Effect of subjective perspective taking during simulation of action: a PET investigation of agency

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Perspective taking is an essential component in the mechanisms that account for intersubjectivity and agency. Mental simulation of action can be used as a natural protocol to explore the cognitive and neural processing involved in agency. Here we took PET measurements while subjects simulated actions with either a first-person or a third-person perspective. Both conditions were associated with common activation in the SMA, the precentral gyrus, the precuneus and the MT/V5 complex. When compared to the first-person perspective, the third-person perspective recruited right inferior parietal, precuneus, posterior cingulate and frontopolar cortex. The opposite contrast revealed activation in left inferior parietal and somatosensory cortex. We suggest that the right inferior parietal, precuneus and somatosensory cortex are specifically involved in distinguishing self-produced actions from those generated by others.

The goal of theory of mind is to explain the ability to predict and understand actions of both oneself and other intelligent agents. Two types of approaches attempt to account for the cognitive mechanism that subserves such a capacity. The theory theorists maintain that this ability is underpinned by a folk-psychological theory of the structure and functioning of the mind (that may be innate and modularized or learned individually)[1]. On the contrary, the simulation theory posits that the attributer tries to covertly mimic the mental activity of the target (for review, see refs. 2, 3), and postulates shared states of mind between the attributer and the target. This theory has generated considerable interest among philosophers of mind, cognitive scientists and, recently, neuroscientists. The question of agency (how a subject attributes an action to himself or to another agent[4,5]) is at the core of the simulation theory.

Motor imagery can be considered a way to access motor intentions or plans, in which the representation of a given action is internally performed without any overt motor output. It can be used as a natural protocol to address the issue of agency within the simulation theory (for review, see ref. 6). So far, motor imagery has always been studied in a first-person subjective perspective, and several neuroimaging studies have consistently demonstrated a striking functional equivalence with actual action. The first-person perspective is associated with activation of the inferior parietal, premotor and SMA on the left side as well as the ipsilateral cerebellum[7–9]. Further evidence in support of shared motor representation between mental simulation of action and motor execution is provided by experiments in patients with impairments in motor imagery following parietal lesions[10,11]. Common brain regions are involved during action generation, action simulation and action observation (for a meta-analysis see ref. 12).

However, there must exist, at the neural level, a distinction between first-person and third-person perspective representation. The objective of this study was to probe the effect of perspective taking on the neural network engaged during mental simulation of action. Subjects were required either to imagine themselves performing a given action (first-person perspective) or to imagine the experimenter performing the same action (third-person perspective). Two perceptual modalities were used to identify brain regions strictly involved in perspective taking during action simulation irrespective of sensory input. These two subjective perspectives were initiated either from photographs of familiar objects or from sentences depicting familiar actions. We used pictures of objects in order to have a reference situation comparable to that used in previous neuroimaging studies, in which motor imagery was mostly visually triggered. However, verbal auditory stimuli were also chosen because of their ecological features. The most natural situation in which one is led to use first- and third-person perspectives is surely linguistic communication (should it be written, spoken or heard). We found that a limited number of brain areas may be specifically involved in self/other distinction, namely right inferior parietal lobe, precuneus and somatosensory cortex.

Results

First-person perspective simulation versus control

First-person perspective simulation, irrespective of the presentation modality of the stimuli, was associated with left hemispheric regional cerebral blood flow (rCBF) increases in the inferior parietal lobe, precentral gyrus, superior frontal gyrus (SMA proper), occipito-temporal junction (MT/V5) and anterior insula. The cerebellum and precuneus were activated in the right hemisphere (A1 – AC and V1 – VC; Table 1; Fig. 1).

Third-person perspective simulation versus control

Third-person perspective simulation, irrespective of the presentation modality, was associated with bilateral rCBF increases in

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Table 1. Areas significantly activated during first-person simulation irrespective of the modality (A1 – AC in conjunction with V1 – VC).

Brain region	L/R	Coordinates			*t*-value	*p* corrected
		x	*y*	*z*		
Inferior parietal lobe	L	–64	–30	30	5.30	0.000
Inferior parietal lobe	L	–56	–32	26	4.61	0.000
Inferior parietal lobe	L	–52	–42	32	4.04	0.000
Superior frontal gyrus (SMA)	L	–12	–2	58	4.90	0.000
Occipito-temporal junction (MT/V5)	L	–56	–66	4	4.15	0.000
Precentral gyrus	L	–26	–16	58	3.81	0.001
Cerebellum	R	44	–54	–32	3.19	0.046
Anterior insula*	L	–30	16	8	2.98	0.128
Precuneus*	R	6	–68	46	2.90	0.188

$p < 0.001$ (corrected for whole brain), $t > 1.88$. *x*, *y*, *z* refer to MNI coordinates. L, left; R, right hemisphere. *Some activated clusters are reported, even though they do not survive correction for the whole brain volume, because we think they are both neurobiologically plausible and relevant in the light of our hypotheses.

the precuneus. On the left side, activation foci were detected in the precentral gyrus, superior frontal gyrus (pre-SMA) and occipito-temporal junction (MT/V5). The inferior parietal lobule and frontomarginal gyrus were both activated on the right side (A3 – AC and V3 – VC; Table 2; Fig. 2).

Areas involved in first- and third-person perspectives

The conjunction analysis ($p < 0.0001$, $t > 1.29$) calculated with the four contrasts (A1 – AC, V1 – VC, A3 – AC, V3 – VC) revealed bilateral rCBF increase in the precuneus ($x = 6$, $y = –68$, $z = 46$; *t*-value, 2.90; *p* corrected, 0.000 and –8, –64, 40; 2.43; 0.001) and in the MT/V5 complex (–58, –60, 12; 2.22; 0.006 and 52, –54, 8*; 1.70; 0.292). The precentral gyrus (–22, –12, 54; 2.25; 0.004) and SMA (–10, 4, 64; 2.14; 0.011) were activated in the left hemisphere.

Third-person versus first-person perspectives

Compared to first-person perspective, third-person perspective simulation was specifically associated with left rCBF increase in

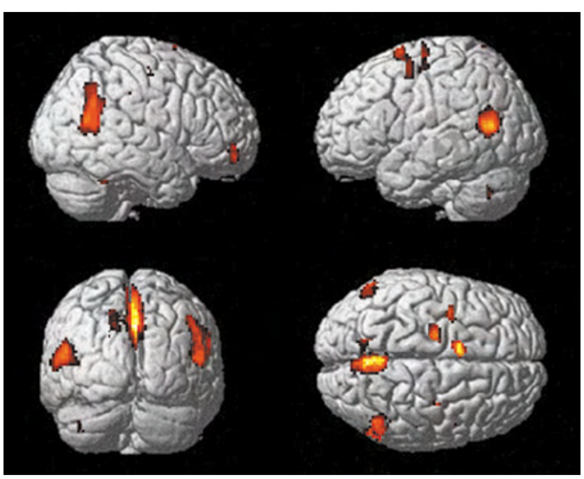

Fig. 2. Brain areas activated by third-person simulation. Foci of activation (A3 – AC in conjunction with V3 – VC) have been superimposed onto lateral (left and right hemispheres), posterior and top views of the single-subject MRI of SPM 99.

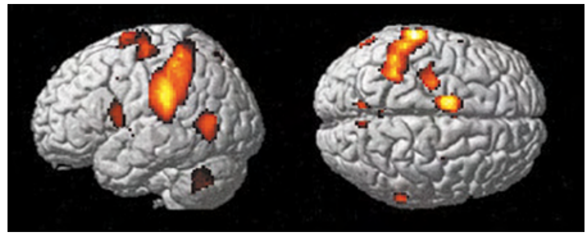

Fig. 1. Brain areas activated by first-person simulation. Foci of activation (A1 – AC in conjunction with V1 – VC) have been superimposed onto the sagittal (left hemisphere) and axial top views of the single-subject MRI of SPM 99.

the posterior cingulate cortex. On the right side, activation foci were detected in the precuneus, the inferior parietal lobule and frontopolar gyrus ((A3 + V3) – (A1 + V1); Table 3; Fig. 3).

First-person versus third-person perspectives

First-person perspective relative to third-person perspective ((A3 + V3) – (A1 + V1), $p < 0.0001$, $t > 3.85$) showed a strong rCBF increase in the inferior parietal lobule (–66, –32, 26; 6.47; 0.000), the posterior insula (–42, –10, –8; 5.46; 0.006) and the postcentral gyrus* (–36, –40, 40; 4.58; 0.142) in the left hemisphere. A bilateral increase was also detected in the inferior occipital gyrus (56, –54, –24; 5.62; 0.003 and –48, –50, –18*; 4.11; 0.498).

Discussion

First- and third-person perspectives correspond to everyday life situations. This study explored the effect of perspective taking on the neural substrates involved in action simulation. All brain regions activated during first-person perspective conditions were consistent with previous neuroimaging experiments that have revealed the neural correlates of motor imagery[7–9,13]. The involvement of these regions, namely the inferior parietal, SMA, precentral gyrus in the left hemisphere and ipsilateral cerebellum (Table 1; Fig. 1), has been interpreted in favor of a functional equivalence between action simulation and action execution[12,14]. When compared with third-person perspective, the main effect of first-person perspective resulted in strong left hemispheric activation of the inferior parietal lobule, as well as increased activation in the somatosensory cortex. This can be interpreted as evidence of a prominent role of left inferior parietal lobe in programming the self's movements, because the programming can potentially be transformed into execution. Detecting a

Table 2. Areas significantly activated during third-person simulation irrespective of the modality (A3 – AC in conjunction with V3 – VC).

Brain region	L/R	Coordinates			*t*-value	*p* corrected
		x	*y*	*z*		
Precuneus	R	6	–64	38	5.09	0.000
Precuneus	L	–10	–62	38	4.14	0.000
Precentral gyrus	L	–22	–14	54	3.70	0.002
Occipito-temporal junction (MT/V5)	L	–50	–64	16	3.50	0.008
Superior frontal gyrus (SMA)	L	–8	4	62	3.39	0.015
Inferior parietal lobe*	R	48	–58	38	2.93	0.166
Frontomarginal gyrus*	R	28	50	–8	2.39	0.878

See Table 1 legend.

Table 3. Areas significantly and specifically activated during third-person simulation compared to first-person simulation ((A3 + V3) – (A1 + V1)).

Brain region	L/R	Coordinates *x*	*y*	*z*	*t*-value	*p* corrected
Posterior cingulate	L	–12	–50	38	5.55	0.004
Precuneus	L/R	0	–66	34	5.36	0.009
Parieto-occipital fissure	R	8	–68	24	5.30	0.012
Inferior parietal lobe	R	44	–64	24	4.94	0.042
Inferior parietal lobe*	R	50	–58	30	4.68	0.105
Frontopolar gyrus*	R	14	72	10	4.37	0.266

$p < 0.0001$ (corrected for multiple comparisons), $t > 3.85$. See Table 1 legend.

somatosensory area only and precisely when first-person perspective is compared to third-person perspective is of particular interest, and reveals the area's participation in distinguishing self from other, as previously suggested[15]. The activation of MT/V5 complex shows that this region is involved not only in actual motion perception, but also in imagined movement, which is conveyed by action simulation. This is consistent with other studies that have demonstrated activation in MT/V5 by apparent motion[16,17], illusory motion[18], imagined motion[19] and static images with implied motion[20].

According to the simulation theory, there should be an overlap between regions involved in first- and third-person perspectives. Our results show that this is partly true. Imagining someone else's action is associated with activation in several areas that are common to first-person simulation, namely, the SMA, precentral gyrus, precuneus and MT/V5 (Table 2; Fig. 2 and the conjunction analysis; A1 – AC, V1 – VC, A3 – AC, V3 – VC). However, this overlap is not complete. There were specific increases in the parietal, cingulate and frontal cortices for third-person perspective simulation when compared to first-person perspective simulation (Table 3; Fig. 3). Left inferior parietal activity, which was very strong for first-person perspective simulation, disappeared when imagining someone else's action. In addition, a strong increase was detected in the right inferior parietal lobe during the third-person perspective experiment (Figs. 1, 2 and 4). In parallel, specific rCBF augmentations were detected in the precuneus, left posterior cingulate cortex and right frontopolar gyrus. The specific activation of both right inferior parietal cortex and precuneus during third-person simulation may account for a neural mechanism that is important in the determination of agency. This interpretation is supported by evidence from clinical neuropsychology, and from brain imaging studies in both normal volunteers and schizophrenic patients.

The right inferior parietal cortex is activated when subjects watch other people in an effort to imitate them[21,22]. Moreover, a patient with an abscess in the right parietal cortex has been described, in a neuropsychological case study, to have believed that his body was being controlled by external forces. This patient made statements such as, "My head is empty," "I have no thoughts," and "I feel hypnotized"[23]. Schizophrenic patients show hyperactivation of the right inferior parietal cortex, and experience passivity as compared to healthy subjects during the performance of freely selected joystick movements[24]. It was proposed that such abnormal responses in the parietal lobe cause the misattribution of self-generated acts to external entities.

Furthermore, in a PET experiment exploring the neural correlates of hypnosis, rCBF decreases were found in the right inferior parietal lobule, left posterior cingulate gyrus and left precuneus[25]. Deactivation of the precuneus, in particular, was considered to be an important metabolic feature of this unconscious state[26]. In agreement with those results, it has been suggested that the right posterior parietal lobe has a determinant role in high-order body or self representation[27,28].

From the viewpoint of cognitive psychology, having a unified perspective involves keeping track of the relationship between what is perceived and what is done, and hence being aware of agency. In this sense, it has been suggested that perspective taking already involves self-consciousness[29]. Thus, at the physiological level, the brain may need to create a particularly vivid representation of the self to discriminate between self and other. During third-person perspective simulation, one needs especially to be aware of who the self is, in order to be able to imagine another person with the same neural resources as the self. So as not consciously to confuse third-person simulation with first-person simulation, regions that are critical for body schema or corporeal awareness may be highly recruited. Although this interpretation is speculative, during the third-person perspective simulation, specific rCBF increases occurred precisely in brain regions where decreases were found during the hypnotic state (right inferior parietal lobule, posterior cingulate and precuneus). A neuroimaging study of self versus non-self judgments has provided further results in favor of this hypothesis. Judgments about either face pictures or personality trait words were indeed associated with activation in the precuneus only in the case of self processing[30]. In our study, although the precuneus was activated in both perspectives, it was much more involved during third-person perspective (Fig. 4), which was consistent with our hypothesis (that is, overactivation of regions involved in self-representation during third-person perspective). According to those converging results, we suggest that the right inferior parietal lobe and the precuneus are critically involved in discriminating the self from others, by way of their involvement in the representation of the self.

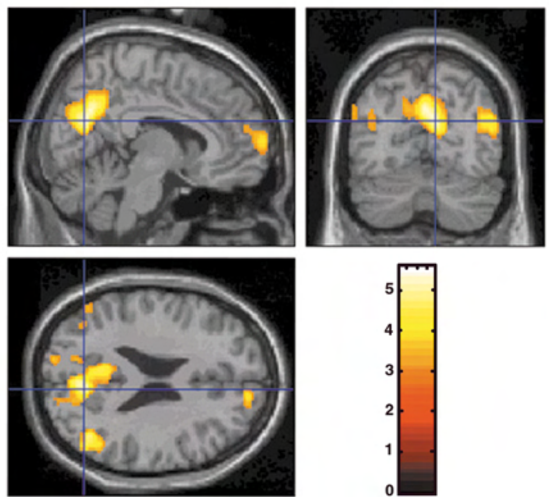

Fig. 3. Brain areas activated by third- versus first-person simulation. Sagittal, axial and coronal sections of the brain ($x = 8$, $y = –68$, $z = 24$) showing specific areas of activation associated with third-person simulation when compared to first-person simulation ((A3 + V3) – (A1 + V1)).

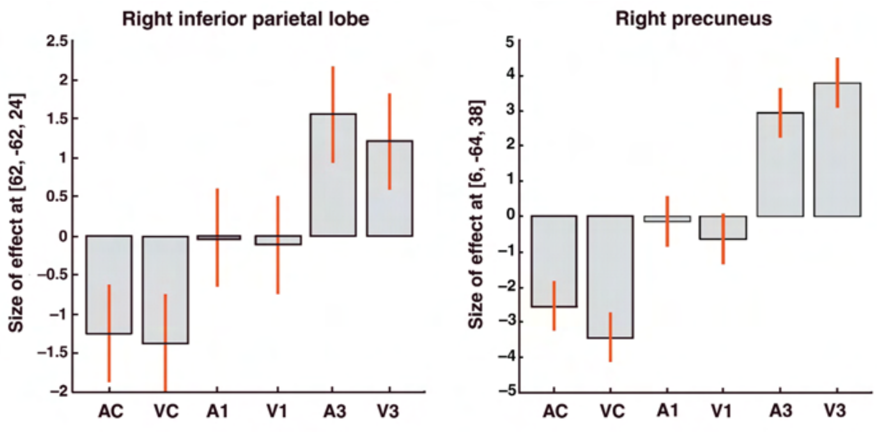

Fig. 4. Activation profiles for clusters in the right inferior parietal and precuneus across activation conditions. The histogram bars represent the relative adjusted regional cerebral blood flow values. A1, first-person simulation with auditory stimuli; A3, third-person simulation with auditory stimuli; AC, auditory control; VC, visual control; V1, first-person simulation with visual stimuli; V3, third-person simulation with visual stimuli. Both precuneus and right inferior parietal show stronger activation for third-person perspective simulation, less activation for first-person perspective simulation, and very low activation for control situations in which self-representation is not required for the task.

To take a third-person perspective, subjects have to be aware of what the actor intends to do before simulating the actor's action. This awareness could be compared to a kind of theory of mind process. The posterior cingulate activation in particular could be associated with such processing, as several imaging studies have demonstrated its involvement during tasks requiring mind-reading[31,32].

The specific activation in the frontopolar gyrus during third-person perspective simulation could be interpreted as demonstrating the existence of an inhibitory phenomenon during third-person perspective simulation. An ANCOVA analysis, performed using frontopolar activity as a covariate of interest and subjects as a confound, provided results that allowed us to formulate this hypothesis, because left inferior parietal lobule (56, –30, 26) was significantly negatively correlated with the frontopolar gyrus ($t = 4.06$). Our assumption of an inhibitory role of the frontopolar region is also in accordance with neuroanatomical deficits that have been discovered in schizophrenic patients. Inhibitory neurons (GABA neurons) in the anterior cingulate and in the frontopolar cortex are lacking in the brains of patients who are susceptible to confusing the self and other[33,34]. In addition, patients with lesions of this part of the frontal cortex may exhibit utilization behavior, which has been interpreted as a consequence of impaired inhibition[35].

Our study demonstrates that it is possible, at a representational level, to identify which brain regions are involved in first-person perspective, and which are involved in third-person perspective. Several cortical areas (right inferior parietal, precuneus and somatosensory cortex) are proposed to be engaged in distinguishing the self from the other, and should be investigated further to better understand agency disorders in both neurological and psychopathological patients.

Methods

Subjects. Ten right-handed healthy male volunteers were recruited (24.2 ± 2.9 years old). All subjects gave written informed consent according to the Helsinki declaration. The study was approved by the local ethical committee (CCPPRB, Centre Léon Bérard, Lyon), and subjects were paid for their participation.

Activation protocol. Subjects were scanned during four target conditions (A1, A3, V1, V3), and two control conditions (AC, VC), which were duplicated once and presented in a pseudorandomized order, counterbalanced across subjects (12 scans per subject). Half the conditions were composed of visual stimuli (V1, V3, VC), and half were composed of auditory stimuli (A1, A3, AC). During the scanning procedure, auditory and visual conditions were never mixed; half the subjects saw the visual conditions block first, and half saw the auditory block first. All actions selected for this study required the use of the right hand.

During each visual condition (V1, V3, VC), subjects were presented with photographs of familiar objects (for example, a razor, shovel or ball). Each stimulus was presented for 5 s on a dark background. In the V1 condition, subjects were instructed to imagine themselves (that is, using the first-person perspective) acting with the object for as long as it appeared on the screen. In the V3 condition, subjects were instructed to imagine the experimenter acting with the object (that is, using the third-person perspective). The same set of photographs of objects ($n = 14$) was used across these two conditions. In VC condition, subjects were asked to passively watch another set of photographs of objects.

During the auditory conditions (A1, A3, AC), subjects were presented with verbal sentences recorded onto CD in the experimenter's voice. Each sentence lasted approximately 2 s and was followed by a blank period of 3 s. At the end of the blank period, a beep (300 ms) warned the subject that the next sentence would arrive. Each auditory condition included 14 sentences. In the A1 and A3 conditions, the same series of sentences using familiar actions (for example, stapling sheets of paper, peeling a banana) were used. These sentences were declined at the present tense and the subject of the verb was either 'you' in condition A1 (for example, "You are stapling a sheet of paper") or 'I' in condition A3 (for example, "I am stapling a sheet of paper"). In those two conditions, subjects had thus to imagine what the experimenter said (that is, in A1, with first-person perspective; in A3, with third-person perspective). In the AC condition, the sentences described landscapes that did not include humans, motion or animals (for example, "You are seeing a field of wheat"). Subjects were instructed to imagine themselves contemplating these landscapes.

All subjects were extensively trained in each of the experimental conditions. They were familiarized with the experimental setup, the experimenter's voice and physiognomy, and also with first- and third-person perspectives of action simulation. For the latter, they were trained to imagine the experimenter in a three-quarters view so that no right/left conflict could arise during imagination. The stimuli used in the training session were different from those used in the PET experiment.

Scanning procedure. A Siemens CTI HR+ (63 slices, 15.2 cm axial field of view) PET tomograph with collimating septa retracted operating in three-dimensional mode was used. Sixty-three transaxial images (slice thickness of each, 2.42 mm) without gaps between them were acquired simultaneously. A venous catheter to administer the tracer was inserted in an antecubital fossa vein in the left forearm. Correction for attenuation was made using a transmission scan collected at the beginning of each study. After a 9-mCi bolus injection of $H_2{}^{15}O$, scanning was started when the brain radioactive count rate reached a threshold value and continued for 60 s. Integrated radioactivity accumulated in 60 s of scanning was used as an index of rCBF.

The three visual conditions used a NEC projector (800 × 600 pixels) to display colored photographs on a screen located at the back of the camera. A mirror placed in front of the subjects' eyes allowed them to see the projected images by reflection. The resultant distance from the eyes to the screen was approximately 50 cm (corresponding field of view, 42° in the horizontal dimension and 32° in the vertical direction). A Power Macintosh computer (Apple, Cupertino, California) with the SUPERLAB software was used to control the display processing.

Data analysis. Images were reconstructed and analyzed with the Statistical Parametric Mapping software (SPM99, Wellcome Department of Cognitive Neurology, UK[36]; implemented in MATLAB 5, Math Works, Natick, Massachusetts). For each subject, images were realigned to the first scan and then normalized into the MNI stereotaxic space. Data were convolved using a Gaussian filter with a full-width half maximum (FWHM) parameter set to 12 millimeters.

The design for statistical analysis in SPM was defined as 'multi-subjects and multi-conditions' with 105 degrees of freedom. Global activity for each scan was corrected by grand mean scaling. The condition (covariate of interest) and subject (confound, fixed effect) effects were estimated voxelwise according to the general linear model. Linear contrasts were assessed to identify the significant difference between conditions, and were used to create an SPM $\{t\}$, which was transformed into an SPM $\{z\}$ map. The SPM $\{z\}$ maps were thresholded at $p < 0.001$ (corrected for whole brain) for conjunction analysis and at $p < 0.0001$ (corrected for whole brain) for main effect analysis. Anatomical identification was done using atlases both of Talairach and Tournoux[37] and of Duvernoy[38].

Three conjunction analyses were done. The first was designed to focus on regions activated during first-person simulation compared to control conditions, irrespective of the presentation modality (A1 – AC in conjunction with V1 – VC). The second was designed to detect brain areas involved in third-person simulation compared to control, irrespective of the presentation modality (A3 – AC in conjunction with V3 – VC). The third was designed to formally identify regions commonly involved in first- and third-person perspectives (A1 – AC, V1 – VC, A3 – AC and V3 – VC).

Two main effect analyses were done to reveal the brain areas specifically involved in third-person perspective simulation compared to first-person perspective ((A3 + V3) – (A1 + V1)) and the reverse ((A1 + V1) – (A3 + V3)).

Post hoc analysis was used to assess task-related regional activity. The analysis represented rCBF adjusted values in each task to demonstrate the differential involvement of a given brain area in the six experimental conditions.

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