Selective responses in right inferior frontal and supramarginal gyri differentiate between observed movements of oneself vs. another

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ABSTRACT

The fact that inferior frontal (IFg) and supramarginal (SMg) gyri respond to both self-generated and observed actions has been interpreted as evidence for a perception-action linking mechanism (mirroring). Yet, the brain readily distinguishes between percepts generated by one's own movements vs. those of another. Do IFg and/or SMg respond *differentially* to these visual stimuli even when carefully matched? We used BOLD fMRI to address this question as participants made repetitive bimanual hand movements while viewing either live visual feedback or perceptually similar, pre-recorded video of an actor. As expected, bilateral IFg and SMg increased activity during both conditions. However, right SMg and IFg responded differentially during live visual feedback vs. matched recordings. These mirror system areas may distinguish self-generated percepts by detecting subtle spatio-temporal differences between predicted and actual sensory feedback and/or visual and somatosensory signals.

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1. Introduction

In monkeys, 'mirror neurons' in the inferior frontal gyrus (IFg) and inferior parietal lobule (IPL) respond both when the monkey executes an action and when it observes that same action made by an experimenter (di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996). This discovery provides a potential mechanism to match one's own actions with the actions of others, a link between perception and action via a shared parieto-frontal representation. In these studies, monkeys view their own movements (seen from the 1st-person perspective) or those of an actor (seen from the 3rd-person perspective).

Functional neuroimaging data indicates that the IFg and the supramarginal gyrus (SMg) of the IPL in the human brain also respond to the observation of others' actions (Grèzes & Decety, 2001; Rizzolatti & Craighero, 2004). Whether these same regions are also involved during the execution of equivalent actions is still controversial. With repetition suppression techniques, adaptation across execution and observation has been found in right

IPL (Chong, Cunnington, Williams, Kanwisher, & Mattingley, 2008), and in IFg (Kilner, Neal, Weiskopf, Friston, & Frith, 2009), providing support for a mirror neuron system in humans. However, see Dinstein, Hasson, Rubin, and Heeger (2007) and Lingnau, Gesierich, and Caramazza (2009) for counterevidence using the same technique. Similar debates involving the existence of a human mirror system arise when multivoxel pattern analysis is used (Dinstein, Gardner, Jazayeri, & Heeger, 2008; Oosterhof, Wiggett, Diedrichsen, Tipper, & Downing, 2010). Furthermore, with few exceptions (Frey & Gerry, 2006; Jackson, Meltzoff, & Decety, 2006; Shmuelof & Zohary, 2008), investigations of this 'mirror system' have tended not to manipulate viewing perspective. Instead, stimuli used in the vast majority of studies on action observation have consisted primarily of others' actions as seen from a 3rd-person perspective. The effects of perspective change on IFg and SMg, or lack thereof, may provide valuable insights into what is being represented in this system.

On the basis of the mirror system account, one might expect that the IFg and SMg would respond equivalently to visual percepts attributable to our own movements vs. those of another actor. However, it is obvious that the brain is also able to distinguish between percepts arising from these two fundamentally different sources. Is this essential yet overlooked ability attributable to selective responses in IFg and/or SMg, or a separate mechanism? Here we perform the critical test of this hypothesis, by measuring the brain's responses to observation of actions generated by oneself vs. another as seen from both the 1st- and 3rd-person perspectives.

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During the acquisition of whole-brain fMRI data, healthy adults performed aurally paced, bilateral thumb-finger sequences while viewing either live visual feedback (*Self* condition) or carefully matched pre-recorded video of an actor performing the same task (*Other* condition). We reasoned that if the IFg and SMg are sensitive to subtle perceptual differences between these conditions, then they should exhibit selective responses. Evidence for a right cerebral hemisphere asymmetry in self recognition (Uddin, Iacoboni, Lange, & Keenan, 2007), suggests that these conditional differences might be lateralized. We also varied perspective (*1st-* or *3rd-person*) in both *Self* and *Other* conditions in an effort to determine the effects of this variable on these responses.

2. Materials and methods

2.1. Subjects

Participants included fourteen healthy, right-handed volunteers (18–36 years, 7 females) with normal or corrected-to-normal vision and no history of psychiatric or neurological disease. Written informed consent was obtained.

2.2. fMRI design and procedure

Prior to the experiment, participants were given instructions and performed a short practice set of trials in a mock MRI scanner. Participants rested supine with their heads in the scanner, a cloth draped over their bodies, forearms on thighs and palms aligned in the vertical plane with thumbs facing up. Head and upper arms were padded to reduce motion artifacts. Other than performing the instructed hand movements, participants remained as still as possible.

Participants performed a sequential bimanual thumb-finger sequencing task (TFST) in synchrony with a 1.5 Hz pacing tone under two conditions, *Self* and *Other*. These were distinguished by aural presentation of the word "execute" or "imitate" 2 s prior to each block. Blocks of each condition lasted 18 s and were followed by a 12 s rest interval consisting of a black screen. A central fixation circle was always present. In the *Self condition*, participants viewed their own movements via live video feedback. Images of participants' hands were reflected off an 18 in. × 18 in. mirror above the scanner bed. An MRI-compatible, remotely controlled digital video camera captured this reflection. This video stream was then back-projected onto a screen at the head of the scanner bore and viewed by participants on a 5 in. × 2 in. mirror attached to the head coil. In the *Other condition* participants performed the aurally paced TFST task while viewing a pre-recorded digital video of an actor performing the same task in the scanner. This video was created prior to the experiment using the same setup. Thus, the perspective, FoV, and lighting conditions of the video were matched as closely as possible to the live feedback. Participants were explicitly informed about the difference between *Self* and *Other* and received 15–20 min of practice. To avoid possible confusion between conditions, participants wore green gloves and the actor in the video wore purple gloves. The orientation of the visual stimuli was also manipulated. For both conditions, 50% of the counterbalanced blocks presented visual stimuli (live or pre-recorded) from the perspective of the participant (*1st-person perspective*), and the remaining 50% were rotated by 180° (*3rd-person perspective*) (Fig. 1A).

Several steps were taken to ensure spatial and temporal correspondence between participants' movements and those of the actor. First, participants practiced beforehand, while the experimenter watched to make sure that they understood the instructions and were performing the tasks correctly. Second, participants' hand postures were matched with those of the actor depicted in the recorded video. Just before the experiment, participants were shown a semi-transparent digital still frame (1st-person perspective) of the recorded video overlaid on a live video feed of their hands (Fig. 1B). They were instructed to align their hands with those of the actor and remain in this position throughout the study. Third, to facilitate synchronization, participants were instructed to initiate TFST movements beginning with the index finger after two preparatory tones and then performed them along with the actor in sync with the auditory pacing tone. Hand movements were recorded with digital video for offline verification of compliance.

Participants completed four (8.6 min) runs. Each run consisted of 2 blocks of each of the four conditions (2 types (*Self, Other*) × 2 perspectives (*1st-person, 3rd-person*)). Two other types of blocks (*Observe, Imagine*) will not be discussed here. Condition order was counterbalanced across runs. Runs were counterbalanced across participants.

To control for possible variations in attention across conditions, participants performed a secondary task that required counting features of the observed movements (Fig. 2). The central fixation circle's color changed periodically (range 18–30 times per run) from red to blue coincident with the pinkie finger contacting the thumb. Participants reported cumulative values at the end of each run. The change occurred with equal likelihood during each condition. Participants performed this somewhat difficult task with a mean of 88% correct indicating that they were attending to the movement in all conditions (Fig. S1).

2.3. Data acquisition

Scans were performed on a Siemens (Erlangen, Germany) 3T Allegra MRI scanner. BOLD echoplanar images (EPIs) were collected using a T2*-weighted gradient echo sequence, a standard birdcage radio-frequency coil, and these parameters: TR = 2000 ms, TE = 30 ms, flip angle = 90°, 64 × 64 voxel matrix, FoV = 220 mm, 34 contiguous axial slices acquired in interleaved order, thickness = 4.0 mm, in-plane resolution: 3.4 mm × 3.4 mm, bandwidth = 2790 Hz/pixel. The initial four scans in each run were discarded to allow the MR signal to approach a steady state. High-resolution T1-weighted structural images were also acquired, using the 3D MP-RAGE pulse sequence: TR = 2500 ms, TE = 4.38 ms, TI = 1100 ms, flip angle = 8.0°, 256 × 256 voxel matrix, FoV = 256 mm, 176 contiguous axial slices, thickness = 1.0 mm, in-plane resolution: 1 mm × 1 mm. DICOM image files were converted to NIFTI format using MRIConvert software (http://lcni.uoregon.edu/~jolinda/MRIConvert/).

Structural and functional fMRI data were preprocessed and analyzed using fMRIB's Software Library [FSL v.4.1.2 (http://www.fmrib.ox.ac.uk/fsl/)] (Smith et al., 2004) and involved several steps: motion corrected using MCFLIRT, independent components analysis conducted with MELODIC to identify and remove any remaining obvious motion artifacts, fieldmap-based EPI unwarping performed to correct for distortions due to magnetic field inhomogeneities using PRELUDE+FUGUE with a separate fieldmap (collected following each run) for each run, non-brain matter removed using BET, data spatially smoothed using a 5 mm full-width at half-maximum Gaussian kernel, mean-based intensity normalization applied, in which each volume in the data set is scaled by the same factor, to allow for cross-sessions and cross-subjects statistics to be valid, high-pass temporal filtering with a 100 s cut-off was used to remove low-frequency artifacts, time-series statistical analysis was carried out in FEAT v.5.98 using FILM with local auto-correlation correction, delays and undershoots in the hemodynamic response accounted for by convolving the model with a double-gamma HRF function, registration to the high-resolution structural with 7 degrees of freedom and then to the standard images with 12 degrees of freedom (Montreal Neurological Institute [MNI-152] template) at a 2 × 2 × 2 voxel resolution implemented using FLIRT, and registration from high resolution structural to standard space was further adjusted using FNIRT nonlinear registration (Andersson, Jenkinson, & Smith, 2007).

2.4. Whole brain analysis

For every participant, each of the 4 fMRI runs containing *Other* and *Self* conditions viewed from either a *1st-* or *3rd-person* perspective, were modeled separately at the first level. Orthogonal contrasts (one-tailed *t*-tests) were used to test for differences between each of the experimental conditions and resting baseline. Orthogonal contrasts were also used to test for differences between conditions. Because the only differences for contrasts of the *1st-* vs. *3rd-person perspectives* were in visual areas, we collapsed across perspective.

The resulting first-level contrasts of parameter estimates (COPEs) then served as inputs to higher-level analyses carried out using FLAME Stage 1 to model and estimate random-effects components of mixed-effects variance. *Z* (Gaussianized *T*) statistic images were thresholded using a cluster-based threshold of $Z > 3.1$ and a whole-brain corrected cluster significance threshold of $p = 0.05$. First-level COPEs were averaged across the 4 runs for each subject separately (level 2), and then averaged across participants (level 3).

In order to test for the main effects of PERSPECTIVE and TASK and for the interaction between these two factors, a 2 (PERSPECTIVE: *1st, 3rd*) × 2 (TASK: *Self, Other*) repeated-measures ANOVA (*F*-tests) was performed on second-level COPEs.

Anatomical localization of brain activation was verified by manual comparison with an atlas (Duvernoy, 1991). In addition, the multi-fiducial mapping algorithm in Caret (http://www.nitrc.org/projects/caret/) (Van Essen et al., 2001) was used to overlay group statistical maps onto a population-average, landmark- and surface-based (PALS) atlas for the human brain (Van Essen, 2005).

2.5. Post hoc ROI analysis

We also calculated mean percent signal change relative to the resting baseline across all voxels within the significant clusters of activation in IFg and SMg identified by the contrast of *Self* vs. *Other* in the whole-brain analysis. These values were calculated separately for each participant and condition using FSL's Featquery. Repeated-measures ANOVAS were also conducted to test for differences between conditions in these regions of interest (see Supplemental material).

3. Results

3.1. Self or other

3.1.1. Self vs. rest and Other vs. rest contrasts

Relative to resting baseline, both *Self* (Fig. 3A) and *Other* (Fig. 3B) conditions were associated with increased bilateral activity within fronto-parietal areas (including both IFg and SMg) as well as