

Self-awareness and action

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In this review we discuss how we are aware that actions are self-generated. We review behavioural data that suggest that a prediction of the sensory consequences of movement might be used to label actions and their consequences as self-generated. We also describe recent functional neuroimaging experiments and studies of neurological and psychiatric patients, which suggest that the parietal cortex plays a crucial role in the awareness of action.

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Abbreviations

fMRI functional magnetic resonance imaging
PET position emission tomography

Introduction

‘She raised one hand and flexed its fingers and wondered, as she had sometimes before, how this thing, this machine for gripping, this fleshy spider on the end of her arm, came to be hers, entirely at her command. Or did it have some little life of its own? She bent her finger and straightened it. The mystery was in the instance before it moved, the dividing moment between not moving and moving, when her intention took effect. It was like a wave breaking. If she could only find herself at the crest, she thought, she might find the secret of herself, that part of her that was really in charge. She brought her forefinger closer to her face and stared at it, urging it to move. It remained still because she was pretending, she was not entirely serious, and because willing it to move, or being about to move it, was not the same as actually moving it. And when she did crook it finally, the action seemed to start in the finger itself, not in some part of her mind. When did it know to move, when did she know to move it?’

Ian McEwan, *Atonement*

In this review, we discuss studies on action and awareness in the context of a well-established framework of motor control. This framework proposes that our actions and interactions with objects are represented in the form of internal models [1]. The crucial component of the forward model, a type of internal model, is the predicted sensory consequence(s) of movement, which can be compared with the actual sensory consequence(s) of movement and used to optimise motor control [1,2, Davidson and Wolpert, this issue]. Here, we suggest that this sensory prediction may be one important component of our awareness of action.

What aspects of action are we aware of?

Being aware of initiating and controlling actions is a major component of conscious experience, but many aspects of action occur without our awareness. Evidence that sensations associated with actual movements are unavailable to awareness comes from a study in which the sensory consequences of movement were made to deviate from a subject’s expectations [3]. In this study, the subject’s task was to draw a straight line on a computer screen. Subjects could not see their arm or hand and were given false feedback on the screen about the trajectory of their arm movement. Thus, they had to make considerable deviations from a straight movement to achieve their goal. However, verbal reports indicated that subjects were unaware that they were making deviant movements – they claimed to have made straight movements. These results suggest that we are aware of the movements we intend to make rather than those we actually make. There is some evidence to suggest that the exact threshold above which the discrepancy between the intended and actual movement becomes available to awareness depends to some extent on the task at hand [4*,5]. When the task is to detect the mismatch between the movement and the sensory (visual) consequences, subjects seem to become aware that the movement is not their own when the two components are discrepant by 15 degrees spatially or by 150 ms temporally [4*]. If subjects are not asked to detect a mismatch, however, they appear not to notice any discrepancy, even when the sensory (tactile) consequences of their movements are delayed by 300 ms [5].

In his studies of motor consciousness, Libet investigated the time at which awareness emerges during the generation of an action. Libet [6] asked healthy volunteers to estimate retrospectively the time at which they initiated a finger movement (the time at which their finger started to move; the ‘M’ judgement). The volunteers consistently anticipated the actual starting time of the movement by 50–80 ms. Recently, Haggard and Magno [7] carried out a

series of experiments that were based on the Libet paradigm. They showed that the perceived time of movement onset is slightly delayed (by about 75 ms) if the motor cortex is stimulated using transcranial magnetic stimulation (TMS), whereas this stimulation causes a far greater delay (of around 200 ms) in the initiation of the actual movement [7]. These observations support the idea that our awareness of initiating a movement is not derived from sensory signals arising in the moving limb — because such signals are not available until after the limb has started moving. Instead our awareness appears to be linked, at least in part, to a signal that precedes the movement. One signal that is available before a movement is initiated is the prediction of the sensory consequences of the movement. Perhaps one signal that we are aware of when making a movement is this prediction, rather than the movement itself. Sensory feedback from the movement would also be important to check the movement was completed as planned.

Action in the imagination

Sensory prediction might underlie the ability to prepare and imagine movements. It is well established that imagining a movement and preparing to move activate a subset of brain regions that are also activated by executing a movement [8–10,11*,12**]. Healthy subjects can confuse actions performed in the imagination and in reality when they are asked to recall such actions two weeks later [13*]. A recent functional magnetic resonance imaging (fMRI) study scanned subjects while they executed movements or imagined making the same movements. A direct comparison between brain activity during imagined and executed movements revealed that imagining movements activates the left posterior and inferior parietal lobe to a greater extent than executing the same movement [14]. Subjects show a speed-accuracy trade off for imaginary as well as real movements, but this effect is lost in the imaginary movements of patients with parietal lesions [15,16*]. Taken together, these data suggest that the parietal lobe plays an important role in the generation of motor images, and may store motor representations that are necessary for motor imagery. The same lack of speed-accuracy trade off is seen in imagined movements made by schizophrenic patients with delusions of control [17*]. This is in line with the proposal that delusions of control are associated with a faulty internal representation of action [18,19].

Awareness of intentions

Are we aware of our intentions to move? In a second task, Libet asked volunteers to indicate the time at which they became aware of having the ‘urge’ to make a movement (that is, of their will or intention to move; the ‘W’ judgement; [6]). Subjects’ W judgements consistently precede the production of the movement by about 300 ms. Interestingly, this is well after the onset of the readiness potential, the negative potential arising from

the supplementary motor area (SMA), which precedes the movement by one second or more. On the basis of these results, Libet concluded that, “The brain... decides to initiate... or prepares to initiate the act at a time before there is any reportable subjective awareness that such a decision has taken place” [6].

Using a similar paradigm, Haggard and Eimer [20] asked subjects to indicate the time at which “they first began to prepare the movement” and related this to various components of the readiness potential. In this study, subjects moved either their left or their right index finger. The onset of the lateralised readiness potential (occurring at around 500 ms before the movement), rather than earlier components of the readiness potential (starting more than 1 s before the movement), co-varied with the perceived time at which preparation of the movement began. This suggests that the awareness of preparing to move is associated with the exact specification of the movement (which finger will be moved) rather than some more abstract representation of action, such as the goal of the movement.

A sense of agency

An important aspect of awareness of action is our sense of agency; the feeling that we cause movements and their consequences. In a recent study, Haggard and co-workers [21**] investigated the consequences of a sensory event being causally linked to a subject’s action. Subjects made a key-press, which on some trials was followed 250 ms later by an auditory tone. The subject’s task was to judge the time at which they were aware of pressing a key or the time at which they were aware of hearing a tone. When their key-press caused a tone, subjects judged the timing of their key-press as occurring about 15 ms later and the tone as occurring 46 ms earlier than if the two events occurred alone. This ‘temporal attraction’ seems to depend on the perceived causal relationship between an action and its sensory consequence(s). In a second experiment, a varying delay (250, 450, or 650 ms) was introduced between the key-press and the tone. The further apart the key-press and the tone, the more the temporal attraction of the tone to the key-press was diminished. Furthermore, the temporal attraction between the perception of actions and their sensory consequences did not occur when an involuntary movement (caused by stimulating the motor cortex using TMS) was followed 250 ms later by a tone, or when subjects judged the timing of two causally related external sensory events. The temporal attraction between self-generated actions and their sensory consequences binds together these events, and enhances our experience of agency.

If an explicit goal is suggested just prior to the action that achieves that goal, then the action will be perceived as intended. Wegner and Wheatley [22] have shown that this can lead to errors in the perception of intention. A

naive subject and a confederate simultaneously used a single mouse to control the position of a pointer on a screen. If the attention of the subject was drawn to an object on the screen and the pointer stopped near that object shortly afterwards, then the subject frequently believed that s/he had intentionally moved towards the object. In reality, his/her arm had been moved passively by the confederate. As long as the action did not conflict with some explicitly suggested goal then the action was perceived as intended.

How do we recognise our own actions?

A clever paradigm that has been used to investigate self-movement recognition involves subjects viewing the visual consequences of their own hand movements, which can be manipulated so that the ownership of the hand is ambiguous. The subject sees on a television screen a hand that is either their own or the experimenter's performing movements that are either congruent or incongruent with the subject's own hand movements. Using this paradigm, Daprati and co-workers [23] showed that normal subjects confuse their own hand movements with those of the experimenter about 30% of the time when the movements are similar. Thus, even in an ambiguous situation in which the experimenter's hand makes the same movements as the subject's hand, the subject is able to recognise their own hand movements 70% of the time, and recognition is better for the dominant hand than the non-dominant hand [24*].

A recent series of experiments by Knoblich, Prinz and co-workers [25*,26*] has shown that subjects are adept at recognising their own actions when they are played back to them. In one study, subjects drew various characters, and their movement patterns were recorded. A week later they were presented with films of a moving dot, which represented either their own pre-recorded movements or the movements of someone else drawing the same character. Subjects were easily able to recognise which movements were their own. Velocity seemed to be the crucial component — self-movement recognition was not possible when the moving dot that represented their movement was made to move at constant velocity while all other factors remained the same as during the original recording [25*].

We are easily able to distinguish our own movements from those of other people. How is this achieved, given the overlapping neural system that is involved in the execution and the observation of movement? A significant part of the motor system is activated both when we execute an action and when we observe a similar action being executed [27–30,31*,32**,33]. If my brain 'mirrors' observed actions, how do I know that it is someone else, and not me, who is moving when I observe an action? Accumulating evidence indicates that the parietal cortex plays a role in the distinction between self-produced

actions and actions generated by others. The right inferior parietal cortex is activated when subjects mentally simulate actions from someone else's perspective but not from their own (Figure 1; [34*]). This region is also activated when subjects observe their own actions being imitated by someone else, but not when they imitate someone else's action [35*], and when subjects attend to someone else's actions rather than their own [36*,37]. It seems that the inferior parietal cortex is involved in classifying movements as external as well as in representing imagined movements.

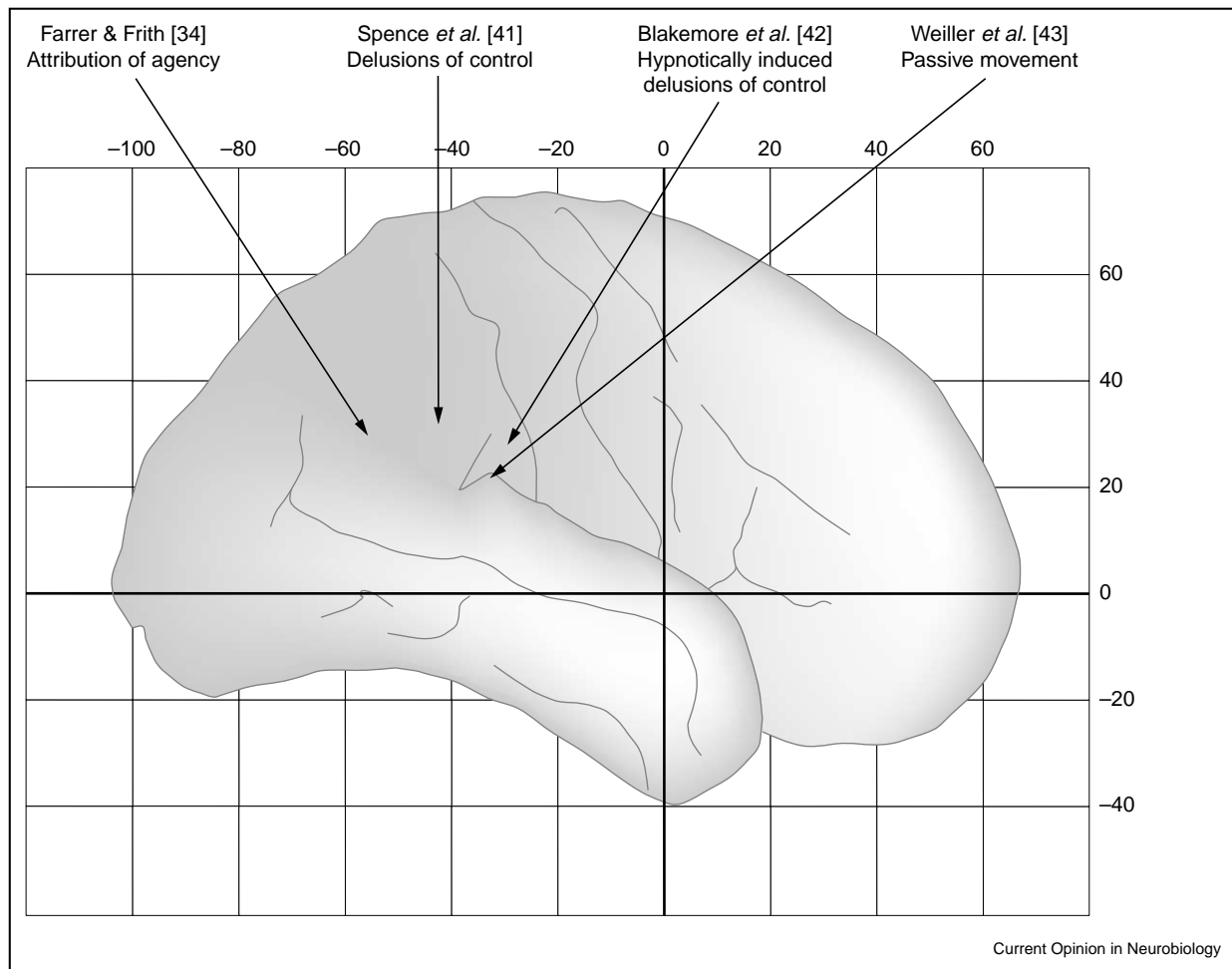
Confusing our own actions with other people's actions

The observation that patients with left parietal lobe damage, with and without apraxia, are more likely to confuse their hand movements with those of another agent supports the idea that the parietal lobe is involved in producing a sense of agency [38]. Conversely, a recent case study demonstrated that a patient with neglect and somatoparaphrenic delusions caused by a right thalamo-temporo-parietal lesion tended to deny that his left hand was his own [28].

Certain psychiatric symptoms are characterised by an inability to distinguish self- and externally produced actions. Many patients with schizophrenia describe 'passivity' experiences in which actions, speech and thoughts are controlled by some external agent rather than by their own will. The experience of alien control could arise from a lack of awareness of the predicted limb position [18,19]. Under normal circumstances, the awareness of initiating a movement must depend on the predicted limb position, because awareness of initiating a movement precedes the actual movement and any feedback about actual limb position ([6]; see above). Patients with delusions of control are aware of their goal, of their intention to move and of their movement having occurred, but they are not aware of having initiated the movement. This could relate to the problem of imagining movements, which we have already discussed [17*].

Several studies have shown that patients that have delusions of control confuse self-produced and externally generated actions. Using the paradigm in which subjects see feedback of their own hand movement or that of the experimenter's hand making similar movements, Daprati and co-workers [23] found that schizophrenic patients that have delusions of control are more likely than control subjects to confuse their hand with that of the experimenter. Such people are less able to detect a discrepancy between their movement and its consequences than schizophrenic patients that do not have delusions of control or control subjects. They become aware that a movement is not their own when their movement and its sensory (visual) consequences are discrepant spatially by 30 degrees or temporally by 300 ms, compared with 15

Figure 1



Schematic diagram showing the lateral surface of a brain. Arrows indicate regions of parietal cortex that were activated by; the attribution of movement to an external source for visually guided movements [34], delusions of control in schizophrenia [41], hypnotically induced delusions of control in the healthy brain [42] and passive movements [43].

degrees and 150 ms, respectively, for control subjects [4]. One explanation for this is that the schizophrenic patients that have delusions of control only have proprioceptive and visual feedback to rely on for recognition, whereas control subjects are additionally able to compare the sensory prediction with sensory feedback from the movement.

Because a movement is predicted, its sensory consequences can be perceptually attenuated relative to external sensations [5]. There is evidence that the confusion between self and others in subjects with delusions of control is a consequence of an abnormal sensory prediction [5]. Patients with delusions of control do not show this perceptual attenuation of self-produced sensory stimulation [39]. The normal perceptual attenuation of the sensory consequences of movement is accompanied by, and might be attributable to, a reduction in activity in the

parietal operculum (secondary somatosensory cortex) and the anterior cingulate cortex during self-produced tactile stimulation compared with external tactile stimulation [40]. If delusions of control are associated with an impairment in sensory prediction, we would expect to see no attenuation of the activity in sensory regions. This was precisely the result of a study in which schizophrenics with and without delusions of control were scanned in position emission tomography (PET) while they performed a movement task (Figure 1; [41]). The presence of delusions of control was associated with over-activity in the right inferior parietal cortex. Moreover, activity in this region returned to normal levels when the schizophrenics were in remission. Over-activity of the inferior parietal cortex might reflect a heightened response to the sensory consequences of movements the schizophrenic patients made during the scan, contributing to the feeling that movements are externally controlled.

This result was supported by a recent study that investigated brain activity associated with delusions of control experiences in healthy control subjects (Figure 1; [42]). In this study, hypnosis was used to induce a misattribution of self-generated movement to an external source in healthy individuals. PET was employed to investigate the neural correlates of active movements correctly attributed to the self, compared with identical active movements misattributed to an external source. Active movements attributed to an external source resulted in higher activations in the parietal cortex and cerebellum than identical active movements correctly attributed to the self. The brain activations associated with the misattribution of active movements resembled brain activity associated with passive movements (Figure 1; [43]). Together with the results of Spence *et al.* [41], these results suggest that delusions of control may be associated with overactivation of the cerebellar-parietal network.

Conclusion

We have briefly reviewed recent evidence that suggests that many aspects of action occur without awareness. We have argued that one aspect of an action that might be available to awareness is the prediction of the sensory consequences of that action. This prediction might underlie the ability to distinguish between self-produced and externally generated actions, a process that appears to involve the parietal cortex. This brain region has also been implicated in psychotic symptoms, in which patients confuse their own actions with externally produced actions. Future studies using new paradigms are needed to elucidate the hypothesis that the forward model prediction contributes to the awareness of action. In particular, the study of motor awareness in patients with poor sensorimotor prediction might be fruitful in this context.

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References and recommended reading

Papers of particular interest, published within the annual period of review, have been highlighted as:

- of special interest
 - of outstanding interest
1. Wolpert DM, Ghahramani Z, Jordan MI: **An internal model for sensorimotor integration.** *Science* 1995, **269**:1880-1882.
 2. Wolpert DM, Flanagan JR: **Motor prediction.** *Curr Biol* 2001, **11**:R729-R732.
 3. Fournier P, Jeannerod M: **Limited conscious monitoring of motor performance in normal subjects.** *Neuropsychologia* 1998, **36**:1133-1140.
 4. Franck N, Farrer C, Georgieff N, Marie-Cardine M, Dallery J, d'Amato T, Jeannerod M: **Defective recognition of one's own actions in patients with schizophrenia.** *Am J Psychiatry* 2001, **158**:454-459.
 5. Blakemore S-J, Frith CD, Wolpert DW: **Spatiotemporal prediction modulates the perception of self-produced stimuli.** *J Cog Neurosci* 1999, **11**:551-559.
 6. Libet B, Gleason CA, Wright EW, Pearl DK: **Time of conscious intention to act in relation to onset of cerebral activity (readiness potential): the unconscious initiation of a freely voluntary act.** *Brain* 1983, **106**:623-642.
 7. Haggard P, Magno E: **Localising awareness of action with transcranial magnetic stimulation.** *Exp Brain Res* 1999, **127**:102-107.
 8. Jeannerod M, Frak V: **Mental imaging of motor activity in humans.** *Curr Opin Neurobiol* 1999, **9**:735-739.
 9. Stephan KM, Fink GR, Passingham RE, Silbersweig D, Ceballos-Baumann AO, Frith CD, Frackowiak RS: **Functional anatomy of the mental representation of upper extremity movements in healthy subjects.** *J Neurophysiol* 1995, **73**:373-386.
 10. Decety J, Perani D, Jeannerod M, Bettinardi V, Taday B, Woods R, Mazziotta JC, Fazio F: **Mapping motor representations with positron emission tomography.** *Nature* 1994, **371**:600-602.
 11. Nyberg L, Petersson KM, Nilsson LG, Sandblom J, Aberg C, Ingvar M: **Reactivation of motor brain areas during explicit memory for actions.** *Neuroimage* 2001, **14**:521-528.
- This PET study demonstrated that verbal retrieval of action phrases is associated with reactivation of the left ventral motor cortex and the left inferior parietal cortex for actions that were either overtly or covertly performed during encoding. Reactivation of the left dorsal parietal cortex and the right cerebellum was restricted to actions that were originally performed overtly.
12. Naito E, Kochiyama T, Kitada R, Nakamura S, Matsumura M, Yonekura Y, Sadato N: **Internally simulated movement sensations during motor imagery activate cortical motor areas and the cerebellum.** *J Neurosci* 2002, **22**:3683-3691.
- In this PET study, the neural correlates of an illusory wrist movement elicited by tendon vibration was compared with motor imagery of the same type of wrist movement. Motor imagery and the illusory kinesthetic sensation activated a common network of contralateral motor areas and the ipsilateral cerebellum. Together, these results suggest that it may be the kinesthetic sensation during mental imagery that activates these motor regions of the brain.
13. Thomas AK, Loftus EF: **Creating bizarre false memories through imagination.** *Mem Cognit* 2002, **30**:423-431.
- Subjects were presented with statements of bizarre or familiar actions, and had to either perform or imagine those actions 24 h later, subjects imagined performing a new set of actions, some of which had been presented in the first session. Two weeks later, subjects were tested for their memory of those actions. Actions that had been imagined in the first two sessions were more likely to be classified as performed actions than actions that had only been imagined in the first session. The more an action is imagined, the more likely it is to be confused with a performed action.
14. Gerardin E, Sirigu A, Lehericy S, Poline JB, Gaymard B, Marsault C, Agid Y, Le Bihan D: **Partially overlapping neural networks for real and imagined hand movements.** *Cereb Cortex* 2000, **10**:1093-1104.
 15. Sirigu A, Duhamel JR, Cohen L, Pillon B, Dubois B, Agid Y: **The mental representation of hand movements after parietal cortex damage.** *Science* 1996, **273**:1564-1568.
 16. Danckert J, Ferber S, Doherty T, Steinmetz H, Nicolle D, Goodale MA: **Selective, non-lateralized impairment of motor imagery following right parietal damage.** *Neurocase* 2002, **8**:194-204.
- Normally there is a speed-accuracy trade-off for movements performed both in reality and in the imagination. Here, a subject with a right temporoparietal lesion was tested on his ability to imagine and perform visually guided arm movements. There was a relationship between the speed and accuracy of his visually guided actions, but not between the accuracy and

speed of his imagined movements. This result is interpreted as demonstrating the role of the right parietal cortex in generating and updating internal forward models of action.

17. Maruff P, Wilson PH, Currie J: **Abnormalities of motor imagery • associated with somatic passivity phenomena in schizophrenia.** *Schiz Res*, in press.
This study demonstrated that patients with delusions of control do not show the normal speed-accuracy trade off for imagined as for real movements. These data support the notion that delusions of control are associated with an abnormal internal representation of action.
18. Frith CD: *The Cognitive Neuropsychology of Schizophrenia*. Hove: Lawrence Erlbaum Associates; 1992.
19. Frith CD, Blakemore S-J, Wolpert DM: **Abnormalities in the awareness and control of action.** *Phil Trans Roy Soc Lond: Biol Sci* 2000, **355**:1771-1778.
20. Haggard P, Eimer M: **On the relation between brain potentials and the awareness of voluntary movements.** *Exp Brain Res* 1999, **126**:128-133.
21. Haggard P, Clark S, Kalogeris J: **Voluntary action and conscious • awareness.** *Nat Neurosci* 2002, **5**:382-385.
This paper reports an elegant series of experiments investigating the awareness of actions and their sensory consequences. These experiments demonstrated a temporal 'binding' effect between actions that cause sensory stimuli (tones). This attraction between actions and their consequences may be a possible mechanism for classifying sensory events as self-generated.
22. Wegner DM, Wheatley T: **Apparent mental causation – sources of the experience of will.** *Am Psychol* 1999, **54**:480-492.
23. Daprati E, Franck N, Georgieff N, Proust J, Pacherie E, Dalery J, Jeannerod M: **Looking for the agent: an investigation into consciousness of action and self-consciousness in schizophrenic patients.** *Cognition* 1997, **65**:71-86.
24. Daprati E, Sirigu A: **Laterality effects on motor awareness. • Neuropsychologia** 2002, **40**:1379-1386.
The ability of right-handers and left-handers to recognise their own hand movements was tested using a paradigm in which subjects saw on a computer screen either the visual feedback of their own hand movements or the experimenter's hand movements. When the experimenter pantomimed the subjects' hand movements, thus producing an ambiguous situation, subjects were more accurate in recognising their dominant hand than their non-dominant hand. This is the first study to show that the ability to recognise self-generated movements is affected by motor dominance.
25. Knoblich G, Prinz W: **Recognition of self-generated actions from • kinematic displays of drawing.** *J Exp Psychol Hum Percept Perform* 2001, **27**:456-465.
This study showed that subjects are adept at recognising their own handwriting strokes when the strokes are played back to them, as long as the strokes are replayed at the correct velocity.
26. Knoblich G, Seigerschmidt E, Flach R, Prinz W: **Authorship effects • in the prediction of handwriting strokes: evidence for action simulation during action perception.** *Q J Exp Psychol A* 2002, **55**:1027-1046.
Subjects observed parts of earlier self-produced and other-produced writing strokes and were instructed to predict the following stroke. With no constraints, subjects are better at predicting strokes of their own writing than of other people's writing. When the writing strokes were made under constraints, however, the subjects were as good at predicting other people's writing strokes as their own. This was taken as evidence for action simulation.
27. Grafton ST, Arbib MA, Fadiga L, Rizzolatti G: **Localization of grasp representations in humans by positron emission tomography. 2. Observation compared with imagination.** *Exp Brain Res* 1996, **112**:103-111.
28. Decety J, Grezes J, Costes N, Perani D, Jeannerod M, Procyk E, Grassi F, Fazio F: **Brain activity during observation of actions. Influence of action content and subject's strategy.** *Brain* 1997, **120**:1763-1777.
29. Grezes J, Decety J: **Functional anatomy of execution, mental simulation, observation, and verb generation of actions: a meta-analysis.** *Hum Brain Mapp* 2001, **12**:1-19.
30. Iacoboni M, Koski LM, Brass M, Bekkering H, Woods RP, Dubeau MC, Mazziotta JC, Rizzolatti G: **Reafferent copies of imitated actions in the right superior temporal cortex.** *Proc Natl Acad Sci USA* 2001, **98**:13995-13999.
31. Perani D, Fazio F, Borghese NA, Tettamanti M, Ferrari S, Decety J, Gilardi MC: **Different brain correlates for watching real and virtual hand actions.** *Neuroimage* 2001, **14**:749-758.
This study investigated the neural processing of the observation of real hand movements and hand movements produced in three-dimensional virtual reality. Only real actions in a natural environment activated a visuospatial network including the right posterior parietal cortex. This study suggests that the brain treats real and virtual hand movements differently.
32. Buccino G, Binkofski F, Fink GR, Fadiga L, Fogassi L, Gallese V, Seitz RJ, Zilles K, Rizzolatti G, Freund HJ: **Action observation activates premotor and parietal areas in a somatotopic manner: an fMRI study.** *Eur J Neurosci* 2001, **13**:400-404.
In this fMRI study, subjects observed actions that were performed with the mouth, the hand or the foot, and which did or did not involve an object. Different regions of premotor cortex were activated by actions that involved different body parts, roughly representing the homunculus in premotor cortex. The parietal lobe was activated when actions involved an object, and again the activation pattern in this region was different for different actions. This was the first study to demonstrate that action observation activates parts of the motor system in a functionally specific manner.
33. Avikainen S, Forss N, Hari R: **Modulated activation of the human SI and SII cortices during observation of hand actions.** *Neuroimage* 2002, **15**:640-646.
34. Ruby P, Decety J: **Effect of subjective perspective taking during • simulation of action: a PET investigation of agency.** *Nat Neurosci* 2001, **4**:546-550.
Subjects were scanned using PET while imagining actions either from their own or from a third-person perspective. The parietal lobe was activated by action simulation in the third person perspective.
35. Decety J, Chaminade T, Grezes J, Meltzoff AN: **A PET exploration • of the neural mechanisms involved in reciprocal imitation.** *Neuroimage* 2002, **15**:265-272.
The parietal cortex was differentially activated when subjects imitated the experimenter compared with when the experimenter imitated the subject.
36. Farrer C, Frith CD: **Experiencing oneself vs another person as • being the cause of an action: the neural correlates of the experience of agency.** *Neuroimage* 2002, **15**:596-603.
Subjects were scanned in PET while controlling a moving dot on a computer screen. In some trials, subjects were in control of the dot's movement, whereas in other trials the dot was controlled by someone else and moved along a different trajectory from the subject's movements. The parietal cortex was activated more when someone else was in control of the dot's movement than during self-produced movements of the dot.
37. Chaminade T, Decety J: **Leader or follower? Involvement of the inferior parietal lobule in agency.** *Neuroreport* 2002, **13**:1975-1978.
38. Sirigu A, Daprati E, Pradat-Diehl P, Franck N, Jeannerod M: **Perception of self-generated movement following left parietal lesion.** *Brain* 1999, **122**:1867-1874.
39. Blakemore S-J, Smith J, Steel R, Johnstone E, Frith CD: **The perception of self-produced sensory stimuli in patients with auditory hallucinations and passivity experiences: evidence for a breakdown in self-monitoring.** *Psychol Med* 2000, **30**:1131-1139.
40. Blakemore S-J, Wolpert DM, Frith CD: **Central cancellation of self-produced tickle sensation.** *Nat Neurosci* 1998, **1**:635-640.
41. Spence SA, Brooks DJ, Hirsch SR, Liddle PF, Meehan J, Grasby PM: **A PET study of voluntary movement in schizophrenic patients experiencing passivity phenomena (delusions of alien control).** *Brain* 1997, **120**:1997-2011.
42. Blakemore S-J, Oakley DA, Frith CD: **Delusions of alien control in the normal brain.** *Neuropsychologia* In press.
43. Weiller C, Juptner M, Fellows S, Rijntjes M, Leonhardt G, Kiebel S, Muller S, Diener HC, Thilmann AF: **Brain representation of active and passive movements.** *Neuroimage* 1996, **4**:105-110.