

Nonvisual motor learning influences abstract action observation

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Nonvisual Motor Learning Influences Abstract Action Observation

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Summary

Neuroimaging studies have recently provided support for the existence of a human equivalent of the “mirror-neuron” system as first described in monkeys [1], involved in both the execution of movements as well as the observation and imitation of actions performed by others (e.g., [2–6]). A widely held conception concerning this system is that the understanding of observed actions is mediated by a covert simulation process [7]. In the present fMRI experiment, this simulation process was probed by asking subjects to discriminate between visually presented trajectories that either did or did not match previously performed but unseen continuous movement sequences. A specific network of learning-related premotor and parietal areas was found to be reactivated when participants were confronted with their movements’ visual counterpart. Moreover, the strength of these reactivations was dependent on the observers’ experience with executing the corresponding movement sequence. These findings provide further support for the emerging view that embodied simulations during action observation engage widespread activations in cortical motor regions beyond the classically defined mirror-neuron system. Furthermore, the obtained results extend previous work by showing experience-dependent perceptual modulations at the neural systems level based on nonvisual motor learning.

Results

In the current event-related functional magnetic resonance imaging (fMRI) experiment, subjects were confronted with motion stimuli that constituted visual representations of the resulting paths of previously trained yet unseen movement sequences. The presented study had two main goals. First, we wanted to investigate whether the actions implied by the observed dynamically drawn paths would be “matched” to the neural representation of the corresponding (yet unseen) actions executed earlier. Second, we wanted to assess the relation between the amount of physical practice that had been invested to learn each of the movement sequences and the activation levels of the involved brain

regions during their observation. Such an experience-dependent modulation would suggest that the observer’s own motor repertoire influences the way in which (the perceptual consequences of) observed actions are perceived. The displayed motion paths were based on movement sequences that the subjects had previously learned by continuously tracing a set of predefined two-dimensional maze trajectories (Figure 1A; [8–10]). In the first scanning session, two maze trajectories were introduced. Afterwards, one of them was extensively trained over 3 days in order to allow a comparison between both trajectories in terms of invested training during a second scanning session 4 days later. Importantly, the required tracing movements were performed with closed eyes and without having seen the trajectories beforehand. Consequently, subjects could rely only on somatosensory cues and proprioceptive feedback while learning the movement sequences, by tracing through a groove to which their pen movements were restricted. Subjects were subsequently asked to discriminate between the traced trajectories and similar nonencountered trajectories in a visually presented matching task (Figures 1B and 1C). By including both the actual execution and the observation of the same actions, the applied design allowed us to assess the specificity of the recorded neural responses. Additionally, any effects of visual familiarity on observation-related activations could be ruled out because the paradigm involved only nonvisual motor-learning conditions.

Motor Learning

A set of regions of interest (ROIs) was functionally defined based on the maze-tracing data from the first scanning session, by contrasting motor learning conditions (in which novel maze trajectories were traced) with appropriate control conditions (in which a familiar square-shaped trajectory was traced either fast or slowly and no additional learning occurred). The identified ROIs included the bilateral dorsal (PMd) and ventral (PMv) premotor cortex, the inferior postcentral sulcus (InfPCS), the anterior intraparietal sulcus (aIPS), the posterior superior parietal lobule (SPL), and a region in the left medial IPS/posterior SPL (see Figure 2A). Note that these ROIs did not differentiate between the fast and slow square-tracing conditions when contrasting these control conditions directly, implying that the observed activations truly reflected learning (i.e., instead of the accompanying increase in tracing velocity). This was furthermore corroborated by the finding that the specified ROIs changed their activation levels as learning progressed, showing learning-related decreases both within and across sessions.

Visual Matching

For the visual matching task, a conjunction of the different trial types separately contrasted with the intertrial baseline revealed activations in a widely distributed

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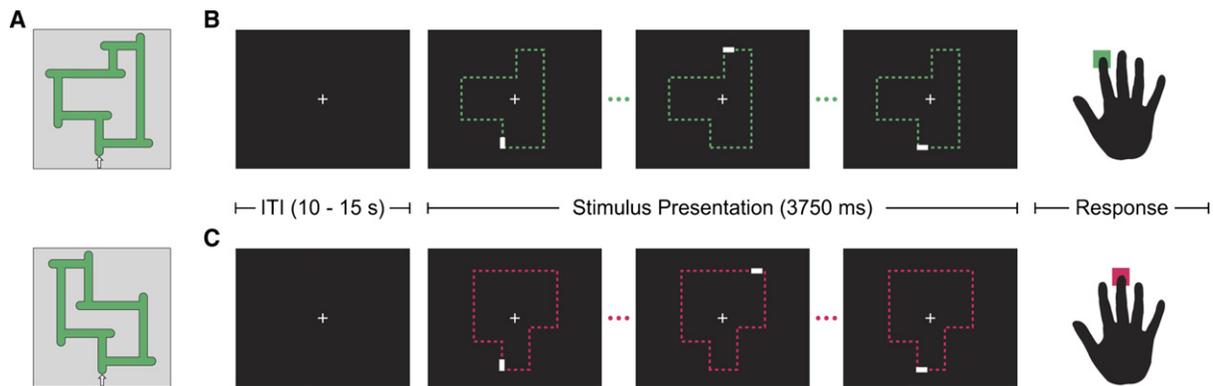


Figure 1. Traced Trajectories and Visual Matching Design

(A) One of the movement sequences represented by the mazes shown here was extensively trained over the course of several days in between two scanning sessions. The white arrows at the bottom indicate the starting points, and in both cases the total trajectory was 260 mm long. Note that the correct movement sequences needed to be learned by trial and error, in the absence of any visual feedback.

(B) An example of a trial as presented during the visual matching task, in which a matching trajectory was displayed. After a variable intertrial interval (ITI), a small white rectangle started to move along an invisible path (depicted by the green dashed line). Subjects were instructed to covertly follow the movements of the rectangle (while fixating the fixation cross) and compare its trajectory with the movement sequences they had previously performed themselves. Once the rectangle arrived at its starting point again, subjects should indicate whether the observed trajectory matched with one of the performed movement sequences or not (via a forced-choice button press).

(C) A similar example, but now showing a nonmatching trajectory and the response that should be given correspondingly.

network of areas, which was highly replicable across sessions (Figure S2 in the Supplemental Data available online). Interestingly, performing the visual matching task reactivated the brain areas specifically implicated in learning the novel motor routines, even though subjects did not execute any overt movement sequences at that point. To rule out that the observed reactivations were simply related to the production of the required button presses, the data from the “button press control” task (BPC; see Experimental Procedures) were contrasted with the responses obtained during the matching task. The resulting activation map is depicted in

Figure 2B and still clearly includes all learning-related areas (marked by white contours). The role of the learning-related areas in matching was also confirmed by additional random effects analyses at the ROI level, indicating that the responses during the matching task exceeded the responses in the BPC task in all considered ROIs (as exemplified in Figure 3).

Separate random effects ROI GLMs on the data from the second scanning session revealed that a large majority of the learning-related areas differentiated between matching and nonmatching trajectories, by responding more strongly to the displayed trajectories

Table 1. Results from the Random-Effects ROI Analyses Related to the Visual Matching Task Data from Session Two

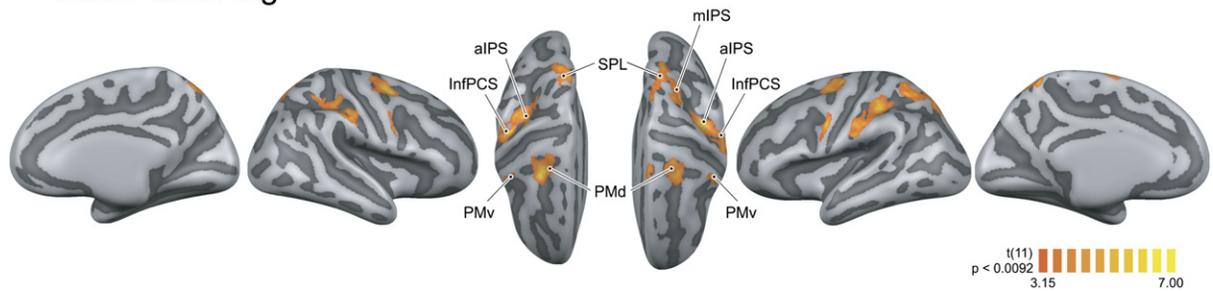
Region of Interest	Hemisphere	Talairach Coordinates [mm]			Significance of Differential Responses ^a									
					OVER/OLD/NONM > BPC		OVER/OLD > NONM		OVER > NONM		OVER > OLD		OLD > NONM	
		x	y	z	t	(p)	t	(p)	t	(p)	t	(p)	t	(p)
PMd	LH	-21	-9	52	6.92	(0.000)**	3.33	(0.003)**	2.84	(0.008)*	0.72	(0.242)	2.57	(0.013)*
	RH	25	-8	48	6.94	(0.000)**	2.04	(0.033)*	2.35	(0.019)*	1.60	(0.069)	0.94	(0.185)
PMv	LH	-52	-1	34	6.30	(0.000)**	2.19	(0.026)*	2.98	(0.006)*	1.62	(0.067)	0.44	(0.335)
	RH	52	2	34	6.31	(0.000)**	1.53	(0.078)	1.70	(0.058)	0.76	(0.233)	0.22	(0.415)
InfPCS	LH	-54	-21	32	5.15	(0.000)**	3.13	(0.005)*	3.86	(0.001)**	1.91	(0.041)*	0.84	(0.209)
	RH	49	-24	37	6.88	(0.000)**	3.93	(0.001)**	4.91	(0.000)**	1.17	(0.134)	1.54	(0.076)
alPS	LH	-39	-33	42	6.57	(0.000)**	2.71	(0.010)*	3.44	(0.003)**	1.61	(0.068)	1.02	(0.165)
	RH	36	-35	39	8.74	(0.000)**	3.55	(0.002)**	2.55	(0.014)*	0.09	(0.467)	2.26	(0.023)*
mlPS	LH	-26	-53	51	8.03	(0.000)**	5.53	(0.000)**	4.97	(0.000)**	1.06	(0.156)	1.75	(0.054)
	RH	-	-	-	-	-	-	-	-	-	-	-	-	
SPL	LH	-17	-66	52	5.37	(0.000)**	3.79	(0.002)**	4.10	(0.001)**	0.83	(0.213)	1.78	(0.051)
	RH	13	-59	53	6.92	(0.000)**	2.56	(0.013)*	2.90	(0.007)*	1.00	(0.170)	1.09	(0.149)

The table lists the relevant contrasts related to the visual matching task for all included ROIs. Note that all ROIs were functionally defined in the first scanning session based on their involvement in learning to perform the novel movement sequences. The results indicate that: (1) all ROIs showed enhanced responses during the matching task as compared to the button press control task; (2) a consistently stronger response when observing the overlearned sequence (compared to nonmatching trajectories) was found across all ROIs (except right PMv). Even though the OVER > OLD contrast was only on the verge of significance in a subset of the studied ROIs, a clear activation pattern became evident in which the response to the OLD sequence reached an intermediate position between the OVER and NONM responses, as depicted in Figure 4. Note that the listed p values are based on one-tailed t tests. Abbreviations as in Figures 2 and 3.

^aShown are t values and probabilities based on random effects ROI-GLM contrasts (n = 12).

*p < 0.05 (uncorrected); **p < 0.0045 (Bonferroni-corrected for the number of included ROIs).

A Motor Learning



B Visual Matching versus BPC

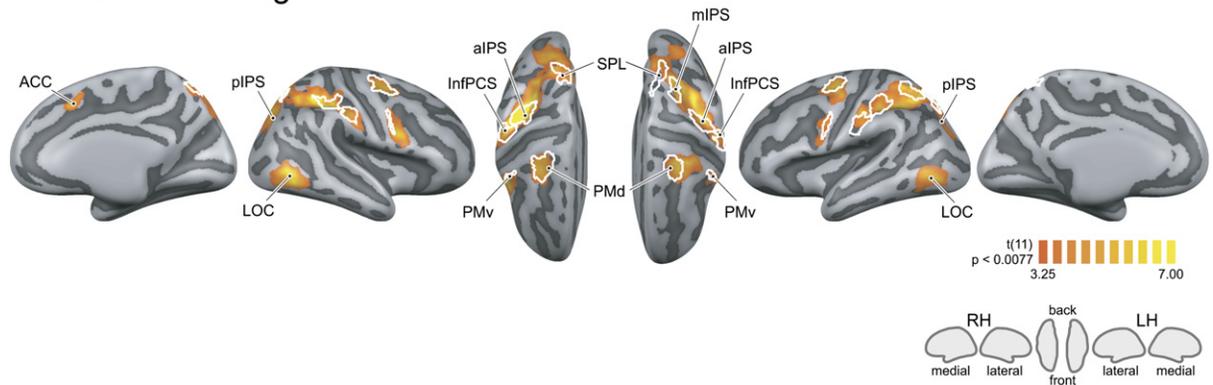


Figure 2. Group Activation Maps Showing Regions Implicated in Motor Learning and Their Reactivation during Visual Matching

(A) The network of learning-related areas as identified during the maze-tracing task in scanning session one, projected on the inflated version of the average group cortex mesh (random effects; $t(11) = 3.15$; $p(\text{uncorr}) < 0.0092$). The implicated areas showed stronger responses when subjects learned to execute the novel movement sequences, compared to the control conditions in which a known square was traced either fast or slowly.

(B) The displayed map shows the regions that were significantly more active during the visual matching task compared to the button press control (BPC) task. Importantly, all learning-related ROIs (depicted by white contours) that were defined during the physical execution of the corresponding movement sequences were reactivated again. Note that the currently described analyses focused on the data from session two, because of the relatively large fraction of incorrectly classified trajectories in session one (see Figure S1). Abbreviations: PMd, dorsal premotor cortex; PMv, ventral premotor cortex; InfPCS, inferior postcentral sulcus; aIPS, anterior intraparietal sulcus; mIPS, medial intraparietal sulcus; SPL, superior parietal lobule; ACC, anterior cingulate cortex; pIPS, posterior intraparietal sulcus; LOC, lateral occipital complex; RH, right hemisphere; LH, left hemisphere.

matching the actively learned and repeatedly performed sequences (Table 1 and Figures 3A and 3B).

Moreover, as additional analyses in which the overlearned (OVER) and less extensively trained (OLD) sequences were separately contrasted with the non-matching stimuli established, this effect was mainly caused by a stronger response to the overlearned sequence (Table 1; third contrast). Except for the right PMv, all areas implicated in learning tended to respond more vigorously whenever a trajectory was presented that matched the extensively trained sequence (Figure 4). Because the sequence that was overlearned was counterbalanced across subjects, these enhanced responses cannot be related to a specific set of sequential movements per se, but really reflect the overlearned status of the corresponding movement pattern. Finally, the observation that differential response patterns for matching and nonmatching trajectories were restricted to the learning-related motor areas and were not found within a wider set of regions (e.g., the lateral occipital complex [LOC], see Figure 3D) suggests that this divergence is not related to a general “deallocation” of attention in the case of the nonmatching stimuli.

Discussion

In the current study, subjects were confronted with the visual counterpart of previously performed but unseen movement sequences. The dynamic nature of the presented visual stimuli and the feature that previous positions along the path were not highlighted (i.e., no trace was visible), probably reinforced the use of the already stored motor representations to accomplish the outlined task. Interestingly, the areas that were specifically involved in learning to execute the trained sequences were recruited again while performing the visual matching task, as part of a more extended network including areas previously shown to be implicated in, for example, the multimodal processing of object shapes (LOC; [11]) and covert spatial attention (e.g., pIPS; [12]). In part, the observed reactivations comprised regions that have been typically associated with mirror-system functions, such as the PMv [13, 14] and the InfPCS, which, based on [15], might at the cytoarchitectonic level be considered part of the anterior inferior parietal lobule [16]. On the other hand, several other regions (PMd, aIPS, mIPS, and SPL) were additionally

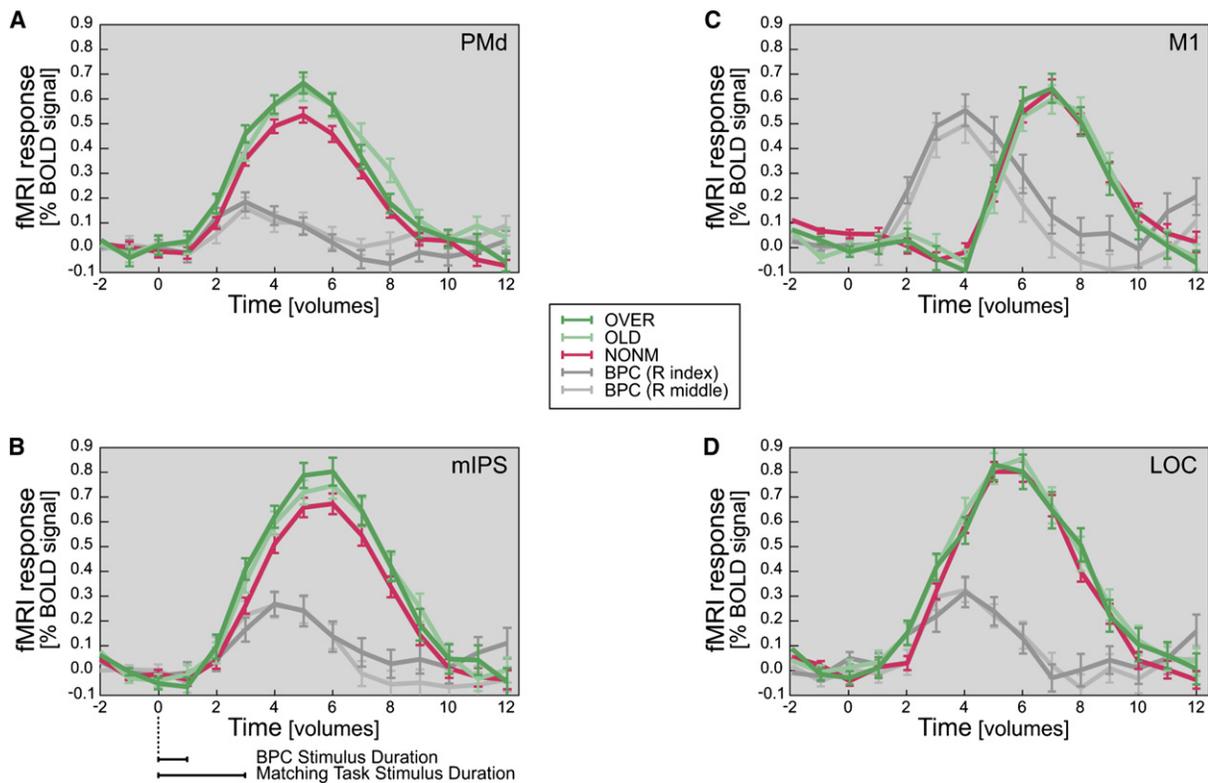


Figure 3. Representative Event-Related Responses during Visual Matching

This figure shows event-related responses averaged across subjects for (A) the left PMd, (B) the left mIPS, (C) the left primary motor cortex (M1), and (D) the left lateral occipital complex (LOC). Error bars represent standard errors of the mean. Note that in (A), (B), and (D), the responses during the matching task by far exceed the activation amplitude associated with the BPC task. In contrast, the responses shown in (C) are similar in both conditions and the shift in onset during the visual matching task clearly indicates their relation to the required button press. Furthermore, only the PMd and mIPS ROIs show an enhanced response during the observation of matching compared to nonmatching trajectories. Finally, the (nondifferential) responses observed in the LOC are depicted to illustrate that the divergent response pattern in the learning-related ROIs is not confounded by differences in the general amount of attention deployed to matching and nonmatching trajectories. Abbreviations: OVER, over-learned sequence; OLD, previously encountered but not extensively trained sequence; NONM, nonmatching trajectory; BPC, button press control task; R, right hand.

involved in the matching task, supporting the emerging view that a more widespread network of regions is implicated during action observation (see also [17–19]). These findings were highly replicable both across subjects and across sessions. Moreover, it was shown that the potential confounding effect of having to respond via button presses (which by itself might explain the involvement of motor-related areas) could not account for the observed reactivations. Rather, the involvement of the learning-related motor areas suggests that observing a novel visual representation of the previously performed movements goes beyond passive sensory processing and involves an active simulation of the corresponding motor act.

This interpretation is in accordance with the general notion that nonvisual motor training can enhance visual perception capabilities (e.g., [20]) and previous neurophysiological data showing that neurons in the monkey PMd discharge both when actually performing a reaching task and while only observing the visual events associated with the task when performed by another unseen party [21]. Additionally, these PMd neurons started to discharge even before any visual motion could be detected once enough information was provided regarding which event could be expected next. This

preparatory activity highlights that the responses recorded during the observation condition were not purely “reactive” but part of an active simulation process. Similarly, such proactive responses have been reported in humans via eye-movement recordings [22] and electroencephalogram measurements [23]. Another interesting aspect of the reported study is related to the nature of the used stimuli. Although there is still an ongoing debate concerning the question of whether the human mirror system is “biologically tuned” in the sense that it preferentially responds to natural movements performed by other human beings (e.g., [19, 24–26]), the present results suggest that even rather abstract visual stimuli conveying minimal information concerning the underlying movement can trigger the corresponding motor representations.

The obtained results additionally are in line with the hypothesis that the extent to which a given stimulus succeeds in activating the mirror system depends on the existing motor repertoire of the observer (e.g., see [27]). Two interesting fMRI studies involving professional dancers recently showed that an observer’s proficiency at performing certain movements influences the neural responses elicited by the sight of the same movements being performed by somebody else [28,

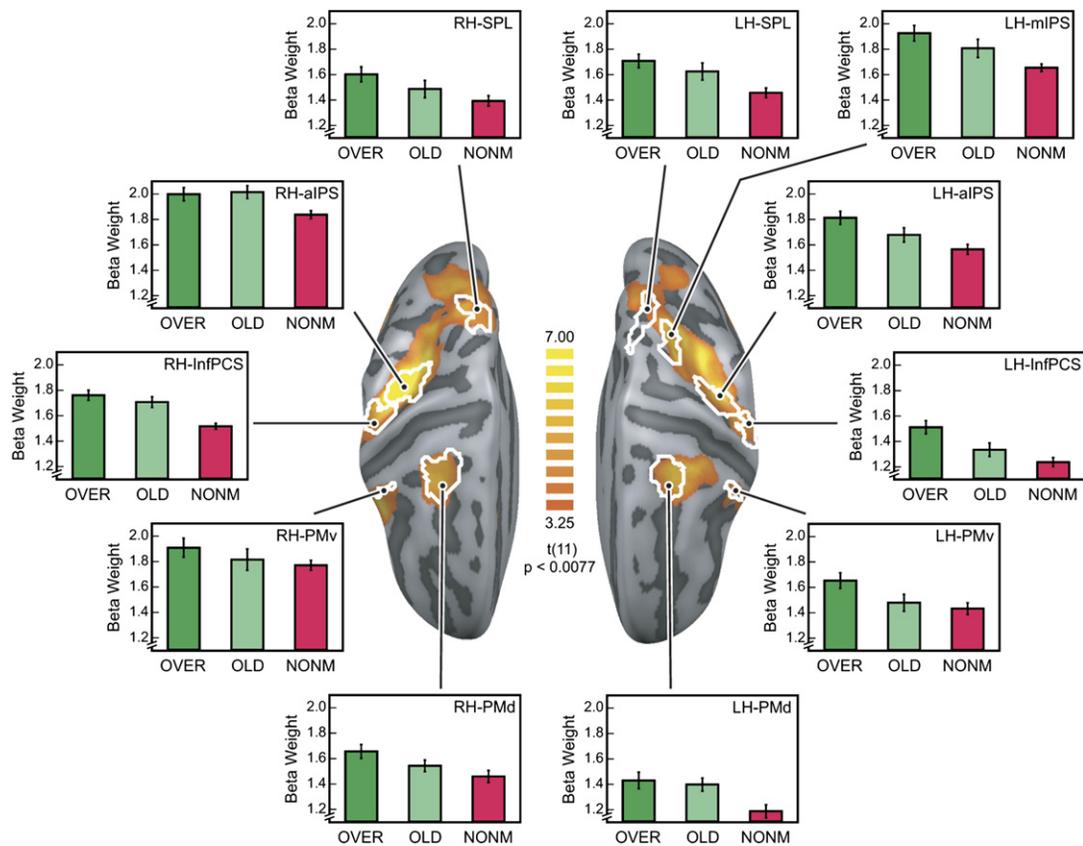


Figure 4. Overview of the Responses to the Different Visual Matching Conditions for All Identified ROIs

This figure gives an overview of the activation levels across the different visual matching conditions for all functionally defined ROIs, based on the estimated beta weights. Note that in nearly all ROIs, a similar pattern emerges in which a path matching the overlearned sequence gives rise to the strongest response, whereas a nonmatching trajectory produces the weakest activations. Error bars indicate the standard error of the mean after a normalization procedure in which the grand mean across subjects and conditions was first subtracted from each subject's own mean beta across conditions, and subsequently this resulting value was subtracted from the subject-specific beta's per condition. Abbreviations as in Figures 2 and 3.

29]. There are several commonalities between these imaging experiments and the study presented here. First, as pointed out in [29], earlier studies on action simulation required subjects to imagine a given action without any external guidance. Instead, the provided visual stimuli in the studies discussed here were intended to guide and constrain the ongoing simulation, leading to a more homogeneous sampling of the process of interest. Additionally, the simulation was behaviorally controlled in the present study by including a forced-choice matching task that enabled the evaluation of the subjects' simulation performance post hoc. Second, all three studies lend further support to the notion that the observation-guided simulation of motor sequences relies on some of the same areas that are also active during the overt execution of the corresponding movements. However, in contrast to both dance observation studies, this equivalence was explicitly established in the present study by including appropriate motor learning conditions. Third, and in line with other imaging results (e.g., [18, 19]), all three studies suggest that simulating perceived actions involves areas for which the assessment of mirror responses at the single-cell level is still lacking to date. Finally, the listed findings are in agreement with the hypothesis that the neural activity

that is related to the simulation of an observed action is modulated by the experience of the observer, in the sense that formerly trained (i.e., embodied) action sequences lead to stronger activations. The current study extends previous findings regarding this latter issue in two ways. First, the level of expertise of the subjects in the current study was objectively assessed and quantified by monitoring their performance during the actual production of the movement sequences. Moreover, it could be shown that the very same regions were recruited in both the early and late stages of learning, ensuring that the equivalence between the networks observed during motor execution and visual matching was preserved throughout the learning process. The second point is related to the visual familiarity of the presented stimuli. Complementary to the findings from an elegant follow-up study by Calvo-Merino et al. [30], the current results show that visual familiarity cannot constitute a confounding factor when interpreting the observed experience-dependent modulations, given that the displayed stimuli corresponded to previously unseen movements.

In sum, the presented results indicate that when perception guides the internal simulation of previously executed (yet unseen) movement sequences, a distributed

network of areas specifically involved in learning to overtly execute these movements will be recruited again. Furthermore, the degree to which these learning-related regions are reactivated is dependent on how well the observed information matches the observer's direct experience in performing the corresponding movement. Since the used matching task necessitates the continuous online simulation of an acquired movement sequence, the processes it taps into might be more tightly coupled to the matching of sensory events to stored motor representations than the more end-goal-driven coding as observed in the classically defined mirror-neuron system in monkeys.

Experimental Procedures

Participants

12 healthy volunteers with normal visual acuity (6 males; mean age = 25 years, standard deviation = 1.4 years) participated in the current study. All subjects gave written informed consent according to procedures approved by the local research ethics committee. Right-handedness was used as an inclusion criterion and was assessed via the Edinburgh Handedness Inventory [31] (mean score = 94, standard deviation = 9).

Experimental Paradigm

All subjects participated in two separate scanning sessions, both consisting of two main parts: a motor learning task, in which different movement sequences were learned and repeatedly executed with closed eyes (see [Supplemental Data](#) for details), and a subsequent visual matching task, in which subjects were asked to discriminate between the actually traced trajectories and other nonmatching trajectories based on a visually presented representation of the corresponding movements. In both scanning sessions, the visual matching task immediately followed the motor learning task within the same functional run. Throughout the matching task, a fixation cross was shown in the middle of the display. In each trial, a small white rectangle appeared and started to continuously move along an invisible trajectory until ending up at its starting position again. There were two types of trajectories: the path that the white rectangle followed either coincided with one of the movement sequences previously executed by the subject ([Figure 1B](#)) or represented one of four different sequences that were not encountered before ([Figure 1C](#)). Subjects were instructed to pay attention to the entire trajectory that the white rectangle traversed, without moving their eyes away from the fixation cross. Their task was to decide whether the presented trajectory constituted a match or a nonmatch with one of the previously performed movement sequences. In order not to contaminate the neural responses to the visually presented trajectory with the activations related to the button presses, subjects were furthermore instructed to wait until the white rectangle again reached its starting position before responding.

Finally, an additional button press control (BPC) task including visually cued button presses was performed in the second scanning session to rule out that potential activations in areas related to motor learning might be present because of the use of button presses as behavioral responses (see [Supplemental Data](#)).

Data Acquisition and Analysis

The (f)MRI data were acquired on a 3T Siemens Magnetom Allegra head-scanner (Siemens Medical Systems, Erlangen, Germany) and analyzed with BrainVoyager QX (v1.7; Brain Innovation, Maastricht, The Netherlands). See [Supplemental Data](#) for details on scan parameters, preprocessing, the applied cortex-based alignment procedures, and subsequent random-effects statistical analyses.

Supplemental Data

Two figures, Results, Discussion, and Experimental Procedures are available at <http://www.current-biology.com/cgi/content/full/17/14/1201/DC1/>.

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