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Experiencing Oneself vs Another Person as Being the Cause of an Action: The Neural Correlates of the Experience of Agency

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The present study is aimed at identifying the neural correlates of two kinds of attribution: experiencing oneself as the cause of an action (the sense of agency) or experiencing another person as being the cause of that action. The experimental conditions were chosen so that they differed only in their requirement to attribute an action to another person or to oneself. The same motor task and the same visual stimuli were used in the experimental conditions. Subjects used a joystick to drive a circle along a T-shaped path. They were told that the circle would be driven either by themselves or by the experimenter. In the former case subjects were requested to drive the circle, to be aware that they drove the circle, and thus to mentally attribute the action seen on the screen to themselves. In the latter case they were also requested to perform the task, but they were aware that action seen on the screen was driven by the experimenter. In accord with previous studies, the results showed that being aware of causing an action was associated with activation in the anterior insula, whereas being aware of not causing the action and attributing it to another person was associated with activation in the inferior parietal cortex. These two regions are involved in the perception of complex representations of the self and of its interactions with the external world. We suggest that the anterior insula is concerned with the integration of all the concordant multimodal sensory signals associated with voluntary movements. The inferior parietal cortex, in contrast, represents movements in an allocentric coding system that can be applied to the actions of others as well as the self.

INTRODUCTION

Most studies concerned with consciousness have focused on the awareness of some aspects of the outside world. However, another important aspect of consciousness concerns awareness of our own actions and our sense of being in control of them (the sense of agency). One of the key questions asked in this domain is, how can we distinguish our actions and their effects from those of other people? How do we refer the origin of an action to its proper agent? This ability has been called "attribution of action judgement" (Georgieff and Jeannerod, 1998; Jeannerod, 1999). This question is important because most of our actions are realized in a social context in which we have to interact with other people. Appropriate interactions require that an action is continuously and correctly referred to its agent, thus differentiating the actions caused by oneself from those caused by others.

Agency has been assigned a key role in self-consciousness. According to Gallagher (2000) self-consciousness is constituted in part by a "minimal self" defined as consciousness of oneself as an immediate subject of experience, unextended in time. This immediate self-awareness includes self-ownership, or the sense that "it is my body that is moving," and self-agency, or the sense that "I am the initiator of the action and thus that I am causally involved in the production of that action" (Gallagher, 2000). In the normal experience of voluntary or willed action, the sense of agency and the sense of ownership coincide and are indistinguishable.

In this study we focus on this sense of agency and extend it to a more general ability, that is, to be aware of who has caused the action (oneself or another person). This capacity has been described by Georgieff and Jeannerod (1998) as a "Who" system that permits us to refer the origin of an action to its proper agent and thus to distinguish the self from others. This Who system would have a major role in the consciousness of action and self-consciousness.

The operation of this Who system will depend, in part, on the sensory signals that result from actions. There are two kinds of signal. An arm movement causes a direct effect on the somatosensory system whether the movement is active or passive. There are

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also indirect effects of arm movements such the sight of a moving mouse pointer or the sound of a key press. There is evidence that the direct somatosensory signals caused by our own actions are attenuated, presumably on the basis of corollary discharge derived from the signals associated with the motor commands that generated the movement (Blakemore *et al.*, 1998). This attenuation permits a distinction between active and passive movements and, thus, identifies the agent. In this study, however, we were concerned only with the indirect consequences of an action. Our subjects always performed an action and experienced the appropriate somatosensory feedback, but what they saw on the screen was sometimes the consequences of the experimenter's action rather than their own.

Our study is aimed at identifying the neural correlates of two different judgments of attribution; experiencing oneself as the cause of an action (the sense of agency) or experiencing another person as being the cause of that action. The experimental conditions were chosen so that they differed only in their requirement to attribute an action to another person or to oneself. The same motor task and the same visual stimuli were used in all the experimental conditions. Subjects manipulated a joystick and saw a colored circle moving on a screen. Sometimes the subject caused this movement and sometimes the experimenter. This paradigm allowed us to study the sense of agency without any confounding from the sense of ownership. To achieve this subjects were requested to execute an action during all the different experimental conditions. By doing so the effect related to the sense of ownership (I am performing an action) would be present in all conditions and would be canceled in the various contrasts. We used an event-related fMRI technique to measure hemodynamic activity related to a single event (the attribution judgment). This technique also allowed us to randomize the order of presentation of the different events and thus avoid any habituation effects or anticipation in the subjects. The majority of the previous studies of this topic have used blocked designs with PET.

In previous studies attribution of actions to another has been consistently associated with activity in the right inferior parietal lobe. Patients with delusions of control who erroneously attributed their actions to another showed abnormally high activation in this region (Spence *et al.*, 1997). Subjects imagining someone else acting showed greater activity in this area than when they imagined themselves making the action (Ruby and Decety, 2001). Subjects reading words who heard the sound of someone else's voice instead of their own also showed greater activity in this area (McGuire *et al.*, 1996). In this last study, hearing the distorted sound of one's own voice was associated with activity in the left anterior insula. Activity was also seen in this area, among others, in the study of Ruby and Decety (2001), when subjects imagined themselves acting. Activity in the right anterior insula has been observed in the same area in two studies involving self-attribution, although not in the context of action. Kircher *et al.* (2000, 2001) observed activity here when subjects had to recognize their own face or descriptions of themselves in words. Fink *et al.* (1996) saw activity here when subjects identified their own memories. On the basis of these previous studies we expected to observe different brain activity in the right inferior parietal cortex during attribution of action to another and in the anterior insula when action was attributed to the self.

MATERIAL AND METHODS

Twelve right-handed volunteers (4 females, 8 males) with a mean age of 29 years gave written informed consent. None had a history of neurological or psychiatric disease. The study was approved by the Ethics Committee of the National Hospital for Neurology and Neurosurgery.

The main purpose of this experiment was to compare brain activity associated with attributing an action to oneself and attributing an action to another person. Subjects used a joystick to drive a colored circle along a T-shaped path of the same color (Fig. 1). A cross appeared on the right or the left of the screen to inform the subject into which branch of the T he had to drive the circle. The joystick was held with two fingers (the thumb and the index) of the right hand in order to avoid any movement of the shoulders during the execution of the task.

This experiment used a 2 × 2 factorial design. The first factor referred to the type of attribution judgment made by the subject. He was told that the circle would be driven either by himself or by the experimenter (in reality the circle was driven by either the subject or the computer). In the former case subjects were requested to drive the circle, to be aware that they drove the circle, and thus to mentally attribute the visualized action to themselves. In the latter case they were also requested to perform the task, but they were aware that the experimenter was driving the circle and so attributed the visualized action seen on the screen to her. To emphasize the fact that they were not driving the circle in this latter case, the subject was told that the circle would go through the branch of the T opposite to the one indicated by the cross.

The second experimental factor referred to the predictability of the situation. In the predictable situation the subject knew from the beginning of the trial whether he or the experimenter would be driving the circle. In the unpredictable situation the subject did not know at the beginning who would be driving the circle. He could only discover who was driving the circle halfway through the trial. If the circle went

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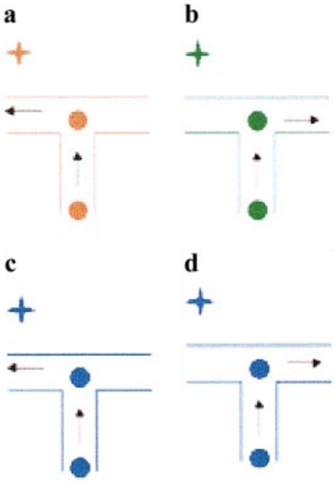

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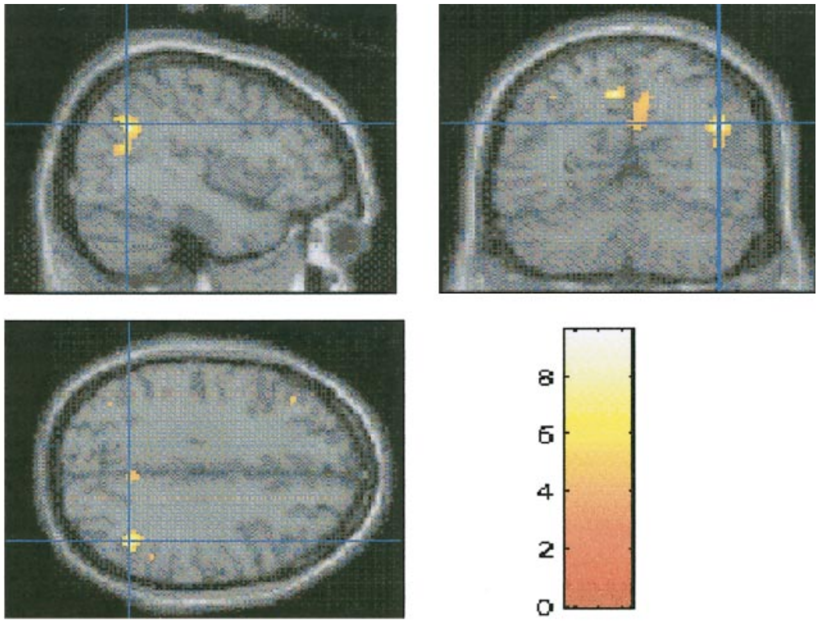

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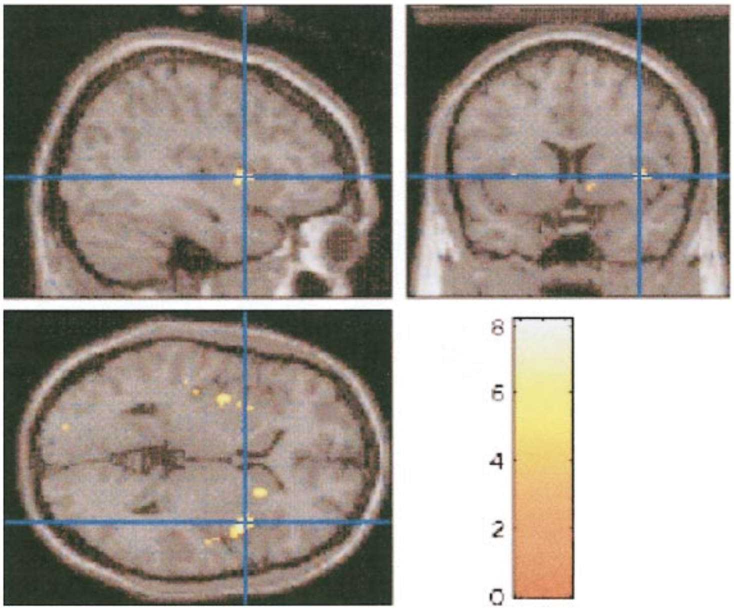

FIG. 1. Schema of the different experimental conditions of the 2 × 2 factorial design. (a) Self-attribution in the "predictable" situation. (b) Other-attribution in the "predictable" situation. (c) Self-attribution in the "unpredictable" situation. (d) Other-attribution in the "unpredictable" situation.

FIG. 2. Attributing an action to another person activates the angular gyrus bilaterally. The SPM thresholded at $P < 0.0001$ (uncorrected) and superimposed on sagittal, coronal, and transverse sections of the T1 image shows the activation in the right angular gyrus ($x = 44$; $y = -58$; $z = 32$), $Z = 4.86$.

FIG. 3. Attributing an action to oneself activates the anterior insula bilaterally. The SPM thresholded at $P < 0.0001$ (uncorrected) and superimposed on sagittal, coronal, and transverse sections of the T1 image shows the activation in the right anterior insula ($x = 40$, $y = 8$, $z = 2$), $Z = 4.55$.

through the branch of the T indicated by the cross then he was driving it. If the circle went through the branch opposite the cross then he could attribute the action to the experimenter. Each of the factors was divided into two levels: driving the circle either to the right or to the left. Information about the type of attribution and the predictability of the situation was given by a specific color. Four colors were used: one color informed the subject that he was in a predictable situation and that he was driving the circle. Another color informed the subject that he was in a predictable situation but the circle was being driven by the experimenter. A third color informed the subject that he was in an unpredictable situation and thus could not attribute the action until the circle went through one of the two arms of the T. Two low-level control conditions were represented by a fourth color. The subject watched the circle moving either to the right or to the left, without doing anything. The information given by a color was counterbalanced across subjects to avoid any confounding with the processing of colors. Thus all the conditions were determined only 3 times by the same color. Finally, null event conditions in which subjects did nothing and saw nothing were included. As far as the subject was concerned these events were experienced simply as longer gaps between trials. Each of these 11 conditions lasted 5 s and was repeated 20 times. The condition onset asynchrony was variable between 5 and 5.6 s. The experiment was divided into two sessions of 10 min each to allow subjects to keep up their level of concentration.

Functional Imaging

Data were acquired with a 2-T Magnetom Vision whole-body MRI system (Siemens, Erlangen, Germany) equipped with a head volume coil. T1-weighted anatomical images and contiguous multislice T2*-weighted echoplanar images (echo time 40 ms, 80.7 ms/image, 64×64 pixels (19.2×19.2 cm)) were obtained. Volumes were acquired continually every 2 s. Each volume comprised 26 slices (slice thickness of 3 mm). Two sessions of 10 min each were recorded. Three hundred ten scans were acquired for each session. Five "dummy" volumes were acquired at the start of each session to allow for T1 equilibration effects. The interval between the scan impulse and the start of the stimulus presentation was randomized by introducing jitters of TR/1 TR/3 TR/4, TR/5, and TR/6 s. Their order was randomized.

Image Processing

Image and statistical analyses were performed using statistical parametric mapping (SPM99). All volumes were realigned to the first volume to correct for interscan movement and then resliced using a sinc interpolation in space (Friston *et al.*, 1995a). To correct for their different acquisition times, the signal measured in each slice was shifted relative to the acquisition of the middle slice using a sinc interpolation in time (Henson *et al.*, 1999). Each volume was normalized (Friston *et al.*, 1995a) to a standard EPI template volume, based on the Montreal Neurological Institute reference brain (Evans *et al.*, 1994), in the space of Talairach and Tournoux (1988) using nonlinear basis functions. Finally the data were smoothed with a Gaussian kernel of 8 mm full width at half-maximum to compensate for residual variability after spatial normalization and to permit application of Gaussian random field theory to provide for corrected statistical inferences.

Data Analysis

The data were analyzed using SPM99 employing a random-effects model (Holmes and Friston, 1998) implemented with a two-level procedure. To test for the effects of interest we used a conventional analytical approach. We specified five effects of interest: "self-attribution in a predictable situation," "other-attribution in a predictable situation," "self-attribution in an unpredictable situation," "other-attribution in an unpredictable situation," and "control." Each effect of interest lumped together the trials of the two directions of displacement of the circle (to the left and to the right). These effects were modeled by convolving a boxcar function with a standard hemodynamic response function and its temporal derivatives to create regressors of interest. The data were normalized for global effects by proportional scaling. The random-effects analysis involved three stages. First, session-specific parameter estimates pertaining to each type of effect of interest were calculated for each subject for each voxel producing an image of parameter estimates (Holmes and Friston, 1998). Second, the specific contrasts of the parameter estimates (i.e., the appropriate weights which specify the comparisons between the effects of interest) were calculated in a voxel-wise manner to produce, for each subject, one contrast image for that particular comparison. Six contrast images were realized: "self-attribution vs control," "other-attribution vs control," "self-attribution vs other-attribution," "other-attribution vs self-attribution," "main effect of unpredictability," and an interaction term between unpredictability and attribution. Finally, the contrast images (one for each subject) for each effect were entered into a one-tailed t test with 11 degrees of freedom. The set of t values thus obtained constituted a statistical parametric map SPM$\{t\}$ (Friston *et al.*, 1995b). The SPMs for each effect modeled were transformed into SPM(Z)'s. Areas of activation were characterized in terms of their peak heights (Z-value maxima) with their positions specified (in coordinates x, y, and z) according to the stereotactic space of Talairach and Tournoux (1988). We report activations above a threshold corresponding to $P < 0.001$ (uncorrected for multiple comparisons) in the regions for which we had an a priori hypothesis. All other activations reported survived a threshold corresponding to $P < 0.05$ (corrected for multiple comparisons) at the cluster level.

RESULTS

The areas showing significantly increased BOLD signal during conditions in which subjects were required to attribute the visualized action to themselves, in a

TABLE 1

Brain Areas Activated during "Self-Attribution" Conditions Compared to Control Conditions

Area	x	y	z	Z value
Anterior insula L*	−40	2	2	3.74
SMA L	−8	−4	70	4.58
Lateral premotor cortex L	−26	−10	62	3.73
Primary sensorimotor cortex R	34	−32	44	4.16
Primary sensorimotor cortex L	−46	−30	60	3.76
Cerebellum	0	−66	−22	3.64

predictable situation, compared to the control condition were the primary sensorimotor cortex bilaterally, the left lateral premotor cortex, the left SMA, and the cerebellum. Activity was also evident in the left anterior insula. The coordinates of the areas activated, the Z values, and their corresponding probability values are shown in Table 1.

The areas showing significantly increased BOLD signal during conditions in which subjects were required to attribute the visualized action to the experimenter, in a predictable situation, compared to the control condition were the primary sensorimotor cortex bilaterally, the lateral premotor cortex bilaterally, the left SMA, and the left supramarginal gyrus. Activity was also seen in the right occipitoparietal fissure, in the cerebellum bilaterally, in the right precuneus, and in the right intraparietal sulcus. The coordinates of the areas activated, the Z values, and their corresponding probability values are shown in Table 2.

The areas showing significantly increased BOLD signal during conditions in which subjects were required to attribute the visualized action to the experimenter, in a predictable situation, compared to conditions in which subjects were required to attribute it to themselves were the precuneus bilaterally, the left lateral premotor cortex, and the angular gyrus bilaterally (Fig. 2). The coordinates of these areas, the Z values, and their corresponding probability values are shown in Table 3.

TABLE 2

Brain Areas Activated during "Other-Attribution" Conditions Compared to Control Conditions

Area	x	y	z	Z value
SMA L	−8	−4	54	4.75
Lateral premotor cortex R	34	−6	54	4.26
Lateral premotor cortex L	−24	−12	58	4.06
Primary sensorimotor cortex L	−38	−26	54	3.96
Primary sensorimotor cortex R	32	−30	42	4.35
Intraparietal sulcus R	44	−32	48	3.62
Supramarginal gyrus L	−30	−44	54	4.21
Parieto-occipital fissure R	18	−60	32	5.26
Precuneus R	8	−68	−46	3.38
Cerebellum R	16	−56	−24	3.64
Cerebellum L	−22	−64	−26	3.81

TABLE 3

Brain Areas Activated during "Other-Attribution" Conditions Compared to "Self-Attribution" Conditions

Area	x	y	z	Z value
Angular gyrus R	44	−58	32	4.86
Angular gyrus L	−48	−52	40	4.04
Precuneus L	−6	−58	50	4.62
Precuneus R	2	−50	44	3.76
Lateral premotor cortex L	−38	28	48	3.65

The areas showing significantly increased rCBF during conditions in which subjects were required to attribute the visualized action to themselves, in a predictable situation, compared to conditions in which they attributed it to the experimenter were the anterior insula bilaterally (Fig. 3). The coordinates of the areas activated, the Z values, and their corresponding probability values are shown in Table 4.

No significant increases in brain activity were revealed for the main effect of unpredictability and for the interaction term between the unpredictability and the attribution factors.

DISCUSSION

In this study we used event-related fMRI to investigate neural activity related to the judgment of attribution that refers the origin of an action to its agent. We found that the two effects of interest (attributing an action to oneself and attributing it to another person) elicited hemodynamic changes in distinct brain systems.

The restricted comparison of the "attribution to another" condition to the "attribution to the self" condition revealed activations in the angular gyrus bilaterally, in the left lateral premotor cortex, and in the precuneus (Table 3). Activity in these regions was also seen in the comparison of "attribution to another" with the control conditions (Table 1). This demonstrates that these regions increased in activity during the "attribution to another" condition rather than decreasing in the "attribution to self" condition.

The observation of greater activity in the parietal lobe, more markedly on the right, when attributing an

TABLE 4

Brain Areas Activated during "Self-Attribution" Conditions Compared to "Other-Attribution" Conditions

Area	x	y	z	Z value
Anterior insula R	40	8	2	4.55
Anterior insula L	−36	−2	2	4.21

action to another is consistent with previous imaging studies (McGuire *et al.*, 1996; Spence *et al.*, 1997; Ruby and Decety, 2001). There is also evidence that lesions in this region can lead to disorders in the attribution of action. Lesions in the right parietal cortex have been associated with disturbances in the feeling of belonging of the patient's limbs. In the neurological syndrome of the "alien hand," which can follow a right-sided parietal lesion, the limb is not only outside the control of the subject (as it might be in forms of alien hand produced by lesions of medial premotor cortex or corpus callosum), but is also perceived to be under the control of another person (Leiguarda, 1993; Bundick and Spinella, 2000). Other patients with right parietal lesion do not recognize their limbs as their own and perceive them as belonging to others (Critchley, 1953; Nightingale, 1982; Daprati *et al.*, 2000).

Metabolic abnormalities in the right inferior parietal cortex have been associated with self-awareness disorders in psychiatric and neurological patients. Spence *et al.* (1997) observed hyperactivity in the right inferior parietal lobule when schizophrenic patients experienced alien control (feeling of being controlled by another agent) during a movement selection task. Alteration of the subjective experience of the relationship of the self to the physical body occurring in patients with depersonalization disorder has also been associated with hyperactivity in the right inferior parietal lobe (Simeon *et al.*, 2000).

In our study, activation of the right inferior parietal lobe was observed when the subject was aware that he did not cause the action visualized on the screen and correctly attributed this to another person. This situation is close to that of the neurological and psychiatric patients described above who experience external control of their own actions. This result confirms experimentally the role of this region in the relationship of the self to the physical body.

The only region specifically associated with attribution to the self was the anterior insula bilaterally (Table 4). This result is consistent with previous imaging studies (McGuire *et al.*, 1996; Fink *et al.*, 1996; Kircher *et al.*, 2000, 2001; Ruby and Decety, 2001) in which subjects have made self-attributions. Furthermore lesions of the insula cortex have been shown to provoke somatic hallucinations in epileptic patients (Roper *et al.*, 1993). However, the function of this brain region is not well established.

Why should the parietal lobe have a special role in attributing actions to others while the anterior insula is concerned with attributing actions to the self? The sense of agency (i.e., being aware of causing an action) occurs in the context of a body moving in time and space. Damasio (1999) has suggested that the sense of agency critically depends upon the experience of such a body. There is evidence that both the inferior parietal lobe and the anterior insula are representations of the body.

The parietal lobe receives cortical afferents from primary and secondary sensory areas and has reciprocal connections with the premotor, cingular, and superior temporal cortices. These multiple connections allow an elaboration of internal representations of the external world and of our interactions with it. Moreover, 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 (Benton and Silvan, 1993).

There is anatomical and physiological evidence to suggest that the anterior insula, in interaction with limbic structures, is also involved in the representation of body schema (Bonda *et al.*, 1995). Neurophysiological studies in the monkey have revealed the involvement of the insula in higher levels of somatic function (Friedman, 1986), and Schneider *et al.* (1993) have identified a modality-specific somatosensory area in this region.

If both these regions contain representations of the body then we need to identify in what way these representations differ and how these differences relate to the attribution of actions to self or other. Jeannerod (1999) has suggested that making agency judgments about who has performed an act is likely to be made on the basis of central representations coded in allocentric coordinates. A common coding system of this kind is needed since it is not possible to represent the actions of others in the egocentric coordinates used for generating our own actions. There is strong physiological evidence that the inferior parietal cortex involved the kind of remapping process (Andersen *et al.*, 1985) that would be needed to generate representations of body movements in allocentric coordinates. Furthermore, activity is seen in the right inferior parietal cortex when subjects observe the actions of others in order to imitate them (Grèzes *et al.*, 1998)

There is some evidence that the anterior insula has a special role in integrating signals across modalities. In terms of anatomical connections the anterior insula is likely to be involved in integrating autonomic and visceral information (Flynn *et al.*, 1999). A number of studies have shown that the anterior insula is involved in verbal imitation (Wise *et al.*, 1999). The critical requirement for this task is to relate sounds to the articulatory movements being made to produce them. A recent imaging study found that the anterior insula was involved in integrating visual and auditory signals of movement (Lewis *et al.*, 2000). These results suggest that the anterior insula might be a polysensory integration area.

One aspect of the experience of agency that we feel when we move our bodies through space is the close correspondence between many different sensory signals. In particular there will be a correspondence between three kinds of signal: somatosensory signals directly consequent upon our movements, visual and auditory signals that may result indirectly from our movements, and last, the corollary discharge associated with motor commands that generated the movements. A close correspondence between all these signals helps to give us a sense of agency. In our experiment, subjects would be aware of the correspondence between their movements and the movement of the colored circle on the screen in the "self-attribution" condition. In the "other-attribution" condition, however, they would not expect a correspondence between the movements they made and the movements of the circle.

We suggest that the activation of the anterior insula when subjects attribute an action to themselves and the activation of the right inferior parietal lobe when they attribute the action to another agent reflect a shift in attention. During self-attribution attention is directed toward representations integrating the many sensory signals associated with the action. These representations are found in the anterior insula. During other-attribution attention is directed toward representations of actions in allocentric coordinates. Such representations are found in inferior parietal cortex especially on the right.

In conclusion, Georgieff and Jeannerod (1998) have postulated the existence of a Who system allowing the organism to refer the cause or origin of an action to its agent. This system would be complementary to the "What" and "Where" systems already described, which relate to awareness of external reality (see Jeannerod, 1997, for review). Our results suggest that the anterior insula and the right inferior parietal lobule may play a crucial role in the functioning of this Who system. The sense of agency or more generally of being aware of who has caused an action is related to the sense of a body acting in time and space. Our results confirm that the judgment of attribution is mainly associated with brain areas involved in the perception of complex representations of the self and of its interactions with the external world.

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