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REVIEW

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Action prediction in the cerebellum and in the parietal lobe

Abstract The ability of the central nervous system to predict motor behaviour is a central issue in experimental and computational studies of motor control. The parietal cortex and the cerebellum have been proposed to play a role in sensorimotor prediction. Here we discuss the roles of these two brain regions in various aspects of sensorimotor prediction according to results of recent empirical studies using a variety of techniques including electrophysiology, psychophysics, functional neuroimaging and the investigation of neurological patients.

Keywords Prediction · Internal model · Forward model · Parietal cortex · Cerebellum · PET · fMRI · Motor control

Introduction

Prediction is fundamental to several aspects of motor behaviour such as postural compensation, tracking moving objects and planning an arm trajectory. The ability of the central nervous system to simulate and anticipate the behaviour of the motor apparatus is a central problem in experimental and computational studies of motor control. Human subjects can use prediction to improve a motor skill or induce sensorimotor plasticity through movement execution or even simply through mental rehearsal. It has been proposed that the CNS implements prediction by using internal models (Wolpert et al. 1995). There are two types of internal model: 'inverse models' and 'forward models'. Inverse models calculate the motor commands required to achieve a certain goal based on the desired state. Forward models make predictions about the behaviour of the motor system and its sensory consequences (Wolpert et al. 1995; Wolpert and Flanagan 2001; Desmurget and Grafton 2000). When a movement is made, an efference copy (Holst and Mittelstaedt 1950) of the motor command, in combination with state variables such as the configurations of parts of the body, is used to make a prediction of the sensory consequences of the movement (Wolpert et al. 1995). This sensory prediction can then be compared with the actual sensory feedback from movement and used to optimise motor control.

Prediction can be used by the CNS in several ways. Predictions of the sensory consequences of the motor command can be used to anticipate and cancel the sensory effects of movement (re-afference), as is the case during eye-movements (Helmholtz 1867; Holst and Mittelstaedt 1954). This process effectively accentuates externally produced sensory stimulation (ex-afference). Prediction can be used to maintain accurate performance in the presence of feedback delays, such as those that occur between the issuing of a motor command and the perception of its sensory consequences. Prediction can be used to estimate the actual outcome of the motor command without delay and compare this to the desired outcome before sensory feedback is available (Miall et al. 1993). It has recently been proposed that multiple forward models can be used to identify the context of a movement (Wolpert and Kawato 1998). Finally, discrepancies between the predicted and actual consequences of movement can be used to update the forward model in order to maximise motor learning (Wolpert and Ghahramani 2000).

Both the parietal lobe and the cerebellum have been proposed to play a role in sensorimotor prediction. There is evidence that the cerebellum acts as a component of a forward model system that provides rapid predictions of the sensory consequences of motor actions, which are compared with the actual sensory consequences (Ito 1970; Kawato and Gomi 1992; Miall et al. 1993). The main input to the cerebellum, the climbing fibres from the inferior olive, has been proposed to act as a comparator between expected and achieved movement, signalling errors in motor performance (Oscarsson 1980). Evidence

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for this comes from electrophysiological studies demonstrating that neurons in the inferior olive of cats respond to passively applied cutaneous stimuli but not to similar stimuli produced by a voluntary movement of the cat, except when stimuli are unexpectedly encountered during movement (Gellman et al. 1985). Similarly, inferior olive neurons fire when a cat walking on a horizontal ladder encounters a rung that unexpectedly gives way (Andersson and Armstrong 1985). Accordingly, inferior olivary neurons have been proposed to act as somatic 'event detectors' responding particularly reliably to unexpected, unpredictable stimuli (Oscarsson 1980; Simpson et al. 1995).

It is also well established that the parietal lobe is involved in predicting actions. Electrophysiological studies have demonstrated that the parietal cortex intervenes at an early stage of motor planning. In a proportion of neurons in the monkey lateral intraparietal sulcus (area LIP) the location of the receptive field shifts transiently before an eye movement (Duhamel et al. 1991). Parietal neurons respond when an eye movement brings a previously flashed stimulus into the receptive field. These results demonstrate that the parietal cortex anticipates the retinal consequences of eye movements and updates the retinal coordinates of remembered stimuli in order to generate an accurate representation of visual space. Thus, parietal neurons can predict sensory changes in anticipation of intended movements.

Anderson and Buneo (2002) have proposed that the parietal cortex is a suitable candidate region for creating high level cognitive plans for movement, given its central role in combining sensory and motor information within a common reference frame. According to this view different subregions within posterior parietal areas contain maps of intention related to the planning of different movements such as eye movements, reaching movements and grasping movements (Anderson and Buneo 2002). If the parietal regions generate intentions directly related to the planned movement, this reveals a contribution of these areas to the early stages of motor preparation before movement itself begins. Compared with the proposed role of the cerebellum in motor prediction, the parietal cortex might be involved in prediction involved in plans and goals of movement well before the movement has occurred.

In this paper we review studies investigating the roles of the cerebellum and parietal cortex in prediction with an attempt to emphasise their differential roles.

Predictive grip force modulation

Forward models are proposed to play a fundamental role in coordinative behaviour such as that used when manipulating objects. When an object is picked up and moved, the load force (tangential to the surface of the object) on the fingers changes because of the acceleration of the gripped object. Without a corresponding change in grip force (normal to the surface of the object), the object would slip. Despite sensory feedback delays associated with the detection of load force by the fingertips, when movement of an object is self-generated grip force is modulated in parallel with load force (Johansson and Cole 1992; Flanagan and Wing 1997). Conversely, when the motion of a gripped object is externally generated, grip force lags 60–100 ms behind load force and subjects make intermittent catch up responses in their levels of grip force (Johansson et al. 1992a, 1992b; Blakemore et al. 1998a). The zero lag between load force and grip force fluctuations when movement of an object is self-generated suggests that the load force is being accurately predicted based on forward models of the object and the arm's dynamics (Flanagan and Wing 1997). In contrast, the lag between load force and grip force fluctuations during external loading of an object suggests a reactive response to external perturbation of the object, which cannot be predicted.

The cerebellum appears to be critically involved in predictive grip force modulation. Neurons in the cerebellum fire before movement onset when monkeys reach and grasp objects (Espinosa and Smith 1992; Smith et al. 1993). Human subjects with degenerative cerebellar lesions exhibit a lack of co-ordination of grip and load force when performing lifting tasks (Muller and Dichgans 1994a). In these patients grip and load force are decoupled – during self-generated movement the two forces do not always change in parallel (Muller and Dichgans 1994b; Babin-Ratté et al. 1999). This impairment in predictive grip force appears to be restricted to the hand ipsilateral to the cerebellar lesion (Serrien and Wiesendanger 1999). Functional neuroimaging studies in humans have demonstrated cerebellar activity during grip force–load force coupling (Tamada et al. 1999).

These findings support the suggestion that the cerebellum is critically involved in predicting the sensory consequences of action. Normally during self-produced manipulation of objects, grip-load force coupling occurs entirely automatically and effortlessly—subjects do not report being aware of constantly changing the force of their grip when manipulating objects (Blakemore et al. 1998a). This suggests that the prediction made by the cerebellum is a rapid process that occurs continuously during the active manipulation of objects and may be unavailable to awareness.

Motor learning

Motor learning can be achieved by comparing the predicted consequences of an action to the actual result of the action and updating the prediction accordingly (Wolpert and Kawato 1998). It has been proposed that the cerebellar cortex can acquire internal models through motor learning (Ojakangas and Ebner 1992). Several foci in the human cerebellar cortex are activated during the early (e.g. Seitz et al. 1994; Imamizu et al. 2000; Tracy et al. 2001) and late phases of motor learning (Ghilardi et al. 2000; Tracy et al. 2001) in functional imaging studies. In terms of the forward model, activation of the cerebellum early in learning might correspond to the error signals originating from the comparison between the predicted and actual outcomes of movements, which are used to refine the forward model's predictions and guide the acquisition of new internal models (Wolpert and Kawato 1998).

Kawato and his colleagues have proposed that multiple internal models exist in the cerebellum and that they compete to learn new environments and tools (Kawato 1999). Recently, this group has proposed that the phylogenetically newer part of the cerebellum acquires internal models of objects in the external world (Imamizu et al. 2000). Subjects where scanned in fMRI while they tracked a moving square target with a cursor on a screen using a normal computer mouse during the baseline condition. During the test condition, the position of the cursor on the screen was rotated by 120° from the position of the computer mouse, so that the tool (the computer mouse) was now novel to the subjects. Two types of cerebellar activity were observed. At first, during the test period, large regions of the cerebellum were activated compared with their activity during the baseline task. This activation decreased after repeated test trials, and the decrease was proportional to the reduction in tracking errors made by the subjects as they learned to use the novel tool. The authors proposed that this activity corresponds to the acquisition of internal models during learning. In addition, certain sub-regions of the cerebellum, near the posterior superior fissure, continued to be activated even after subjects had learned to use the novel tool. It was suggested that this remaining activity represents an internal model that is acquired during the repeated test trials, and which defines the new relationship between movement of the cursor and of the mouse.

Recognising the sensory consequences of action

Information about motor commands can be used to distinguish the sensory consequences of our own actions from externally produced sensory stimuli (Frith et al. 2000). In order to achieve this, the predicted sensory consequences of movement are compared with the actual consequences of the movement. Self-produced sensations can be accurately predicted on the basis of motor commands and this accurate prediction can be used to cancel the ensuing sensory stimulation. In contrast, externally generated sensations cannot be predicted on the basis of efference copy, and are not cancelled. Such a system can be used to cancel or attenuate sensations induced by self-generated movement, thereby accentuating sensations originating externally, such as contact with objects or external touch.

There is evidence that self-produced stimuli are attenuated perceptually relative to external stimulation. Subjects rate self-produced tactile stimulation as less tickly and intense than an identical stimulus produced externally (Blakemore et al. 1999), supporting the demonstration that people cannot tickle themselves (Weiskrantz et al. 1971). Experiments examining the perceptual effects of altered correspondence between self-generated movement and its sensory consequences demonstrated that the perception of a self-produced sensation is related to the accuracy of the sensory prediction made by the forward model (Blakemore et al. 1999). Using a robotic interface, delays of 100, 200 and 300 ms and trajectory rotations of 30°, 60° and 90° were introduced between the movement of the left hand and the tactile stimulus on the right palm. The result of increasing the delay or trajectory rotation is that the sensory stimulus no longer corresponds to that which would be normally expected based on the efference copy. As the delay or trajectory rotation is increased, the sensory prediction becomes less accurate and the discrepancy between the predicted and actual feedback from movement increases. Subjects reported a progressive increase in the tickly rating as the delay and trajectory rotation increased. This occurs without any explicit awareness of the perturbation in the case of the delays. This suggests that the perceptual attenuation of self-produced tactile stimulation is due to a precise attenuation of the sensory stimulation, based on specific sensory predictions.

The cerebellum and the parietal lobe both appear to be involved in the cancellation of self-produced sensory stimulation. Activity in the bilateral parietal operculum (secondary somatosensory cortex) was higher during externally produced tactile stimulation of the palm than during self-produced tactile stimulation (Blakemore et al. 1998b). This relative attenuation of parietal opercular activity during self-produced sensory stimulation requires the sensory consequences of movement to be predicted accurately. The cerebellum appears to be involved in this sensory prediction. This study revealed that there was less activity in the right cerebellar cortex during a self-generated movement that generated a tactile stimulus than during an identical movement that did not result in any tactile consequence. This pattern of activity suggests that activity in the cerebellum depends on the specific consequences of a movement.

Further evidence for this proposal was obtained in a PET study that employed parametric increases in the perturbation between movement and its consequences (Blakemore et al. 2001). By using two robots so that the tactile stimulus could be delivered under remote control by the subject, delays of approximately 0, 100, 200 and 300 ms were introduced between the movement of the right hand and the resulting tactile stimulus on the left palm. In all conditions the motion of the right hand determined the tactile sensation on the left palm. Only the temporal correspondence between the action of the right hand and the sensory effect on the left palm was altered. Blood flow in the right lateral cerebellar cortex increased as the delay increased, supporting the proposal that the cerebellar cortex signals the sensory discrepancy between the predicted and actual sensory feedback. In this study, subjects were not warned about the delays, and in a post-experimental debriefing none of the subjects claimed to have been aware of the delays. The fact that subjects could not explicitly report the perturbations suggests that the sensory discrepancy signalled by the cerebellum is not available to awareness.

Mismatches between movement and its visual consequences

The parietal lobe also plays an important role in detecting mismatches between the desired and actual movement particularly when visual feedback is important. In a recent study, Desmurget et al. (1999) asked normal subjects to point to visual targets while vision of the arm was prevented. In some trials, target location progressively changed position while in others it remained stationary. In the stationary trials subjects readily corrected the initial movement trajectory by pointing to the new target location. However, after applying single focal transcranial magnetic stimulation (TMS) to the left intraparietal sulcus, subjects missed the new target location and pointed to the first seen position. A similar result was found for a patient with bilateral damage in the posterior parietal cortex (Pisella et al. 2000). Like normal subjects' performance after TMS to the intraparietal sulcus, the parietal patient failed to correct her arm trajectory when the target jumped to another spatial position, whereas her behaviour was normal when targets remained stationary. Both studies demonstrate the importance of parietal regions in updating limb movements when visual feedback about the arm movement trajectory is not available.

When a mismatch exists between vision and action, the motor system can rapidly adapt to solve the conflict. In a recent study the role of both the parietal cortex and the cerebellum in this process, as well as the way these two brain regions adapt during the visuomotor mismatch, was examined using fMRI in normal volunteers while they performed a simple hand movement (Giraux et al. 2002). A mismatch was produced using a closed-circuit video system, which enabled the presentation of an inverted mirror-image view of the moving hand, thus giving the subject the impression of moving the opposite hand. Subjects were either given normal feedback about the hand movement (the subject moves his right hand and sees his right hand moving) or inverted feedback (the subject moves his right hand and sees his left hand moving). The time course of the adaptation was investigated by alternating two series of the two experimental conditions. The results demonstrated a selective increase of activity in the intra-parietal sulcus contralateral to the moving hand for the inverted visual feed-back condition relative to the normal visual feed-back condition. The same comparison yielded a selective activation in the intermediate zone of the posterior lobe of the cerebellum ipsilateral to the moving hand. Thus activation in both regions was driven by the acting hand and not by the hand the subject was seeing. There was an important difference between the activation in each region. The intra-parietal sulcus exhibited fast adaptive properties especially for the right (dominant) hand, whereas the cerebellum activity decayed slowly in time for both hands during the conflict condition.

These results suggest that detection of and adaptation to a simple visuomotor conflict involves both the intra-parietal sulcus and the medio-lateral cerebellum. These findings support the hypothesis that the parietal cortex and the cerebellum work as a functional loop for estimating the current status of the motor system throughout movement execution.

Distinguishing self-produced and external movements visually

In human subjects, the parietal lobe seems to become involved when explicit distinctions are made about self-generated and other-generated actions. A paradigm that has been used extensively 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 (Daprati et al. 1997). The subject sees on a television screen a hand that is either their own or that of the experimenter performing movements that are either congruent or incongruent with the subject's own hand movements. Using this paradigm, Daprati and her colleagues showed that normal subjects confuse their own hand movements with the hand of the experimenter when the movements are similar about 30% of the time (Daprati et al. 1997).

A significant part of the motor system is activated both when we execute an action and when we observe a similar action being executed (Grafton et al. 1996; Grèzes and Decety 2001). How then is the distinction made between self-produced and other-produced movements? There is accumulating evidence that the parietal cortex plays a role in this distinction. The right inferior parietal cortex is activated when subjects observe their own actions being imitated by someone else compared with when they imitate someone else's action (Decety et al. 2002), and when subjects lead, rather than follow, someone else's actions (Chaminade and Decety 2002). The same region is activated less when subjects experience themselves as the agent of a movement than when the movement is controlled by someone else (Farrer and Frith 2001). When subjects mentally simulate actions from someone else's perspective the inferior parietal cortex is activated more than when they imagine themselves performing the same action (Ruby and Decety 2001). These studies suggest that the inferior parietal cortex is involved in the conscious classification of actions. This proposal is supported by the observation that patients with left parietal lobe damage are more likely to confuse their hand movements with those of another agent (Sirigu et al. 1999).

Further evidence for the parietal lobe role in storing representations of movement come from brain damaged patients who lose feeling in the limb contralateral to the lesion. Jeannerod et al. (1984) describe a patient with hemianaesthesia after damage involving the right inferior parietal lobe. The patient could initiate simple single-component movements, but could not make complex multi-component movements with his left hand in the absence of visual feedback. Another patient 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 (Wolpert et al. 1998). Her experience of a constant tactile stimulus or a weight also faded away, but changes in such sensations could be detected. Slow reaching movements to peripheral targets with the right hand were inaccurate, but reaching movements made at a normal pace were unimpaired. In this case there seemed to be a circumscribed problem with the representation of the current limb position in that it could not be maintained in the absence of changing stimulation. Following these results Wolpert and colleagues postulated that the parietal cortex is involved in both maintaining and updating an internal body state issued from sensory and motor signals.

Imagining movement

It has been proposed that prediction underlies the ability to prepare and imagine movements. The parietal lobe seems to play a critical role in movement imagery. Several brain regions, including the cerebellum, parietal cortex and premotor cortex, are activated by both imagining and executing movement (Decety et al. 1994; Jeannerod and Frak 1999). However, a recent fMRI study that directly compared movement execution with movement imagination demonstrated that imagining a movement activates the left posterior and inferior parietal lobe to a greater extent than executing the same movement (Gerardin et al. 2000). Furthermore, parietal lesions impair the ability to use mental motor imagery. 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 (Sirigu et al. 1995; Decety and Jeannerod 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). To our knowledge, there is no evidence that patients with cerebellar lesions have the same kind of deficits in motor imagery.

Taken together these results show that the parietal cortex is particularly important for motor imagery. Motor imagery comprises the very conscious and effortful ability to simulate a movement in the imagination, which requires retrieving a stored forward model of that particular movement. It has been argued that parietal patients' motor imagery impairment is due to a failure to generate and monitor a forward model of movement (Sirigu et al. 1996; Danckert et al. 2002). The parietal regions may be involved in monitoring the motor outflow via the efference copy received from downstream motor areas (Sirigu et al. 1996, 1999).

Conclusion

We have reviewed some of the evidence that the cerebellum and the parietal lobe are involved in predicting the sensory consequences of movement. The results discussed in this paper strongly implicate these two brain structures in motor prediction processes. Their differential roles in prediction, however, are not clear. The goal of this paper, rather than providing answers about the differential ways the cerebellum and the parietal structures accomplish motor prediction, was simply to highlight this issue, which is rarely addressed in motor control studies.

Although we have attempted to highlight the differential roles of the parietal cortex and the cerebellum in motor prediction, it is highly likely that these two regions work as a functional loop for estimating the current status of the motor system throughout movement execution. The parietal cortex receives input from the cerebellum via the thalamus (Clower et al. 2001), and there are connections in the opposite direction via the pons (Glickstein 2000). It is likely that these two regions work in parallel to predict the sensory consequences of movement, and to monitor and to make corrections to movement.

Clues from the results discussed in this review lead us to suggest that the differential roles of the cerebellum and the parietal cortex in this process may occur at the level of awareness ascribed to the prediction in each case. In the case of research on the cerebellum, investigators have used simple tasks involving basic motor adjustments, which are usually performed outside conscious control. These studies suggest that the cerebellum makes rapid predictions about the sensory consequences of self-generated movement at a very low level of movement execution, presumably without awareness. In contrast, the parietal cortex predictive functions have been addressed using tasks tapping the most cognitive aspects of movement.

It is possible that the prediction made by the cerebellum is unavailable to awareness, whereas the prediction made by the parietal lobe is concerned more with high-level prediction such as strategic planning actions. Perhaps the predictions made by the parietal cortex can be made available to conscious awareness. This is purely speculative because the methods used in the field of motor control, to date, have not explicitly addressed this issue. Few studies have directly addressed the joint contribution of the cerebellum and the parietal cortex to motor performance. Future research using new paradigms is required to investigate directly the hypothesis that different levels of motor awareness are provided by these two brain regions.

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