

Learning of Audio-motor skill is sensitive to the lateral relationship between trained hand and ear

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Running title: Audiomotor integration across hands and ears

Keywords: audiomotor learning, monaural stimulation, lateral feedback

Abstract:

Performance of goal-directed actions requires integration of motor commands with their expected sensory outcome. Nevertheless, the process by which the brain links actions to their sensory consequences is poorly understood. A salient feature of motor and sensory circuits is their contralateral hemispheric bias, which might play a role in the integration process and affect learning of sensorimotor skills. In the current behavioral study, we examined this issue by manipulating the lateral relationship between sound-producing hand and stimulated ear, on the learning process of an audio-motor task. Four groups of right-handed participants (total N=117) trained for two days on playing a piano sequence using either their right or left hand while auditory feedback was presented monaurally, either to the right or left ear. All subjects showed improvement on the task across learning blocks and days. However, participants in the groups that received auditory feedback to the ear contralateral to the trained hand performed better than participants in the groups that received feedback to the ipsilateral ear. Our results suggest that sensorimotor integration is sensitive to the lateral relationship between the neural circuits controlling actions and those processing their sensory consequences and that integration of neural activity across hemispheres may facilitate learning.

Introduction:

Performance of goal-directed actions requires integration of motor and sensory information. For example, when learning to play the piano, one needs to learn the association between specific keystrokes and corresponding sounds. At the neural level, it is assumed that this is achieved through cross-talk between motor and sensory circuits that are engaged during task performance (Scott 2004, Crochet, Lee et al. 2019). Nevertheless, despite well-documented reciprocal interactions between behavioral and neural aspects of perception and action (Schutz-Bosbach and Prinz 2007, Gallivan and Culham 2015, Rizzolatti and Sinigaglia 2016), the process by which the brain links actions to their sensory consequences is not well understood. Previous studies have demonstrated that actions with sensory consequences modulate perception of sensory stimuli and corresponding neural activity in sensory regions, relative to otherwise identical sensory stimuli generated by an external

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source (Weiss, Herwig et al. 2011, Hughes, Desantis et al. 2013, Kiltner and Ehrsson 2019, Reznik, Guttman et al. 2021). For example, in the auditory domain, perceived amplitude of sounds that are the consequence of self-generated actions is modulated relative to the perceived amplitude of identical sounds from an external source (Weiss, Herwig et al. 2011, Reznik, Henkin et al. 2015). At the neural level, the amplitude of the auditory evoked EEG/MEG signal component (N100/M100) is reduced when sounds are the consequence of voluntary actions (Martikainen, Kaneko et al. 2005, Horvath 2015). Such modulatory effects are often explained by models suggesting that during execution of goal directed actions with sensory consequences, motor pathways responsible for action execution send a predictive (efference) signal to relevant sensory regions thereby modulating their neural state and ensuing stimulus-evoked activity (Wolpert, Ghahramani et al. 1995).

A salient feature of motor circuits is their lateral bias to one hemisphere relative to the controlled effector. At the cortical level, this bias is mostly to the contralateral hemisphere and at the cerebellar level mostly to the ipsilateral hemisphere (Kandel, Schwartz et al. 2012). Similar to the lateral biases in motor circuits, anatomical and functional evidence in the auditory system point to a contralateral bias between the stimulated sensory organs (left/right ears) and auditory cortex processing incoming auditory stimuli (Jancke, Wustenberg et al. 2002, Stecker, McLaughlin et al. 2015, Behler and Uppenkamp 2016). Thus, processing of monaural stimuli delivered to the right ear is biased to the left hemisphere (and vice versa for the left ear).

Given the anatomical distribution of neural circuits across hemispheres described above, it is plausible that differences in the hemispheric relationship between motor and sensory circuits engaged during performance of a sensorimotor task will affect integration processes and subsequent behavior. For example, shorter anatomical pathways connecting motor and sensory circuits and corresponding shorter conduction latencies (as when the two circuits reside within the same hemisphere), might facilitate integration of information compared to longer transmission pathways (as when the two circuits reside across hemispheres). This notion is supported by studies reporting shorter reaction times when the lateral relationship between responding hand and sensory stimulus do not require hemispheric crossing (Marzi 1999, Woelfle and Grahn 2013). Thus, participants' responses with the right hand (for example) are faster when stimuli are presented to the right (vs. the left) visual field (and vice versa with the left hand). The longer RTs in the crossed condition are ascribed to the additional processing time required for integration of the sensory and motor commands across the two hemispheres. Neurophysiological studies support this notion by demonstrating correlations between RT differences between crossed and un-crossed conditions and integrity of the corpus callosum (Tettamanti, Paulesu et al. 2002, Iacoboni and Zaidel 2004, Schulte, Sullivan et al. 2005, Westerhausen, Kreuder et al. 2006). An alternative possibility is that engagement of motor and sensory circuits that reside in opposite hemispheres enhance cross-talk that in turn may actually facilitate integration and learning. Cross-talk across large cortical regions and engagement of more neural circuitry has been suggested to play an important role in conscious perception (Mashour, Roelfsema et al. 2020).

We have recently demonstrated in the auditory domain that indeed the lateral relationship between motor and sensory circuits influences perception (Reznik, Henkin et al. 2014). Monaural hearing thresholds were lower when participants triggered sounds using the hand ipsilateral (vs. contralateral) to the stimulated ear (i.e. sound detection in the right ear was better when sounds were triggered by the right, as opposed to left, hand; and vice versa for left ear stimulation). Compatible with this behavioral result, using neuroimaging we also found hand dependent differences in auditory cortex. While inside an fMRI scanner, participants used either their right or left hand to generate sounds that were presented binaurally. Despite identical sounds produced by the two hands, evoked responses in auditory cortex were stronger when the lateral relationship between cortex and hand was contra (vs. ipsi) lateral. In other words, fMRI signal in left auditory cortex was stronger when participants generated the sounds with their right vs. the left hand (and vice versa for the right auditory cortex). Together, these behavioral and imaging results support the notion that the lateral relationship between motor and sensory circuits plays a role in perception and auditory-evoked neural activity. Nevertheless, whether the lateral relationship between motor and sensory circuits plays a role in sensory-motor integration and learning is not known.

In the current behavioral study, we address this question by using a 2x2 design in which training hand (left/right), and feedback-receiving ear (left/right) were manipulated across four groups of participants who trained across two days to perform an audio-motor task. Our findings point to differential learning across lateral relationship, with enhanced learning when hand and ear are contralateral to each other.

Methods:

Participants:

One hundred and forty-six right-handed healthy participants, naïve to the purpose of the experiment were recruited. All participants had normal hearing, normal or corrected to normal vision and no ~~prior~~previous musical training on a piano. Data from twenty-nine participants were discarded (seventeen participants did not complete the second session, six subjects were discarded due to technical error, and another six due to high number of errors during task performance or extreme values- see below), leaving data from one hundred and seventeen participants (36 males, mean age 25.19, range 18-35 years). The study conformed to the guidelines that were approved by the ethical committee in Tel-Aviv University. All participants provided written informed consent to participate in the study and were compensated for their time.

Materials and procedure:

In order to assess the effect of feedback laterality on audio-motor learning, participants were randomly assigned to one of four training conditions: left-hand ipsilateral ear stimulation (n=28), left-hand contralateral ear stimulation (n=30), right-hand ipsilateral ear stimulation (n=30) or right-hand contralateral ear stimulation (n=29). Participants completed two training sessions on two consecutive days during which they learned to play an 8-note sequence on a digital keyboard (MIDI Teensy) using five-fingers (see figure 1A). The sequence participants trained to perform was 1-4-1-2-3-4-5-3 where the numbers represent fingers that were mapped to notes as follows: 1 (little finger, G), 2 (ring finger, F), 3 (middle finger, E), 4 (index finger, D), and 5 (thumb, C). Throughout the experiment, participants were instructed to play the correct sequence of notes as accurate as possible relative to a target rhythm. Participants performed the task sitting in a chair in front of the keyboard while receiving auditory feedback via headphones (Audio Technica ATH-M50X). Instruction slides were presented on a computer using Psychtoolbox-3 (www.psychtoolbox.com) on MATLAB 2019b (The MathWorks, Inc., Natick, Massachusetts, United States).

Each of the two training days included a main training phase, which was preceded and followed by evaluation phases (see figure 1A). At the beginning of day 1, participants also underwent a short familiarization phase in which they were allowed to interact with the MIDI keyboard and verify they understand the task. This phase included 4 trials (2 sequence repetitions for each hand) in which participants executed the sequence in a self-paced manner. During the main training phase of each session, participants executed the sequence using either their right or left hand while receiving monaural auditory feedback according to their assigned condition (ipsilateral or contralateral ear with respect to their training hand). Participants were informed they would receive auditory feedback only to one ear during this phase. In addition, a metronome beat (25 bpm) was presented to the same ear as a reference for rhythm performance (2.4s between consecutive beats). Before training began, participants listened to a playback of two metronome beats (4.8s), followed by an image of headphones cueing them to listen to 5 repetitions of the 8-note sequence in the correct rhythm. Each note was 150ms long and the inter-press interval (IPI) between consecutive note onsets was 300ms. Thus, a single 8-note sequence fit between two consecutive metronome beats. Each training session included 20 blocks, each block consisted of 5 continuous repeats of the 8-note sequence, followed by 15 seconds rest period cued by a white screen (see Fig 1B). Within each training block, metronome was initiated by participant's first note press. Participants were instructed to execute each 8-note sequence between two consecutive metronome beats and use equal IPI between notes.

Another measure of learning is the degree of generalization – performance on a similar task under different conditions. In the current study we examined two types of generalization through the use of performance evaluation phases before/after training (Figure 1A). During each evaluation phase, participants performed the same

note sequence as during training however we removed the metronome cue as external temporal reference and auditory feedback was provided to both ears. Another form of generalization we examined was inter-manual transfer – i.e., task performance with the non-trained hand. Thus, each evaluation phase included assessment of both the trained and untrained hands. During each evaluation phase, participants were instructed to execute the note sequence as accurately as possible relative to the reference sequence. During each evaluation, participants were first presented with an image of headphones cueing them to listen to 5 repetitions of the 8-note sequence (same as in the training phase). Next, participants were instructed to execute the sequence repeatedly on the MIDI keyboard in a constant rhythm as similar as possible to the reference performance they just heard. The evaluation phase consisted of 4 blocks; 2 blocks performed using each hand. Each block included 5 repetitions of the 8-note sequence and was followed by 15 seconds of resting period cued by a white screen (see figure 1C). In order to minimize hand-switching between evaluation/training phases, in the pre-training evaluation phase, the first two blocks were performed with the untrained hand and the following two blocks were performed with the trained hand. In the Post-training evaluation, hand order was reversed (see figure 1A).

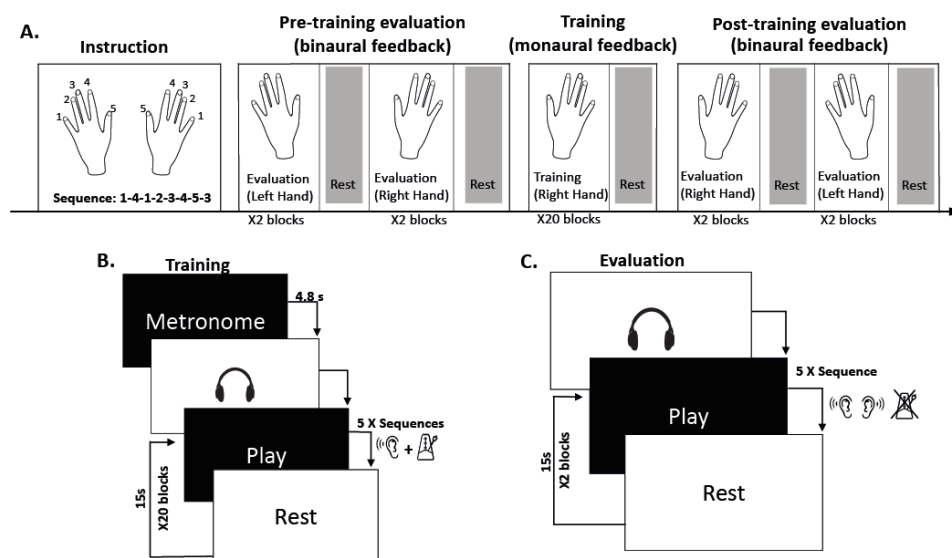


Figure 1: Experiment design. A – experiment timeline (example for right-hand training groups). B – training block. Participants were requested to play the sequence as accurately as possible between consecutive metronome beats . Auditory feedback of generated notes and metronome was provided to one ear (either left or right) according to group assignment. C – evaluation block. Participants

were requested to execute the sequence as accurately as possible, relative to the same reference sequence. During evaluation no metronome cue was provided, and auditory feedback was delivered binaurally.

Data preprocessing and analysis:

In order to compare sequence playing performance between the four training groups, we calculated two dependent measures from each participants' data: inter-press-interval (IPI) and number of errors. IPI was defined as the time between the initiation of one note and the initiation of the next note. For each IPI we calculated its absolute difference from 300ms (perfect performance; delta IPI). Error notes were defined as pressing the wrong key with respect to the correct sequence or notes with IPI greater than 1s. For each block of each participant (total of 40 key presses/39 IPIs), we calculated the median delta IPI across correct note pairs, as the representative IPI of the block. Data from blocks with 20 or more errors was discarded from analysis. Participants with more than 10 discarded blocks in the training session (out of 40 total) were discarded from analysis (total of 3 participants, 2 in the left- hand ipsilateral ear group and 1 in the left- hand contralateral ear group). Participants with less than 10 discarded blocks remained in analysis, considering only their valid blocks (total of 12 discarded blocks from 6 participants; range 1-5 blocks each in the training session; 9 blocks in the left- hand contralateral ear group and 3 blocks in the left- hand ipsilateral ear group. We also discarded 1 block from 1 participant in the left- hand ipsilateral ear group in the pre-training evaluation). In addition, we discarded additional 3 participants from analysis that demonstrated deviant training trends (2 in the left-hand ipsilateral ear group and 1 in the right ear contralateral group), leaving data from 117 participants for further analysis.

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Results:

Training data:

In order to compare learning across days and conditions, we averaged each participant's performance across training blocks separately for the first and second training day. Overall, regardless of training group, we found a significant improvement in performance between the two training sessions, such that participants' average performance across blocks on the second day was significantly better than their average performance across blocks on the first day (i.e. had smaller difference from perfect performance - Δ IPI; *Second day* $M=28.30\text{ms}$ $SD=14.61\text{ms}$; *First day* $M=44.04\text{ms}$ $SD=21.38\text{ms}$; Paired sample t test: $t(116)=11.90$, $p<0.01$). We also found a significant reduction in the number of errors committed across days (first day: $M=3.43$ $SD=2.86$ errors; second day: $M=1.32$ $SD=1.92$ errors; Paired-sample t test: $t(116)=9.84$, $p<0.01$; see figure 2A).

In order to compare learning across conditions, we used a 2X2 ANOVA with trained hand (right / left) and feedback laterality (ipsilateral /contralateral relative to training hand) as between-subjects factors. During the first training day, we did not find a difference in performance (Δ PI) between feedback laterality groups (ipsilateral groups: $M=44.67$ ms $SD=19.45$ ms; contralateral groups: $M=43.41$ ms $SD=23.44$ ms; $F(1,113)=0.12$ $p=0.73$). We also did not find a significant difference between trained hands (Right Hand groups: $M=41.54$ ms $SD=17.17$ ms; Left Hand groups: $M=46.57$ ms $SD=24.69$ ms; $F(1,113)=1.62$ $p=0.21$) or an interaction effect ($F(1,113)=0.1$ $p=0.76$). Similarly, we did not find a significant difference in terms of committed errors between feedback laterality groups (Ipsilateral Feedback groups: $M=3.78$ $SD=2.85$ errors; Contralateral Feedback groups: $M=3.10$ $SD=2.81$ errors; $F(1,113)=1.80$, $p=0.18$), trained hand groups (Right Hand: $M=3.01$ $SD=2.29$ errors; Left Hand: $M=3.87$ $SD=3.27$ errors; $F(1,113)=2.82$, $p=0.10$), or an interaction between the two ($F(1,113)=0.51$ $p=0.48$). Together, these results point to similar baseline performance levels between training groups during the first day.

During the second training day, we found a significant difference in performance between feedback laterality groups, such that groups that trained with auditory feedback to the ear contralateral to the trained hand had better performance (smaller Δ PI values) than groups that trained with auditory feedback to the ipsilateral ear ($M=25.63$ ms $SD=12.41$ ms vs. $M=31.01$ ms $SD=16.49$ ms; $F(1,113)=4.22$ $p=0.04$). With respect to trained hands, we did not find a significant difference between the groups (Right Hand groups: $M=26.45$ ms $SD=13.44$ ms; Left Hand groups: $M=30.18$ ms $SD=15.49$ ms; $F(1,113)=2.12$ $p=0.15$), or an interaction effect between feedback laterality and trained hand ($F(1,113)=0.41$ $p=0.52$, see figure 2B).

With respect to number of errors committed on the second training day, we found no difference between feedback conditions (Ipsilateral Feedback groups: $M=1.57$ $SD=2.25$ errors; Contralateral Feedback groups: $M=1.07$ $SD=1.47$ errors; $F(1,113)=2.22$, $p=0.14$). We found a trend toward significance between trained hands (Right Hand groups: $M=1.02$ $SD=1.43$ errors; Left Hand groups: $M=1.63$ $SD=2.26$ errors; $F(1,113)=3.23$ $p=0.08$), and no interaction effect between trained hand and feedback type ($F(1,113)=1.97$, $p=0.16$).

Taken together, all groups performed better following training (as expressed by smaller deviations from perfect performance Δ PI, and lower error rates). Groups that trained with auditory feedback delivered to the ear contralateral to the training hand learned better than groups that trained with auditory feedback delivered to the ear ipsilateral to the training hand, while error rates remained similar across groups.

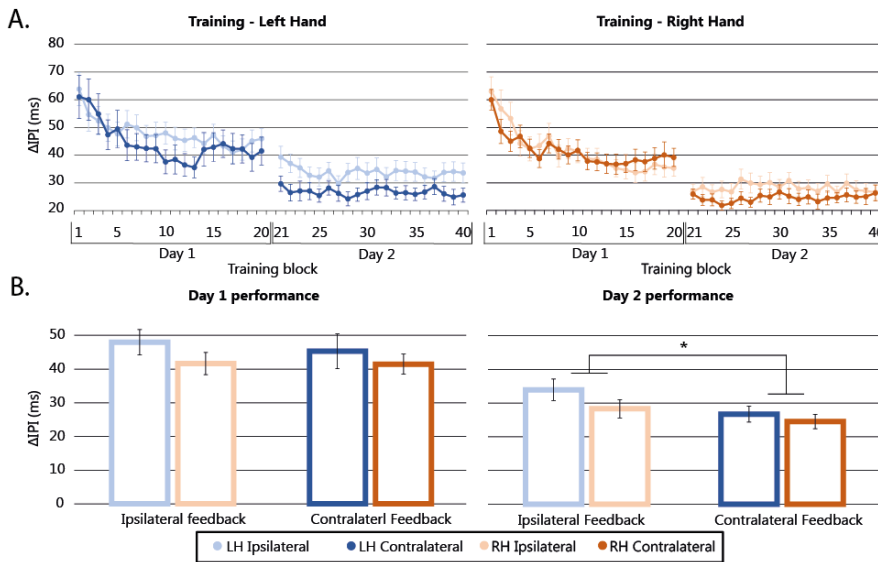


Figure 2: performance on the training sessions.

A - performance (ΔIPI) across training blocks for the left hand (blue) and right hand (red) groups according to feedback condition (ipsilateral ear – light colors; contralateral ear – dark colors).

B - mean performance across blocks on the first (left) and second (right) training days. On the second day, participants who received auditory feedback to the ear contralateral to the active hand had lower ΔIPI (were more accurate), than participants who received ipsilateral feedback during training.

Generalization to binaural feedback: performance with the trained hand

In order to examine generalization of training to performance without external reference cue (metronome), we evaluated participants' performance before and after training (see methods). With respect to evaluations of the trained hand irrespective of training group, we found a significant difference between pre-training evaluation on the first day and the post-training evaluation on the second day, such that participants' performance on the last evaluation was significantly more accurate (ΔIPI : $M=28.97ms$ $SD=12.90ms$ vs. $M=77.52ms$ $SD=56.32ms$; Paired sample t test: $t(116)=9.94$, $p<0.01$). In addition, subjects committed less errors during the post training evaluation ($M=0.65$ $SD=1.39$ errors) relative to pre training evaluation ($M=3.30$ $SD=2.81$ errors; Paired sample test: $t(116)=9.86$ $p<0.01$).

Before training, we found no significant difference in performance (ΔIPI) between feedback laterality groups (Ipsilateral Feedback groups: $M=79.63ms$ $SD=47.58ms$; Contralateral Feedback groups: $M=75.44ms$ $SD=63.69ms$;

$F(1,113)=0.20$ $p=0.66$). We also found no difference in performance between right and left hand training groups (Right Hand groups: $M=68.71$ ms $SD=41.35$ ms; Left Hand groups: $M=86.49$ ms $SD=67.09$ ms; $F(1,113)=2.92$ $p=0.09$), or interaction effect between feedback laterality and trained hand ($F(1,113)=0.06$ $p=0.81$). With respect to errors, we did not find a significant difference between feedback laterality groups (Ipsilateral feedback groups: $M=3.64$ $SD=3.26$ errors; Contralateral Feedback groups: $M=2.97$ $SD=2.21$ errors; $F(1,113)=1.71$ $p=0.19$), hand groups (Right Hand groups: $M=3.12$ $SD=2.60$ errors; Left Hand groups: $M=3.48$ $SD=3.00$ errors; $F(1,113)=0.54$ $p=0.46$), or an interaction effect between these conditions ($F(1,113)=0.64$ $p=0.43$). Together, these results indicate no inherent difference in baseline performance across groups on the first day.

In the post-training evaluation blocks performed on the second day, we found no significant difference in performance across feedback laterality training groups either (Ipsilateral Feedback groups: $M=30.36$ ms $SD=13.59$ ms; Contralateral Feedback groups: $M=27.61$ ms $SD=12.03$ ms; $F(1,113)=1.72$ $p=0.19$). A significant difference in performance between hands was found, such that right hand performance of participants who trained with their right hand ($M=26.24$ ms $SD=11.11$ ms) was better than left hand performance of participants who trained with their left hand ($M=31.75$ ms $SD=13.96$ ms; $F(1,113)=6.25$, $p=0.01$). We also found a significant interaction effect between feedback laterality and trained hand ($F(1,113)=10.02$ $p<0.01$). Post hoc analysis revealed that in the Left Hand training groups, there is a significant difference between feedback conditions (Ipsilateral Feedback group: $M=36.98$ ms $SD=15.20$ ms; Contralateral Feedback group: $M=26.87$ ms $SD=10.58$ ms; Unpaired t-test: $t(56)=2.91$, $p<0.01$), but no such difference was found in the Right Hand training groups (Ipsilateral Feedback: $M=24.18$ ms $SD=7.91$ ms; Contralateral Feedback: $M=28.37$ ms $SD=13.32$ ms; $t(57)=1.30$ $p=0.20$; see figure 3A). With respect to errors, did not find a significant difference between feedback laterality groups (Ipsilateral feedback groups: $M=0.59$ $SD=1.64$ errors; Contralateral Feedback groups: $M=0.72$ $SD=1.09$ errors; $F(1,113)=0.24$ $p=0.62$), trained hand groups (Right Hand groups: $M=0.58$ $SD=1.04$ errors; Left Hand groups: $M=0.72$ $SD=1.67$ errors; $F(1,113)=0.29$ $p=0.59$), or an interaction effect between these groups ($F(1,113)=3.08$ $p=0.08$).

Thus, all groups showed generalization, as expressed by improved post-training performance on the task without an external cue (metronome). Although no main difference across laterality groups was found, in the left-hand groups we did find a significant advantage for the contralateral vs. ipsilateral training condition.

Generalization to binaural feedback: performance with the untrained Hand

Another type of generalization we examined is inter-manual transfer – assessed by sequence performance with the untrained hand. Collapsed across groups, we found a significant improvement in performance with the untrained hand following training,

such that participants' performance accuracy with the non-trained hand on the last evaluation (ΔIPI : $M=36.26\text{ms}$ $SD=19.59\text{ms}$) was significantly better than their performance with the non-trained hand on the first evaluation ($M=92.00\text{ms}$ $SD=61.35\text{ms}$; Paired sample t test: $t(116)=11.99$, $p<0.01$). In addition, subjects performed less errors with the untrained hand following training (Last evaluation: $M=1.26$ $SD=1.57$ errors; First evaluation: $M=4.29$ $SD=3.94$ errors; Paired sample t test: $t(116)=8.15$ $p<0.01$).

Similar to the trained hand evaluations, we found no difference in baseline performance of the untrained hand across groups. In other words baseline left hand performance in right hand training groups was not significantly different than right hand performance in the left hand training groups (Right Hand group (evaluation of left hand): $M=96.25\text{ms}$ $SD=54.55\text{ms}$; Left Hand group (evaluation of right hand): $M=97.76\text{ms}$ $SD=67.55\text{ms}$; $F(1,113)=0.01$ $p=0.91$). We also found no significant difference in the untrained hand between feedback laterality training groups (Ipsilateral Feedback: $M=92.38\text{ms}$ $SD=50.45\text{ms}$; Contralateral Feedback: $M=101.55\text{ms}$ $SD=70.13\text{ms}$; $F(1,113)=0.64$ $p=0.43$), and no interaction effect between trained hand and feedback laterality ($F(1,113)=0.09$ $p=0.77$). With respect to errors, we did not find a significant difference between feedback laterality groups (Ipsilateral feedback groups: $M=4.59$ $SD=3.98$ errors; Contralateral Feedback groups: $M=4.02$ $SD=3.86$ errors; $F(1,113)=0.60$ $p=0.44$), hand groups (Left hand performance in Right Hand training groups: $M=3.76$ $SD=3.38$ errors; Right hand performance in Left Hand training groups: $M=4.82$ $SD=4.38$ errors; $F(1,113)=2.12$ $p=0.15$), or an interaction effect between Feedback Laterality and Hand groups ($F(1,113)=0.15$ $p=0.69$). Thus before training, there was no inherent difference in performance with the hand that was not to be used during subsequent training.

Following training, we did not find a significant effect of laterality group on inter-manual transfer (Ipsilateral Feedback: $M=37.63\text{ms}$ $SD=19.48\text{ms}$; Contralateral Feedback: $M=34.92\text{ms}$ $SD=19.61\text{ms}$; $F(1,113)=0.58$ $p=0.45$). Thus, transfer to the untrained hand was not different following ipsilateral or contralateral training. We also did not find a main effect of trained hand group (Right Hand groups (evaluation of left hand performance): $M=37.20\text{ms}$ $SD=21.46\text{ms}$; Left Hand groups (evaluation of right hand performance): $M=35.31\text{ms}$ $SD=17.44\text{ms}$; $F(1,113)=0.24$ $p=0.63$) but did find a significant interaction effect between trained hand and feedback laterality on performance with the untrained hand ($F(1,113)=4.92$ $p=0.03$). Similar to the results in the trained hand, post hoc analysis revealed that in the Left Hand training groups, there is a significant difference between feedback conditions such that transfer to the right hand was better following contralateral training (Contralateral Feedback group: $M=30.14\text{ms}$ $SD=14.33\text{ms}$; Ipsilateral Feedback group: $M=40.85\text{ms}$ $SD=18.73\text{ms}$; Unpaired t-test: $t(56)=2.41$, $p=0.02$). In the right hand groups no such difference was found and transfer to the left hand was similar for the contralateral and ipsilateral feedback groups (Contralateral: $M=39.87\text{ms}$ $SD=22.85\text{ms}$; Ipsilateral: $M=34.63\text{ms}$ $SD=19.68\text{ms}$; $t(57)=0.83$ $p=0.41$; see figure 3B). With respect to errors, we found a main effect of feedback laterality conditions, such that the groups trained with

Ipsilateral feedback ($M=1.56$ $SD=1.88$ errors) committed more errors in the untrained hand than the groups trained with Contralateral Feedback ($M=0.97$ $SD=1.10$ errors; $F(1,113)=4.19$ $p=0.04$). We did not find a difference in the number of errors between hand groups (Left hand errors in Right Hand training group: $M=1.20$ $SD=1.44$ errors; Right hand errors in Left Hand training group: $M=1.33$ $SD=1.68$ errors; $F(1,113)=0.24$ $p=0.63$) or an interaction effect between feedback laterality and trained hand ($F(1,113)=0.44$ $p=0.51$). Taken together, in terms of temporal accuracy, left hand training with contra (vs. ipsi) lateral auditory feedback results in better transfer to the right hand, and training with ipsilateral auditory feedback (irrespective of hand) results in more errors in the untrained hand.

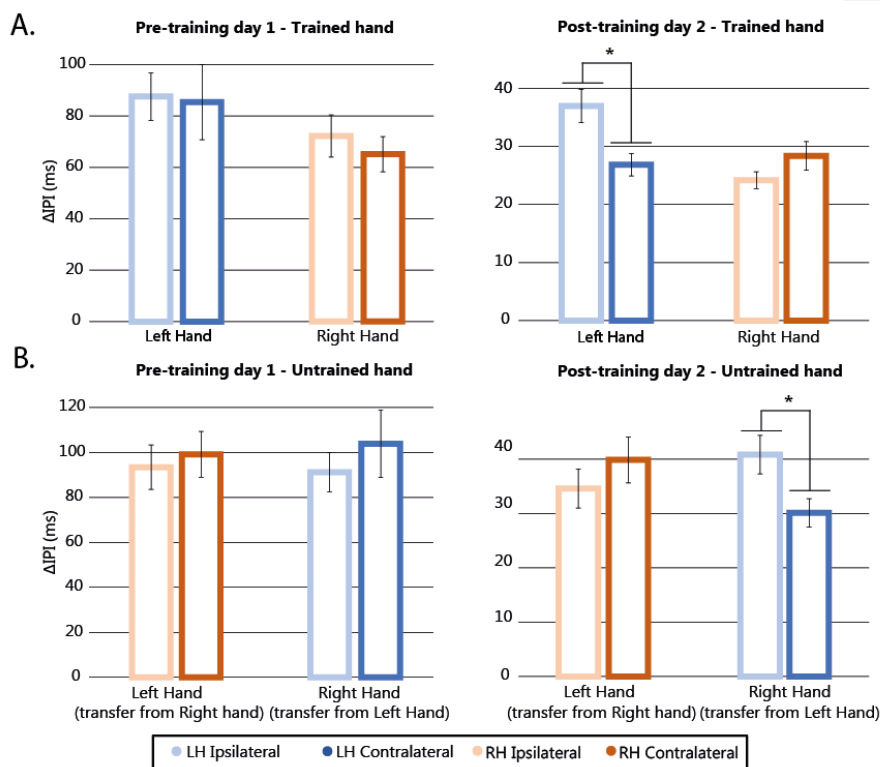


Figure 3: Performance results in the evaluation phases (generalization).

A – performance with the trained hand before the first training session (left) and after the second training session (Right). After the second training session, we see a significant advantage of the contralateral over ipsilateral feedback in the Left-Hand training groups. During the first evaluation, we see no differences between groups.

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B – performance with the untrained hand (transfer). Similar to the trained hand results, we see that between the left- hand training groups, the group that trained with contralateral feedback had better right-hand performance relative to the left-hand group that trained with ipsilateral feedback. No such difference was found between the right-hand training groups.

Discussion

In the current study, we examined whether the lateral relationship between hand (motor output) and ear (auditory input channel) during training affects performance and learning of an audio-motor task. Our measures included sequence and temporal accuracy – assessed by the deviation from a target sequence with temporal interval of 300ms between notes. During monaural training with an external cue (metronome), we find a significant advantage for a contralateral configuration between hand and ear such that subjects exhibited less errors and smaller temporal deviations from the target sequence. In addition, we assessed generalization of monaural training to performance in a binaural task without external cueing by a metronome. In this generalization conditions, we found a significant laterality effect in the binaural task for left hand training, such that training with contralateral feedback leads to better performance in the evaluation. This effect was found for the trained (left) hand and the untrained (right) hand.

- Contra is better than ipsi

האם כשלומדים מטלה יש קשר בין אקטיבציה חזקה יותר ללמידה טובה יותר?

האם יש קשר בין תפיסה ולמידה? עוצמת גירוי?

למידה מוטורית שונות בזמן למידה, תנועות גסות יותר בתחילת הלמידה

- Lateral modulation (Reznik 2021, 2014). At the behavioral level, converging evidence point to attenuated perception of stimulus attributes when they are the consequences of self (vs. other)
- **Hand**-dependent modulation. We have recently shown that sensory cortex is sensitive not only to the physical attributes of the stimulus in the relevant modality (auditory/visual), but also to the hand.... (Buaron; Reznik 2014; and action-locked modulations in the contralateral auditory cortexMEG)
- Sensory modulations: we previously found stronger modulations within hemisphere. Here we find that learning is facilitated when the hand and ear are in a contralateral configuration suggesting that stronger sensory modulations interfere with learning.
- In the right hand the difference is smaller (floor effect?)
- Generalization across **tasks and hands**

Commented [BB5]: 1. More activation after learning, correlation between activation level and performance (stronger bold = better learning). Linguistic task: <https://www.ineurosci.org/content/33/22/9295.full> 2.

Commented [BB6]: Im not sure what id the difference from the previous point

Commented [BB7]: Inhibitory interactions are thought to be crucial during the preparation of unilateral actions to counteract the production of default mirror movements²⁸ — that is, involuntary movements of one hand that accompany the voluntary actions of the other hand. From a lateralization viewpoint, there is evidence to suggest that in right-handers inhibitory effects between both motor cortices are greater from the left to the right hemisphere than vice versa²⁹. This type of functional distinction could contribute to hemispheric differences in motor control and probably emerges in early childhood, during which certain inhibitory processes in the hemispheres assume an asymmetrical developmental course³⁰. Serrien et al 2006

- [difference start on second day – offline effect?](#)

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Acknowledgments

The study was supported by the Israel Science Foundation (grant No. 2392/19 to R.M.). The authors thank lab members for constructive comments and fruitful suggestions.

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