



Observing one's hand become anarchic: An fMRI study of action identification

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Abstract

The self seems to be a unitary entity remaining stable across time. Nevertheless, current theorizing conceptualizes the self as a number of interacting sub-systems involving perception, intention and action (self-model). One important function of such a self-model is to distinguish between events occurring as a result of one's own actions and events occurring as the result of somebody else's actions. We conducted an fMRI experiment that compared brain activation after an abrupt mismatch between one's own movement and its visual consequences with an abrupt mismatch between one's own movement and somebody else's visually perceived hand movement. A right fronto-parietal network was selectively active during a sudden mismatch between one's own observed and performed hand action.

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1. Introduction

The first intuition one has when thinking about the self is that it is a unitary entity that remains relatively stable across time. Accordingly, social psychologists and memory researchers have long treated the self as if it were a mental concept to which perceptions, emotions, memories, etc. become linked (e.g., Baumeister, 1998). However, recent work in philosophy (Metzinger, 2003), psychology (Neisser, 1994; Wegner, 2002), and neuroscience (Frith & Frith, 1999; Jeannerod,

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1999; Kircher & David, 2003; Ruby & Decety, 2001) suggests that the self actually needs to be conceptualized as consisting of a number of interacting subsystems that often involve perception, intention, and action (Proust, 2000). Together, these subsystems might form a self-model that underlies our subjective experience (Metzinger, 2000). One important function of such a self-model is the ability to distinguish between events that occur as a result of one's own actions and events that occur as the result of somebody else's actions (Blakemore & Decety, 2001; Knoblich & Flach, 2001; van den Bos & Jeannerod, 2002). Before we report an functional magnetic resonance imaging (fMRI) study that further explored which brain networks implement this ability, we provide a short overview of prior research on brain networks that allow one to distinguish between the consequences of our own and others' actions.

2. Previous research

A first relevant area of research is the study of brain systems responsible for conflict monitoring. It is now well established that there are areas in the brain that are selectively active as soon as action conflicts arise. The most important structure in this context is the anterior cingulate cortex (ACC, cf. Botvinick, Braver, Barch, Carter, & Cohen, 2001). This area is active for instance, when an incongruent stimulus is presented in the Stroop task, when attention needs to be divided in order to carry out two simultaneous tasks, or when a person internally corrects an erroneous response. It is possible that the type of conflict monitoring implemented in the anterior cingulate cortex also plays an important role in detecting conflicts between one's own intentions and the events occurring in the outside world. This, in turn, would provide a way to distinguish the results of self- and other-generated actions, because there would only be a conflict when somebody else's actions are observed. Another brain area that might be involved in conflict monitoring mechanisms is the dorsolateral prefrontal cortex (DLPFC). This brain area seems to be especially activated when a cognitive conflict between one's own intention and sensory feedback emerges. This has been shown in a PET study that used a mirror to manipulate visual feedback (Fink et al., 1999). Participants were instructed to open and close both hands repetitively, either in-phase or out-of-phase, while observing their hand's movements. A mirror was used in some conditions to alter visual feedback such that both the volunteer's intention and proprioceptive feedback indicated out-of-phase hand actions while the mirror showed in-phase hand actions. The mismatch between intention, proprioception, and visual feedback specifically activated the right dorsolateral prefrontal cortex.

A second relevant area of research is the study of patients with disorders of the self(-model). Of particular interest are results obtained from schizophrenic patients suffering from delusions of control (Kircher & David, 2003). Patients with these symptoms often experience their own actions as being controlled by others. A number of recent studies have demonstrated that their ability to distinguish between their own and others' actions is reduced. Daprati et al. (1997) found that patients compared to healthy participants more often accepted hand actions of an experimenter imitating them as being their own. Further studies demonstrated that these patients have problems with detecting angular and temporal deviations between their actual actions and the perceived consequences of these actions (Fournernet, Franck, Slachevsky, & Jeannerod, 2001; Franck et al., 2001; see Blakemore, Smith, Steel, Johnstone, & Frith, 2000 for a study that explored the

tactile domain). Accordingly, it has been suggested that these patients have difficulties with predicting the sensory consequences of actions (Frith, 1992; Frith, Blakemore, & Wolpert, 2000) and/or difficulties with comparing what is intended with what is observed (Georgieff & Jeannerod, 1998; Jeannerod, 1999; Knoblich, Stottmeister, & Kircher, submitted). A recent PET study demonstrated that patients experiencing passivity phenomena and delusions of control show hyper-activation of parietal and cingulate cortices (Spence et al., 1997). In particular, the right parietal cortex has previously also been implicated in the aetiology of alienation in organic brain disorders (Leiguarda, Starkstein, Nogués, Berthier, & Arbeláiz, 1993; Mesulam, 1981).

A third relevant area of research addressed the assumption that self-recognition is based on a comparison of the predicted and actually observed consequences of self-generated actions. According to this theory, a forward model simulates the future consequences of each motor program that is issued. The predictions of this model attenuate re-afferent signals (Blakemore, Frith, & Wolpert, 1999; Von Holst & Mittelstaedt, 1954). Support for these assumptions was obtained in an fMRI study (Blakemore, Wolpert, & Frith, 1998) that addressed the well-known phenomenon that one cannot tickle oneself (Weiskrantz, Elliott, & Darlington, 1971). The study compared conditions in which participants tactily stimulated themselves via a robot arm. Different extents of temporal delay were introduced between the movement of the robot arm and its tactile consequences (long delays are experienced like being touched by somebody else). The somatosensory cortex was less activated when there was no temporal delay. The cerebellum was more active when there was a temporal delay. This is consistent with the assumption that the cerebellum provides predictions of the sensory consequences of movements that in turn attenuate re-afferences and therefore lead to a reduced activation of sensory areas for the sensory consequences of one's own movements. Thus, it is possible that one can identify the consequences of one's own actions, because they are attenuated by the predictions.

The fourth relevant area of research addressed the question of how actions are represented in the brain such that similarities between self and other are perceived (Knoblich & Prinz, 2001; Knoblich, Seigerschmidt, Flach, & Prinz, 2002; see also Rizzolatti, Fogassi, & Gallese, 2001 for research on a "mirror system" in monkeys), but confusion between self and other does not occur (Decety, Chaminade, Grezes, & Meltzoff, 2002). This research addressed the domains of action observation (Decety & Grèzes, 1999), imitation (Decety et al., 2002; Iacoboni et al., 1999), and action imagery (Ruby & Decety, 2001). Some of these studies provide evidence that left frontal and parietal areas are active when one carries out an action, imagines to carry it out, or observes somebody else performing the same action. However, the right parietal cortex seems to be specifically activated when another person imitates an action one has performed earlier (Decety et al., 2002), or when one is asked to mentally imagine somebody else performing an action (Ruby & Decety, 2001).

3. The present study

The present study aimed to further explore the brain networks that contribute to identifying one's own actions. In particular, we were interested in the question of which brain areas enable us to attribute visually perceived hand movements to our own or somebody else's actions. In earlier studies, this question has been addressed by assessing brain activity in response to either

temporally distorted feedback (Blakemore, Frith, & Wolpert, 2001; Leube et al., in press) or spatially distorted feedback (Farrer et al., 2003). As mentioned above, other studies compared brain activation during action perception, action imagery, and action execution. With our newly developed paradigm we took a somewhat different approach by directly comparing an abrupt mismatch between one's own hand movements and observation of their visual consequences with an abrupt mismatch between one's own hand movements and the observation of somebody else's synchronized hand movements.

In each experimental trial (see Fig. 1), participants opened and closed their hands four times, in a constant rhythm (1 Hz). While they performed the first and second open–close cycle (Interval 1) they received no visual feedback. While they performed the third and fourth open–close cycle (Interval 2) they observed the visual consequences recorded during the first interval as visual feedback. Because of the cyclic nature of the actions, the visual feedback matched the actually performed actions. Also, participants were instructed to stay synchronized with the observed actions at all times. For the second interval participants reported the subjective experience that the visual feedback reflected their own actions, although the display actually showed an action they had carried out two cycles earlier.

In the control condition, the same participants observed the action of a foreign, gloved hand (the participant's own hand was not gloved). In all conditions participants stopped their hand action after the fourth cycle. Thus, during Interval 3 they observed either their own hand or the foreign hand performing two open–close cycles (observe SELF vs. observe OTHER). Observing one's own hand moving, although having stopped the action, caused an experience that participants described as rather strange, sometimes funny. Observing the foreign hand did not cause the same experience, despite the abrupt mismatch between motor performance and visual feedback.

The rationale behind these manipulations was that the sudden switch from synchrony between the performed action and its visual consequences should cause a complete mismatch (seeing one's own hand moving without performing an action) and should activate the brain network that detects conflicts between the actions one performs and the actions one observes. These networks should become activated at the moment when the mismatch arises and only if one observes one's own hand moving. Thus, contrasting the SELF with the OTHER-condition during Interval 3 allowed us to determine, which of the several areas that have been associated with the ability to keep the visual consequences of one's own and others' actions apart, are sensitive to a clear mismatch. Contrasting the SELF and OTHER-condition during Interval 2 allowed us to

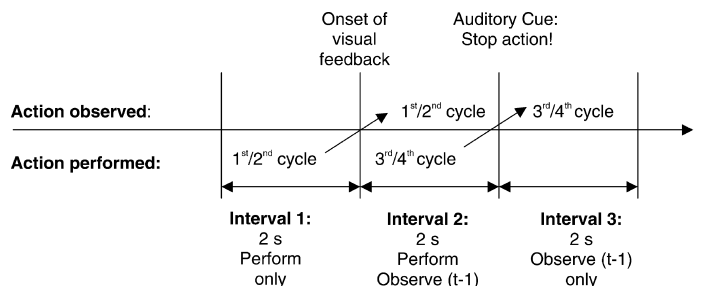


Fig. 1. Illustration of an experimental trial.

determine, whether observing one's own hand actions activates different brain areas, when there is (almost) no mismatch to the actions performed.

4. Method

Six healthy right-handed participants lay in the scanner in a supine position. They wore ear-phones and looked into a mirror that reflected a screen. As soon as they heard an acoustical signal they started to continuously open and close their right hand with a frequency of approximately 1 Hz for the whole open–close cycle. In the open position fingers were fully extended. In the closed position the fingers formed an open fist. The action was filmed with an MRI compatible video camera (Wild et al., 2000). There were two different conditions (see Fig. 1). In the SELF-condition the participants performed two open–close cycles (2 s) without receiving visual feedback (Interval 1). Then, the screen came on and displayed the earlier performed cycles (Interval 2). Participants were instructed to always stay synchronized with the visual display. After participants had performed the third and fourth full cycle they heard a second acoustic signal that told them to stop their actions. However, the earlier performed action was further displayed via visual feedback with a delay of 2 s (Interval 3). Thus, during this phase participants observed how their own hand continued to move without actually moving it.

The OTHER condition was exactly the same with the only difference that participants did not receive visual feedback from their own ungloved hand, but observed another gloved hand performing the open–close actions. Before the main experiment started, subjects went through a training session in the scanner. During this training session they were familiarized with both experimental conditions (SELF and OTHER). The experimental procedure was explained to each participant, and therefore fully transparent. The foreign hand movement was played back from a data file. A total of 76 SELF and 76 OTHER trials were collected from each subject in a random order during four runs. The stimulus onset asynchrony (SOA) varied between 10 and 14 s.

Scanning was performed with a 1.5 T scanner (Siemens, Sonata). Functional images consisted of echo-planar image volumes sensitive to BOLD contrast (TE 40 ms, TR 2 s). The volume covered the whole brain with a 64×64 matrix and 22 slices with in plane resolution of $3 \times 3 \text{ mm}^2$. Four runs, consisting of 253 volumes each, were acquired. To insure that a steady state magnetization had been reached, the first six acquired volumes were discarded. A trigger signal from the scanner, the button press of the subject and the onset of the stimuli were registered in a protocol, together with the timeline, on a separate computer. A T1 weighted data set (MP-RAGE; $1.5 \times 1 \times 1 \text{ mm}^3$) was collected to serve as an anatomical reference.

For image processing, and all statistical analyses SPM99 (Wellcome Department of Cognitive Neurology, London) was used. The images of each subject were corrected for acquisition delay (slice timing) and motion by realigning to the first scan of the block as reference. T1 anatomical images were co-registered to the mean of the functional scans and aligned to the SPM T1 template in the MNI space [Montreal Neurological Institute, mean brain]. The calculated nonlinear transformation was applied to all images for spatial normalization. Finally, the images were smoothed with a 12 mm full-width half-maximum (FWHM) Gaussian filter. A high pass filter with a cutoff period of 40 s and a low pass filter with a cutoff period of 4 s were used. In a fixed effect model differential contrasts between SELF-violation and OTHER-violation trials were

modeled. Because of the small number of participants, we used a fixed effect model. Therefore, one cannot generalize the results obtained to the whole population. Accordingly, the data have an exploratory and preliminary character until a bigger group has been investigated using a random effects model.

For the differential contrasts two different models were constructed, each with different timing parameters. The first model covered the second interval in which participants performed an action and either observed their own or a foreign hand moving (2 s length blocks convolved with the hemodynamic response function (hrf) starting with the onset of the visual feedback). The second model covered the third interval in which the participants had stopped their own action but continued to observe their own or a foreign hand moving (2 s length blocks convolved with the hrf starting with the second acoustic trigger). Activations are reported if they exceeded a significance level of 5%, corrected for multiple comparisons on the single voxel level. Only activations that had an extent of more than three coherent voxels are reported.

5. Results

5.1. Brain regions active while observing one's own hand actions

5.1.1. Perform and observe (Interval 2)

For this differential contrast, brain activation in the OTHER condition was subtracted from the brain activation during the SELF condition. Thus, the remaining brain activations indicate higher brain activity, when participants observed their own hand actions compared to foreign hand actions. Table 1 shows the results. The only regions that were more active while observing one's own actions were in the right inferior occipital cortex and the left middle occipital cortex. It is likely that the differential activation of these visual brain areas is due to differences in the stimulus.

5.1.2. Perform–observe mismatch (Interval 3)

Again, the brain activation in the OTHER condition was subtracted from that in the SELF condition. The remaining brain activations are higher, when participants observed their own hand moving on, after having stopped their hand movement. Similar to the signal changes during the second interval occipital areas were more active in the SELF condition (see Table 2). In the right hemisphere, the occipital activation extended into inferior temporal areas. This indicates that there were differences in early visual processing due to differences in the stimuli. Two further areas were more active in the SELF condition. The first was in the right superior parietal cortex (BA 7, see Fig. 2A). The second was in the right prefrontal cortex (BA 44, see Fig. 2B). Note that these

Table 1
Differential contrast SELF minus OTHER, Perform and Observe (Interval 2)

Cerebral area	Side	MNI x, y, z	T -value
Inferior occipital	R	36, -78, -3	5.10
Middle occipital	L	-30, -81, 21	5.05

Table 2
Differential contrast SELF minus OTHER, Perform–Observe Mismatch (Interval 3)

Cerebral area	Side	MNI x, y, z	T -value
Inferior occipital	R	39, -75, -6	10.35
Inferior temporal	R	42, -60, -9	8.38
Middle occipital	R	36, -72, 24	7.03
Middle occipital	L	-30, -81, 21	6.36
Inferior frontal	R	45, 9, 24	5.25
Superior parietal	R	27, -51, 63	4.99

are the only activations that selectively occurred during the third interval and not during the second interval. This indicates that these areas were selectively activated, when a mismatch occurred between performing and observing one's own hand movements.

5.2. Brain areas active while observing foreign hand actions

In order to determine, which brain areas were selectively active when participants observed foreign hand actions, differential contrasts (OTHER minus SELF) were computed for the second interval (Perform and Observe, see Table 3) and the third interval (Perform–Observe Mismatch, see Table 4). Right primary visual areas (Lingua and Cuneus) were more active during both intervals, again indicating differences in early stimulus processing. In addition, the anterior cingulate was more active when observing foreign hand actions, which could reflect that conflict monitoring is more important when one observes foreign hand actions. Finally, the cerebellum was more active during the second interval. This might have to do with the fact that fine-grained timing information about the action performed was internally available in the SELF condition, but not in the OTHER condition. Note that there was no area selectively more active, when a mismatch between the performed action and the observed foreign action occurred (except one primary visual area).

6. Discussion

The main result of the present study is that a right fronto-parietal network was selectively active, when a sudden mismatch between one's own observed and performed hand action occurred. This mismatch consisted in observing one's hand moving on, despite having stopped the actual action. Thus, the fronto-parietal network seems to have become active when an established self-attribution of visually observed actions was violated. There seem to be two highly selective conditions for this network to become active. First a self-attribution of an observed movement must be established (I am performing an action and the observed action is my own). Second, a violation of this relationship needs to occur (my hand moves, although I am actually not moving it).

The results of the present experiment are consistent with earlier findings and may shed some new light on the mechanisms underlying self-attribution of visually observed actions. Frontal areas in the right cortex have been associated with distinguishing perceptions that are congruent

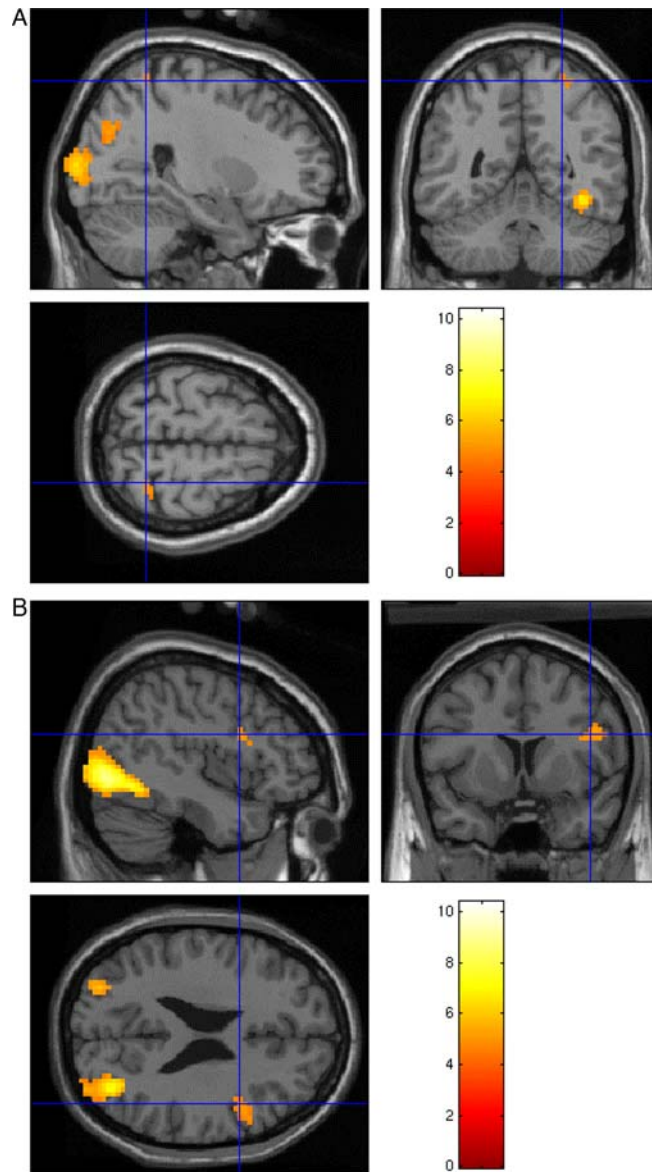


Fig. 2. Differential contrast between observing one's own unexpected hand action and a foreign hand action (SELF minus OTHER), after a sudden de-synchronization of performed and observed action (Interval 3). The right superior parietal (A) and the right lateral frontal (B) cortex was significantly more activated when subjects watched their own hand move on (p less than 0.05, corrected; extent threshold $k = 3$ voxels).

or incongruent with a concurrently performed action. In an earlier study the right DLPFC was more activated when there was a mismatch between an intention to perform an action and the visual consequences observed (Fink et al., 1999). Parietal areas in the right cortex have been associated with keeping self and other apart in mental imagery tasks (Ruby & Decety, 2001) and

Table 3
Differential contrast OTHER minus SELF, Perform and Observe (Interval 2)

Cerebral area	Side	MNI x, y, z	<i>T</i> -value
Lingual	R	12, -87, -6	5.89
Anterior cingulum	R	9, 36, 27	5.07
Cerebellum	L	-36, -57, -42	4.67

Table 4
Differential contrast OTHER minus SELF, Perform–Observe Mismatch (Interval 3)

Cerebral area	Side	MNI x, y, z	<i>T</i> -value
Lingual	R	12, -87, -6	7.35
Anterior cingulum	R	9, 39, 24	5.29
Cuneus	R	9, -87, 27	4.99

imitation tasks (Decety et al., 2002). In these tasks, the right parietal lobe was more activated when a third person perspective was imagined, or when one observed somebody else imitating one's own actions.

Although the frontal and parietal areas that were selectively active for the Observe–Perform Mismatch, the activations observed in the present study did not exactly correspond to the ones reported in the earlier studies. Most importantly, we observed a difference in activation in the superior parietal cortex rather than the inferior parietal cortex (Decety et al., 2002; Ruby & Decety, 2001; and an activation in BA 44 frontally rather than BA 46 (Fink et al., 1999). Nevertheless, our results provide converging evidence for the assumption that detecting mismatches between one's movements and their visual consequences mainly relies on a fronto-parietal network in the right hemisphere. The differences might be due to specifics of the respective tasks used.

There is a possibility that the frontal and parietal areas in this network serve different functions. An earlier study has described the function of the frontal component of the network as detecting conflicts between intentions and the senses (Fink et al., 1999). Such a conflict also arose in our task. The present results show that the same activation did not occur when a sudden de-synchronization occurred between actions the participants performed and a foreign hand's actions the participants observed. This suggests that the frontal part of the network is involved in detecting specific mismatches between one's own actions and their visual consequences. It is unlikely that the differential activation is due to an unspecific mismatch between action and perception—such a mismatch was present in the SELF as well as the OTHER condition during the third interval. There was no indication that the conflict monitoring that seems to take place in the anterior cingulum (Botvinick et al., 2001) was selectively involved in detecting the mismatch in the SELF condition. There was also no indication of a selective activation of the cerebellum that has been previously implied in detecting differences between the predicted and observed consequences of actions (cf. Blakemore et al., 1998).

The right parietal component of the network has been shown to be involved in more complex attribution processes of actions comprising goal-directed behavior and perspective taking in mental imagery. In an earlier study (Ruby & Decety, 2001) this activation occurred together with activation in a left fronto-parietal network that has been interpreted as a system coding one's own and others' actions in a commensurate representational format (Blakemore & Decety, 2001;

Decety & Grèzes, 1999; Knoblich & Prinz, 2001; Prinz, 1997). This network is often considered to be a human homologue of the mirror system that Rizzolatti & colleagues (2001) discovered in monkeys. It is active, regardless of whether one observes somebody else's action, imagines performing an action, or actually performs it. The right parietal cortex was selectively active when participants were asked to imagine another person performing a movement (Ruby & Decety, 2001) or observed another person imitating their own actions (Decety et al., 2002). In a further study, the right parietal cortex was preferentially activated when an angular bias was introduced between joystick movements participants performed and the corresponding visual feedback (Farrer et al., 2003). Finally, the right parietal lobe was also more activated when an action was attributed to oneself compared to somebody else, while observing the same physical event (Farrer & Frith, 2002).

Together these results suggest that the right parietal lobe is activated in situations when a distinction between oneself and another is critical and ambiguous (e.g., when oneself is being imitated by another person). In such cases its activation might be important to signal an alienation. This is supported by the experiments where is no physical difference in the stimuli but differential activation of the right parietal cortex builds up on a mere cognitive act (third person perspective, action attribution to another person). Such an alienation is also present in our experiment when an initially self-attributed movement is changed in character by an overt mismatch with one's own motor programs.

In conclusion, our study provides further support for the claim that fronto-parietal areas in the right hemisphere contribute to identifying one's own action by (1) detecting mismatches between an intention and the visual input and (2) by merging all available information to generate a correct attribution of the perceived movements to self or other. We would like to suggest that this fronto-parietal network implements important parts of the self-model (Metzinger, 2003), namely to ensure self-integrity by detecting discrepancies, in physical reality and mental imagery, between actions performed and actions perceived.

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