophysical data; Mills, 1960). As the slope of the ILD-versus-azimuth function decreases with increasing azimuth, high-frequency ILD-mediated spatial acuity, like low-frequency ITD-mediated spatial acuity (Fig. 1C), should deteriorate. However, as seen in Fig. 1D, this purely acoustic (constant-ILD-acuity) prediction deviates substantially from reported MAA values at even modest azimuths, for which the slope of ILD versus azimuth remains steep and informative. This discrepancy suggests that magnitude-dependent variation in the acuity of ILD sensitivity may also impact performance.

3.2. Two separate tasks demonstrate magnitude-dependence of human ILD sensitivity

We assessed spatial variation in behavioral ILD sensitivity using two complementary psychophysical tasks that controlled for confounding monaural intensity cues (see Materials and Methods). In the first task, human listeners ($n=7$) were asked to judge the lateral position of stimuli carrying randomly varied ILDs. Lateralization responses were modulated most steeply near the midline (Fig. 2A), with weaker differentiation at large ILD values. Lateralization means and standard deviations were used to compute ILD discrimination thresholds (see Materials and Methods), revealing a steady increase in threshold with increasing ILD magnitude (Fig. 2B), with estimated thresholds at the largest tested ILD (16 dB) on average twofold greater than those at the midline (paired t-test $t_{6}=3.468$, $p=0.013$). The same held true for a second set of measurements at a frequency of 8 kHz (Fig 2B inset, paired t-test for 16 dB versus 0 dB, $t_{6}=3.133$, $p=0.020$), consistent with the expected frequency invariance of ILD sensitivity (Mills, 1960; Jones et al. 2015). In a second task, discrimination thresholds were measured at 4 kHz over a larger range of ILDs (see Materials

and Methods). Listeners ($n=5$) were presented with a reference stimulus carrying a randomly selected ILD (0, 8, 16, or 24 dB) followed by a target stimulus carrying a smaller or larger ILD. The smallest reliably detectable change in ILD (at $d'=1$) was then determined. Listeners were on average threefold worse at ILD discrimination at the largest tested reference ILD (24 dB) than for a midline reference (0 dB), with graded reductions in sensitivity at intermediate ILDs (Fig. 2C), in good agreement with the shift in lateralization-based thresholds (mean ILD discrimination threshold at reference of 0 dB = 1.04 dB, mean at reference 16 dB = 2.26 dB [paired t-test vs. 0 dB, $t_4=3.472$, $p=0.0255$], mean at reference 24 dB ILD = 3.17 dB [paired t-test vs. 0 dB, $t_4=11.10$, $p=0.0004$]). These data demonstrate that ILD perceptual acuity is significantly magnitude dependent (Carlile et al., 2016, but cf. Hershkowitz and Durlach, 1969; Hafter et al., 1977; see Discussion), such that high-frequency spatial acuity should be expected to reflect such dependence.

3.3. Magnitude dependent ILD acuity better accounts for classic high-frequency MAA data

Next, measures of variation in ILD acuity and acoustic ILD across azimuth were combined to predict high-frequency auditory spatial acuity (MAA). The prediction procedure was the same as described for purely acoustic predictions (section 3.1), excepting that the azimuth-invariant discrimination threshold was replaced with an azimuth-dependent ILD discrimination function. This function, $discrim(ILD) = 0.933 \times e^{0.05129ILD}$ was derived from the empirical discrimination data of the present report (fit to mean discrimination thresholds, dotted line of Fig 2C, $R^2=0.98$), see Methods and Materials). As illustrated in Fig. 3A, the incorporation of an ILD magnitude-dependent sensitivity function results in a sharp increase in predicted MAA with increasing azimuth. Compared to the prediction obtained with azimuth-invariant sensitivity, this prediction better captures the effect of sound source azimuth on high-frequency auditory spatial acuity, with predictive error decreasing at several different frequencies for which acoustic measurements and empirical discrimination performance data were both available (Figs. 3A, B; Mills, 1958). Across frequencies of 4, 6, 8 and 10 kHz for azimuths from 0° - 60° (the MAA could not be determined at 75° for most frequencies in Mills, 1958; see Materials and Methods), the mean absolute error of prediction decreased on average by 44% with the incorporation of spatially-dependent sensitivity (error decrease ranged from 17% [8 kHz] to 71% [6 kHz]).

3.4. Neural correlates of magnitude dependence in ILD acuity

The demonstration of significant magnitude dependence in ILD acuity, and evidence that such dependence may impact auditory spatial acuity *per se*, led us to consider the nature and extent of magnitude dependence in neurons that encode ILD. Sensitivity to ILD arises in neurons that are excited by sound to one ear and inhibited by sound to the opposite ear (Boudreau and Tsuchitani, 1968). As the relative level of sound across the ears varies (i.e., as the ILD changes due to changing source azimuth), the relative strength of excitatory and inhibitory input varies, giving rise to a characteristic sigmoidal ILD tuning function. The fundamental form of such tuning appears to be well-conserved across species and auditory nuclei (Tollin, 2003; Grothe et al., 2010; cf. Yao et al., 2015). Typically, maximal inflection occurs near the midline (0 ILD) – perhaps the expected outcome for a neuron receiving balanced input from the two ears – and neural ILD acuity is correspondingly best at small

ILD magnitudes (Tollin 2003, Grothe et al. 2010). However, in the present context, the acuity of such a neuron at large ILD magnitudes is also of interest. Although behavioral ILD acuity decreases with increasing ILD magnitude, it is hardly eliminated, even at the more extreme ILD values encountered in the free field. In contrast, for a neuron modulated *only* near the midline, acuity *is* eliminated at sufficiently large ILDs, for which responses are saturated and the neuron is unable to distinguish between even very different ILDs (e.g., 15 and 30 dB may elicit the same response). We were thus interested to examine how acuity is – or is not – preserved in a population of neurons across ILD magnitude. In one scenario, acuity might be maintained across a range of magnitudes by neurons that are less sharply modulated, but are modulated (and thus carry information) across a broader range of ILDs. In another scenario, acuity at more extreme ILDs could depend on subsets of neurons that are sharply modulated at non-zero ILDs. Alternatively, the entire population's response might saturate at modest ILD magnitudes, suggesting the involvement of other processes/correlates of performance at extreme magnitudes.

We measured ILD response functions in a population of midbrain neurons in a common auditory model species that is audiometrically similar to humans (in its hearing across frequency and use of binaural cues), the chinchilla (Heffner and Heffner, 1994). As noted above, the fundamental form of ILD coding appears to be well-conserved across species (Tollin, 2003; Grothe et al., 2010), but some aspects of the ILD pathway (e.g., the morphology of the lateral superior olive) vary across species, and distributions of ILD sensitive neurons could also vary. The data that follow should certainly be contextualized in this sense (see Discussion). A typical ILD tuning function is illustrated in Fig. 4A. Such sigmoidal tuning was evident across the neurons of our sample ($n=146$) (which possessed a range of characteristic frequencies, a factor that does not appear to influence ILD tuning parameters, consistent with the frequency-invariance of ILD sensitivity, Jones et al., 2015). As expected, the steepest modulation of firing generally occurred near 0 dB ILD (i.e., around the midline, Fig. 4B; population half-maximal ILD, point of steepest rate/ILD slope = $-0.11 \text{ dB} \pm 12.2 \text{ dB std. dev.}$). However, while the distribution of the population was centered near the midline, many neurons exhibited more eccentric half-maximal ILDs (Fig. 4C), with a substantial proportion at ILD magnitudes greater than 10 dB (40%), and some at magnitudes greater than 20 dB (12%).

In order to assess acuity across reference ILD, we next computed Fisher information for each neuron (Fig. 5A), which (as applied here) quantified the ability of neurons to differentiate adjacent values of ILD. Paired “left” and “right” neurons were then combined to compute neural ILD discrimination thresholds across the population (Fig. 5B; see Materials and Methods). This analysis is distilled in the upper panel of Fig. 5B, which illustrates normalized ILD acuity (re: the midline) in an “average” neuron, or equivalently, across the population, as a function of reference ILD magnitude. Acuity was best near the midline and quite stable within ~ 10 dB of center. Thresholds increased approximately threefold as the ILD magnitude increased from 10 dB to 30 dB. Therefore, while most neurons (60%) were most steeply modulated near the midline, yielding a clear medial bias in sensitivity, a large subset of neurons was steeply modulated away from the midline, mitigating the decrease in acuity with increasing ILD at the population level. Reports from other species also suggest substantial numbers of “off-midline” ILD-sensitive neurons

despite an overall medial tendency in the population (e.g., gerbil, Sanes and Rubel 1988; cat, Irvine and Gago 1990, Tollin et al. 2008; guinea pig, Orton et al. 2016). Recognizing species-specific caveats and the correlational nature of these observations, this pattern of responses (a relatively broad distribution of half-maximal ILDs across reference ILD) suggests one means by which ILD acuity might be conserved at large ILDs/azimuths.

4. Discussion

The observations reported here demonstrate that (1) sensitivity to ILD, the dominant spatial acoustic cue for high-frequency sound localization, is ILD magnitude-dependent, and (2) such magnitude dependence may better account for cross-azimuth variation in high-frequency spatial acuity than acoustic factors alone. Previous psychophysical studies of magnitude dependence in ILD acuity have yielded mixed conclusions, with some suggesting little or no dependence of ILD sensitivity on reference cue magnitude, with variable performance in few subjects (Hershkowitz and Durlach, 1969; Hafter et al., 1977), others implicitly or explicitly suggesting that ILD sensitivity can be considered spatially invariant (e.g., Shinn-Cunningham et al., 2000; Wood and Bizley, 2015), and others suggesting that notable magnitude dependence may exist (Yost and Dye, 1988; Carlile et al. 2016). In the first investigation of this matter, Hershkowitz and Durlach (1969) found little evidence of variation in ILD acuity across reference ILD, concluding "...of interest in these results is the finding that the [threshold ILDs]... do not necessarily increase as the reference condition moves away from the midline." In the most recent investigation, Carlile et al. (2016) found clear evidence for magnitude dependence in ILD acuity commensurate with that demonstrated in the present report, and also of magnitude-*independence* in ITD sensitivity (cf. Smith and Price, 2014). Measurements of ILD thresholds across reference ILD drawn from the psychophysical literature are summarized in Fig. 6. It is possible that methodological constraints (such as lack of monaural level/loudness cue mitigation, e.g. Hershkowitz and Durlach, 1969), or differences in stimuli, experimental paradigm, or listeners have led to the mixed state of evidence. Here, being careful to limit monaural cues, testing across multiple listening paradigms, stimulus frequencies, and experimental subjects, we have provided evidence for significant variation in the precision of ILD sensitivity (ILD acuity) with reference ILD magnitude.

4.1. Implications of magnitude-dependent ILD acuity for spatial acuity and localization

Measurements of auditory spatial acuity (i.e., spatial discrimination, the MAA) are frequently discussed in the binaural and spatial hearing literature and are foundational to certain models and arguments concerning mechanisms of binaural cue encoding. However, genuine acuity data are relatively sparse. Acuity data measured using narrowband stimuli, which enable careful specification of the pertinent acoustic cues, are even rarer. Mills' classic study (1958) remains, to the best of our knowledge, the most comprehensive set of spatial discrimination measurements across frequency and reference azimuth. Most spatial discrimination studies that measure or estimate acuity directly have considered only broadband stimuli (e.g., Heffner et al., 1988; Perrott and Saberi, 1990), or low-frequency stimuli (e.g., Hartmann and Rakerd, 1989), for which performance is presumably dominated by ITD sensitivity (Wightman and Kilster, 1992).

Measurements of auditory acuity thresholds (which can approach 1°) require an apparatus with spatial resolution that is usually only achievable by moving the test loudspeaker between reference and target intervals (as done by Mills). A much more common paradigm is to measure localization *accuracy*, wherein subjects “point” toward the perceived source location (for a detailed discussion of differences between acuity and accuracy, see, e.g., Moore et al., 2008). The error (response re: target location) can then be quantified. Such studies also show a decrease in performance at lateral source angles (Stevens and Newman, 1936; Middlebrooks, 1992; Carlile et al., 1997; Yost, 2016), though the decrease is generally less dramatic than that shown by Mills. Most studies, including those isolating high frequencies (Middlebrooks, 1992; Yost, 2016) have used noise bands rather than tones. Yost and Zhong (2014) reported higher errors for tones than for very narrow noise bands ($<1/6$ oct.), with root-mean-square errors at the lateral-most test angle (75°) exceeding 30° in some cases, resembling the pattern evident in Mills’ data. Neither spatial acuity (MAA) nor accuracy (localization) were measured in the present study, but the narrowband tokens employed were similar in spectral extent to tone bursts (25 Hz bandwidth), and we would expect them to yield similar error patterns.

Very narrowband signals potentiate a high rate of front-back confusions (cf. Middlebrooks, 1992), which could manifest differently in acuity versus accuracy tasks: For a lateral target, a front-back reversal will lead to a moderate absolute error, but in a discrimination context could lead to a systematic and persistent incorrect response (e.g. perceiving a 5° leftward shift relative to a 75° reference at 110° (front-back confusion, incorrect rightward response) versus 70° (correct), cf. Mills, 1958). Additionally, apart from front-back confusions, ILDs become non-monotonic at sufficiently large azimuths, and performance may be profoundly affected by such non-monotonicities under some circumstances. For signals in the region of the “bright spot” (especially prominent in the “low-frequency” range of ILD use, ca. 1500-3000 Hz), discrimination may become impossible (see Macaulay et al., 2010 for a detailed treatment of this matter, including discussion of the bright spot in the context of Mills’ data). After accounting for any such constraints, magnitude dependence in ILD sensitivity should act to *further* constrain performance for lateral targets. For “moderately” lateral targets (e.g., 30° - 60°), our analyses suggest that magnitude-dependence might be a primary constraint.

4.2 Limitations and summary

The present report has pooled data from several sources to provide evidence for a fundamental constraint on spatial hearing at high frequencies. Magnitude dependence in the precision of ILD sensitivity appears to be modest, and under some conditions (lateral sources, or even sources near the head that produce very large ILDs, cf. Brungart and Rabinowitz 1999), the influence of such may be substantial. It would be desirable in the future to obtain acoustic ILD, behavioral ILD, and behavioral spatial acuity measures from a common set of subjects. Subject- and frequency-dependent non-monotonicities in acoustic ILD are not captured by continuous approximations (e.g., sinusoidal fitting to generalized/manikin measurements), and we would certainly expect that more precise within-subjects measurements would lead to improved prediction of spatial acuity performance (cf. Middlebrooks, 1992). Separately, it would be desirable to more explicitly examine the link

between neural ILD coding and ILD-mediated spatial acuity at eccentric azimuths in an animal model (such as the chinchilla), and to further establish the prevalence of neurons most sensitive to off-midline ILDs, which could act to mitigate the medial bias of ILD-coding neural population(s).

We have repeatedly used the term “eccentric” to refer to the extreme left- or rightward azimuths at which spatial acuity is worst. However, significant changes in high-frequency acuity are evident at azimuths as small as $\pm 30^\circ$. ILD magnitude-dependent predictions better account for such changes, suggesting that the observable influence of magnitude dependence is not relegated to extreme azimuths. Nonetheless, as many natural sound sources carry both low- and high-frequency (broadband) information, relatively better spatial acuity for low-frequency components – via ITD sensitivity that appears to be less magnitude dependent (Smith and Price, 2014; Carlile et al., 2016) – may work to mitigate poorer acuity at high frequencies. Additionally, while reduced sensitivity for peripheral source locations is expected to reduce the separability of peripheral sources and also the accuracy of initial localization responses (e.g., Yost and Zhong, 2014), head movement in the direction of the source(s) will bring them to the higher-resolution center of auditory space – one likely ecological solution to the problem of peripheral imprecision (Heffner et al., 1994).

Acknowledgements:

This work was supported by the National Institute for Deafness and Other Communication Disorders (NIH Grant Nos. F32-DC013927 [ADB], R01-DC011555 [DJT], and F31-DC014219 [KLA]) and the University of Washington (ADB). We wish to thank Associate Editor Brian Moore and two anonymous reviewers for helpful comments on an earlier version of this manuscript. We thank Drs. Nathaniel Greene, Kanthiah Koka, and Jennifer Thornton for assistance with physiological experiments, and Dr. Brianne Beemer for assistance with psychophysical experiments. The authors declare no competing financial interests

References

- Benichoux V, Rebillet M, Brette R (2016) On the variation of interaural time differences with frequency. *J Acoust Soc Am* 139:1810–1821. [PubMed: 27106329]
- Benichoux V, Brown AD, Anbuhl KL, Tollin DJ (2017) Representation of multidimensional stimuli: Quantifying the most informative stimulus dimension from neural responses. *J Neurosci* 37:7332–7346. [PubMed: 28663198]
- Boudreau JC, Tsuchitani C (1968) Binaural interaction in the cat superior olive S segment. *J Neurophysiol* 31:442–454. [PubMed: 5687764]
- Brown CH, Schessler T, Moody D, Stebbins W (1982). Vertical and horizontal sound localization in primates. *J Acoust Soc Am* 30:237–246.
- Brown AD, Tollin DJ (2016) Slow temporal integration enables robust neural coding and perception of a cue to sound source location. *J Neurosci* 36:9908–9921. [PubMed: 27656028]
- Brungart DS, Rabinowitz WM (1999) Auditory localization of nearby sources. Head-related transfer functions. *J Acoust Soc Am* 106:1465–1479. [PubMed: 10489704]
- Carlile S, Leong P, Hyams S (1997) The nature and distribution of errors in sound localization by human listeners. *Hear Res* 114:179–196. [PubMed: 9447931]
- Carlile S, Fox A, Orchard-Mills E, Leung J, Alais D (2016) Six degrees of auditory spatial separation. *J Assoc Res Otolaryngol* 17:209–221. [PubMed: 27033087]
- Dahmen JC, Keating P, Nodal FR, Schulz AL, King AJ (2010) Adaptation to stimulus statistics in the perception and neural representation of auditory space. *Neuron* 66:937–948. [PubMed: 20620878]

- Goldberg JM, Brown PB (1969) Response of binaural neurons of dog superior olivary complex to dichotic tonal stimuli: Some physiological mechanisms of sound localization. *J Neurophysiol* 32:613–636. [PubMed: 5810617]
- Green DM, Swets JA (1966) *Signal detection theory and psychophysics*. New York, NY: Wiley.
- Grothe B, Pecka M, McAlpine D (2010). Mechanisms of sound localization in mammals. *Physiol Rev* 90:983–1012. [PubMed: 20664077]
- Haftner ER, De Maio J (1975). Difference thresholds for interaural delay. *J. Acoust. Soc. Am.* 57:181–187. [PubMed: 1110279]
- Haftner ER, Dye RH, Nuetzel HM, Aronow H (1977) Difference thresholds for interaural intensity. *J Acoust Soc Am* 61:829–834. [PubMed: 853155]
- Hancock KE, Delgutte B (2004) A physiologically based model of interaural time difference discrimination. *J Neurosci* 24:7110–7117. [PubMed: 15306644]
- Hartmann WM, Rakerd B (1989) On the minimum audible angle—a decision theory approach. *J Acoust Soc Am* 85:2031–2041. [PubMed: 2732384]
- Hershkowitz RM, Durlach NI (1969) Interaural time and amplitude jnds for a 500-Hz tone. *J Acoust Soc Am* 46:1464–1467. [PubMed: 5361515]
- Heffner RS, Heffner HE (1988) Sound localization acuity in the cat: Effect of azimuth, signal duration, and test procedure. *Hear Res* 36:221–232. [PubMed: 3209494]
- Heffner RS, Heffner HE, Kearns D, Vogel J, Koay G (1994) Sound localization in chinchillas. I: Left/right discrimination. *Hear Res* 80:247–257. [PubMed: 7896583]
- Hubel DH, Wiesel TN (1960) Receptive fields of optic nerve fibres in the spider monkey. *J. Physiol* 154:572–580. [PubMed: 13716437]
- Irvine DRF, Gago G (1990) Binaural interaction in high-frequency neurons in inferior colliculus of the cat: Effects of variations in sound pressure level on sensitivity to interaural intensity differences *J Neurophysiol* 63: 570–591. [PubMed: 2329362]
- Jones HG, Brown AD, Koka K, Thornton JL, Tollin DJ (2015) Sound frequency-invariant neural coding of a frequency-dependent cue to sound source location. *J Neurophysiol* 114:531–539. [PubMed: 25972580]
- Kuhn GF (1977) Model for the interaural time differences in the azimuthal plane. *J Acoust Soc Am* 62:157–167.
- Macaulay EJ, Hartmann WM, Rakerd B (2010) The acoustical bright spot and mislocalization of tones by human listeners. *Hear Res* 127:1440–1449.
- McAlpine DA, Jiang D, Palmer AR (2001) A neural code for low-frequency sound localization in mammals. *Nat Neurosci* 4:396–401. [PubMed: 11276230]
- Middlebrooks JC (1992) Narrow-band sound localization related to external ear acoustics. *J Acoust Soc Am* 92:2607–2624. [PubMed: 1479124]
- Mills AW (1958) On the minimum audible angle. *J Acoust Soc Am* 30:237–246.
- Mills AW (1960) Lateralization of high-frequency tones. *J Acoust Soc Am* 32:132–134.
- Moore JM, Tollin DJ, Yin TCT (2008) Can measures of sound localization acuity be related to the precision of absolute location estimates? *Hear Res* 238, 94–109. [PubMed: 18178351]
- Orton LD, Papasavvas CA, Rees A (2016) Commissural gain control enhances the midbrain representation of sound location. *J Neurosci* 36: 4470–4481. [PubMed: 27098691]
- Parsons CH, Lanyon RG, Schnupp JWH, King AJ (1999) Effects of altering spectral cues in infancy on horizontal and vertical sound localization by adult ferrets. *J Neurophysiol* 82: 2294–2309. [PubMed: 10561407]
- Pavao R, Sussman ES, Fischer BJ, Pena JL (2018) Anticipated ITD statistics built-in human sound localization. *bioRxiv* doi.org/10.1101/303347.
- Perrot DR, Saberi K (1990) Minimum audible angle thresholds for sources varying in both elevation and azimuth. *J Acoust Soc Am*:1728–1731. [PubMed: 2341677]
- Porschmann C, Arend JM, Neidhardt A (2017). A spherical near-field HRTF set for auralization and psychoacoustic research. *AES eBrief*:322
- Schone H (1984) *Spatial Orientation*. (Princeton University Press, Princeton, NJ).

- Seung HS, Sompolinsky H (1993) Simple models for reading neuronal population codes. *Proc Nat Acad Sci* 90:10749–10753. [PubMed: 8248166]
- Shinn-Cunningham BG, Santarelli S, Kopco N (2000) Tori of confusion: Binaural localization cues for sources within reach of a listener. *J Acoust Soc Am* 107:1627–1636. [PubMed: 10738816]
- Smith RCG, Price SR (2014) Modelling of human low frequency sound localization acuity demonstrates dominance of spatial variation of interaural time difference and suggests uniform just-noticeable differences in interaural time difference. *PLOS One* 9:e89033. [PubMed: 24558468]
- Stevens SS, Newman EB (1936) The localization of actual sources of sound. *Am J Psychol* 48: 297–306.
- Stevens JC, Choo KK (1996) Spatial acuity of the body surface over the life span. *Somatosens Mot Res* 13: 153–166. [PubMed: 8844964]
- Rayleigh Lord (1907) On our perception of sound direction. *Phil Mag* 13:214–232.
- Tollin DJ (2003) The lateral superior olive: A functional role in sound source localization. *The Neuroscientist* 9: 127–143. [PubMed: 12708617]
- Tsai JJ, Koka K, Tollin DJ (2010) Varying overall sound intensity to the two ears impacts interaural level difference discrimination thresholds by single neurons in the lateral superior olive. *J Neurophysiol* 103: 875–886. [PubMed: 20018829]
- Wichmann FA, Hill NJ (2001) The psychometric function: I. Fitting, sampling and goodness of fit. *Percept Psychophys* 63:1293–1313. [PubMed: 11800458]
- Wightman FL, Kistler DJ (1992) The dominant role of low-frequency interaural time differences in sound localization. *J Acoust Soc Am* 91:1648–1661. [PubMed: 1564201]
- Wood KC, Bizley JK (2015) Relative sound localization abilities in human listeners. *J Acoust Soc Am* 138:674–686. [PubMed: 26328685]
- Yao JD, Bremen P, Middlebrooks JC (2015) Transformation of auditory spatial sensitivity along the ascending auditory pathway. *J Neurophys* 113:3098–3111.
- Yost WA, Dye RH (1988) Discrimination of interaural level differences as a function of frequency. *J Acoust Soc Am* 83:1846–1851. [PubMed: 3403800]
- Yost WA, Zhong X (2014) Sound source localization identification accuracy: Bandwidth dependencies. *J Acoust Soc Am* 136:2737–2746. [PubMed: 25373973]

- Auditory spatial acuity declines at lateral locations, especially at high frequencies
- Interaural level difference (ILD) informativeness also generally declines with azimuth
- However, ILD alone does not appear to account for classic cross-azimuth acuity data
- Incorporating ILD-magnitude-dependent variation in ILD perceptual acuity better accounts for these data
- Modest and similar variation in acuity is evident in ILD-sensitive neural populations

Figure 1:

A. Human auditory spatial acuity (MAA, minimum audible angle) for narrowband signals (pulsed tones) from the classic report of Mills, 1958. At low frequencies, performance is mediated by the interaural time difference cue (ITD); at high frequencies, by the interaural level difference cue (ILD). Arrows/dashed lines indicate that an MAA could not be determined (N) at the given reference azimuth. **B.** Upper panel: Acoustic ITD for lowpass noise (cutoff 0.5 kHz). Lower panel: Acoustic ILD at 6 kHz (25-Hz bandwidth); the shaded region 0-60° indicates the range over which MAA error estimates are given in the present paper (Fig. 3). All cue values were computed from a publicly available database (Porschmann et al., 2017; see Materials and Methods) and fitted with sinusoids. **C.** Predicted MAA at 0.5 kHz (lower panel) based on ITD slope (upper panel) plotted with Mills' data, after Smith and Price (2014). **D.** Predicted MAA at 6 kHz (lower panel) based on ILD slope (upper panel) plotted with Mills' data.

Figure 2:

A. Lateralization magnitude (upper panel) and standard deviation (lower panel) for human subjects (n=7) presented with narrowband 4-kHz noise bursts carrying varied ILDs. **B.** ILD discrimination thresholds assessed using lateralization data from (A) (see Materials and Methods) demonstrate increasing threshold with increasing ILD magnitude; the same pattern is observed at 8 kHz (inset; see text). **C.** Explicit ILD discrimination thresholds measured with directly varied reference ILDs reproduce and extend the trend shown in (B) to a larger reference ILD of 24 dB.

Figure 3:

A. Combining magnitude dependent changes in ILD sensitivity with the changing acoustics of ILD across azimuth improves prediction of high-frequency spatial acuity (MAA values) as reported by Mills (1958), shown here at 6 kHz. **B.** Summary quantification of predictive accuracy (mean absolute error) for azimuths from 0° - 60° at several frequencies for which spatial acuity is mediated by ILD. Magnitude dependent (open bars) predictions are more accurate than constant-sensitivity (solid bars) predictions (see text).

Figure 4:

A. An example rate-ILD tuning curve is shown. Each point gives the mean firing rate observed over 50 stimulus presentations at the specified ILD, ± 1 standard error. Tuning to the ILD cue is well characterized by a logistic function (Eq. 4). **B.** Responses for all neurons in the study population, normalized to the logistic fitted maxima. **C.** The distribution of half-maximal ILDs (inflection points of the fitted logistics, individual data given by open gray circles near abscissa) across the population shows a strong medial bias, but many neurons are most steeply modulated away from the midline (see text).

Figure 5:

A. Fisher information (FI), computed using Eq. 5, is shown for all studied neurons in the study population. The population mean is given by the bold trace. **B.** Across the study population, FI (left ordinate, lower panel) and corresponding neural ILD discrimination thresholds (right ordinate, lower panel) show a central bias. Each bold trace represents the bootstrapped “average” for a pair of neurons ± 1 standard deviation (see Materials and Methods). In a normalized sense, the population neural ILD discrimination threshold was approximately threefold worse at 30 dB ILD than at midline (upper panel; see text).

Figure 6:

Psychophysical measurements of the influence of reference ILD on ILD acuity are summarized. All data are normalized to mean thresholds obtained at a 0 dB reference. Stimuli were as follows: Hershkowitz and Durlach (1969), 500 Hz tone burst; Hafter et al. (1977), high-frequency filtered (3-4 kHz) click; Yost and Dye (1988), 5000 Hz tone burst; Carlile et al. (2016), speech token 'ee' as spoken by female talker. See text and cited references for additional details.