

Computational approaches to motor control and their potential role for interpreting motor dysfunction

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Purpose of review

Computational frameworks, notably internal models and optimal control theory, have led to rapid advances in our understanding of how the brain plans and controls movement. The purpose of this review is to provide an overview of these theoretical ideas, how they have been used to interpret motor control, as well as their potential role for interpreting motor dysfunction.

Recent findings

There are two general types of internal models, neural processes that mimic the mechanical properties of the limb (and environment). Forward internal models parallel the normal causal flow of the motor periphery and estimate limb motion from motor commands. Inverse internal models perform the reverse process by estimating motor commands from signals related to intended limb motion and/or spatial targets. This framework has led to several important behavioural observations on motor planning, control and learning, and has also been influential for interpreting neural activity in awake, behaving non-human primates. A more recent framework for interpreting motor function is optimal control theory, which recognizes that noise or errors are an inherent feature of the motor system and may influence strategies to plan and control movement.

Summary

Internal models and optimal feedback control both provide frameworks for interpreting motor performance, and may be of value for interpreting many motor dysfunctions associated with neurological injuries. Advanced technologies such as robots that have played a key role in these frameworks may be also of considerable value for motor assessment and rehabilitation.

Keywords

motor control, internal models, optimal feedback control, motor disorders, motor rehabilitation

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Introduction

Humans possess an impressive array of highly adaptable motor skills allowing us to move in and interact with the environment. Skilled motor performance involves a careful interplay between central and peripheral motor systems, each possessing considerable complexity in their structure and organization. However, even small injuries to the motor system can greatly reduce motor performance, creating weak, uncoordinated and inaccurate movements.

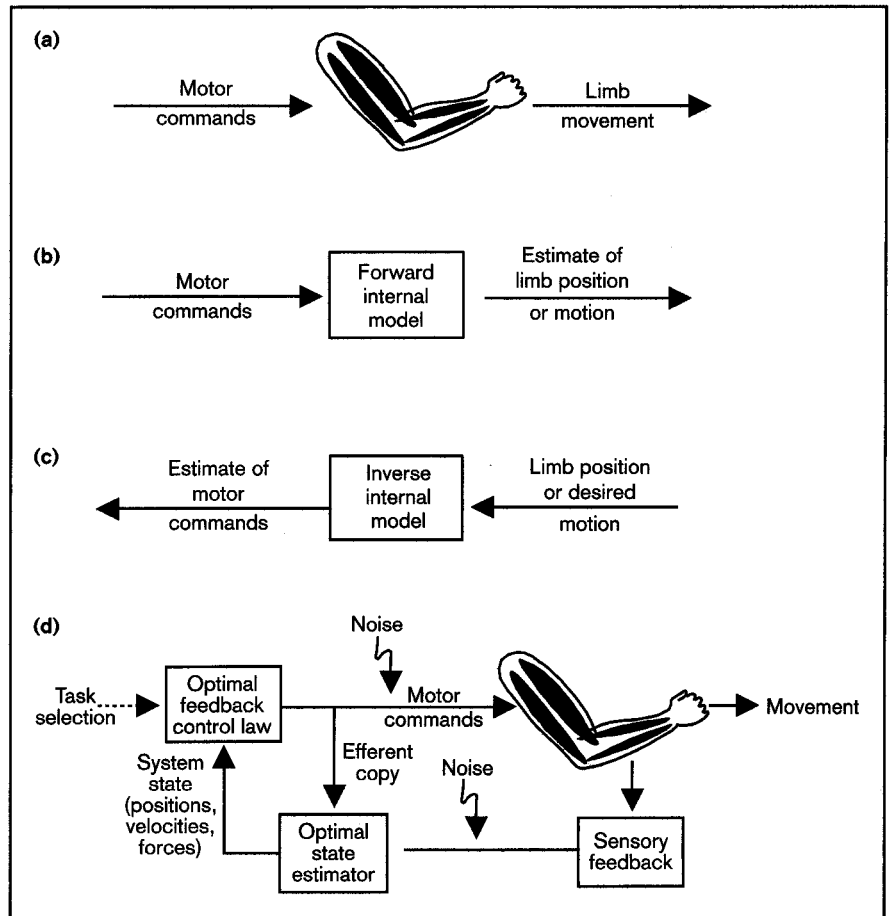
Our understanding of how the brain plans and controls limb movement is increasingly influenced by the use of computational frameworks to guide behavioural and neural studies on motor performance. The present article highlights some of these theoretical advances, notably the idea of internal models [1,2] and optimal control [3*,4]. A key feature inherent in both ideas is that the brain has knowledge of the properties of the peripheral motor system and the environment, and uses this information to plan and control movement. Such frameworks may be of potential value for understanding and quantifying motor dysfunction and guiding subsequent rehabilitation and treatment strategies.

Internal models

The musculoskeletal system can be viewed as a complex filter that converts patterns of muscle activity into movements of the limb, dependent on factors such as limb geometry, limb inertia, muscle mechanics and environmental loads (Fig. 1a). An important concept is that the brain controls limb movement by using internal models that mimic the properties of the limb or objects in the environment [1,2,5*]. In general, there are two types of internal models that may be used by the motor system. Forward internal models mimic the normal causal flow, estimating the expected motion of the body based on efference copy of motor commands (Fig. 1b). In contrast, inverse internal models perform the opposite transformation, estimating motor commands (i.e. muscle activity) based on limb kinematics (Fig. 1c). Brain processing to initiate a reaching movement can be viewed as an inverse internal model because patterns of muscle activity are generated from kinematic information related to the spatial target and initial limb position. Both inverse and forward internal models are probably used for movement control and are created through the highly distributed and interconnected regions of the brain involved in sensorimotor control.

Figure 1. Basic definitions of internal models to control upper limb function

(a) The musculoskeletal system converts motor commands to muscles into limb motion. (b) Internal models are neural processes that mimic the properties of the limb (or environment). Forward internal models mimic the normal causal flow by converting motor commands to muscles into estimates of limb motion. (c) Inverse internal models perform the reverse process by converting signals of limb motion into motor commands. (d) Diagram for implementing optimal feedback control as proposed by Todorov and Jordan [3**]. The motor system selects the appropriate feedback control law that converts the state of the system into motor commands to perform a task. Noise can corrupt these motor commands or sensory signals of motor performance. An optimal state estimator uses both sensory signals and efference copy of motor commands to predict the present state of the limb. Within the rubric of internal models, an optimal feedback controller includes both forward and inverse internal models: the optimal state estimator uses a forward internal model to convert motor commands into estimates of limb position, and the optimal feedback controller itself behaves like an inverse internal model converting limb motion into motor commands (diagram adapted from Scott [4]).



Internal models of the musculoskeletal system

By definition, internal models approximate the properties of the limb. It is therefore important to explore what information the brain knows about the musculoskeletal system. Several studies illustrate that the brain has rather substantial knowledge of limb mechanics. A key complexity in multi-joint movements is that muscular force generated across a single joint can create motion at multiple joints [6,7]. These interactions between body segments (i.e. intersegmental dynamics) appear to be anticipated by the motor system because individuals instructed to move the elbow generate shoulder muscular activity to counteract the influence of elbow muscular torque [8,9]. Another feature of multi-joint movements is that the effective inertia of the limb varies with hand movement direction [10]. Does the motor system recognize this inertial anisotropy? Monitoring finger contact force with a flat disc (puck) on a frictionless surface [11] illustrated that individuals modulate finger force in parallel with variations in initial hand acceleration. Such variations in contact force suggest that the brain recognized the consequences of

motor actions, and thus appropriately scaled the finger force to maintain contact with the puck.

There are obvious and clear differences in our ability to throw a baseball with our left and right hands, and recent work has illustrated fundamental differences in control strategies for dominant and non-dominant limbs [12–15]. The findings suggest that the influence of intersegmental dynamics is better controlled by the central nervous system for the dominant arm [13], whereas the use of sensory feedback to correct for motion errors is better controlled for the non-dominant arm [14]. Within the rubric of internal models, such studies suggest that the brain uses or has access to different types of knowledge for controlling the two arms.

These internal models of the motor periphery appear to be reflected in the discharge pattern of neurons in brain regions during behaviour. Muscle activity to move the limb in different spatial directions changes when movements are performed from different initial hand positions. A recent study illustrated parallel changes in cell

activity in the primary motor cortex, including changes in discharge rate and directional preference (movement direction for which cells are maximally active) when reaching movements were performed in similar directions but with different initial hand positions [16^{*}]. Many studies have shown that neural activity in primary motor cortex is sensitive to force output [17]. Other factors that influence the response patterns of neurons in primary motor cortex during reaching include variations in joint power [18] and limb geometry [19]. All these observations illustrate that the discharge pattern of neurons in primary motor cortex reflects specific information about the mechanics of the musculoskeletal system: neural correlates of an internal model of the limb.

Internal models of the environment

Motor learning studies were instrumental in initiating interest in the concept of internal models for interpreting motor control [20,21]. Individuals reaching to spatial targets normally make relatively straight hand paths with bell-shaped velocity profiles [22]. Loads applied to the limb initially perturb the hand trajectory, but individuals return to straight paths with practice. Abrupt removal of the load results in large deviations in hand trajectory in the direction opposite to the initial perturbation, suggesting that the initial motor commands were adjusted to take into account the influence of the load on performance, an internal model of the mechanical load.

There have been several important advances in our understanding of motor learning and how we interact with the mechanical environment [23^{**}], as well as neocortical mechanisms associated with motor learning [24^{*}]. For example, adaptive strategies as one learns to move against mechanical loads rely on motor performance from only the last few trials [25]. Furthermore, individuals appear to be able to predict the consequences of their motor actions even before they learn to control their actions [26^{*}]. Stable, predictable loads result in changes in motor patterns that reflect the load's mechanical properties. However, individuals learning to move with inherently unstable loads appear to use a different strategy in which limb stiffness is selectively increased to counteract the load [27]. Recent work has explored the activity of individual neurons in primary motor cortex when novel loads are being learned [28]. Whereas neurons show relatively stable discharge patterns for repeated performance of the same well-learned task [19,29], cell activity appears to be more labile as individuals learn to interact with novel loads [28].

One general problem in motor control is that we interact with many different types of mechanical objects (throwing a baseball, gripping a styrofoam cup, sweeping with a

broom), and move in different mechanical environments (under water, gusty winds). Individuals are clearly able to learn multiple load contexts given sufficient practice [29–31], but individuals have difficulties switching quickly between two contexts that have recently been learned [32], and in many cases have difficulty learning multiple novel loads and visuomotor perturbations simultaneously [33,34]. It has been proposed that the motor system manages the broad range of mechanical contexts by using multiple internal models, each specialized for different mechanical contexts [35,36]. Although this idea has been influential for generating interest in the problem of motor context, evidence for multiple internal models remains equivocal. Functional magnetic resonance imaging has been used to illustrate that different regions of the cerebellum were activated for a computer tracking task when the relationship between a joystick and cursor motion were varied [37]. In contrast, there was considerable overlap in the response of individual neurons in the primary motor cortex recorded in awake, behaving non-human primates making reaching movements with and without viscous loads applied to the shoulder, elbow or to both joints [29]. The change in a cell's activity when loads were applied to both joints simultaneously could be predicted from its response to single-joint loads. However, all loads examined in that study were velocity dependent; more selective changes in activity may occur for different types of mechanical loads (i.e. position versus velocity dependent).

A key aspect of motor learning is the ability to generalize learning from one context to other situations [38–40]. One consistent finding is that the generalization of learning mechanical loads appears to occur within a joint-based framework even if loads are applied directly at the hand [38,39,41–43]. For example, learning to make reaching movements with a novel load in one arm position does not generalize equally to all areas in the workspace [39]. Rather, generalization is best with arm geometries similar to that used during learning, and degrades for arm trajectories with very different patterns of joint motion. Generalization is also better when loads maintain a constant relationship with joint motion compared with those related to hand motion [42]. Finally, loads applied at a joint tend to be associated with motion at that joint, suggesting that a default strategy for learning may be a local association between motion and torque [43].

Optimal feedback control

Another important theoretical advance in motor control has been the notion that the brain may behave like an optimal feedback controller [3^{**}]. Such controllers can be viewed as a special form of internal model including both forward and inverse components (see Fig. 1d). A

crucial feature of optimal feedback controllers is how they manage noise or error, an inevitable property of the sensorimotor system and the environment. It has been suggested that a strategy implemented by the brain is to minimize the effect of this noise [44–46]. Instead of attempting to minimize all noise, optimal feedback control selectively reduces noise if it influences the global goal of the task, and ignores noise if it does not influence the goal.

The simplest way to think about optimal feedback control is to consider a system with two control signals and a prescribed goal to generate the value two. Nominally the system tries to set each control signal to one ($1 + 1 = 2$), but noise corrupts these signals. In one instance, both signals become 1.1, so the optimal controller reduces the value of both signals to approach the goal of a total signal of 2. In another, one control signal equals 1.1 and the other equals 0.9. In this case, the values for each signal are corrupted by noise, but the global goal of the task has been attained (total equals 2). If each variable were controlled independently, the controller would adjust each value towards one, but this is not necessary and, in fact, could lead to more error. The key feature of an optimal feedback controller is that it recognizes that the global goal has been attained and thus does not adjust the control signals.

There are several emergent features of optimal feedback controllers. First, they predict that movements are successful yet variable. This variability occurs in very selective ways that do not interfere with the task completion [47–50]. Second, optimal feedback controllers behave as though the system directly controls the global goal of the task, but can be created entirely by low-level signals each only concerned with a small portion of the entire system. In other words, relatively straight hand trajectories and bell-shaped hand velocities can be created by an optimal feedback controller based on only relatively low-level signals related to joint motions and muscle activities.

How these feedback laws are implemented within the distributed motor circuitry remains an important question for further study, but this theory re-emphasizes the important role that supraspinal feedback plays in motor performance. There is a large body of literature on the highly adaptable long-loop reflex principally generated by the transcortical reflex pathway through primary motor cortex. As expected for an optimal controller, this reflex pathway considers the influence of intersegmental dynamics when converting proprioceptive errors into patterns of muscle activity [51], and is modified as novel motor tasks are learned [52]. The notion of optimal feedback control should provide an important framework

in the next few years both for exploring how the motor system creates complex emergent behaviour, while also focusing attention on the neural circuitry that underlies this behaviour.

Clinical implications

Internal models and optimal control theory may also be of considerable value for interpreting how neurological injuries disrupt motor performance, whether of insidious or abrupt onset. The value lies in the focus on the physics of limb movements, and how the brain has and uses this knowledge to plan and control movement. Neurological disorders can be viewed as situations in which the neural system has reduced knowledge of the peripheral motor system and its interaction with the environment. The neurological injury may reduce knowledge about how to initiate movements (i.e. inverse internal model), or about how properly to select and manipulate afferent feedback to create smooth and accurate movements of the limb (i.e. optimal feedback control). In addition, many brain disorders frequently lead to secondary changes at the level of the spinal cord (e.g. spasticity) and of the mechanical properties of the limbs (e.g. reduced muscle length and extensibility). When movement function is thus impaired, the impairment may arise not merely from the changes themselves, but also from the brain's reduced ability to adjust to them.

In most neurodegenerative disorders, neural loss or dysfunction is occurring long before a clinical diagnosis can be confirmed. The use of paradigms to explore learning and adaptive motor skills provides a tremendous opportunity to assess subtle deficits in motor function. Novel tasks involving complex visuomotor transformations or mechanical loads stress the motor system and may reveal specific anomalies in motor performance. For example, individuals with genetically confirmed Huntington's disease but not yet any clinically documented impairments have been shown to have deficits in adapting to novel mechanical loads [53]. Deficits in motor performance from cerebral palsy are consistent with the perspective that the neural damage reduces the brain's ability to learn or use knowledge of the physics of limb movements. Errors in motor execution by individuals with progressive cerebellar diseases have been shown to be caused by a lack of knowledge of intersegmental dynamics [54,55,56*].

An abrupt loss of neural function, such as occurs from stroke, can result in a range of movement dysfunctions, from subtle changes to profound impairment. In many cases, some degree of improvement occurs spontaneously and this improvement can be optimized by well-designed rehabilitation. In the recovery of dysme-

tria after cerebellar stroke, a multistage process has been described: first, achieving less dysmetria in movements without load than in movements with load; next, recovery of normal timing in the initiation of antagonist muscle activity; subsequently, eliminating dysmetria in movements without load; and finally, eliminating dysmetria in movements with load [57]. The same paradigm has revealed motor deficits in otherwise clinically silent lesions of the cerebellum: these individuals showed no dysmetria in unloaded movements but produced overshoot when inertial load was added [58].

The concept of clinically silent or subtle impairments that can be revealed with these paradigms also applies to the consequences of cerebral stroke. The most obvious deficits in upper limb movements are, of course, those contralateral to the lesion. However, the ipsilateral upper limb is affected [59–61], and the errors are consistent with the studies regarding the control of the dominant and non-dominant limbs (see the section on Internal models). Left stroke impairs the ability to control reversal in the left upper limb smoothly in a reciprocal aiming task. Left stroke also leads to greater difficulty in coordinating arm and trunk movements [60]. These findings reflect that the left hemisphere may have a better knowledge of the influence of dynamics. In contrast, right stroke leads to difficulty in accurately guiding the right arm to a target, consistent with the idea that the right hemisphere is better able to use sensory feedback to correct for motion errors.

Finally, robotic and virtual reality technologies are playing a growing role in studies in this field, and such technology will probably be valuable for motor rehabilitation and in particular for motor assessment. The ability to create automated, standardized tasks is ideal for generating objective quantitative measures of motor function and dysfunction. Such technologies will not replace existing ordinal scales (e.g. Fugl-Meyer Assessment, Unified Parkinson Disease Rating Scale), which provide a brief assessment of a wide range of motor skills. Rather, robotic technology provides the opportunity to explore fully an element of the motor system (e.g. whole-limb function), allowing more in-depth characteristics of motor performance that may also reflect a broad pattern of disturbances in motor performance inherent in the entire motor system.

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