Abnormalities in the awareness of action

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Optimal motor control relies on internal representations of the actual, desired and predicted states of our limbs and the external world. Only certain components of these internal representations are available to awareness. We suggest that impairments of the components of internal representations might underlie a broad variety of neuropsychiatric symptoms, including the anarchic hand sign, phantom limbs, utilization behaviour and delusions of control.

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In this article we present a framework that can account for several disparate abnormalities in the awareness and control of action. Our framework is based on an established model of normal motor learning and control [1]. In the first section of the article we summarize this model of motor control and speculate on which of its components are available to awareness. In the second section we outline how this model can be used to understand specific signs and symptoms of various neuropsychiatric disorders in which motor control or awareness of motor control is impaired.

Internal models of the motor system

It has been proposed that the central nervous system (CNS) contains internal models, which represent aspects of one's own body and its interaction with the external world, in order to optimize motor control and learning [1–3]. Recent research has focused on two types of internal model. The 'forward model' uses efference copy to predict the sensory consequences of motor commands whenever movements are made [1–5]. By contrast, the 'inverse model' provides the motor commands necessary to achieve some desired outcome [6,7]. Internal models and their functions are described in detail elsewhere [1,5].

Awareness of the motor system

The question of which component processes of internal models of motor control are available to awareness and which are not does not currently have a clear answer, although we can speculate. We are clearly aware of the goals and desired states underlying most movements we make. However, it is unlikely that we have conscious access to all our motor commands and every fine adjustment made to a movement. Take the simple example of picking up a cup. You are aware of the goal and desired state of the action (to grasp and lift the cup without breaking it or letting it slip), but you are probably unaware of all the fine adjustments in muscle contraction, movement velocity, grip aperture, grip force and so on, which are necessary to achieve the goal. These adjustments seem to be made without awareness. This suggests we do not have conscious access to the computations of the inverse model or to motor commands.

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By contrast, predictions made by the forward model may be available to awareness. The forward model makes two types of prediction. First, it predicts the actual outcome of the motor command and compares this to the desired outcome – this comparison occurs before a movement has been made [8]. This prediction is used to estimate the state of the motor system, which is not directly observable by the CNS, and to make fine adjustments to ongoing motor commands before reafferent feedback from the movement is available. Second, the forward model predicts the sensory consequences of movement and compares this with the actual feedback – this comparison occurs after a movement is made. This prediction can be used to anticipate and compensate for the sensory effects of movement, attenuating the component that is due to self-movement from that due to changes in the outside world [9]. The results of several studies suggest that this prediction, which is based largely on the efference copy of the motor command, is available to awareness (see Box 1). The experiments described in Box 1 also suggest that the actual state of the motor system and the actual sensory consequences of a movement are normally unavailable to awareness. Furthermore, we seem to be unaware of the results of the comparison between the predicted and intended outcome of motor commands, and the comparison between the predicted and actual sensory feedback, as long as the desired state is successfully achieved.

Abnormalities in the control and awareness of action

In the remainder of this article we discuss a variety of neuropsychiatric symptoms and suggest that the model of the motor system illustrated in Fig. 1 provides a useful and unifying framework for understanding these various disorders. We do not speculate on possible neurophysiological underpinnings of the components of this model of motor control and their impairments, which have been explored elsewhere [10]. The strength of the framework is in the parsimonious nature with which it can address many seemingly disparate disorders.

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Box 1. To what extent are we aware of our motor systems?

There are several observations that demonstrate that the motor system can function in the absence of awareness. Goodale *et al.* report an experiment in which subjects were required to point at a visual target [a]. During a saccade the target was occasionally displaced by several degrees. Although the displacement of the target went unnoticed by the subjects, they nevertheless adjusted the trajectory of their moving hand to the new target position. In this case, the subjects were not aware of the sensory information that elicited the movement correction or of the change in the motor programme that was elicited. Similarly, Castiello *et al.* found that awareness of an unexpected target jump occurred more than 200 ms after the motor system had initiated an appropriate movement correction [b]. We propose that there is only limited awareness of the actual state of the motor system whenever it has been successfully predicted in advance. We suggest that under normal circumstances we are aware only of the predicted consequences of movements.

Libet demonstrated that subjects are aware of initiating a movement about 80 ms before the actual movement occurs [c]; see also [d]. This suggests that the awareness of initiating a movement depends on the predicted sensory consequences of the movement, which are available before the sensory feedback from the movement. We may only be aware of the actual sensory consequences of our movements when they deviate from what we expect. However, in some circumstances we are unaware of even relatively large deviations of actual movements from those expected. This seems to happen as long as the desired state is successfully achieved. For example, Fourneret and Jeannerod gave false feedback about the trajectory of an arm movement so that subjects, who could not see their arm or hand, had to make considerable deviations from a straight movement in order to generate a straight line on a computer screen [e]. The subjects could achieve the desired result of drawing a straight line by making deviant movements. However, verbal reports indicated that they were unaware that they were making deviant movements.

Knoblich and Kircher recently performed a similar study (pers. commun.). Subjects were instructed to draw circles with a pen, which they saw reproduced by a moving dot. Parametric degrees of velocity change were introduced between the subjects' movement and its visual consequences (the movement of the dot), and subjects were instructed to lift the pen as soon as they detected a change. The results clearly demonstrated that subjects tended to compensate for the velocity changes well before they were aware of the discrepancy (before they lifted the pen).

These results suggest that there are different levels of awareness of the motor control system. It seems that the inverse model system continually makes fine adjustments to the motor commands so that the actual movement achieves the goal (desired state). These fine adjustments are normally unavailable to awareness. This makes sense – we would be overloaded with information if we were aware of all the minor errors in and fine adjustments made to our movements. Only when the discrepancy between the intended and actual movement is large does it becomes available to awareness. The exact threshold above which the discrepancy becomes available to awareness is currently unknown.

A rather different experiment in which the correspondence between movement and its sensory consequences was altered provides further evidence that subjects are unaware of the actual consequences of movement. In this study, 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 [f]. Without the subject's knowledge, 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. Delays are not predicted by the forward model and therefore produce a discrepancy between the predicted and actual feedback from movement. Subjects rated the sensation of the tactile stimulation in each condition, and although there was a striking correlation between delay and the perceived 'tickliness' of the stimulus, none of the subjects had noticed the delays. This demonstrates that the delays, because they are not predicted, result in less cancellation of the sensory signal, which is perceived as more tickly. However, at another level, subjects were unaware of discrepancy between the predicted and actual consequences of movement. It seems then, that we are largely unaware of sensory feedback about the actual state of our motor system as long as our intentions have been achieved.

References

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Optic ataxia

Patients with optic ataxia (Bálint's syndrome) have difficulty grasping objects that they can see relatively clearly ([11] translated by [12],[13]). Despite being clumsy, the attempted movement matches the patient's intentions and the patient is aware of having a problem with reaching [14]. In terms of our characterization of the motor system, the problem in optic ataxia occurs because the inverse models are not properly finely 'tuned' by the immediate context. In other words, the inverse models do not use the affordances offered by the shape of the object to be grasped appropriately when computing the motor commands required to make an action (Fig. 2).

'Anarchic hand' sign

Patients showing the anarchic hand sign (or 'alien hand' sign, see Ref. [15]) have a hand that moves 'of its own accord', without the will of the patient. In one case it was noted that 'the patient had picked up a pencil and had been scribbling with the (affected) right hand... She then indicated that she had not herself initiated the original action of the right arm... She experienced a feeling of dissociation from the actions of the right arm, stating...that "it will not do what I want it to do"' [16]. Patients with an anarchic hand clearly recognize that there is a discrepancy between what the hand is doing and their desired actions.

In many ways the patient with an anarchic hand shows the converse problem to the patient with optic ataxia. The patient with optic ataxia fails to form representations of objects in the immediate environment in terms of the appropriate movements needed to reach and grasp them. In the patient with an anarchic hand these representations are activated inappropriately. The sight of an object is sufficient to elicit the movement even though this does not fit with the patient's current goals. In terms of our characterization of the motor system, the movements

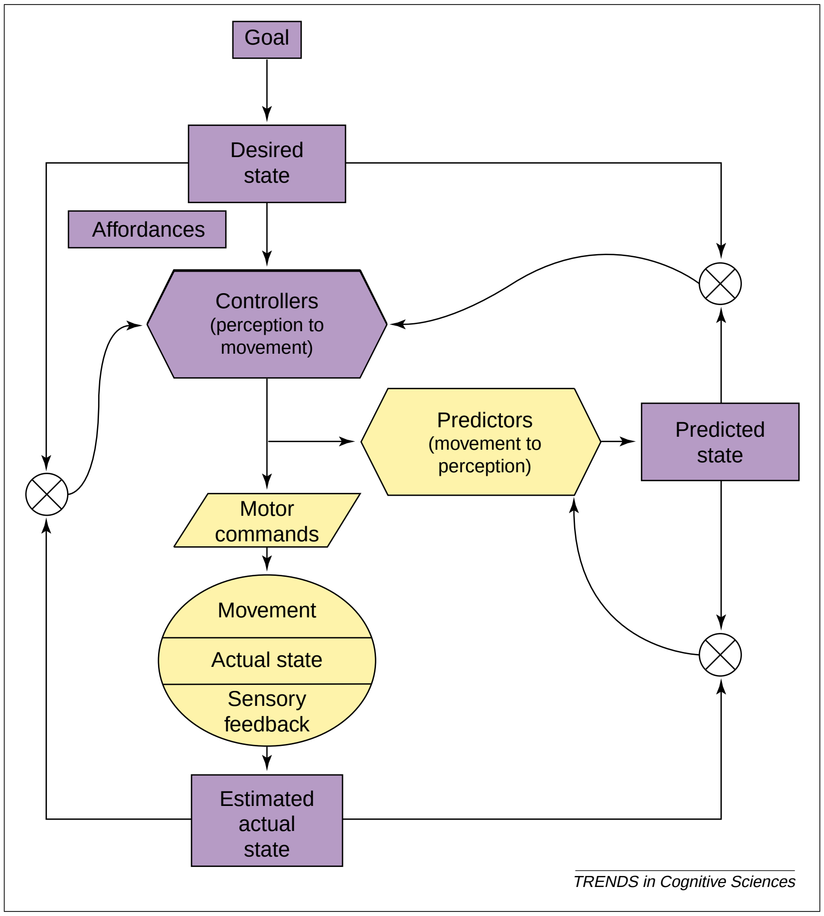

Fig. 1. Our framework of the motor control system postulates several kinds of motor representation, some of which are available to awareness (in mauve), some of which are not (in yellow). (1) The actual state of the system is not directly available to the central nervous system. Instead, an **estimated actual state** of the system is inferred on the basis of the stream of motor commands, predictions based on motor commands and sensory feedback. (2) The representation of the **desired state** of the system holds the instant goal of the system and is available to awareness. (3) The next **predicted state** of the system provides an estimate of the future state of the system derived from the predictors. The predicted state seems to be available to awareness (see Box 1). (4) **Motor commands** are derived from the controllers and are fine-tuned by sensory information (**affordances**) about the current state of the world (such as visual information about the position and shape of the object that is to be grasped). We are not aware of motor commands, nor of fine adjustments made to them. (5) **Sensory feedback** is the consequence of the action performed, plus any environmental events. Experiments suggest that we have only limited awareness of the consequences of actions.

of the anarchic hand occur because the effects of the affordances supplied by the immediate visual environment are no longer inhibited by the currently intended action (Fig. 2). However, representations of the intended and actual positions of the hand are available, so the patient knows that the behaviour of the hand does not conform to his or her intentions.

Utilization behaviour

Some patients with damage to the frontal lobes show 'utilization behaviour' [17,18], in which they utilize objects inappropriately. The sight of an object elicits a stereotyped action, which is inappropriate in the wider context [17]. Unlike patients with the anarchic hand sign, the patient showing utilization behaviour does not perceive a discrepancy between his actions and his intentions. On being asked why he performed the actions, the patient will 'rationalize'; saying that he performed the action because he thought that is what the examiner wanted him to do. Our formulation of utilization behaviour is that the patient's actions are involuntarily elicited by objects in the environment, but that the patient erroneously experiences these actions as intended.

We suggest that the problem causing utilization behaviour occurs at an earlier stage in the development of an action than that causing the anarchic hand. The problem has two components. First, there is no awareness of goals and intended actions (Fig. 3). The patient is not aware of what he is going to do until after he has done it. Second, inappropriate responses elicited by objects in the environment are not inhibited.

Phantom limbs

After amputation of a limb many patients experience a phantom limb: they still feel the presence of the limb although they know it does not exist [19]. It has been suggested that neural plasticity plays a role in the experience of phantom limbs. After amputation of a limb there is reorganization of the deafferented region of cortex. As a result, stimulation of the skin of distant areas such as the face or the chest can elicit sensations in a phantom arm [20,21].

Some patients report being able to move their 'phantoms' voluntarily, whereas others experience their phantom as paralysed and cannot move it even with intense effort. If the limb was paralysed before amputation the phantom normally remains paralysed. If not, then typically immediately after amputation the patient feels that they can generate movement in the phantom. However, with time, patients often lose this ability [22]. Our explanation of these phenomena is that the estimated position of a limb is not based solely on sensory information, but also on the stream of motor commands issued to the limb muscles. On the basis of these commands the forward model can estimate the new position of the limb before any sensory feedback has been received. We have suggested that the normal experience of the limb is often based on this predicted state, rather than the actual state (Box 1). Even in the absence of a limb, streams of motor commands can still be issued. If these commands lead to the prediction of movement then the phantom will be experienced as moving. However, the motor control system is designed to adapt to changing circumstances. Because the limb does not actually move, there is a discrepancy between the predicted and the actual consequences of the motor commands. With time, the forward models will be modified to reduce these discrepancies – the prediction will be altered so that eventually no movement of the limb is predicted even when motor commands to move the limb are issued. Such adaptation in the forward models could explain why patients eventually lose the ability to move their phantoms.

Such adaptation of the forward models would also explain how Ramachandran and Rogers-Ramachandran were able to reinstate

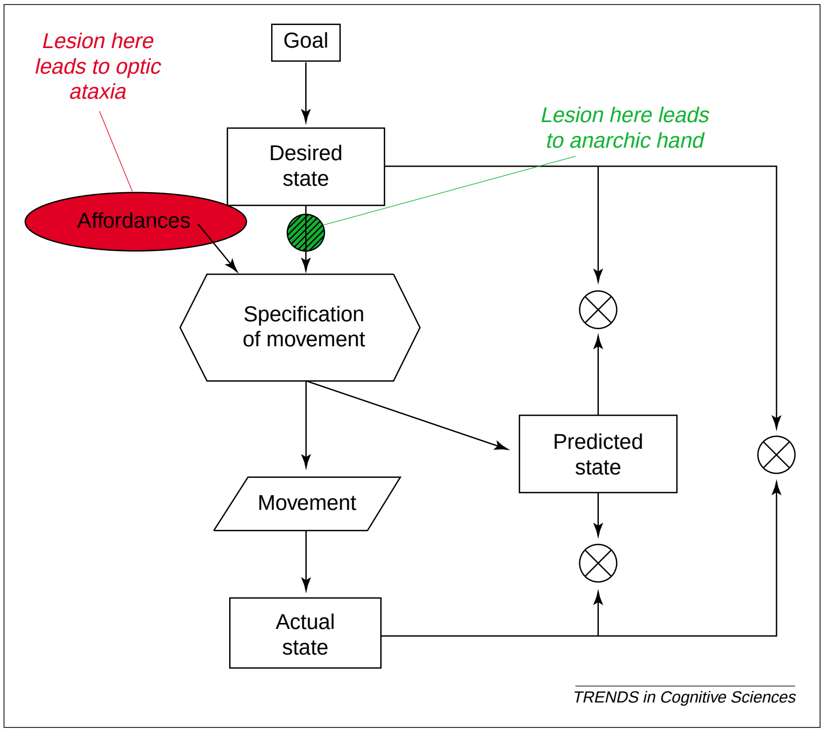

Fig. 2. The underlying disorders leading to optic ataxia (in red) and anarchic hand (in green). In optic ataxia, the fine-tuning of grasping actions afforded by the precise shape and position of objects is no longer available to the patient. The patient is aware that actions are clumsy. In anarchic hand syndrome, actions of the hand are no longer controlled by the intentions of the patient. Instead, the hand makes stereotyped responses to objects in the environment. The patient is aware of the discrepancies between intentions and the actions of the hand.

voluntary movement of the phantom by providing false visual feedback of a moving limb corresponding to the phantom [23]. This was achieved by placing a mirror in the mid-sagittal plane. With the head in the appropriate position it was possible for the patient to see the intact limb at the same time as the mirror reflection of this limb. For most patients, moving their hand in this mirror box rapidly leads to the perception that they are now able to move the phantom limb again. In a reformulation of the proposals of Ramachandran and Rogers-Ramachandran [23], we suggest that the false visual feedback supplied by the mirror box allows the forward models to be updated. As a result, efference copy produced in parallel with the motor commands now generates changes in the predicted position of the missing limb corresponding to what the patient had seen in the mirror.

Fading limbs

In some cases of peripheral deafferentation of a limb, patients become unaware of the existing limb unless it can be seen [24]. Similar problems can occur in brain-damaged patients who are no longer aware of a (non-paralysed) limb contralateral to their lesion. For example, patient PJ had a large cyst in the left parietal lobe and reported the experience of the position and presence of her right limbs fading away over seconds if she could not see them [25]. Her experience of a constant tactile stimulus or a weight also faded away, but she could detect changes in such sensations. Thus, the representation of the current limb position could not be maintained in the absence of changing stimulation.

In such cases, visual signals provide the only sensory information for making accurate movements. They provide information about the position of a limb prior to movement and provide feedback about the accuracy of the movement. As a result, the motor control system will learn to predict the outcome of movements and estimate the current state of the system without using somatosensory and proprioceptive signals, which are unavailable. It will learn to base such estimates solely on the stream of motor commands and upon visual information. In the absence of visual signals, the estimates cannot be made and the limb seems to fade away.

Delusions of control or passivity experiences associated with schizophrenia

Many patients with schizophrenia describe 'passivity' experiences in which actions, speech, thoughts or emotions are made for them by some external agent rather than by their own will. 'My fingers pick up the pen, but I don't control them. What they do is nothing to do with me' [26]. In most cases the actions made when the patient 'feels' that he is being controlled by alien forces are not discrepant with his intentions.

In a reformulation of an earlier model [27], we suggest that the experience of alien control arises from a lack of awareness of the predicted limb position. 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 (see Box 1). The patient with delusions of control is aware of his goal, of his intention to move and of his movement having occurred, but he is not aware of having initiated the movement. It is as if the movement, although intended, has been initiated by some external force. Abnormalities in forward model prediction might underlie this misinterpretation of action. Normally the sensory consequences of self-generated movements are attenuated and classified as self-produced [9]. This attenuation and classification relies on an accurate prediction by the forward model. We suggest that, in delusions of control, the prediction mechanism is faulty, and as a consequence self-generated movements are not attenuated and are wrongly classified as externally generated. The patient is not aware of the predicted consequences of a movement and is therefore not aware of initiating a movement (Fig. 3). In parallel, the patient's belief system is faulty so that he interprets this abnormal sensation in an irrational way. In a variation on this theme, Spence has suggested that the problem is to do with the timing of awareness. Spence suggests that, in the presence of delusions of control, the awareness of the sensory consequences of the movement precedes the awareness of initiating the movement, which is in the opposite order to the normal experience of our own agency [28].

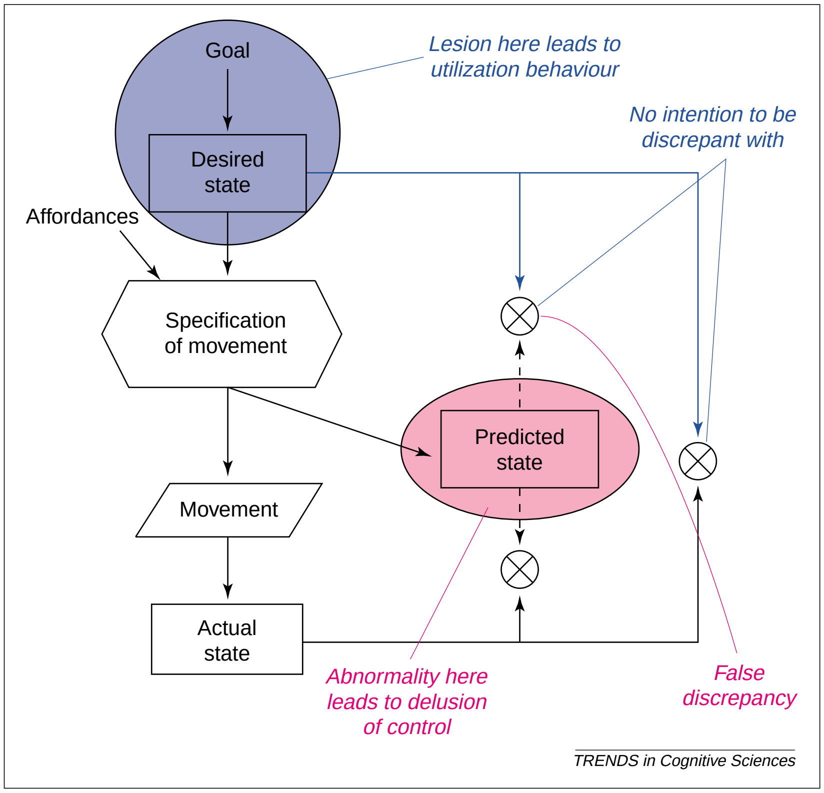

Fig. 3. The underlying disorders leading to utilization behaviour (in blue) and delusions of control (in pink). The patient with utilization behaviour does not form any intentions and so makes stereotyped responses to objects in the environment. The patient is not aware that these responses are inappropriate. The patient with delusions of control formulates the action appropriate to his intention and the action is successfully performed. The patient is aware that the action matches the intention, but has no awareness of initiating the action or of its predicted consequences. The patient feels as if his actions are being made for him by some external force.

Several experiments confirm that there are subtle problems consistent with a lack of awareness of predicted actions. Patients with delusions of control fail to make rapid error corrections based on awareness of discrepancies between intended and predicted limb positions, although they have no difficulty correcting errors based on visual feedback about actual limb positions [29,30]. These patients have difficulty distinguishing between correct visual feedback about the position of their hand and false feedback when the image of the hand they see is in fact that of another person attempting to make the same movements as the patient [31]. Normally the sensory consequences of self-produced movements can be predicted accurately on the basis of efference copy, and are cancelled relative to external sensations (see p. 237). Attenuation of self-produced stimulation occurs in normal control subjects and psychotic patients without passivity symptoms or auditory hallucinations. By contrast, the perception of self-produced stimulation is not attenuated relative to externally produced stimulation in patients with passivity symptoms and/or auditory hallucinations [32]. These results support the proposal that such symptoms are associated with an abnormality in the forward model mechanism that normally predicts and cancels self-produced relative to externally produced sensations.

Conclusions

In this article we have attempted to develop a framework based on well-established principles of motor control in such a way that the components of the system can be related to the subjective experience of motor control. Impairments of different components of the system may underlie various neurological and psychiatric disorders. The strength of this model is the parsimonious nature in which it can account for a broad range of disorders.

Questions for future research

- Under what circumstances do the components of internal models become available to awareness?
- What are the neural systems underlying motor representations?
- In particular, what are the underlying brain mechanisms of the predictor and comparator mechanism in forward models?
- What is the role of prior knowledge and beliefs to our awareness of the motor system?
- Does the same kind of predictive system underlie cognitive processes such as understanding other people's minds?

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Conscious thought as simulation of behaviour and perception

Germund Hesslow

A ‘simulation’ theory of cognitive function can be based on three assumptions about brain function. First, behaviour can be simulated by activating motor structures, as during an overt action but suppressing its execution. Second, perception can be simulated by internal activation of sensory cortex, as during normal perception of external stimuli. Third, both overt and covert actions can elicit perceptual simulation of their normal consequences. A large body of evidence supports these assumptions. It is argued that the simulation approach can explain the relations between motor, sensory and cognitive functions and the appearance of an inner world.

It might be said that cognitive science rests upon the assumption that human behaviour cannot be understood by taking only perceptual and motor processes into account and that distinct *cognitive* mechanisms are required to explain behaviour. Yet, developments in several fields during the last couple of decades suggest that cognitive and sensorimotor mechanisms are intimately connected. Among these are emerging ideas about embodied cognition [1,2] and findings that imagery relies heavily on sensory mechanisms and that certain kinds of problem solving involves motor structures.

The view to be defended here, is that this somewhat paradoxical situation can be resolved by what we might call the ‘simulation hypothesis’, essentially a combination of some ideas originally formulated by British empiricist philosophers in the 18th century [3] and their associationist descendants [4]. This hypothesis states that thinking consists of simulated interaction with the environment, and rests on the following three core assumptions:

(1) Simulation of actions: we can activate motor structures of the brain in a way that resembles activity during a normal action but does not cause any overt movement.

(2) Simulation of perception: imagining perceiving something is essentially the same as actually perceiving it, only the perceptual activity is generated by the brain itself rather than by external stimuli.

(3) Anticipation: there exist associative mechanisms that enable both behavioural and perceptual activity to elicit other perceptual activity in the sensory areas of the brain. Most importantly, a simulated action can elicit perceptual activity that resembles the activity *that would have occurred* if the action had actually been performed.

Simulation of behaviour

In his remarkably insightful book, *The Senses and the Intellect* from 1868, Alexander Bain suggested that thinking is essentially a covert or ‘weak’ form behaviour that does not activate the body and is therefore invisible to an external observer [4]. ‘Thinking’, he suggested, ‘is restrained speaking or acting’ (p. 340). This idea, which was central to behaviourism [5,6], was thought to have been disproved when it was shown that subjects paralysed by curare were still able to think [7]. It may have been prematurely rejected, however and a slightly modified version of it has lived on.

Behaviour is generated in a hierarchical fashion in the frontal lobes. Activity in sensory cortex is signalled via both intra- and sub-cortical pathways to the anterior parts of the frontal lobe. The main signal flow is then posteriorly through supplementary and premotor cortex to the primary motor cortex. Single muscle contractions are controlled by neurons in the primary motor cortex. More complex movements, such as gripping an object or saying a word, which require temporally organized activation of several muscles, are elicited by higher-level command signals in more anterior neurons. In the prefrontal cortex only the most global aspects of behaviour are controlled. At all levels, the frontal cortex interacts

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