Leader or follower? Involvement of the inferior parietal lobule in agency

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Received 2 August 2002; accepted 10 August 2002

Agency is the sense that I am the one generating an action. In this neuroimaging experiment, subjects controlled a circle with a mouse while requested either to lead another circle (i.e., being the agent) or to follow it (i.e., being acted upon). Clusters within the right intraparietal sulcus were associated with following for the most rostral and leading for the most caudal ones. Bilateral activity in the inferior parietal lobule in conditions involving confusion about the origin of the action confirmed its role in agency. A lateralization effect was also found in these conditions, the response being stronger in the left inferior parietal lobule when subjects were not the agent of the performed action, and in the right when they were. *NeuroReport* 13:1975–1978 © 2002 Lippincott Williams & Wilkins.

Key words: Action; Agency; Human; Imitation; Inferior parietal lobule; Neuroimaging

INTRODUCTION

We have the idea of ourselves as agents, demonstrated by our use of 'I' when referring to our actions. Recently, interest in the self has been renewed both in developmental psychology and in cognitive neuroscience. An ecological sense of self is exhibited from birth [1], and neonatal imitation demonstrates that the other is recognized as being of the same sort as oneself [2]. This PET experiment was designed to explore the brain correlates of agency. The sense of agency has been defined as the sense that I am the one who is causing or generating an action, and is different to the sense of ownership, which is the sense that I am the one who is undergoing an experience [3]. In Shaun Gallagher's model, the coincidence between the sense of agency and the sense of ownership leads one to consider himself as the agent of an action. From a neurocognitive perspective, Gallagher's model can be translated into the framework of motor control based on internal models [4].

Reciprocal imitation paradigms are suited to tackle the question of agency. Visual and motor components are similar when one imitates or is imitated and can be related to the sense of ownership. The key distinction is the agent controlling the action. We previously demonstrated that the superior temporal gyrus and the inferior parietal lobule are involved in reciprocal imitation of hand manipulations of objects [5]. We hypothesized that the former region should be specific to the imitation of hand actions [6], while the latter would be involved in the sense of agency [5,7].

To test this hypothesis, we designed an experiment in which subjects were presented with two circles moving on a white screen. Subjects controlled one of these circles with a mouse, and were told that another person controlled the other circle. According to the experimental conditions, subjects were either leading or following the other circle.

We expected that the inferior parietal lobule would be activated when confusion between self's and other's actions may occur, reflecting its involvement in the sense of agency. Moreover we predicted that the hemodynamic response would be stronger in the right hemisphere when the subjects lead, and in the left hemisphere when they follow, the other [5].

MATERIALS AND METHODS

Subjects: Nine healthy right-handed male volunteers (age 22 ± 3 years) gave written informed consent according to the declaration of Helsinki, and were paid for their participation. The study was approved by the local Ethics Committee (CCPPRB, Centre Léon Bérard, Lyon).

Experimental apparatus: Subjects laid in the PET scanner with a mouse pad centered on their midline. A projection screen and a projector placed behind the PET-scanner displayed the visual input to subjects. A mirror placed in front of their eyes in the PET scanner allowed subjects to see the reflection of the screen. A Java program running on a PC was created for presenting two colored circles moving across a white screen and recording their positions every 20 ms. Subjects controlled the blue circle using right-hand movements with a mouse. The computer program controlled the red circle.

Experimental conditions In the 'leading the other' condition (A) subjects were instructed to move the mouse controlling the blue circle at will, while seeing the red circle following it. In the 'following the other' condition (B) subjects were instructed to move the mouse controlling the blue circle to follow the red circle. When 'acting at will' (condition C) subjects were instructed to move the mouse controlling the blue circle at will, while watching the red circle's unrelated movements. When 'observing the other' (condition D) subjects were instructed not to move the mouse and to observe the red circle's movements.

For the leading condition, the algorithm controlling the red circle was designed to depict biological motion. For other conditions, 2 min movements were recorded and used randomly to control the red circle.

PET acquisition: A Siemens CTI HR+ (63 slices, 15.2 cm axial field of view) PET tomograph with collimating septa retracted operating in 3D mode was used. A total of 63 transaxial images with a slice thickness of 2.42 mm with no gap were acquired simultaneously. Correction for attenuation was made using a transmission scan collected at the beginning of each subject's session.

A venous catheter to administer the tracer was inserted in an antecubital fossa vein in the left forearm. 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 the regional cerebral blood flow. Twelve scans were acquired per subject, representing three replications of the four experimental conditions.

Data analysis: The average speed of the mouse movements were calculated and were two-way *t*-tested for behavioral differences between the experimental conditions.

Functional imaging analysis was performed with statistical parametric mapping software (SPM99) [8] implemented in Matlab 5.3. The scans from each subject were automatically realigned and stereotactically normalized into the space of the MNI template used in SPM99. Images were then smoothed with a Gaussian kernel of 10 mm full-width at half-maximum. The voxel dimensions of each reconstructed scan was $2 \times 2 \times 4$ mm in the x, y and z dimension, respectively.

Data were analyzed modeling the experimental conditions for all subjects in the context of the general linear model. Comparisons across conditions were made using t statistics. The SPM{t} maps were transformed into Z distributions (SPM{Z}). Masking procedures implemented in SPM were used to distinguish between common and specific activated clusters when comparing contrasts be-

Table 1. Cerebral areas of increased regional cerebral blood flow in the contrasts between conditions A and B, and controls C (left), and D (right).

Localisation	x	y	z	Size	Z value	x	y	z	Size	Z value
			A−C masked exclusively with B−C					A−D masked exclusively with B−D		
Bilateral MI/SI/SMA proper/cingulate gyrus/left inferior parietal lobule						−42	22	58	6119	11.65
Fundus of right intraparietal sulcus						22	−60	56	33	5.36
Right inferior parietal lobule						58	−26	40	93	6.07
Pre-SMA	6	−2	72	13	4.08	6	4	68	197	7.59
Fundus of right intraparietal sulcus (posterior part)						24	−72	48	21	4.66
Cingulate gyrus						0	12	34	143	5.15
			B−C masked exclusively with A−C					B−D masked exclusively with A−D		
Right precentral gyrus	20	−18	66	24	4.43	22	−18	62	29	5.43
Left intraparietal sulcus (posterior part)						−40	−56	60	12	4.47
Right intraparietal sulcus (anterior part)	44	−58	54	17	4.27	44	−56	56	18	4.75
Fundus of right intraparietal sulcus (anterior part)	32	−50	52	40	4.85	30	−50	50	42	5.31
Left lateral occipital cortex	−34	−86	0	47	5.42	−50	−72	−2	18	4.24
Right lateral occipital cortex	46	−84	−8	203	4.89	46	−74	−10	22	4.28

The size of clusters corresponds to the number of voxels. MI and SI are the primary motor and sensory cortices, respectively. SMA, supplementary motor area.

tween the two conditions of interest (A and B) and the controls (C and D). For commonality, contrasts A–C and A–D were inclusively masked with the corresponding contrasts B–C and B–D, and thresholded at $p < 0.05$ corrected for multiple comparison with an extent of superior to 15 voxels. For specificity, contrasts describing the activity in condition A (*vs* B) were exclusively masked with the similar contrasts describing condition B (*vs* A) and thresholded at $p < 0.0001$ uncorrected with an extent of superior to 15 voxels. All masks were thresholded at $p < 0.05$ uncorrected. Anatomical identification was performed with reference to the atlas of Duvernoy [9]. Analysis of the clusters of interest was performed using condition-specific parameter estimates which reflect the adjusted regional cerebral blood flow in the different conditions relative to the fitted mean expressed as a percentage of whole brain mean blood flow.

RESULTS

Behavioral results showed a similar amount of mouse movement in the two conditions of reciprocal imitation (A and B) with no significant difference between them ($p = 0.1$). Movement in condition C was significantly greater than in conditions A and B (both $p < 0.01$).

Neuroimaging results are given in Table 1. Activated clusters in the intraparietal sulcus demonstrate the existence of several functional areas related to the experimental tasks along the rostrocaudal axis (Fig. 1). Bilateral activated clusters in the inferior parietal lobule were further analyzed using condition-specific parameter estimates (Fig. 2), which showed an increase of activity in conditions with action (A, B and C) compared to observation (D), as well as an additional increase in both hemispheres when the actions performed by the self and the other coincide (A and B). Finally, regional cerebral blood flow increased in condition A compared to B in the right hemisphere, and it increased in condition B compared to A in the left hemisphere.

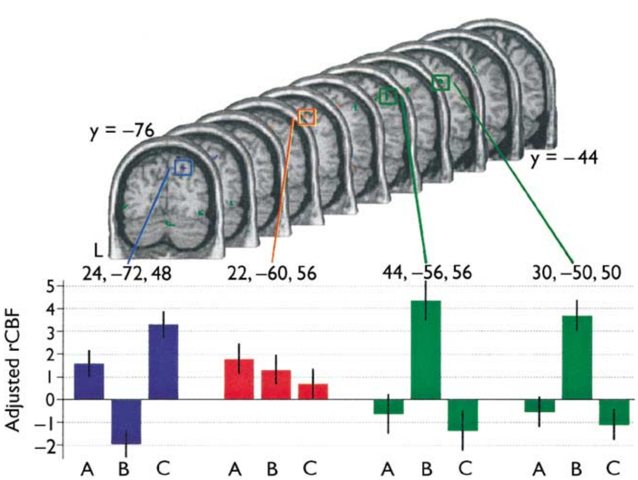

Fig. 1. Activity in the right intraparietal sulcus. Clusters located within the right intraparietal sulcus given in Table 1 (red: A–D masked inclusively with B–D; blue: A–D masked exclusively with B–D; green: B–D masked exclusively with A–D) are superimposed onto successive coronal sections (inter-slice distance 3 mm) of a standard brain (L: left hemisphere). Graphs show the parameter estimates of the four intraparietal sulcus clusters at the x, y and z coordinates indicated above each.

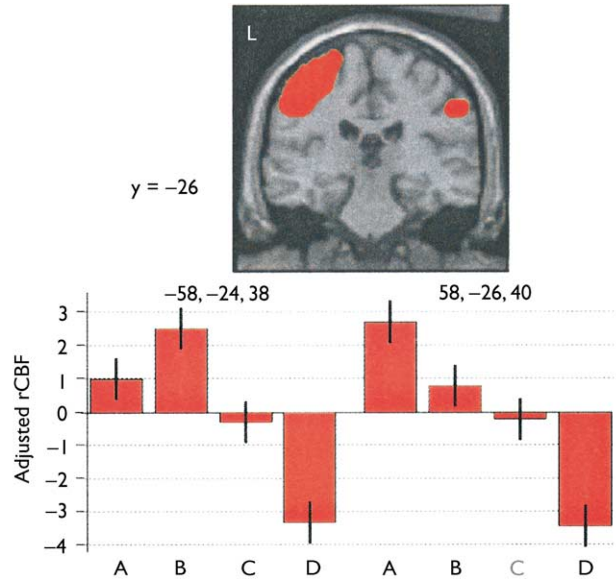

Fig. 2. Activity in the inferior parietal lobule. Active areas common to contrasts A–D and B–D given in Table 1 are superimposed onto a coronal section of a standard brain (L: left hemisphere). Graphs show the parameter estimates of the left and right inferior parietal lobule clusters on the left and right respectively at the x, y and z coordinates indicated above.

DISCUSSION

Investigation of the neural basis of agency was performed using a paradigm in which the subjects either led (A) or followed (B) the other, in a computerized environment free of explicit reference to body parts. Behavioral results indicate that the quantity of movement was similar in the two conditions of reciprocal imitation, A and B. The sense of ownership, related to motor control, and the sense of agency, related to the intentional aspect, can be segregated in the analysis.

The two conditions of interest are associated with different clusters of activity in sensory association areas (Table 1). Bilateral activation of the lateral occipital cortex, which plays a general role in analyzing object shape [10], is systematically associated with condition B. Its involvement is consistent with sustained attention to the model circle in the condition in which subjects had to follow the other. This result parallels the previous finding [5] of left superior temporal gyrus activity associated with attention to the model's hand [6] when object-directed hand actions are imitated. Interestingly, activated clusters are segregated along the rostrocaudal axis of the intraparietal sulcus (Fig. 1). Recent neuroimaging experiments suggest that the intraparietal sulcus, involved in visuomotor control, may be fragmented into several functional regions similar to those reported in neurophysiological studies of the monkey intraparietal sulcus [11]. The most caudal area engaged in conditions A and C corresponds to the putative human homologue of the lateral intraparietal (LIP) area, involved in visual tracking and saccades [12]. In conditions A and C subjects acted freely so that the visual tracking of the other's actions was separated from hand control. The two clusters associated with condition B are located in the most rostral position within the sulcus, which is acknowledged to underly visually guided action [13]. Lastly, the central cluster commonly activated in the three conditions that involve action can be associated with the visually guided manipulation of the mouse [14]. The present results therefore reveal a rostrocaudal gradient within the intraparietal sulcus, from visuomotor to visual tracking functions.

Previous functional imaging studies have demonstrated inferior parietal lobule activation when subjects watch actions performed by others [15]. There is plenty of evidence that the inferior parietal lobule plays a key role in corporeal awareness [16–18] and recent neuroimaging studies have suggested that it could play a key role in the attribution of action to its correct agent [5,7]. We recently demonstrated that the left hemisphere is more activated when the self imitates the other whereas the right hemisphere is more activated when the self is imitated [5], as well as when subjects mentally simulate observing someone else's actions [19]. In the present experiment, the hemodynamic activity is the lowest in both hemispheres in the condition without action, and is significantly increased when subjects and the other were performing similar actions (Fig. 2). Moreover, the activity in the left inferior parietal lobule is stronger when the subjects reproduced the other's action (condition B), whereas the right area is more activated when the other reproduced actions initiated by the subjects. Interestingly, abnormal increased activity in the right inferior parietal cortex has been observed in schizophrenic patients experiencing passivity phenomenon [20]. Taken together, these results suggest that the lateralization of the inferior parietal lobule activity may be critical for distinguishing consequences of actions generated by the self from those initiated by others, especially when confusion may occur.

An alternative explanation of these results involves attention-related activity. Reproducing a modeled action, as in condition B, requires an increased attention in comparison to acting freely. Since subjects were not asked to pay any particular attention to the fact that they were being followed in condition A and not in condition C, these two conditions are similar in term of attention. A motor attention function has been proposed for the left inferior parietal cortex [21] and could satisfyingly explain the increase of activity when subjects followed the other (condition B). But it would fail to explain the difference of activity between the two conditions in which subjects acted freely (conditions A and C), or the profile of activity in the right inferior parietal region which shows a large difference between conditions A and C. Lastly, in the absence of direct reference to body parts, only visuospatial and visuomotor attention are likely to be involved in this experiment. Both attentional components have been attributed to superior parietal areas [22], in agreement with our previous discussion concerning the activity within the intraparietal sulcus.

Finally, the computational framework for the control of action [4] could be used to explain the link between agency and activity in the inferior parietal lobule if we consider that this region plays a critical role in updating internal models of action performed by the self [23]. In the left hemisphere, dominant for praxis in right-handers, this region would perform the inverse computation necessary to map the self's actions on the others. In the right hemisphere, it would compare the computed internal representation of the expected state of the body and the sensory feedback, associated with sensory areas [6] to inhibit the sensory feedback of an internally triggered action. Discrepancies between the expected state and the sensory feedback would engage this region.

CONCLUSION

The different contribution of the inferior parietal cortex in the sense of agency is supported by this study and a model of its function, in particular concerning the lateralization, is proposed within the framework for the control of action based on the existence of internal models of the motor system.

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Acknowledgements: The authors thank Jean Laurens for the Java programming, Luc Cinotti, Didier Le Bars, and Franck Lavenne from the CERMEP for medical and technical assistance, and Sarah-Jayne Blakemore for helpful discussions on the manuscript. This research was supported by the INSERM, and by the University of Washington Center for Mind, Brain and Learning through funding from the Talaris Research Institute.