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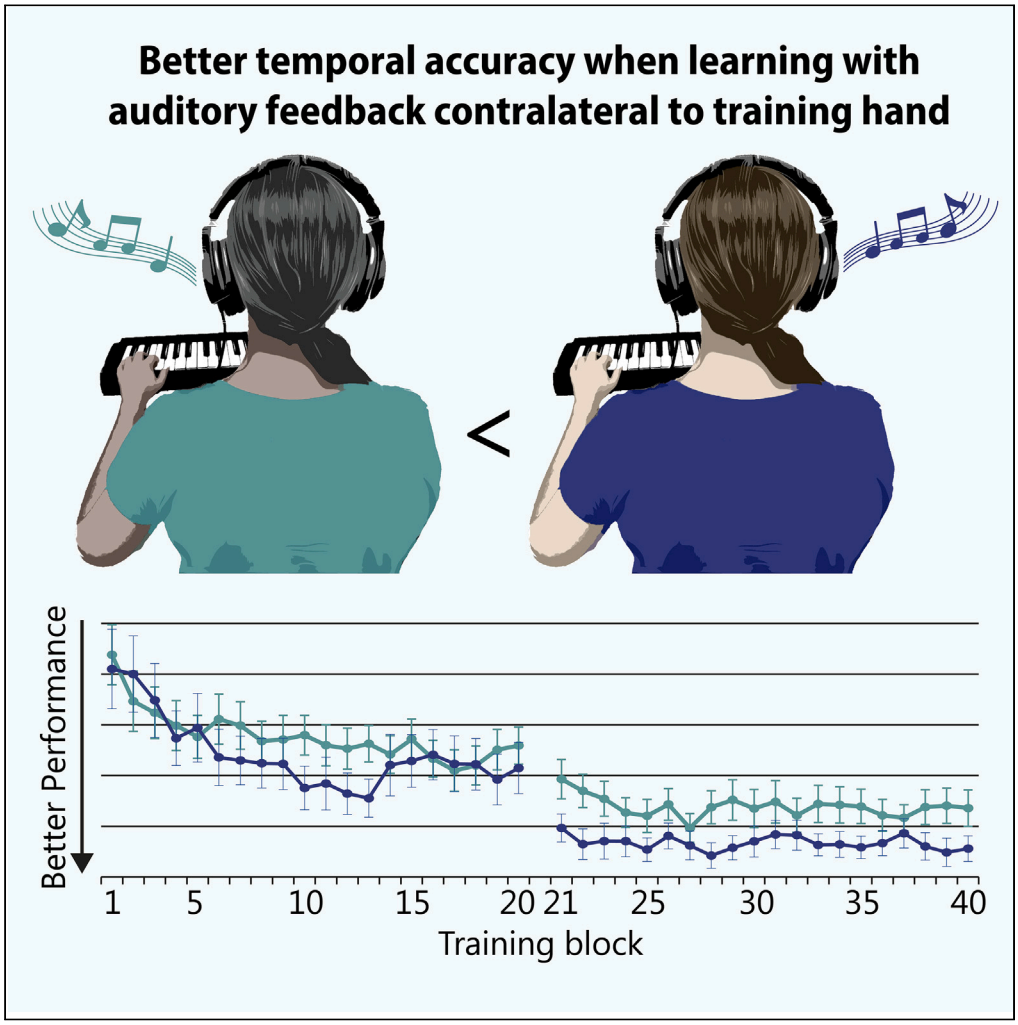

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Highlights

Audio-motor learning is sensitive to the lateral configuration between hand and ear

Contralateral hand-ear configuration during training facilitates learning

Contralateral training advantage with left hand generalizes to untrained conditions

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Playing with your ears: Audio-motor skill learning is sensitive to the lateral relationship between trained hand and ear

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SUMMARY

A salient feature of motor and sensory circuits in the brain is their contralateral hemispheric bias—a feature that might play a role in integration and learning of sensorimotor skills. In the current behavioral study, we examined whether the lateral configuration between sound-producing hand and feedback-receiving ear affects performance and learning of an audio-motor skill. Right-handed participants (n = 117) trained to play a piano sequence using their right or left hand while auditory feedback was presented monaurally, either to the right or left ear. Participants receiving auditory feedback to the contralateral ear during training performed better than participants receiving ipsilateral feedback (with respect to the training hand). Furthermore, in the Left-Hand training groups, the contralateral training advantage persisted in a generalization task. Our results demonstrate that audio-motor learning is sensitive to the lateral configuration between motor and sensory circuits and suggest that integration of neural activity across hemispheres facilitates such learning.

INTRODUCTION

Performance of goal-directed actions requires the 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 in order to produce a melody. At the neural level, it is assumed that this is achieved through crosstalk between motor and sensory circuits that are engaged during task performance.[1–3] Nevertheless, despite well-documented reciprocal interactions between behavioral and neural aspects of perception and action,[4–7] 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 the perception of sensory stimuli and their corresponding evoked neural activity in sensory regions, relative to otherwise identical sensory stimuli generated by an external source.[8–11] 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.[10,12] At the neural level, the amplitude of auditory-evoked responses is reduced when sounds are the consequence of voluntary actions.[11,13,14] 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 signal to relevant sensory regions, thereby modulating their neural state and the ensuing stimulus-evoked activity.[15]

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, with crossing fibers through the thalamus connecting cerebral and cerebellar motor circuits.[16] Similar to the lateral biases in motor circuits, anatomical and functional evidence in the auditory system points to a contralateral bias between the stimulated sensory organs (left/right ears) and auditory cortex processing incoming auditory stimuli.[17–19] At the cerebellar level, similar to motor circuits, evidence points to an ipsilateral bias with stimulated ear, and functional connections with the contralateral auditory cortex.[20] Thus, the processing of monaural stimuli delivered to the right ear is biased to the left auditory cortex/right cerebellum (and vice versa for the left ear).

Given the anatomical distribution of neural circuits across hemispheres described earlier, 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. We have previously demonstrated in the auditory domain that indeed the lateral relationship between motor and sensory circuits influences perception,[21] such that 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

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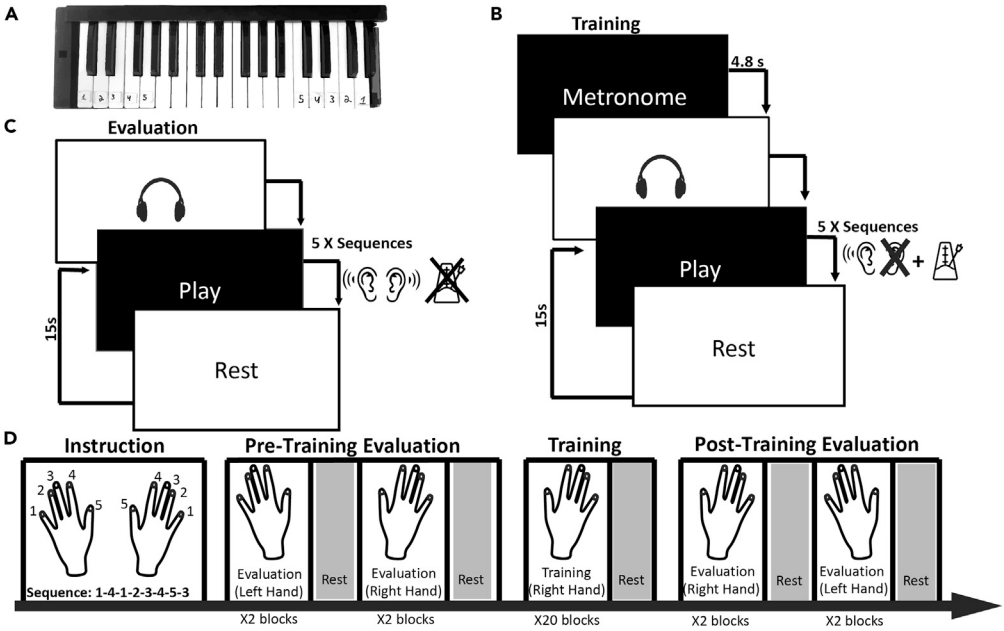

Figure 1. Experiment design

(A) MIDI layout, numbered keys were mapped to notes and fingers as follows: 1 - little finger, G; 2 - ring finger, F; 3 - middle finger, E; 4 - index finger, D; 5 - thumb, C. Notes were identical for playing with the right (right keys) and left (left keys) hand.

(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 the 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 to both ears.

(D) experiment timeline in each training day (example for right-hand training groups).

hand-dependent differences in auditory cortex activity. While inside an fMRI scanner, participants used either their right or left hand to generate sounds that were presented binaurally. Evoked responses in a given auditory cortex (right or left) were stronger, when the hand used to generate the sounds was on the opposite side. In other words, fMRI signal in (for example) left auditory cortex was stronger when participants generated sounds with their right vs. the left hand. The opposite pattern was found in the right auditory cortex. Thus, stronger auditory-evoked fMRI signals were found when the auditory cortex and engaged motor cortex resided in the same hemisphere vs. opposite hemispheres.[21] 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 yet known.

In the current behavioral study, we address this question by using a 2 × 2 design in which the training hand (left/right) and feedback-receiving ear (ipsilateral/contralateral to trained hand) were manipulated across four groups of participants learning an audio-motor task across two days. Thus, participants were trained to perform a specific sequence of notes on a piano keyboard while note identity and temporal accuracy were measured. Our findings point to differential learning between lateral configurations of ears and hands, with enhanced learning when hand and ear are contralateral to each other.

RESULTS

Participants performed a sequence of notes on a digital piano while their accuracy (number of incorrect notes) and temporal precision (absolute deviation from a target inter-press interval of 300 ms [ΔIPI]) were measured. Performance was assessed across 20 blocks of training in each of two training days (see Figure 1 and STAR methods section for details). Each participant was assigned to a single training configuration, in which they used one hand (right or left) and received auditory feedback to one ear (ipsilateral or contralateral to the hand) during training.

Training data

For all groups, participants' performance, in terms of accuracy and timing (ΔIPI, see STAR methods), improved with training (see Figure 2A). 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

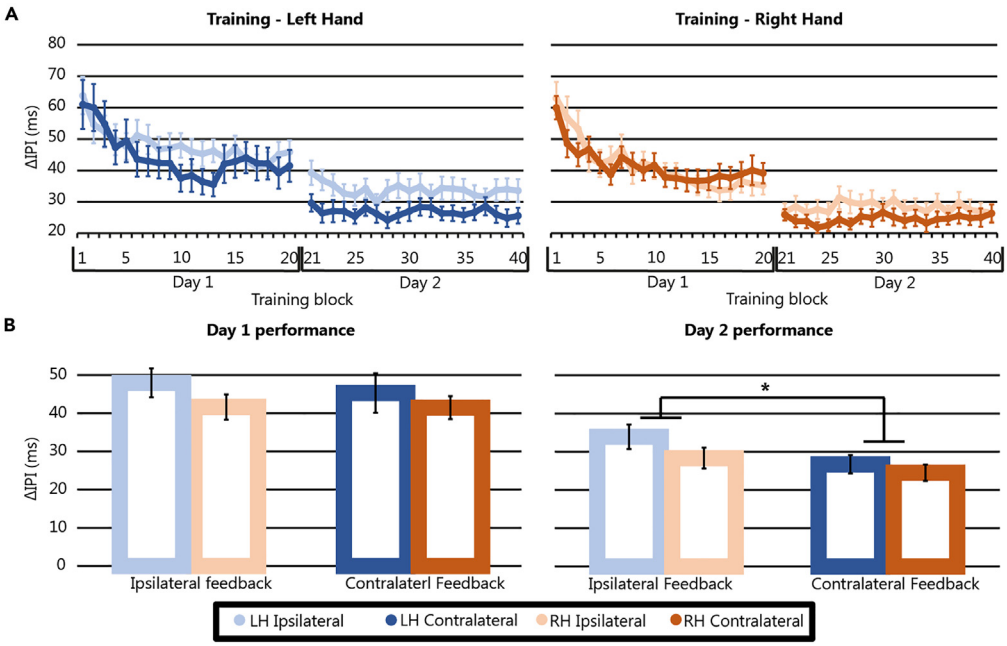

Figure 2. performance on the training sessions

(A) performance (ΔIPI) across training blocks for the Left-Hand (blue) and Right-Hand (red) groups according to Feedback Laterality (Ipsilateral Feedback – light colors; Contralateral Feedback – dark colors). Error bars represent SEM across subjects.

(B) mean performance averaged 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 trained hand had lower ΔIPI (were more accurate) than participants who received ipsilateral feedback during training. Error bars represent SEM across subjects, * indicates p<0.05.

performance across blocks on the first day. With respect to timing, participants had a smaller difference from perfect performance (ΔIPI) on the second day of training (First day M = 44.04 ms, SD = 21.38 ms; *Second day* M = 28.30 ms, SD = 14.61 ms; Paired sample t test: $t(116) = 11.90$, $p = 8.074*10^{-22}$, Cohen's d = 1.1). In terms of accuracy, 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: $t(116) = 9.84$, $p = 5.671*10^{-17}$, Cohen's d = 0.91).

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 timing accuracy (ΔIPI) between feedback laterality groups (Ipsilateral Feedback groups: M = 44.67 ms, SD = 19.45 ms; Contralateral Feedback groups: M = 43.41 ms, SD = 23.44 ms; $F(1,113) = 0.12$, $p = 0.73$, $\eta^2p=0.001$). We also did not find a significant difference between trained hand groups (Right-Hand groups: M = 41.54 ms, SD = 17.17 ms; Left-Hand groups: M = 46.57 ms, SD = 24.69 ms; $F(1,113) = 1.62$, $p = 0.21$, $\eta^2p=0.014$) or an interaction effect ($F(1,113) = 0.1$, $p = 0.76$, $\eta^2p=8.61*10^{-4}$). Similarly, we did not find a significant difference in terms of number 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; $F(1,113) = 1.80$, $p = 0.18$, $\eta^2p=0.016$), trained hand groups (Right-Hand: M = 3.01, SD = 2.29 errors; Left-Hand: M = 3.87, SD = 3.27 errors; $F(1,113) = 2.82$, $p = 0.10$, $\eta^2p=0.024$), or an interaction between the two ($F(1,113) = 0.51$, $p = 0.48$, $\eta^2p=0.005$). 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 performed better (smaller ΔIPI 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; $F(1,113) = 4.22$, $p = 0.04$, $\eta^2p=0.036$). 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; $F(1,113) = 2.12$, $p = 0.15$, $\eta^2p=0.018$), or an interaction effect between feedback laterality and trained hand ($F(1,113) = 0.41$, $p = 0.52$, $\eta^2p=0.004$, see Figure 2B). With respect to the number of errors committed on the second training day, we found no difference between feedback laterality conditions (Ipsilateral Feedback groups: M = 1.57, SD = 2.25 errors; Contralateral Feedback groups: M = 1.07, SD = 1.47 errors; $F(1,113) = 2.22$, $p = 0.14$, $\eta^2p=0.019$), no difference between trained hands (Right-Hand groups: M = 1.02, SD = 1.43 errors; Left-Hand groups: M = 1.63, SD = 2.26 errors; $F(1,113) = 3.23$, $p = 0.08$, $\eta^2p=0.028$), and no interaction effect between trained hand and feedback laterality ($F(1,113) = 1.97$, $p = 0.16$, $\eta^2p = 0.017$).

Taken together, all groups performed better following training (as expressed by smaller deviations ΔIPI from perfect performance and lower error rates). During the second day of training, groups that trained with auditory feedback delivered to the ear contralateral to the

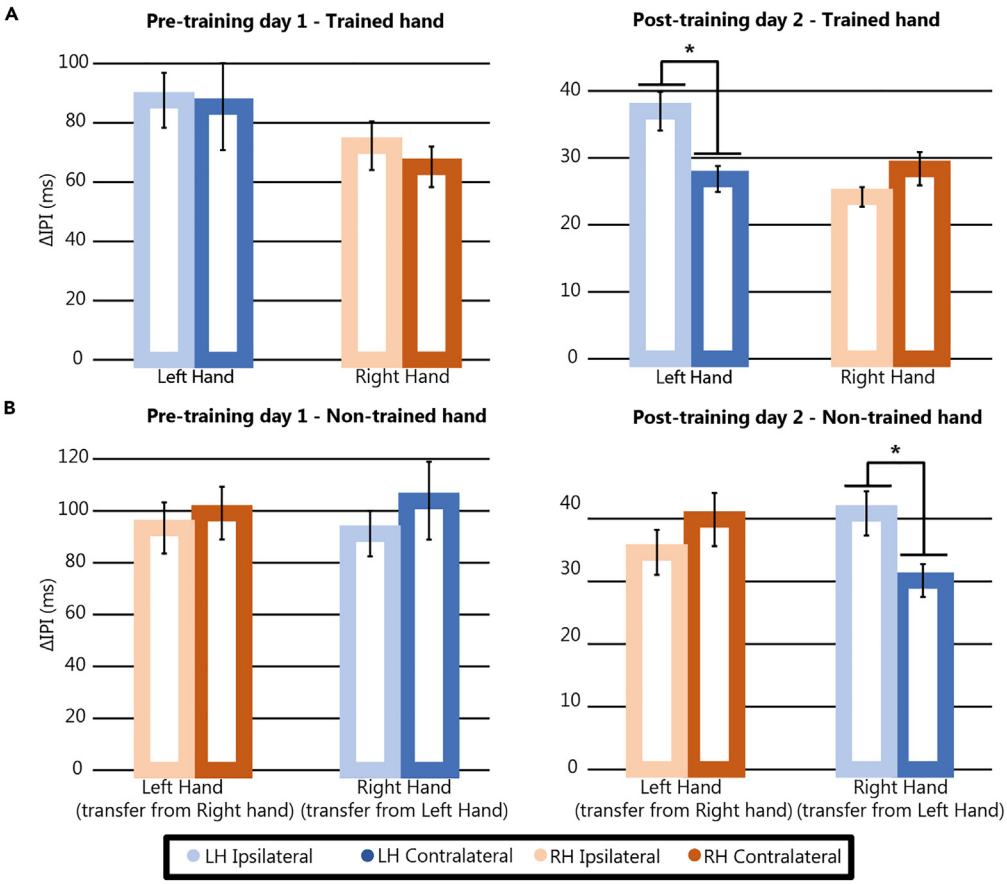

Figure 3. Performance results in the evaluation phases (generalization)

(A) performance with the trained hand before the first training session (left) and after the second training session (right). Note the change in scale on the second day (indicative of better post-training performance). After the second training session, there was a significant advantage of the contralateral over ipsilateral feedback condition in the Left-Hand training groups. During the first evaluation, no significant difference between groups was found. Error bars represent SEM across subjects.

(B) Performance with the non-trained hand (inter-manual transfer). Group that trained with their left hand and received contralateral feedback had better right-hand performance relative to the group that trained with ipsilateral feedback (similar to the contralateral advantage in the trained hand). No such difference was found in left-hand performance between laterality conditions in the right-hand training groups. Error bars represent SEM across subjects, * indicates p<0.05.

training hand performed better than groups that trained with auditory feedback delivered to the ear ipsilateral to the training hand, while error rates remained similar across groups.

Generalization to no-metronome binaural feedback: Performance with the trained hand

We also examined the generalization of the monaural stimulation training with a metronome to performance on a similar task, but with binaural feedback and without a metronome. To this end, we evaluated participants' performance in such conditions before and after training (see STAR methods). With respect to evaluations of the trained hand irrespective of stimulated ear, we found a significant difference between the 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 pre-training: M = 28.97 ms, SD = 12.90 ms vs. post-training: M = 77.52 ms, SD = 56.32 ms; Paired sample t test: $t(116)$ = 9.94, p = $3.199*10^{-17}$, Cohen's d = 0.92). In addition, participants committed fewer errors during the post-training evaluation (M = 0.65, SD = 1.39 errors) relative to the pre-training evaluation (M = 3.30, SD = 2.81 errors; Paired sample t test: $t(116)$ = 10.08, p = $1.519*10^{-17}$, Cohen's d = 0.93). These results are indicative of generalization between the training and testing conditions (see Figure 3A).

Before training, we found no significant difference in performance (ΔIPI) between feedback laterality groups (Ipsilateral Feedback groups: M = 79.63 ms, SD = 47.58 ms; Contralateral Feedback groups: M = 75.44 ms, SD = 63.69 ms; $F(1,113)$ = 0.20, p = 0.66, η^2p=0.002). 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, η^2p=0.025), or an interaction effect between feedback laterality and trained hand ($F(1,113)$ = 0.06, p = 0.81, η^2p=$5.12*10^{-4}$). 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, η^2p=0.015), 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, η^2p=0.005), or an interaction effect between these conditions (F(1,113) = 0.64, p = 0.43, η^2p=0.006). Together, these results indicate no inherent difference in baseline performance on the generalization task 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 (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, η^2p=0.015). 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, η^2p=0.052). We also found a significant interaction effect between feedback laterality and trained hand ($F(1,113)$ = 10.02, p = 0.002, η^2p=0.081). Post hoc analysis revealed that in the Left-Hand training groups, there was 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: $t(56)$ = 2.41, p = 0.005), but no such difference was found in the Right-Hand training groups (Ipsilateral Feedback group: M = 24.18 ms, SD = 7.91 ms; Contralateral Feedback group: M = 28.37 ms, SD = 13.32 ms; $t(57)$ = 1.30, p = 0.20; see Figure 3A). With respect to errors, we 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, η^2p = 0.002), 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, η^2p=0.003), or an interaction effect between these groups (F(1,113) = 3.08 p = 0.08, η^2p = 0.026).

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 (similar to what we found for the main trained condition).

Generalization to no-metronome binaural feedback: Performance with the non-trained hand

The second type of generalization we examined is inter-manual transfer—assessed by sequence performance with the non-trained hand. Collapsed across groups, we found a significant improvement in performance with the non-trained hand following training, such that participants' performance accuracy with the non-trained hand on the last evaluation (ΔIPI: M = 36.26 ms, SD = 19.59 ms) was significantly better than their performance accuracy with the same hand on the first evaluation (M = 92.00 ms, SD = 61.35 ms; Paired sample t test: $t(116)$ = 11.99, p = $4.842*10^{-22}$, Cohen's d = 1.11). In addition, participants performed fewer errors with the non-trained 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: $t(116)$ = 9.76, p = $8.485*10^{-17}$, Cohen's d = 0.90). These results are indicative of generalization of the training to the non-trained hand.

Similar to the trained hand evaluations on the generalization task, we found no difference in baseline performance (ΔIPI) of the non-trained hand across groups. In other words, baseline left-hand performance in Right-Hand training groups was not significantly different than right-hand performance of the Left-Hand training groups (Right-Hand training groups [evaluation of left hand]: M = 96.25 ms, SD = 54.55 ms; Left-Hand training groups [evaluation of right hand]: M = 97.76 ms, SD = 67.55 ms; $F(1,113)$ = 0.01 p = 0.91, η^2p=$1.03*10^{-4}$). We also found no significant difference in the non-trained hand between feedback laterality training groups (Ipsilateral Feedback groups: M = 92.38 ms, SD = 50.45 ms; Contralateral Feedback groups: M = 101.55 ms, SD = 70.13 ms; $F(1,113)$ = 0.64, p = 0.43, η^2p=0.006), and no interaction effect between trained hand and feedback laterality ($F(1,113)$ = 0.09, p = 0.77, η^2p=$7.88*10^{-4}$). 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, η^2p=0.005), 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, η^2p=0.018), or an interaction effect between feedback laterality and hand groups (F(1,113) = 0.15, p = 0.69, η^2p=0.001). Thus, before training, there was no inherent difference in performance with the hand that was not to be used during subsequent training—both in terms of temporal accuracy and errors.

Following training, we did not find a significant effect of laterality group on timing performance (ΔIPI) in the non-trained hand (Ipsilateral Feedback groups: M = 37.63 ms, SD = 19.48 ms; Contralateral Feedback groups: M = 34.92 ms, SD = 19.61 ms; $F(1,113)$ = 0.58, p = 0.45, η^2p=0.005). Thus, transfer to the non-trained 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 ms, SD = 21.46 ms; Left-Hand groups [evaluation of right-hand performance]: M = 35.31 ms, SD = 17.44 ms; $F(1,113)$ = 0.24, p = 0.63, η^2p=0.002) but did find a significant interaction effect between trained hand and feedback laterality on performance with the non-trained hand ($F(1,113)$ = 4.92, p = 0.03, η^2p=0.042). In the Left-Hand training groups, post hoc analysis revealed that, similar to the results in the trained hand generalization, there was a significant difference between feedback conditions such that performance with the right-hand was better following contralateral training (ΔIPI; Contralateral Feedback group: M = 30.14 ms, SD = 14.33 ms; Ipsilateral Feedback group: M = 40.85 ms, SD = 18.73 ms; Unpaired t test: $t(56)$ = 2.41, p=0.02). In the Right-Hand groups no such difference was found, and performance with the left hand in the contralateral and ipsilateral groups was not significantly different (ΔIPI; Contralateral Feedback group: M = 39.87 ms, SD = 22.85 ms; Ipsilateral Feedback group: M = 34.63 ms, SD = 19.68 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 with the non-trained hand than the groups trained with contralateral feedback (M = 0.97, SD = 1.10 errors; F(1,113) = 4.19, p = 0.04, η^2p=0.036). 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; $F(1,113) = 0.24$, $p = 0.63$, $\eta^2p=0.002$) or an interaction effect between feedback laterality and trained hand on this measure ($F(1,113) = 0.44$, $p = 0.51$, $\eta^2p=0.004$). Taken together, the results show that contralateral training (irrespective of trained hand) results in less errors in the non-trained hand and better temporal accuracy in the Left-Hand group.

DISCUSSION

In the current study, we examined how the lateral relationship between hand (motor output) and ear (auditory input channel) engaged during training affects learning of an audio-motor task. Our measures of learning included temporal accuracy—assessed by the deviation from a target temporal interval of 300 ms between notes (ΔIPI)—and sequence accuracy—assessed by the number of incorrect notes played during sequence performance. During monaural training with an external cue (metronome), we find a significant advantage for a contralateral configuration between hand and ear, such that participants exhibited less errors and smaller temporal deviations from the target interval relative to the ipsilateral training groups. In addition, we assessed generalization of training to task performance on a binaural condition with no external metronome cueing. In the Left-Hand training groups, we find that training with contralateral feedback leads to better performance in the generalization condition—both in their trained (left) and non-trained (right) hand. In the Right-Hand training groups, no such configuration-dependent differences in the generalization task between contralateral and ipsilateral training were found.

Results from the training task are in agreement with our previous studies showing sensory-motor interactions that depend on the lateral relationship between sensory cortex and the active motor cortex in stimulus generation (ipsilateral/contralateral to the sensory cortex). At the behavioral level, we have previously found that auditory stimuli are perceived better (i.e., hearing thresholds are lower) when the stimulated ear is ipsilateral (vs. contralateral) to the sound-triggering hand.[21] In the visual modality, we have shown stronger modulations of perceived stimulus brightness when the stimulus-triggering hand is ipsilateral (vs. contralateral) to the visual field in which the stimulus is presented.[22] These studies point to stronger motor-induced modulations in perceptual tasks when motor and sensory circuits reside within the same hemisphere. Our current results expand the scope of sensitivity to the lateral configuration between active effector and feedback-processing hemisphere to a more complex task such as learning to play a piano sequence. Nonetheless, in contrast to our previous results showing an advantage for the ipsilateral (vs. contralateral) configuration in simple perceptual tasks, our current results point to an advantage of the contralateral configuration in learning and generalization of an audio-motor task.

We believe a possible explanation for the difference in lateral configuration advantage between the current and previous studies may relate to differences in the degree of task complexity. While within-hemispheric processing may facilitate performance on simple tasks (as in stimulus detection), engagement of both hemispheres is beneficial when task demands increase (as in audio-motor learning). Supporting evidence for this comes from several lines of research. In the visual modality, a bilateral processing advantage (BPA) has been previously reported[23,24] in which participants show superior enumeration and stimulus comparison abilities when visual information is distributed across the left and right visual fields (engaging both visual cortices) vs. when presentation is limited to a single visual field (engaging mostly the contralateral visual cortex). Importantly, this bilateral processing advantage becomes more prominent as task difficulty and cognitive demand increase. In simpler tasks, there is no bilateral advantage, and in some cases even a within-hemisphere advantage.[25–28] Crosstalk across large cortical regions and engagement of more neural circuitry have been also suggested to play an important role in other high cognitive processes including conscious perception[29] and motor learning.[30] In contrast, in the context of simple stimulus-response tasks, processing within-hemisphere seems advantageous for sensorimotor integration as participants respond faster when the lateral relationship between responding hand and sensory stimulus does not require hemispheric crossing.[31,32] Thus, responses with the left hand are faster to stimuli presented to the left visual field vs. the right visual field (and vice versa for right-hand responses). Neurophysiological data further demonstrate that such differences in reaction time between crossed and un-crossed conditions correlated with integrity of the corpus callosum.[33–36] Thus, performance on a simple stimulus-response task benefits from within-hemisphere processing. With respect to the current results, learning to perform an audio-motor task (such as playing a piano sequence with specific temporal constraints) may be more cognitively demanding compared to stimulus detection or stimulus comparison tasks for which we previously found advantage for the ipsilateral configuration. As such, learning may benefit from activation of more cortical resources and recruitment of both hemispheres—as is the case in the contralateral training configuration. Note that in the current study we did not examine performance on a binaural feedback training condition since the focus of the study was to compare the configural relationship between motor and auditory circuits during training. Thus, it remains an interesting open question how the superior learning we find in the contralateral monaural configuration ranks compared to traditional binaural training in light of this cortical activation theory.

Interestingly, differences between ipsilateral and contralateral training groups were prominent only on the second day of training, whereas on the first day of training no significant differences between groups were found. Previous studies have shown the importance of sleep for learning motor tasks.[37,38] Our current results show that sleep-dependent consolidation processes may be affected by the training regimen and sensitive to the lateral configuration between trained hand and stimulated ear during earlier training. Further studies examining the influence of sensory-motor feedback configuration during training on sleep-related consolidation processes can help shed light on the neural mechanisms underlying skill acquisition.

In addition to performance levels on the trained task, we also examined performance on a similar, but not identical, task (i.e., generalization). Thus, performance of all participants was evaluated pre/post-training in a binaural condition with no external pacing cue (metronome). Generalization was evaluated by examining performance separately in both the trained and the non-trained hand of each participant. In

general, for all training configuration groups we found significant pre/post-training performance gains on the generalization task in both the trained and non-trained hands. These results are in agreement with previous studies showing post-training benefits that generalize to non-trained conditions in the trained[39,40] and non-trained[41,42] hands.

With respect to audio-motor configuration during training, which is the focus of the current study, our data show that similar to the advantage of the contralateral training configuration on performance of the trained task, this configuration advantage generalizes to the non-trained task. However, generalization of this contralateral advantage in performance was only found following left-hand training. In other words, left-hand training with auditory feedback presented to the right ear resulted in better performance on the non-trained task (relative to the left-hand training group that received left ear feedback). In contrast, right-hand training groups showed no configuration-dependent performance differences in the non-trained task. It is possible that the dominant right hand has reached ceiling performance in both configurations and that with further training left-hand performance across configurations will converge. This is supported by the overall better performance of right (vs. left) hand training in the generalization task—suggesting the left hand has further room for improvement. Alternatively, the preserved sensitivity to the audio-motor configuration following left-hand training also in the generalization task may imply that the neural circuits controlling the left (vs. right) hand are more sensitive to the context of training. Evidence for differences between left/right motor circuits in the context of generalization across hands was previously reported.[42–44]

Taken together, our current results show that the lateral configuration between active hand and feedback-processing sensor affects performance and learning of an audio-motor skill. In addition to the intriguing theoretical implications discussed, our results may also have practical implications for training regimens in healthy participants and in clinical populations. For example, binaural auditory stimulation was shown to improve motor actions in Parkinson's disease patients.[45–47] An open question for future study is whether manipulating the lateral configuration between motor and auditory circuits, and their relationship to the more clinically affected side in such patients, may facilitate motor behavior.

Limitations of the study

In the current study, we focused on the differences between specific hand-ear configurations in learning of an audio-motor task and find a contralateral configuration advantage. One limitation of our study is that our dataset did not include a binaural condition group for reference—which is the more common and natural learning condition. Therefore, the relationship between contralateral configuration and binaural stimulation remains open for future study. Another limitation of our study is the lack of neurophysiological measures. Although our theoretical framework and motivation are based on current knowledge about functional neuroanatomy, further studies will be needed to address the neural mechanisms of the behavioral effects we described.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

- KEY RESOURCES TABLE
- RESOURCE AVAILABILITY
  - Lead contact
  - Materials availability
  - Data and code availability
- EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS
  - Experimental models
  - Participants
- METHOD DETAILS
- QUANTIFICATION AND STATISTICAL ANALYSIS

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AUTHOR CONTRIBUTIONS

Conceptualization, H.D. and R.Mukamel.; Methodology, H.D., B.B., and R. Mukamel.; Software, H.D. and R.Mazinter.; Formal Analysis, H.D. and B.B.; Investigation, H.D., B.B., R.Mazinter, and S.L.; Writing – Original Draft, B.B. and R. Mukamel.; Supervision and Funding Acquisition, R. Mukamel.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Training and Test piano play data	Mendeley Data https://doi.org/10.17632/psgnvsfr5b.1	RRID:SCR_002750
Software and algorithms		
MATLAB (2019b)	MathWorks	RRID:SCR_001622
JASP (v.0.16.0.0)	JASP Team	RRID:SCR_015823

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources should be directed to and will be fulfilled by the lead contact, Prof. Roy Mukamel (rmukamel@tau.ac.il).

Materials availability

This study did not generate any new materials.

Data and code availability

- Participants training and test raw data can be found in Mendeley Data and are publicly available as of the date of publication. DOI is listed in the key resources table.
- This paper does not report any original code.
- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

Experimental models

- human subjects
- Caucasian
- mean age: 25.19 (range: 18–35) years
- 36/117 males

Participants

One hundred and forty-six right-handed healthy participants were recruited for this study. All participants were naive to the purpose of the experiment, had normal hearing, normal or corrected to normal vision and no previous musical training on a piano. Handedness of participants was assessed by self-report and by the Edinburgh inventory.[48] Data from twenty-nine participants were discarded (seventeen participants did not complete the second session of the experiment, six participants were discarded due to technical error, and another six due to a 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 ethics committee in Tel-Aviv University. All participants provided written informed consent to participate in the study and were compensated for their time.

METHOD DETAILS

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 training with ipsilateral ear stimulation (n = 28), left-hand training with contralateral ear stimulation (n = 30), right-hand training with ipsilateral ear stimulation (n = 30) or right-hand training with 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. 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; see the piano layout in Figure 1A). Finger mapping to notes was identical for playing with right and left hand, introducing no sensory differences between the groups. Throughout the experiment, participants were instructed to play the correct 8-note sequence as accurately as possible within two consecutive metronome beats. This corresponded with a 300 ms interval between notes. 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 and sounds were delivered 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 1D). 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 understood 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 groups (ipsilateral or contralateral ear with respect to training hand). Participants were informed they would receive auditory feedback only to one ear during this phase. In addition, a metronome beat 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 150 ms long and the inter-press interval (IPI) between consecutive note onsets was 300 ms. Thus, a single 8-note sequence fits between two consecutive metronome beats. Each training session included 20 blocks, and each block consisted of 5 continuous repeats of the 8-note sequence, followed by a 15 s rest period cued by a white screen (see Figure 1B). Within each training block, metronome was initiated by the 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.

In addition to measuring performance (IPI) during the learning phase, we also measured participants' degree of task generalization – performance on a similar task under different conditions. In the current study we examined two types of generalizations (Figure 1D). In the first type of generalization, we evaluated participants' performance in the same task they trained on while auditory feedback was provided to both ears, and no metronome cue was provided as external temporal reference. Evaluation of the second type of generalization was similar to the first (i.e., binaural, no metronome), only participants performed the evaluation task with their non-trained hand (inter-manual transfer). Both generalization evaluations were conducted before and after training. Thus, each evaluation phase included an assessment of both hands. During each evaluation phase, participants were instructed to execute the note sequence as accurately as possible relative to the reference sequence. 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 s 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 non-trained hand and the following two blocks were performed with the (to-be) trained hand. In the Post-training evaluation, hand order was reversed such that we first evaluated performance of the trained hand on the generalization task, and then evaluated performance in the non-trained hand (see Figure 1D).

QUANTIFICATION AND STATISTICAL ANALYSIS

In order to compare sequence playing performance between the four training groups, we calculated two dependent measures from each participant's 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 (ΔIPI) from 300 ms (the target IPI). The delta-IPI metric provides a measure of the variability around perfect performance. Lower delta-IPI values correspond with better performance (i.e., less deviation from perfect performance). 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 ΔIPI across correct note pairs and used it as the representative IPI of the block. Data from blocks with 20 or more errors were discarded from analysis. Participants with more than 10 discarded blocks in the training session (out of 40 total blocks across 2 days) 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). In the remaining participants, only IPIs from valid blocks were used for analysis (total of 12 discarded blocks across 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. 1 block from 1 participant in the Left-Hand ipsilateral ear group was also discarded in the pre-training evaluation). In addition, we discarded additional 3 participants from analysis since they demonstrated deviant performance (ΔIPI that was more than 2.5 standard deviations from all participants' average ΔIPI for more than 3 consecutive blocks; 2 in the Left- Hand Ipsilateral ear group and 1 in the Right-Hand Contralateral group), leaving data from 117 participants for further analysis. Data analysis was conducted using JASP (JASP Team 2022. Version 0.16.0). Specific statistical tests used are described in the results section.