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Deluding the motor system

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Abstract

How do we know that our own actions belong to us? How are we able to distinguish self-generated sensory events from those that arise externally? In this paper, I will briefly discuss experiments that were designed to investigate these questions. In particularly, I will review psychophysical and neuroimaging studies that have investigated how we recognise the consequences of our own actions, and why patients with delusions of control confuse self-produced and externally produced actions and sensations. Studies investigating the failure of this 'self-monitoring' mechanism in patients with delusions of control will be discussed in the context of the hypothesis that overactivity in the parietal cortex and the cerebellum contribute to the misattribution of an action to an external source (Spence et al., 1997).

1. Introduction

Delusions of alien control are symptoms associated with schizophrenia in which patients misattribute self-generated actions to an external source (Schneider, 1959). The actions in question can be mundane, such as picking up a cup or combing one's hair. Patients describe their thoughts, speech, and actions as being controlled by those of external agents rather than being produced by themselves: ''My fingers pick up the pen, but I don't control them. What they do is nothing to do with me'' (Mellors, 1970).

Normally, we can readily detect whether a movement is self-generated or externally caused. It has been proposed that an internal predictor, or forward model, uses information about intentions to enable this distinction between self-generated and externally generated sensory events

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(Miall & Wolpert, 1996; Wolpert, Ghahramani, & Jordan, 1995; Wolpert, Ghahramani, & Flanagan, 2001). Forward models use an 'efference copy' of the motor command (von Holst, 1954) to make a prediction of the consequences of the motor act. A *forward dynamic model* makes predictions about the next state of the system and compares this with the desired state. A *forward output model* makes predictions about the sensory consequences of the movement and this prediction is compared with the actual sensory consequences of a movement (see Fig. 1). This comparison can be used to cancel the sensory effect of the motor act, attenuating it perceptually compared with identical stimulation that is externally produced (Blakemore, Frith, & Wolpert, 1999a; Weiskrantz, Elliot, & Darlington, 1971).

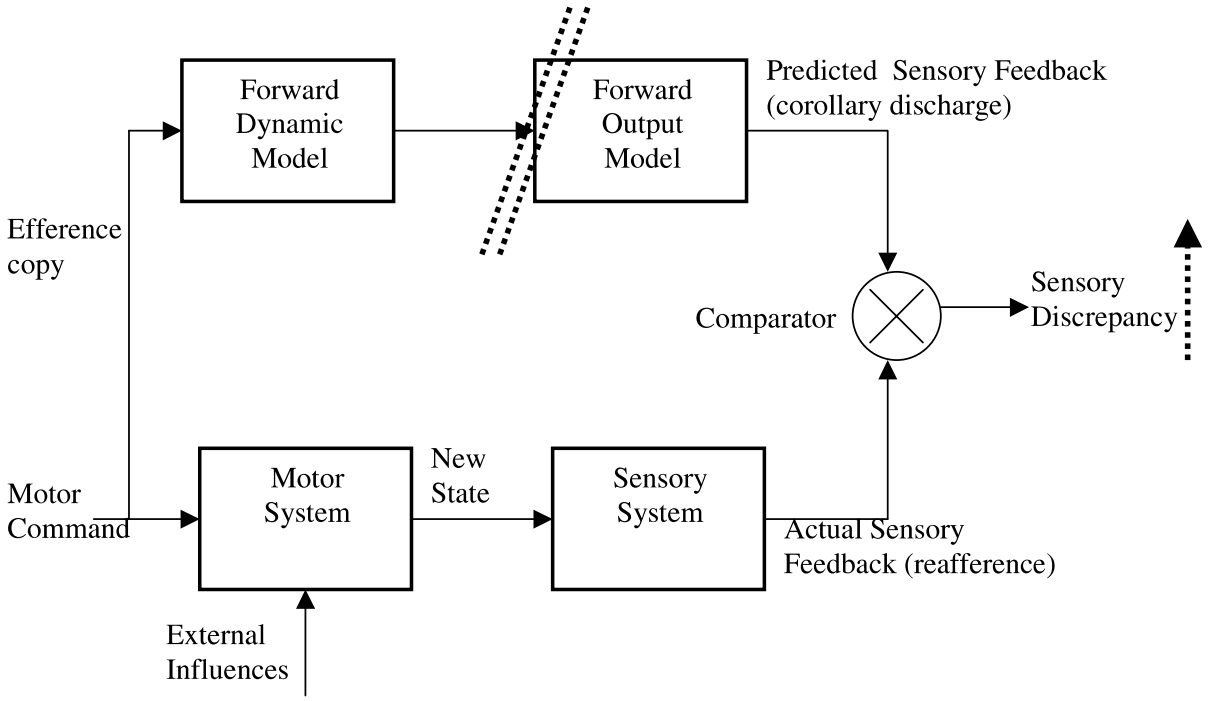

Fig. 1. The forward model of motor control, as proposed by Miall, Weir, Wolpert, and Stein (1993). A forward dynamic model predicts the consequences of motor commands and these are compared with the desired state. The forward output model makes a prediction of the sensory consequences of motor commands, which is compared with the actual consequences of movement (reafference). Discrepancies resulting from this comparison can be used to cancel reafferent inputs and to distinguish self-produced and externally produced signals. The dashed lines indicate the proposed underlying disorder leading to delusions of control, and a possible mechanism by which hypnotic suggestion can alter the experience of a self-produced movement. In both delusions of control and hypnotic suggestion the subject can formulate the action appropriate to his intention and the action is successfully performed. The forward output model is dysfunctional such that it cannot make an accurate prediction of the sensory consequences of the movement based on the efference copy. This might be because the efference copy signals do not reach the forward output model, or that the forward output model cannot make accurate predictions based on the efference copy it receives. This results in a high level of sensory discrepancy (indicated by the dashed arrow) and no cancellation of the reafference, so that the (self-produced) movement feels externally produced.

This predictive system is useful because it can be used to filter incoming sensory signals, picking out sensory information caused externally, such as touch produced by an external object or agent, and distinguishing it from sensory stimulation that occurs as a necessary consequence of self-produced motion. An impairment in such a predictive system could cause a lack of attenuation of the sensory consequences of self-produced actions, which would therefore be indistinguishable from externally generated sensations. This would result in the interpretation of one's own movements as being externally caused—a delusion of alien control (Blakemore, Wolpert, & Frith, 2002; Frith, 1992; Frith, Blakemore, & Wolpert, 2000).

1.1. The role of the cerebellum in predicting the sensory consequences of movement

How does the brain distinguish between self- and externally produced sensory stimulation? The cerebellum is believed to be involved in predicting the sensory consequences of movement (Miall et al., 1993; Wolpert, Miall, & Kawato, 1998). There is neuroimaging evidence that forward models are stored in the lateral cerebellar cortex (Imamizu et al., 2000). A similar region of the cerebellum is differentially activated according to the specific consequences of movement (Blakemore, Wolpert, & Frith, 1998). In this fMRI experiment subjects moved a foam-tipped rod with their left hand to produce a tactile stimulus on the palm of their right hand. In another condition in this study subjects made an identical movement of their left hand but this time the movement did not result in tactile stimulation on their left palm. The only experiential difference between these two conditions was the specific sensory consequences of the movement. The only significant difference in brain activity between these two conditions was located in the right lateral cerebellar cortex. This suggests that activation in this region depends on the specific sensory consequences of a movement.

A second experiment supported this proposal (Blakemore, Frith, & Wolpert, 2001). In this experiment, subjects were scanned using PET while generating a tactile stimulus on the palm of their hand, as before. This time, however, the tactile stimulation was produced under remote control via a robotic interface. Subjects moved a robotic arm with their left hand and this movement caused a second foam-tipped robotic arm to move across their right palm. Thus, motion of the left hand determined the tactile stimulus on the right palm. By using this robotic interface, delays of 0, 100, 200, and 300 ms were introduced between the movement of the left hand and the tactile stimulus on the right palm. Under all delays the left hand made the same movements and the right hand experienced the tactile stimulus. Only the temporal correspondence between the movement of the left hand and the sensory effect on the right palm was altered. The assumption behind this design was that delays are not predicted by the forward model because normally movements and objects do not have inherent delays. Therefore as the delay increases, the forward model prediction becomes less accurate and the sensory discrepancy between the predicted and actual sensory feedback from movement increases. Although subjects reported being unaware of the delays, there was a significant increase in the tickliness ratings for the tactile stimulus with increasing delay, supporting the notion that the amount of perceptual attenuation possible is proportional to the accuracy of the predicted sensory feedback from movement (Blakemore et al., 1999a). Blood flow in the right cerebellar cortex significantly correlated with delay (Blakemore et al., 2001). This suggests that activity in this region increases as the actual feedback from movement deviates from the predicted sensory feedback.

1.2. The role of the parietal cortex in the distinction between the self and the other

There is accumulating evidence that the parietal cortex is also involved in distinguishing self-produced actions and actions generated by others. Activity in the parietal operculum (secondary somatosensory cortex) is attenuated during self-initiated movements compared with passive movements (Weiller et al., 1996), and during self-produced compared with external sensory stimulation (Blakemore et al., 1998). In the fMRI experiment described in the previous section, subjects received a tactile stimulus on the palm of their right hand that was produced either by the movement of their own right hand or externally by the experimenter. In these two conditions, the tactile stimulus was identical, only the source of the stimulus differed. After excluding activity caused by subject arm movement per se, the remaining difference in brain activity between these two conditions was located in the parietal operculum as well as the anterior cingulate cortex and right cerebellar cortex. These areas were significantly more active when the tactile stimulus was externally produced compared with when it was self-produced. This might explain why self-produced touch feels less intense and tickly than the same tactile stimulation when it is externally produced (Blakemore et al., 1999a; Weiskrantz et al., 1971).

There is evidence from neurological patients that the parietal cortex plays a role in the distinction between the self and the other. Patients with left parietal lesions tend to confuse the ownership of hand movements when they are shown someone else's hand making movements similar to those they are making themselves (Sirigu, Daprati, Pradat-Diehl, Franck, & Jeannerod, 1999). A recent case-study reported a patient with a right hemisphere lesion in which the white matter underlying cortex including the parietal operculum had been damaged. This patient suffered from the delusional belief that her left limb belonged to her niece (Bottini, Bisiach, Sterzi, & Vallar, 2002).

Parietal lesions impair the ability to use mental motor imagery, a process believed to involve an internal model of action. In order to imagine an action you need some kind of stored representation that action. Parietal patients are unable to predict the time necessary to perform finger movements and visually guided pointing gestures using their imagination. Normally imagined and executed movement times are highly correlated, Fitts' Law accounting equally well for both types of movement (Decety & Jeannerod, 1995; Sirigu et al., 1995). This was found to be true for a patient with motor cortex damage, whereas in patients with parietal lesions actual movement execution was modulated by target size but motor imagery was not (Sirigu et al., 1996). More recently, using similar tasks, a patient with a right temporo-parietal lesion was tested on his ability to imagine and perform visually guided hand movements. It was found that, unlike his performance for visually guided actions, there was no relationship between accuracy and speed for imagined movements (Danckert et al., 2002).

Functional neuroimaging studies have also demonstrated that the parietal cortex is involved in the distinction between self and other. Right inferior parietal cortex is activated when subjects simulate actions from someone else's perspective but not from their own (Ruby & Decety, 2001). This region is activated when subjects observe their own actions being imitated by someone else compared with when they imitate someone else's action (Decety, Chaminade, Grezes, & Meltzoff, 2002). In this case, knowledge of who is producing the movements to imitate, and who is doing the imitating is involved in the imitation. The inferior parietal cortex is differentially activated according to whether subjects attend to someone else's actions or their own (Farrer & Frith, 2002) and whether they lead or follow another person's actions (Chaminade & Decety, 2002).

1.3. Delusions of control and the cerebellum and parietal cortex

Overactivity of the parietal cortex appears to contribute to the feeling that active movements are externally controlled in delusions of alien control (Spence et al., 1997). In this PET study, patients with delusions of control were scanned while they performed a simple motor task in which they were required to move a joystick in one of the four directions, chosen at random. This 'willed action' task was compared with a similar task in which the joystick movements were paced. The patients with delusions of control showed overactivity in superior parietal cortex and in the cerebellum relative to normal controls and to patients who did not have delusions of control. Normally, activity in parietal cortex is more typical of passive movements than active ones (Weiller et al., 1996). Thus, at the experiential level, when the patient makes an active movement it can feel like a passive movement. It is this feeling that leads to the belief about alien control. Further support for this suggestion came from the finding that parietal activity had returned to 'normal' levels when, some months later, the same patients who were scanned in the initial study and whose symptoms had now subsided were re-scanned performing the same task.

1.4. Inducing delusions of control in the normal brain

Further evidence that overactivity of the parietal cortex and cerebellum are involved in generating the feeling that a movement is externally produced comes from a recent study in which experiences of alien control were induced in healthy control subjects (Blakemore, Oakley, & Frith, 2003). In this study, hypnosis was used as a cognitive tool to create delusions of alien control in normal, healthy subjects. 'Ideomotor movement' is a frequently demonstrated hypnotic phenomenon in which self-produced actions are attributed to an external source (Heap & Aravind, 2002). A typical example involves suggesting to the hypnotised subject that their arm is being raised upwards passively by an external device, such as a helium balloon attached to their wrist. This suggestion causes highly hypnotisable subjects to produce an appropriate movement. Despite generating the movement themselves, subjects describe the raising and lowering of their arm as being involuntary and typically claim that it was caused by the helium balloon.

In our study, PET was used to scan highly hypnotisable subjects during a similar 'alien control' experience. In an Active Movement condition, subjects were instructed to move their left arm up and down, which they correctly attributed to themselves. In another condition (the Deluded Passive Movement condition), subjects were told that their left arm would be moved up and down by a pulley, but in fact the pulley did not move and resulting arm movements were self-generated. This suggestion induced the subjects, who were all highly hypnotisable according to the Harvard Hypnotisability Scale (Shor & Orne, 1962), to move their arm up and down in the suggested manner. However, crucially, subjects misattributed this movement to the pulley. All conditions were performed while subjects were hypnotised. Thus, movements in the Active Movement and Deluded Passive conditions were identical—subjects made the same self-generated arm movements in both conditions. The only difference between these two conditions was the source to which the movement was attributed.

Using this paradigm we were able to compare brain activation during active movements that are correctly attributed to the self with identical active movements that are misattributed to an external source. The results demonstrated the cerebellum and parietal operculum were

differentially activated depending on whether an active movement was experienced as truly active or as passive. Parietal-opercular and cerebellar activity was significantly higher and more widespread in the Deluded Passive condition in which movements were misattributed to an external source than in the Active Movement condition in which identical movements were correctly attributed to the self.

In terms of the forward model (Fig. 1), which is believed to be stored in the cerebellum (Imamizu et al., 2000; Miall et al., 1993), the abnormality in the Deluded Passive condition might lie in the forward output model, and not the forward dynamic model. The forward dynamic model compares the estimated state with the desired state and the results of this comparison are used to adjust motor commands in order to optimise motor control and learning. Subjects produced the same smooth arm movements in the deluded passive and active movement conditions. Therefore, the motor system appears to be functioning normally in terms of motor control in the Deluded Passive condition. In contrast, the forward output model compares the predicted consequences of motor commands with the actual consequences of movement (reafference), and discrepancies resulting from this comparison can be used to cancel reafferent inputs and to distinguish self-produced and externally produced sensory signals.

Rainville, Carrier, Hofbauer, Bushnell, and Duncan (1999) noted that introducing specific suggestions to hypnotised subjects was accompanied by widespread increased in rCBF in frontal cortical areas, mainly on the left. We proposed that hypnotic suggestion in the Deluded Passive condition, possibly mediated by top-down signals from prefrontal cortex, which was activated only in this condition, prevents the motor intentions from reaching the forward output model. In this case, the forward output model would no longer be able to make an accurate prediction of the sensory consequences of the movement. This would lead to a discrepancy between predicted and actual sensory feedback, which would result in no attenuation of the sensory feedback, making the (self-produced) movement feel externally produced. If the cerebellum signals sensory discrepancies between predicted sensory feedback of movements and their actual sensory consequences (Andersson & Armstrong, 1985; Blakemore et al., 2001), increased cerebellar activation would be expected in the Deluded Passive condition.

According to evidence from patient and neuroimaging studies described above, the parietal cortex appears to be involved in inducing the feeling that an action or sensory event is external. Activity in the parietal cortex seems to be required for an arm movement to feel as if it is externally generated. The inferior parietal lobe is the direct target of output from the cerebellum (Clower, West, Lynch, & Strick, 2001) and parietal-opercular cortex activity can be influenced by cerebellar activity (Blakemore, Wolpert, & Frith, 1999b). In the Deluded Passive condition, if the cerebellum signals a discrepancy between predicted and actual sensory feedback, then no parietal-opercular attenuation would occur, which is what normally occurs during externally produced sensory stimulation.

There is an alternative—or additional—explanation for the parietal activity in the Deluded Passive condition. It is well established that attention to a particular sensory modality or feature increases activity in the brain region that processes that feature even in the absence of a sensory signal (Driver & Frith, 2000). It has also been suggested that hypnotic suggestion, by focussing attention, can produce increased activity in specific brain areas, which causes a modulation of sensory experience (Rainville, Duncan, Price, Carrier, & Bushnell, 1997). It is possible that, in our study, subjects' attention is more highly focussed on the sensations associated with passive

movement in the Deluded Passive condition than in the Active Movement condition. This increased attention produces activation in brain regions that process such sensations (the parietal operculum). It is the activation in this region that causes the movement to feel external.

A similar mechanism may underlie the disorder leading to delusions of control in schizophrenia and other clinical conditions. In particular, it has been proposed that delusions of control are caused by an impairment in the forward model system that predicts the sensory consequences of one's own actions (Frith et al., 2000). This could cause a lack of attenuation of the sensory consequences of self-produced actions, which would therefore be indistinguishable from externally generated sensations, hence causing a confusion between the self and the other (Frith, 1992; Frith et al., 2000).

There is one crucial difference between delusions of control in clinical populations and the misattribution of movement in the hypnotised subjects in this study. The patient with delusions of control has an intention to move and misattributes his movement to someone or something else, whereas the hypnotised person is not aware of the intention to move and experiences his movement as passive. We have suggested that the patient with delusions of control is aware of her intention, makes a movement based on this intention, but no cancellation of the consequences of the movement occurs, so the movement, even though it matches the intentions, feels like an externally caused movement (Blakemore et al., 2003). The hypnotised subject, on the other hand, is not aware of his intention to move, moves due to the hypnotic suggestion to move, but no sensory cancellation occurs, and his movement is experienced as passive.

The ability to distinguish between active and passive movements is an important part of a 'who' system, which allows one to link an action with its cause (Georgieff & Jeannerod, 1998). Our results suggest that overactivation of a cerebellar–parietal network during self-generated actions is associated with the misattribution of those actions to an external source. Overactivity of the parietal cortex and cerebellum occurs during self-generated movements in patients with delusions of alien control, and subsides when the same patients are in remission (Spence et al., 1997). It is possible that malfunctioning in this network leading to overactivity produces the feeling of 'otherness' associated with self-produced movements in delusions of alien control.

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