The rapid decline in interaural-time-difference sensitivity for pure tones is explained by a single frequency-channel model

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ABSTRACT

The interaural time difference (ITD) is a primary horizontal-plane sound localization cue computed in the auditory brainstem. ITDs are accessible in the temporal fine structure of pure tones with a frequency of no higher than about 1400 Hz. Explaining how listeners' ITD sensitivity transitions from very best sensitivity near 700 Hz to impossible to detect within 1 octave currently lacks a clear physiological explanation. Here, it was hypothesized that the rapid decline in ITD sensitivity is dictated not to a central neural limitation but by initial peripheral sound encoding, specifically, the low-frequency edge of the cochlear excitation pattern produced by a pure tone. To test this hypothesis, ITD sensitivity was measured in 16 normal-hearing listeners as a joint function of frequency (900-1500 Hz) and level (10-50 dB sensation level). Performance decreased with increasing frequency and decreasing sound level. The slope of performance decline was 90 dB/octave, consistent with the low-frequency slope of the cochlear excitation pattern. Consequently, fine-structure ITD sensitivity near 1400 Hz may be conveyed primarily by "off-frequency" activation of neurons tuned to lower frequencies near 700 Hz. Physiologically, this could be realized by a single narrow channel near 700 Hz that conveys fine-structure ITDs. Such a model is a major simplification and departure from the classic formulation of the binaural display, which consists of a matrix of neurons tuned to a wide range of relevant frequencies and ITDs.

(Number of words: 230/250)

SIGNIFICANCE STATEMENT

Human sensitivity to fine-structure interaural time differences declines with increasing frequency at an incredible rate of 90 dB/octave above 1200 Hz. This is best explained by initial peripheral processing (auditory filtering and off-frequency processing), not a central neural limitation such as a decline phase locking. A binaural model with a single dominant channel near 700 Hz can explain these data, which contradicts the classic formulation of binaural display that utilizes a matrix of neurons tuned to a range of best frequencies and interaural time differences.

(Number of words: 85/120)

INTRODUCTION

Humans can precisely localize sounds in the horizontal plane. When a sound is located away from the midline, the extra distance that the sound travels to the far ear generates an interaural time difference (ITD) (1). There is an obvious central physiological substrate for ITD processing in the medial superior olivary complex of the mammalian auditory brainstem, which consists of neurons that primarily respond to low frequencies and receive bilateral frequency-matched inputs from the anteroventral cochlear nucleus from cells that have short-latency and secure synaptic connections with superior temporal precision (2-5).

The most important ITD cues for sound localization occur at frequencies below 1500 Hz (6, 7) and are conveyed in the acoustic waveform's temporal fine structure, the temporal aspects of the rapid variation in pressure that the auditory nerve can precisely

encode. There are two notable features to ITD frequency dependence below 1500 Hz. First, the best sensitivity in ITD discrimination for pure tones is exquisitely good, on the order of 10 µs. This occurs for pure tones near 700 Hz (8-10), which coincides with the often-called ITD frequency "dominant region" (i.e., a region of very high relative weight) for lateralization of narrowband noises, transients, and complex tones that exceed a single peripheral cochlear filter width (11-15). Second, ITD discrimination sensitivity for pure tones declines at a remarkable slope previously estimated to be at least 46-78 dB/octave as frequency is increased from 1200 to 1400 Hz (10, 16). This is much steeper than the 12 dB/octave decline in temporal information conveyed by auditory nerve phase locking (17) (i.e., the ability to generate action potentials during a preferred phase of the waveform), making the decline in neural phase locking a relatively poor explanation for this phenomenon. The question posed in this study is whether the dominant region and the upper limit of fine-structure ITD processing are related. This could be a result of some unique aspect of binaural processing at 700 Hz that allows for very effective conveyance of fine-structure ITD.

Most studies that investigate the frequency dependence of ITD discrimination sensitivity present stimuli at a fixed level, for example 65 dB SPL (9) or 70 dB SPL (10, 16), comparable to the level of conversational speech. Lower level sounds (e.g., 10 dB sensation level, SL) are perceived relatively nearer the midline (18) and have worse ITD discrimination thresholds (19). For low-frequency pure tones, Zwislocki and Feldman (8) measured ITD discrimination thresholds in up to six normal-hearing listeners as a function of level (10-110 dB SL) and frequency (250, 500, 1000, and 1250 Hz). ITD performance decreased as the frequency increased from 1000 to 1250 Hz, and as the level

116 decreased from 70 to 10 dB SL. At 10 dB SL and 1250 Hz, the ITD discrimination
117 threshold was not measurable, which places the upper limit of fine-structure ITD
118 processing at a frequency that is much lower than the typically reported 1400 Hz for
119 higher level tones (10).
120
121 (Figure 1 about here)
122
123 Another stage of the auditory system that shows an incredibly steep slope occurs
124 at the auditory periphery in the cochlea (inner ear), where there is a high-resolution
125 frequency decomposition of sound; in the cochlea, sound is effectively passed through a
126 bank of narrowly tuned bandpass filters (20). The low-frequency edge of the cochlear
127 excitation pattern (i.e., the representation of the effective amount of excitation produced
128 by a stimulus or internal spectral representation of a stimulus) (21) generated by one of
129 these peripheral bandpass auditory filters is approximately 100 dB/octave at 1000 Hz (20,
130 22). This means that tonal excitation at a frequency just above the ITD frequency
131 dominant region extends downward to induce activity in dominant region neurons tuned
132 near 700 Hz, but this activity would decrease rapidly with increasing tone frequency and
133 decreasing tone level (Fig. 1). Moreover, at some frequency near 1400 Hz, activity of
134 neurons in the dominant region would cease altogether regardless of the tone level due to
135 the exceptionally steep cochlear excitation pattern. That expectation is consistent with the
136 abrupt cessation of the ability to use fine-structure ITDs near 1400 Hz. Such a
137 relationship can be understood if the upper limit of fine-structure ITD processing was
138 investigated as a function of level. Such measurements, however, have not been made

with adequate resolution to quantify the slope of ITD sensitivity decline with adequate precision. Therefore, this study measured this upper limit as a function of frequency and sound level. It was hypothesized that the upper limit of fine-structure ITD processing decreases with decreasing level with a slope near 100 dB/octave, suggesting it is a consequence of peripheral auditory filtering, the low-frequency edge of the cochlear excitation pattern. Through the confirmation of this hypothesis, we have shown that these data are best explained by the initial peripheral encoding, and that fine-structure ITD is conveyed through responses of a single dominant channel tuned near 700 Hz, contradicting the classic formulation of the binaural display.

RESULTS AND DISCUSSION

The upper limit of fine-structure ITD sensitivity decreases from 1400 to 900 Hz with decreasing sound level

Individual ITD discrimination data are shown in Fig. 2 for all 16 normal-hearing human listeners. The average performance across all tested conditions is reported in each panel. While there is variability in the overall performance, the patterns in the data are consistent across listeners and testing sites. Two listeners (M6 and B3) had great difficulty with this task, with an average performance <60%. These two listeners were removed from subsequent group analyses. For all other listeners, ITD discrimination performance decreased systematically with increasing frequency and decreasing sound level.

(Figure 2 about here)

The average ITD discrimination data are shown in Fig. 3(A) for 14 listeners. A three-way repeated-measures analysis of variance was performed on ITD discrimination performance transformed to rationalized arcsine units (23) with factors frequency (7 levels: 900-1500 Hz), level (4 levels: 10, 20, 30, 50 dB SL), and testing location (3 levels: Maryland, Nebraska, Colorado). The Greenhouse-Geisser correction was used to address sphericity assumption violations. There were significant effects of frequency [$F(2.8,5.6)=73.7$, $p<0.0001$, $\eta_p^2=0.87$] and level [$F(1.6,3.2)=99.4$, $p<0.0001$, $\eta_p^2=0.90$]. There was a significant frequency×level interaction [$F(4.4,8.8)=13.9$, $p<0.0001$, $\eta_p^2=0.56$]. The effect of testing location was not significant [$F(2,11)=0.265$, $p=0.772$, $\eta_p^2=0.05$], and there were no significant interactions with testing location ($p>0.05$ for all).

(Figure 3 about here)

The upper limit of fine-structure ITD processing (defined as 75% correct ITD discrimination performance) was found for each presentation level and for each listener by fitting the data with a logistic regression (24). The frequency boundaries are shown in Fig. 3(B). These data generally agree with others that show that the upper limit of fine-structure ITD processing is near 1400 Hz for sound levels above 50 dB SPL.(8-10, 16) Across listeners, the frequency that yielded 75% correct ITD discrimination was 1264.8±95.4 Hz (range=1168–1483) for 50 dB SL tones. For better comparison to past studies estimating the upper frequency boundary at higher levels, the data in Fig. 3(B)

were fit by a three-parameter exponential rise to maximum function. The best fitting equation (r=0.74, p<0.0001) was $y = 775.9 + 587.6 \times (1 - e^{-0.039x})$, where y is the frequency boundary and x is the sensation level. Evaluating this function at 70 dB SL yielded an estimated upper frequency boundary of 1326 Hz with a 95% confidence interval from 1212 to 1437 Hz, the latter which encompasses the upper frequency boundary measured in other studies (8-10, 16).

Any other small discrepancies in the upper limit of fine-structure ITD processing between the current study and others can be explained by methodological differences. For example, our stimuli had slow diotic ramps minimizing contributions from onset ITD (25). We also tested more listeners than previous studies, and thus may have included more listeners that were not operating at a point near the absolute limits of human binaural processing, including two that were middle aged (26, 27). Similarly, Klug and Dietz (10) and Best and Swaminathan (28) tested a relatively large number of normal-hearing listeners (n=9), and reported relatively larger ITD thresholds compared to some studies with relatively smaller (potentially more selective) samples. It may also be that more extensive training would improve ITD discrimination performance to the levels of the best listeners in this study (29), including the two who had <60% total correct responses and were omitted from the average data and slope calculations (described below).

These data also agree with other studies that show declines in ITD discrimination performance with decreasing sound level (8, 19, 28). This decrease in performance with decreasing level causes the 75% correct performance point to shift from about 1400 to 900 Hz [Fig. 3(B)]. It is notable that changing the stimulus level from 50 to 30 SL

207 produces a marked change in the upper limit given that both stimuli are clearly audible;
208 this result is difficult to reconcile with a phase locking explanation, which reaches a
209 maximum within ~20 dB of neural threshold (30). Hence, it is important to account for
210 the stimulus sound level when considering the upper limit of fine-structure ITD
211 processing.
212

213 The rate of fine-structure ITD sensitivity decline is 90 dB/octave, best 214 explained by peripheral cochlear filtering

215 A linear fit between the sound level (in dB SL) and the frequency boundary (in
216 octaves relative to 1000 Hz) determined the slope of the ITD performance change. The
217 10 dB SL point was omitted from the calculation for 2 of the 14 listeners (M3 and C2)
218 because they did not have an estimate of the frequency boundary at 75% correct (i.e.,
219 they were guessing in this condition). The resulting fit slopes are shown in Fig. 3(C). The
220 median slope was 90.5 dB/octave (range=40.7–244.6). The linear fits explained a median
221 of 88% in the variance of the data points (range=74–99.8).

222 The most important addition to our knowledge that results from this study is that
223 the slope of ITD discrimination performance decline was measured to be 90 dB/octave
224 [Fig. 3(C)]. Such a steep slope of decline limits the possible explanations for the
225 physiological mechanisms that are involved in the upper limit of fine-structure ITD
226 processing. For example, Klug *et al*. showed that phase locking in the auditory nerve
227 across animal models declines at approximately 12 dB/octave (17). Therefore, the decline
228 in phase locking by itself cannot account for these data because the slopes are so
229 different. In contrast, one well-known stage of the auditory system that does have such a

steep slope is the low-frequency edge of the cochlear excitation pattern, which is approximately 100 dB/octave near 1000 Hz (20, 22).

Fine-structure ITD sensitivity as a function of frequency appears to be a result of off-frequency listening to a single channel near 700 Hz

If the peripheral cochlear filtering interpretation of these data is correct, it has a further important corollary. It suggests that ITD sensitivity for stimulus frequencies between 1000-1500 Hz are primarily driven by lower-frequency neurons, such as those tuned between 500-1000 Hz–in other words, the region where the best ITD sensitivity is observed (9) and location of the ITD frequency dominant region for ITD (Fig. 1) (13). There could be a narrow band of neurons near 700 Hz in humans that is responsible for conveying fine-structure ITD, which in turn yields the exquisite sensitivity to fine-structure ITDs and carries most of the localization weight for broadband stimuli. Indeed, examination of the functional form of ITD sensitivity as a function of frequency [see Fig. 9 in Klug and Dietz (10)] resembles the neural response area of a high level tone (i.e., a shallow low-frequency portion, a minimum at 700 Hz, a sharp high-frequency portion; the inverse of the excitation patterns shown in Fig. 1), which would suggest the possibility of a single dominant channel for fine-structure ITD processing. To the extent that neurons tuned to 1000-1500 Hz contribute to fine-structure ITD sensitivity, they are clearly less important than those between 500-1000 Hz because the observed transition slope does not extend near the high-frequency edge of their tuning, which would be 2 kHz or higher. They may, in fact, not contribute at all. In other words, the dominant region neurons are highly weighted even for pure tones.

Future behavioral and physiological experiments that examine ITD sensitivity as a function of frequency and level are required to better understand the properties of the neurons that convey fine-structure ITD information. Such experiments include animal studies in mammalian models to determine if they have a single dominant fine-structure ITD channel and its location in frequency. For example, primates may have a dominant channel near the same frequency region as humans but in animals with smaller heads like cats, ferrets, and chinchillas, it could be higher, if it exists at all. (31)

The proposed "dominant channel theory," having only a single narrow band of ITD sensitive neurons near 700 Hz, is starkly different than the classic binaural display proposed by Jeffress (11, 32, 33), which consists of a matrix of frequency- and ITD-tuned neurons. Such a reimagining of human ITD processing overlaps with past discussions about mammalian vs avian binaural-processing models, the distribution and length of neural delay lines, and how the binaural system processes physiologically plausible and implausible ITDs (2, 4, 33-35). This dominant channel theory can be formulated to be consistent with the idea that the binaural system evolved in a manner to emphasize ecologically valid range of ITDs that provide unambiguous location information(36), helping to reconcile the discrepant interpretation of data from several past binaural-hearing studies.

In summary, the rapid 90 dB/octave rate of decline in fine-structure ITD sensitivity is best explained by initial peripheral cochlear filtering. This suggests that listeners are performing off-frequency listening to a single dominant channel tuned near 700 Hz. Such a model contradicts the classic binaural display that utilizes a matrix of

neurons that yield maximum firing rates at their best frequency and best interaural time difference.

METHODS

Listeners and Equipment

Sixteen young to middle-aged (mean=30.1 years, range=20-51 yrs) normal-hearing listeners (10 female) were tested in this study. Hearing thresholds were measured at octave frequencies from 0.25-8 kHz. Hearing thresholds were ≤20 dB hearing level (HL) for all listeners except C1, who had slightly higher thresholds ≥6 kHz. Interaural asymmetry in hearing thresholds was ≤10 dB except it was 15 dB at 1000 Hz for listener M5. Data from the authors (listeners M1, B1, B2, and C1) were included.

The testing was done at three locations (Maryland, Nebraska, and Colorado), three to seven listeners at each location. Each location used the same testing software and type of circumaural headphones (HD280 Pro, Sennheiser; Hannover, Germany). Stimuli were generated and the experiment was conducted on a personal computer using MATLAB (the Mathworks; Natick, MA). Procedures were reviewed and approved by the University of Maryland, Boys Town National Research Hospital in Nebraska, and the University of Colorado School of Medicine Multiple Institutional Review Boards for use of human subjects.

In Maryland, testing was performed in a double-walled sound booth (IAC; North Aurora, IL). Stimuli were presented to listeners via an external sound card (Sound Blaster PLAY! 3, Creative Labs; Milpitas, California). In Nebraska, testing was performed in a double-walled electromagnetically shielded sound booth (ETS-Lindgren; Cedar Park,

TX). Stimuli were presented to listeners via USB audio interface (RME Fireface UFX; Haimhausen, Germany). In Colorado, testing was performed in a single-walled custom-built sound booth. Stimuli were presented to listeners via an external digital-to-analog converter (Schitt Modi, Schitt Audio; Newhall, CA) and headphone amplifier (Schitt Magni 3+, Schitt Audio; Newhall, CA).

Stimuli

The stimuli were pure tones that were 250 ms in duration, with frequencies of 900-1500 Hz in 100-Hz steps. For audiometric threshold measurements, tones were presented diotically. For ITD discrimination testing, tones started with the left channel in sine (0°) phase and the right channel had the same phase or a phase that yielded ±167-µs ITDs. Then a diotic raised-cosine temporal ramp applied that had a 100-ms rise-fall time. In other words, ITD was applied in only the temporal fine structure. The tone amplitude was 10-, 20-, 30-, and 50-dB SL.

Procedure

<u>Pure-Tone Audiometric Threshold Measurements</u>

Pure tones were presented diotically. An experimenter controlled the timing of presentation and level of the stimulus by using buttons that could adjust the level by 0, ±1, ±2, or ±6 dB. Listeners indicated when they heard a tone. Experimenters adjusted the sound level above and below the level that produced threshold (transition from response to no response) at least twice to determine a final threshold level (TL), which defines 0 dB SL, at each test frequency. The frequencies were tested in increasing order. The threshold at each frequency was tested twice for most listeners. If the two thresholds differed by >5 dB, additional threshold levels were measured and the average of the last

321 two measurements were used. Across-frequency averaging was implemented to smooth
322 out small variations in TL during later periods of testing (listeners M6, B4, B5, B6): the
323 average TL at each frequency was computed as the average of levels from the target and
324 adjacent frequencies, rounded to the nearest integer. For example, the TL at 1200 Hz was
325 based on the six measurements from 1100, 1200, and 1300 Hz. Adjustments due to
326 averaging were small–generally, less than 2 dB; on average <1 dB over all listeners and
327 frequencies–and yielded comparable results to unsmoothed TLs used for other listeners.

328 Left-right ITD Discrimination

329 Listeners performed a two-interval forced-choice discrimination task based on the
330 task described by Füllgrabe and Moore (26). Each interval presented a sequence of four
331 250-ms tone bursts with sinusoidal envelopes. In the reference interval, all four tone
332 bursts had zero ITD. In the target interval, the ITD alternated twice between right and left
333 leading ±167-μs ITDs (i.e., right-left-right-left). This ITD magnitude was chosen because
334 it corresponds to one-quarter of the stimulus period at 1500 Hz, which was the highest
335 frequency tested in this study. Hence, this ITD should yield the maximum performance at
336 1500 Hz and avoids the descending portion of the cyclical psychometric function. There
337 was a 200-ms silent interval between the target and reference intervals. The order of the
338 intervals was randomized with a probability of 50%. The task of the listener was to
339 identify which interval contained the target alternating ITD.

340 The task was self-paced because listeners initiated each trial. After the stimulus
341 was presented, the listener indicated the target interval by pressing a button on the screen.

342 Pre-experiment training was performed to ensure the listener understood the task
343 and had no apparent problems with binaural processing. Listeners were initially presented

with 10 trials at 500 Hz and 70 dB SL. Training in 10-trial blocks continued until performance was 100% correct. Almost all the listeners needed only the initial 10 practice trials to proceed.

For the main experiment, a method of constant stimuli was performed where all combinations of frequency and level were presented in random order, consisting of seven frequencies (900–1500 Hz in 100-Hz steps) and four levels (10, 20, 30, and 50 dB SL). Therefore, there were 112 trials per block (7 frequencies×4 level×4 trials), and each block took ~10 minutes to complete. Testing breaks were provided between blocks as needed. Listeners performed 60 trials/condition, which took ~3 hours. Three listeners were provided less than 60 trials (minimum of 56 trials) for at least one condition and four listeners were provided more than 60 trials (maximum of 83 trials) for at least one condition because of computer or experimenter error. Correct answer feedback was provided after each trial, which helped keep the listener attentive during testing blocks.

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Figures and Captions:

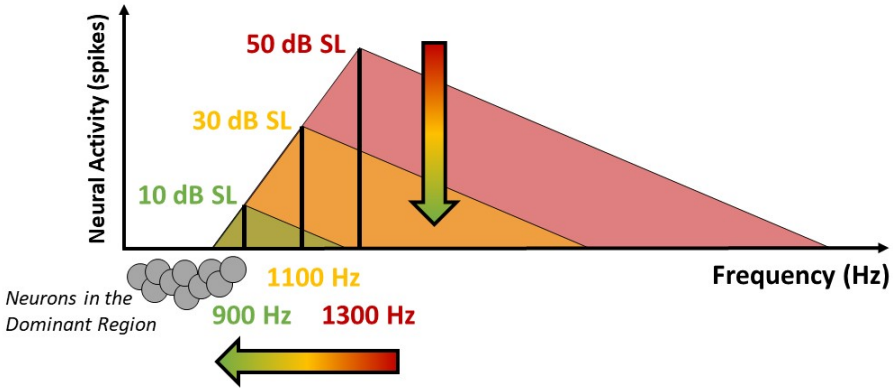

Fig. 1: Illustration of the transformation of input acoustic tones into their effective neural spectral representations (i.e., their excitation patterns, which have a steep low-frequency slope and shallow high-frequency slope) and their relationship to the experimental hypothesis. If fine-structure ITD is primarily conveyed by neurons in the ITD frequency dominant region near 700 Hz, decreasing the stimulus level will decrease the highest frequency that demonstrates fine-structure ITD sensitivity at approximately the same slope as the low-frequency edge of the cochlear excitation pattern, about 100 dB/octave.

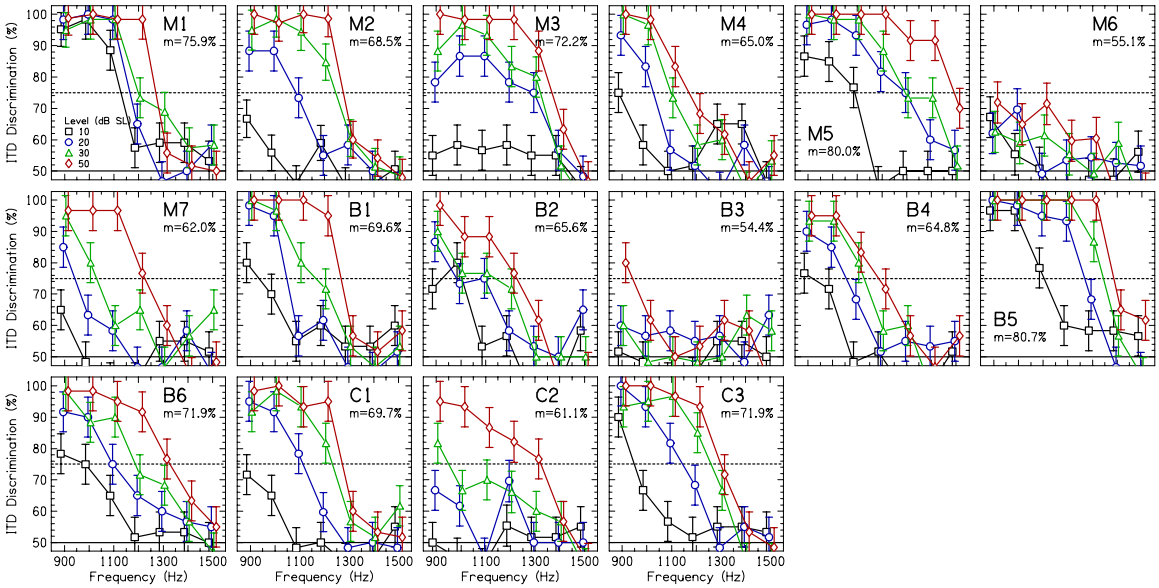

Fig. 2: Percent correct as a function of frequency and level (in dB SL) for 16 listeners. Error bars show 95% confidence intervals. The average percent correct over all conditions is reported in each panel.

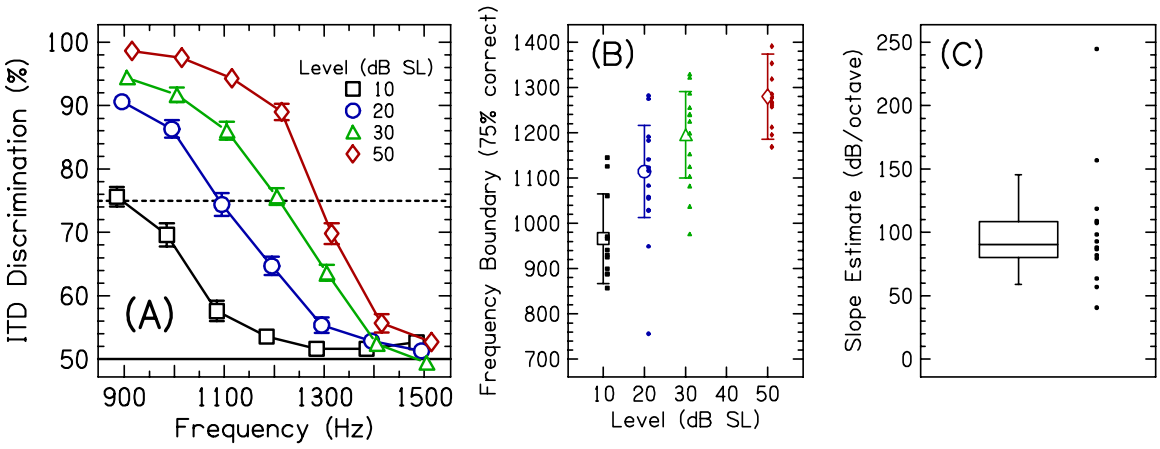

Fig. 3: (A) Percent correct as a function of frequency and sensation level for 14 listeners. Error bars represent ±1 standard error. Some conditions had error bars that were smaller than the symbol. (B) Frequency boundaries that yield 75% correct ITD discrimination performance. Small closed symbols show individual data. Large open symbols show the data averaged over listeners. The error bars represent ±1 standard deviation. (C) Linear slope estimates between sound level (in dB SL) and frequency (in octaves). Small closed symbols show the slope for the individual listeners. The box length represents the interquartile range, and the median is shown within the box. Whiskers extend to 10th and 90th percentiles.