Behavioral and neural effects of congruency of visual feedback during short-term motor learning

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A B S T R A C T

Visual feedback can facilitate or interfere with movement execution. Here, we describe behavioral and neural mechanisms by which the congruency of visual feedback during physical practice of a motor skill modulates subsequent performance gains. 18 healthy subjects learned to execute rapid sequences of right hand finger movements during fMRI scans either with or without visual feedback. Feedback consisted of a real-time, movement-based display of virtual hands that was either congruent (right virtual hand movement), or incongruent (left virtual hand movement yoked to the executing right hand). At the group level, right hand performance gains following training with congruent visual feedback were significantly higher relative to training without visual feedback. Conversely, performance gains following training with incongruent visual feedback were significantly lower. Interestingly, across individual subjects these opposite effects correlated. Activation in the Supplementary Motor Area (SMA) during training corresponded to individual differences in subsequent performance gains. Furthermore, functional coupling of SMA with visual cortices predicted individual differences in behavior. Our results demonstrate that some individuals are more sensitive than others to congruency of visual feedback during short-term motor learning and that neural activation in SMA correlates with such inter-individual differences.

Introduction

Vision provides a rich source of information supporting the performance of motor acts. For instance, consider what would happen to the performance level of a basketball player when shooting a free throw with eyes closed or to a painter drawing a sketch with no visual cues. Behavioral studies examined the effects of visual input on action performance (Sturmer et al., 2000; Brass et al., 2001; Kilner et al., 2003) and how the motor system adapts to manipulations in visual feedback (Wolpert et al., 1995; Kagerer et al., 1997). A study by Saunders and Knill revealed that humans use continuous visual feedback to correct their concurrent movements (Saunders and Knill, 2003), suggesting a real-time integration between action and visual feedback (Wolpert and Ghahramani, 2000; Desmurget and Grafton, 2003).

In the context of learning new motor skills, online visual feedback has been shown to facilitate motor learning. For example, Shea and Wulf trained different groups of subjects to maintain their balance on a stabilometer with and without visual feedback (Shea and Wulf, 1999). Their results showed enhanced learning in subjects that were provided with feedback compared to no-feedback. Others have shown that at the group level, visual feedback was the most effective source of sensory input during motor training (Adams et al., 1975; Proteau, 1992). While a great deal of previous research has focused on the effect of visual input on executed movements at the averaged group level (Smith and Bowen,

1980; Carlton, 1992; Collins and Luca, 1995; Kilby et al., 2017), it is acknowledged that some individuals learn better than others (Ackerman, 1987; Unsworth and Engle, 2005; Tubau et al., 2007; Sigrist et al., 2013).

At the neural level, individual differences in motor learning have been shown to correlate with structural (anatomical) differences and changes in blood-oxygen level dependent (BOLD) levels during training (Della-Maggiore et al., 2009; Tomassini et al., 2011). Importantly, variations in learning have been found to correlate with activation in visuomotor networks (Kincses et al., 2008). Evoked activity within these regions during action observation and imitation has also been reported (Grezes and Decety, 2001; Tanaka and Inui, 2002; Gazzola et al., 2006), supporting their importance in integrating visual information to motor performance during training.

In a recent study we reported that manipulated (incongruent) visual feedback during short-term unimanual motor training facilitates learning in the untrained hand. Furthermore, activity in the superior parietal lobule correlated with individual differences in learning (Ossmy and Mukamel, 2016b). Here, we examine the link between congruency of visual feedback during training and individual differences in performance gains with a focus on the physically trained hand. Healthy subjects were trained inside a functional magnetic resonance imaging (fMRI) scanner to perform sequences of right hand finger movements with (i) no visual feedback (ii) congruent visual feedback of a right virtual hand simulating subject's real right hand movement in real-time or (iii)

incongruent visual feedback of a left virtual hand moving in sync with the subject's real right hand movement.

Materials and methods

Subjects

Eighteen healthy subjects (10 females, mean age: 27.4, range: 22–34 years) participated in the study after providing informed consent. All subjects were right handed with normal or corrected-to-normal vision and no reported cognitive deficits or neurological problems. Subjects were recruited according to the standard safety criteria for fMRI studies. Subjects were naïve to the purpose of the study and participated in the experiment either for course credit or money (55 NIS per hr). The study was conducted in accordance with the protocol approved by the Ethics Committee of Tel-Aviv University and the Helsinki committee at the Tel-Aviv Sourasky Medical Center.

Experimental design

Subjects completed five experimental sessions (5 consecutive runs) in which they learned unique sequences of finger movements. Fingers were numbered from index (1) to little finger (4) and subjects were asked to learn a different sequence in each session (5 different sequences: 4-1-3-2-4, 4-2-3-1-4, 3-2-4-1-3, 3-1-4-2-3, 2-3-4-1-2; see Fig. 1a). Subjects lied supine with their arms to the side of their body and palms facing up. Subjects could not see their real hands during the scans. We recorded the subjects' finger movements using MR compatible gloves (5DT Data Glove Ultra) that allowed yoking the movements of virtual hands presented on a screen to real hand movements during relevant experimental conditions. The two virtual hands were presented on a screen with black background (see Fig. 1b). In the scanner, subjects viewed the screen through a tilted mirror mounted in front of their eyes.

In the beginning of each session (see design of single session in Fig. 1c), subjects were presented with an instructions slide depicting two hand illustrations with numbered fingers and a 5-digit sequence underneath representing the sequence of finger movements to be learned. The instructions slide was presented for 12 s followed by a pre-training evaluation stage in which baseline performance level of each hand was separately assessed. During the evaluation, subjects performed the required sequence with one hand repeatedly as fast and as accurate as possible for 30 s (hand order right\left was counter balanced across all sessions). At this stage real-time visual feedback consisted of a simultaneous display of two virtual hands whose finger movements were yoked in real-time to the subjects' actual finger movements recorded by the gloves. After initial performance evaluation of the two hands, subjects trained under one of the following 5 training conditions: 1. Congruent visual feedback - subjects physically trained with their right hand while receiving congruent real-time visual feedback of right virtual hand movement on the screen (condition RH-RH); 2. Incongruent visual feedback - subjects physically trained with their right hand while receiving real-time corresponding visual feedback of left virtual hand movement (RH-LH); 3. No visual feedback - subjects physically trained with their right hand while no visual feedback (black screen) was presented (RH-None); 4. Right hand observation only - subjects passively observed the virtual right hand performing the sequence, while both their real hands were immobile (None-RH); 5. Left hand observation only – subjects observed the virtual left hand performing the sequence, while both their real hands were immobile (None-LH). The current study focuses on the first 3 conditions in which subjects actively performed the finger sequences with their right hand. The order of the active training conditions was counter balanced across subjects, and the finger sequence to be learned was randomized across conditions. Results from the training by observation conditions (None-RH, and None-LH) have been

recently reported (Ossmy and Mukamel, 2016b). When visual feedback was provided (all conditions except condition 3) both virtual hands appeared on the screen, while movement of the relevant virtual hand (depending on experimental condition) was yoked to real right hand finger movement. For each experimental condition, a unique sequence of finger movements was learned. Following the pre-training evaluation stage, a "Start Training" slide appearing for 9 s cued the subjects to the upcoming training stage in which they performed the sequence of finger movements in a self-paced manner. In the training by observation conditions (None-RH, and None-LH) the pace of virtual hand finger movement was set based on the average pace of the subject's finger movements during previous execution conditions (see (Ossmy and Mukamel, 2016b) for further details). The training stage consisted of 20 training blocks. Each training block lasted 15 s followed by 9 s of a yellow blank screen that served as cue for resting period. After the training stage, subjects' performance level was re-evaluated as previously for 30 s in each hand. For each training condition, the same sequence was used in the pre/post evaluation stages. During both pre- and post-training evaluation stages, subjects were instructed to repeatedly execute the sequence as fast and as accurately as possible while visual feedback of virtual hand movement, congruent to real hand movement, was provided (regardless of the type of training condition).

Behavioral analysis

Each sensor of the glove provided the angle of each finger joint (sampling rate = 16 ms), and allowed us to calculate subject's performance (P) by counting the number of correctly performed complete 5-digit sequences within 30 s in all evaluation stages. We considered individual finger movement as correctly performed only when the angle between the proximal phalange and the metacarpal reached 90°. Subject's performance gain (G) following training was calculated using the formula below:

$$G = \frac{p_{post_{training}} - p_{pre_{training}}}{p_{post_{training}} + p_{pre_{training}}}$$

Where $P_{post\_training}/P_{pre\_training}$ corresponds to the subject's performance in the post/pre training evaluation stage. Therefore, a positive G index reflects improvement in performance following training. We calculated right hand performance gain index for each subject and experimental condition. The effect of visual feedback on motor learning at the individual subject level was calculated relative to the no-feedback condition using the formulas below:

$$T_C = G_{RH-RH} - G_{RH-None}$$

$$T_I = G_{RH-LH} - G_{RH-None}$$

where T_C (training congruent) is the difference between G index after training with congruent feedback (RH-RH) and the G index after training with no feedback (RH-None). Similarly, T_I (training incongruent) is the difference between G index after training with incongruent visual feedback and the G index after training with no visual feedback. Subject's sensitivity to visual feedback during training was termed *VS* and calculated as the sum of the absolute values of T_C and T_I above:

$$VS = |T_C| + |T_I|$$

Data from the motion detection gloves were used as previously reported (Ossmy and Mukamel, 2016b), to verify that the subjects did not move their fingers during the observational training conditions (None-RH and None-LH). For each subject, we also used the data from the gloves' sensors in each training block (20 blocks per training condition) to compare the total amount of self-paced movements performed during training across the different conditions.
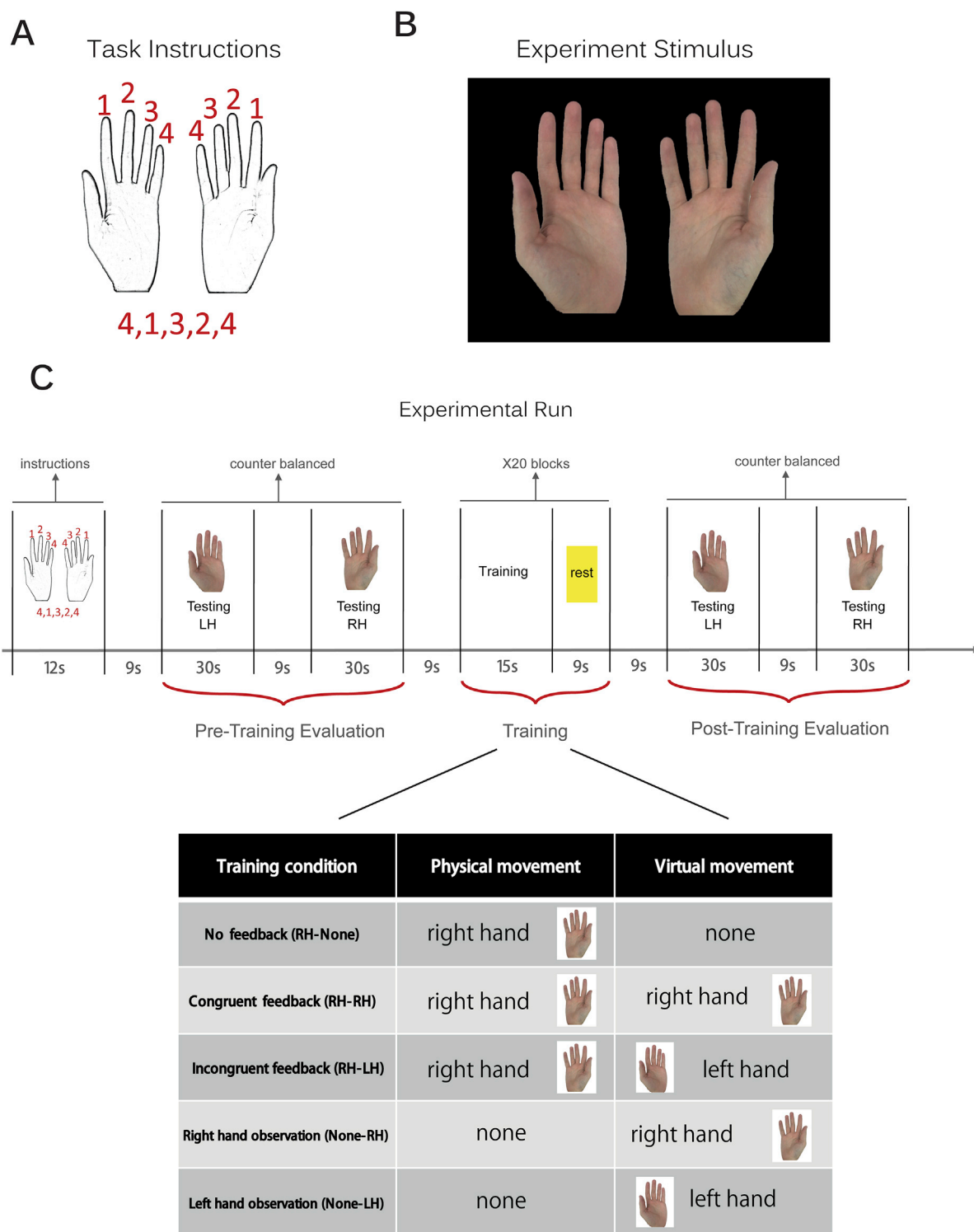
Fig. 1. Experiment details. (**a**) Instructions – At the beginning of each session, a unique sequence of numbers together with a sketch of the mapped fingers was presented. (**b**) Stimuli - picture of the virtual hands used as visual feedback during training. (**c**) Schematic illustration of one experimental session. After instructions, subjects performed the sequence as accurately and rapidly as possible using their right hand (RH) and their left hand (LH) separately for initial evaluation of performance. Next, subjects were trained under a specific training type, and finally the evaluation test was repeated. Each subject underwent a total of 5 different training sessions corresponding to five different conditions and unique finger sequences. Order of the active training sessions was counter-balanced across subjects.

fMRI data acquisition

Blood oxygenation level dependent (BOLD) contrast was obtained on a 3T General Electric scanner with an 8 channel head coil located at the Tel-Aviv Souraski Medical Center, Tel-Aviv, Israel. An echo-planar imaging sequence was used to obtain the functional data (39 contiguous ascending interleaved axial slices, 4 mm thickness, slice gaps = 0; TR = 3000 ms; flip angle = 90°; TE = 30 ms; in-plane resolution = 1.72×1.72 mm; matrix size = 128×128). In addition, anatomical reference was obtained by T1-weighted scan (voxel size = $1 \times 1 \times 1$ mm) for each subject.

fMRI preprocessing

All fMRI data were processed using the BrainVoyager QX software (version 2.6, Brain Innovation, Maastricht, Netherlands). Prior to statistical analysis, a preprocessing procedure was performed on all functional images and included cubic spline slice-time correction, trilinear 3D motion correction, and high-pass filtering (above 0.006 Hz). In addition, we assessed head movements and verified no scans contained head movement exceeding 2 mm. The 2D functional images were co-registered to the anatomical images and the complete dataset was transformed into the Talairach coordinate system for multi-subject comparisons (Talairach and Tornoux, 1988).

ROI analysis

We defined brain regions of interest (ROIs) relevant to the perceptual-motor task by performing a general linear model (GLM) analysis on the fMRI data obtained during the training stage. Since we were interested in motor regions that are sensitive to visual input we used the conjunction contrast: RH-None > rest ∩ None-RH > rest. In addition, 'visual-only' ROIs within the visual cortex that are sensitive to visual input during mere observation were defined by the contrast None-RH > rest U None-LH > rest. The ROIs were chosen based on the multi-subject map, however the exact coordinates of each ROI were defined by the peak activation using the same contrasts at the individual subject level. All the resulting maps were corrected for multiple comparisons by controlling the False Discovery Rate (Benjamini and Hochberg, 1995) and thresholded at q(FDR) < 0.05, with a minimum cluster size of 30 contiguous voxels. In each ROI, we examined the correlation between fMRI activation in the different experimental conditions (type of visual feedback) and the corresponding behavioral effect (performance gain) across subjects. As neural measure, for each ROI in each of the eighteen subjects, we calculated the average contrast value across all voxels during training with congruent feedback relative to training without visual feedback (obtained from the GLM contrast: RH-RH > RH-None), yielding a vector of 18 average contrast values. As behavioral measure, we took the corresponding T_c value. In a similar fashion, we performed the same correlation analysis using the data from the incongruent feedback condition (taking the contrast values obtained from the GLM contrast: RH-LH > RH-None) and the corresponding T_I values.

Multivariate analysis

To examine whether activation patterns across voxels in each ROI are sensitive to the type of visual feedback provided during right hand training (congruent/incongruent), we used a multivoxel pattern analysis (MVPA) classifier approach in each one of the 18 subjects separately. We used a Matlab implementation of a support vector machine classifier (Chang and Lin, 2011) to discriminate activation patterns during RH-RH and RH-LH trainings as belonging to congruent/incongruent feedback type. Classification of feedback type was based on left-out trial activation patterns. For classification model construction we used radial basis function (RBF) kernel with factor C = 1 and γ = 0.008. Data from each experimental block was represented as the average signal amplitude in the 3 time points corresponding to 6-, 9- and 12-sec following block onset (TR = 3sec). Signal amplitude was expressed as percent signal change relative to baseline – defined as the average signal at time points −3 s and 0 s relative to the beginning of the block. Thus, the time-course of each voxel in the ROI was reduced to two 1×20 vectors (20 experimental blocks per condition, and one vector for each type of feedback). For each ROI, the following classification procedure was implemented: First, data from all voxels in the ROI were extracted - resulting in a 20xM matrix of values for each feedback type, where M is the number of voxels in the ROI. In order to keep the number of voxels identical across all ROIs, we used M = 125. Therefore, in each ROI we extracted data from the 125 voxels nearest to the voxel with the highest p-value in the GLM map.

Next, we randomly chose data from one training block from each condition to be used as test set and the classifier was modeled based on the remaining two datasets of 19 blocks. Following the model construction, classification performance was assessed on the test set ('leave-one-trial-out'). The average performance level across all 400 possible combinations of train/test sets (20 trials per condition) was assigned to the ROI. In order to assess statistical significance of classification performance level, we performed an identical classification procedure as described above using the same data but with shuffled labels across conditions as input to the classifier. In order to obtain a distribution of shuffle-labeled classifications accuracies, this was repeated 1000 times. For each one of the 18 subjects, an ROI was defined as significantly coding feedback type if the real classification level exceeded the shuffle-labeled distribution with significance level of α = 0.01.

Functional connectivity analysis

We conducted whole-brain functional connectivity analysis using the activation in relevant ROI defined as seed region for each subject. Regressors were generated by calculating the mean activation across all voxels in the seed region during RH-LH and RH-RH trainings separately (training duration = 480sec/TR = 3sec, yielding a regressor of 160 time points which include rest periods between training blocks). The design matrix of each subject consisted of RH-LH or RH-RH regressors from the seed region. Multi-study whole-brain contrast was performed to identify the regions that show the strongest functional connectivity during RH-LH and RH-RH training across subjects.

Results

Sensitivity to visual manipulation - behavior

Subjects performed a total number of 126 ± 11.6 full sequence movements during each training type (Mean ± SD across subjects and training types) which was not significantly different across training conditions (minimal p = .34 across subjects; rmANOVA). Fig. 2a depicts the right hand group average performance gains following physical training (conditions RH-None, RH-RH and RH-LH; See also Table 1). Physical training with no visual feedback yielded significant performance gains ($G_{RH-None} = 0.09 \pm 0.03$, Mean ± SEM; p = .02; two-tailed unequal variance *t*-test compared to zero). The addition of congruent visual feedback during training resulted in significantly enhanced learning at the group level ($G_{RH-RH} = 0.25 \pm 0.04$; $p = 8 \cdot 10^{-3}$ two-tailed paired *t*-test compared to $G_{RH-None}$). Conversely, following training with incongruent feedback, performance gain was significantly reduced relative to training with no visual feedback ($G_{RH-LH} = -0.01 \pm 0.06$; p = .04 two-tailed paired *t*-test compared to $G_{RH-None}$), and was not significantly different than zero (p = .8; two-tailed unequal variance *t*-test). Interestingly across individual subjects, the increased gains for congruent visual feedback (Tc) and decreased gains for incongruent visual feedback (Ti) - correlated (r = −0.55, p = .01; Spearman correlation; See Fig. 2b). This result suggests that with respect to short term motor skill learning, individual subjects exhibit different sensitivity levels to visual feedback, and that this sensitivity can work in both directions (either enhance or interfere) depending on feedback type (congruent/incongruent). We further examined this effect by applying k-means clustering method (Likas et al., 2003) with k = 2 to obtain the optimal partitioning of subjects to two groups based on their sensitivity to visual feedback during learning (VS; see Materials and methods). This analysis yielded a group of 6 subjects who were significantly more sensitive to feedback than the other twelve (See Fig. 2c; VS = 0.75 ± 0.08 compared to VS = 0.14 ± 0.02; p = .001; two-tailed unequal variance *t*-test). Pre-training performance of the subjects found sensitive to visual feedback was not significantly different from pre-training performance of non-sensitive subjects (mean performance = 10.5 vs. 11.25 respectively; p = .76, unequal variance *t*-test).
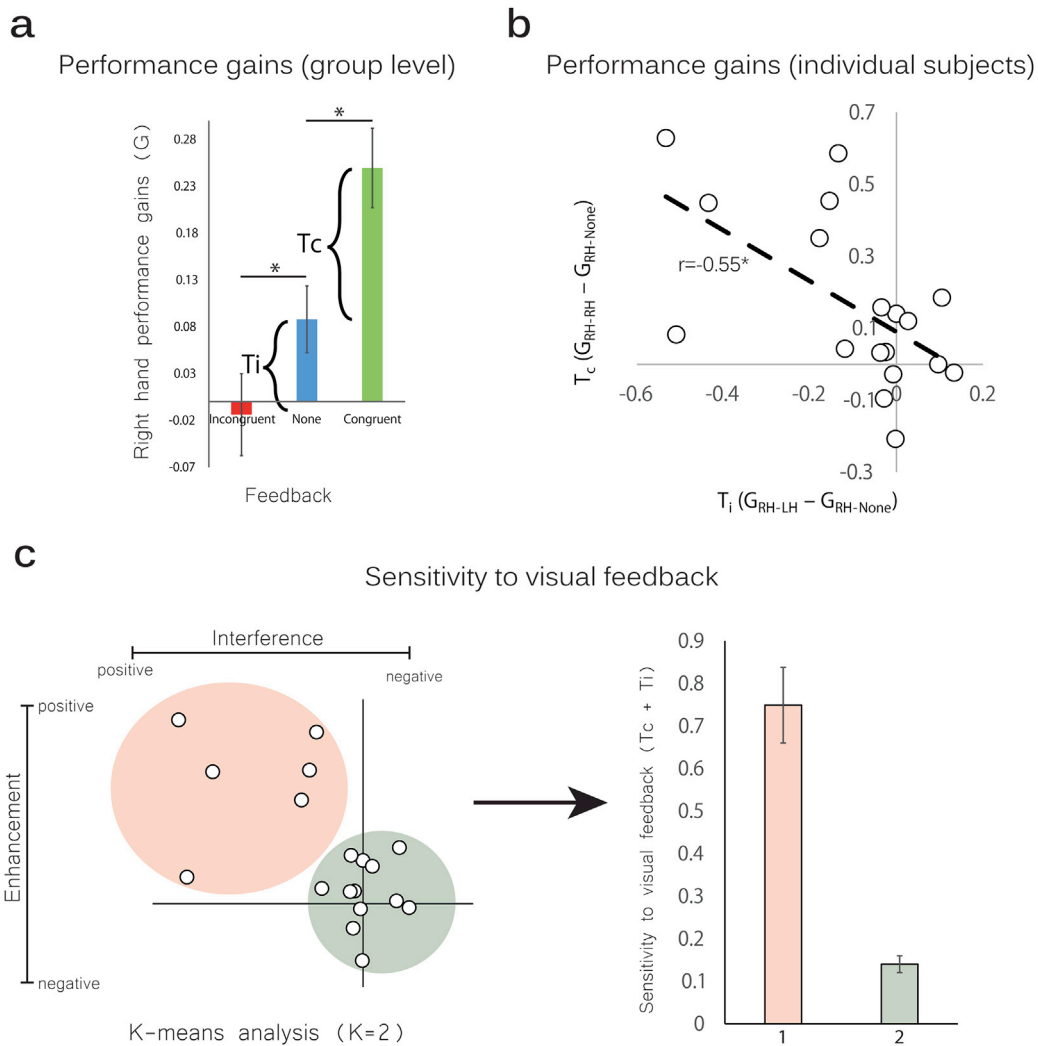
a
Performance gains (group level)

b
Performance gains (individual subjects)

c
Sensitivity to visual feedback

K-means analysis (K=2)

Fig. 2. Behavioral results. (**a**) Group performance gains after training with congruent visual feedback (green) were significantly higher than performance gains following training without visual feedback (blue). Similarly, group performance gains after training with incongruent feedback were significantly lower than performance gains following training without visual feedback (red) (p < .05 denoted by asterisks). (**b**) Negative correlation across subjects between T_C and T_I such that subjects showing higher gains following training with congruent visual feedback had lower gains following training with incongruent visual feedback. (**c**) Individual subject sensitivity to visual feedback. K-means analysis (K = 2) on the performance enhancement (Tc) and interference (Ti) effects shown in panel a. One group (red; n = 6) was significantly more sensitive to visual feedback ($T_c + T_i$) than the other group (green; n = 12; p = .001).

Table 1
Right hand – performance gains. Individual subject's performance during pre- and post-training evaluation stages. Each cell represents the number of correctly performed complete 5-digit sequences within 30 s. S – subject number.

# S	RH-RH			RH-LH			RH-None		
	Pre training	Post training	G index	Pre training	Post training	G index	Pre training	Post training	G index
1	3	10	0.53	13	9	−0.18	11	10	−0.04
2	7	10	0.17	3	6	0.33	6	9	0.2
3	2	5	0.42	13	2	−0.73	3	2	−0.2
4	7	19	0.46	16	14	−0.06	12	15	0.11
5	17	22	0.12	20	23	0.06	24	29	0.09
6	4	15	0.57	15	8	−0.3	10	13	0.13
7	10	15	0.2	16	7	−0.39	15	19	0.11
8	11	16	0.18	17	21	0.1	13	13	0
9	13	14	0.03	16	13	−0.1	16	13	−0.1
10	5	18	0.56	12	11	−0.04	12	15	0.11
11	13	16	0.1	14	15	0.03	13	15	0.07
12	4	8	0.33	6	14	0.4	2	5	0.42
13	14	21	0.2	11	26	0.4	8	19	0.4
14	13	17	0.13	11	15	0.15	13	18	0.16
15	8	11	0.15	15	14	−0.03	6	6	0
16	7	7	0	14	17	0.09	6	6	0
17	11	14	0.12	18	19	0.02	10	10	0
18	15	20	0.14	27	26	−0.01	18	21	0.07

ROIs sensitive to visual input

All subjects performed the evaluation and training stages while undergoing a whole-brain fMRI scan. Fig. 3 demonstrates the random effect multi-subject maps relative to rest of: physical training with no feedback (RH-None; Fig. 3a), training by right hand observation (None-RH; Fig. 3b) and physical training with congruent\incongruent feedback (RH-RH, RH-LH; Fig. 3c). To define motor regions that are sensitive to visual input, we performed a GLM conjunction analysis on the fMRI data obtained during right-hand physical training without visual feedback, and training by right-hand observation (RH-None > rest ∩ None-RH > rest). The conjunction contrast using training by left-hand observation (RH-None > rest ∩ None-LH > rest), yields a similar map – in agreement with our previous report showing similar activations for None-RH > rest and None-LH > rest; (see Ossmy and Mukamel, 2016a). The conjunction revealed 2 regions at the multi-subject level (see Fig. 4a): bilateral supplementary motor area (SMA; size at the group level: 239 voxels; peak activation Talairach coordinates in the multi-subject map: $x = -3$; $y = -5$; $z = 58$) and the left superior parietal lobule (lSPL; size at the group level: 127 voxels; peak activation Talairach coordinates: $x = -34$; $y = -56$; $z = 52$). These regions were chosen as ROIs for further analysis at the individual subject level. The exact coordinates of these ROIs were defined at the individual subject level (for peak activation Tailarach coordinates in each subject using the same conjunction analysis see Table 2).

Sensitivity to visual feedback - multivariate fMRI analysis

We examined whether the pattern of activation in each ROI is sensitive to the type of visual feedback (congruent\incongruent) during physical training with the right hand. To that end, we employed multivariate pattern analysis (MVPA; See Materials and methods). For each one of the 18 subjects separately, we constructed a classifier that was provided with labeled stimuli (according to the type of visual feedback) and corresponding SMA or L-SPL response patterns. ROI selection (based on the conjunction contrast: RH-None > rest ∩ None-RH > rest), was independent to the input to the classifier (activation patterns during training with congruent/incongruent visual feedback: RH-RH and RH-LH respectively; See Materials and methods). At the individual subject level, subjects with strong behavioral modulations depending on training type (i.e. high VS levels found in k-means clustering analysis; see Fig. 2c) showed significant classification with high accuracy levels based on their fMRI activation patterns in SMA (see Fig. 4b, red for individual subject classification levels; average classification accuracy across subjects = 73.2%, N = 6; p < .05). The same classification analysis based on SMA activation patterns in the subjects with weak behavioral modulations, was not significantly different from that obtained from shuffled label data (see Fig. 4b, green for individual subject classification level; average classification accuracy across subjects = 52.09%, N = 12). Activation patterns in L-SPL did not yield significant classification levels relative to corresponding accuracy levels obtained when condition labels were shuffled (mean classification accuracy across subjects with strong
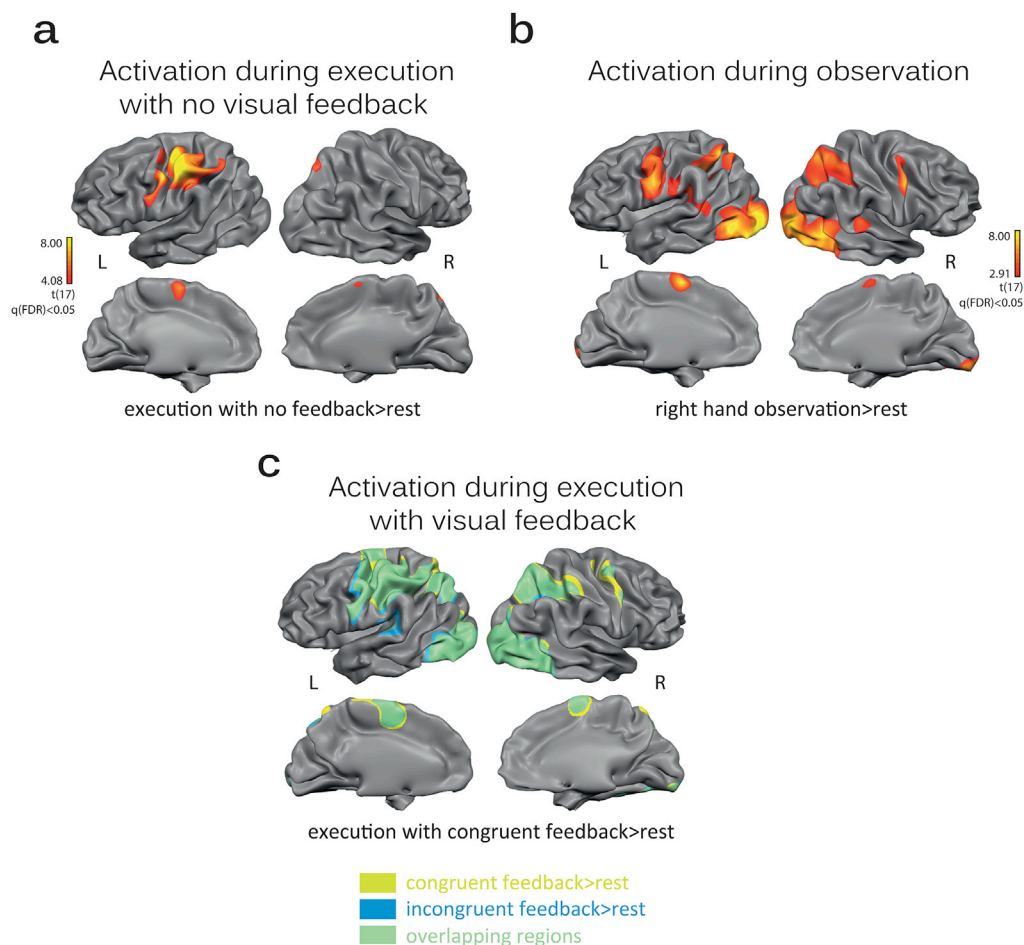

Fig. 3. Activation maps during the different conditions. Random effect multi-subject activation maps (N = 18) from the training stage corrected using q(FDR) < 0.05, displaying significant regions obtained from the GLM contrast (**a**) RH-None > rest, (**b**) None-RH > rest, and (**c**) RH-RH > rest (yellow) and RH-LH > rest (blue). Green regions correspond to overlapping regions between the two. Direct contrast: RH-RH > RH-LH yielded an empty map.
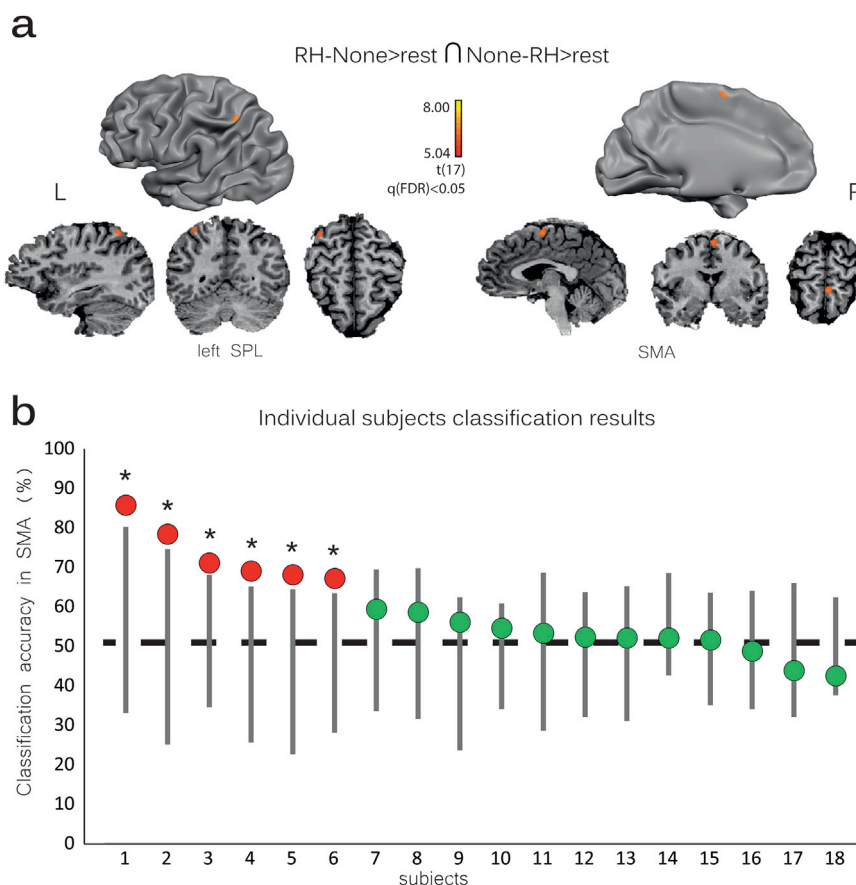
Fig. 4. Classification of visual input. (**a**) ROI analysis. Random effect multi-subject activation map (N = 18) displaying significant regions obtained from the GLM contrast: RH-None > rest ∩ None-RH > rest during the training period (q(FDR) < 0.05; see Materials and methods). (**b**) Across the two ROIs, SMA activation patterns significantly classified the type of visual feedback in all the subjects with strong behavioral modulations (red; see Fig. 2c). Classification accuracies in the subjects with weak behavioral modulations (green; see Fig. 2c) was not significantly different than shuffled-labeled classification accuracies (gray bars) and chance level (black dashed line).

Table 2

ROI coordinates. Talairach coordinates of each subject's peak voxels in the SMA and left SPL ROIs defined by the contrast RH-None > rest ∩ None-RH > rest at the individual subject level (Fig. 4a).

Subject	SMA coordinates	Left SPL coordinates
1	[−4−2 57]	[−31−63 50]
2	[−1−6 64]	[−44−61 46]
3	[−4−6 56]	[−32−54 48]
4	[1−3 55]	[−33−56 52]
5	[−2−7 58]	[−37−49 48]
6	[−4−10 53]	[−30−52 45]
7	[−2−8 53]	[−21−64 40]
8	[−6−10 61]	[−30−55 55]
9	[−2−6 58]	[−42−45 52]
10	[−4−1 56]	[−21−55 59]
11	[−4−6 55]	[−29−58 50]
12	[−6−9 58]	[−30−64 50]
13	[−5−8 65]	[−30−52 45]
14	[−1−5 69]	[−37−51 52]
15	[−5−12 50]	[−28−53 52]
16	[−4−7 57]	[−28−72 45]
17	[−9−1 49]	[−34−37 45]
18	[−1−15 61]	[−26−58 52]

behavioral modulations = 53.9%, minimal p > .25 across subjects; mean classification accuracy across subjects with weak behavioral modulations = 54.9%, p > .17). This provides evidence for the sensitivity of SMA activation patterns to the type of visual feedback during physical training which also corresponds with subsequent behavioral changes of individual subjects.

Correlation between neural activation patterns and performance gains

Activation in the SMA was also examined with respect to corresponding behavioral changes in right hand performance (enhancement and interference effects; see Materials and methods). We found that the average contrast across training blocks (RH-RH vs. RH-None) in the bilateral SMA significantly correlates with T_C during training with congruent visual feedback (see Fig. 5a; Spearman r = 0.53; p < .05 Bonferroni corrected for 2 ROIs). Similarly, the contrast (RH-LH vs. RH-None) in bilateral SMA correlates negatively with T_I values during training with incongruent visual feedback (see Fig. 5b; Spearman r = −0.57; p < .05 Bonferroni corrected for 2 ROIs). We did not find significant correlation between differences in SMA activation and absolute performance levels in both congruent (RH-RH vs. RH-None; post-training behavior - p = .15, r = −0.35; pre-training behavior – p = .1, r = 0.39) and incongruent condition (RH-LH vs. RH-None; post-training – p = .11, r = 0.38; pre-training – p = .78, r = −0.07; see Table 1). Contrast in the L-SPL also yielded significant correlation with T_C values during training with congruent visual feedback (Spearman r = 0.61; p < .05) but not with T_I values during training with incongruent visual feedback (Spearman r = 0.009; p = .97). In addition, we did not find significant correlations between the contrast in the visual regions with T_C values during training with congruent visual feedback (left visual – p = .42, r = 0.2; right visual - p = .35, r = 0.23) or T_I during training with incongruent visual feedback (left visual – p = .21, r = −0.31; right visual - p = .06, r = −0.45). Taken together, the results suggest that during physical training, the modulation of SMA activity due to the addition of visual feedback (congruent or incongruent) corresponds with the modulation in behavior rather than the absolute performance level at the
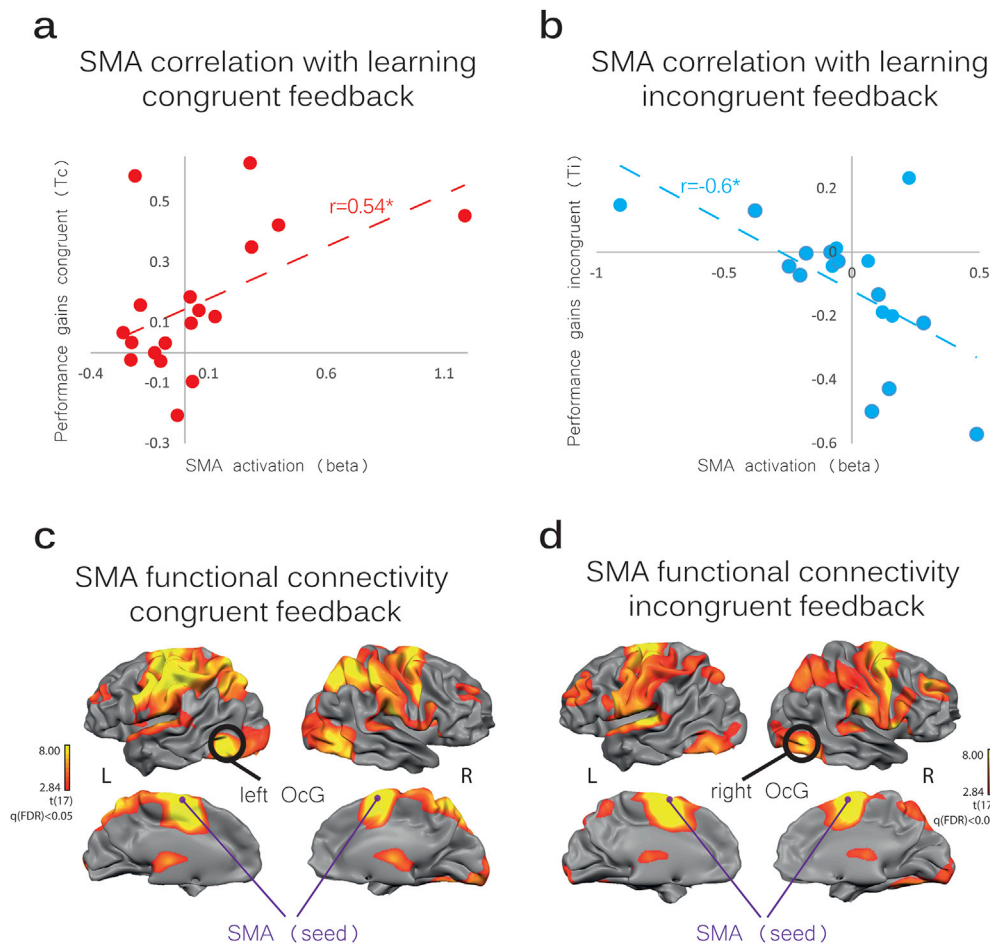
Fig. 5. Correlation of neural activation with behavior. (a) Scatter plot showing individual subject contrast in SMA during training with congruent feedback (RH-RH vs. RH-None) plotted against subsequent performance enhancement (Tc). (b) Contrast of activation in SMA during training with incongruent feedback (RH-LH vs. RH-None) plotted against subsequent performance interference (Ti). (c) Functional connectivity map with SMA as seed region (see Fig. 4a) during training with congruent feedback (q(FDR) < 0.05). The degree of coupling between SMA and a patch of voxels in the left OcG (black circle) correlated with subsequent performance gains (see Materials and ,ethods). (d) Functional connectivity map with SMA as seed region during training with incongruent feedback (q(FDR) < 0.05). The degree of coupling between SMA and a patch of voxels in the right OcG (black circle) correlated with subsequent performance gains (see Materials and methods).

beginning or end of practice.

Neuroimaging: functional connectivity analysis

To further examine the neural network underlying sensitivity to visual feedback, we performed a functional connectivity analysis. First, we used the activation in SMA during training with congruent feedback as seed (see Materials and methods). This analysis revealed clusters in left primary motor cortex, left pre-motor cortex, bilateral superior parietal lobule, bilateral thalamus, bilateral striatum, left and right visual cortex and right cerebellum. Interestingly, we found that in a patch of voxels located in the left occipital gyrus (left OcG), the strength of connectivity with SMA during training with congruent feedback significantly correlated with subsequent performance gains across subjects (r = 0.64; p = .003; Spearman correlation). Other regions did not yield significant correlation (See Fig. 5c).

Finally, we performed a similar analysis using the same SMA voxels as seed region but this time using their activation during training with incongruent feedback. The functional connectivity map revealed similar regions to the ones obtained during training with congruent feedback (79% overlap). We found that in a patch of voxels located in the right occipital gyrus (right OcG), the strength of connectivity with SMA during training with incongruent feedback exhibited a significant negative correlation with subsequent performance gains across subjects (r = −0.66; p = .002; Spearman correlation). In other words, stronger

functional connectivity between SMA and right OcG during training with incongruent visual feedback implied smaller subsequent behavioral right-hand performance gains (i.e. stronger interference). Other regions did not yield significant correlation (See Fig. 5d). Taken together, this shows that subjects exhibiting stronger functional connectivity (crosstalk) between SMA and visual regions contralateral to the observed moving hand are also more susceptible at the behavioral level to the influence of visual feedback.

Discussion

The human eye provides rich and important feedback during the acquisition of a new motor skill (Salmoni et al., 1984; Sigrist et al., 2013). Previous studies have noted that visual feedback can facilitate or interfere with motor learning (Shea and Wulf, 1999). The present study was designed to determine how different types of visual feedback during physical training modulate short-term learning. Examining performance gains in the trained hand revealed enhanced learning following training with congruent visual feedback and attenuated learning following training with incongruent visual feedback (relative to training with no visual feedback). Interestingly we found that across subjects these two effects correlated, suggesting that some individuals are behaviorally more sensitive than others to visual feedback and its congruency level.

Our results are in agreement with previous studies showing that congruency of visual input affects performance of executed actions at the

group level (Sturmer et al., 2000; Kilner et al., 2003). Previous studies did show that individual experts are more sensitive to visual information than novices (Williams and Ward, 2003; Dicks et al., 2010; Steinberg et al., 2016). However, most behavioral studies examining the role of congruency of visual feedback in motor learning did not focus on the variation in individual subjects.

At the neural level, we examined regions in which the representation of observed and executed actions overlapped. We found that the bilateral SMA and left SPL were active both during training by observation and training by physical practice without visual input. These findings are consistent with data obtained in previous neuroimaging research which reveal that action observation evokes activation within various regions traditionally associated with motor function (Grezes and Decety, 2001; Garry et al., 2005; Gazzola et al., 2006). It was further shown that these regions are engaged in learning by observation/imitation (Iacoboni et al., 1999; Ossmy and Mukamel, 2016b).

Motor regions such as the inferior frontal gyrus (IFG) and right SPL have been also shown to be sensitive to visual input (Buccino et al., 2001; Jeannerod, 2001). Indeed we found these regions to respond during our observation condition (Fig. 3b). However, these regions did not survive our observation/execution conjunction analysis for ROI analysis. This might be explained by our experimental design in which no visual feedback was provided during the execution condition (RH-None). This is opposed to traditional studies of the human mirror system that either use an observation condition (Cross et al., 2008) or use an execution condition that is accompanied by visual input (such as during imitation) (Iacoboni et al., 1999; Rizzolatti et al., 2001; Higuchi et al., 2012; Molenberghs et al., 2012).

At the group level, both SMA and left SPL were active during congruent/incongruent training but activation level did not differentiate the two training types. Activation maps of the two training types overlapped and direct comparison between them yielded an empty map. Nonetheless, examining the data at individual subject level reveals a different picture. Activation patterns in the SMA differentiate the type of training in a subset of subjects in which visual input induced strong behavioral modulations. This result emphasizes the importance of looking beyond group results.

In the context of learning, visual input has been shown to induce plastic changes at the neural level. McGregor and Gribble, report changes in resting state functional connectivity between primary motor and somatosensory cortex following learning by observation of movements in a force field (McGregor and Gribble, 2017). Across subjects, these changes correlate with individual differences in learning. In another study, Mayhew and colleagues report that during physical training, performance levels on a grip force task correspond with fMRI signal in bilateral thalamus, posterior parietal cortex, and dorsal pre-motor cortex only when visual feedback is provided (Mayhew et al., 2017). We extend these previous findings by showing that the degree of coupling between SMA and visual regions is higher in subjects with strong behavioral modulations that depend on the congruency of visual feedback during physical training. Importantly, visual-only ROIs did not yield a similar dependency, thus the individual differences are unlikely to be due to differences in mere perception. Interestingly in the current data-set, activity level in SMA during mere observation did not correspond with individual differences in performance level (Ossmy and Mukamel, 2016a). Only in conditions where visual input was coupled to executed actions (as described here) did such correlations emerge, suggesting a different role for vision when it is coupled with motor output. This is in agreement with our recent behavioral finding in which we report differences in sensitivity to visual input of hand size depending on whether or not the visual signal is coupled to motor output (Ossmy and Mukamel, 2017). Thus the addition of visual input during training seems to induce selective changes in coupling within visuo-motor networks which deserve further study.

It is an open question whether our results are limited to simple motor tasks or short-term training. With respect to the number of sequence repetitions, our study is compatible with equivalent short-term studies reported in the literature (Mattar and Gribble, 2005; Gabitov et al., 2015). However, further research should be undertaken to investigate sensitivity to congruency of visual feedback across multiple training sessions spanning longer time periods (e.g. days or weeks).

In summary, by examining the effects of manipulation of visual feedback on motor learning, we show that some individuals are more susceptible than others to visual input during short-term motor learning. Furthermore, we show that such behavioral variability might be explained by differential coupling between SMA and visual areas across individuals during the training process. Such activation patterns allow predicting subsequent modulations in performance gains. These findings have implications to the ongoing endeavor of optimizing motor training.

Conflicts of interest

The authors declare that no competing interests exist.

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