



Tel Aviv University
The Gershon H. Gordon Faculty of Social Sciences
The school of Psychological Sciences

Laterality of auditory feedback in motor learning and cross-education

The paper was submitted as the thesis for M.A. degree by

Hadar Dery

The study was carried out under the supervision of

Prof. Roy Mukamel

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Abstract

Actions with sensory consequences require integration of motor and sensory information. In recent studies, we found that actions with sensory consequences (visual/auditory), modulate perception and neural activity in relevant sensory cortices (visual/auditory respectively) in a hand dependent manner. These results imply that sensory regions code not only the sensory consequences of the action, but also the identity of the active effector involved.

In the current behavioral study, we examined whether manipulating the identity of the sensor (rather than the effector), would also differentially affect sensorimotor integration as examined by the learning process of a sensorimotor skill. Right-handed subjects (N=60) trained for two days to perform an audiomotor task using their left hand. The task involved performing a repeated finger sequence with a constant inter-press-interval (IPI) on a digital piano. Auditory feedback in each group was presented monaurally, either to the left or right ear. Subjects in both groups showed improved IPI and reduced errors across learning blocks and days. However, subjects who received auditory feedback to the right ear had more accurate IPIs than subjects who received feedback to the left ear.

It remains to be seen whether this advantage can be ascribed to right-ear advantage or rather to contralateral relationship between the active hand and stimulated ear. Taking into account previous neuroimaging and behavioral results, current results are in agreement with a model in which sensorimotor integration is sensitive to whether the neural representation of actions and their sensory consequences reside within or across hemispheres.

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1. Introduction

Learning a motor skill usually relies on integrating motor and sensory information to enhance performances and establish a new behavior. For example, learning to play on a piano is a complex behavior that demands integrating motor actions with multi-sensory information, such as tactile feedback from the pressed keys, visual feedback from the hand's movement on the piano keyboard, and the corresponding auditory feedback frequency evoked by the pressed key. According to the ideomotor theory, action and perception are linked in a bidirectional manner and share a common representation of information at behavioral and physiological levels [1]. The origin of the transmission defines the direction of the transmitted information. While 'forward' indicates that motor commands are mapped onto their sensory consequences, 'inverse' indicates the opposite direction, meaning that sensory products are transmitted into the motor commands that would achieve it [2]. In this sense, sensory and motor systems have a mutual effect on changing the neural state in those regions and modify behavior.

1.1 *Perception modulates action*

Our ability to learn motor behavior, to some extent, depends on 'inverse' transmission of perceptual information, such as observing someone else performing a learned action. Behavioral studies provide supporting evidence in which action observation plays a role in motor learning [35]. Similar findings were found in the auditory domain, showing that passive listening to a learned audio-motor sequence improved motor performance even a week after the initial learning [6]. At the physiological level, Rizzolatti and colleagues' (1996) famous discovery of 'mirror neurons' demonstrated how sensory information changes neural activity in motor regions. They found neurons in the macaque monkey's premotor cortex that discharge when executing an action, observing other monkeys or humans performing a similar action and even when hearing the related sounds [89]. In humans, fMRI studies revealed a functional network that includes frontal and parietal regions such as the premotor cortex and SMA. This network, named the 'action-observation-network' (AON), is activated following visual perception of actions performed by others [10].

Several studies have shown supporting evidence of neurons with audio-motor mirroring properties similar to the AON, suggesting a similar network in the auditory domain [1114]. In a study by Lahav et al. (2007), non-musician subjects learned to play a novel melody on a MIDI (musical instrument digital interface) keyboard for five days. After subjects reached error-free performance, they underwent an fMRI session while they passively listened to a short passage of either learned melody (trained-music), novel melody comprising of the same notes as the learned melody (untrained-same-notes-music), or to a novel melody composed by entirely different notes (untrained-different-notes-music). They found an audio-motor network activation, including primary and secondary auditory cortices and frontoparietal regions such as the posterior inferior frontal gyrus and premotor cortex only when subjects listened to the trained-music. Importantly, this network was found to be active in the absence of motor

execution, suggesting that experience shapes activity of frontoparietal mirror neurons. Similarly, Stephan, Lega, and Penhune (2018) have demonstrated that after training subjects to play a melody, auditory tones of the learned melody automatically cues the movement that would produce that tone as measured by motor evoked potentials (MEP). Specifically, applying single-pulse TMS over subjects' M1 while listening to a trained melody revealed increased corticospinal excitability for specific finger muscles before auditory tone onset in the absence of motor execution. These findings demonstrate that similar to neural modulation during action-observation, once auditory-motor representation occurs, auditory information may modulate motor regions and even facilitate motor learning.

1.2 Action modulates perception

As mentioned earlier, the relation of action and perception representation is bidirectional. Studies over the past decades have demonstrated that motor actions evoke neural activity in sensory regions. Nevertheless, identical sensory stimuli are perceived differently if they are the consequence of self-generated actions relative to identical stimuli generated by an external source [15]. These differences in perception are known as sensory modulations, and evidence from behavioral studies revealed both sensory attenuation [16-17] and sensory enhancement of self-generated stimuli [18-19]. According to the forward model [20], when planning to execute a motor action, 'efference copy' is sent from the motor system to the relevant sensory region. These efference copies predict the sensory consequences of the motor command and modulate activity in the sensory regions according to the predicted outcome. For example, Blakemore et al. (1999) used a robotic manipulator to investigate whether an externally generated tactile stimulus would be perceived differently than self-triggered stimulus in terms of tickliness as measured by participants' subjective ratings. They found that tactile stimuli are perceived as less intense when they are self-generated relative to identical external stimuli, suggesting sensory attenuation for self-generated tactile stimuli. A similar phenomenon was also found in the visual domain, where a Gabor patch was perceived as less intense (lower contrast) when it was self-initiated relative to an identical stimulus passively presented [21].

In the auditory modality, self-generated sounds are perceived differently compared to externally generated identical sounds. Supra-threshold sounds that are self-initiated were perceived as less loud than similar sounds that were externally generated [17-18]. However, sounds near the hearing threshold result in the opposite pattern such that self-generated sounds are perceived louder than identical externally generated sounds [18-22]. Besides the change in perception at the behavioral level, self-generated sensory consequences evoke different neural responses in sensory regions than those evoked by external source stimuli with identical characteristics. Intracellular recordings from cricket's auditory neurons during self-generated acoustic stimulation revealed inhibited firing patterns, suggesting that this inhibition allows the cricket to respond while also remaining sensitive to an external sensory source of acoustic stimulation [23]. In non-human primates, studies on marmosets have shown that during self-

generated vocalization, neurons in the auditory cortex are inhibited, and this suppression is believed to play a role in self-monitoring [24], increased sensitivity to auditory feedback, and to inform the system if prediction errors were made relative to the expected outcome [25]. In humans, while some studies have shown attenuated auditory neural responses to self-generated sounds using EEG [2627], fMRI studies reported enhanced BOLD response in the auditory cortex for self-generated sounds [22-28].

1.3 Action modulates perception in a lateralized manner

In general, the representation of sensory and motor information in our brain is lateralized. One of the most prominent examples comes from the motor system in which limbs on one side of our body are controlled by the motor cortex residing in the contralateral hemisphere [29]. Studies using non-invasive methods have demonstrated motor cortex activity contralateral to the executing hand [30] and lower limb (e.g., knee, ankle, or toe) [31] movements. Similarly, contralateral activations are also found in the tactile [32], visual [33], and auditory modalities [22-34].

Given the premise that efference copies are sent from the motor regions generating the action and the robust laterality effects of both the motor and sensory systems, it has been suggested that the degree of sensory modulations would be significantly different depending on the identity of the stimulus-generating effector. In a previous study conducted in our lab, Reznik et al. (2014) showed that when sounds are generated with the hand ipsilateral to the stimulated ear, the monaural auditory threshold is lower than for sounds generated with the hand contralateral to the stimulated ear. At the physiological level (using fMRI), they also demonstrated stronger enhancement of neural responses to self vs. externally generated stimuli in the superior temporal gyrus (STG) that resides within the same hemisphere as the active motor cortex. Following these results, the authors suggested that when sensory regions reside within the same hemisphere as the active motor cortex, efference copies will evoke more robust modulation than in sensory regions that reside in the contralateral hemisphere. In the visual domain, Buaron et al. (2020) has demonstrated stronger sensory modulation (e.g. subjects perceived the visual stimulus as either more or less bright) when visual stimuli were presented to visual field that is ipsilateral to the stimulus triggering hand. At the physiological level, evoked neural activity in the visual cortex was different depending on the stimulus triggering hand. These findings demonstrate that there are differences in motor-sensory coupling that depend on whether the active motor cortex resides within or across the hemisphere as the relevant sensory region [22]. However, it remains an open question whether such hand-specific modulations relate to motor learning.

1.4 Cross-education

Cross-education is the process whereby physical training of one limb results in increased performance gains of the opposite one, thus learning of a motor skill ‘transfers’ from a trained

to an untrained effector after a period of unilateral training [36]. This effect has been demonstrated for a wide range of motor tasks including maze tracing [37], the serial reaction time task [38], finger movement sequence [39] and ballistic index finger abduction task [40]. In a study conducted in our lab, Ossmy and Mukamel (2016) highlight the role of sensory feedback on inter-manual skill transfer. Using VR headset, they manipulated visual feedback that was presented to subjects during training on a finger sequence task. Subjects trained to perform the sequence using their right hand while receiving online visual feedback of a left virtual hand performing the task. Subjects significantly improved their performance in the untrained (left) hand evaluation test. At the neurophysiological level, bilateral neural activity in the superior parietal lobe correlated with left hand performance gains across subjects. Moreover, subjects that exhibited high left hand performance gains, also showed a stronger functional connectivity between the left superior parietal lobe (L-SPL) and the left motor cortex (L-M1) during training. These findings suggest that stronger within-hemisphere connections between sensory and motor regions may facilitate learning. Therefore, manipulating the stimulated sensory region (e.g. stimulated ear in the auditory modality) might affect cross-education when learning a finger sequence task.

1.5 Research goals and hypotheses

In the current study, we examine the effect of lateralized auditory feedback on motor learning performances and skill transfer to the untrained-hand. Based on Reznik et al. (2014) model, we hypothesized differences in learning as a function of stimulated sensory system and active motor system, such that within hemisphere activity would improve learning while across hemisphere might improve cross education. To examine these hypotheses, we conducted a behavioral study on two consecutive days where participants trained with their left hand on performing an audiomotor task that measured rhythm and notes press accuracies. During training, participants received monaural auditory feedback to either left or right ear. Before and after training, evaluations were conducted on each hand separately with binaural auditory feedback. We expected that monaural auditory feedback during learning would result in different performance gains in the evaluation stage at the end of the session on the second day.

2. Methods

2.1 Participants

Sixty-seven 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 musical training playing on a piano. Data from seven participants was discarded (four participants did not complete the second session and three due to technical error), leaving data from sixty participants (25 males, mean age 26.71, range 19-34 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.

2.2 Materials and procedure

In order to assess the effect of lateralized auditory feedback on audiomotor learning and offline gains, participants were randomly assigned to one of two training conditions: left ear stimulation (LE) or right ear stimulation (RE) (30 subjects in each group). Participants completed two 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 Fig 1A). Each session included a pre-training evaluation phase, a training phase, and a post-training evaluation phase. The finger sequence the subjects 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). Participants performed the audiomotor task sitting in a chair in front of the keyboard while receiving auditory feedback via headphones (Audio Technica ATH-M50X) (see Fig 1C). Instruction slides were presented on a computer using Psychtoolbox-3 (www.psychtoolbox.com) on MATLAB 2019b (The MathWorks, Inc., Natick, Massachusetts, United States).

At the beginning of the first session, participants underwent a short familiarization phase to allow them to interact with the MIDI keyboard (see Fig 1B) 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. Next, participants underwent pre-training evaluation in which baseline performance level of each hand was separately assessed. Participants were presented with an image of headphones cueing them to listen to 5 repetitions of the 8-note sequence. Each note duration was 150ms and the inter-stimulus interval (ISI) between notes onset was 300ms. After this hearing phase, participants were instructed to execute the sequence repeatedly on the MIDI keyboard in a constant rhythm as accurate as possible with respect to the reference sequence they just heard. The evaluation consisted of 4 blocks, each block included 5 consecutive trials of the 8-note sequence and was followed by 15 seconds of resting period cued by a white screen (see Fig 2A). In the pre-training evaluation phase, the first two blocks were performed with the right hand and the following two blocks were performed with the left hand. Post-training evaluation was in reverse order (see Fig 1A). During the evaluation phase, binaural auditory feedback was provided.

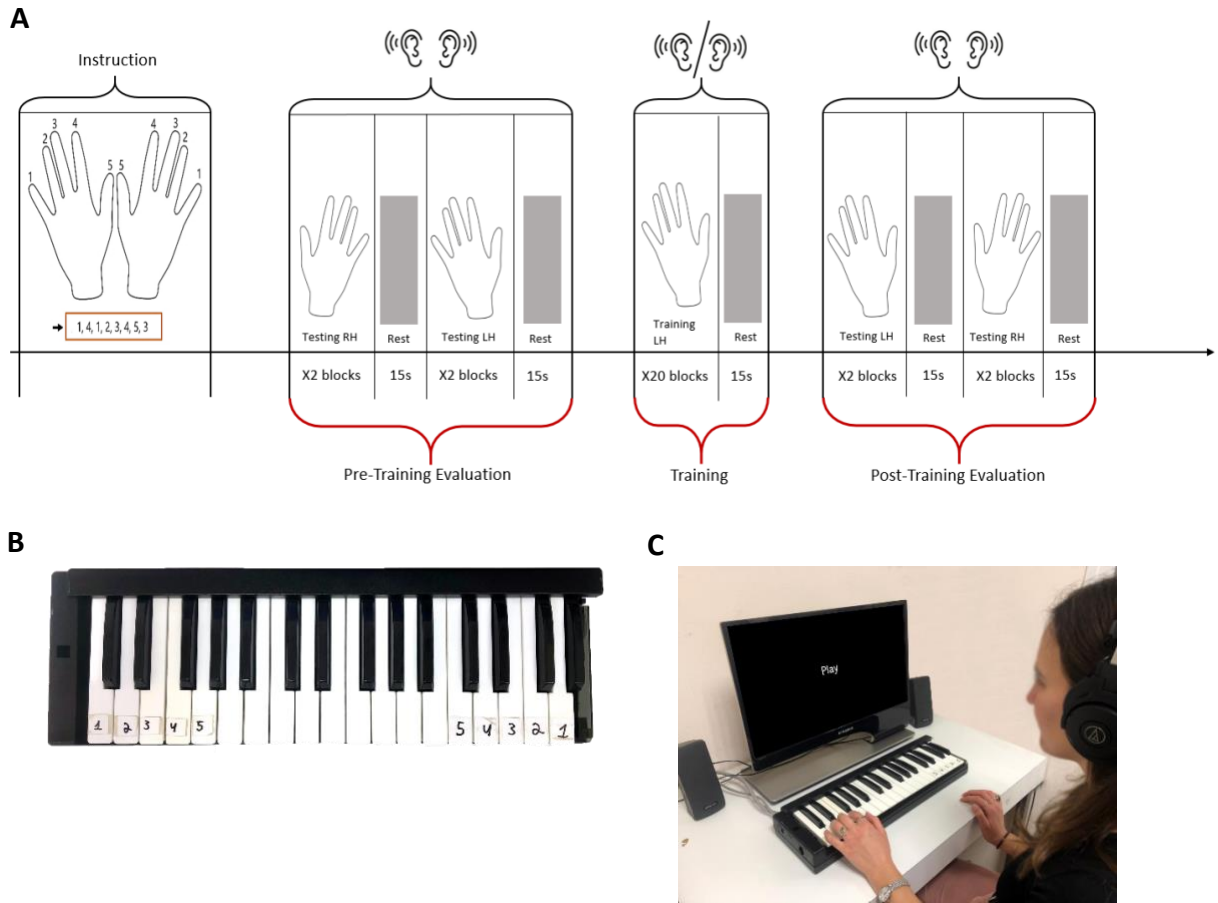


Figure 1: Experimental design **(A)** Illustration of experimental design for one session. The 8-note sequence was presented in the instruction slide. Pre-training evaluation was performed with the right hand (RH) and left hand (LH) separately with binaural auditory feedback for initial evaluation of performance. During the training phase subjects repeatedly performed the 8-note sequence while receiving monaural auditory feedback (either right or left ear) according to their assigned group condition. After training, participants performed an identical evaluation test starting with their left hand (LH). Subjects performed two sessions on two consecutive days. **(B)** The MIDI keyboard with finger mapping. **(C)** The audiomotor skill task performed with the left hand.

In the training phase, participants trained on sequence execution with their left hand while receiving monaural auditory feedback according to their assigned condition (left or right ear). In addition, a metronome (25 bpm) was presented to the same ear as a reference for rhythm performance. Within each block, metronome was initiated by participant's first note press. Metronome beats were separated by 2.4 s, thus participants had to execute the 8-note sequence within the interval between two consecutive metronome beats and use equal IPI between notes. The training phase consisted of 20 blocks, each block consisted of 5 continuous repeats of the 8-note sequence, followed by 15 seconds resting period (see Fig 2B). Before training phase began, participants listened to playback of two metronome beats (4.8 s), followed by headphones image slide as mentioned above. This was done to allow participants to get familiar with the metronome auditory feedback before training. Participants were informed they would receive auditory feedback only to one ear.

2.3 Data analysis

We assessed performance using two measures: error and accuracy. Error was measured by the proportion of incorrect sequences that were played by the participant within each block out of five possible sequence repetitions (e.g. if the participant did not complete a sequence in the correct order the entire sequence counted as error). Accuracy of rhythm (inter-press-interval; IPI) was measured by calculating the mean of absolute difference in time between the target ISI of 300ms and the actual IPI performed by the subject in each block. Delays between note pressing that exceeded 1 s were discarded. Accuracy of rhythm was calculated only on error-free trials. Participants with error rates greater than 70% and IPI score ± 2.5 SD (relative to the average IPI across participants) in the trained hand pre-training evaluation were excluded from further analysis on the grounds of poor performance.

To assess improvements in trained and non-trained hand performance between sessions, a two-tailed independent t-test was conducted on the accuracy and error measures of the pre-training evaluation session from the first day and the post-training evaluation session on the second day. In order to evaluate off-line gains, we calculated the difference between the average IPI/error from the last 3 blocks of the first training session and the average of the first 3 blocks of the second training session. Off-line gains were compared across conditions using 2 X 1 repeated measures ANOVA with IPI/error rates as dependent variable and group (LE/RE) as independent variable. Finally, in order to compare performance gains across hands (trained/non-trained; CE), we performed Pearson correlation of IPI measures between hands across subjects. Analysis was performed using JASP (JASP team, 2020; jasp-stats.org).

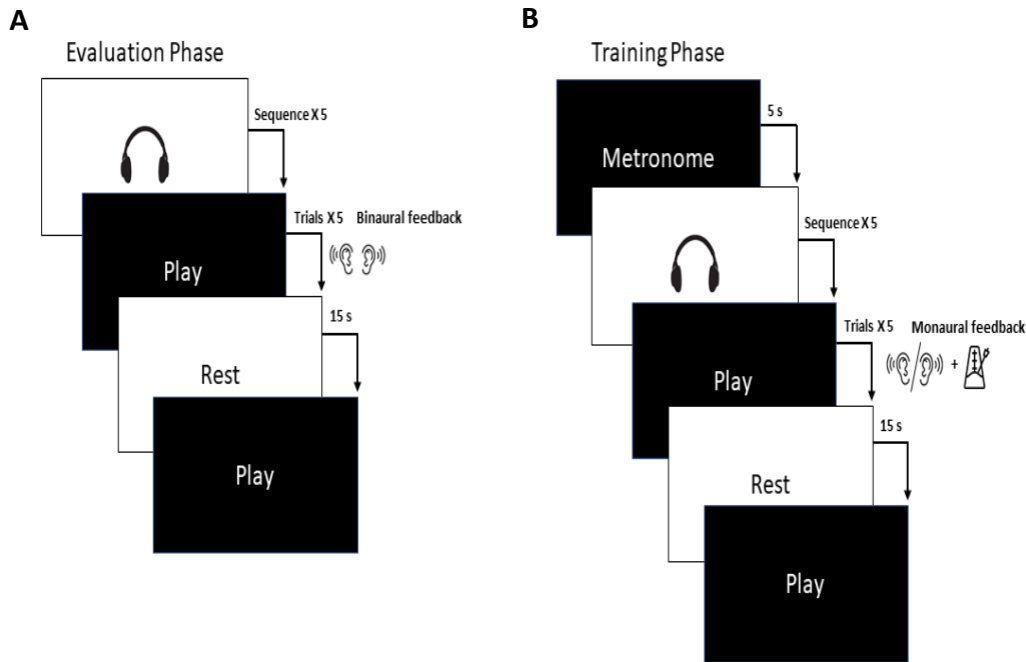


Figure 2: (A) binaural auditory feedback evaluation phase time-course. Each block consisted of 5 sequence repetitions. (B) Time-course of monaural auditory feedback training phase. Each block consisted of 5 sequence repetitions. Metronome and auditory feedback delivered to one ear (either left or right) according to assigned training group.

3. Results

Two participants from the LE condition group and one participant from the RE condition group were excluded from further analysis due to poor performance in the pre-training evaluation (see Methods), leaving data from 57 participants (25 males, mean age 26.77, range 19-34).

3.1 Trained hand performance gains evaluation

First, we assessed baseline performance of the trained (left) hand using IPI and error measures. An independent sample t-test revealed no significant differences between groups on the IPI measure ($M = 140.59$ ms, $SD = 81.49$ LE condition; $M = 120.22$ ms, $SD = 80.63$ RE condition; $t(55) = 0.94$, $p = 0.34$) and proportion of error ($M = 0.27$, $SD = 0.20$ LE condition; $M = 0.23$, $SD = 0.23$ RE condition; $t(55) = 0.63$, $p = 0.52$). In addition, we conducted a Bayesian factor analysis in favor of the H_0 hypothesis. BF_{+0} for IPI and error measures (2.56 and 3.15,

respectively), indicate moderate evidence for no group differences. Taken together, these results point to similar baseline performance levels across groups

Next, we compared the two groups' post-training performance in the evaluation phase of the second session. Results of an independent sample t-test showed that participants who received monaural auditory feedback to their right ear (RE) during training had significantly lower IPI compared to participants who received left ear (LE) monaural auditory feedback (RE $M = 34.05$ ms, $SD = 17.23$; LE $M = 51.98$ s, $SD = 42.64$, $t(55) = 2.09$, $p < 0.05$) (see Fig 3A). In terms of error, no significant difference was found between the groups ($M = 0.09$, $SD = 0.12$ RE condition; $M = 0.07$, $SD = 0.15$ LE condition, $t(55) = -0.58$, $p = 0.56$, independent sample t-test).

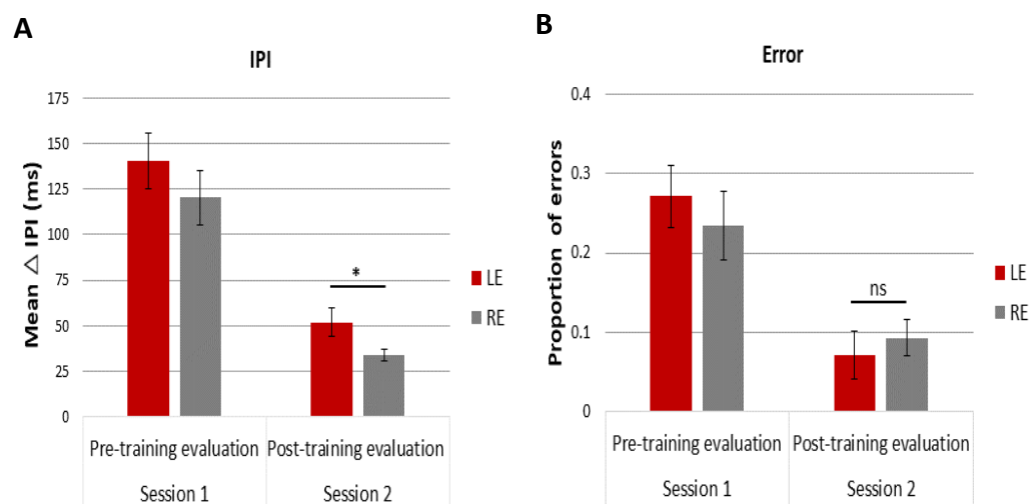


Figure 3: Trained-hand pre/post training evaluations (A) Group IPI means. The mean IPI in RE condition was significantly lower compared with LE condition following training ($N = 55$; $t = 2.09$; $*p < 0.05$). **(B)** Group error means. Error means were not significantly different between RE and LE conditions following training ($N = 55$; $t = -0.58$; $p = 0.56$). Error bars represent S.E.M.

3.2 Learning curves and off-line gains

The time-course of learning is shown in Figure 4 for LE and RE groups. We assessed offline gains by comparing performance at the end of session 1 and beginning of session 2 (see methods). Repeated measure ANOVA on IPIs revealed a significant main effect for Session [$F(1,55) = 40.23$, $p < 0.001$]. There were no significant main effect for Group [$F(1,55) = 2.14$, $p = 0.14$] or Session X Group interaction [$F(1,55) = 1.82$, $p = 0.18$]. Similarly, ANOVA of errors revealed significant main effect of Session [$F(1,55) = 20.32$, $p < 0.001$] and no significant effects of Group [$F(1,55) = 0.56$, $p = 0.45$] or Session X Group interaction [$F(1,55) = 0.33$, $p = 0.56$]. Taken together, these results indicate that across training sessions with monaural auditory feedback, subjects exhibited significant offline gains that were similar across groups.

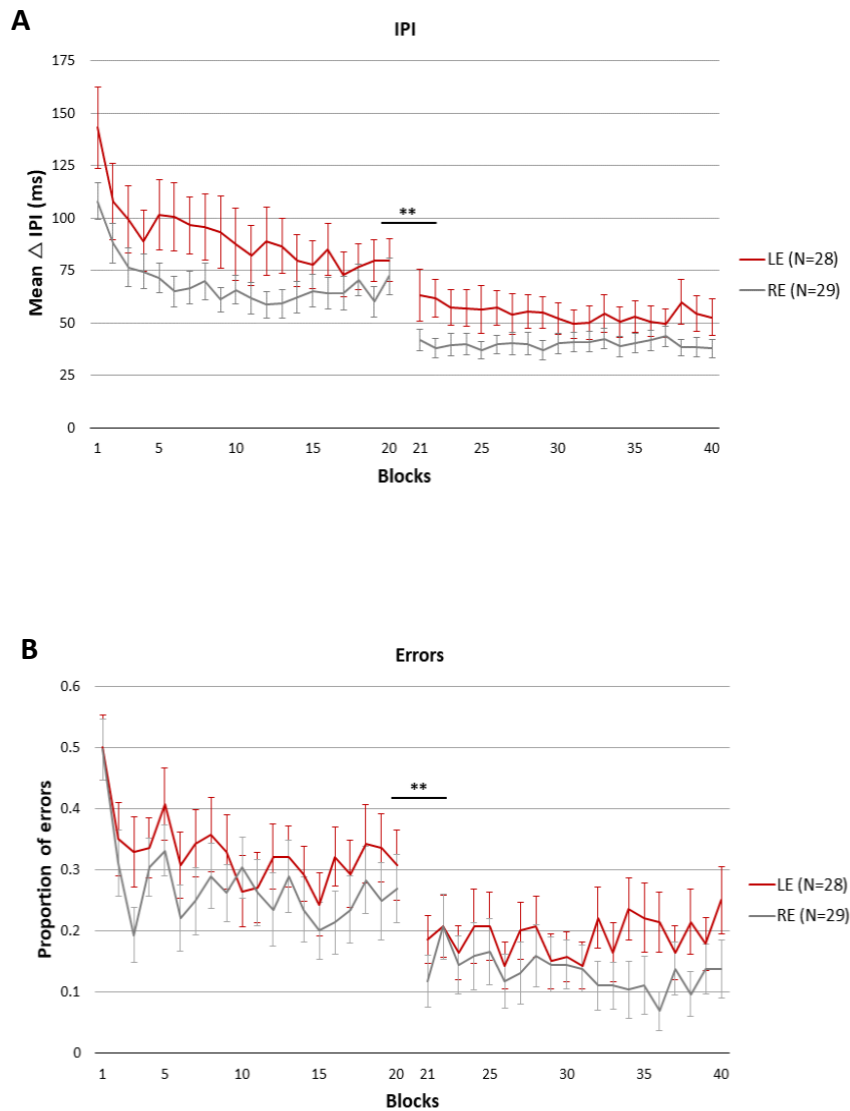


Figure 4: Training phase learning curves and between sessions offline gains. Lines represents group means and error bars denote S.E.M across subjects. Throughout training, both groups improved (A) IPI performance (0 value in the y-axis represent the ISI of 300 ms), (B) reduced errors and exhibit between sessions offline gains (N = 57; repeated measures ANOVA; ** $p < 0.001$).

3.3 Cross-education performance gains evaluation

In addition to participants that were excluded due to poor performance in the left hand evaluation phase, two participants from the LE condition group and three participants from the RE condition group were excluded from untrained-hand analysis due to poor performance in the right hand evaluation phase (see Methods), leaving data from 52 participants (21 males, mean age = 26.86, age range 19 – 34).

Similar to trained (left) hand analysis, we compared IPI and error baseline performances in the non-trained (right) hand. At the pre-training evaluation phase of the first session, an independent sample t-test on IPIs revealed no significant difference in performance between LE ($M = 152.43$ ms, $SD = 81.62$) and RE ($M = 143.84$ ms, $SD = 93.65$) groups ($t(50) = 0.35$, $p = 0.72$ with $BF+0$ of 3.41). Levene's test of equality of variances revealed unequal proportion of error variances [$F = 4.72$, $p < 0.05$], therefore we use a Mann-Whitney a-parametric test. Similarly, no significant difference between groups was found in baseline error performance ($M = 0.25$ $SD = 0.13$ LE condition; $M = 0.24$, $SD = 0.20$ RE condition; $U = 368.50$, $p = 0.57$, $BF+0 = 3.50$).

In order to assess cross-education, we compared groups non-trained hand (right) post-training evaluation performances in the second session. An independent sample t-test on IPIs revealed no significant difference between groups ($M = 60.49$ ms, $SD = 45.67$ LE condition; $M = 46.26$ ms, $SD = 29.49$ RE condition; $t(50) = 1.33$, $p = 0.18$). Similarly, no significant difference between groups was found in error performance ($M = 0.14$, $SD = 0.15$ LE condition; $M = 0.15$, $SD = 0.22$ RE condition; $t(50) = -0.21$, $p = 0.83$). Interestingly, although IPI performance did not significantly differ between groups, it displayed a similar trend to what was significantly found in the trained hand, namely that RE stimulation had a minor advantage over LE stimulation (see Fig 5A).

Finally, we assessed the relationship between the magnitude of CE (e.g. the transfer of learning between hands), and the magnitude of learning in the trained hand. To this end, we calculated across subjects the correlation between IPI performance gains of the two hands. We found a strong positive correlation between trained hand and CE performance gains ($r(52) = 0.74$, $p < 0.001$ (see Fig 5C), demonstrating a link between the magnitude of improved performance across hands.

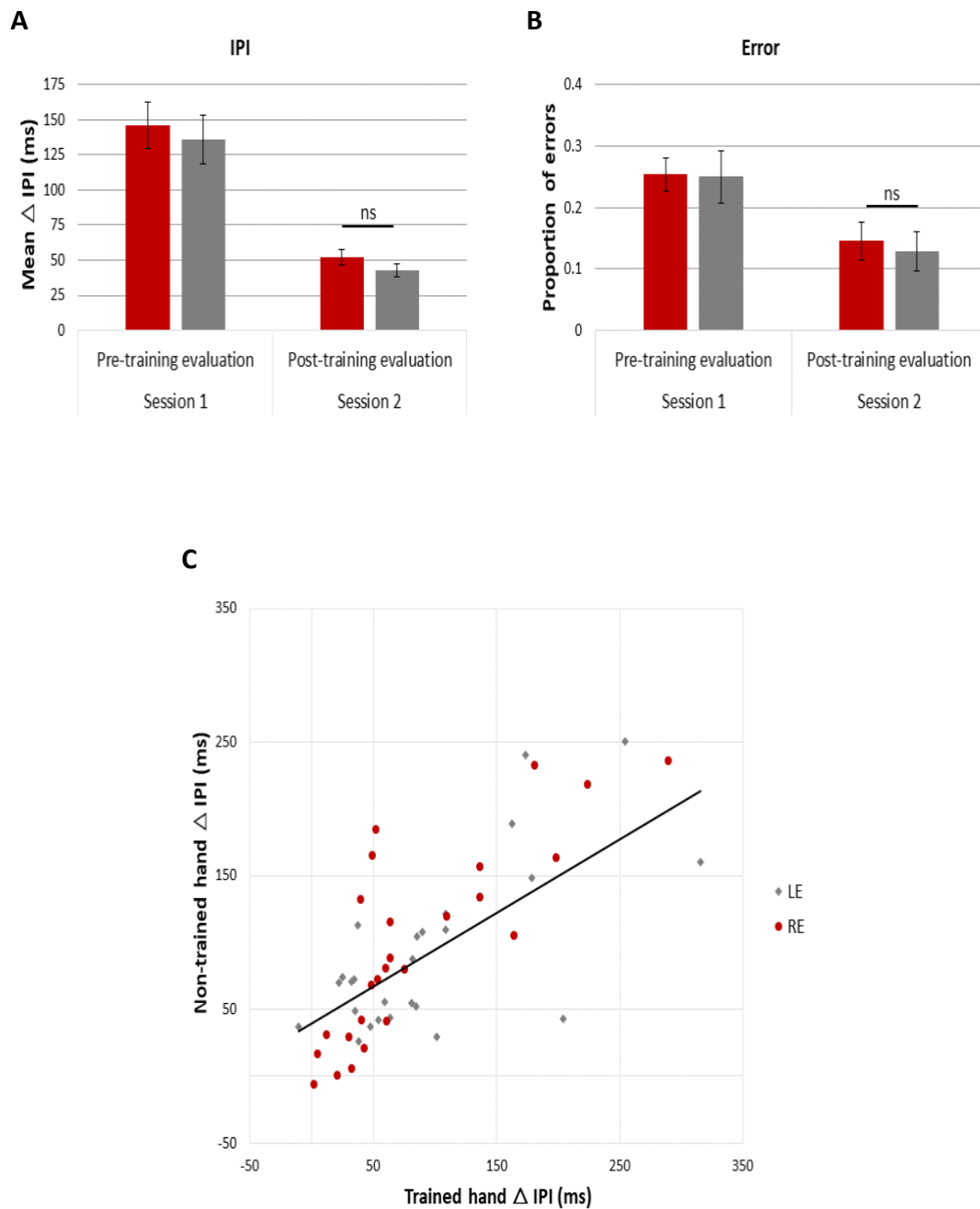


Figure 5: Non-trained hand pre/post evaluation (A) Group IPI means. Similar to figure 3 for the untrained (right) hand. No significant difference between groups IPI performance ($N = 50$; $t = 0.35$; $p = 0.72$). (B) Group error means. Error means did not significantly differ between RE and LE conditions ($N = 50$; $U = 368.50$; $p = 0.57$). Error bars represent S.E.M. (C) IPI Gains across hands (collapsed across conditions). Significant positive correlation between trained and untrained hands ($N = 52$; $r = 0.74$; $**p < 0.001$).

4. Discussion

In the present study, we examine the effect of lateralized auditory feedback on audiomotor learning and skill transfer across hands. In agreement with our hypothesis, our behavioral experiments' findings revealed that lateralized auditory feedback during training sessions of audiomotor skill resulted in differences in trained hand performance between-group conditions. However, as opposed to our expected outcome, trained hand performance with binaural auditory feedback was better in rhythm accuracy when the stimulated ear during training was contralateral to the performing hand. Contrary to our hypothesis, we did not find a cross-education effect between groups' performance, meaning that lateralized auditory feedback during training did not yield any performance gains advantage. Finally, we have shown that both groups exhibit offline gains between the two training sessions, indicating that substantial learning was achieved in both group conditions.

Our trained hand post-training evaluation of the second session revealed better IPI performance when participants' right ear was stimulated during left-hand training. One interpretation could be an advantage when the sensor is contralateral to the effector such that providing monaural auditory feedback to the ear contralateral to the performing hand is better in sensorimotor integration of audiomotor skill learning. In terms of perceptual abilities, sensitivity for sounds near the hearing threshold is better when the sound triggering hand is ipsilateral to the stimulated ear. This behavioral sensitivity to sound detection correlates with more robust sensory enhancement when the motor and auditory cortices reside within the same hemisphere [22]. These findings imply a functional advantage in sensorimotor integration when the stimulated ear is ipsilateral to the active hand. However, in terms of audiomotor skill learning, our result suggests that sensorimotor integration is more efficient when the stimulated ear is contralateral to the performing hand. These contradicting phenomena indicate that integrating motor and sensory information differs depending on the intended task goal. It has been suggested that inter-hemispheric processing rises as a function of cognitive load, such that while simple tasks can be processed in a single hemisphere, tasks that are more complex and increase the working load require inter-hemispheric cooperation [41-42]. This inter-hemispheric dynamic processing implies that the underlying mechanism of 'efference copies' in sensorimotor integration may be mediated by the cognitive system load evoked according to tasks' requirements.

An alternative explanation could rely on left-hemisphere dominance. Therefore, right ear stimulation may be sufficient for improving task performance, regardless of the trained hand identity. While the left-hemisphere advantage is mostly known for speech-language processing [43], recent studies provide evidence for a more general temporal processing role [44-45]. Specifically, the left superior temporal gyrus (STG) was found to be involved in many auditory-motor integrations such as perception and reproduction of speech [46], reproduction of melodic stimuli [47], and musical improvisation [48]. Interestingly, evoked left STG neural activity was found during temporal sequence performance regardless of stimulus properties (e.g., visual or

auditory) [44] and has been suggested to have an essential functional role in sequencing and transformation of auditory representation into motor responses [4749]. It is plausible that during left-hand training, participants who received right ear stimulation evoked left STG neural activity that results in a more robust auditory-motor representation of the learned sequence. However, to determine whether our finding can be ascribed to inter-hemispheric relations or left-hemisphere dominance, a similar experiment should be conducted using right-hand training.

Our cross-education analysis revealed no significant differences between groups at the post-training evaluation on the second session. Although participants across conditions exhibit significant IPI performance gains in the non-trained hand, stimulated ear manipulation during training did not yield any group advantage. Indeed, using visual manipulation improved performance gains in a finger movement sequence task, and these performance gains correlated with more robust connectivity between motor and sensory regions residing within the same hemisphere [39]. Importantly, this effect seems to rely on visual manipulation of the moving hand rather than visual field per se. We did not find any cross-education effect using monaural auditory feedback, presumably, given that the manipulated sensor was participants' ear and that the sensory information did not convey visual non-trained hand movement. Thus, it is possible that skill transfer performance gains to the non-trained hand mostly relies on transmitting motor information that conveys sensory information of the effectors' physical movement.

The nature of lateralized auditory feedback contribution to sensorimotor learning remains an open question. Understanding processes underlying motor and sensory coupling would shed light on involved neural mechanisms in sensorimotor learning and potentially improve sensorimotor learning paradigms. Future studies should examine the effect of monaural auditory feedback on audiomotor skill performance using right-hand training and investigate the neural representation of such sensor manipulation on sensorimotor learning and cross-education.

4.1 Conclusions and summery

Our findings show that sensorimotor integration while learning an audiomotor skill is sensitive to whether the stimulated ear is ipsilateral or contralateral to the performing hand, such that left-hand training with monaural auditory feedback to the right ear results in better IPI performance gains in binaural post-training evaluation. Moreover, the cross-education effect seems to be less sensitive to manipulated monaural auditory feedback. These findings provide the first step for a better understanding of sensorimotor integration mechanisms in sensorimotor learning.

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תקציר

פעולות שיש להן תוצאות סנסוריות דורשות אינטגרציה של מידע מוטורי וסנסורי. במחקרים שנערכו לאחרונה, מצאנו שפעולות עם תוצאות סנסוריות (של ראייה או שמיעה), משנות את התפיסה והפעילות עצבית באזורים הסנסורים של קליפת המוח (של ראייה או שמיעה בהתאמה) באופן התלוי ביד. תוצאות אלה מצביעות על כך שהאזורים הסנסורים מקודדים לא רק את התוצאות הסנסוריות אלא גם את זהות האיבר הפעיל המעורב.

במחקר ההתנהגותי הנוכחי, בדקנו אם מניפולציה של החוש (ולא של האיבר) תשפיע באופן דיפרנציאלי גם על האינטגרציה הסנסורית-מוטורית כשהיא נבחנת באמצעות תהליך הלמידה של מיומנות סנסורית-מוטורית. משתתפים שידם הימנית היא הדומיננטית ($N=60$) התאמנו במשך יומיים כדי לבצע משימה אודיו-מוטורית בידם השמאלית. המשימה דרשה ביצוע של רצף אצבוע חוזר עם הפסקה קבועה בין הלחיצות (IPI) על פסנתר דיגיטלי. המשוב האודיטורי הוצג לשתי הקבוצות המשתתפות באוזן אחת: לקבוצה אחת באוזן שמאל ולשניה באוזן ימין. המשתתפים בשתי הקבוצות שיפרו את ה-IPI ומספר הטעויות שלהם פחת לאורך האימונים והימים. אולם, למשתתפים שקבלו את המשוב האודיטורי באוזן הימנית היו הפסקות (IPI) מדויקות יותר מאלה שקבלו את המשוב לאוזן השמאלית.

עדיין יש לבדוק אם יתרון זה נובע מגירוי האוזן הימנית או מן היחס המנוגד בין היד הפעילה והאוזן המגורה. בהתחשב בתוצאות התנהגותיות ובתוצאות הדמיה קודמות, התוצאות של הניסוי הנוכחי מתיישבות עם המודל שבו אינטגרציה סנסורית-מוטורית קשורה למיקום שבו מתקיים הייצוג העצבי של פעולות ותוצאותיהן הסנסוריות – בתוך ההמיספירות או ביניהן.



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בית הספר למדעי הפסיכולוגיה**

**התפקיד של משוב אודיטורי בטרליות של למידה מוטורית והעברת הלמידה
בין ידיים**

**M.A. חיבור זה הוגש כעבודת גמר לקראת התואר "מוסמך אוניברסיטה" –
באוניברסיטת תל אביב**

על ידי:

הדר דרעי

העבודה הוכנה בהנחיית:

פרופ' רועי מוכמל

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