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Modulating the experience of agency: a positron emission tomography study

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Abstract

This study investigated agency, the feeling of being causally involved in an action. This is the feeling that leads us to attribute an action to ourselves rather than to another person. We were interested in the effects of experimentally modulating this experience on brain areas known to be involved in action recognition and self-recognition. We used a device that allowed us to modify the subject's degree of control of the movements of a virtual hand presented on a screen. Four main conditions were used: (1) a condition where the subject had a full control of the movements of the virtual hand, (2) a condition where the movements of the virtual hand appeared rotated by 25° with respect to the movements made by the subject, (3) a condition where the movements of the virtual hand appeared rotated by 50°, and (4) a condition where the movements of the virtual hand were produced by another person and did not correspond to the subject's movements. The activity of two main brain areas appeared to be modulated by the degree of discrepancy between the movement executed and the movement seen on the screen. In the inferior part of the parietal lobe, specifically on the right side, the less the subject felt in control of the movements of the virtual hand, the higher the level of activation. A reverse covariation was observed in the insula. These results demonstrate that the level of activity of specific brain areas maps onto the experience of causing or controlling an action. The implication of these results for understanding pathological conditions is discussed.

Introduction

When we act, we normally feel ourselves causing and controlling our own action. There are situations, however, where this feeling can be altered. Normal subjects can sometimes experience confusion between the actions or intentions of other agents and the actions they themselves perform or intend. For example, when playing a mutual video game we may experience difficulties in deciding whether an action has been caused by ourselves or by our partner (Wegner and Wheatley, 1999). Such situations reveal that our sense of agency can be confused. This may lead to misattribution not only of one's own actions to another agent, but also of the actions of another agent to oneself. Studying the ability to attribute the origin of an action to its proper agent is important for the understanding of consciousness and self-consciousness in relation to action.

The feeling of being causally involved in an action (the sense of agency, Gallagher, 2000) is a constituent of the sense of the self. Georgieff and Jeannerod (1998) have postulated the existence of a "who" system that allows an agent to refer an action to its proper origin. Neuroimaging techniques have already provided clues for the existence of a cerebral network specifically devoted to this process. Attribution of action to another agent has been associated with increased activity in the right inferior parietal lobe (McGuire et al., 1996; Spence et al., 1997; Ruby and Decety 2001; Farrer and Frith, 2002). Activity in the insula has been observed when subjects recognize aspects of themselves. Fink et al. (1996) reported an activation of the

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anterior–midposterior insula when subjects identified their own memories. Kircher et al. (2000, 2001) observed anterior insula activation when subjects had to recognize their own face or recognize descriptions of themselves in words. Finally, in a recent study, Farrer and Frith (2002) found an activation of the anterior insula when subjects attributed an action to themselves.

The above-mentioned studies established the existence of neural network correlated with attribution judgments made by an acting subject. In the present study, we conjectured that processes underlying the sense of agency or consciousness of action should not be all or none states, but should rather be continuous being based on monitoring of the different action-related signals, from sensory (kinesthetic, visual) and central (motor command) origin. To test this hypothesis, we devised an experimental situation where the visual feedback provided to the subjects about their own movements could be either veridical or distorted to a variable degree. The degree of distortion went up to the point where the seen movements were completely unrelated to the executed ones. Thus, in the veridical condition, the subjects were likely to feel in full control of their own movements, whereas in the maximally distorted condition, they were likely to feel that they were not in control, but rather watching the movements of another agent.

Our results provide a significant expansion of the results reported previously. The level of activity in the main areas already shown to be activated during attribution judgments (e.g., posterior parietal cortex and insula) was found to covary with the amount of discordance between what the subjects did and what they saw. This new finding provides a dynamic view of the mental processes used to determine what does or does not pertain to the self and, ultimately, to establish a boundary between the self and the other.

Materials and methods

We studied 8 healthy right-handed male subjects (mean age 34 ± 6.71 years). None had a history of neurological or psychiatric disease. All the subjects gave written informed consent. The study was approved by the local ethics committee (CCPPRB, Centre Léon Bérard, Lyon). The subjects were paid for their participation.

The subjects underwent 12 perfusion scans with positron emission tomography (PET) in a single session. Subjects lay in the scanner with head movements minimized by a mask.

Radioactivity was administered as an intravenous injection of H_2O^{15} by a plastic canula placed in the left cubital vein.

The subjects held a joystick with their right hands and were instructed to execute random movements at a constant rate throughout the 70-s block. They were requested to move the joystick back to the center after each excursion in a given direction. This procedure ensured that the movements were similar across conditions and subjects. The movements of the joystick controlled an image of a virtual hand holding a joystick. This system provided a dynamic representation of the movements of the joystick held by the subjects with an intrinsic delay of less than 30 ms.

The joystick was attached to a table above the bed of the scanner. The image of the virtual hand holding the joystick was projected onto a mirror placed in front of the subjects. The angle of visualization of the image in the mirror was adjusted so as to coincide with the real position of the joystick actually held by the subjects. The position of the subject's forearm was adjusted so as to coincide with the direction of the virtual forearm seen in the mirror. A black cloth was then hung above the subject's forearm so as to prevent him or her from seeing his or her forearm and the device controlled by the experimenter.

Angular distortions could be introduced into this system, modifying the direction of the movement actually performed by the subjects with respect to the movement displayed on the computer screen. The experiment involved four experimental conditions. In the first condition ("0° condition") the subjects could see the movements of the virtual hand in perfect concordance with their movements made with the joystick. In the second condition ("25° condition"), they saw the movements of the virtual hand deviating by 25° from their hand's actual trajectory. In the third condition ("50° condition") the value of the deviation was 50°. In the latter two conditions, the deviation was to the right on half of the sessions and to the left on the other half. In the fourth condition ("other condition"), the subjects saw the movements of the joystick controlled by another agent (the experimenter).

During each session subjects were asked to direct their attention to the origin of the movement they saw: was it their own movement, their own movement distorted, or the movement of another agent?

Two low-level control conditions (C1 and C2) were also included. In condition C1 the subjects had to execute random movements without seeing anything on the screen. In condition C2 they had to watch the virtual hand moving by itself without doing anything.

At the beginning of the experiment subjects performed a practice session to get acquainted with the device and to experience generating random movements. They sat in front of the monitor and executed random movements in three different conditions: 0° condition, distorted condition (the deviation was 35°) and other condition. When the subjects were lying in the scanner they had a second practice session so that they could familiarize themselves with the new angle of visualization caused by their supine position. Only the 0° and the distorted conditions were performed in this final practice session.

PET scanning comprised two blocks of each of the six conditions of 70 s each. The interval between each start time was 8 min. The order of the conditions was randomized and reversed within and between subjects. Each trial was initiated by an auditory stimulus.

Table 1
Brain areas showing increased rCBF from 0° to other conditions: (25–0°) in conjunction with (50–25°) and (other–50°)

Area	x	y	z	Z	P
R inferior parietal lobe*	56	−56	36	4.72	0.021*
L inferior parietal lobe	−64	−58	32	4.43	<0.0001
Pre-SMA	0	14	54	4.27	<0.0001
R rostral dorsal premotor cortex	50	10	58	4.20	<0.0001
R anterior cingulate gyrus	12	30	42	4.07	<0.0001

* $P < 0.05$ corrected at the voxel level with a search volume correction in the inferior parietal lobe and the intraparietal sulcus. All other areas are reported for a $P < 0.0001$ uncorrected at the voxel level; voxel extent threshold 10, $Z \geq 3.80$.

Image acquisition

The PET images were acquired using a Siemens CTI HR+ (63 slices, 15.2-cm axial field of view) PET tomograph with collimating septa retracted operating in 3D mode. Relative rCBF was measured by recording the regional distribution of cerebral radioactivity using $H_2{}^{15}O$ as a tracer. After a 9-mCi bolus injection of $H_2{}^{15}O$, scanning 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. A transmission scan collected before the first emission scan permitted correction for radiation attenuation.

Data analysis

Image analysis: preprocessing

The data were analyzed with SPM99 (Wellcome Department of Cognitive Neurology, London, UK).

Each subject's PET data were realigned to the first scan of the time series. The estimates extracted from the rigid body transformation (described as three translations (*X, Y, Z*) and three rotations about the axes) were used to realign the images and to perform a mathematical adjustment (minimizing the sum of the squares of differences in intensity between each image and the reference) to remove movement-related components. The images were then spatially normalized into the system of reference of Talairach and Tournoux (1988) using as template a representative brain from the Montreal Neurological Institute series (Evans et al., 1994). The first step of spatial normalization was to determine the optimal affine transformation (correction for the variation in position and size) that mapped a brain image onto the template (minimization of first the sum of the squares of the differences between those two images and also the squared distance between the parameters and their known expectation). Residual differences between each pair of images were corrected using nonlinear basis functions (Friston et al., 1995). The normalization parameters were subsequently applied to the PET images. Finally PET images were filtered with the use of a low-pass Gaussian filter (FWHM = 11.1 13.2 14.5 mm) to reduce noise and maximize signal. The smoothness was achieved by forcing the deformations to consist of a linear combination of predefined smooth spatial basis functions.

Statistical model and inference

The data were modeled so as to partition the rCBF of each voxel into components of interest, confounds of no interest, and an error term. The data were first adjusted for the effect of global image signal using proportional scaling. The fraction of mean signal over the whole brain was specified for thresholding signal intensities above the gray matter value. Since the subjects were requested to move the joystick freely, there were some differences in the amount of movement between subjects and between conditions. To eliminate this bias, the coordinates of the position of the joystick were recorded so as to obtain a measure of the distance covered by the joystick. This reflected the amount of movement made by each subject in each condition. These measures were modeled as confounds in the analysis so as to remove variations in blood flow that were related to the amount of movement.

The analysis of regionally specific effects was realized using the general linear model. We specified six effects of interest: 0°, 25°, 50°, other, C1, and C2. The 25° and 50° effects of interest lumped together the trials in the two directions of deviation (to the left and to the right). We were interested in finding brain areas showing increased or decreased rCBF as a function of the discrepancy between the movements made by the subjects and the movements of the virtual hand on the screen. To achieve this aim the four experimental conditions (0°, 25°, 50°, and other) were modeled as independent covariates and two conjunction analyses (Price and Friston, 1997) of three contrasts were performed. The first one identified brain areas showing

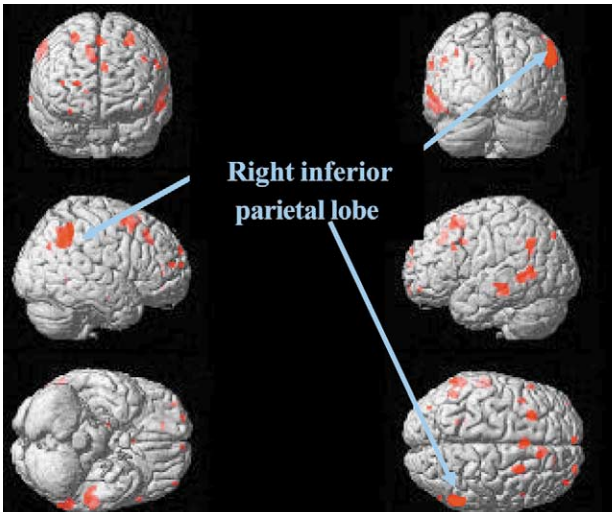

Fig. 1. Brain areas showing increased rCBF from 0° to other conditions: (25–0°) in conjunction with (50–25°) and (other–50°) ($P < 0.0001$ uncorrected for multiple comparisons).

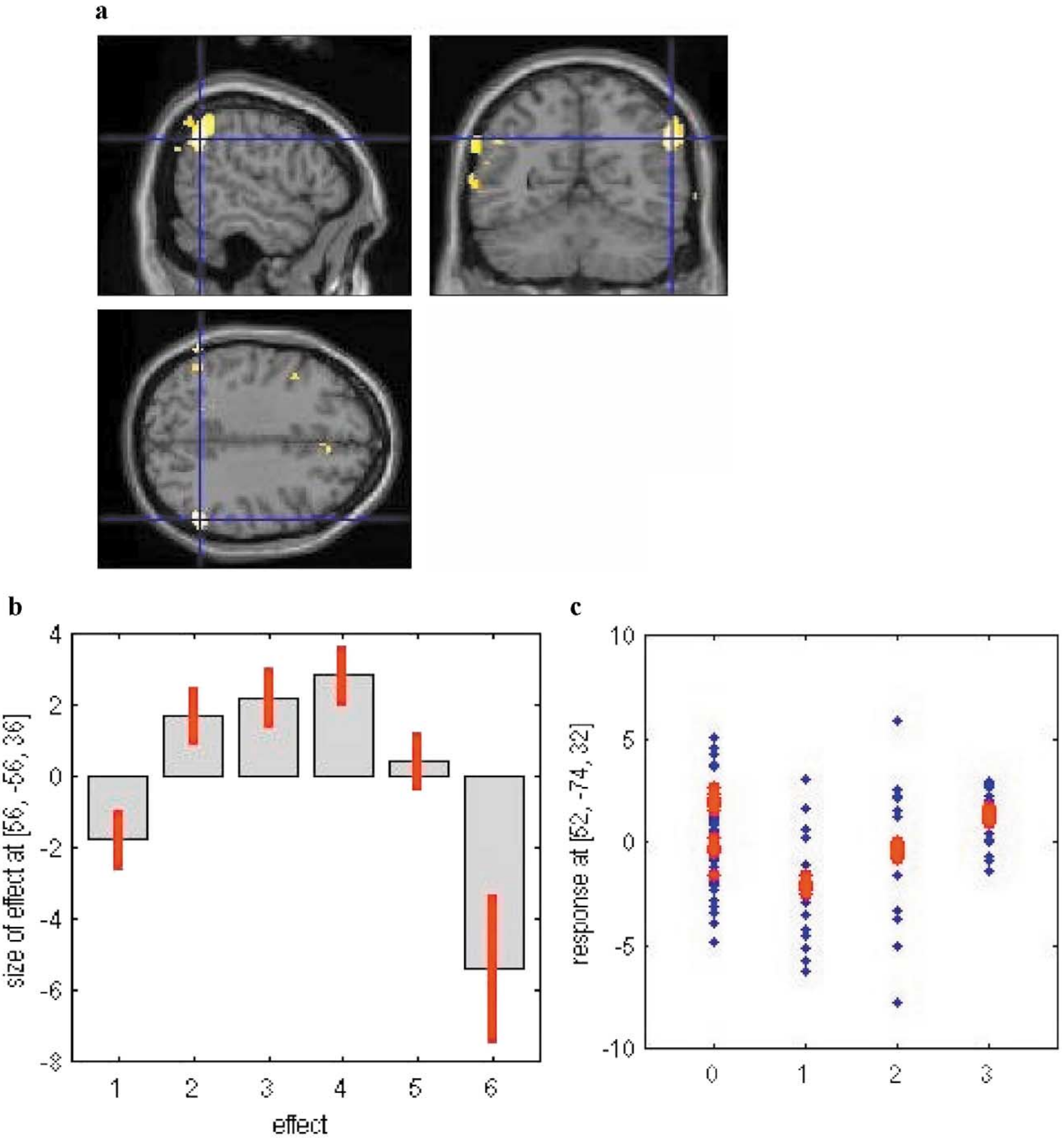

Fig. 2. (a) The peak activation in the right inferior parietal lobe (*x* = 56; *y* = −56; *z* = 36; *Z* = 4.72) from the conjunction analysis between the contrasts (25–0°); (50–25°); and (other–50°). This activation is superimposed on sagittal, coronal, and transverse sections of the T1-weighted MRI. (b) Parameter estimates at the same coordinates. The effects of interest are 0° (1); 25° (2); 50° (3); other (4); C1 (5); C2 (6). This graph clearly shows increased rCBF in the right inferior parietal lobe from 0° to other conditions. (**c**) Fitted and adjusted responses in the right inferior parietal lobe (*x* = 52; *y* = −74; *z* = 32; *Z* = 3.77). The effects of interest are 0° (1); 25° (2), and 50° (3). The effect of interest (0) regroups the other and the two control conditions. This graph clearly shows parametric increased rCBF conditions in the right inferior parietal lobe from 0 to 50°.

increased rCBF with increasing distortion from the 0° condition to the other condition ((25–0°) in conjunction with (50–25°) and (other–50°)). The second analysis allowed us to determine brain areas showing decreased rCBF with increasing distortion from the 0° condition to the other condition ((0–25°) in conjunction with (25–50°) and (50°–other)). An exclusive masking procedure with the contrast ((0° + 25° + 50° + other) − C1) was applied to each conjunction analysis to eliminate hemodynamic activity related to visual feedback and eye movements. In the C1 condition the subjects were requested to move the joystick while fixating on the center of the blank screen.

We were also interested in identifying brain areas showing parametric increased or decreased rCBF as a function of the discordance for the first three conditions (0°, 25°, 50°). These conditions were modeled as three levels of a same covariate "distortion." The regression with this covariate was then calculated for every voxel in the whole brain.

The models were framed in terms of a statistical parametric map of a t value SPM $\{T^3\}$ for the conjunction analysis and of a SPM$\{t\}$ transformed into SPM (Z) for the regression analysis. Since we were interested in brain activity in the right inferior parietal and in the anterior insula and we had strong a priori hypotheses, we first defined search volume corrections in a region involving the inferior parietal lobe and the intraparietal sulcus and in a second region involving the insula and the circular insular sulcus. To look for other brain regions showing a modulation of their activity as a function of the discordance, we analyzed the SPM (Z) thresholded at $P < 0.0001$ uncorrected for multiple comparisons at the voxel level or thresholded at $P < 0.05$ corrected at the cluster level. Only activations with a $Z \geq 3.80$ were taken into account. Finally, brain activity localization was identified using the atlas of neuroanatomy by Duvernoy (1992).

Results

Behavioral results

After each experimental condition the subjects were requested to indicate whether the movements they saw on the screen exactly corresponded to their executed movements (self response) or if they deviated (distorted response) or were controlled by the experimenter (other response). Subjects gave 100% of correct responses for the 0° trials and for the other trials. However, errors were observed in the distortion conditions. Errors were found in 21.9% of cases (self response) for the 25° trials and in 6.2% of cases (other response) for the 50° trials. These results indicate that subjects were able to distinguish between the different conditions. The occasional confusion of 50% distortion with other justifies the treatment of the other condition as an extreme form of distortion rather than a qualitatively different effect.

Measurements of rCBF

Brain areas increasing their activity as a function of the degree of discordance between the executed and the seen movements

The conjunction analysis between (25–0°), (50–25°), and (other–50°) allowed us to identify brain areas that show significant rCBF increase from the 0° condition to the other condition (Table 1). The less the subjects felt in control of the movements of the virtual hand, the more these areas were found to be activated. This analysis indicated activation in the right inferior parietal lobe in both the right angular gyrus and the right supramarginal gyrus (see Fig. 1).

The comparison using a search volume correction (localized in the inferior parietal lobule and the intraparietal sulcus) revealed a significant peak activation in the right angular gyrus at $x, y, z = 56\ -56\ 36$ ($P = 0.02$ corrected for multiple comparisons, $k_E = 257$) (see Fig. 2a). Increased activation of this region from the 0° to the other conditions can be observed in Fig. 2b showing the parameters estimates in the right angular gyrus. The same conjunction analysis was used without using a region of interest in order to identify brain activations that were not predicted. We only report brain areas with a $Z \geq 3.80$ ($P < 0.001$ uncorrected for multiple comparisons). This analysis revealed activation in the right inferior parietal lobe and activations in the left inferior parietal lobe, the pre-SMA, the right rostral dorsal premotor cortex, and the right anterior cingulate.

We were also interested to see whether brain areas revealed in the conjunction analyses were parametrically modulated across the first three conditions (0°, 25°, 50°). A regression analysis involving these conditions revealed increased rCBF in the angular gyrus bilaterally ($P < 0.001$ corrected at the cluster level). In the right hemisphere, the maxima was at $x, y, z = 52\ -74\ 32$ with a Z score $= 3.77$). Fig. 2c shows parametric increased rCBF in the right inferior parietal lobe from 0 to 50°. We also observed activation in the right pre-SMA ($P < 0.001$ uncorrected for multiple comparisons).

Brain areas decreasing their activity as a function of the degree of discordance between the executed and the seen movements

The conjunction analysis between (0–25°), (25–50°), and (50°–other) identified brain areas showing significant decreased rCBF from the 0° condition to the other condition. The more the subjects felt in control of the movements of the virtual hand, the more these areas were activated. A first comparison using a search volume correction (localized in the insular cortex bilaterally) revealed activation in the right posterior insula at $x, y, z = 40\ -10\ 16$ ($P = 0.064$ corrected for multiple comparisons) (see Fig. 3a). Increased activation of this region from the other to the 0° conditions can be easily observed in Fig. 3b showing the parameters estimates in the right posterior insula. To investigate whether other brain areas showed significant decreased rCBF, we looked at brain areas with a $Z \geq 3.80$ ($P < 0.001$ uncorrected for multiple comparisons) without defining a region of interest. This comparison revealed activations in the right cerebellum (see Table 2).

Finally, we evaluated whether activation in these brain areas was parametrically modulated across the first three conditions (0°, 25°, 50°). The regression analysis revealed decreased rCBF in the posterior insula bilaterally ($P < 0.001$ corrected at the cluster level). In the right hemisphere, the maximum was at $x, y, z = 42\ -16\ 10$ with a Z score $= 3.65$). Fig. 3c shows parametric decreased rCBF in the right posterior insula from 0 to 50° conditions. We also observed activation in the cerebellum bilaterally ($P < 0.001$ uncorrected for multiple comparisons).

All experimental conditions vs observation control condition (C2)

Contrasting all experimental conditions with the observation of action condition (C2) revealed significant activation ($P < 0.001$ uncorrected for multiple comparisons) in brain areas typically associated with motor tasks involving the right hand (the right cerebellum, the right cerebellar vermis, the left primary motor cortex, the right ventral opercular premotor cortex, and the right inferior parietal cortex). Most of these activations did not survive correction for multiple comparisons. Additional activation was found in the left anterior orbital gyrus, the left medial orbital gyrus, and the right posterior orbital gyrus. The coordinates of these areas, the Z values, and the probability score uncorrected for multiple comparisons are shown in Table 3.

All experimental conditions vs execution control condition (C1)

Contrasting all experimental conditions with the execution control condition (C1; making movements without visual feedback) revealed significant activation ($P < 0.001$ corrected for multiple comparisons) in brain areas associated with visual perception. Activation was observed with a peak in the right cuneus extending into the precuneus, the inferior occipital cortex, the medial occipital cortex, and the superior occipital cortex bilaterally. As anticipated, this network included the motion area V5/MT bilaterally. This region was predicted since the subjects watched the movements of a virtual hand in each experimental condition.

Discussion

This study aimed at evaluating whether the feeling of being in control of one's action can be correlated with brain activity. The feeling of being in control depends on the concordance between the subject's intention (e.g., to move the hand in a certain direction) and information provided by his senses (e.g., seeing one's hand moving in the intended direction). This feeling is the basis for attribution judgments (e.g., "I am the one causing this movement" or "Somebody else must be causing this movement"). In our experiment, the introduction of a systematic and graded discordance between subject's intention and reafferent information was used to produce a parametric variation in the feeling of being in control.

Increased activity with decreasing feeling of controlling the movements

Right inferior parietal cortex

Our findings demonstrate that a decreasing feeling of control due to larger and larger degrees of distortion was associated with increased rCBF in the right inferior parietal lobule and, to a lesser extent, in a symmetrical zone on the left side.

Interestingly, the peak activation in the right hemisphere (56, −56, 36) is located a few millimeters more lateral than the fMRI activation (44, −58, 32) reported by Farrer and Frith (2002). In their study, this activation was observed when the subjects attributed an action to another agent, compared to a self-attribution condition. Our experiment further shows that this activation was modulated as a function of the feeling experienced by the subject of being in control of the action. Activation of the right inferior parietal lobule at closely similar coordinates in these two studies using two very different paradigms is thus a strong argument for the role of this region in the process of self-attribution of an action. As mentioned in the introduction, the right inferior parietal cortex has previously been identified as a key area for this type of process (Ruby and Decety, 2001 [50, −58, 30]; Farrer and Frith, 2002 [56, −56, 36]; Decety et al., 2002) [56, −46, 28]).

The integration of visual and somatosensory signals processed in the parietal–occipital junction around the angular gyrus confers on this region a role in the elaboration of an image of the body in space and in time (see review in Benton and Silvan, 1993). Self-recognition is a highly consistent process which depends on a vailable cues from the visual position of the hand with respect to the body and from the presence of movements (Van den Boos and Jeannerod, 2002). The graded activation of the right inferior parietal lobe that we observed in the present study would thus relate to the increased degree of discordance between central signals arising from the motor command and visual and kinesthetic signals arising from movement execution. The mismatch between normally congruent sets of movement-related signals is likely to result in an increased level of processing of these signals.

We have proposed the activity seen in inferior parietal cortex relates to the feeling of loss of agency associated with the discrepancy between intended actions and sensory feedback. However, from the experiment discussed so far it is possible that the activity in this region relates solely to the sensory discordance. The feeling of agency might relate to activity in other regions. We think this is unlikely on the basis of various pathological cases in which the primary disorder concerns the feeling of agency rather than sensory discordance. Lesions of the inferior parietal cortex, especially on the right side, have been associated with delusions about the patient's limb that may be perceived as an alien object or as belonging to another person (Critchley, 1953; Nightingale, 1982; Leiguarda, 1993; Bundick and Spinella; 2000; Daprati et al., 2000).

In a different pathological context, abnormal hyperactivity in the right inferior parietal cortex has also been associated with disorders of feelings of agency in psychiatric and neurological patients (Spence et al., 1997 [36, −32, 36];

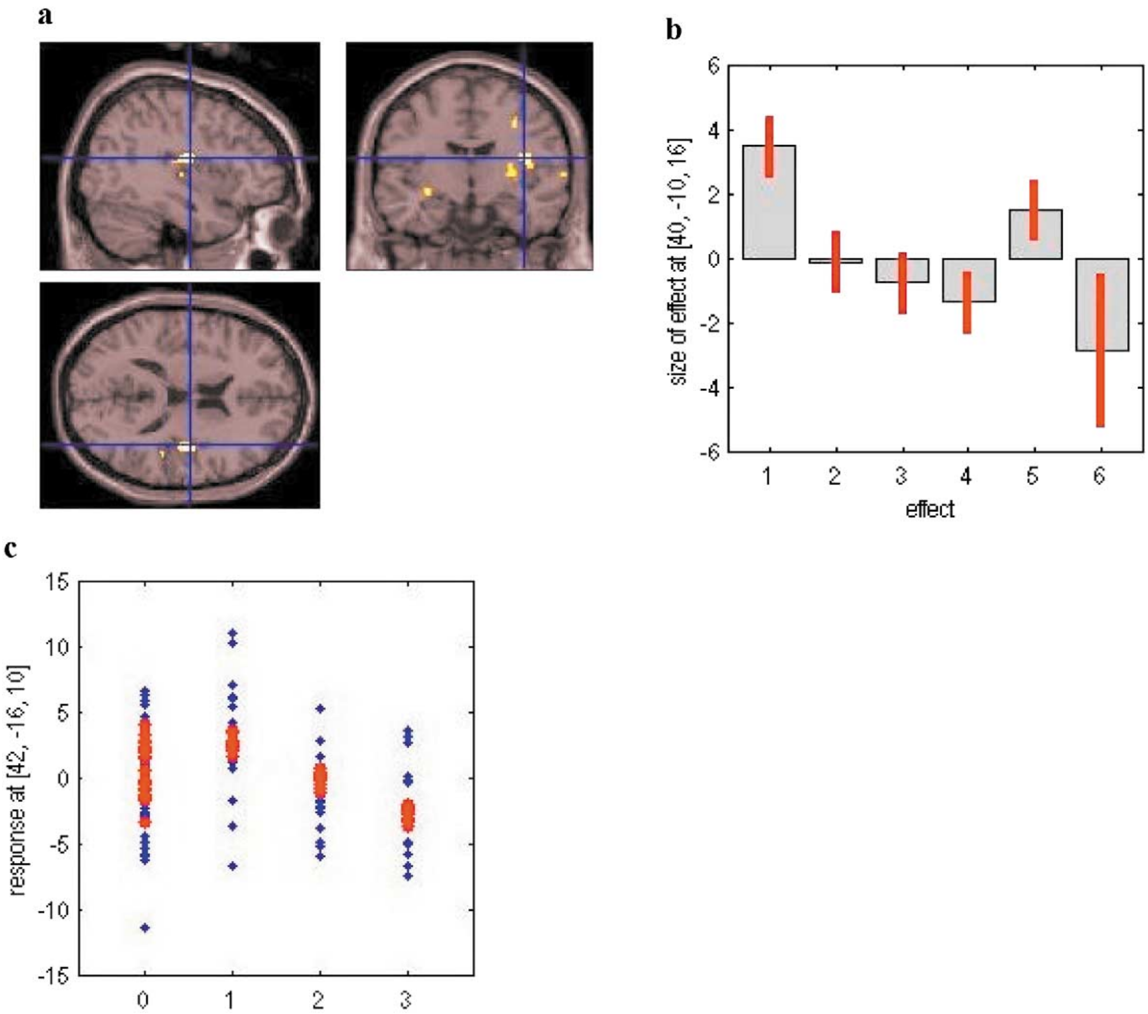

Fig. 3. (a) The peak activation in the right posterior insula ($x = 40$; $y = -10$; $z = 16$; $Z = 4.42$) from the conjunction analysis between the contrasts (0–25°); (25–50°); and (50°–other). This activation is superimposed on sagittal, coronal, and transverse sections of the T1-weighted MRI. (b) Parameter estimates at the same coordinates. The effects of interest are 0° (1); 25° (2); 50° (3); other (4); C1 (5); C2 (6). This graph clearly shows decreased rCBF in the right posterior insula from 0° to other conditions. (c) Fitted and adjusted responses in the right posterior insula ($x = 42$; $y = -16$; $z = 10$; $Z = 3.64$). The effects of interest are 0° (1); 25° (2); and 50° (3). The effect of interest (0) regroups the other and the two control conditions. This graph clearly shows parametric decreased rCBF in the right posterior insula from 0 to 50° conditions.

Simeon et al., 2000; Franck et al., 2002). These patients report that they do not have control over their own actions.

The effects of the distortion were not confined to inferior parietal cortex. Other areas were also found to be activated, namely, the rostral part of the dorsal premotor cortex, the pre-SMA, and the right anterior cingulate gyrus.

Table 2
Brain areas showing decreased rCBF from 0° to other conditions: (0–25°) in conjunction with (25–50°) and (50°–other)

Area	*x*	*y*	*z*	*Z*	*P*
R posterior insula*	40	−10	16	4.42	0.064*
R cerebellum	20	−38	−28	4.38	<0.0001

* *P* corrected at the voxel level with a search volume correction in the insula. All other areas are reported for a $P < 0.0001$ uncorrected at the voxel level; voxel extent threshold 10, $Z \geq 3.80$.

Premotor cortex

Activation in the frontal lobe was localized in the rostral subdivision of the dorsal premotor cortex (PMdr) and the pre-SMA. These activations cannot be due to residual motor activity, because the conjunction analysis eliminated brain activity related to execution. Also, the quantity of movements in each condition was taken into account and removed in the analysis so as to eliminate brain activity related to possible differences between conditions.

Evidence from a variety of studies suggest that the PMdr and the pre-SMA are more involved in cognitive processes than in motor processes and that PMdr has more in common with the pre-SMA than the SMA (Picard and Strick, 2001, for review). Studies in monkeys have found that neuronal properties of the PMdr reflect more sensory and attentional signals than motor preparation (Boussaoud and Wise,

Table 3
Brain areas activated during all the experimental conditions contrasted to observation control condition (C2)

Area	*x*	*y*	*z*	*Z*	*P*
R cerebellum	14	−50	−24	5.05	0.01*
R cerebellum	34	−40	−38	4.73	0.042*
R vermis	6	−54	−6	4.29	<0.0001
L anterior orbital gyrus	−22	46	−26	4.47	<0.0001
L medial orbital gyrus	−20	34	−28	3.8	<0.0001
R posterior orbital gyrus	32	34	−32	4.2	<0.0001
L primary motor cortex	−36	−38	72	4.05	<0.0001
R ventral opercular premotor cortex	52	8	4	3.95	<0.0001
R inferior parietal lobe	70	−40	36	3.92	<0.0001

* $P < 0.05$ corrected. All other areas are reported for a $P < 0.0001$ uncorrected at the voxel level; voxel extent threshold 10.

1993a, 1993b). A recent fMRI study in humans confirmed this result in showing a rostrocaudal specialization within PMd with attention-related activation in the rostral and medial parts of the PMd and motor preparation-related activity in the caudal part (Simon et al., 2000). Increased activation in the premotor cortex may thus reflect increased visuospatial attention to the movements of the virtual hand on the screen. As the visual feedback was increasingly distorted, visuospatial attention was modified across the conditions of distortion, in an attempt to compensate for the loss of action control.

Anterior cingular gyrus

Activation of anterior cingulate cortex is commonly associated with error detection between the subject's intention and the executed corresponding action. In the ERP study of Milner et al. (1997), a negative deflection was recorded when subjects received feedback indicating incorrect performance in a time-production task. The scalp distribution of this potential was consistent with a distributed source involving the anterior cingulate cortex. Implication of this area in error processing has also been shown recently by Menon et al. (2001) using event-related fMRI. Error related brain activation during Go/NoGo response inhibition involved a neural circuit including the rostral part of the anterior cingulate. In the present study, increased discordance between the expected sensory outcome and the visual outcome would lead the subjects to expect errors; this would be associated with an increased activation of the anterior cingulate cortex.

Decreased activity with decreasing feeling of controlling the movements

Looking at decreased rCBF associated with increased discordance between movements executed by the subjects and the movements of the virtual hand showed activation in the right posterior insula. Activation was also observed in the right cerebellum.

Posterior insula

The posterior insula is a multimodal sensory association area in which input from the five senses converge (see Flynn et al., 1999, for review). Berthier (1987) has reported a case of a patient with a right insular lesion in which there was a multimodal sensory neglect. According to Craig et al. (1996) this area would be involved in a pathway implied in self-awareness. In a recent study, bilateral activation of the anterior insula was observed when subjects were requested to attribute an action to themselves compared to a condition where they attributed it to another person [40, 8, 2] and [−36, −2, 2] (Farrer and Frith, 2002). Activity in the right anterior midposterior insula has also been observed in other studies involving self-attribution, although not in the context of action (Fink et al., 1996; Kircher et al., 2000 [49, −3, 4], 2001 [40, −3, 4]). We have no explanation as to why the localization of the activated areas differ in these studies, except that we know that these two regions are densely and reciprocally connected. In addition, both include somesthesic representations and are considered multimodal areas.

Decreased activation of the insula while the subjects experience discordance between what they do and what they see suggests that, in contrast to parietal cortex, activity in the insula correlates with the degree of match between the different signals related to action. When the two are perfectly matched, the activity in the insula would be at its maximum. Farrer and Frith (2002) have already proposed that the sense of agency would be associated with a shift of attention toward representations integrating the different signals associated with the action and that this integrating process might involve the insula.

Cerebellum

The cerebellum has been shown to be involved in predicting the sensory consequences of an action (see Wolpert et al., 1998, for a review). Blakemore et al. (1998, 2001) have shown an increased activation in this area when subjects experienced externally produced tactile stimulation compared to self-produced tactile stimulation. These authors suggested that the cerebellum differentiates between movements depending on their specific sensory consequences.

A system for attributing actions to the self?

The problem raised by the present results is to determine how the modulation of activity for different degrees of discordance between an intended and an executed action, mainly in the posterior parietal cortex and in the insula, can be at the origin of the feelings of being in control of an action and attributing an action to oneself.

One must be aware that the changes in activity that we observed in these regions cannot be dissociated from possible changes in other cortical areas. Several studies point to the role of prefrontal cortex in intentional actions. Frith et al. (1991a) showed that willed action produces an increase in activation in the dorsolateral prefrontal cortex and the anterior cingulate. This increased activity is associated with a decrease of activity in the angular gyrus. Similarly, in a word generation task, Frith et al. (1991b) showed a concomitant activation of the prefrontal cortex and deactivation of the superior temporal cortex. According to Frith and Dolan (1996), the frontotemporal interactions observed in this task would label inner representations as resulting from intrinsic actions. For these authors, the modulation of perceptual areas by the activity of areas concerned with action generation serves to identify the source of perceptions (internal or external).

Fink et al. (1999), using a situation similar to the one used in the present study and creating a similar conflict between intention and action, found a specific activation in the right dorsolateral prefrontal cortex. However, this study differs in a number of ways from the present one. The subjects in the study of Fink et al. (1999) knew that no other agent was involved and were not therefore required to make attributions about agency. In our study the subjects knew that other agents were sometimes involved and were explicitly instructed to direct their attention to the origin of the movement they saw. This difference could be one of the reasons why dorsolateral prefrontal activation was not observed in the present study or in the study by Farrer and Frith (2002).

Conclusion

The findings of this study first suggest that the factors which ultimately determine the sense of agency are based not on discrete, but on continuous mechanisms. Modulating the sense of causing or controlling an action, induced by distorting the relationship between the different action-related signals, modulates the activity of brain areas that are involved in higher-order representations of the body. The greater the correspondence between the different signals, the greater the sense of agency and the greater the activity in right posterior insula. In contrast, the weaker the correspondence, the greater the activity in the right inferior parietal lobe.

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