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Trading of interaural differences in high-rate Gabor click trains

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Abstract

In this study, combinations of interaural time differences (ITD) and interaural level differences (ILD) were applied to trains of 4000 Hz Gabor clicks (Gaussian-filtered impulses) and presented to listeners over headphones. ITD / ILD equivalence functions, or “trading ratios” (TR) were estimated using two different procedures: a “closed-loop” procedure in which subjects adjusted (via head-turn) the ILD of a target click train to counteract the effects of an imposed ITD, and an “open-loop” procedure in which subjects indicated (also via head-turn) the lateral position of click trains containing independent combinations of ITD and ILD. For both tasks, TR values increasingly favored ILD over ITD as inter-click interval (ICI) decreased from 10 to 2 ms. Subsequent analysis confirmed that this change reflected a loss of sensitivity to envelope ITD at short ICI rather than a gain in sensitivity to ILD, consistent with prior studies demonstrating rate-limited processing of ongoing envelope ITD. Significant intersubject differences in the data included two subjects whose TR values obtained under both procedures were consistently lower (greater influence of ITD) than other subjects', and did not vary with ICI. Such differences suggest that multiple mechanisms of ITD/ILD combination may be utilized to varying degrees by individual listeners. By at least one of those mechanisms, ITD sensitivity (but not ILD sensitivity) is limited to low modulation rates.

Keywords

binaural hearing; time-intensity trading; onset dominance; rate limitation

1. Introduction

The primary acoustic cues for sound localization in azimuth are interaural differences in time (ITD) and level (ILD) of sound arriving at the two ears. These cues result from interactions of the sound field with the head and pinnae, and vary systematically with both the spatial location of a sound source and the frequency content of the sound. The largest and most informative ILD cues arise from sound with energy at high frequencies, where attenuation at the far ear (“head shadowing”) is most effective. In contrast, the most informative ITD cues arise from low-frequency sounds. That distinction is embodied in Rayleigh's “duplex theory” (Strutt, 1907) of pure-tone localization. For complex tones, ITD is carried not only by the fine structure of the stimulus waveform, but also by fluctuations in the temporal envelope occurring at sound onset or offset or due to ongoing amplitude

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modulation. Sensitivity to these “envelope ITDs” at high carrier frequency can be comparable to fine-structure ITD sensitivity at low-frequencies (Bernstein and Trahiotis, 2002). Sensitivity to ongoing envelope ITD, however, is limited to amplitude modulation rates below approximately 200–500 Hz, beyond which onset ITD plays a more significant role (Nuetzel and Hafter, 1976; McFadden and Moffitt, 1977; Burns and Colburn, 1977; Freyman et al., 1997; Hafter and Dye, 1983; Saberi, 1996; Bernstein and Trahiotis, 2002; Stecker and Brown, 2010b; Brown and Stecker, 2010).

Azimuthal localization of complex sounds, therefore, relies upon a combination of cues including ILD (especially at high frequencies), fine-structure ITD (especially at low frequencies), and envelope ITD carried by onsets, offsets, and ongoing modulations. In the absence of competing sound sources and acoustically reflective surfaces (i.e., in the free field), the various cues should agree and suggest a common sound-source direction. When echoes and reverberation are present, however, both the temporal fine structure and the temporal envelope of the sound at the ears become distorted. In that case, the ongoing interaural differences may fluctuate over time and fall into conflict with one another or with the veridical sound-source direction.

Notably spared from the deleterious effects of echoes and reverberation is the first-arriving wavefront, and so one strategy that the auditory system employs in such situations is to emphasize the binaural cues carried by sound onsets (Wallach et al., 1949; Hafter and Dye, 1983; Hafter et al., 1983; Litovsky et al., 1999; Freyman et al., 1997; Stecker and Hafter, 2002). This onset dominance, or precedence effect applies to ITD and ILD (Hafter et al., 1983), as well as to monaural spectral cues for localization in elevation (Blauert, 1971; Litovsky et al., 1997). Another strategy is to weight the various cues according to their expected informativeness, as suggested by the “plausibility hypothesis” of Rakerd and Hartmann (1985). According to that hypothesis, localization is based on a weighted combination of information from multiple cues (e.g., ITD and ILD) which may each be affected in specific ways by echoes and reverberation. The relative weights reflect an estimation of the reliability or plausibility of each cue. For example, Rakerd and Hartmann (1985) presented 500 Hz tones from an array of loudspeakers in the presence of a single reflective surface (side wall). For loudspeakers located closest to the wall, in-ear recordings revealed significant distortion of the ITD, such that large changes in ITD occurred with small changes in source location and implausibly large values of ITD were commonly observed. In that case, listeners' localization responses relied upon the ILD. Thus, the plausibility hypothesis suggests that combinations of ITD and ILD are localized in an adaptive manner that is sensitive to the specific acoustic effects of echoes and reverberation.

A majority of studies investigating onset dominance for interaural cues have focused on single cue types (e.g., ITD) presented in isolation from other cues (ILD). For example, Hafter and Dye (1983), Freyman et al. (1997), and Stecker and Brown (2010b) measured ITD discrimination thresholds for click trains with ILD held at 0 dB, and found strong onset dominance when inter-click intervals (ICIs) were shorter than 3–5 ms (i.e., modulation rates above 200–300 Hz). In separate experiments parallel to the ITD measurements, Hafter et al. (1983) and Stecker and Brown (2010b) measured ILD thresholds while ITD was held at 0 μ s. Hafter and colleagues reported onset dominance for ILD that was similar to that observed for ITD. Stecker and Brown (2010b), however, reported no onset dominance for ILD. Although in disagreement with the former result, the latter result suggests that when both cues are present (i.e., in the free field), listeners might rely more heavily on ILD at high modulation rates.

Stecker and Hafter (2002) measured “temporal weighting functions” (TWF, a plot of relative sensitivity to spatial cues distributed over the duration of a brief sound) for high-frequency

click trains presented in the free field. Consistent with results obtained using ITD alone (Hafters and Dye, 1983; Hafters and Buell, 1990; Saberi, 1996; Stecker and Brown, 2010b), they reported evidence of strong onset dominance at short ICI (≤ 3 ms). Additionally, however, and different from ITD studies, they reported “upweighting” of clicks occurring near the end of the train (Stecker and Hafters, 2002, 2009). That result is consistent with an enhanced role of ongoing ILD in localization at high rates, in the sense that upweighting could reflect the contribution of ongoing ILD information available in the freefield but absent in pure-ITD studies. Further consistent with that view, a pair of recent studies measuring TWFs for the two cues presented in isolation of one another both revealed relatively greater weighting of ongoing ILD than ITD (van Hoesel, 2008; Brown and Stecker, 2010).¹ The current study tests the hypothesis that relative weighting of ITD and ILD in the lateralization of click trains carrying both cues will vary with modulation rate, such that ILD plays a greater role in the lateralization of high-rate stimuli.

1.1. Trading of ITD and ILD

The current study follows the logic of a number of classic studies that investigated the relative contributions of ITD and ILD cues to sound localization by presenting the two cues in opposition to one another (Shaxby and Gage, 1932; Feddersen et al., 1957; David et al., 1959; Deatherage and Hirsh, 1959; Moushegian and Jeffress, 1959; Harris, 1960; Whitworth and Jeffress, 1961; Hafters and Jeffress, 1968). To the extent that ITD and ILD are translated into a common representation at some level of auditory processing, the lateral position of a sound with ITD favoring one ear can be shifted toward the interaural midline by applying an appropriate ILD favoring the opposite ear. Adjusting the two cues to produce a centered acoustic image gives the point of equivalence between the two cues, and the ratio of ITD to ILD in that situation gives the ITD/ILD “trading ratio” (TR). The TR varies with stimulus parameters including frequency (Harris, 1960; Moushegian and Jeffress, 1959), intensity (Deatherage and Hirsh, 1959; David et al., 1959; Hafters and Jeffress, 1968), and duration (Hafters and Jeffress, 1968). The TR also varies significantly as a function of which cue the subject adjusts (Trahiotis and Kappauf, 1978; Lang and Buchner, 2008), and across individual subjects (Moushegian and Jeffress, 1959). The current study assesses the extent to which TR varies with the inter-click interval (ICI) of a narrowband click train.

1.2. Closed-loop versus open-loop tasks

A second question addressed by the current study is whether the task employed plays a major role in determining the measured TR. Typically, trading studies have employed closed-loop² adjustment tasks in which the subject makes a series of adjustments to the ITD or ILD of the target or a separate pointer stimulus. Successive adjustments are interleaved with presentations of the stimuli, and subjects are instructed to successively reduce the perceptual difference between target and pointer positions.³ Subjects indicate an acceptable match upon minimizing that difference. This approach raises two types of concerns for investigators interested in relating the results to typical localization behavior. One concern is that with repeated exposure to the stimulus, listeners might focus on specific cues that may not have been clearly apparent on the first presentation. For example, the “buildup” of

¹Both van Hoesel (2008) (testing bilateral cochlear implantees) and Brown and Stecker (2010) demonstrated onset-dominated TWFs for short-ICI stimuli carrying ILD, but the degree of onset dominance was significantly reduced compared to TWFs for the stimuli carrying ITD. Brown and Stecker (2010) reported that whereas listeners' discrimination of ITD at short ICI was well predicted by the direction of the onset ITD, discrimination of ILD closely followed the mean ILD across clicks. Similarly consistent with greater averaging of ongoing ILD information, Stecker and Hafters (2009) reported weights to increase gradually toward the end of each train (a “recency” effect), and suggested that result to reflect “leaky” temporal integration of available ongoing ILD information (Akeroyd and Bernstein, 2001).

²The terms “closed-loop” and “open-loop” are taken from control theory, and refer to systems that do and do not utilize continuous feedback to minimize error.

³Or between target and midline, in some methods.

precedence effect (Freyman et al., 1991) suggests that onset dominance might increase with repeated stimulation. Alternatively, subjects might change their adjustment strategy multiple times during the sequence (minimizing the error with respect to different aspects of the sound over the sequence of the trial). Thus, the relative weighting of ITD and ILD might differ significantly from that which occurs during overt open-loop localization in which successive error-correction is not possible. A second related concern is that closed-loop adjustment makes different demands upon memory for location than does the localization of real sounds in space. Whereas open-loop responses require that spatial percepts or responses be encoded and maintained during the stimulus-response interval, closed-loop tasks may be performed without resort to spatial memory encoding and maintenance, relying instead on “sensory-trace” processing (Durlach and Braida, 1969) for direct comparison of target and reference. Thus, memory-related effects such as primacy and recency effects (Stecker and Hafter, 2009) might manifest differently in open- and closed-loop tasks. To address these issues, two methods were employed in separate experiments: Experiment 1 utilized a closed-loop adjustment procedure modified from Hafter and Jeffress (1968), while Experiment 2 utilized an open-loop procedure collecting one absolute (pointing) response on each trial following a single presentation of the sound.

2. Experiment 1: Closed-loop adjustment

In this experiment, a method similar to that of Hafter and Jeffress (1968) was employed to measure ITD/ILD trading ratios for filtered click trains varying in ICI. As in that earlier study, “traded” stimuli carrying ITD and ILD in opposite sign were presented in alternation with diotic reference stimuli, and subjects were asked to adjust the traded stimulus to match the perceived location of the diotic reference. By including an objective reference, this procedure seeks to avoid ambiguity associated with subjective centering of a traded stimulus presented in isolation. In contrast to Hafter and Jeffress (1968), who imposed ILD and asked listeners to adjust ITD using a rotary knob, the present method imposed ITD and asked listeners to adjust ILD by means of a head turn. Use of the head turn offers an intuitive response mode for most listeners and facilitates comparison to head-centered orienting tasks as used in Experiment 2. The results may be considered equivalent to those obtained using more “traditional” adjustment procedures (e.g., Hafter and Jeffress, 1968), except for differences in the perceived locations of target and pointer stimuli and the expectation that trading ratios typically favor the adjusted cue—ILD in this case—(Trahiotis and Kappauf, 1978).

The hypothesis under test in this experiment is straightforward: if the processing of ongoing envelope ITD is impaired for high-rate stimuli (Hafter and Dye, 1983; Saberi, 1996; Bernstein and Trahiotis, 2002), but the processing of ILD is not (Stecker and Brown, 2010b), then ITD/ILD trading ratios should change as a function of modulation rate. Specifically, larger ratios (indicating relatively greater influence of ILD) should be obtained at modulation rates above around 200 or 300 Hz (3–5 ms ICI) than at lower rates. In this experiment, we tested three values of ICI spanning this critical range: 10, 5, and 2 ms (100, 200, and 500 Hz modulation rate).

2.1. Methods

All procedures, including recruitment, consenting, and testing of human subjects followed the guidelines of the University of Washington Human Subjects Division and were reviewed and approved by the cognizant Institutional Review Board.

2.1.1. Subjects—Eight subjects participated in this experiment. One (0501) was the first author, and two (0502, and 0503) were undergraduate research assistants working in the lab. The remainder (0601, 0701, 0702, 0801, 0803) were paid subjects naive to the purpose of

the experiment. All subjects reported normal hearing and demonstrated pure-tone detection thresholds < 15 dB HL over the range 250-8000 Hz.

2.1.2. Apparatus—Stimulus generation and audio presentation was conducted using TDT RX6 hardware (Tucker-Davis Technologies, Alachua FL) under computer control using MATLAB. Sounds were amplified (TDT HB6) and presented to listeners via open-backed circumaural headphones (Sennheiser HD485). Listeners' head position and orientation was measured, in 3 dimensions of translation and 3 of rotation, using an electromagnetic position sensor (Polhemus Fastrak, Colchester VT), whose transmitter was suspended in a wooden frame approximately 3-6 inches above the listener's head, and whose receiver was affixed to the top of the headphones. Fastrak data were accessed via TDT HTI3, which communicated with the RX6 used for stimulus generation. Responses were collected via custom handheld button box connected to a logic input of the RX6.

2.1.3. Stimuli—Stimuli consisted of trains of narrowband Gabor clicks (Gaussian-windowed tone bursts). Each click consisted of a 4 kHz cosine multiplied by a Gaussian temporal envelope with $\sigma = 221 \mu\text{s}$. (The resulting spectral bandwidth was also Gaussian, with $\sigma = 750 \text{ Hz}$, or half-maximal bandwidth $\approx 1.8 \text{ kHz}$). Trains of 16 clicks with peak-to-peak ICI equal to 2, 5, or 10 ms were synthesized at 48.848 kHz. Click trains were presented via headphones at 61–68 dB SPL (time-averaged sound level varied with ICI). ITDs were imposed on the test sounds by delaying the waveform presented to one ear. ILDs were imposed by increasing the level in one ear and attenuating the level in the other ear, each by 1/2 the ILD.

2.1.4. Procedure—At the start of each run, subjects were instructed to face forward and press the handheld button to begin. In response to the button press, head position and angle was recorded to define a default, or “head-forward” position. Throughout the remainder of the run, head-position measurements were made relative to this reference position. Stimulus presentation began following a 2 s delay.

On each trial, “reference” and “test” stimuli were presented in alternation with an interstimulus interval (ISI) of 500 ms (onset to onset). The diotic reference stimulus was presented with zero ITD and zero ILD. The test stimulus ITD was selected pseudorandomly on each trial, with values ranging from $-225 \mu\text{s}$ (left-leading) to $+225 \mu\text{s}$ (right-leading) in $50 \mu\text{s}$ steps. The ILD of the test stimulus was under subject control via head position. Immediately prior to each presentation of the test stimulus, the listener's head azimuth θ (left/right angle, in degrees) was measured and used to compute a *compensatory ILD* applied to the test stimulus. The compensatory ILD was computed in real time by polynomial approximation to published measurements at 5000 Hz (Shaw, 1974; Gulick et al., 1989):

$$ILD(\text{dB}) = -1.2e^{-5}\theta^3 + 0.22\theta \quad (1)$$

to be consistent with a head-centered sound-source azimuth equal in magnitude but opposite in sign to the head azimuth θ . That is, the compensatory ILD corresponded to that of a fixed sound source located at 0° azimuth in the original (head forward) reference frame.

Rotation of the listener's head in the direction of the imposed ITD therefore resulted in an oppositely-directed ILD, and shift of the combined image back toward interaural midline. Similarly, head rotation toward the opposite side of space increased the ILD in the direction of the ITD, shifting the combined image away from center. To the extent that listeners were able to trade ITD and ILD in these stimuli, a centered image could be produced by turning the head to produce an ILD of sufficient magnitude to cancel the effects of imposed ITD.

Subjects were instructed to rotate the head slowly until the apparent location of the test stimulus matched, as closely as possible, that of the diotic reference stimulus (the apparent location of which remained fixed with respect to the head at all times). In the event that multiple or broad spatial images were perceived, subjects were instructed to match the leftmost image (or leftmost edge, in the case of a broad image) (Whitworth and Jeffress, 1961; Hafter and Jeffress, 1968). Subjects indicated the match by pressing a handheld button, following which they returned to head-forward position. A new trial began following a 2 s delay.

Each run consisted of 40 trials (4 for each of 10 ITD values, presented in random order). Separate runs were completed for each value of ICI tested. The order of ICI testing was assigned randomly for each subject and each repetition. Subjects completed at least 2 runs per ICI. Subjects 0501, 0502, and 0801 each completed a third run at each ICI.

2.1.5. Analysis—To accommodate differences in the bias or range of responses across experimental session, individual-trial data were normalized to z-scores by subtracting the overall mean and dividing by the overall standard deviation of responses in each experimental run. Subsequently, data for each subject were restored to units of ILD by multiplying by the subject's overall standard deviation and adding the overall mean across all responses. Stimulus-specific mean ILDs for each combination of test-stimulus ITD and ICI were then computed and used to generate trading functions (Fig. 1) for each ICI. ITD/ILD trading ratios were computed by linear regression of the adjusted (compensatory) ILD onto the imposed ITD across all trials, separately for each combination of subject and ICI:

$$\widehat{ILD} = \beta ITD + k \quad (2)$$

The regression slope β defines the trading ratio in dB ILD per μ s ITD. For consistency with past studies, its inverse was computed to define the trading ratio TR in units of μ s ITD per dB ILD:

$$TR = 1/\beta. \quad (3)$$

Statistical confidence intervals on β were computed at the $\alpha = .05$ level using standard techniques, and transformed following Equation 3 to compute confidence intervals on TR, plotted in Fig. 2. With respect to comparisons across conditions for individual subjects, statements of statistical significance refer conservatively to non-overlapping 95% confidence intervals of this type (i.e., $p < .01$)⁴, whereas statements indicating lack of significant difference refer to situations where at least one of the compared estimates falls within the 95% confidence interval of the other (i.e., $p > .05$).

2.2. Results

Figure 1 plots trading functions for individual subjects (panels). Within each panel, the mean adjusted ILD (vertical axis) is plotted against imposed ITD (horizontal axis) for each tested value of ICI (lines). Although clear individual differences in the overall slope of the trading function (i.e., the trading ratio) are apparent, all subjects demonstrated a reliable negative slope, indicating that negative ILD was required to compensate for imposed positive ITD, and vice versa. Note the expanded ILD range plotted for subjects 0601 and 0701. Compared to other subjects, these subjects required significantly more ILD to counter a given value of

⁴For distributions of approximately equal variance, non-overlapping 95% confidence intervals correspond to $\alpha \approx .005$ (see Payton et al., 2003).

ITD, regardless of ICI. That result suggests that the relative salience of the two cues was not constant across subjects. The remaining 6 subjects demonstrated shallower slopes, indicating a relatively greater contribution of ILD, as well as a dependence of slope on ICI, with shallower slopes for the shortest ICI (2 ms) compared to other ICIs. That difference is further summarized in Fig. 2, which plots the ITD/ILD trading ratio in $\mu\text{s}/\text{dB}$ (vertical axis) across subjects and ICI conditions. Overall, trading ratios depended significantly on ICI (repeated-measures ANOVA, $F_{(2)14} = 6.45$, $p < .05$). Consistent with Fig. 1, trading ratios were smallest overall for subjects 0601 and 0701, and did not vary with ICI for those subjects. The remaining subjects showed higher trading ratios (indicating relatively greater dependence on ILD), which varied a great deal across subjects. Despite individual differences in overall trading ratio, however, 5 of the 6 subjects demonstrated a consistent dependence of trading ratio upon ICI, with significantly lower ($p < .01$) trading ratios observed at 10 ms ICI (mean = $72.4 \mu\text{s}/\text{dB}$, excluding 0601 and 0701) than at 2 ms ICI (mean = $118.7 \mu\text{s}/\text{dB}$).

3. Experiment 2: Open-loop lateralization

The goal of Experiment 2 was to replicate the findings of Experiment 1 using an open-loop (non-adjustment) method. Rather than asking subjects to adjust the value of one cue (ILD) to subjectively offset the other (ITD) as in Experiment 1, single stimuli carrying specific combinations of ITD and ILD were presented, and listeners were asked to indicate the subjective location of each stimulus combination with a single head turn (that is, by orienting to the perceived location). The advantage of this open-loop procedure is twofold: First, by eliminating the feedback available due to repeated stimulus presentation, we can measure localization functions corresponding to the first impression of a stimulus, which more directly relates to the requirements of localizing brief sounds in natural listening. Second, independent manipulation of the two cues (ITD and ILD) allows us to separate the trading ratio into its underlying components and determine if changes to the trading ratio reflect increasing (or decreasing) contributions of one or both cues.

Ideally, the orientation task of experiment 2 would involve the localization of sounds which are clearly externalized (Toole, 1970), so that head turns would map in a systematic way to behavior in free-field localization tasks. However, reliable externalization was not expected in the current study because the stimuli lack features typical of external sound sources, such as monaural spectral cues and consistent ITD/ILD combinations. One may thus expect some subjects to experience difficulty when asked to turn their heads in the direction of an intracranial image. Here, subjects were instructed to produce a head turn that scaled with the perceived lateral position of the sound image. None reported difficulty in determining appropriate responses, and indeed spontaneous comments indicated that most subjects treated the task as one of pointing the nose in the direction of a sound's location in space. Notably, all subjects had previously completed testing in experiment 1, and that prior experience may have helped subjects to learn a mapping between image location and head angle. Regardless, the computation and interpretation of ITD/ILD trading functions depends only on the reliability of that mapping, and does not require that subjects perceived the sounds themselves to be externally located in the direction of the head turn.

3.1. Methods

The same eight subjects tested in Experiment 1 participated in Experiment 2. The methods of Experiment 2 corresponded closely to those of Experiment 1, with the following exceptions:

3.1.1. Stimuli

Stimuli were trains of 16 Gabor clicks identical to those used in experiment 1, but with ITD and ILD manipulated differently to accommodate an open-loop testing procedure (see below).

3.1.2. Procedure

As in Experiment 1, subjects began each run of trials by facing forward and pressing the handheld button to define the “head-forward” position. Stimulus presentation began following a 2 s delay.

On each trial, a single stimulus was presented with a specific combination of ITD and ILD. Tested values of ITD ranged -225 to $+225 \mu\text{s}$ (right-leading) in $50 \mu\text{s}$ steps; tested values of ILD ranged -5 to $+5$ dB in steps of 2 dB. As in Experiment 1, positive ITD or ILD values favored the right ear. All 60 combinations of ITD and ILD were tested, in random order, twice per run of 120 trials. Immediately after hearing the sound, subjects were instructed to rotate the head so that their nose pointed in a direction corresponding to the perceived location of the sound, and then press a button to record their response. As in Experiment 1, subjects were instructed to indicate the leftmost image in any case where multiple images were apparent, or the leftmost edge in any case where a broad image was perceived. Responses were recorded in units of degrees azimuth head position. Following response collection for a given trial, subjects returned to head-forward position, and a new trial began following a 2 s inter-trial interval.

Each run consisted of 120 trials. Subjects completed at least 2 runs per ICI (2, 5, and 10 ms). Subjects 0501, 0502, 0801, and 0803 each completed a third run at each ICI.

3.1.3. Analysis

Individual-trial data were normalized across runs by subtracting the overall mean of responses across each experimental run. Stimulus-specific mean ILDs for each combination of test-stimulus ITD and ICI were then computed and used to generate trading functions (Fig. 3) for each ICI. ITD/ILD trading ratios were computed by multiple linear regression of the response angle θ onto the imposed ITD and ILD across all trials, separately for each combination of subject and ICI:

$$\hat{\theta} = \beta_T \text{ITD} + \beta_L \text{ILD} + k \quad (4)$$

The trading ratio TR was computed from the ratio of ITD slope β_T and ILD slope β_L . As in Experiment 1, TR has units of μs ITD per dB ILD.

$$\text{TR} = \beta_T / \beta_L. \quad (5)$$

Statistical confidence intervals on $\log(\text{TR})$ were computed by parametric bootstrap estimation. 10,000 random samples were generated independently from normal distributions defined by each slope (β_T and β_L) and the standard error of each slope. A random estimate of $\log(\text{TR})$ was computed for each of these 10,000 pairs of coefficients according to Eq. 5. The widths of 95% confidence intervals were computed from the resulting distribution of $\log(\text{TR})$. This procedure was completed separately for each combination of subject and ICI.

3.2. Results

Figure 3 plots mean localization functions for each combination of subject (rows) and ICI (columns). Clear individual differences are evident in both the overall range of response azimuth and in its relative dependence on ITD and ILD. Consistent with the results of Experiment 1, for example, subjects 0601 and 0701 exhibited a strong dependence of response azimuth on ITD (apparent in the slopes of individual curves). Subject 0503, in contrast, exhibited a stronger dependence on ILD (apparent in the vertical separation of curves). For six of the eight subjects, localization functions suggest weaker effects of ITD at 2 ms as compared to 10 ms ICI.

Open-loop TR is plotted across subject and ICI in Fig. 4. The data reiterate the results of Experiment 1 (Fig. 2). Overall, TR significantly depended on ICI (repeated-measures ANOVA, $F^{(2)14} = 10.91, p < .01$). Compared to other subjects, subjects 0601 and 0702 exhibited lower overall TR, which did not change significantly with ICI. Other subjects exhibited greater TR and a consistent pattern of increasing TR as ICI shortened from 10 to 2 ms. Consequently, TR was significantly greater at 2 ms ICI (across-subject mean of $184.7 \mu\text{s}/\text{dB}$, omitting 0601 and 0702) than at 10 ms ICI ($80.2 \mu\text{s}/\text{dB}$) in 5 of 6 remaining subjects. Subject 0502 exhibited a similar trend of TR with ICI, but the difference was not statistically significant, due to increased variance in the TR estimate at 2 ms ICI.

One concern with open-loop measurement of TR as employed here reflects the choice of values at which to test each cue. Large values of one cue, for example, might overwhelm the contribution of the other cue, leading to non-linear (compressed) localization functions. In that case, estimates of TR could become biased, as the compressed response range causes β to systematically under-estimate the influence of the cue assigned the larger value. To examine this possibility, TR was recomputed separately using only trials with large ($\pm 5 \text{ dB}$) or small ($\pm 1 \text{ dB}$) ILD. Those ranges correspond to the outermost or innermost curves plotted in Fig. 3, respectively. Response data were filtered to select only trials matching the selected ILD range, and TR recomputed following Equations 4 and 5. Fig. 5 plots the TR values separately for the two ILD ranges. A 2-way repeated-measures analysis of variance (ANOVA) detected significant main effects of ICI ($F_{(2)14} = 6.8, p < .01$) and ILD range ($F_{(1,7)} = 31.0, p < .001$), but no significant interaction between the two factors ($F_{(2,14)} = 0.1, p > .05$). Altogether, the results suggest that larger values of TR (i.e., TR more strongly favoring ILD) were obtained for larger ILD than for smaller ILD,⁵ but that the effects of ICI were similar across the tested range of ILD.

3.2.1. Specific contributions of ITD and ILD to open-loop TR

The systematic increases in TR with shorter ICI observed in both current experiments are consistent with decreasing influence of ITD, increasing influence of ILD, or both. Figure 6 plots the two components of TR measured in Experiment 2 (β_T and β_L) separately to compare ITD and ILD sensitivity across subjects and conditions. Mean values for individual subjects (symbols) are plotted for each ICI (10 to 2 ms, light to dark shading) and interconnected with line segments. In general, the line segments progress systematically and horizontally from right to left with decreasing ICI, indicating little change in β_L with ICI. That is, changes in TR (indicated by contour lines projecting from the origin) with ICI reflect decreases in β_T rather than increases in β_L , consistent with a rate-dependent loss in sensitivity to envelope ITD but not ILD.

⁵The dependence of TR on ILD range is consistent with compression of responses to stimuli carrying large values of ITD and ILD (see Fig. 3).

3.2.2. Comparison of TR across methods

Values of TR are compared across the closed-loop (Experiment 1) and open-loop (Experiment 2) procedures in Fig. 7 for each combination of subject (symbol) and ICI (symbol shading). Overall, the two measures were significantly correlated ($r = 0.76, p < .0001$). A 2-way repeated-measures ANOVA revealed a significant main effect of ICI ($F_{(2,14)} = 12.9, p < .001$)—consistent with the dependence of TR on ICI found for individual subjects in both experiments—along with a significant main effect of procedure ($F_{(1,7)} = 7.2, p < .05$), but no significant procedure-by-ICI interaction ($F_{(2,14)} = 1.8, p > .05$). For a majority of subjects, TR values were somewhat higher (by factors ranging 1:1 to 2:1) when measured using the open-loop procedure than the closed-loop procedure.

4. Discussion

4.1. Implications for temporal weighting of binaural cues

The current results are consistent with recent work in our lab showing greater onset-dominance for ITD than for ILD at high click rates (Stecker and Brown, 2010b; Brown and Stecker, 2010). Together with other studies, the overall results support a rate-limitation in the processing of ongoing envelope ITD at high frequency (Haftner and Dye, 1983; Bernstein and Trahiotis, 2002), which results in a shift toward the remaining intact cues: onset ITD (Haftner and Dye, 1983; Saberi, 1996; Stecker and Haftner, 2002; Stecker and Brown, 2010b) and ILD.

Apparently inconsistent with the current results is the observation of Haftner et al. (1983) that binaural adaptation affects ILD in a manner identical to ITD. Based on the results of that study, one would expect TR to be largely independent of ICI, as ongoing cues of both types (ILD and envelope ITD) are affected similarly by increasing stimulus rate. While we currently lack an adequate explanation of that discrepancy, it has been noted and discussed previously by Stecker and Brown (2010b). Their study compared listeners' discrimination of ITD or ILD cues appearing at the onsets or offsets of trains of 16 Gabor clicks. They found that ITD discrimination at 2-ms ICI was significantly impaired for offsets compared to onsets, but that ILD discrimination was equivalent regardless of the temporal placement of the cue. Noting the discrepancy with results of Haftner et al. (1983), they suggested the possibility that “U-shaped” temporal weighting of ILD cues (cf. Stecker and Haftner, 2009) affords similar sensitivity to onsets and offsets, despite an ICI-dependent reduction in sensitivity to ILD carried by intermediate clicks.⁶ Recent work in our laboratory has begun to explore this possibility, and consistent with the suggestion of U-shaped TWFs, reveals greater sensitivity to ILD carried by the endpoints than by the “interior” of a high-rate click train (Stecker and Brown, 2010a).

4.2. Individual differences in TR values

Consistent with previous studies (e.g., Moushegian and Jeffress, 1959), the current results demonstrated significant individual differences in overall TR, which ranged from less than 40 to over 250 $\mu\text{s}/\text{dB}$ across subjects, for physically identical stimuli. Intersubject differences in the current data were similar across both types of tasks, suggesting that such differences were primarily intrinsic to the subjects themselves rather than due to effects of the specific task or to random, session-to-session variation. Of particular interest in the current data are two subjects—0601 and 0702—who demonstrated the lowest overall TR in both experiments. Unlike the majority of other subjects, those two exhibited TR which did

⁶Increasing the click train duration, as Haftner et al. (1983) did, moves the onset and offset further apart in time. With U-shaped temporal weighting, the additional interior clicks make progressively weaker and weaker contributions to ILD processing (Stecker, 2010).

not vary significantly with ICI. That is, the two low-TR subjects differed from other subjects not only in the *magnitude*, but also in the *pattern* of their data, suggesting the possibility that they utilized a qualitatively different strategy than other subjects.

4.2.1. Two-image lateralization—It is worth noting that prior reports of individual differences in ITD/ILD trading have demonstrated the existence of two distinct auditory images with different sensitivity to the two cues (Whitworth and Jeffress, 1961; Hafter and Jeffress, 1968). One, the “time image” is dominated by the ITD ($TR < 10\mu s/dB$ for 500 Hz tones, $2 - 35\mu s/dB$ for high-pass clicks), while the other “intensity image” is strongly affected by both cues ($TR \approx 20-50\mu s/dB$ for tones, $80 - 150\mu s/dB$ for clicks) (Hafter and Jeffress, 1968). Well-practiced subjects can be trained to match either or both images (Hafter and Jeffress, 1968); unpracticed subjects may differ in their preference, with some matching the “time” image and others matching the “intensity” image. Hafter and Jeffress (1968) suggested that differences in the propensity of unpracticed subjects to match one or the other image might explain a significant portion of individual variability observed in prior studies, and that argument may be similarly applied here. That is, the low TRs of subjects 0601 and 0702 in the current study appear consistent with the “time” image, whereas those of other subjects appear more similar to the “intensity” image, based on the TR ranges described by Hafter and Jeffress (1968) for high-pass clicks. If so, a further hypothesis may be drawn from the data: the “time” image appears to be unaffected by ICI of stimuli used in this study, whereas the TR of the “intensity” image is strongly ICI-dependent. In other words, only the “intensity” image is affected by the rate-limitation for ongoing envelope ITD, a distinction that may in turn relate to differences in the dynamics of ITD processing in binaural brainstem nuclei (see section 4.4.2).

4.2.2. Individual differences in onset dominance—To the extent that TR is sensitive to the degree of onset dominance affecting the ITD cue, individual differences in TR might additionally reflect differences in the degree of onset dominance experienced by different listeners. In a pair of studies, Saberi and colleagues (Saberi and Antonio, 2003; Saberi et al., 2004) studied the ability of listeners' to discriminate the ITD or ILD of a lag click that followed a diotic lead click by a 2-ms ICI. Lag-click thresholds were elevated approximately two-fold compared to thresholds for single isolated clicks. The ratio of threshold elevation, however, varied across listeners from less than 1 (indicating no onset dominance) to over 4 (for ITD, Saberi and Antonio, 2003) or 6 (for ILD, Saberi et al., 2004). Assuming similar variability across listeners tested in the current study might suggest similarly large differences in TR, and especially in the effects of ICI upon TR. Because Saberi and colleagues did not measure threshold ITDs and ILDs in the same listeners, however, it remains unclear whether differences in the relative weighting of ITD and ILD might reflect differences in the degree of onset dominance for one or the other cue.

4.3. Implications for measurement of ITD/ILD trading functions

The current study employed a pair of novel procedures for measuring ITD/ILD trading functions in individual listeners. Although the closed-loop procedure of Experiment 1 was modeled closely on prior studies using closed-loop adjustment (e.g., Hafter and Jeffress, 1968), both it and the open-loop procedure of Experiment 2 required listeners to make tracked head-turn responses. The methods were apparently successful, in that (1) response functions were systematic and sensitive to the interaural differences in the stimuli (Figs. 1 and 3) and (2) TR values were roughly consistent with prior studies. Informal comments by listeners indicated that the response method was quick and intuitive, consistent with listeners' presumed familiarity with orienting to sound sources outside of the lab. Aside from issues of experimental convenience, we have no reason to suspect different outcomes using more traditional adjustment (knob-turning) or scaling responses (magnitude estimation,

visual-analog scaling, etc.). Future studies might directly compare the reliability of spatial scaling across such methods.

Comparison of results across Experiments 1 and 2 revealed a significant difference between TR measured using open-loop and closed-loop tasks. Although both tasks presumably measured the same underlying percept (perceived location), the difference might have reflected procedure-dependent biases. Previous studies have demonstrated closed-loop adjustment tasks to be sensitive to the choice of which cue is adjusted, with TR values biased in favor of the attended or adjusted cue (Young and Levine, 1977; Trahiotis and Kappauf, 1978; Lang and Buchner, 2008). In Experiment 1 of the current study, listeners adjusted ILD. Therefore, the past results suggest a bias toward ILD (i.e., toward larger TR). Since the open-loop procedure of Experiment 2 did not involve attention to or adjustment of either cue, one would expect little if any systematic bias in that case. Thus, the overall effects of bias should have been in favor of greater TR for closed-loop adjustment over the open-loop task, but the opposite result was found (greater TR in the open-loop task). The discrepancy cannot be addressed within the context of the current data alone, and we cannot offer an explanation at this time.

4.4. Implications for neural mechanisms

To understand the effects of ICI on ITD/ILD trading requires a view of how the two cues are processed (individually and together) in the auditory nervous system. It is thus informative to consider the neural mechanisms by which ITD and ILD might potentially interact. Here, we briefly consider the effects of ITD and ILD on auditory peripheral responses, and subsequently the sites of ITD/ILD convergence in central structures.

4.4.1. Effects of the auditory periphery on ITD/ILD trading

Reduction in neural modulation depth at high rates: When an impulse is delivered to the ear of a listener, it sets the basilar membrane into motion that decays over time. If a subsequent impulse is delivered during the period of initial vibration, the two responses will overlap in time such that the overall vibration fails to demonstrate the temporally discrete nature of the impulses. A straightforward consequence of this behavior is that the ability of auditory neurons to encode temporal variation in a click-train stimulus is limited to low rates (long ICI), especially at apical (low frequency) regions of the cochlea, where the basilar membrane impulse response is long. It can reasonably be expected that obscuration of temporal envelope features in this way would impact the processing of envelope-ITD more strongly than ILD cues (Hartmann and Constan, 2002) and thereby increase TR at short ICI. Although the current results are consistent with that general view, the relatively high carrier frequency suggests a minimal role for this type of effect at the tested ICI values.⁷ Previous results demonstrating rate-limited and onset-dominated ILD processing (Hafer et al., 1983, 1988) further suggest the need to consider other possible mechanisms.

Level-to-time conversion: A second relevant aspect of auditory peripheral function is embodied in the *latency hypothesis* presented by Jeffress (1948) to describe how ILD sensitivity might emerge within a purely ITD-sensitive mechanism. Jeffress suggested that increasing the intensity at one ear might reduce the latency of that ear's response and thereby induce a neuronal ITD favoring the louder ear (see also Deatherage et al., 1959; Whitworth and Jeffress, 1961). Possible mechanisms for this level-to-time conversion include intensity-dependent changes in cochlear vibration as well as the intrinsic response thresholds of

⁷The Gabor click trains used in the current study had a carrier frequency of 4000 Hz. Modeling of the cochlear response to these stimuli by Gammatone filtering (Akeroyd, 2001) suggests 100% modulation at 5 ms ICI. Shortening the ICI to 2 ms reduces the modulation depth to approximately 75%, whereas a 1-ms ICI preserves less than 10% modulation. (Stecker, 2009).

auditory neurons. The latency hypothesis has been addressed in a number of physiological studies of ITD/ILD trading in the auditory brainstem, reviewed by Joris et al. (2008). Of particular consequence to the dynamics of binaural-cue processing, level-to-time conversion may have large effects at sound onset, where intensity-dependent latency shifts can be on the order of milliseconds (Kiang et al., 1965). Effects on ongoing responses to sustained sounds are rather more limited, to a maximum TR of about $10\mu\text{s}/\text{dB}$ (Joris et al., 2008), and observed mainly for low-frequencies where little acoustic ILD is experienced for free-field sound (Joris et al., 2008).

4.4.2. Convergence of ITD and ILD in the central auditory system—Binaural processing in the auditory brainstem originates within two major structures of the superior olivary complex: the medial superior olive (MSO) and the lateral superior olive (LSO). A major distinction between the two structures lies in the nature of the binaural inputs. Where MSO neurons demonstrate excitatory-excitatory (EE) binaural interactions as a consequence of excitatory input from both ears, LSO neurons demonstrate inhibitory-excitatory (IE) interactions, due to ipsilateral excitation and con-tralateral inhibition. Although recent evidence suggests an important role of inhibition in MSO neurons (cf. Grothe, 2003), the primary determinant of MSO responses is the timing of inputs from the two ears; thus MSO neurons demonstrate exquisite tuning to ITD. Their predominantly EE-type responses suggest little sensitivity to ILD beyond that afforded by level-to-time conversion in the periphery. Consistent with that view, studies of ITD/ILD trading in mammalian MSO have reported TR around $5\text{--}8\mu\text{s}/\text{dB}$ (Crow et al., 1978; Kuwada and Yin, 1983; Yin and Kuwada, 1983; Yin and Chan, 1990), roughly in line with the “time” image described by Whitworth and Jeffress (1961). In contrast to MSO neurons, the IE-type responses of LSO neurons suggest a major role for the processing of ILD. That role is further consistent with the preponderance, in LSO, of neurons tuned to high frequencies where the behavioral relevance of ILD processing is highest (Strutt, 1907). The timing of both excitatory and inhibitory inputs to LSO, however, is nearly as precise as that to MSO, facilitating sensitivity to ITD along with ILD. Many LSO neurons are thus sensitive to ITD in the fine structure of low-frequency sounds (Tollin and Yin, 2005) or envelopes of high-frequency sounds, with TR $\approx 80\mu\text{s}/\text{dB}$ in the cat (Joris and Yin, 1995) and $40\text{--}50\mu\text{s}/\text{dB}$ in the free-tailed bat (Pollak, 1988; Park et al., 1996)—roughly in line with the “intensity image” measured psychophysically in human listeners (Haftner and Jeffress, 1968).

Trading of ITD and ILD might thus reflect processes intrinsic to MSO and LSO, but it might additionally involve the subsequent convergence of outputs from the two nuclei. That convergence occurs initially at the level of the auditory midbrain, within the dorsal nucleus of the lateral lemniscus and central nucleus of the inferior colliculus (ICC). At least some ICC neurons combine inputs from both the MSO and LSO pathways (McAlpine et al., 1998), and ITD/ILD trading in the responses of such cells could reflect the relative weighting of those inputs. Many other ICC neurons, however, maintain the binaural tuning of their MSO and LSO inputs, suggesting the opportunity for ITD/ILD trading at subsequent stages within the central auditory system. For example, Furukawa and Maki (2006) measured ITD/ILD trading in the middle-latency response of guinea pig auditory cortex, reporting TR $\approx 30\mu\text{s}/\text{dB}$ across multiple recordings. Notably, the ITD sensitivity of cortical responses appeared dominated by the envelope ITD and insensitive to ongoing fine-structure ITD (ongoing envelope ITD was not explicitly tested). Although it is not clear whether the results of Furukawa and Maki (2006) reflected trading that occurred within the auditory cortex itself or at an earlier stage of processing, other electrophysiological evidence in cats (Middlebrooks et al., 1980) and humans (Schroger, 1996; Yamada et al., 1996; Ungan et al., 2001; Tardif et al., 2006) suggests that the two pathways are maintained separately at least to the level of primary auditory cortex. The results of the current study might therefore

involve relatively high level mechanisms in addition to the peripheral and brainstem mechanisms described above.

4.5. Limitations of the study

Choice of ILD function in Experiment 1. One potential methodological concern of the current study is the appropriateness of azimuth-ILD mapping embodied in Equation 1. Incorrect fitting would have led to ILD changing by a larger or smaller amount than necessary to offset the subject's head turn, spoiling the illusion that the traded image remained spatially fixed during the adjustment procedure. Informal comments by subjects suggested that this did not occur. More importantly, the ultimate response on each trial was collected when the subject judged the traded stimulus to match the lateral position of the diotic reference, regardless of changes in the lateral position over the course of adjustment. Thus, the measurement of ILD necessary to offset an imposed ITD should not have been affected by the mapping of head azimuth onto ILD.

Non-linearity of response functions—A second potential concern, which applies to all studies that describe the ITD/ILD equivalence function using a single linear slope (TR), is the degree to which equivalence functions can be described as linear. Of note are a number of localization functions appearing in Fig. 3 that demonstrate nonlinearity in the form of compressed responses for large interaural differences. In such cases, fitting a linear function over the entire tested range leads to an underestimate of the response slope β (Eq. 4). Constraining the fit to use only small interaural differences (Fig. 5) revealed somewhat different overall values of TR but little change in the dependence of TR upon ICI. Thus, although a nonlinear function might have more accurately fit the shapes of localization functions in Experiment 2, the primary results of the study appeared unaffected by the choice of function.

Frequency content of the stimuli—A final limitation of the study stems from the fact that only stimuli of 4000 Hz carrier frequency were tested. TR is known to vary with the spectral content of the test stimuli (e.g., Harris, 1960), and to the extent that “time” and “intensity” images may involve mechanisms operating over different frequency ranges (Haft and Jeffress, 1968; Furukawa, 2008) different results might be expected when testing different frequencies. Of related concern is the propensity of subjects to utilize cues available in different frequency regions. For example, “off-frequency listening” might afford performance on the basis of deeper envelope modulations in auditory filters with high characteristic frequencies. Similarly, nonlinear interactions of the cochlear partition might give rise to low-level intermodulation distortion products at low frequencies. To the extent that listeners are able to detect and utilize that content, the trading results might be expected to follow those of past studies using low-frequency tonal stimuli Whitworth and Jeffress (1961). Future work could test this possibility by selectively masking or directly manipulating the frequency content of stimuli.

5. Summary and conclusions

1. For a majority of listeners, ITD/ILD trading ratios for 4000 Hz Gabor click trains varied systematically with click rate (ICI). In those listeners, larger TR (indicating greater relative influence of ILD) was obtained at 2 ms ICI than at 10 ms ICI. The dependence of TR on ICI was similar across closed-loop adjustment (Exp. 1) and open-loop lateralization (Exp. 2) tasks.
2. Increases in TR with ICI primarily reflected decreases in listener sensitivity to ITD at high rates, and were not strongly associated with increases in ILD sensitivity. That result is consistent with binaural adaptation (Haft and Dye, 1983) or rate

limitation (Bernstein and Trahiotis, 2002) that affects the processing of ongoing envelope ITD—but not ILD—at high frequency. The result is inconsistent with past results demonstrating binaural adaptation for ILD (Haft et al., 1983).

3. Consistent with prior studies, TR varied widely across individual listeners. For individual subjects, TR was consistent across tasks (though higher overall in the closed-loop than the open-loop task), suggesting that differences did not result from session-to-session variability. The individual differences may be in part attributable to population differences in onset dominance (Sabeti et al., 2004), or to listeners' dependence on “time” versus “intensity” images, as suggested by Haft and Jeffress (1968). Notably, two subjects with the lowest overall TR (i.e., those most consistent with use of the “time” image) did not exhibit changes in TR with ICI.

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List of abbreviations

ANOVA	analysis of variance
EE	excitatory-excitatory
HL	hearing level
ICC	central nucleus of the inferior colliculus
ICI	inter-click interval
IE	inhibitory-excitatory
ISI	inter-stimulus interval
ITD	interaural time difference
ILD	interaural level difference
LSO	lateral superior olive
MSO	medial superior olive
TR	trading ratio
TDT	Tucker-Davis Technologies
TWF	temporal weighting function

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Figure 1.

Closed-loop trading functions obtained in Experiment 1. Within each panel, the mean adjusted ILD (y-axis) is plotted against imposed ITD (x-axis) for each value of ICI (separate lines). Individual panels plot data for individual subjects. The inverse slope of the ILD/ITD trading function gives the ITD/ILD trading ratio TR (see Fig. 2), which varies between individuals (note the expanded ILD range for subjects 0601 and 0701) and across ICI. For most subjects, slopes were shallower (indicating greater relative influence of ILD over ITD) at 2 ms ICI than at 5 or 10 ms ICI.

Figure 2.

Closed-loop trading ratios obtained in Experiment 1. Bars plot the overall ITD/ILD trading ratio TR (y-axis) for each combination of subject and ICI. Error bars indicate 95% confidence intervals on the TR estimate. Five of the eight tested subjects exhibited a greater TR at 2 ms than 10 ms ICI, consistent with relatively greater contribution of ILD at high rate (short ICI). Of the remainder, note that subjects 0601 and 0702 produced TRs which were significantly lower overall compared to other subjects and not significantly dependent on ICI. 47

Figure 3.

Open-loop localization functions obtained in Experiment 2. Each panel plots the mean response (degrees of head turn in azimuth) as a function of ITD (y-axis) and ILD (parameter) for a specific combination of subject (rows of panels) and ICI (columns). From left to right, columns correspond to ICI of 10, 5, and 2 ms ICI. Subject identifiers are given in the top left corner of the leftmost panel in each row. Shaded lines indicate values of the ILD imposed on each stimulus; from top to bottom, curves correspond to +5, +3, +1, -1, -3, and -5 dB ILD. Error bars indicate standard error of the mean response azimuth for each stimulus. Overall ITD/ILD trading ratio (TR, in $\mu\text{s} / \text{dB}$) is indicated in the lower right corner of each panel.

Figure 4. Open-loop trading ratios obtained in Experiment 2. Bars plot the overall ITD/ILD trading ratio TR (y-axis) for each combination of subject and ICI. Error bars indicate 95% confidence intervals on the $\log(\text{TR})$ estimate

Figure 5.

Open-loop trading ratios obtained in Experiment 2 at specific values of ILD. In each panel, bars plot the ITD/ILD trading ratio TR (y-axis) for each combination of subject and ICI. Separate panels indicate TR estimated by linear regression of response azimuth onto ITD for each of the indicated ILD values. Asterisk (*) indicate values outside range of plot. Left panel: subject 0702 at 2-ms ICI: $TR=934\mu s/dB$ due to near-zero weight on ITD. Right panel: subject 0502 at 10-ms ICI: $TR=74\mu s/dB$ due to near-zero weight on ILD. Shading as in Fig. 4. Error bars omitted for clarity.

Figure 6.

Decomposition of open-loop TR into ILD and ITD sensitive components. Symbols plot ILD slope (β_L in Eq. 4, y-axis) against ITD slope (β_T , x-axis) for each combination of subject (symbol type) and ICI (symbol shading). Large symbols plot slopes computed across all runs, with black lines connecting symbols for adjacent ICI values (i.e. between 2 and 5 ms ICI, and between 5 and 10 ms ICI). Smaller symbols plot data for individual runs. Gray lines extending from the origin indicate contours of equal TR (numbers). Note that, with few exceptions, the progression from 2 to 5 to 10 ms ICI is horizontal, indicating similar ILD sensitivity across ICI. Changes in TR with ICI are thus associated primarily with decreasing sensitivity to ITD and not with increasing sensitivity to ILD.

Figure 7.

Comparison of TR across closed-loop and open-loop tasks. Symbols plot mean TR, for each combination of subject (symbol type) and ICI (shading), measured in Experiment 1 (y-axis) and Experiment 2 (x-axis). For reference, the dashed line indicates 1:1 agreement of TR across procedures, while the dotted line indicates a 2:1 relationship, with larger values for open-loop TR.