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Binaural spatial adaptation as a mechanism for asymmetric trading of interaural time and level differences

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ABSTRACT:

A classic paradigm used to quantify the perceptual weighting of binaural spatial cues requires a listener to adjust the value of one cue, while the complementary cue is held constant. Adjustments are made until the auditory percept appears centered in the head, and the values of both cues are recorded as a *trading relation* (TR), most commonly in μs interaural time difference per dB interaural level difference. Interestingly, existing literature has shown that TRs differ according to the cue being adjusted. The current study investigated whether cue-specific adaptation, which might arise due to the continuous, alternating presentation of signals during adjustment tasks, could account for this poorly understood phenomenon. Three experiments measured TRs via adjustment and via lateralization of single targets in virtual reality (VR). Targets were 500 Hz pure tones preceded by silence or by adapting trains that held one of the cues constant. VR removed visual anchors and provided an intuitive response technique during lateralization. The pattern of results suggests that adaptation can account for cue-dependent TRs. In addition, VR seems to be a viable tool for psychophysical tasks. https://doi.org/10.1121/10.0001622

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I. INTRODUCTION

Interaural time differences (ITDs) and interaural level differences (ILDs) comprise the dominant cues for sound localization in azimuth and for in-head lateralization of headphone-delivered sound. Varying either cue produces systematic changes in apparent lateral position, such that several different combinations of ITD and ILD values can produce the same lateral percept. The relative weight by which ITD and ILD contribute can be measured by asking listeners to adjust one cue to offset an opposing cue of the other type to "center" the resulting intracranial image (David *et al.*, 1959; Deatherage and Hirsh, 1959; Harris, 1960; Lang and Buchner, 2008; Shaxby and Gage, 1932; Stecker, 2010). The ratio of cue values gives the relative weight in μs ITD per dB ILD, i.e., the *trading ratio* (Shaxby and Gage, 1932) or trading *relation* (TR) (Lang and Buchner, 2008). A variety of observations suggest that obtained values of TR depend on which cue is adjusted as if adjusting one cue increases the weight that listeners assign it (e.g., Banister, 1926; Hafter and Jeffress, 1968; Whitworth and Jeffress, 1961; Young and Levine, 1977). Competing theories to account for that effect include biased regression (Trahiotis and Kappauf, 1978) and attentional explanations (Lang and Buchner, 2008, 2009). The purpose of the current study was to test an alternative hypothesis, namely, that the influence of the non-adjusted cue is reduced by repeated exposure that induces neural or rapid perceptual adaptation.

A. TR bias toward the adjusted cue

Young and Levine (1977) measured TRs in separate centering tasks, where listeners adjusted the ITD or ILD of a 500 Hz tone. They reported a TR of 40.4 μs/dB when participants adjusted the ITD to offset a fixed 8 dB ILD. However, when participants adjusted the ILD in the presence of a fixed 500 μs ITD, the TR increased to 79.4 μs/dB. Contemporary studies often refer to this phenomenon as the "shift-back" effect (e.g., Ignaz *et al.*, 2014; Lang and Buchner, 2008). Initial accounts attempted to relate this phenomenon to the perception of "dual images" (Hafter and Carrier, 1972; Whitworth and Jeffress, 1961): that listeners experience two independent percepts (one dominated by the time cue and the other by the level cue). If so, perhaps adjusting one cue caused greater emphasis of one or the other image. Young and Levine (1977) note their participants did not report perceiving dual images, but might have been responding to one image or the other without realizing it.

Trahiotis and Kappauf (1978) proposed that a judgmental bias from a reference stimulus can account for the cue-specific trading data reported by Young and Levine (1977). They cited similar differential results in the psychophysical literature at large when using the method of adjustment (MOA) to measure a common function obtained by matching variables of different dimensions. They state, "the observer's matching settings regress toward the level of the

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standard on the dimension being adjusted" (Kappauf, 1975). By this account, adjusting the ILD of a pointer to match a diotic standard results in a smaller ILD denominator because the adjusted ILD value would regress toward 0 dB, resulting in an artificially large (ILD-dominant) trading value. The opposite effect occurs when the ITD is adjusted (i.e., a smaller numerator results in a smaller, ITD-dominant, ratio).

Lang and Buchner (2008, 2009) proposed another theory that did not involve a reference stimulus. They attributed cue-dependent TRs to attentional upweighting of the cue being adjusted; they argued increased perceptual salience of the adjusted cue rendered it more effective than the fixed cue. In an elegant experiment, Lang and Buchner (2009) first recorded the final ITD and ILD cue values of the TR required to center a 500 Hz pure tone using the MOA. Second, they played those same cue values as single presentations using a method of constant stimuli (MOCS) lateralization task. The results revealed that perceptions were no longer centered when the midline TR values from the MOA centering task were presented during the MOCS lateralization task. Instead, the perceived azimuth deviated away from midline, moving toward the perceived location of the fixed cue during adjustment. That is, the adjusted cue value was no longer sufficient to offset the complementary cue to midline, resulting in perceptions "shifted back" toward the fixed cue (i.e., the shift-back effect).

Existing work investigating both theories using similar tasks has been inconclusive (e.g., Ignaz *et al.*, 2014), with the evidence effectively supporting either theory. However, while regression is rooted in behavioral bias and attentional upweighting invokes cognitive processes, neither proposed explanation considers how the method of stimulus presentation itself may contribute to cue-specific TRs. Because differential TRs are specific to the MOA and do not occur using the MOCS (e.g., Lang and Buchner, 2009), a further look into the differences between methods is warranted. In particular, it is possible that the rapid, repeated presentations of stimuli during the MOA centering task could lead to perceptual changes through adaptation.

B. Adaptive localization aftereffects

Thurlow and Jack (1973) systematically explored the impact of adaptors on both ITD and ILD cues. They found that eccentric adaptors of either cue type caused judgments of the same cue type to shift toward the midline, while midline adaptors caused probes to shift away from the midline. Importantly, they always noted a shift in the probe away from the adaptor. The phenomenon of a perceptual shift of the auditory image away from a preceding adapting stimulus has been well documented, and is commonly referred to as the *auditory localization aftereffect*. Previous work has shown the effect to be present under headphones as well as in the sound field (e.g., Canévet and Meunier, 1994, 1996; Kopčo *et al.*, 2007), using pure tones as well as broadband noise (Meunier *et al.*, 1996), in reverberation (Braasch, 2003), and across various frequencies and interstimulus intervals (ISIs) (Kashino and Nishida, 1998). Most germane to the present study, Phillips *et al.* (2006) demonstrated that ITD adaptors can cause a shift in the perception of ILD probes, and vice versa. Consistent with the earlier literature, they found the probe was always displaced away from the adaptor. It seems quite possible that repeated presentations of the fixed cue during a centering task could function as an adaptor to the adjusted cue, shifting its perceived location. Kopčo *et al.* (2007) showed that displacement of a probe in the presence of a preceding stimulus can occur with a single adaptor presentation, and with an adaptor duration of only 2 ms. The presence of a perceptual shift in probe location during adjustment would necessarily impact the reported position of the auditory percept.

Another crucial similarity across MOA and MOCS adaptation tasks is the ISI. The ISIs used in MOA studies of binaural interaction typically range from roughly 200 to 500 ms (e.g., Hafter and Carrier, 1972; Lang and Buchner, 2008). This range overlaps with ISIs known to produce localization aftereffects (e.g., Kashino and Nishida, 1998; Kopčo *et al.*, 2007; Phillips *et al.*, 2006). Furthermore, the standard and target in MOA tasks have often been of the same frequency (e.g., Lang and Buchner, 2009; Whitworth and Jeffress, 1961), which has been shown to produce spatial adaptive aftereffects of the greatest magnitude (e.g., Kashino and Nishida, 1998).

Taken together, the similarities in experimental parameters between the MOA centering tasks and MOCS localization aftereffect studies suggest that TRs obtained using the MOA task could be contaminated by adaptive shifts in perceived location. The approach used in the current study was to compare MOA TRs directly to MOCS TRs obtained with and without adaptors.

C. Response measurement

In addition to stimulus presentation, it is important to consider response measurement. Gilkey *et al.* (1995) devised a method of participant reporting using a sphere positioned in front of the listener. They compared localization data from their "God's eye localization pointing" to data from a study that recorded perceived azimuth by asking listeners to call out coordinates (Wightman and Kistler, 1989), and to a study that instructed listeners to point their heads in the direction of the perceived source (Makous and Middlebrooks, 1990). Gilkey *et al.* (1995) found the head-pointing technique produced results that most closely matched the actual sound-field locations of the stimuli. Other studies showed that head-pointing can also be used to obtain reliable judgments of in-head lateralization, without training listeners to externalize headphone-presented sound (Jeffress and Taylor, 1961; Stecker, 2010).

In light of the superior reporting accuracy with no additional need for practice, the current study used a head-pointing technique combined with a virtual reality headset and environment to enhance further the ecological validity of the response paradigm. Van Veen *et al.* (1998) advocate

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that virtual reality offers several benefits to laboratory tests (see also Stecker, 2019). For instance, they mention the precise control of stimuli, easy manipulation of parameters, interactivity between subject and environment, improved multisensory realism, and multiple methods of recording responses. The current study utilized VR to simulate an outdoor, free-field environment. This step reduces perceptual mismatch between auditory and visual experience of the laboratory setting (e.g., speakers, wall, and floor patterns). VR also offers the potential for consistent visual input when testing across studies and physical laboratory locations. The aims of this study do not concern the influence of visual cues or VR on TRs; rather, the use of VR in this study was a first step toward using VR in future studies for increased face validity, more complex manipulation of audiovisual interaction, and improved consistency across laboratory testing.

D. Purpose

This study investigated the potential influence of the auditory localization aftereffect on binaural cue TRs. Trading relations were obtained using a repeated-stimulus centering task (MOA) that could lead to cue adaptation and a head-pointing technique where adaptive influences could be systematically manipulated. Three experiments were carried out. Experiment 1 measured TRs obtained using the MOA. Listeners adjusted the amount of ITD required to center a stimulus containing one of several fixed ILDs, and vice versa. Experiment 2 used the MOCS to measure TRs using a head-pointing technique similar to Stecker (2010). Combinations of ITD and ILD were presented in isolation, and the oriented head angle indicated perceived azimuth. Experiment 3 was identical to Experiment 2, with the addition of an adapting train preceding each probe.

It was hypothesized that the results from Experiment 1 and Experiment 3 (the MOA task and the adaptation MOCS paradigm) would produce similar TRs consistent with the shift-back effect. That is, adaptation present in the MOCS adaptor conditions would reproduce the cue-dependent effects obtained in the MOA task. Accordingly, the results obtained from Experiment 2 (the No-Adaptor head-pointing task) would differ from Experiments 1 and 3, because the No-Adaptor MOCS task does not induce consistent localization aftereffects. Specifically, if auditory spatial adaptation is involved in trading ITDs and ILDs during MOA centering tasks, the TR from the No-Adaptor MOCS task should lie between those obtained in ITD and ILD conditions of the other experiments.

II. GENERAL METHODS

The study was conducted at Vanderbilt University Medical Center, Nashville, TN. All procedures, including recruiting, consenting, and testing of human subjects, followed guidelines of the Vanderbilt University Human Research Protections Program and were reviewed and approved by the cognizant Institutional Review Board.

A. Participants

Nine adult listeners were recruited from Vanderbilt University and participated in this study. One additional participant was recruited but reported being unable to alter perceived lateral position via adjustment, and did not complete testing. Initial analyses confirmed that participant's adjustment responses were effectively random on all trials. The remaining nine participants (aged 24–33 years; mean = 28 years; 8 females; 1 male) completed all three experiments. All participants had normal, symmetrical hearing at octave frequencies from 250 to 8000 Hz (<25 dB hearing level, HL), verified using standard audiometric procedures for air conduction thresholds. There was no history of neurogenic or otologic disease, as evidenced by self-report. All participants reported normal, or corrected normal visual acuity and color vision. Participants were compensated for their time.

B. Testing environment and apparatus

All sessions were conducted in a sound-attenuating room. Participants wore an Oculus Rift virtual reality headset (Oculus Rift, Menlo Park, CA), while seated in a chair approximately 1 m from mounted position sensors. The custom virtual environment was coded using the Unity3D game engine (version 5.6.1f1, Unity Technologies, San Francisco, CA) on a custom-built PC running Steam VR (version 2017-01-30, Valve Corporation, Bellevue, WA). The virtual environment placed the participant in the center of a circular platform, with red helium balloons positioned around the outer platform perimeter in 1-degree steps. The balloon at 0° azimuth (midline) was colored green to serve as the only directional orienting cue in the environment. The larger area was an outdoor setting consisting of a uniform, green "grass" floor and clear blue "sky" to avoid visual reference points, while also creating the visual equivalent of a free field (Fig. 1).

Participants interacted with the environment to make responses via standard Oculus handheld controllers. Each controller had two push buttons, a thumbstick button, a

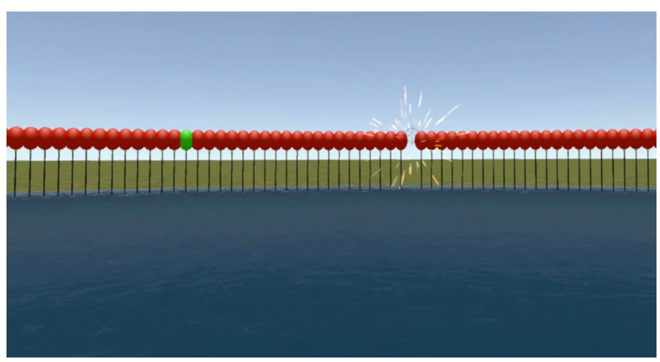

FIG. 1. (Color online) The virtual reality environment seen during the localization experiments. The scene was uniform except for a single (green) balloon to indicate midline. The reticle (shown here over the popping balloon) moved with the head and was used to indicate perceived azimuth. Pulling the trigger on the handheld controller recorded head azimuth and provided visual feedback with a balloon-pop animation.

trigger, and a grip button. Various input methods were used for each experiment (described in the methods for each experiment). The spatial position and orientation of the head-mounted device (HMD) was tracked using the Rift's onboard position sensors.

A reticle in the center of the visual field followed participant head movements and allowed aiming at individual balloons simply by orienting the head. This paradigm was also used to maintain proper head position at the onset of each trial. Participants were instructed to keep the reticle centered on the green balloon (midline) either throughout the experiment (Experiment 1), or at the beginning of each new trial after head pointing (Experiments 2 and 3). If the reticle moved outside the "home position" (within 3 deg azimuth/elevation of the green balloon), the experiment stopped, and a green box appeared to illustrate the home position. Once the reticle was returned to home position, the green box disappeared, and the experiment resumed after 2 s.

A second PC (Dell, Inc., Round Rock, TX) running MATLAB (Mathworks, Natick, MA) communicated with the presentation computer via transmission control protocol/Internet protocol (TCP/IP). Behavioral tasks for all experiments were coded in MATLAB scripts, which also controlled the virtual reality environment via TCP/IP messages by calling custom Unity3D functions (e.g., balloon pop, reset environment), collecting responses, and reading HMD position data.

C. Stimuli

All sounds were synthesized using MATLAB. Because synchronization between auditory and visual stimuli was not of importance to the study, no timing calibration measurements were made between the audio onset and Unity3D function execution. Auditory stimuli were synthesized at 48.828 kHz (Tucker-Davis Technologies RP2.1, Alachua, FL) and presented via ER-2 insert earphones (Etymotic, Elk Grove Village, IL). Stimuli were presented from the MATLAB PC, bypassing the Unity3D audio device completely. All stimuli consisted of 500 Hz pure tones with a duration of 500 ms. Unless modified by introducing an ILD, all stimuli were presented at a level of 65 dB SPL (A-weighted). Tones were gated using raised cosine ramps of 20 ms duration to avoid spectral transients. Differences in arrival time at the two ears were computed by shifting the whole waveform (amplitude ramp and fine structure) of one channel relative to the other in time. Level differences were achieved by halving the desired ILD and applying offsets as a reduction to one channel, and an increase to the other channel.

III. EXPERIMENT 1

A. Method

1. Stimuli

The stimuli in Experiment 1 were synthesized using the parameters described in Sec. II. Trials consisted of looped, alternating presentations of standard and target tones. The standard tone always carried a 0 dB ILD and a 0 μs ITD. The target tone consisted of either a target ILD (0, $\pm$3, $\pm$6, or $\pm$9 dB), or a target ITD (0, $\pm$100, $\pm$200, or $\pm$300 μs) and an adjustable complimentary cue used by the participant to center the test tone to midline. This yielded 14 different conditions. On each trial, the adjustable cue started at a random value ranging from $\pm$(3 to 9 dB) ILD or $\pm$(100 to 300 μs) ITD. The standard and target tones were separated by a 400-ms ISI. Each standard-target pair was separated by a silent interval of 600 ms.

2. Procedure

Participants completed a centering task with insert earphones. Stimuli were presented using the MOA. Participants initiated each trial by pulling the trigger on the right Oculus Rift controller. A brief animation (three balloons bobbing) indicated the trigger pull had been read and the trial had begun. In this experiment, the virtual environment served to ensure participants kept their heads centered during the task and to provide visual consistency across experiments, but otherwise, there was no interaction with the VR surroundings for the MOA task. The adjustable cue of the target tone was adjusted by the participant, using buttons on the handheld Oculus Rift controllers, until the target tone was perceived as coming from the midline (i.e., matching the standard tone in perceived azimuth). The right buttons increased the time or level advantage to the right ear (arrival time lead or higher level). The left buttons increased the time or level advantage to the left ear. One button on each controller ("fine") adjusted the target by 10 μs ITD or 0.1 dB; another button ("coarse") adjusted the target by 100 μs ITD or 1 dB. Adjusted cue values were limited to a maximum range of $\pm$900 μs ITD or $\pm$15 dB ILD. After participants were satisfied with centering (i.e., with the match between standard and target lateralization), they pressed a separate button (the thumbstick) on the right controller to end the trial and record the cue value. The adjustment duration for an individual judgment was typically less than one minute. Participants were instructed to report verbally if they were unable to center the percept.

Each session began with at least eight practice trials. During this time, participants could ask questions and were given as much time as necessary to familiarize themselves with the controls. After eight practice trials, additional practice was provided until a participant reported comfort with the task. Practice data were inspected to ensure performance was broadly consistent with expectations, e.g., a fixed, right-ear level advantage was perceptually centered by the participant introducing a left-ear time advantage. Following training, a total of eight judgments were made during data collection for each of the 14 conditions (112 recorded responses). The final cue value chosen to center the static, complementary cue was recorded at the end of each trial.

Four of the nine participants made judgments on a single cue type (ITD or ILD) during any given session (the

Fixed group). This procedure of fixing cue type across blocks is consistent with existing literature, where ITD and ILD adjustments were often completed in separate experiments within a single study (e.g., Lang and Buchner, 2009; Whitworth and Jeffress, 1961). To investigate this convention, the remaining five participants were presented trials randomly from any of the 14 possible ITD (0, ±100, ±200, or ±300 μs) and ILD (0, ±3, ±6, or ±9 dB) fixed cue values. That is, those five participants adjusted both cue types intermixed within the same session or day (the Mixed group).

3. Data analysis

Data from all nine participants contributed to the results. All participants reported an inability to center the auditory percept in the target ILD conditions of ±6 and ±9 dB with any amount of ITD. These trials were marked, and later inspection of the final values indicated the ITD had been adjusted to the maximum permissible value. Thus, only data from fixed ILD values of 0 and ±3 dB were used for the remainder of the study. Potential explanations for the truncated range of testable ILD values are considered in Sec. VI.

Data analysis was completed using *R* Version 3.3.2 (R Core Team, 2016). The eight judgments per condition were averaged into a single data point by taking the arithmetic mean, after removing outliers (absolute deviation from median >2.5 times the median absolute deviation; Leys *et al.*, 2013). A total of 28 outliers were removed across all participants and conditions (approximately 6.5% of data points). The data points for ITD and ILD fixed cue values were fit using linear regression. The resulting slope was taken as the TR in that condition. In other words, each participant produced two TRs: one based on the slope of the data points when adjusting the ITD (henceforth ITD_{adj}), and one based on the slope of the data points when adjusting the ILD (henceforth ILD_{adj}).

B. Results and discussion

1. Mixed vs Fixed groups

Unequal variance *t*-tests (Welch two-sample test) comparing the Mixed and Fixed group TRs revealed no significant differences between the Mixed and Fixed groups for either the $\mathrm{ITD_{adj}}$ TR [mean $\mathrm{TR_{mixed}} = 25.8\ \mu\mathrm{s/dB}$; mean $\mathrm{TR_{fixed}} = 30.5\ \mu\mathrm{s/dB}$; $t(4.5) = 0.6$, $p = 0.58$] or the $\mathrm{ILD_{adj}}$ TR [mean $\mathrm{TR_{mixed}} = 37\ \mu\mathrm{s/dB}$; mean $\mathrm{TR_{fixed}} = 41.5\ \mu\mathrm{s/dB}$; $t(4.3) = 0.33$, $p = 0.75$], suggesting the MOA is not sensitive to intermixing cue types within a session. Because there were no statistical differences between groups, subsequent analyses of the MOA took place on the pooled data.

2. Trading relations

Figure 2 displays the results of Experiment 1 for the 9 participants individually, presenting data for both conditions in the same plot. Adjusted ITD values are plotted on the vertical axis, against target ILD values along the horizontal. For ILD adjustments, the ordinate and abscissa are reversed to plot adjusted ILD values on the horizontal axis, against target ITD values along the vertical. The mean TR while adjusting the ITD was 27.9 μs/dB [range = 15 to 44.9 μs/dB, standard error of the mean (SEM) = 3.45 μs/dB]. The mean TR while adjusting the ILD was 39 μs/dB (range = 19.9 to 69.1 μs/dB, SEM = 5.79 μs/dB).

A bootstrapped paired-samples *t*-test (10 000 replications) comparing TRs across conditions revealed a significant difference between the $\mathrm{ITD_{adj}}$ (mean TR = 27.91 μs/dB) and $\mathrm{ILD_{adj}}$ (mean TR = 39.01 μs/dB) for the MOA task [$t(8) = 3.87$, 95% CI (−1.88, 1.81), $p = 0.003$, $d = 1.29$]. Individual (thin lines) and mean (thick lines) slopes are superimposed in Fig. 3. This result is generally consistent with the existing literature (e.g., Whitworth and Jeffress, 1961; Young and Levine, 1977), indicating greater weight on the adjusted cue (i.e., smaller values of the adjusted cue were sufficient to center the auditory percept).

The relationship between TRs obtained in this study replicate existing findings showing the $\mathrm{ITD_{adj}}$ produces a smaller TR (i.e., shallower slope) compared with the $\mathrm{ILD_{adj}}$ TR. These results serve as a basis for comparison with TRs obtained using the MOCS, with and without adaptors, in the same individuals (Experiments 2 and 3).

IV. EXPERIMENT 2

A. Method

1. Stimuli

The stimuli in Experiment 2 were synthesized using the parameters described in Sec. II. Similar to Experiment 1, cue combinations consisted of target ILD values (0, ±3, ±6, or ±9 dB), and fixed ITD values (0, ±100, ±200, or ±300 μs). In this experiment, all combinations of ITD and ILD were used, resulting in 49 different combinations.

2. Procedure

Participants completed a virtual localization task with insert earphones. That is, unfiltered pure tones resulted in intracranial images that participants mentally extrapolated into space (Jeffress and Taylor, 1961; Stecker, 2010). Stimuli were presented using the MOCS. Participants wore the Oculus HMD and were immersed in the same virtual environment as Experiment 1 (see Fig. 1). Participants were seated and held the right Oculus controller. Pulling the trigger button started a brief animation (three balloons bobbing) to indicate the beginning of each run. Participants positioned the head-locked reticle into a green box at midline (marking "home position" as in Experiment 1) to initiate the trial. After holding home position for a delay of 2 s, a single 500-ms tone was presented with one of the 49 possible cue combinations. Trials were presented in random order. Participants were required to keep their heads centered until the stimulus had completely finished playing. Participants were then instructed to indicate perceived azimuth by

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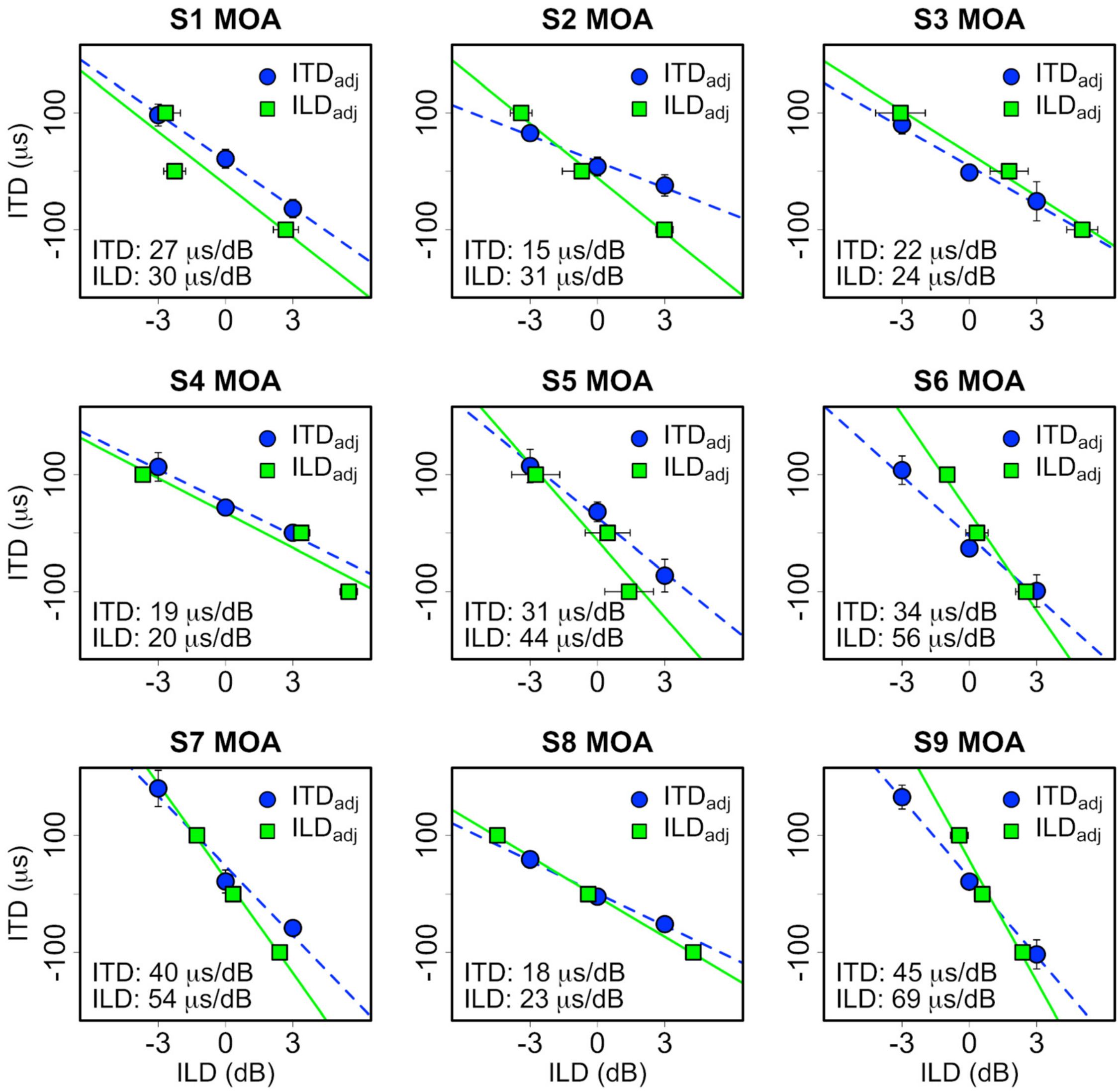

FIG. 2. (Color online) Individual TRs from Experiment 1. Circles indicate the required ITD (μs) to offset a variety of fixed ILDs (fixed values labeled along the abscissa in dB). Squares indicate the required ILD (dB) to offset a variety of fixed ITDs (fixed values labeled along the ordinate in μs). Error bars denote standard error of the mean. Each panel represents data from one participant. The slopes of the respective data points were taken as trading relations and are given in the lower left of the panels.

positioning the reticle over the appropriate balloon via head turn. Consistent with existing reports (e.g., Jeffress and Taylor, 1961; Stecker, 2010), participants had no difficulty reliably extrapolating the lateralized stimulus to an external location. Once the reticle was satisfactorily aligned with the perceived azimuth of the tone, the participant pulled the trigger button on the Oculus Rift controller. Immediately after the trigger pull, the selected balloon silently "popped," providing visual confirmation of the selection, and the head position was recorded by MATLAB. The next trial began after the participant returned the reticle to home position, with a delay of 2 s. Participants completed eight trials per cue combination (392 total), distributed across eight runs of 49 trials each.

There were no mixed or fixed presentation patterns for this experiment, due to the nature of the task: all stimuli consisted of single presentations from the same pseudorandomly-chosen 49 cue combinations.

3. Data analysis

The response azimuth was computed from head orientation on each trial. To account for differences in potential bias and range of responses across the session, azimuth judgment data were normalized to *z*-scores per participant. The arithmetic mean of the eight judgments per condition was used for plotting and analyses. Data are displayed using response heatmaps created with the R package *lattice* (Sarkar, 2008). The heatmaps show mean normalized response azimuth in a 7×7 matrix of ILD (on the horizontal axis) and ITD (vertical axis) combinations. Each square represents the mean judgment of a single cue combination. The scale ranges from dark (blue) for leftward azimuths, to light (tan) for rightward azimuths. For reference, idealized heatmaps are given in Fig. 4. They represent maps resulting from a completely dominant ITD, a completely dominant ILD, and equal effectiveness between the cues.

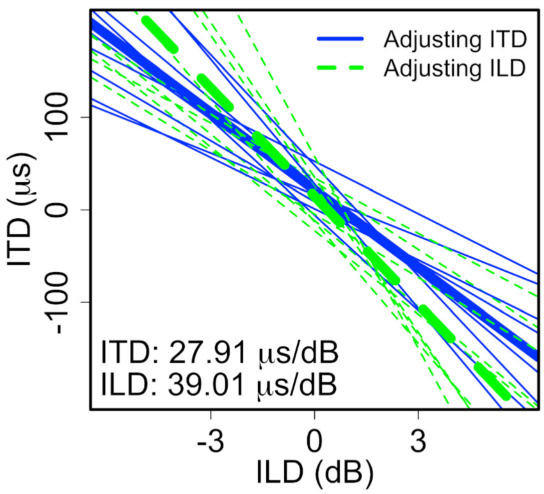

FIG. 3. (Color online) Mean TRs from Experiment 1. Thin, solid lines represent the slopes from all participants while adjusting the ITD. Thin, dashed lines represent the slopes from all participants while adjusting the ILD. Thick lines (solid and dashed) show the group mean slopes (i.e., TRs) when participants adjusted the ITD and ILD, respectively.

TR values were calculated from an individual's data by fitting contour lines to the heatmaps in *R* Version 3.3.2 (R Core Team, 2016). Contours were plotted by connecting points of similar response azimuth across all values of ITDs and ILDs using base *R*. The contour line fitted to the MOCS heatmaps at zero indicates ITD/ILD combinations that produced centered percepts, which is a condition analogous to the centered percepts from the MOA task. For this reason, comparisons were made from the slopes of the contour lines at zero (note the contour slopes at other values were largely consistent with those at zero). The contour line was fit using linear regression, and the slope was taken as the TR. A Shapiro-Wilk normality test revealed the TR data for this experiment were normally distributed.

Based on data from Experiment 1, predicted TRs for the idealized conditions included ∼28 μs/dB or lower for a dominant ITD and ∼39 μs/dB or greater for a dominant ILD. The prediction for equally dominant cues depended on the relationship between the ITD and ILD during adjustment. If either the ITD or ILD were dominant during adjustment, the predicted TR would be similar to the corresponding value from Experiment 1. If neither cue was strongly dominant during adjustment, the predicted TR for equally dominant cues would likely be ∼34 μs/dB (i.e., a value between those found during adjustment).

B. Results and discussion

1. TRs obtained using the MOCS and MOA

Response heatmaps for individual participants are shown in Figs. 5(A) (Mixed group) and 5(B) (Fixed group), leftmost columns. Individual and mean slopes of the contour line at 0 (i.e., TRs) are shown in Fig. 6. The mean TR was 40.8 μs/dB (range = 20.2 to 64 μs/dB; SEM = 5.08 μs/dB), which is nearly identical to the $\mathrm{ILD_{adj}}$ TR of 39 μs/dB (see Fig. 3). A bootstrapped paired samples *t*-test confirmed no

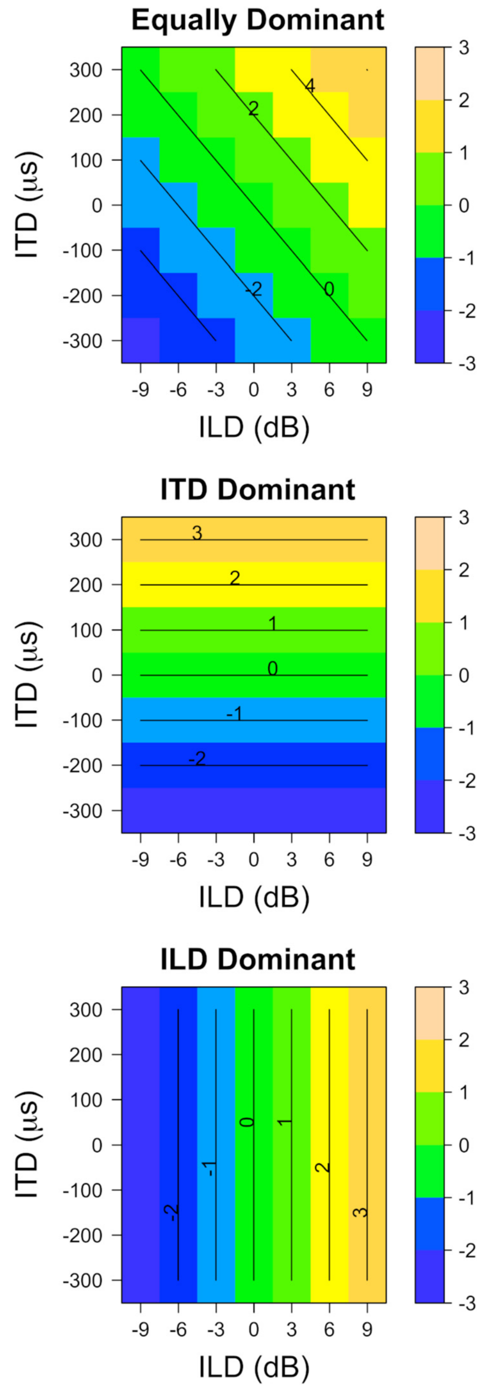

FIG. 4. (Color online) Idealized heatmaps for the MOCS task showing scenarios where the ITD and ILD cues are equally dominant (top), where the ITD is dominant (middle), and where the ILD is dominant (bottom). Fixed cue values are plotted along the axes. The response parameter is perceived azimuth. Darker (blue) squares and negative numbers indicate perception to the left of midline. Lighter (tan) squares and positive numbers indicate perception to the right of midline. Predicted TRs for ITD- or ILD-dominant scenarios were the values obtained from Experiment 1 (∼28 μs/dB and ∼39 μs/dB, respectively). In the case of equal cue dominance the predicted TR would be a value between those from Experiment 1 (i.e., ∼34 μs/dB).

statistical difference between the $\mathrm{ILD_{adj}}$ and No-Adaptor conditions [$t(8) = 0.55$, 95% CI(−1.85, 1.85), $p = 0.59$, $d = 0.18$]. Conversely, the TRs obtained from the $\mathrm{ITD_{adj}}$ and No-Adaptor conditions differed significantly [$t(8) = 3.57$,

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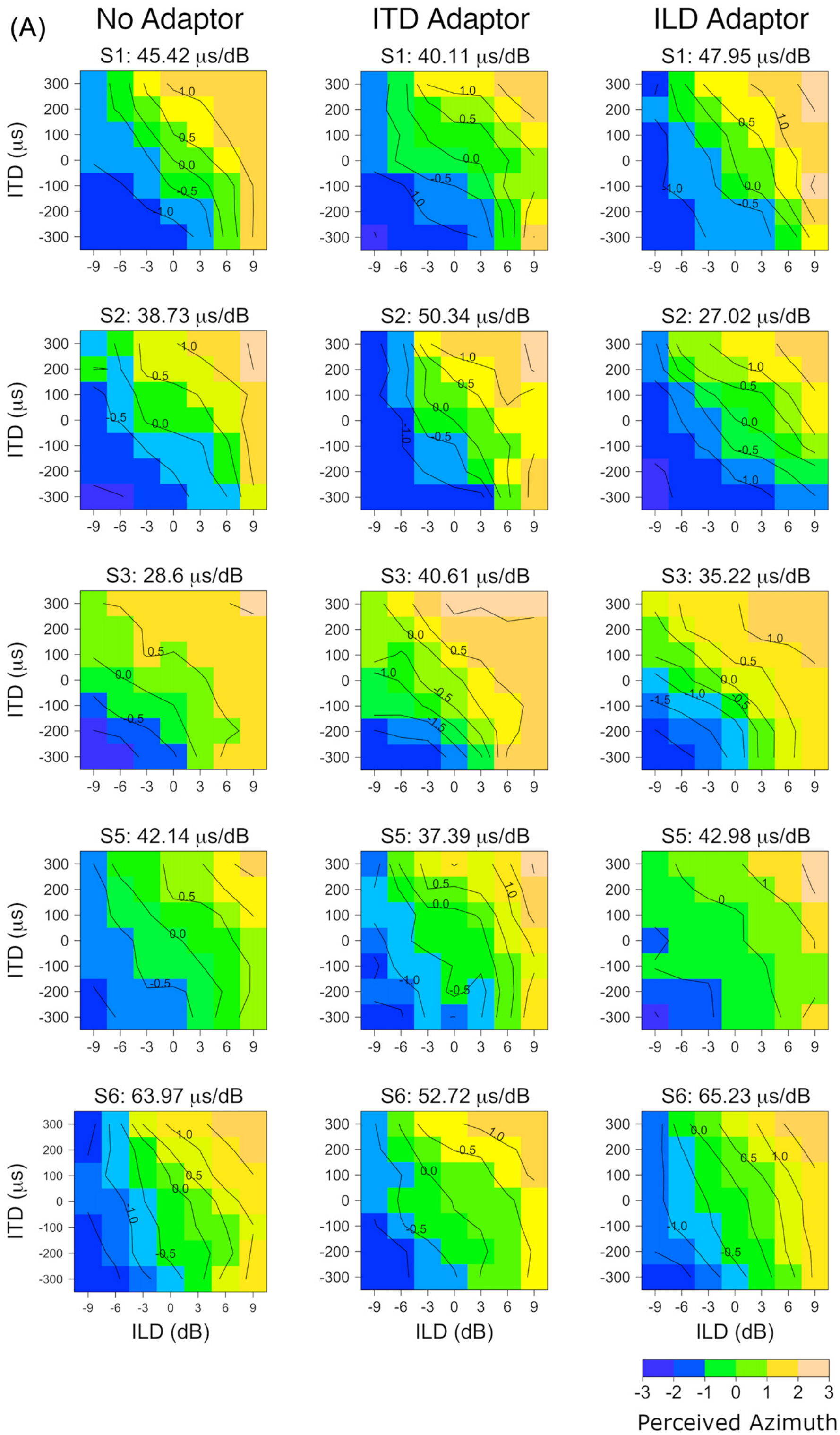

FIG. 5. (Color online) Individual perceived-azimuth heatmaps for Experiments 2 (left column) and 3 (middle and right columns). (A) Data for the Mixed group. (B) Data for the Fixed group. All heatmaps plot ITD along the ordinate and ILD along the abscissa. The parameter is perceived azimuth. Darker squares and negative numbers indicate perception to the left of midline. Lighter squares and positive numbers indicate perception to the right of midline. Trading relations for a given participant and condition are above each plot. The left column shows heatmaps from the No-Adaptor condition (Experiment 2). The middle column shows heatmaps from the ITD-Adaptor condition of Experiment 3. The right column shows heatmaps from the ILD-Adaptor condition from Experiment 3.

95% CI(−1.87, 1.86), $p = 0.006$, $d = 1.19$]. Implications of these findings are discussed in Sec. VI B.

It is noteworthy that in Experiment 1 participants were unable to center the intracranial percept at preset ILD values greater than 3 dB using the MOA, yet there are several instances of centered percepts at 6 and 9 dB in Experiment 2 using the MOCS. In comparison with Lang and Buchner (2009), who measured MOA TRs up to ±7.5 dB ILD, the

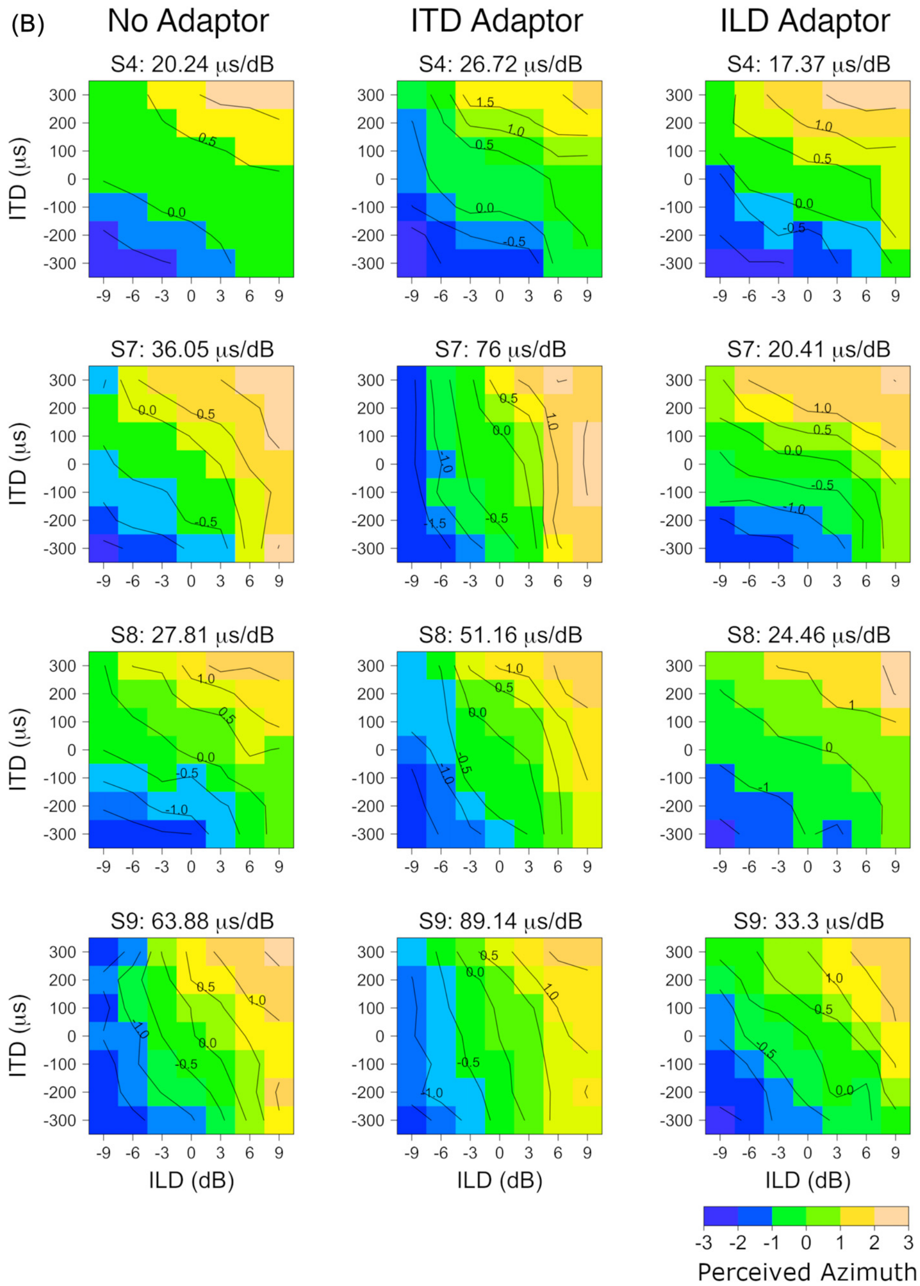

FIG. 5. (Color online) (*Continued*)

current study did not provide a visual depiction of the cue adjustment controls and used discrete step sizes. It is possible these methodological differences altered listener perception in the current study. Another potential factor could be the effect of active decision-making during adjustment, compared with the more passive orientation task in Experiment 2. Further investigation is needed into visual controls and discrete vs continuous adjustments in MOA tasks.

The MOCS No-Adaptor condition avoids the adaptive effects of repeated stimuli inherent to the MOA task by using a single stimulus presentation. Lang and Buchner (2008, 2009), described the "shift-back" effect in terms of deviation from perceived midline, while this study considers the No-Adaptor condition a baseline where the binaural cues are unbiased by repetition. One interpretation of the similarity between the No-Adaptor and ILD_{adj} TRs is that the ILD was the dominant cue during the MOA task. However, the overall diagonal pattern of the heatmaps indicates that ITD and ILD both contributed to most cue combinations (i.e., opposing cues often led to a midline percept; see Fig. 4). Experiment 3 provides a more complete picture (and suggests the latter is true). Data from the heatmaps therefore suggest adjusting the ILD gives a more unbiased estimate of the TR than adjusting the ITD in MOA tasks.

V. EXPERIMENT 3

To explore the possibility that TR differences between ILD_{adj} and ITD_{adj} obtained in the MOA task (Experiment 1) arose due to adaptation of the target cue, the MOCS task

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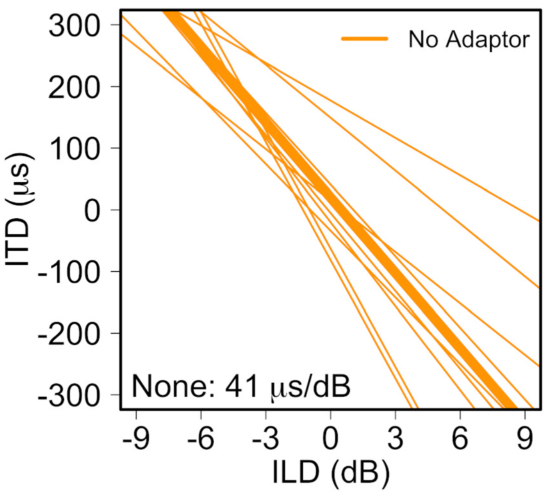

FIG. 6. (Color online) Mean and individual slopes (i.e., TRs) for Experiment 2 (thick and thin lines, respectively). Slopes were derived from the 0 contour lines of the heatmaps (cue combinations at which listeners perceived the stimulus at midline). The contour at zero azimuth corresponds to ITD/ILD combinations that produced centered percepts in the MOCS task and is thus most relevant for comparison to the MOA centering task (Experiment 1). The value of the mean slope (i.e., mean TR) is given in the lower left-hand corner.

was repeated with the addition of cue-specific adaptors preceding each test stimulus and judgment. It was hypothesized that adapting the ILD would lead to a greater perceptual dominance of the ITD, yielding a TR similar to the ITD_{adj} condition (i.e., smaller than the No-Adaptor MOCS TR). Conversely, adapting the ITD would result in perceptual dominance of the ILD, leading to a TR larger than the No-Adaptor MOCS condition.

A. Method

1. Stimuli

Stimuli were identical to those of Experiment 2, with the addition of an adaptor train of 5 pure tones preceding the probe. The number of adaptors was chosen based on a combination of 5-s "refresher" adaptors in the localization aftereffect literature (e.g., Kashino and Nishida, 1998), and the ability to elicit a change in perception with one and eight adaptors from Kopčo *et al*. (2017). Pilot testing suggested five adaptors achieved a reasonable balance. All tones in the train were synthesized using the parameters given in Sec. II so that the adaptor train and the probe stimuli were identical (e.g., 500 Hz, 500 ms in duration) except for the binaural cues they carried. In each case, the adaptor cue value was identical to that of the probe, while the complementary (unadapted) cue was set to zero.[1] As in Experiment 2, the probe was presented with one of 49 ITD/ILD combinations, selected from the same range as in Experiment 2 (i.e., ±300, ±200, ±100, and 0 μs, or ±9, ±6, ±3 and 0 dB, for ITD and ILD, respectively). Participant responses culminated in two response heatmaps per listener (one per adaptor condition), where each square represents the mean response azimuth from eight trials.

In order to approximate the parameters used in the MOA task, each tone in the entire stimulus (five adaptors and one probe) was separated by an ISI of 400 ms; the same ISI separating the standard and target tones in the MOA task of Experiment 1.

2. Procedure

The task was identical to that in Experiment 2 other than the presentation of the adaptor train. Participants were instructed to ignore the first five tones (i.e., the adaptor train), and to indicate via head turn the perceived azimuth of the last tone (the probe) only. Participants were required to keep their heads centered by holding the reticle in home position until the entire stimulus finished playing. A single adaptor type (ITD or ILD) was presented for all 49 combinations in any given block of trials. Listeners made eight judgments for each type of adaptor, for a total of 784 responses ($49_{combination} \times 8_{judgment} \times 2_{adaptor}$).

As in Experiment 1, the participants were divided into Mixed and Fixed groups. Participant group assignment was the same as in Experiment 1. Five participants completed blocks with the adaptor type selected in random order within each session (the Mixed group), and four listeners completed blocks with the same adaptor type on a given testing day (the Fixed group). Trials for the Fixed group also began with 1 s of binaurally uncorrelated Gaussian white noise to reduce carryover effects from one trial to another due to the constant exposure to a single adapted cue type (e.g., Ignaz *et al*., 2014). Each Fixed trial thus consisted of Noise → 1.5 s Silence → Stimulus. The noise was presented at a root-mean-square level of 65 dB SPL (A-weighted).

3. Data analysis

Heatmaps of response azimuth were generated for each cue combination, and TRs were computed from linear regression of the 0-azimuth contour as in Experiment 2. The results of a Shapiro-Wilk normality test revealed the data were normally distributed. Bartlett's test for homogeneity of variance across adaptor types revealed the assumption of homogeneity was valid. Therefore, TR data were analyzed using a two-way mixed model analysis of variance (ANOVA), with a single within-subjects factor of adaptor type (ITD-Adaptor, ILD-Adaptor), and a between-subjects factor of stimulus presentation group (Mixed, Fixed). Mauchly's test for sphericity failed to reject the null hypothesis, indicating variances were not significantly different from equal; therefore, no corrections were applied to the degrees of freedom.

B. Results and discussion

Recall that in the ITD-Adaptor condition, the ILD is expected to be the dominant cue as a result of the adaptation associated with repeated presentations of the probe ITD value. That is, with ILD plotted along the abscissa, an ITD adaptor would lead to ILD dominance and therefore steeper heatmap slopes. Conversely, the ILD-Adaptor condition predicts a dominant ITD cue, and subsequently shallower slopes.

1. Mixed vs Fixed groups

Individual heatmaps are plotted in Figs. 5(A) and 5(B), with the ITD-Adaptor condition heatmaps in the middle column, and the ILD-Adaptor condition heatmaps in the rightmost column. The analysis revealed no main effect of Mixed vs Fixed Group [$F(1,7) = 0.04$, $p = 0.72$], but did show a main effect of Adaptor Type [$F(1,7) = 9.11$, $p = 0.004$, $\hat{\eta}^2_G = 0.31$] and a significant Group X Adaptor interaction [$F(1,7) = 8.58$, $p = 0.006$, $\hat{\eta}^2_G = 0.29$]. The interaction effect reveals that mixed-cue groups and fixed-cue groups differed significantly in how they responded as a function of adaptor type, therefore data for this experiment were analyzed separately for the Mixed and Fixed groups.

2. TRs obtained using ITD and ILD adaptors

a. Fixed group. Mean TRs for the Fixed group were 60.8 μs/dB for the ITD-Adaptor condition (range = 26.7–89.1 μs/dB), and 23.9 μs/dB for the ILD-Adaptor condition (range = 17.4–33.3 μs/dB). Individual (thin lines) and mean (thick lines) TRs for each adaptor type are given in Fig. 7(A). A bootstrapped, paired-samples t-test compared the TRs between the ITD-Adaptor and ILD-Adaptor conditions. The result revealed a significant difference [$t(3) = 3.22$, 95% CI(-2.14, 2.13), $p = 0.03$, $d = 1.61$], suggesting adaptor type differentially influenced perceived azimuth for listeners in the Fixed group.

Consistent with the hypothesis that cue-specific adaptation influences ITD/ILD trading, presentation of adaptor trains significantly biased the perceived azimuths of probe tones using a modified MOCS task, at least for the Fixed group. Because this experiment used the same stimulus parameters as Experiment 1, it seems reasonable to infer that adaptation due to cue repetition also occurred during

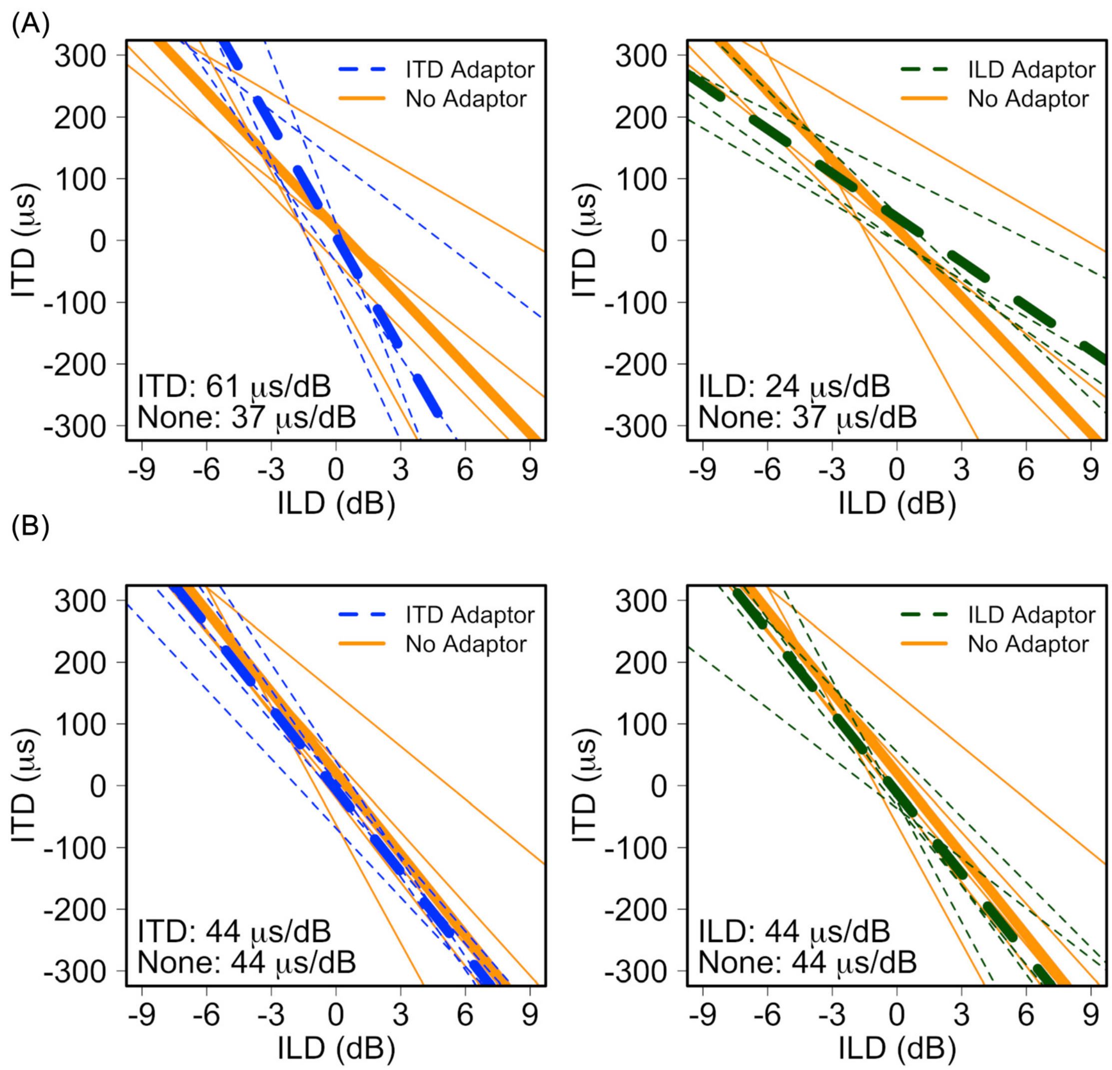

FIG. 7. (Color online) Mean and individual slopes (i.e., TRs) for Experiment 3 (thick and thin lines, respectively). (A) Data from the Fixed Group. (B) Data for the Mixed Group. Slopes are plotted on the same scale as the heatmaps, where they were derived from the 0 contour lines (cue combinations at which listeners perceived the stimulus at midline).

the MOA task. Furthermore, because Experiment 1 used MOA parameters common in the literature, it also seems reasonable to assume existing work showing cue-specific TRs obtained using an MOA task were also affected by binaural adaptation.

b. Mixed group. Individual (thin lines) and mean (thick lines) slopes for each adaptor type are displayed in Fig. 7(B). The mean TR for the Mixed group was 44.2 μs/dB for the ITD-Adaptor condition (range = 37.4–52.7 μs/dB), and 43.7 μs/dB for the ILD condition (range = 27–65.2 μs/dB). A bootstrapped, paired-sample t-test revealed no effect of the adaptors on listeners' responses in the Mixed group [$t(4) = 0.09$, 95% CI(-2.21, 2.16), $p = 0.94$]. See Sec. VI F 1 for discussion.

VI. GENERAL DISCUSSION

A. Main findings across experiments

Results from all three experiments are displayed in Fig. 8. Because there was no statistical difference between the Mixed and Fixed group data in Experiments 1 and 2, the data were collapsed for those experiments to increase statistical power ($n = 9$). Due to the lack of adaptive effects on the Mixed group in Experiment 3, those data were not included in the following analyses. Thus, the following planned comparisons should be interpreted with caution due to the small sample size of the Fixed group ($n = 4$). Note, however, that the pattern of results remains the same when only Fixed group data are considered for each experiment. Comparisons were carried out using bootstrapped t-tests.

It should also be noted that due to the different psychophysical methods across experiments, participants necessarily heard the most presentations overall during the MOA task due to its iterative nature. That is, the spatial adaptation observed in the MOA task was elicited by an average of ~12 s of exposure to the non-adjusted cue per judgment (~24 presentations of 500 ms each), while the spatial adaptation observed in the MOCS task was elicited by a 4-s adaptive train.

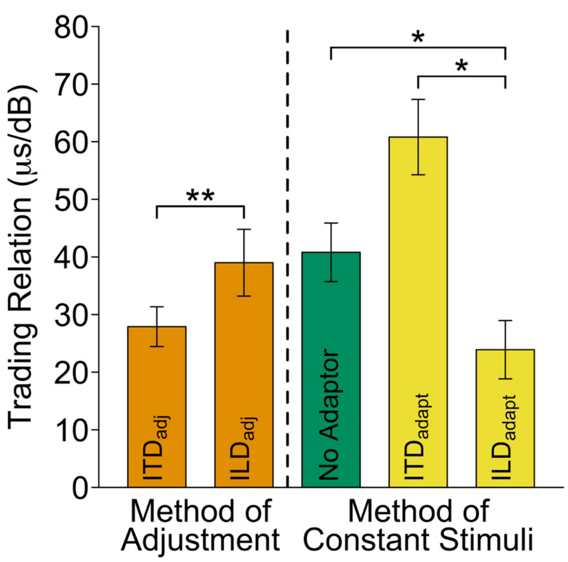

FIG. 8. (Color online) Comparison of trading relations across experiments and conditions. Error bars denote standard error around the mean. *$p < 0.05$. **$p < 0.005$.

1. Experiments 1 and 3

When comparing the data, it is important to recall that the MOCS adaptors mirror the MOA adjustments. That is, repeated presentations of the ILD occurred in both the MOCS ILD-Adaptor condition and the MOA ITD_{adj} condition, and repeated presentations of the ITD occurred in both the MOCS ITD-Adaptor and MOA ILD_{adj} conditions. Strikingly, those mirrored conditions across methods of presentation led to similarly biased TRs, lending credence to the involvement of adaptation in the cue-dependent TRs obtained using the MOA. The TRs obtained from the conditions with repeated ILDs (i.e., the ITD_{adj} and ILD-Adaptor TRs) both yielded small TRs (mean TR = 27.9 and 23.9 μs/dB, respectively), and did not differ significantly from each other [$t(8.72) = 0.82$, 95% CI(-1.71, 2.27), $p = 0.43$, $d = 0.32$]. The TRs obtained from the repeated ITD conditions (i.e., the ILD_{adj} and ITD-Adaptor TRs) both produced large TRs (mean TR = 39 and 60.8 μs/dB, respectively), and did not result in statistically different values [$t(4.1) = 1.45$, 95% CI(-1.82, 2.19), $p = 0.21$, $d = 0.47$]. It should be noted that the lack of statistical difference for the latter comparison may be due to the small sample size of the Fixed group, as visual inspection of the data suggests the ILD_{adj} and ITD-Adaptor TRs were different. What is clear, is that the repeated ITD conditions consistently yielded relatively larger TRs than the repeated ILD conditions. These findings support the occurrence of binaural spatial adaptation during the MOA task.

2. Experiments 2 and 3

Comparison of the No-Adaptor (mean TR = 39 μs/dB) and ILD-Adaptor (23.9 μs/dB) conditions revealed a significant difference [$t(10.9) = 2.75$, 95% CI(-1.71, 2.21), $p = 0.03$, $d = 0.86$]; however, the No-Adaptor and ITD-Adaptor (mean TR = 60.8 μs/dB) conditions did not differ significantly [$t(3.84) = 1.36$, 95% CI(-1.68, 2.26), $p = 0.22$, $d = 0.45$], despite a larger difference between the mean TRs than the former comparison. Given the overall pattern of the data, it is likely the lack of significance stems from the small sample size of the Fixed group ($n = 4$). Therefore, it seems reasonable to assume there is at least a trend for the data from Experiments 2 and 3 to agree with the hypothesis that overtly adapting a binaural spatial cue results in dominance of the unadapted cue.

B. Relative effectiveness of adaptation

What is particularly interesting is that while the pattern of MOCS data suggests that adaptation leads to TRs greater and lesser than the No-Adaptor condition, it was shown in Experiment 2 that the No-Adaptor MOCS condition did not differ from the ILD_{adj} condition (analog of the ITD-Adaptor condition). One interpretation of these data is that adaptation only affected the ITD_{adj} TR (analog of the ILD-Adaptor condition). In order to understand this phenomenon, it is useful to recall the parameters used in this study and the known effects those parameters have on binaural cues. There are three main points to consider. First, the ITD is known to drive perception in wideband stimuli (e.g., Macpherson and Middlebrooks, 2002), giving rise to the general rule that the ITD is the dominant cue when low frequency information is available (e.g., at 500 Hz used in these experiments). Second, low frequency ILDs are contrived stimuli that primarily exist under headphones, and therefore may be more easily ignored by the auditory system. Third, Harris (1960) found that larger values of ILD created diffuse percepts that proved difficult to lateralize. Taken together, a reasonable conclusion is that, under the conditions used in this study, the ITD was the more coherent cue, while the ILD was more diffuse and less effective.

There is precedent for this cue relationship. Stecker (2010) showed that decreasing the interclick interval between Gaussian-filtered impulses below 5 ms abolished the envelope cues necessary to extract ITD. This led to a shift in the TR that favored the ILD. Subsequent analysis confirmed the shift was due to weakened ITD cues, rather than an increase in ILD effectiveness. This reasoning can also account for the difference in TRs between the ILD_{adj} (susceptible to ITD dominance) and the ITD-Adaptor TR (ITD overtly adapted out resulting in ILD dominance). It is also worth noting that existing work has shown lead-lag pairs changing in ITD to be more robust against breakdown of the precedence effect compared to lead-lag pairs changing in ILD (e.g., Brown and Stecker, 2013; Krumbholz and Nobbe, 2002). Within the context of the current study, investigations into the precedence effect suggest a more cohesive ("fused") ITD percept and a more diffuse (i.e., separated lead-lag pairs) ILD percept. If percepts based on the ITD are generally more unified, they could also be more susceptible to adaptive effects than the ILD, which could partially explain the lack of difference between the ILD_{adj} and No-Adaptor MOCS conditions.

However, counter to the current findings, Lang and Buchner (2008, 2009) showed evidence of the shift-back effect regardless of the cue being adjusted, while the results of the current study predict the shift-back effect would only occur when the ITD was adjusted (i.e., the ILD_{adj} TR did not differ significantly from the No Adaptor condition). To explore this discrepancy further, TRs were calculated from the MOA data provided in Figs. 1 and 3 from Lang and Buchner (2009), over a range similar to the current study: preset ILD = 0 and ±2.5 dB; preset ITD = 0 and ±200 μs. The calculated TRs were ≈15 μs/dB for the ITD_{adj} condition, and ≈53 μs/dB for the ILD_{adj} condition. These values most closely match the adapted TRs from the current Experiment 3; this is noteworthy because the MOA TRs from the current Experiment 1 are the most methodologically equivalent to the TRs calculated from Lang and Buchner (2009).

The ITD-Adaptor and ILD-Adaptor TRs from the current study are 7.4 μs/dB and 8.8 μs/dB greater than their respective counterparts from Lang and Buchner (2009). Thus, while the absolute values differ by approximately 8 μs/dB, the relative difference between cue-specific TRs is nearly identical (∼38 μs/dB). This finding could indicate the influence of spatial adaptation during the MOA phase of Lang and Buchner (2009). A very similar difference between TRs is also found in data from Young and Levine (1977), who also investigated binaural cue trading using the MOA at 500 Hz. While the absolute values of the TRs differed from both the current study and Lang and Buchner (2009) ($ITD_{adj} = 40.4$ μs/dB; $ILD_{adj} = 79.4$ μs/dB), the difference between values remains 39 μs/dB.

The discussion above raises the question of why the current study's MOA task yielded a difference between ITD_{adj} and ILD_{adj} of only 11 μs/dB (i.e., a relatively small amount of adaptation). The reason for this may be methodological in nature. First, participants in Lang and Buchner (2009) used a continuous slider to change the value of the adjusted cue, while the present study made use of discrete step sizes with handheld controllers and a virtual environment. Second, Lang and Buchner (2009) did not use a reference tone to indicate midline in their MOA task, whereas the current study alternated between the adjusted percept and a diotic reference. Ignaz *et al.* (2014) showed that the presence of a reference tone in a MOA task led to shallower slopes (i.e., smaller TRs) compared with a MOA task without a reference tone. It is possible these two methodological differences sufficiently changed the stimulus context to reduce adaptation in the current study.

C. Adaptation, attention, and regression

Previous explanations for cue-dependent TR values have focused on attention (Lang and Buchner, 2008, 2009), regression (Trahiotis and Kappauf, 1978), and combinations of the two (Ignaz *et al.*, 2014). The current results suggest binaural spatial adaptation as a more parsimonious and cohesive account of these effects. Such an account would also be consistent with a large and growing body of evidence for adaptation to binaural cues in the auditory pathway, as revealed through psychophysical (e.g., Phillips *et al.*, 2006; Kopčo *et al.*, 2007) and physiological (Magnusson *et al.*, 2008; Dahmen *et al.*, 2010; Stange *et al.*, 2013) studies. Specific mechanisms for such adaptation potentially include balancing of excitatory and inhibitory inputs (Magnusson *et al.*, 2008), synaptic gain control (Stange *et al.*, 2013), and dynamic-range adaptation (Dean *et al.*, 2005; Dahmen *et al.*, 2010, Gleiss *et al.*, 2019). One consequence of normalizing the perception of auditory space to recently experienced cues could be perceptual shifts (Lingner *et al.*, 2018), such as those observed in the current study and in Lang and Buchner (2009).

Lang and Buchner (2008, 2009) demonstrated that when a fixed cue favored the left during adjustment, the MOCS task revealed a shift in perceived azimuth to the left (and vice versa). While these results could have been due to an attention-mediated increase in salience of the adjusted cue, it is equally likely the seeming dominance of the adjusted cue was due to the lateral percept being deflected away from the fixed cue. Taking into account that Lang and Buchner (2008) used an ISI of 500 ms during their MOA task, which is within the range of adaptive spatial effects, it is plausible they inadvertently introduced the localization aftereffect. In fact, the "shift-back" could very well have been a "shift-away."

Binaural spatial adaptation can also account for the results from Ignaz *et al.* (2014), who investigated the effect of an interleaved diotic reference tone (as employed in Experiment 1 here) on TRs obtained from an MOA centering task. They found a greater "shift-back" in the presence of a reference tone compared to a task without a reference tone. The interpretation offered by Ignaz *et al.* (2014) was that cue-specific attention was largely responsible for cue-dependent TRs in the absence of a reference tone, but the addition of reference tone likely biased listener responses as described by Trahiotis and Kappauf (1978). However, the localization aftereffect provides an even simpler solution: a repeated, midline reference tone can serve as an adaptor, which would result in larger shifts of the probe away from center compared with conditions lacking a reference tone. Indeed, Kopčo *et al.* (2007) showed that even a single preceding reference can lead to a shift in perception of the target away from the reference.

D. Processing of binaural spatial cues

Early models of ITD/ILD trading explained binaural percepts of laterality as originating solely from time or level differences via conversion from one cue to another in the cochleae (e.g., Deatherage and Hirsh, 1959; van Bergeijk, 1962). However, more recent work has largely shown these peripheral conversion processes can account for only a small portion of the overall perception of laterality (e.g., Joris *et al.*, 2008; Joris *et al.*, 1998). Neuroanatomical and neurophysiological data similarly provide mixed evidence for the integration of binaural spatial cues. Projections from the medial superior olive (MSO; largely low-frequency / ITD sensitive) and lateral superior olive (largely high-frequency / ILD and ITD sensitive) to the central nucleus of the inferior colliculus (ICC) include both segregated and convergent patterns, suggesting a mixture of independent and integrated processing of ITD and ILD in the ICC (Loftus *et al.*, 2004). Mixed evidence of cue integration is also found at the level of the cortex. Brugge *et al.* (1969) were able to offset ILD using timing differences within a single neuron in cat auditory cortex, and Higgins *et al.* (2017) found overlapping regions of cortical sensitivity to ITDs and ILDs using fMRI in humans. It is important to note, however, that Higgins *et al.* (2017) also found patches of non-overlapping ITD- and ILD-sensitive cortical regions, suggesting that cue integration may not be complete even in the auditory cortex. The current study demonstrated that binaural spatial cues are sufficiently independent for one cue to adapt the other, at some level of processing (see also Phillips *et al.*, 2006). This suggests that ITD and ILD could be coded as separate but related perceptual features, perhaps within complementary perceptual channels. Comparison of information within and across these channels could occur throughout the auditory pathway.

Physiological evidence suggests that adaptation to binaural cue values occurs within cue-specific pathways of the auditory brainstem, for example within the lateral superior olive (LSO) (Magnusson *et al.*, 2008) and also in nuclei which may integrate across cues, such as ICC (Dean *et al.*, 2005). Such evidence suggests a basis for cue-specific adaptation as observed here. Differences in the degree of adaptation to ILD vs ITD cues could then reflect intrinsic differences within the LSO and MSO pathways, or to various combinations of cue-specific and cue-independent adaptation along the ascending pathway.

E. VR

A novel methodological aspect of this study was that all experiments were conducted using VR for display of visual information and collection of responses. The reliability of participant responses suggests the use of VR did not negatively affect the quality of the data. Furthermore, TR values obtained in this study were comparable to those obtained using a variety of technologies, ranging from analog circuits (e.g., Deatherage and Hirsh, 1959) to touch-screen tablets (Stecker, 2010).

Establishing the use of VR as a standard tool for psychophysical studies is useful for several reasons. In this case, VR reduced irrelevant visual distractions of the lab environment and supported a natural and intuitive response technique (turning to "look" at a stimulus, pulling a trigger to "pop" balloons). Spontaneous participant comments revealed the more interactive tasks (i.e., MOCS) were noticeably more enjoyable than the less interactive tasks (i.e., MOA). These comments imply interactive virtual environments may lead to more engaged listeners, potentially delaying the effects of mental fatigue and reducing the overall number of visits required to complete data collection. VR tasks can also be easily shared across labs, potentially improving data consistency in replication and multi-site research.

F. Study limitations

1. Effects of adaptation across groups

The stimulus presentation pattern specific to each group provides some insight into the differential effectiveness of adaptation. The Fixed group was presented blocks of only a single adaptor type during an experimental session. Conversely, the Mixed group was presented blocks of either adaptor type during a single experimental session, and there was no Gaussian noise between trials; these differences could relate to the lack of an adaptation effect in that group. It may be that trial-by-trial adaptation is insufficient to influence perceived azimuth consistently, such that behaviorally relevant adaptation requires extended exposure to a single adaptor type. Perhaps introducing noise between stimulus presentations rendered trial-by-trial adaptation more potent, or a combination of these factors might be required to see effects. Unfortunately, the current study design cannot distinguish between these possibilities.

The discussion of Mixed and Fixed cue groups in this experiment is interesting because previous studies reporting cue-dependent TR values have been of the fixed-cue type (i.e., susceptible to adaptation) by nature of the study design: studies either measured a single type of cue interaction (e.g., adjusting only the ITD; Harris, 1960) or tested cues separately in different experiments (e.g., Lang and Buchner, 2009). The finding that listeners in the Mixed group were not sensitive to adaptive effects during an MOCS task thus has implications for future study design and reinforces the sensitivity of cue trading to task and stimulus parameters. It is also interesting to note that neither the MOA task nor the No-Adaptor MOCS task showed differences between Mixed and Fixed groups. More work is needed to investigate this phenomenon.

2. Sample size

The major drawback of splitting the participants into two groups was the subsequent reduction in sample size. Data from only four of the nine listeners were available from Experiment 3. This resulted in a lack of statistical significance between the No-Adaptor and ITD-Adaptor MOCS conditions. While the effect size was robust and the data exhibited a trend toward significance, the findings of this study would be strengthened by replication with a larger Fixed group sample size. Furthermore, a larger sample size would be more appropriate when making Fixed-group comparisons across ITD-Adaptor vs ILD_{adj}, and ILD-Adaptor vs ITD_{adj}.

3. Range of tradable ILD values

While the cue-specific biasing of TRs of this study were generally consistent with the existing literature, there were also some differences. Most notably, participants were unable to center images for fixed ILD values of 6 or more dB. Previous studies using the pointing method (which does not require centering a combined image) have obtained responses up to ±9 dB ILD (e.g., Hafter and Jeffress, 1968; Moushegian and Jeffress, 1959; Whitworth and Jeffress, 1961). However, concerning the method used in this study, Harris (1960) stated: "As the ILD is increased, the image spreads out and becomes harder to locate. For large intensity differences, the image sometimes splits." For this reason, he restricted the range of fixed ILDs to no greater than 6 dB. Despite this precaution, he still found that centering accuracy decreased with increasing ILD. Lang and Buchner (2009) measured TRs with fixed ILD values up to ±7.5 dB. They included a "Not enough" option participants could use if they were unable to center the stimulus. The "Not enough" option was checked most often when the fixed ILD value was ±7.5 dB. Conversely, Young and Levine (1977) mentioned no difficulty obtaining TRs with preset ILDs of up to 8 dB ILD and only observed cue specific TRs at the largest values (4, 6, and 8 dB). This pattern is in contrast to the findings of the current study, as well as Lang and Buchner (2009), where cue-specificity was observed at ILDs as small as 3 and 2.5 dB, respectively. Young and Levine (1977) made use of a diotic noise marker, which may have interfered with adaptive effects at lower cue values.

VII. SUMMARY AND CONCLUSIONS

(1) **Binaural spatial adaptation can account for the variation in trading relations observed across a variety of ITD/ILD trading tasks reported in the literature.** The regression theory and the shift-back effect can both be reconciled as adaptive localization aftereffects. Instead of a response bias or an upweighting in perceptual weight of the adjusted cue, the use of adaptors in this study demonstrated a displacement in perceived azimuth that corresponded to cue-specific TRs previously reported.

(2) **Introducing adaptors to a MOCS task increases the relative dominance of the unadapted cue.** The perceived azimuth of each cue type was shifted away from the perceived location of repeated presentations of the complementary cue. Stimulus parameters reported in previous MOA tasks were used in the MOCS task, suggesting the auditory localization aftereffect can be present during MOA tasks.

(3) **Virtual reality was successfully implemented in the experiments in this study.** Adapted trading relations obtained in this experiment indicate the same amount of cue specificity as values reported from studies using traditional methods. Furthermore, anecdotal reports from participants revealed a strong preference for experimental conditions that involved more VR interaction.

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[1]For example, a probe of +200 μs/−3 dB would be preceded by an ITD adaptor of +200 μs/0 dB or an ILD adaptor of 0 μs/−3 dB.

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