Passively Induced Contextual Plasticity in Sound Localization in Real and Virtual Environments

Norbert Kopčo [1], Stanislava Linková [1], Gabriela Andrejková [1]

[1] *Institute of Computer Science, Faculty of Science, P. J. Šafárik University, Košice, 04180, Slovakia*

Abstract.

Two experiments examined a localization aftereffect, called contextual plasticity (CP), induced by repeated exposure to transient stimuli presented from a fixed location. The first experiment tested whether passive exposure to the context is sufficient to induce CP in a reverberant classroom. The second experiment tested it in a virtual environment (anechoic or reverberant). Targets (2-ms noise bursts) and adaptors (trains of 12 such bursts) were presented on separate interleaved trials and subjects localized the targets while passively listening to the adaptors. The passively received adaptor caused responses to the targets to be displaced by up to 16° away from the adaptor location. This effect was strongest and fastest in the virtual anechoic environment, while only reaching 5° in real reverberation. Response standard deviations were also affected, increasing in the real environment while having a complex effect in the virtual environments. Finally, Information Transfer Rate was evaluated, showing that target spatial resolvability decreased near the adaptor location in all environments. Overall, these results show that passive listening to the context is sufficient to induce CP. However, the effect is exaggerated in virtual environments, where listeners might modify their localization strategy, using the adaptor as an anchor, which causes additional performance deterioration.

I. INTRODUCTION

Horizontal sound localization can be influenced by exposure to preceding sounds on multiple time scales. Early studies examining the auditory *localization aftereffects* (LA) showed that prolonged presentation of an "adapting" sound (with duration on the order of seconds) causes the subsequent target sound to shift away from the adaptor location (Flügel, 1920; Thurlow and Jack, 1973). Later studies showed that the effect is present under headphones as well as in the sound field (Canévet and Meunier, 1996; Carlile et al., 2001), for stimuli with various frequency content (Canévet and Meunier, 1996; Laback, 2023; Meunier et al., 2018), and across a range of interstimulus intervals (Kashino and Nishida, 1998). Additionally, several studies examined spatial discriminability effects induced by an adaptor (e.g., Getzmann, 2004; Maddox et al., 2014; Maier et al., 2010). Notably, all these studies used adaptor stimuli that were relatively long, with durations of at least several hundred milliseconds.

Kopčo et al. (2007) examined the effect of preceding stimuli on localization of brief 2-ms "click" sounds and found a more complex pattern. On one hand, for brief inter-stimulus intervals (ISIs) up to 100 ms, the *adaptor* click induced an attractive shift in the perceived location of the subsequent target click towards the adaptor location, likely due to mechanisms related to precedence effect and precedence buildup (Brown et al., 2015). On the other hand, the cumulative effect of multiple adaptor presentations was that the targets, when presented alone without any immediately preceding adaptor, shifted away from their reference location, possibly due to the same mechanism that causes the LA. The later phenomenon, called *contextual plasticity* (CP), is likely to be related to the LA as it involves similar shifts away from the adaptor (Andrejková et al., 2023; Hládek et al., 2017; Kopčo et al., 2015).

While the LA has been examined for longer stimuli, CP only has been examined for brief clicks, for which it builds up very slowly over the time course of seconds and minutes. Also, many aspects of CP are currently unknown. For example, all the studies in which it has been examined so far used an active listening task on the adaptor trials, not only on the target trials (the subject performed a localization task on the adaptor trials which contained both an adaptor and a target with a brief ISI), and they were performed in real anechoic and reverberant environments.

The current study presents two experiments. Experiment 1 examined the role of active listening in CP. Active listening has been shown to be important for many aspects of sound localization (Deouell et al., 2007; Higgins et al., 2017). And, while the previous CP studies used active listening tasks on adaptor trials, the LA studies typically used passive exposure to adaptor stimuli. Therefore, assuming that CP and LA are related, the current Experiment 1 examined whether passive listening to the adaptors is sufficient to induce CP as well.

Experiment 1, as well as all the previous CP studies, was performed in a real environment. Virtual environments are becoming more common both in everyday listening and in auditory research (Carlile, 1996). Their limited veridicality, caused by limitations in simulation and reproduction accuracy, can cause differences in performance as well as in the strategies used by the listeners. For example, they can induce biases or increased variability in responses, and listeners might try to rely more on the use of relative cues than absolute cues for sound localization (Kopčo et al., 2010; Recanzone et al., 1998). To evaluate these possibilities, experiment 2 was performed in virtual environment, both reverberant (similar to the real reverberant environment of Experiment 1) and anechoic. It also examined whether the changes in the CP strength, rate of buildup, and response variability change between these environments, as shown for real stimuli (Andrejková et al., 2023; Kopco et al., 2007).

The mechanisms of CP and LA are not well understood, even though several studies proposed models of different aspects of LA (Carlile et al., 2001; Dingle et al., 2012; Laback, 2023; Lingner et al., 2018). Traditionally, it has been assumed that the LA adaptation is a result of a local suppression or “fatiguing” in the spatial channels near the adaptor (Carlile et al., 2001; Dingle et al., 2012), resulting in response biases away from the adaptor location and decreased discriminability of sources near the adaptor. Lingner et al. (2018) proposed an alternative model that suggests that the effect of adaptor is to increase spatial separability of sources near the adaptor and the biases are a side effect of that benefit. While the current study does not directly measure discriminability, it introduces the Information Transfer Rate (ITR; Nelken and Chechik, 2007) as a related measure based on localization. It compares ITR with response standard deviation (SD) and Pearson correlation coefficient (CC) as localization-based measures related to discriminability to evaluate whether the current data are more consistent with the models of Carlile or Dingle vs. the Lingner model. Finally, current analysis also explores whether CP and LA are more consistent with models that assume spatial auditory processing channels are relatively narrow (Carlile et al., 2001) vs. broad hemispheric (Lingner et al., 2018), or some mixture of the two (Dingle et al., 2012).

The main hypotheses explored here are: (1) that CP and LA are at least partially related, predicting that CP will be induced by passive exposure to the adaptor; (2) that CP is influenced not only by bottom-up adaptation in spatial representation but also by top-down factors—such as subjects employing different response strategies (absolute vs. relative) in different environments—predicting that the magnitude of CP effects will vary across environments; and (3) that the neural representation underlying CP consists of relatively narrow processing channels, predicting that CP effects will align with the Carlile et al. (2001) model.

II. METHODS

The data described here were collected in two experiments. Experiment 1 was done in real reverberant and experiment 2 in virtual anechoic and reverberant environment. Setup, stimuli, and procedures were similar to the previous CP studies (Hládek et al., 2017; Kopčo et al., 2007, 2015).

A. Subjects

Eight subjects (three females), with ages ranging from 19 to 28 years, participated in Experiment 1. Ten different subjects (five female), nine with ages ranging from 19 to 29 years plus one 70 years old, participated in experiment 2. All subjects, except for the 70-year-old one, had normal hearing as confirmed by audiometric screening (all thresholds within 15 dB hearing level) and gave informed consent as approved by the of P. J. Šafárik University's Ethics Committee (the 70-year-old subject's thresholds ranged from 15 to 65 dB HL, with higher thresholds at higher frequencies; the subject was not excluded since the hearing loss was primarily in the high-frequency region not critical for horizontal sound localization, and since the subject's data were not identified as outliers). One subject from experiment 2 was excluded due to not following instructions. For three other subjects, data from one whole session of experiment 2 were excluded, identified as outliers based on anomalous baseline performance (importantly, as a session included all combinations of conditions, this exclusion influenced data for all conditions equally).

B. Setup and listening environment

Both experiments were performed in a quiet darkened midsize reverberant room (5.5 x 4.7 x 2.8 m; broadband T_{60} = 1.1 s) using identical stimuli and similar setup. Eleven loudspeakers were placed in a semicircle with a radius of 1.2 m at azimuths spanning -45° to +45° (step of 11.25°) and two at ±90° (Fig. 1A), approximately at the level of the subjects' ears. The speakers were covered with a dark acoustically transparent fabric so the subjects could not see their locations. Subjects were seated on a chair at the center of the semicircle, facing the middle speaker, with their heads supported by a headrest. A Polhemus Liberty position tracker was used to monitor the subject's head position and orientation.

A custom-made system consisting of a silent projector (Mitsubishi PK10), a 20 x 250 cm projector screen attached above the loudspeakers spanning the azimuths of ±60°, and a numeric keypad was used to collect the subject's responses. The projector provided instructions to the subject. During the trials, a unique 2-character combination (consisting of decimal digits and symbols "*", "-", "+", and "/") was shown at each azimuth from -59° to 59° in 1° steps (the 2-character combinations were randomly permutated on each trial). The subject responded by entering on the numeric keyboard the character pair nearest to the perceived stimulus location and pressing Enter. On the adaptor trials, the subject responded by only pressing Enter, i.e., without any engagement in active localization. This system was previously shown to provide the most accurate measurements of the subjects' responses when compared to the hand-held pointing response method (Kopčo et al., 2015). During a training session at the beginning of the experiment, the subjects practiced responding using this method until they were comfortable doing it without looking at the keypad.

A personal computer, placed outside the experimental room, controlled the experiments using custom-written MATLAB code. Experiment 1 used the loudspeakers in the experimental room (Fig. 1A), 5 to present adaptors (locations: 0°; ±45°; ±90°) and 6 to present targets (locations: ±11.25°; ±22.5°; ±33.75°). Experiment 2 used virtual stimuli while the subjects sat in the same experimental room (Fig. 1B), with 3 simulated locations to present adaptors (0°; ±50°) and 6 simulated locations to present targets (±10°; ±20°; ±30°). The 90° adaptor was omitted from experiment 2 to make its duration comparable to experiment 1 while using two different virtual environments.

C. Stimuli and procedure

Two types of stimuli were used (Fig. 1C). The target (T) was a 2-ms frozen broad-band white noise burst (a "click"), as used in the previous CP studies. The adaptor (A) was a train of 12 such identical clicks presented at the rate of 10 Hz (T = 100 ms). Note that the total duration of the target and adaptor stimuli (as well as the silent adaptor used in the baseline) was fixed for each stimulus presentation. Thus, the target stimulus was zero-padded prior to the click onset. The stimuli were presented at the level of 64 dBA (peak RMS value, measured using a long version of the stimulus) in experiment 1 and at a perceptually matched loudness in experiment 2 (achieved by adjusting the virtual reverberant stimulus level while listening to interleaved real and virtual stimuli by the authors). The experiment 2 stimuli were presented in a virtual environment created using a single set of non-individualized binaural room impulse responses (BRIR) measured in a similar room on a subject that did not participate in this study, using procedures and devices that were, unless specified otherwise, identical to previous studies (Kopčo et al., 2012; Shinn-Cunningham et al., 2005). The reverberant room simulations used the whole BRIRs, while the anechoic ones used a pseudo-anechoic HRTF obtained by windowing the corresponding BRIR prior to the first reflection. The stimuli were generated using a digital-to-analog converter (RME Fireface UFX), amplified (Knoll MX1255) and sent to loudspeakers (Canton Plus X3) in experiment 1 or sent to headphones (Sennheiser HD 800) in experiment 2.

Each experiment contained 3 sessions, each performed on a different day. A session consisted of runs, one run for each fixed adaptor position (including a no-adaptor baseline), resulting in six runs in experiment 1 and eight runs in experiment 2 (four each for the anechoic and reverberant environments). The experimental runs consisted of three parts: pre-adaptation (12 trials, target stimuli only), adaptation (168 trials – adaptors and targets randomly interleaved with equal probability), and post-adaptation (18 trials, target stimuli only). The target presentation order was pseudo-random such that each target was presented at least once before any target was presented for a second time etc. Thus, runs could be sub-divided into subruns corresponding to groups of trials in which each target was presented exactly once. The baseline runs were identical to the adaptor runs except that the adaptor was replaced by silence. The experiment was self-paced, with average trial duration of approximately 4 seconds, including stimulus presentation, response, and a 0.5-second pause before the next trial. One run lasted approximately 11-12 minutes. After each run the subjects could take a break. With the breaks, one session took approximately 2 hours in experiment 1 and 2.5 hours in experiment 2.

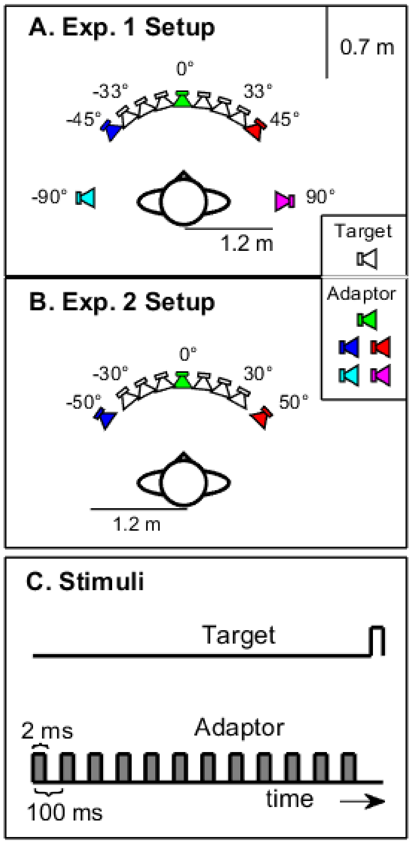

FIG. 1. Experimental setup and stimuli. A) Setup of the real reverberant environment used in experiment 1. B) Setup of the simulated sources used in the virtual anechoic and reverberant environments in experiment 2. White speakers represent targets. Colored speakers represent adaptors, each color corresponding to one adaptor location (results in the following figures use the same color code to represent different adaptor locations). C) Stimuli used in the experiments. The target stimulus was a 2-ms click. Adaptor was a train of 12 such identical clicks.

D. Analysis

All subject responses were recorded as discrete angles from -59° to 59°. Outliers were removed from the adaptation part (subruns 3—16) of each run, separately for each subject and target angle. An outlier was defined as a response with absolute value deviating by more than 4 times the median absolute deviation re. the median response in a given run (Leys et al., 2013). Around 2% of the experiment 1 data and 5% of the experiment 2 data were excluded. Response biases were computed as an average across the whole adaptation part of each run, while the response standard deviations (SDs) only considered the final 10 subruns (subruns 7-16) of each run when the responses reached a stable state.

All reported statistical analyses were performed as multi-way repeated measures or mixed analyses of variance (ANOVAs), using CLEAVE software (Herron, 2005). The reported statistical values were corrected for potential violations of sphericity using the Greenhouse–Geisser epsilon. All t-tests were two-tailed and used Bonferroni correction (unless specified otherwise). The significance level of $\alpha = 0.05$ was used in all tests.

Two overall performance measures were considered, Pearson's correlation coefficient *r* and the Information Transfer Rate (Nelken and Chechik, 2007; Sagi and Svirski, 2008). The *r* represents the extent to which the responses are linearly related to the actual target locations, while the ITR is a measure of how much information about the actual target location can be extracted by observing the responses, and it does not assume a linear relationship. For both measures, the responses for targets from one hemisphere (e.g., +10, +20, and +30°) of the final 10 subruns in a run were considered to compute the value. To compute the ITR, the procedures of Vlahou et al. (2021) were applied, with bin size of 1° used to estimate the probability distributions. Specifically, we defined $ITR = H(X;Y)/H(X)$, where $H(X;Y) = \sum_{x,y} \mathrm{p(x,y)} \log\left(\mathrm{p(x,y)}/\mathrm{p(x)p(y)}\right)$, $\mathrm{H(X)} = -\sum_{x} \mathrm{p(x)} \log\left(\mathrm{p(x)}\right)$. Variable p(x) is the probability of occurrence of stimulus x, p(y) is the probability of occurrence of response y, and p(x, y) is the probability of the joint occurrence of x and y (Miller and Nicely, 1955).

III. RESULTS

Results from both experiments are presented in parallel to allow a direct comparison of the effects in real vs. virtual environments. First, we analyze the effects of adaptor on response biases and SDs for data averaged across time. Then, overall performance is assessed using ITR and correlation measures to evaluate the data against two alternative models of auditory spatial adaptation. Finally, we examine the temporal profile of the buildup of contextual bias on data averaged across target locations.

A. Response Bias

The upper panels of Fig. 2 show the across-subject mean response location as a function of target location, separately for the different adaptor conditions (5 or 3 adaptor locations + no adaptor; encoded by color) and the two experiments (panel A for the real-room experiment 1; panels B and C, respectively, for the virtual reverberant and anechoic environments of experiment 2). Overall, the responses are fairly accurate in all conditions (all lines are near the diagonal). Considering the no-adaptor baseline, there is a slight underestimation of the response azimuths in the real environment and an overestimation in the virtual environments (black line shows bias towards the midline in panel A and away from the midline in panels B and C). The individual adaptors caused consistent effects with respect to the baseline in all environments. For example, the adaptors on the left induced a rightward bias (blue and cyan lines fall above the black lines), while the adaptors on the right induced a leftward bias (red and magenta lines fall below the black lines). Also, all the graphs are largely left-right symmetrical (blue lines are above the black lines mostly on the left, while the red lines are below the black lines mostly on the right).

To focus on the effects of adaptors, the data are replotted in the lower row of Fig. 2 such that each lower panel shows the same data as the corresponding upper panel after subtracting out the baseline and after combining the left-right symmetrical conditions (e.g., the blue point at -33° in each lower panel was obtained by averaging the -33° blue point and the negative of the +33° red point from the corresponding upper panel). Thus, in the lower panels, the graphs in the left-hand portion (locations -33° to -11°) are identical to those in the right-hand portion (locations +11° to +33°) after a rotation about the origin and a swapping of the red/magenta and blue/cyan colors; the green lines, corresponding to the 0° adaptor, are themselves symmetric about the origin). To stress this symmetry, the right-hand half of each graph is shown using a thick line, while the left-hand half is shown using a thin line. (Note that, analogically, the data above and below the x-axis are reflected and flipped copies of each other. For example, the red line is obtained by rotating the blue line around the origin). Therefore, the description below only considers the red, magenta, and green data to describe different effects.

In experiment 1 (Fig. 2A), repulsion away from the adaptor was observed in most conditions, with maxima ranging from 4-5° for the lateral adaptors (magenta and red lines at 33°) to 3° for the frontal adaptor (green line at 33°). For the lateral adaptors, the bias decreased for targets further away from the adaptor (red and magenta lines increase from right to left) while for the frontal adaptor the effect grew with distance from the adaptor or stayed stable (green line grows from left to right). Finally, the two lateral adaptors had similar but slightly different effects, with the 90° adaptor causing a stronger repulsion for the nearby targets (magenta is below red at 33°) while the 45° adaptor caused a stronger repulsion for the contralateral targets (red is below magenta at -11° to -33°). These results were confirmed by ANOVA with the factors of target location (11°, 22°, 33°) and adaptor location (-90°, -45°, 0°, 45°, 90°) which found a significant main effect of adaptor (F(4, 28)=57.3, p<0.001), target (F(2, 14)=11.30, p=0.001), as well as their interaction (F(8, 56)=9.25, p<0.001). A follow-up partial ANOVA performed on the frontal-adaptor data found a significant effect of target (F(2, 14)=8.1; p<0.005) and a partial ANOVA performed on the lateral adaptor data with the factors of adaptor (90°, 45°) and target (-33°, -22°, -11°, 11°, 22°, 33°) found a significant interaction between the factors adaptor x target (F(5, 35)=4.74; p=0.0021) as well as significant main effect of target (F(5, 35)=20.44; p<0.001), confirming that the effects of the two lateral adaptors were slightly but significantly different.

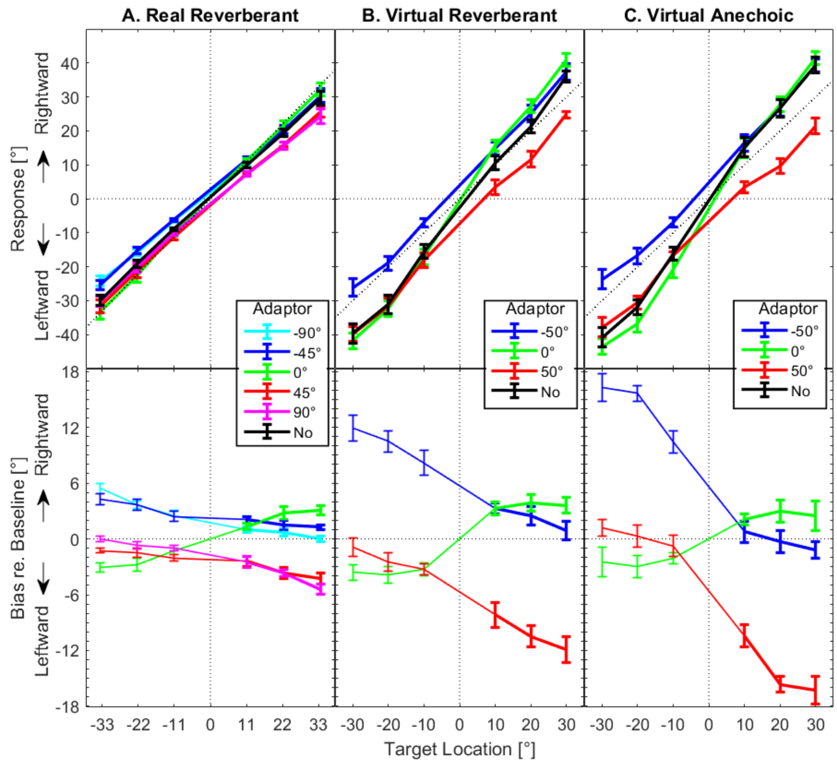

FIG. 2 Upper panels show a mean response (± SEM) in target trials in experiment 1 (panel A) and experiment 2 (panels B and C), plotted as a function of target location separately for each adaptor condition (including no-adaptor baseline). For each panel in the upper row, a panel in the lower row shows the bias (±SEM) in responses of each adaptor re. no-adaptor baseline after mirroring the data, assuming the effects are left-right symmetric. Thick lines highlight the subset of data points that are independent after the mirroring.

In experiment 2 (Figs. 2B and 2C), the central adaptor effects were similar to those of experiment 1 (compare the green lines across all three panels), while the lateral adaptor effects were much stronger, in particular in the virtual anechoic environment (red line in panel C reaches -16°, while it reaches around -12° in panel B). These results were confirmed by ANOVA performed on the biases with factors of target (10°, 20°, 30°), adaptor (-50°, 0°, 50°) and environment (reverberant and anechoic) which found significant main effects of the factors adaptor ($F(2,16)=146.43$, $p<0.001$), environment ($F(1,8)=6.13$, $p=0.038$), and target ($F(2,16)=3.73$, $p=0.0003$), as well as a significant adaptor x target interaction ($F(4,32)=7.22$, $p=0.002$).

1. Discussion

The results of experiment 1 confirm the hypothesis that engagement in active localization task is not required to induce CP. The bias sizes induced here by a 12-click adaptor in a passive listening condition (3°-5°), however, are smaller than those induced in previous studies by an 8-click adaptor in similar setups using active listening (9°-10°; Andrejková et al., 2023; Hládek et al., 2017). It is possible that engagement in active localization performance on the contextual trials also contributes to CP. Importantly, the setup of the previous studies differed from the current study also in other ways, not only in the active contextual localization task. Given these differences, it is impossible to use these comparisons to draw a conclusion about how large, if any, the contribution of active listening to CP might be.

The two lateral adaptors (45° and 90°) produced a similar, even if statistically different, pattern of biases in experiment 1. This result suggests either 1) that the adaptor effects are hemisphere-specific but approximately independent of the specific adaptor location for lateral adaptors (Kopco et al., 2019; Lingner et al., 2018), or 2) that CP also depends on adaptor laterality, becoming stronger (and more local) as the adaptor moves to the side. The latter alternative suggests that CP actually is stronger for the 90° adaptor because previous studies showed that CP decreases for targets further away from the adaptor (Kopčo et al., 2007) and thus the biases would have been much stronger for targets at 50° to 80° for the 90° adaptor if those locations were included (as shown in Andrejková et al., 2023; Hládek et al., 2017).

The frontal adaptor caused a weaker bias than the lateral adaptors, consistent with the suggestion that the effect strength grows with adaptor laterality. However, the effect is much weaker than that observed for a similar setup by Hládek et al. (2017), in which an 8-click frontal adaptor induced a 9° shift when all the targets were located only on one side of the adaptor, at locations from 11° to 79°. So, it is possible that the reduced biases in the current study were caused by the presence of the targets on both sides of the adaptor. This would suggest that CP is determined by the distribution of all stimuli, including both adaptors and targets, not just the adaptors (Andrejková et al., 2023; Laback, 2023). Finally, the notion that CP is not always strongest near the adaptor and decreasing with adaptor-target separation is also supported by the observation that, for the 0° adaptor in the current study, the bias grew, or stayed flat, with increased adaptor-target separation.

In the virtual environments of experiment 2, the lateral adaptors induced much larger biases than in the real environment of experiment 1, while the frontal adaptor's effect was comparable across all three environments. We are not aware of any previous CP or LA studies that directly compared the effects in virtual and real environments. Moreover, most of the LA studies were performed in virtual environments and they used arbitrary response scales instead of reporting perceived angle (e.g., Dingle et al., 2012; Laback, 2023; Lingner et al., 2018). It is difficult to determine the main reason why the virtual lateral effects are larger in the current study. One possibility is that the virtual environment does not provide any real-world anchors, resulting in increased uncertainty about the percepts and possible changes in response strategy. For example, the listeners might rely more on relative cue values of the targets referenced to the known locations of the adaptors, while in real environments they use the values of the stimulus acoustic cues to directly estimate the absolute location of the target. Such a switching strategy might only affect the lateral-adaptor performance but not the frontal adaptor performance because the 0° reference is always available. Another option is that the effect might have been caused by the fact that no ±90° adaptors were used in experiment 2 and so the subjects expanded their response range to cover the whole perceptual space. However, this explanation is unlikely as it predicts that the frontal adaptor responses also become more biased. Also, note that the subjects overestimated the target azimuths also in the no-adaptor baselines of experiment 2, suggesting that they might be biased to use the whole response range even if the stimuli only come from a limited range, or that they again respond relative to the 0° anchor and in general tend to overestimate the differences they perceive.

Finally, the lateral adaptors induced larger biases in the virtual anechoic than reverberant environment of experiment 2, consistent with larger CP observed in real anechoic than reverberant space (Andrejková et al., 2023). Since the presence of reverberation results in some reflections coming from all the directions, not only from the directions corresponding to actual adaptor and target locations, the distribution of received stimuli becomes more uniform and thereby, on average, more biased towards the median plane, possibly causing the reduced CP.

B. Response Standard Deviations

Figure 3 presents the response standard deviation (SD) results using a layout identical to Fig. 2. The upper panels show the across-subject mean SD as a function of target location separately for the different adaptor conditions (colors) and experiments (panels). Overall, the SDs vary both across the adaptors and experiments, with the smallest SDs of 3°-4°observed in the real environment (panel A) and larger SDs of 4°-7° in the virtual environments (panels B and C). Confirming this, a mixed ANOVA performed only on the baseline data (black lines) of the real reverberant and virtual reverberant environments (panel A vs. panel B) with a within-subject factor of target (6 azimuths) and a between-subject factor of environment (real reverberant vs. virtual reverberant) only found a main effect of environment (F(1, 15)=18.58, p=0.001), while a similar ANOVA performed only on the virtual reverberant vs. virtual anechoic data from experiment 2 found no significant difference.

The adaptor effects also differ across the panels. Adaptors induced increases in SDs in the real environment (non-black lines tend to be above the black lines in panel A) and a complex pattern of increases and decreases in the virtual environment (especially the blue and red lines are at times above and at times below the black line in panels B and C). To focus on the effects of adaptors, SD data were again rearranged such that each lower panel in Fig. 3 shows the corresponding data from the upper panel plotted re. baseline and combined after mirroring them across the left-right symmetric conditions (as in Fig. 2). In experiment 1 (Fig. 3A), considering targets at 11°-33°, the ipsilateral and frontal adaptors induced an increased SD (approx. 0.5°; red, magenta and, green lines), while the contralateral adaptors had no effect (blue and cyan). Confirming this, an ANOVA with the factors of adaptor (-90°, -45°, 0°, 45°, 90°) and target (11°, 22°, 33°) only found a significant main effect of adaptor (F(4, 28)=5.74, p=0.0017). Post-hoc Bonferroni-corrected pairwise comparisons are shown in the table inset in Fig. 3A, which indicates by asterisks the adaptor pairs significantly differing from each other. Based on this, the adaptors can be divided into two groups, the 0°, 45°, and 90° adaptors (green, red, and magenta) and the -45° and -90° adaptors (blue and cyan) such that the pairwise differences are significant for all adaptor pairs between the groups and for none within the groups. Note that the factor of target was not significant, suggesting that the effects were approximately equal across the three targets within a hemisphere.

In experiment 2 (Fig. 3B and 3C) the effect of adaptor on SDs was very different compared to experiment 1, while being similar between the two virtual environments. The lateral adaptor (red line) caused an increase in SDs for the nearest target (30°) as well as for the most distant target (-30°), while it caused a decrease in SD for intermediate targets at 10° to 20°. This effect was much stronger in the virtual anechoic environment (difference of 2° in panel C) than in the virtual reverberant environment (difference of 1° in panel B). For the frontal adaptor (green line), there was a similar very weak trend, with the SD slightly positive for the nearest 10° target and slightly negative for the most distant 30° target. Confirming these observations, an ANOVA with the factors of environment (reverberant, anechoic), adaptor (-50°, 0°, 50°), and target (10°, 20°, 30°) found a significant adaptor x target interaction (F(4,32)=3.63, p=0.037). Partial ANOVAs performed separately for each adaptor only found a significant effect of target for the adaptor at +50° (F(2, 16)=4.68, p=0.028), with post-hoc t-tests finding a significant difference between the 30° and 10° target and the 30° and 20° target.

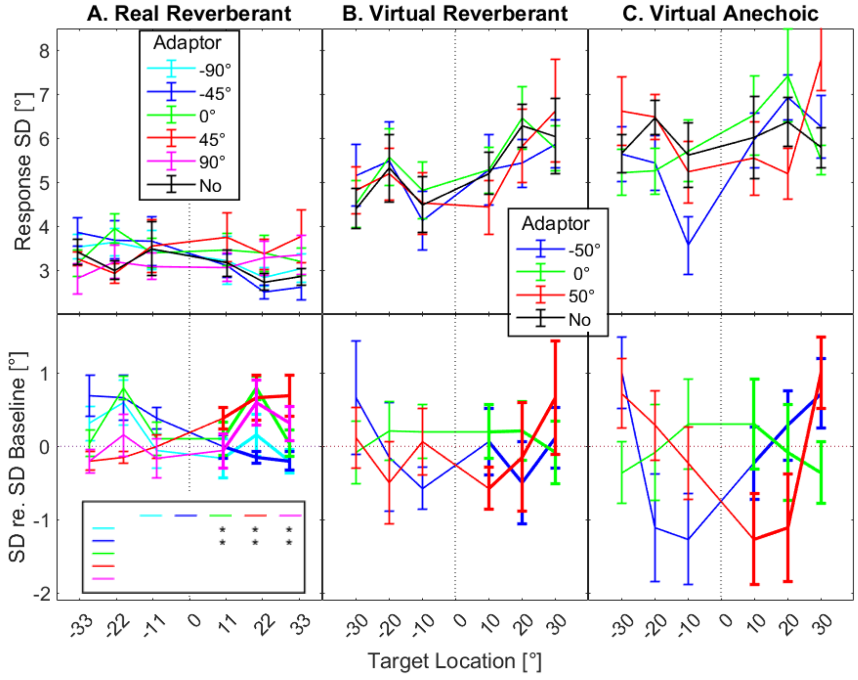

FIG. 3 Upper panels show mean standard deviation (SD) in responses (± SEM) in target trials in experiment 1 (panel A) and experiment 2 (panels B and C), plotted as a function of target location separately for each adaptor condition (including no-adaptor baseline). For each panel in the upper row, a panel in the lower row shows the SD (±SEM) in responses to each adaptor re. no-adaptor baseline after mirroring the data, the effects are left-right symmetric. Thick lines highlight the subset

of data points that are independent after the mirroring. Inset in panel A is a table showing results of post-hoc t-test pairwise comparisons between SDs for different adaptors (indicated by the color of the corresponding line), with asterisks representing significance level of $p<0.05$ (see text for details).

2. Discussion

In the real environment of experiment 1, both the 45° and 90° lateral adaptors had a similar effect, inducing an increase in SDs for the ipsilateral but not for the contralateral targets. Similarly, the 0° adaptor caused an increase in SDs for all the targets. These results are similar to the real room results of Kopčo et al. (2007), again supporting the main hypothesis that passive listening is sufficient to induce CP. Considering the proposed mechanisms of CP, the result is consistent with the mechanism causing a suppression in neural activation after adaptation which then results in noisier responses (Carlile et al., 2001), not with the mechanism where adaptation serves to increase separability of targets, which would predict a reduced SD (Lingner et al., 2018). However, similar to the bias results, it is not clear why the effect of the 45° adaptor is not stronger than that of the 90° adaptor, even though it is much closer to the targets.

In both virtual environments of experiment 2, the lateral adaptor induced an increased SD for the nearest targets and reduced SD for the more distant ipsilateral targets. While the decreased SD provides partial support for the Lingner et al. model of spatial adaptation, which would predict such a reduction for all targets near the adaptor, the overall pattern is not in line with their suggestion that spatial hearing adapts in order to improve separability since the SD actually increased for the targets nearest to the adaptor. Instead, the current results support the alternative suggestion that the subjects changed their strategy when localizing sounds in the virtual environment, as proposed earlier in the discussion of biases. Specifically, if the subjects started to respond relative to the known location of the adaptor which they used as an anchor, then it is possible that, for the intermediate targets, they can respond more consistently (even if with a larger bias) than when responding based on the absolute percept of the target location. And the increased SD for the targets nearest to the adaptor might suggest that the suppression mechanism of Carlile et al. dominates performance even if the response strategy has changed from absolute to relative.

Finally, baseline SDs were smaller in real than virtual environments. This is expected since virtual simulation has limited accuracy, especially when non-individualized BRIRs are used (Carlile, 1996). However, the real SDs were even considerably lower than the 10° SDs observed in the reverberant condition of Kopčo et al. (2007). This decrease is most likely due to a more accurate response method used here (pointer and closed eyes in Kopčo et al. (2007), vs. keyboard input in the current study), as shown in Kopčo et al. (2015).

Comparing virtual anechoic vs. reverberant SDs in current experiment 2 showed that virtual anechoic SDs were larger. In contrast, Kopčo et al. (2007) found anechoic SDs to be lower than reverberant SDs in real environments, consistent with the anechoic binaural cues being less distorted than the reverberant ones (Shinn-Cunningham et al., 2005). It is likely that the larger degradation in virtual anechoic environment is caused by the subjects being more sensitive to the quality of simulation when fewer cues are available, like in the current anechoic HRTFs (which do not include informative early reflections from floor or ceiling), possibly even losing their ability to externalize the simulated sources (Best et al., 2020).

C. Correlation Coefficient and Information Transfer Rate vs. Standard Deviation

One of the main results of the response SD analysis was that it found some support for the hypothesis that the effect of adaptor is to increase spatial separability (Lingner et al., 2018), particularly in virtual anechoic space. To more directly evaluate this hypothesis, we next examined two additional performance measures, Pearson correlation coefficient and the ITR, which consider not only the spread of responses, but also their means.

Figure 4 shows these performance measures for experiments 1 (column A) and 2 (column B and C, respectively, for the virtual reverberant and anechoic environments). The values were computed across the independent target triplets (e.g., the positive azimuths shown by thick lines in Figs. 2 and 3) and considering only the lateral adaptors for which it is clearly defined which adaptor is near (i.e., ipsilateral to the target triplet) vs. far (i.e., contralateral). The upper panels in Fig. 4 show results for SDs, obtained by simply averaging the data from Fig. 3 across the target triplets. The middle row shows the correlations between actual and response target locations computed across the three targets, while the bottom row shows the corresponding ITRs. Note that higher SD values correspond to lower discriminability, while for the other two measures higher values correspond to better performance.

In experiment 1, performance was better with contralateral than ipsilateral adaptor for all three performance measures (blue and cyan are better than red and magenta). ANOVAs with the factors of adaptor absolute azimuth (45°, 90°) and adaptor laterality (ipsi, contra) only found a significant main effect of laterality (SDs: F(1,7)=16.02, p=0.0052; CC: F(1,7)=5.80, p=0.0046; ITR: F(1,7)=6.33, p=0.04).

In experiment 2, there was no significant effect of laterality on SDs or CCs. On the other hand, the contralateral performance was always better in terms of ITR (blue is above red in the bottom row of panels B and C). Finally, in the ITR and CC measures the virtual anechoic performance was worse than virtual reverberant performance, which was worse than the real reverberant performance. Confirming these observations, ANOVAs with the factors of adaptor laterality (ipsi, contra) and environment (virtual anechoic, virtual reverberant) performed separately on the three measures only found a significant effect of adaptor laterality for ITR (F(1,8)=5.38, p=0.049) while the effect of environment was significant for ITR and correlation measures [CC: F(1,8)=29.83, p=0.0006; ITR: F(1,8)=5.69, p=0.044], but not for SDs [F(1,8)=3.06, p=0.12)].

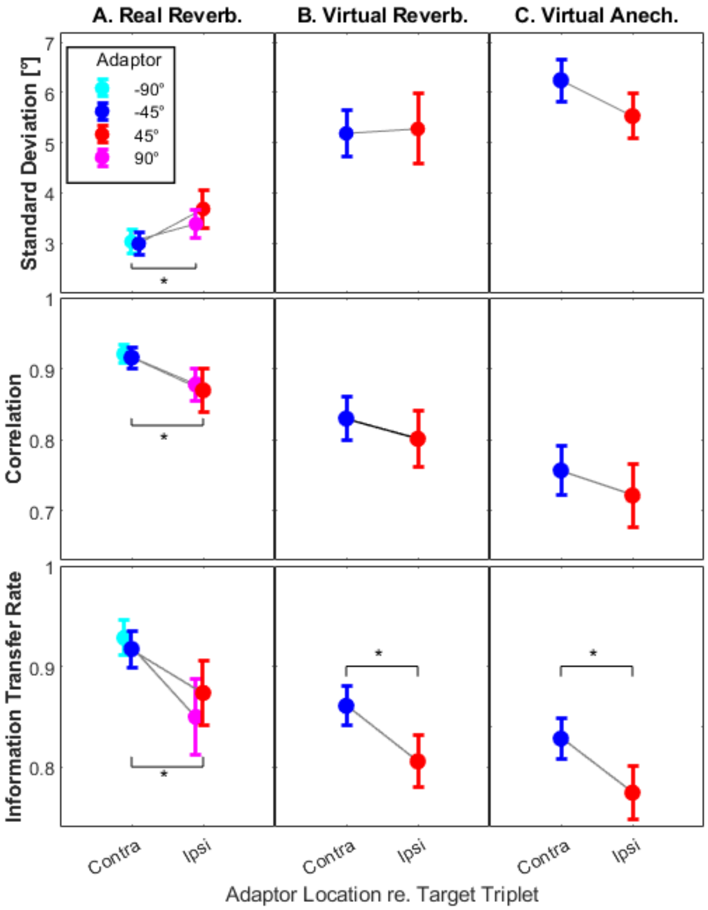

FIG. 4 The effect of ipsilateral and contralateral adaptors on the overall performance evaluated by three different measures (rows) across a triplet of targets at 11° to 33° in experiments 1 and 2 (columns). Upper row: mean of standard deviations across 3 target locations (10°, 20°, 30°)/(11°, 22°, 33°) from Fig. 3. Middle row: Correlation coefficients between subject's responses and actual target locations. Lower row: Values of Information Transfer Rate for the triplets of targets. Asterisks indicate significant difference based on ANOVA ($p<0.05$).

3. Discussion

These results, in particular those based on ITR, are consistent with the notion that source location discriminability is decreased near the adaptor, as would be predicted by the Carlile et al. (2001) model, and contrary to the increased discriminability predicted by the Lingner et al. (2018)

model. Importantly, Lingner et al. (2018) study was performed in virtual anechoic environment, the same environment in which a decreased SD was observed for targets 20-30° away from adaptor in the current study (Fig. 3). Also, a similar study by Getzmann (2004) found increased discriminability near adaptor in a real anechoic environment. Thus, it might be that in anechoic environment the subjects might improve their discriminability for specific targets, e.g. as a consequence of changing their response strategy particularly in anechoic environments, and using relative localization anchored at the known adaptor location when responding to the target.

Overall, only the ITR measure appears to be sufficiently robust and insensitive to possible non-linearities in the stimulus-response mapping to show a significant support for the Carlile et al. (2001) model in all the environments examined here. Also, when comparing performance across the environments, only ITR and correlation confirm the result that performance in the real reverberant environment is the best while in the virtual anechoic environment it is the worst. Thus, SD appears to be the least sensitive measure of discriminability based on localization tasks.

D. Temporal Profile of Contextual Plasticity

Figure 5 plots the temporal profile of CP as a function of subrun within experimental runs. Here, one subrun is defined as a group of trials in which each of the six targets was presented exactly once (note that the target presentation order was pseudo-random such that each target was presented at least once before any target was presented for a second time). The vertical dotted lines separate the pre-/post-adaptation subruns containing only target trials from the adaptation subruns in which adaptor trials and target trials were interleaved. Since the magnitude of the induced biases was similar across the 3 unique targets (10°, 20° and 30°, as shown by the thick lines in the lower panels of Fig. 2), the temporal analysis was performed on data averaged across these targets. The upper panels of Fig. 5 show the bias re. actual target location in the no-adaptor baseline runs, while the lower panels show the bias in the individual adaptor runs re. the baseline from the respective upper panel. The columns again represent the three different environments examined in the two experiments.

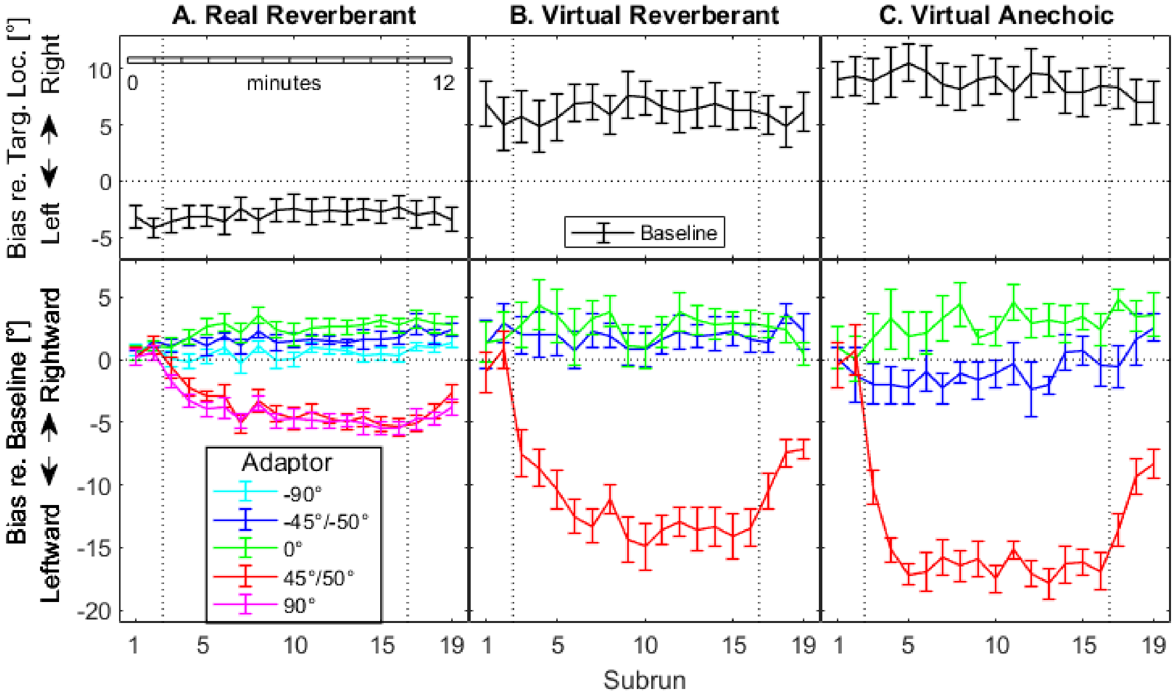

FIG. 5 Temporal profile of CP for the baseline runs (upper row) and adaptor runs (lower row) in experiment 1 (panel A) and experiment 2 (panels B and C). Across-subject mean biases (± SEM) re. actual location (upper row) or re. baseline (lower row) is plotted as a function of subrun within a run, averaged across the 3 unique target locations (10°-30°) after combining the left-right symmetrical data. Pre-adaptation and post-adaptation subruns are separated from the adaptation subruns by dotted vertical lines.

The upper panels show that there were no strong drifts in the baseline runs, with offsets across different panels corresponding to the pattern of overshooting and undershooting observed across the experiments in Fig. 2. The lower panels show strong buildup for the ipsilateral adaptors (45°/50° and 90°, red and magenta lines), while the buildup in the remining adaptor conditions (green, blue and cyan lines) was relatively weak and noisy, making it difficult to estimate specific characteristics of the buildup. Therefore, and since the 90° adaptor had a buildup similar to the 45° adaptor in experiment 1 (magenta vs. red in panel A), this analysis focused on the ipsilateral adaptors at 45°/50° (red lines). The individual data from both experiments were fitted parametrically using first-order exponential function (Andrejková et al., 2023), yielding time constant τ for the adaptation to the context (data of one subject from experiment 1 was excluded as the fitting did not converge). In experiment 1, the buildup was relatively slow ($\tau = 2$ subruns, red line in panel A), while in experiment 2 it was faster in anechoic environment ($\tau=0.93$ subrun, panel C), with the reverberant value falling between the other two ($\tau=1.39$ subrun, panel B). T-tests performed on the τ values only found a significant difference between the real reverberant and virtual anechoic environments ($t(14)=2.45$; $p=0.028$). Finally, in the post-adaptation (subruns 17-19) the effect started to weaken, decreasing to approximately a half of the adaptation peak reached at the end of adaptation in all three environments.

4. Discussion

The main result of this analysis, that the buildup of CP is faster in the virtual anechoic than in real reverberant space, is consistent with the real environment results of Andrejková et al. (2023). As suggested there, if the mechanism driving CP is dependent on the overall stimulus distribution, then the anechoic-vs-reverberant difference might be caused by reverberation being omnidirectional, making the distribution of arriving sounds more uniform than in the anechoic environment. Specifically, assuming that CP is sensitive to the stimulus distribution mean, that mean is shifted off the midline for the lateral adaptors. However, because of the omnidirectionality of reverberation, the extent of that shift is reduced in reverberation, providing an explanation for why the buildup of CP might be slower, and weaker, in reverberation.

An alternative, or additional, factor explaining the difference might be that in the virtual environments, the listeners tend to use more relative response strategy, comparing the target location to the known adaptor location, while in the real environment they use more direct absolute target location estimation (as suggested in the preceding sections). Such a switch in response strategy might occur immediately after the first adaptor presentation, explaining the abrupt onset of CP particularly in the virtual anechoic environment. To further evaluate this hypothesis, we re-analyzed the response biases in the adaptation subruns (shown in Fig. 2) after splitting the data by whether the preceding trial was an adaptor trial or a target trial. This analysis found no effect of the preceding trial type in the real reverberant environment of experiment 1, while the bias was larger immediately after the adaptor trial than after a target trial in experiment 2. Specifically, for the targets near the lateral adaptor, the difference was approximately 2° in virtual reverberant and 6° in virtual anechoic environments (data not shown). Thus, not only at the beginning of the adaptation, but throughout the adaptation portion of each run, responses shifted more away from the adaptor immediately after the adaptor presentation in virtual environments, but not in the real environment. This result supports the idea that in the virtual environments the subjects responded relatively to the adaptor location, and that they consistently overestimated the contrast from it to the target.

Finally, the biases induced during adaptation persisted during the three post-adaptation subruns in all the environments, confirming that the relatively slow adaptation component of CP persists at least over tens of seconds when the adaptor stops being presented, consistent with the time scale previously reported for frontal sources in real environments (Hládek et al., 2017). Importantly, since the relative strategy-switching component in virtual environments likely did not affect the post-adaptation performance (as there was no adaptor to be used as an anchor anymore), these results confirm that there is a slow component of CP that has a comparable temporal profile in real and virtual environments.

IV. GENERAL DISCUSSION

The current study primarily examined two questions about contextual plasticity: 1) whether it can be induced by passive listening to adaptors, and 2) whether it can also be observed in virtual environments. Experiment 1, performed in a real reverberant environment, found that passive listening is sufficient to induce both response biases and increased response SDs for targets near the adaptor (Fig. 2 and 3, respectively). Experiment 2, performed in virtual environments, found 1) that some of the induced biases were larger than in the real environment while the response SDs could either increase or decrease near the adaptor, and 2) that these effects were stronger in the anechoic than the reverberant virtual environment. Consistent across all the environments, overall performance expressed as ITR was always worse near the adaptor than far from the adaptor (Fig. 4). Finally, the buildup of adaptation was faster in the virtual anechoic than the real reverberant environment, with virtual reverberant environment performance falling in between (Fig. 5).

The mechanism underlying contextual plasticity is largely unknown. The current study showed that active responding during adaptation is not necessary to induce CP, supporting the hypothesis that it is caused by passive adaptation in some neural spatial representation whose mechanism is similar to the localization aftereffect (Andrejková et al., 2023). Specifically, it is likely to be driven by changes in the stimulus distribution (Andrejková et al., 2023; Dahmen et al., 2010; Laback, 2023), e.g., by changing the operating point of the neural channels (Dahmen et al., 2010) or by fatiguing of spatial channels due to repeated presentation of the adaptor (Carlile et al., 2001). However, it is still possible that some aspects of active localization on adaptation trials do influence CP, as the current experiment differed from the previous CP studies (e.g., Hládek et al., 2017) also in other ways, not only by the passive listening on the adaptation trials. To determine the contribution of active listening to CP, future studies could directly compare active and passive listening using an otherwise identical setup.

The current study examined CP in new spatial configurations. First, it used midline-symmetric target locations of -33° to 33°, which minimized temporal drifts in the no-adaptor baseline, as observed previously (Andrejková et al., 2023). Second, the adaptor locations were not only at the edge of the target range (45°) as in the previous studies, but also in the middle (0°) or at the extreme azimuth of 90° (only in experiment 1). Considering the 45° and 90° adaptors, if the CP induced by them had similar strength and simply decreased with azimuth, the CP induced by the 45° adaptor was expected to be much stronger than that induced by the more distant 90° adaptor. Contrary to this expectation, the effects of the 45° and 90° adaptor were comparable in terms of both response bias and response SD, with both measures decreasing for targets further away from the adaptors. This result suggests that either the effect is induced in a hemispheric representation not sensitive to the specific adaptor location within the hemisphere (McAlpine et al., 2016), or that the 90° adaptor induces a much stronger and broader effect than the 45° adaptor. It is also worth noting that the effects observed here, particularly in terms of SD, might have been stronger if they were measured also for targets at the adaptor locations, as previously observed in discrimination studies (e.g., Getzmann, 2004).

While the lateral adaptor results are consistent with previous CP studies at least in that the effect strength decreases with adaptor-target separation, the current 0° results do not follow this pattern, as 1) both the biases and SDs are approximately constant across all target locations and 2) the CP induced by this adaptor was much weaker here than in a comparable condition of Hládek et al. (2017). It is likely that both these differences are driven by the change in the spatial arrangement in the current study in which the 0° adaptor was located in the middle of the target range (the adaptor was always on the edge of the target range in Hládek et al. (2017), and other previous studies). This result supports the suggestion that the distribution of all the stimuli including the targets, not only the distribution of adaptors, needs to be considered when determining the size and direction of the

CP biases (Andrejková et al., 2023). However, Andrejková et al. (2023) evaluated the stimulus distribution mean as the statistic predicting the induced bias. Here, the 0° adaptor condition had the same mean as the baseline condition and no adaptation would be predicted based on the distribution mean statistic. Since an expansion of the spatial representation around the adaptor was observed, other distribution statistics, e.g., its standard deviation (Laback, 2023) might need to be considered. Importantly, this result is challenging even for the hemispheric models of auditory spatial representation (Braasch, 2015; Encke and Dietz, 2022; Lingner et al., 2018; McAlpine et al., 2016) as both channels are adapted equally by a central adaptor. Therefore, as a minimum, a third central channel is required to predict the expansion of spatial representation (Dingle et al., 2012).

In the virtual environment, the CP effects pattern was similar to that in the real environment, with two notable differences. First, while the effect of the frontal adaptor was comparable in terms of both biases and SDs, the effect of lateral adaptors was much larger in terms of bias (up to 16° in virtual vs. 5° in real environment) and more complex in terms of SDs (increase in real environment vs. increase followed by decrease in virtual environment). Second, the buildup of adaptation was faster in the virtual environment, especially the anechoic one, in which it had a very transient component that grew after every adaptor trial and disappeared after every target trial. These differences are most likely driven by a much larger uncertainty about how to map the acoustic cues to the physical sources in the virtual environment, as indicated by the increase in the baseline response SDs in virtual environments (5° to 6° vs. 3° in real reverberant environment). It is likely that the subjects use the adaptor, presented from a known location, as an anchor and combine the relative information about the target location re. the recently heard adaptor with a direct absolute estimation of the target location based on its ITD and ILD (Kopčo et al., 2010). Assuming that this relative location gets overestimated for the lateral adaptors, possibly because the subjects know on which side of the adaptor to expect the targets, this mechanism can explain the increased biases as well as the reduced SDs for targets at some locations (e.g., if it is assumed that the relative location estimation is combined with the absolute estimation, resulting in a more stable percept). This mechanism also provides an alternative explanation to the previous adaptation studies which reported increased location discriminability near the adaptor (Getzmann, 2004; Lingner et al., 2018). Specifically, it proposes that the improved discriminability is due to relative response strategy which subjects might use especially in anechoic environment (virtual or real, in which the previous studies were performed). However, note that relative response strategy is in fact required in discrimination studies, thus responding relative to the adaptor might be a more natural strategy there.

To more directly evaluate the proposal by Lingner et al. (2018) that the adaptation is the consequence of the system being tuned to separating sources as opposed to accurately localizing them, the current study evaluated the localization performance using two additional measures: the correlation coefficient and the information transfer rate. Both of these measures have the property that they do not penalize constant biases in responses, thus providing information about how discriminable the sources would be in a discrimination experiment based on localization performance. Contrary to the Lingner et al. proposal, both of these measures (and, in particular, the ITR) show that performance was worse near the adaptors in all three environments examined here, supporting the alternative hypothesis that the adaptation results from fatiguing or suppressing certain spatial channels in the auditory representation (Carlile et al., 2001; Dingle et al., 2012; Thurlow and Jack, 1973).

The current study is, to our knowledge, the first one to introduce the ITR as an overall localization performance measure that is robust against constant biases as well as non-linearities in the stimulus-response mapping. It is shown here that it is more sensitive than CC when evaluating the effect of adaptor on targets near and far from it and it is likely it can be considered as an overall measure of discriminability of stimuli in a localization study or when multiple sources are to be discriminated. Using the ITR, the current study found overall performance to be the best in real reverberant environment, intermediate in the virtual reverberant environment and worst in the virtual anechoic environment (a result that was confirmed also when CC was considered). While the degradation in virtual environments compared to real environments is expected, the lower performance in virtual anechoic compared to virtual reverberant environment is counterintuitive, as in real environments reverberation typically causes degradation in horizontal localization (Devore and Delgutte, 2010; Giguere and Abel, 1993; Hartmann, 1983; Kopčo et al., 2007; Rakerd and Hartmann, 1985, 2004). At least two factors might drive this effect. First, reverberation causes the simulation to be more naturalistic as the reflections arrive from all directions, not only the discrete target locations, improving externalization and mapping from the binaural cues to the horizontal location (Best et al., 2020). Second, some of the reverberant energy provides additional horizontal information, as, in particular, the first reflection typically coming from the floor or the ceiling, has the same azimuthal direction as the direct sound (Shinn-Cunningham et al., 2005).

In summary, the current study advanced our understanding of CP by showing that the effect can be induced by passive listening, and that it can be stronger in virtual than in real environments. These results support the suggestion that CP is related to the localization aftereffect (or, more generally, the precursor effect; Laback, 2023; Lingner et al., 2018; Phillips and Hall, 2005). However, it differs from those effects in that it is induced by very short stimuli and builds up on a slower time scale of tens of seconds to minutes (in the current study, the separation between adaptor and target trials was on average approximately 5 seconds). Moreover, based on the current results, it cannot be excluded that active listening also contributes to CP (e.g., that the effect is stronger when the listeners have to localize a target presented immediately after the adaptor, as in the previous CP studies) or that it is also partially due to the listeners modifying their localization strategy (e.g., from absolute to relative) in presence of the adaptor (Hládek et al., 2017). Additionally, the current results are important for the general understanding of the mechanisms of horizontal sound localization and its adaptation, as similar slow adaptive effects might have influenced also the results of other studies that did not consider them. For example, a binaural trading ratio study of Moore et al. (2020) considered the effect of an immediately preceding adaptor but not of possible slower adaptation to a cue that was fixed throughout a block of trials. Similarly, the Getzman et al. (2004) study mentioned above considered the effect of immediately preceding adaptor but kept that adaptor fixed throughout a block. More generally, many everyday listening situations might cause such slow adaptative effects. For example, consider a listener following – and adapting to – a static talker and then trying to localize an unexpected sound from a new location. Finally, multiple response measures have been proposed to evaluate sound localization accuracy (Culling and Summerfield, 1998). Here, we introduced ITR as a measure that evaluates overall separability between individual target locations while not penalizing for any non-linearities or biases in the stimulus-response mapping.

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AUTHOR DECLARATIONS

Conflict of Interest

The authors have no conflicts to disclose.

Ethics Approval

The current study was approved by the Ethical Review Authority of P. J. Šafárik University in Košice.

DATA AVAILABILITY

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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