REVIEW

Widespread access to predictive models in the motor system: a short review

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Abstract
Recent behavioural and computational studies suggest that access to internal predictive models of arm and object dynamics is widespread in the sensorimotor system. Several systems, including those responsible for oculomotor and skeletomotor control, perceptual processing, postural control and mental imagery, are able to access predictions of the motion of the arm. A capacity to make and use predictions of object dynamics is similarly widespread. Here, we review recent studies looking at the predictive capacity of the central nervous system which reveal pervasive access to forward models of the environment.

(Some figures in this article are in colour only in the electronic version)

Introduction

Predicting the future state of the motor system is thought to be essential for skilled movement because of the delays inherent in the sensorimotor system. Forward models are putative neural systems that mimic physical systems outside the brain. It has been suggested that the sensorimotor system employs forward models to predict the consequences of movements based on efference copies of outgoing motor commands (von Holst and Mittelstaedt 1950, von Holst 1954, Jordan and Rumelhart 1992, Miall and Wolpert 1996). By generating up-to-date estimates of the state of our body and the environment based on our motor commands they also allow the system to generate accurate estimates of current motion. In general, there are other sources of information, such as desired behaviour or sensory feedback, that can be used to estimate the consequences of a movement (Karniel 2002). However, estimates based on these do not require a system which simulates the properties of the motor system and, therefore, here we reserve forward models for systems which make predominant use of the motor command to generate estimates of the outcome (figure 1). Complementary neural systems that implement the inverse transformation, generating

appropriate motor commands based on desired consequences, are known as inverse models (figure 1(c)). Here, we review recent evidence suggesting extensive use of forward models in the motor system.

Evidence for forward models

Recently, evidence for forward models has considerably strengthened on the basis of psychophysical and electrophysiological studies. When holding an object in a precision grip with the fingertips and thumb on either side, sufficient grip force must be generated to prevent slip due to the load force exerted by the object. When the object's behaviour is unpredictable our grip force is modified reactively in response to sensory feedback from the fingertips, with the consequence that grip tends to lag behind increases in load. However, when we direct behaviour towards objects in the environment that exhibit stable properties, predictive control mechanisms can be effectively exploited that could predict the consequences of self-induced load and adjust grip force in anticipation. For example, when the load is increased by a self-generated action, such as moving the arm, grip force increases in parallel with load force with no delay. Sensory
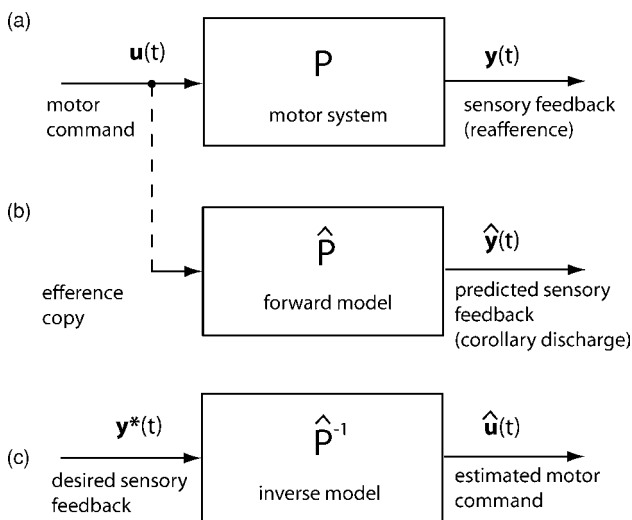
(a)

$$\mathbf{u}(t)$$

| P |
| motor system |

$$\mathbf{y}(t)$$

motor command

sensory feedback (reaference)

efference copy

(b)

| $\hat{P}$ |
| forward model |

$$\hat{\mathbf{y}}(t)$$

predicted sensory feedback (corollary discharge)

(c)

$$\mathbf{y}^*(t)$$

| $\hat{P}^{-1}$ |
| inverse model |

$$\hat{\mathbf{u}}(t)$$

desired sensory feedback

estimated motor command

Figure 1. Internal models mimic the physical properties of real world systems. (a) For example, the motor system P can be considered to transform outgoing motor command $u(t)$ into sensory feedback $y(t)$. (b) A forward model of this system $\hat{P}$ takes a copy of the motor command (termed *efference copy*) and generates an estimate $\hat{y}(t)$ of the sensory feedback likely to result from $u(t)$ (*corollary discharge*). (c) An inverse model performs the opposite transformation. Desired sensory feedback $y^*(t)$ is transformed into an estimate of the motor command $\hat{u}(t)$ necessary to generate this.

detection of the load is too slow to account for this increased grip force, which therefore relies on predictive processes. Such a strategy prevents the object slipping while avoiding excessive grip force which might damage the object or lead to muscular fatigue. This anticipatory adjustment of grip force with load during object manipulation is one longstanding piece evidence for predictive forward models (Johansson and Cole 1992, Flanagan and Wing 1997, Kawato 1999). In principle, the coupling could arise without a forward model if an inverse dynamics model were available (Kawato *et al* 2003). In this scheme, the desired hand trajectory is passed to the inverse model which generates an estimate of load resulting from the planned movement. The load estimate is used to specify appropriate fingertip grip force. However, when arm control is inaccurate the actual and desired trajectories can differ substantially, resulting in inaccurate load force estimates. It has recently been shown that grip force accurately predicts load force even when accurate arm control is still being learned (Flanagan *et al* 2003). In this study it took about 7.5 times longer to establish accurate arm control than to learn appropriate grip forces. This strongly suggests that the grip force pathways include a predictive forward model of object and arm dynamics which is learned more rapidly than the complex inverse dynamics of the arm.

Object manipulation studies with deafferented subjects also support the idea that forward models maintain grip–load force coupling during object manipulation. Forward models must be adaptable and would require a comparison of their output with actual sensory feedback to provide an appropriate error signal for updating the parameters in the forward model. Hence, we would expect a deafferented individual, who lacks

the error signal required to learn a forward model for a novel object, to have problems generating anticipatory control. Nowak *et al* (2004a) had a completely deafferented subject (GL) making point-to-point reaching movements with a hand-held object. GL applied much stronger fingertip forces to the object before, during and after the movements than normal controls. While her grip-force profile was modulated according to load force, as in normal subjects, it was not predictive. This is consistent with an inability to predict the dynamic load forces encountered when moving a hand-held object.

While the psychophysical evidence for forward models is growing, neurophysiological evidence is less widespread. A recent fMRI imaging study suggests that forward models of object and arm dynamics are stored in the cerebellum (Kawato *et al* 2003). The only regions that were differentially activated during anticipatory grip force modulation were the right, anterior and superior cerebellum and the biventer in the left cerebellum. The authors suggest that these regions contain forward models for predicting load force variations caused by arm/object dynamics.

Recently, a neurophysiological study has identified the neural location of a copy of outgoing motor commands, termed efference copy, a key component of a forward model system. Sommer and Wurtz (2002) have suggested that medio-dorsal (MD) thalamic neurons carry a corollary discharge signal from the superior colliculus to the frontal eye fields. This is used to update a forward model of eye position during saccades. The MD neurons fire before saccade onset, demonstrating that their activity is linked to the motor command and not the sensory feedback. When these neurons are inactivated the precision of a saccade to a single target is unaffected. However, in accordance with a failure of updating the current location of the eye based on a forward model prediction, the accuracy of subsequent second saccade in a double-step task shows errors consistent with an inaccurate representation of eye state. Evidence for efference copy is also provided by Roy and Cullen (2001), whose work with rhesus monkeys suggests an efference copy of the neck motor commands is used in cancelling the self-generated component of head angular velocity feedback. Vestibular nuclei neurons that were shown to encode head angular velocity during passive head rotations, and active whole body rotations, failed to do so during active head turns. This is consistent with cancellation of the vestibular feedback by an efference copy of the outgoing motor command when the monkeys actively turn their heads.

Arm dynamics models

It has been known for some time that internal models of arm dynamics play an important role in controlling reaching movements (Atkeson 1989, Shadmehr and Mussa-Ivaldi 1994, Conditt *et al* 1997). Forward models of arm dynamics have also been thought to play an important role in arm control by minimizing the effect of sensorimotor delays (Jordan and Rumelhart 1992, Wolpert *et al* 1995). Anticipatory postural adjustments have long been known to depend on prior knowledge of arm dynamics (Marsden *et al* 1978, Bouisset

and Zattara 1981). More recently, studies of saccadic eye movements, fingertip grip forces, motor imagery and other motor systems have suggested that these disparate systems also have access to forward models of arm dynamics.

The fingertip grip force control system has been shown to have access to important aspects of arm dynamics. The two-link configuration of the human arm means that the effective inertia of the hand varies with movement direction (termed *inertial anisotropy*), and causes corresponding variations in hand acceleration with movement direction. Flanagan and Lolley (2001) have shown that when sliding an object across a frictionless surface to targets located in different directions, subjects vary the force they apply normal to the surface in anticipation of direction dependant changes in initial hand acceleration. Similar information seems to be available in brain regions responsible for motor imagery. The anisotropic inertia of the arm noted in the previous study also causes movements to equidistant targets to be slower in high inertia directions. Noting this property, Gentili *et al* (2004) have shown that the durations of real and imagined movements are tightly correlated regardless of whether subjects are asked to reach or imagine reaches in low or high inertia directions. Furthermore, when the arm dynamics are altered by attaching a 4 kg mass to the wrist, imagined movement duration reduces by the same as actual movement duration. Hence, systems responsible for motor imagery seem to have access to a predictive model of the inertial dynamics of the arm. There is also evidence that the saccadic eye movement system has access to a forward model of arm dynamics. Ariff *et al* (2002) hid subjects' arms from view and had them make reaching movements without visual feedback. They were asked to track the position of their unseen hand with their eyes. Subjects made saccadic movements to a location predicting the position of their hand 196 ms in the future. A brief force pulse was then applied to the hand, thereby altering the state of their arm. After the pulse, saccades were suppressed for 100 ms and then accurate predictive saccades re-emerged. However, when the dynamics of the arm were altered after the perturbation by applying a novel viscous force field, the subsequent saccades were inaccurate. In a further study, the arm's dynamics were altered by applying various external force fields (Nanayakkara and Shadmehr 2003). The eyes were able to make accurate predictive saccades after the force pulse when the externally imposed arm dynamics were predictable. Hence, the saccadic system is able to use new information on arm dynamics to improve its performance. All these results suggest that adaptable internal models of arm dynamics are available to a variety of motor systems. Further studies are required to reveal whether this reflects broad access to a common representation of arm dynamics or multiple, possibly redundant, representations within each motor subsystem.

In addition to the use of prediction for control, prediction is a key element in perceptual processing. Sensory prediction can be derived from state prediction and used to cancel the sensory effects of movement, which is known as reafference. By using such prediction, it is possible to cancel out the effects of sensory changes induced by self-motion, thereby enhancing more relevant sensory information. For example, predictive mechanisms underlie the observation that the same tactile stimuli, such as a tickle (Weiskrantz *et al* 1971, Blakemore *et al* 1999) or constant force (Shergill *et al* 2003), are felt less intensely when self-applied. A predictive mechanism has been supported by studies in which a time delay is introduced between the motor command and the resulting tickle (Blakemore *et al* 1999). The greater the time delay the more ticklish the percept, presumably due to a reduction in the ability to cancel the sensory feedback based on the motor command.

Object dynamics models

There is also evidence that the sensorimotor system maintains forward models of systems other than the arm, including visuomotor relationships (Mehta and Schaal 2002), oculomotor plant and sensor dynamics (Zupan *et al* 2002, Glasauer 2003) and external object dynamics. When lifting an object vertically from a surface we rapidly learn appropriate fingertip grip forces to overcome gravitoinertial-load forces (Johansson and Westling 1988). A memory of appropriate force scaling is maintained and can be recalled later based on visual cues (Gordon *et al* 1991, 1993). Given that the memory is flexible enough to generalize between hands (Gordon *et al* 1994) and to be useful in manipulating combinations of objects (Davidson and Wolpert 2004), it might be expected that explicit knowledge of a simple change in object dynamics could be used to update the internal model. To address this, Nowak and Hermsdorfer (2003) asked subjects to lift a cup full of water with a precision grip (i.e., using their thumb and forefinger). Subjects were then asked to drink half the water in the cup with a straw, before lifting the cup again. The maximum grip force rate used to lift an object provides a reliable estimate of the anticipated weight. It was surprising then that, despite possessing explicit knowledge the cup was lighter after drinking, maximum grip force rate did not reduce for the lighter cup despite subjects' explicit conscious expectations (figure 2). This agrees with previous findings suggesting an inability to use explicit knowledge of mass distribution to form an appropriate forward model (Salimi *et al* 2000). In contrast, explicit knowledge of a relationship between two previously experienced objects can be used to form a new forward model. When two previously experienced objects are stacked, subjects scale their grip force appropriately on the first lift of the combined object (Davidson and Wolpert 2004). Since subjects already possess internal models for the two constituent objects, the result might be explained by an ability to add their outputs (Haruno *et al* 2001).

Interestingly, it has recently emerged that anticipatory grip force scaling learned after lifting an object can be disrupted by pinching an unrelated object with more force than appropriate to the original object. After repeatedly lifting a 4 N object, subjects applied 8 N force to an unrelated object, without lifting, by squeezing it between thumb and forefinger. On the first lift of the 4 N object after pinching, anticipatory grip forces were inappropriately high (Quaney *et al* 2003). The effect has been termed the 'sensorimotor memory' to differentiate it from object-specific memory of appropriate anticipatory force
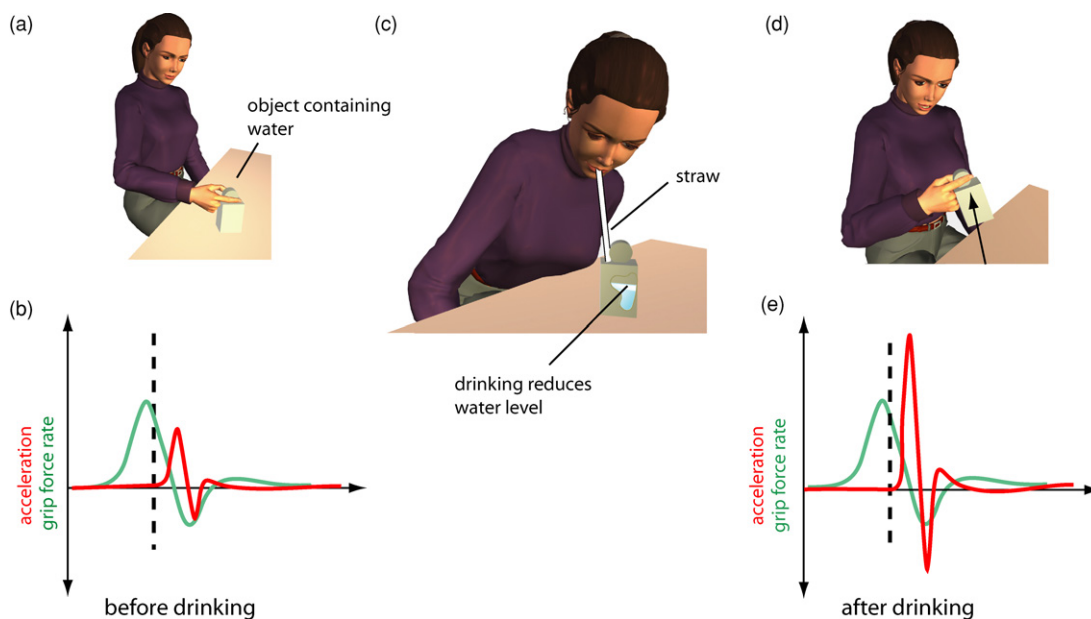
Figure 2. Explicit knowledge of altered object properties is insufficient to alter an existing forward model (redrawn from Nowak *et al* (2003)). When repeatedly lifting an object, subjects learn to precisely scale their applied forces to overcome expected gravitoinertial-load forces. (a) Nowak *et al* (2003) had subjects repeatedly lift an object filled with water. (b) After several lifts, the peak grip force rate (green/light grey) occurred just prior to object lift-off (vertical dashed line) and was scaled appropriately for the object's weight. (c) Subjects drank half the water from the object using a straw. (d) Subjects then lifted the object, aware that they had made the object lighter by drinking the water. (e) Nevertheless, the same grip force (green/light grey) was applied on this lift as used prior to drinking and the object was accelerated (red/dark grey) as if a heavier object, still full of water, was expected.

scaling discussed earlier. Sensorimotor memory appears to dominate object-specific memory under some circumstances. The same effect is observed when the pinch is performed with the opposite hand. Further insight has recently been gained in a study showing that a similar effect can be induced with sensory input alone (Nowak *et al* 2004c). If the muscles contributing to grip force scaling, first interosseus and adductor pollicis, are mechanically vibrated after lifting an object then grip forces will be inappropriately high on the next lift. Again, this effect transfers between hands. These two studies suggest that grip force scaling is influenced by both a forward model output for predictive grip force scaling and a simpler sensory memory of the previous lift.

Prediction of object dynamics is not limited to grip force control. Lamberg *et al* (2003) looked at breathing coordination during lifts with identical looking 150 g and 1000 g objects. They randomly changed the object lifted after every block of five lifts. When the weight of the object was unpredictable (on the first lift of a block) grip force scaling was as for the previous lift and respiratory output prior to the lift was appropriate for the 1000 g object. This suggests an anticipatory strategy where respiratory output is matched to the heavier object regardless of the previous weight, perhaps caused by increased arousal due to anxiety over unpredictability (Poon 1996). When the weight of the object was predictable (on the fifth lift of a block), force application was faster and inspiratory duration and tidal volume were reduced prior to the lift 1000 g lift compared to the 150 g lift. This anticipatory alteration in respiratory output for predictable lifts shows the respiratory system has access to a predictive model capturing the weight of the object.

There is also evidence that forward models of complex external tools are used in arm control. Mehta and Schaal (2002) had subjects learn to balance real and virtual poles on their fingertips. Examining a variety of control schemes they concluded, through a process of elimination, that a forward predictive model was likely to be employed in the task. Mah and Mussa-Ivaldi (2003) showed that when subjects learn to control the tip of a simulated inverted pendulum their internal representation depends on the specific hand trajectories selected. Hence, a less general internal model is formed which only represents the properties of the object experienced while doing the task. In a different study, the same investigators showed that simulated inverted pendulum dynamics are represented as a relationship between torques or muscle commands and object motion (Mah and Mussa-Ivaldi 2003). Learning while the arm was in one posture did not transfer well to a different posture. A recent imaging study has shown that internal models of simpler tools, in this case of mice with differing properties, are stored in structural modules in the lateral regions of the cerebellum (Imamizu *et al* 2003). Subjects learned to perform a tracking task with a normal computer mouse, a rotated mouse (where the cursor movement was rotated $120°$ relative to mouse movement) and a velocity mouse (where the cursor velocity depended on the mouse position). Anatomical regions of activation for each tool varied substantially between subjects, indicating that tools are stored idiosyncratically.

Internal models of object dynamics are capable of adapting to unusual and novel force profiles, including the
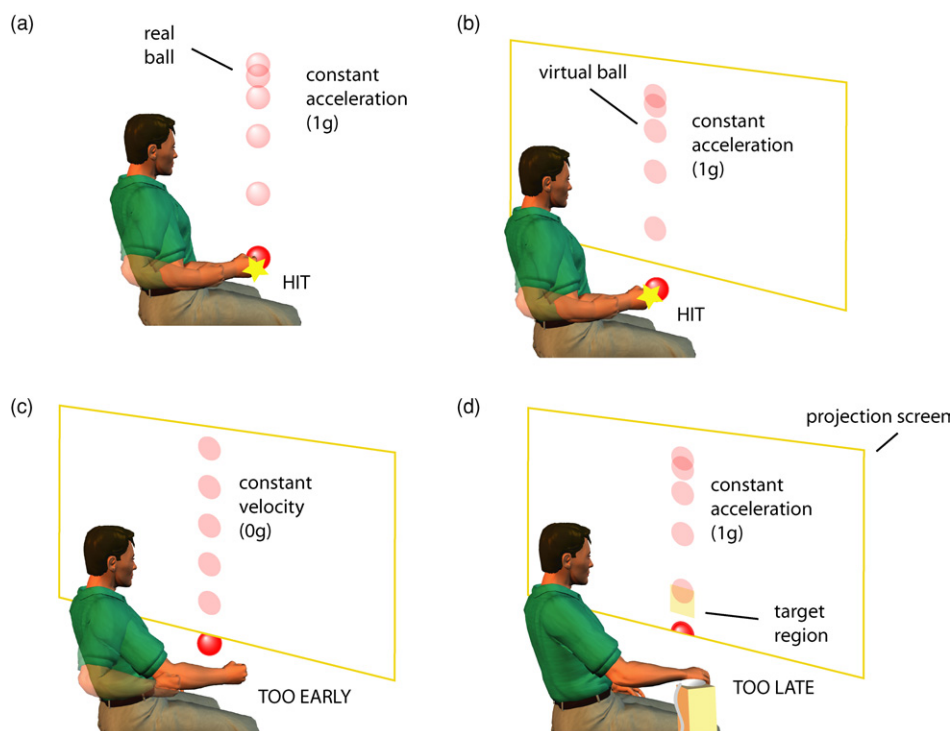
Figure 3. Expected dynamics override observed kinematics in an object interception task (redrawn from Zago *et al* (2004a)). (a) Subjects normally time their interception of a falling ball assuming it moves with constant acceleration due to gravity (1 g). (b) When a real ball, falling behind a projection screen, arrives in synchrony with a virtual ball displayed on the screen, subjects continue to expect the ball to fall under the influence of gravity. (c) Consequently, subjects intercept the real ball correctly when the virtual ball accelerates as it would under gravity, but respond too early when the virtual ball moves with constant velocity (0 g). (d) In contrast, when the ball is intercepted virtually by clicking a mouse button, subjects expect the virtual ball to move with constant velocity. When the virtual ball actually accelerates under simulated gravity (1g) their response is late. The location of the target ball at the expected moment of impact is shown in red/dark grey. Earlier locations of the ball, as seen by the subject, are shown in light red/light grey.

sudden effects of micro and hyper gravity (Augurelle *et al* 2003), and coriolis and centripetal forces (Nowak *et al* 2004b). There are limits to this adaptability, however. McIntyre *et al* (2001) have shown that predictive models are tuned for the effects of gravity. When catching a vertically falling ball, people normally generate accurately timed anticipatory responses to intercept the ball. In the 0 g environment of space, however, these anticipatory responses occur too early, indicating that the CNS employs an internal model of acceleration due to gravity which is inappropriate in a 0 g environment. As subjects spend more time in a 0 g environment the anticipatory response slowly improves, but never reaches the performance achieved in 1 g suggesting a heavy bias to terrestrial gravity. Recent studies have looked at simulated 0 g environments in which objects move with constant velocity (Zago *et al* 2004a). A real ball was released behind the projection screen which displayed an image of a ball falling. Subjects were asked to intercept the real ball, which arrived at the bottom of the screen in synchrony with the simulated ball. Subjects timed their interception assuming gravity was accelerating the simulated ball (1 g condition), even when it actually moved with constant velocity (0 g condition). Subjects altered their response to the unusual ball motion after repeated trials, yet catch trials indicated the 1 g

gravity model persisted and that adaptation was achieved by altering the timing of responses. This suggests predictions of object dynamics override observed kinematics in this task. When the target was intercepted virtually by clicking a mouse button, however, subjects timed their responses appropriately for a constant velocity (0 g) target, even when the target actually accelerated. Hence, the change from a real to a virtual interception task altered subjects' model of the object's mechanical properties (figure 3). The same experimenters have also shown that adaptation to the 0 g condition is acquired rapidly and is remarkably resistant to interference, even when only presented occasionally in a block of 1 g trials (Zago *et al* 2004b).

Conclusions

The studies reviewed here show that otherwise dissimilar systems within the CNS, including those responsible for oculomotor control and mental imagery, have access to forward models of arm dynamics. Similarly, predictive models of external object dynamics are widely available across sensorimotor systems. Evidence from imaging studies suggests at least some of these models are stored in certain regions of the cerebellum. It is tempting, then, to suggest

that the sensorimotor system enjoys widespread access to common encodings of arm and object dynamics located in the cerebellum. Ultimately, we await electrophysiological evidence to confirm this intriguing possibility.

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