

Mirror-image representation of action in the anterior parietal cortex

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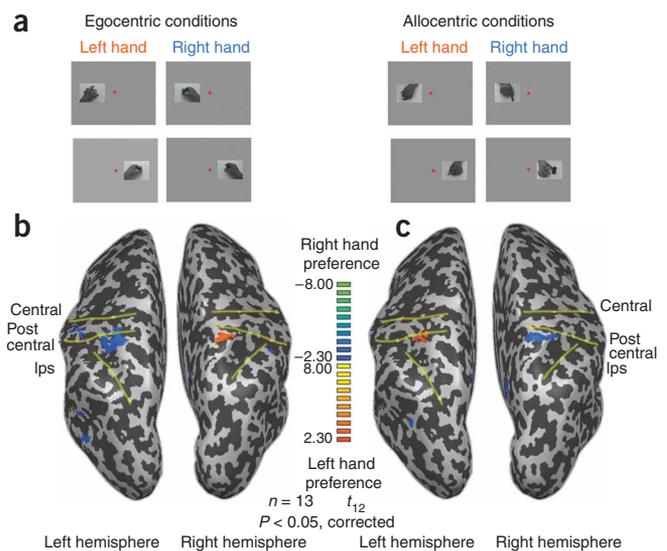
Mimicking hand actions made by someone facing us (that is, allocentric viewpoint) is typically performed with the opposite hand. Using functional magnetic resonance imaging (fMRI), we found a similar mirror-image representation of others' actions in the human anterior parietal cortex. Viewing egocentric-based actions elicited greater fMRI activation in the contralateral hemisphere (as in, self action), whereas observation of action seen from an allocentric viewpoint generated greater activation in the ipsilateral hemisphere. This mirror-like mapping occurs without active imitation, providing further evidence for an automatic action-simulation system in the parietal cortex.

We constantly perceive the outcome of our own actions and learn to refine our movements to better suit our goals. Given the inherent delay

in monitoring of self action, it has been suggested that the CNS uses predictive simulation processes (that is, internal models) to allow online control and correction of movements¹. The direct matching hypothesis suggests that we can also utilize those internal models to understand and predict the actions of others, and to learn new behaviors by means of imitation². This idea is supported by the finding of 'mirror neurons' in the monkey^{3,4}, which discharge when the monkey executes a specific goal-directed action (for example, grasping a peanut) and when the monkey merely observes the experimenter performing the same action. Such neurons are therefore likely to be involved in the simulation of others' actions and may be crucial for the development of imitation in humans⁵.

Although our own actions are naturally seen from an egocentric viewpoint, we observe actions of others from various viewpoints. Notably, we tend to imitate actions of actors that face us (seen from an allocentric viewpoint) in a mirror-like manner^{6,7}. One might posit that a neural 'mirror system', intrinsically involved in imitation, should represent actions seen from an allocentric viewpoint according to the same mapping rule. Recently, we showed that the anterior section of the human superior parietal lobule (aSPL) is selective to the identity of the observed acting hand, showing greater functional magnetic resonance imaging (fMRI) activation during viewed actions made by the contralateral hand than the ipsilateral hand when seen from an egocentric

Figure 1 aSPL shows opposite hand identity preference in the two (egocentric and allocentric) viewing conditions. **(a)** Experimental design. Thirteen right-handed subjects (informed written consent was obtained) viewed object-grasping video clips. We presented eight action observation conditions, each consisting of a unique combination of the acting hand (right/left), the viewpoint of the action (allocentric/egocentric) and its location in the visual field (right/left of the red fixation point) (**Supplementary Methods** and **Supplementary Fig. 3** online). **(b)** Hand-identity preference during the egocentric viewing conditions. A statistical parametric map of the group results, using a random-effect general linear model analysis and cluster-size correction for multiple comparisons, is shown. Direct contrast between observed left-hand actions and right-hand actions seen from an egocentric point of view (egocentric conditions in **Fig. 1a**) revealed a contralateral representation of the seen hand identity in the aSPL. In the left aSPL, significantly higher activation was found during observation of right-hand (egocentric) actions than during left-hand actions (blue clusters, $P < 0.05$). The opposite preference, $P < 0.05$, was found in the right aSPL (red clusters). The center of mass (Talairach coordinates) was $x = 26$, $y = -49$ and $z = 65$ in the right hemisphere and $x = -32$, $y = -45$ and $z = 52$ in the left hemisphere. Yellow lines denote the major sulci in the parietal cortex (central sulcus, post-central sulcus and the intraparietal sulcus, Ips). **(c)** Ipsilateral hand preference in the allocentric viewing conditions. Direct contrast between the clips showing right- and left-hand actions from an allocentric point of view (allocentric conditions, in **Fig. 1a**) revealed an ipsilateral representation of the hand identity in the aSPL. Note the reversal of preference (change in colors) in the same aSPL voxels across the two (egocentric vs. allocentric) viewing conditions. The center of mass was $x = 28$, $y = -47$ and $z = 62$ for the right hemisphere, and $x = -36$, $y = -55$ and $z = 54$ for the left hemisphere.



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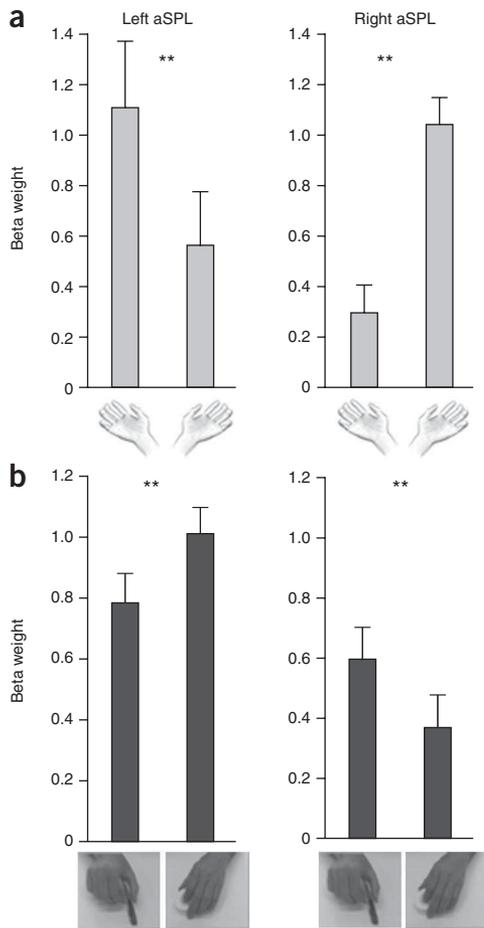


Figure 2 A mirror-inverted representation of action: ROI analysis. ROIs in the aSPL were selected on the basis of their contralateral preference during observation of the egocentric clips (see **Fig. 1b**). **(a)** Specificity for the contralateral hand during self-performed actions. Nine of the subjects performed a somatomotor mapping experiment in which they manipulated a cube with their right or left hand (depicted by icons) without visual feedback of their action. Direct comparison between the activation during object manipulation with the right and left hand revealed a significant contralateral preference for the acting hand during self action in these ROIs (paired *t* test: left aSPL, $P < 0.001$; right aSPL, $P < 0.001$). The bars represent the z-normalized averaged beta weights. Error bars denote s.e.m. $**P < 0.01$. **(b)** Opposite preferences during observation of allocentric action clips. Comparison between observation of right- and left-hand allocentric clips (collapsed across presentations in the two hemifields) revealed a significant ipsilateral hand preference in the same ROIs (paired *t* test: left aSPL, $P < 0.001$; right aSPL, $P < 0.005$; $n = 13$).

point of view⁸. We now capitalize on this clear (motor-like) preference by studying the nature of representation of actions seen from an allocentric perspective.

We started by determining how fMRI activation was modulated by hand identity when the hands were viewed from an egocentric viewpoint (**Fig. 1a**). Direct contrast between the clips that showed right-hand actions and those displaying left-hand actions (from an egocentric point of view) revealed a contralateral representation of the identity of the hand in aSPL (**Fig. 1b**), irrespective of the visual hemifield in which the hand actions were seen. In contrast, the allocentric clips (depicted in **Fig. 1a**) elicited fMRI activation with a clear preference for the ipsilateral hand (compare **Fig. 1b,c**).

To verify that this opposite (mirror-like) pattern of representation can also be seen in the same voxels, we further applied a region of interest (ROI) analysis. To that end, we selected voxel clusters in the aSPL that showed a hand-identity preference in the egocentric conditions (that is, had significantly greater activation ($P < 0.05$, corrected) during the contralateral hand clips compared with the ipsilateral ones in the group contrast). Notably, these selected voxels also showed preference for the contralateral hand (over the ipsilateral one) when subjects executed actions without seeing their own hand action (**Fig. 2a**), as expected from regions that may be part of the human mirror system. Furthermore, the ROI analysis corroborated our statistical parameter mapping data, repeating the inversion of preference when subjects observed clips taken from an allocentric point of view (**Fig. 2b**). This preference was found in both the contralateral and ipsilateral visual fields (**Supplementary Figs. 1 and 2** online).

Mirror-related regions might be expected to be more active during imitation of action, which combines both the visually elicited representation of the action and execution of the observed action, than during observation or execution alone. To test this, we carried out an additional experiment in which a subset of the subjects ($n = 9$) either observed the different object-manipulation clips, imitated the grasping movements shown in the clips with their right hand or executed the same grasping movements without seeing the clip. ROIs were identified in the aSPL on the basis of their mirror-like representation during observation of the clips (**Fig. 3**). In these ROIs, we compared the overall activation during imitation, observation and execution of action (**Fig. 3a**), and assessed the dependence of the evoked fMRI signal on the different observation conditions during imitation (**Fig. 3b**). Consistent with the direct matching hypothesis, we found that the fMRI activation during imitation was significantly higher than during action execution or action observation in the aSPL contralateral to the imitating hand (left hemisphere). Moreover, the patterns of activation in the ROIs during imitation revealed a similar mirror-like preference as in the observation conditions, although the differences between conditions were smaller. This is probably the result of the additional motor and proprioceptive inputs to aSPL that mask the action observation effects.

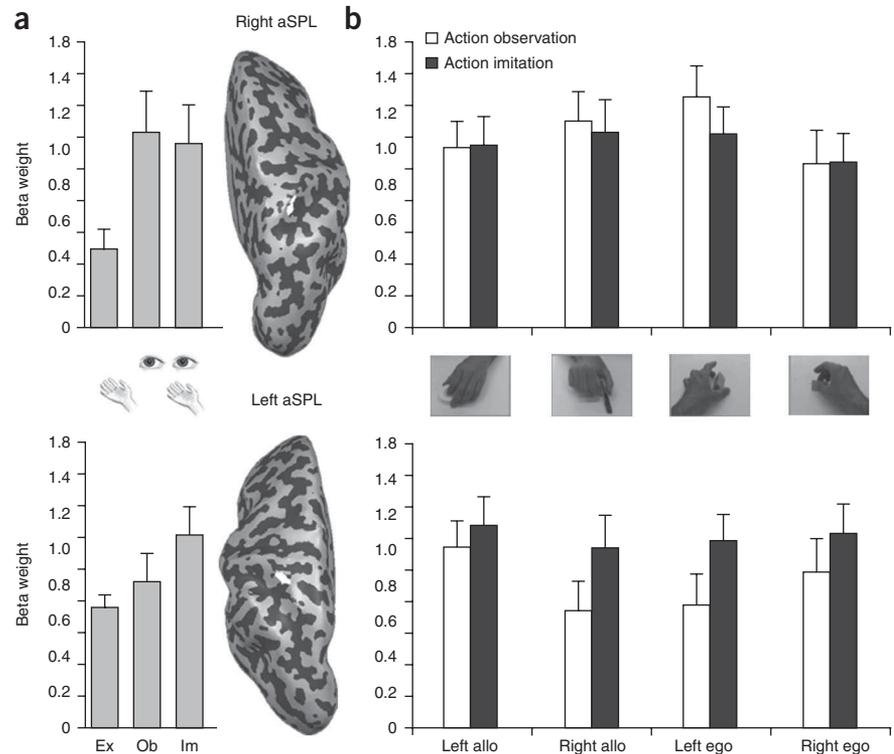
The human anterior parietal cortex is active during grasping execution⁹ and grasping observation⁸. This dual hand-specific activity suggests that it may be engaged in visuomotor control of our own grasping movements. Indeed, a transcranial magnetic stimulation pulse to the anterior intraparietal sulcus disrupts the online correction of object grasping movements¹⁰. Unlike our own (egocentrically viewed) actions, however, actions of others can be seen from various viewpoints. We found that the parietal regions that were active during execution and observation of our own actions (egocentric viewpoint) also mapped actions made by others (allocentric viewpoint), showing an ipsilateral preference. Indeed, similar to egocentric-viewed actions, allocentric-viewed actions also modulate the motor-evoked potential (elicited by transcranial magnetic stimulation in M1) in an action-specific manner¹¹.

Imitation requires a complex transformation of the visual information to a (body-centered) motor frame of reference. Despite that, imitation can already be seen in 21-d-old infants¹². Moreover, when asked to replicate a grasping action made by an actor facing them (such as grasping a disc with the right hand¹³), children younger than 12 years naturally perform the same action with the opposite (left) hand. In adults, mirror-image imitation is less error-prone than anatomical imitation of allocentric actions^{6,7}. According to the associative-sequence learning theory, learned visuomotor associations naturally

Figure 3 Action observation and imitation in the aSPL. The ROI analysis was focused on aSPL voxels (white clusters in inset) showing statistically significant mirror-like representation during the observation conditions (contralateral egocentric + ipsilateral allocentric > ipsilateral egocentric + contralateral allocentric, $n = 9$, $P < 0.05$).

(a) aSPL involvement in action imitation. Comparison between the averaged activation during imitation of action (Im, right), observation of action (Ob, middle) and execution of a similar action (Ex, left) revealed a significant increase in activation during imitation when compared with action observation (paired t test, $P < 0.002$) and with action execution (paired t test, $P < 0.03$) in the left aSPL (contralateral to the imitating hand). In the right aSPL, no significant difference was found between action observation and imitation; however, the execution condition was significantly lower than the imitation condition (paired t test, $P < 0.004$). We verified that observation was not accompanied by unconscious imitation (**Supplementary Fig. 4** online).

(b) Hand identity and viewpoint effects during action imitation. During imitation of action, the differences between the various conditions decreased (compared with the differences seen during observation of the clips). However, a significant interaction between the viewpoint and the identity of the hand during imitation was found in the left aSPL ($F_{1,8} = 5.32$, $P < 0.05$). Allo, allocentric; Ego, egocentric.



arise between motor output circuits and the sensory systems monitoring the action as a result of their co-activation¹⁴. Therefore, on the basis of the associations learned during self actions, egocentrically viewed hand actions generate activity in contralateral visuo-motor regions, even when the action is performed by others. The clear preference for the ipsilateral hand during allocentric-action observation could have evolved simply as a result of our experience in front of the mirror or through common actions in space—for example, when reaching simultaneously with others (facing us) to grab the same object.

We found a mirror pattern of representation in the aSPL but not in classical mirror areas such as the inferior frontal gyrus and inferior parietal lobule. This is consistent with results from action imitation and observation studies demonstrating that while the inferior frontal gyrus and inferior parietal lobule are engaged in representation of the high level, abstract aspects of the action (such as its goal), the SPL represents the specific (kinematic) aspects of the action (for example, how to execute the action and with which hand)^{2,15}. Notably, the aSPL activation in our study was not sensitive to the identity of the observed hand *per se* but was affected by the viewpoint of the action. This result suggests that observed actions are remapped in the aSPL to the hand that will probably be used to replicate the action toward the relevant object in space.

Note: Supplementary information is available on the Nature Neuroscience website.

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AUTHOR CONTRIBUTIONS

L.S. and E.Z. jointly planned the experiments. L.S. conducted the experiments and the data analysis. L.S. and E.Z. wrote the paper together.

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