SYMPOSIUM REPORT

Inconvenient Truths about neural processing in primary motor cortex

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Primary motor cortex (MI) plays an important role in voluntary motor behaviour, yet considerable debate remains on how neural processing within this brain region contributes to motor function. This article provides a brief review of the dominant conceptual frameworks used to interpret MI activity, notably servo-control during the 1970s and early 1980s, and sensorimotor transformations since that time. The former emphasized the use of feedback, but was abandoned because delays in sensory feedback could not permit sufficient feedback gains to generate observed patterns of limb movement. The latter framework focuses attention on identifying what coordinate frames, or representations, best describe neural processing in MI. However, studies have shown that MI activity correlates with a broad range of parameters of motor performance from spatial target location, hand or joint motion, joint torque and muscle activation patterns. Further, these representations can change across behaviours, such as from posture to movement. What do heterogeneous, labile neural representations mean and how do they help us understand how MI is involved in volitional motor control? Perhaps what is required is a new conceptual framework that re-focuses the experimental problem back on processes of control. Specifically, optimal feedback control has been proposed as a theory of the volitional motor system and it is argued here that it provides a rich, new perspective for addressing the role of MI and other brain regions in volitional motor control.

A key feature of primate motor control is the breadth of contexts in which we can move and interact with the environment. We can reach out and grab objects of interest, kick a ball, or trace/draw almost any pattern with our hand. Further, we can adjust our motor patterns to consider the influence of physical objects, whether it is a grasped object such as a coffee mug, or an elbow pad worn during hockey.

Many regions in the brain contribute to voluntary motor function, but there is little doubt that primary motor cortex (MI) plays an important role in volitional motor control (for a general review see Porter & Lemon, 1993; Kandel *et al.* 2000; Shadmehr & Wise, 2005). MI provides the largest contribution to the corticospinal tract. Lesions in MI lead to acute paralysis and long-term difficulties

in coordinating movements such as individuated finger movements. How does MI contribute to the control of motor action?

An important approach for interpreting how MI is involved in controlling sensorimotor function has been to examine the activity of individual neurons in awake, behaving monkeys as they perform various sensorimotor tasks, such as moving the wrist, or reaching towards or maintaining their hand at spatial targets under a range of mechanical conditions. Although neural networks show considerable complexity in processing information, these neurophysiological studies tacitly assume that one can interpret discharge patterns of neurons based on correlations to explicit features of sensorimotor behaviour. These studies have several limitations including the fact that neural activity can only be recorded from large neurons, predominantly corticospinal and other projecting neurons. These studies also cannot address interactions between neurons within MI, although the development and increased use of multielectrode recording systems now permits examination of this

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important level of neural computation (Nirenberg & Victor, 2007). Nevertheless, the use of correlations between neuron discharge and aspects of motor behaviour remain an important and influential approach to examine MI function.

The design of these neurophysiological experiments has been strongly influenced by the conceptual framework used to describe how MI, specifically, and the brain, in general, control movement. Studies may focus on what motor variables are represented or coded in a given brain region, or explore how neural processing parallels formal control processes. As described below, the dominant concept has shifted over the years creating a natural cyclical pattern between studies that examine what variables are represented or coded in the MI (and elsewhere) followed by a period of studies that explore how neural processing parallels formal control processes.

### Single-joint movements, muscles *versus* movements, and servo-control

The first study that examined single neuron activity in MI in awake behaving nonhuman primates was performed in the 1960s by Ed Evarts (Evarts, 1968). These studies focused on a relatively simple question, whether neurons reflected muscles or movements. Wrist flexion/extension movements were performed by the monkeys with or without loads that assisted or resisted movement. Neurons that responded to flexion or extension movement and also modulated their response to loads were identified as muscle-like, whereas those that responded during movement but were not influenced by loads were identified as movement-like. Roughly equal numbers of muscle- and movement-like neurons were found in MI.

Through the 1970s several groups examined single-joint wrist, elbow and finger movements and found that neural processing can correlate with several other features of movement including joint position, force output and even the impending direction of movement (Thach, 1978; for a review, see Porter & Lemon, 1993). However, this line of research started to shift in the mid-1970s to focus less on what variables were represented and more on how neural processing reflected aspects of control. The motor system was viewed as a servo-controller based on sensory feedback from the limb (Fig. 1). MI was viewed as playing a pivotal role in this circuit converting differences between desired and actual joint angle into descending motor commands. Stretch of a muscle was known to elicit a relatively fixed short-latency reflex response, generated by spinal processing ($\sim < 50$ ms), and a more complex, long latency reflex response ($\sim > 50$ ms) (Marsden *et al.* 1983). This latter response could be modulated based on the motor task (Hammond, 1956) and was predominantly supported by a transcortical pathway through MI (Matthews, 1991). The use of servo-control as a conceptual framework led to a broad range of studies on how neurons responded to sensory input and to transient mechanical perturbations, and how this sensory information was transmitted to MI (e.g. Desmedt, 1978).

An inconvenient truth for servo-control

The dominant use of servo-control as a conceptual framework to study neural processing in MI came to an abrupt end in the mid-1980s. At this time, research was starting to uncover the behavioural and mechanical aspects of multijoint motor tasks such as point-to-point reaching. At the behavioural level, hand motion was found to be surprisingly simple with relatively straight hand trajectories and bell-shaped velocity profiles (Morasso, 1981). At the mechanical level, however, these multijoint movements are influenced by intersegmental dynamics such that the activity of a muscle spanning one joint could generate motion at other joints (Hollerbach & Flash, 1982). Therefore, multijoint movements could not be simply a scaled-up version of single-joint movements.
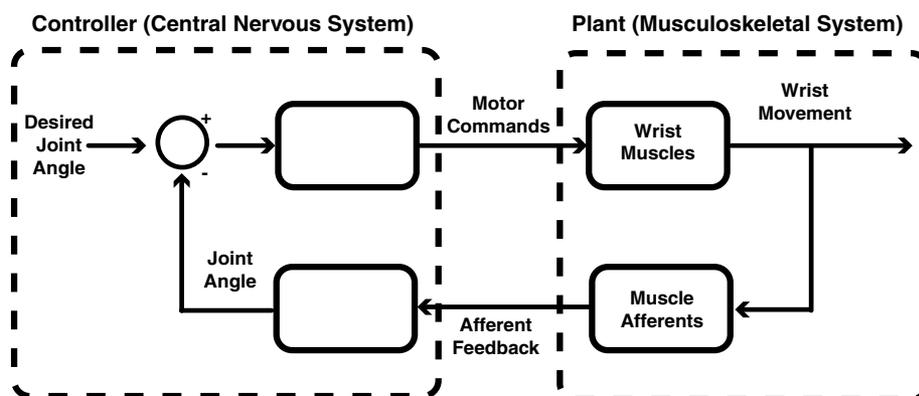
Figure 1. Servo-control as a model of wrist motor control
The difference between desired and present wrist position is first computed and then converted into motor commands that are sent to wrist muscles. Wrist movement is continuously sensed by muscle afferents and sent back to the central nervous system. This framework emphasizes the importance of feedback in motor control.

In theory, servo-control of each joint individually could compensate for these intersegmental dynamics using rapid sensory feedback. However, a fatal problem with this solution was the relatively slow transmission time of afferent information from the periphery (on the order of tens of milliseconds) and leading to instability. The conclusion was that feedback could only have a modest effect on motor output, and thus, the volitional motor system must take advantage of motor programmes, open-loop motor commands that specified the appropriate patterns of motor output (Schmidt & Wrisberg, 2000). With servo-control untenable, there was now a conceptual void for interpreting the neural processing related to volitional motor control.

Whole-limb movements and sensorimotor transformations

A shift in how to examine the motor system occurred in the 1980s from a problem of control back to a problem of what variables were coded in the activity of neurons. In order to reach to a visual target, the brain must convert target information specified in retinal coordinates into activation patterns of proximal limb muscles. Rather than a direct transformation, the idea is that the brain performs a series of sensorimotor transformations using intermediary representations or coordinate frames (Pellionisz, 1988; Soechting & Flanders, 1992; Kalaska *et al.* 1997). Posterior parietal cortex is known to integrate retinal target signals with information on eye, head and body position to specify spatial target position (Kalaska *et al.* 1997). Figure 2 illustrates other putative intermediate representations that could be computed by the brain in converting spatial target location into patterns of muscle activity.

A couple of factors made the concept of sensorimotor transformations and coordinate frames attractive for interpreting neural processing in the motor system. First, sensory systems, notably vision, possessed a hierarchical organization with primary visual cortex (V1) responding to relatively simple stimuli, such as bars of light, and adjacent cortical regions reflecting more sophisticated representations culminating with observations of face sensitive neurons in inferotemporal cortex (Hubel & Weisel, 1968; Perrett *et al.* 1982; Felleman & Van Essen,

1991). It seemed logical that the motor system would perform the reverse sequence of processing from high-level goal-related representations to low-level muscle activation patterns.

A second factor was studies by Georgopoulos and colleagues that illustrated that correlates of hand motion could be observed in MI (Georgopoulos *et al.* 1982). They found neurons were broadly tuned to the direction of hand movement, and across the population of recorded neurons, could roughly predict the direction of hand movement, using the population vector method (Georgopoulos *et al.* 1983, but see Scott *et al.* 2001 and Scott, 2003). These neural correlates of hand motion were an appealing approach for visualizing neural processing. It also seemed reasonable that there must be a link between smooth motion of the hand during reaching and these correlations to neural activity in MI. Thus, the notion of sensorimotor transformations became firmly established in the literature.

Although the ultimate goal for research on MI function was to understand how the volitional motor system controls motor action, it seemed reasonable to focus on a penultimate goal of identifying the coordinate frames. After this neural code was identified, the problem of control could then be addressed.

An inconvenient truth for sensorimotor transformations

However, the last 20 years has been a continued search for the parameters or variables that are reflected in the discharge pattern of neurons. Neural correlates have been found for virtually every movement parameter examined such as spatial target location, hand position or velocity, joint motion and muscle activation (for review see Scott, 2003). This plethora of variables that correlate to neural activity in MI might be due to correlations across variables (Mussa-Ivaldi, 1988; Sanger, 1994; Todorov, 2000). However, even in studies that have carefully dissociated different classes of variables, one can find that neural activity covaries with many variables. The conclusion from these studies is that MI processes both high and low level information about motor action and everything in between.

Figure 2. Putative sensorimotor transformations performed by the brain to generate limb movement
Spatial goals, such as to reach to a location in space, is converted into muscle activity through a sequential series of intermediary representations or coordinate frames. This concept emphasizes the open-loop aspects of motor control and the type of information conveyed in the discharge pattern of neurons in a given brain region.

Recent studies have uncovered even greater complexity and diversity of neural processing in MI (Hatsopoulos *et al.* 2007; Churchland & Shenoy, 2007; Morrow *et al.* 2007; Herter *et al.* 2007; Stark *et al.* 2007). For example, it had been assumed that neural activity should scale linearly with parameters such as movement distance and speed, an assumption now used in neuroprosthetics based on neural recordings in this brain region. Churchland & Shenoy (2007) found that such scaling was rarely observed in MI neurons with tuning magnitude and breadth often changing when speed or distance was varied (Fig. 3).

Another recent study found that neural coding or representations did not always remain constant across behavioural contexts. The activity of neurons in MI was recorded while monkeys maintained a constant arm posture and during reaching movements with flexor, extensor or null loads applied to the shoulder and elbow joints (Kurtzer *et al.* 2005). Loaded and unloaded trials were aligned on movement onset and regression models used to correlate changes in neural activity across loaded and unloaded conditions (Fig. 4). Some neurons responded to loads as the monkey maintained a fixed hand position and when reaching to another spatial target. However, many neurons changed their load sensitivity and in the extreme only responded to loads during reaching, but not during posture, or vice versa. Across the population of recorded MI neurons, there was no correlation between the magnitude of load-related activity during posture *versus* during movement. In effect, neurons appear to switch their representation across motor behaviours so that a neuron could reflect low-level information (responds to loads) during posture, then abruptly switch and code high-level information during reaching.

Given these additional complexities in MI processing, perhaps it is time to re-evaluate what we are learning about MI function from continuing to ask what coordinate frames or neural representations can be found in MI. A broader range of behaviours could be examined and more advanced mathematical tools could be used, but would this added complexity tell us anything more? Artificial neural networks to control movement tend to parallel many of these complexities in the pattern of hidden unit activity (Fetz, 1992). Similarities in the pattern of activity of a hidden unit with a given parameter of movement does not mean that it was destined to code that piece of information. As well, the activity of some hidden units does not parallel any parameter of movement. Does this mean some neurons code movement parameters and others don't? Perhaps it is time to stop pursuing the penultimate goal of identifying the coordinate frame(s) represented in the discharge patterns of MI and again move back to the question of control.

Optimal feedback control as a conceptual framework of MI processing

Control theory for robots and other applications has advanced considerably over the years and provides many new approaches for interpreting biological control. Optimal control theory is a mathematical optimization method that derives control laws based on some cost function (Stengel, 1994; Todorov, 2006). Optimal feedback control (OFC), a subfield of optimal control, computes
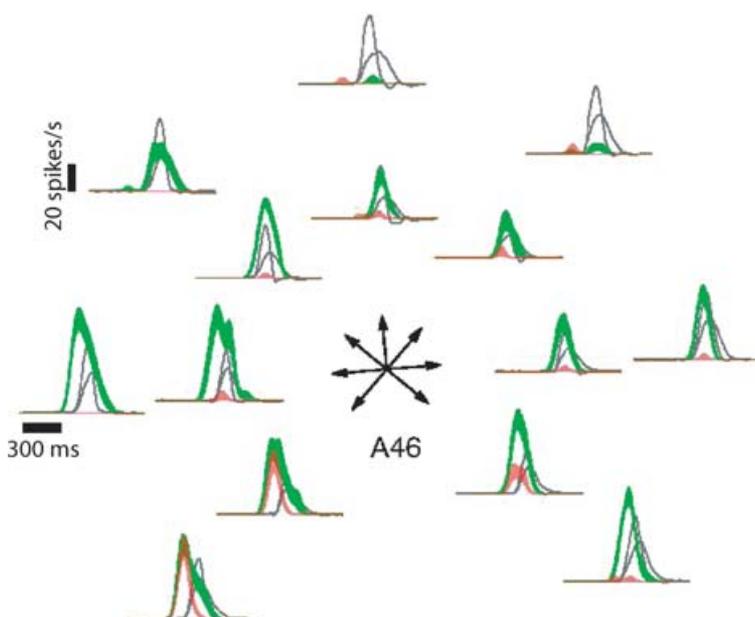
**Figure 3. Response of an exemplar neuron tested in seven directions, two distances and two instructed speeds**
Each subpanel plots data for 1 target location. Grey traces plot mean hand velocity. Red and green traces plot mean firing rate for fast and slow reaches, respectively. Trace widths show ± s.e.m. Vertical calibration bars indicate 20 spikes s^{-1}. Reproduced from Churchland & Shenoy (2007) with permission of the American Physiological Society.

control signals based on the current state of the system and has recently been proposed as a theory of the volitional motor system (Fig. 5; Todorov & Jordan, 2002). Given the inherent noise in biological systems, such controllers predict movements that have trial-to-trial variability, but that remain successful in attaining the behavioural goal. Todorov & Jordan (2002) suggest the use of a minimal intervention principle in which noise/errors are not corrected if they do not influence the goal of the task, but are quickly corrected if they affect completing the task. Irrelevant noise is ignored because attempts to correct these errors may lead to new errors that influence the goal: the best solution is to leave them alone. As a result, patterns of movement variability are not random but show considerable organization dependent on the goal of the motor task (Winter, 1984; Scholz *et al.* 2000). Such controllers also capture other key aspects of motor behaviour such as motor equivalence and muscle synergies.

With regards to the neural basis of control, OFCs resolve the fatal problems in applying servo-control to volitional motor control. The problem of sensory delays for feedback control is resolved through an optimal state estimator that combines efference copy of motor commands to rapidly estimate the state of the system (position, velocity, etc.) with actual sensory feedback as it arrives from the motor periphery and the visual system.

Optimal feedback control provides testable hypotheses related to patterns of motor behaviour. It was not designed to directly describe how neurons in a region of the brain are involved in controlling movement. The formal
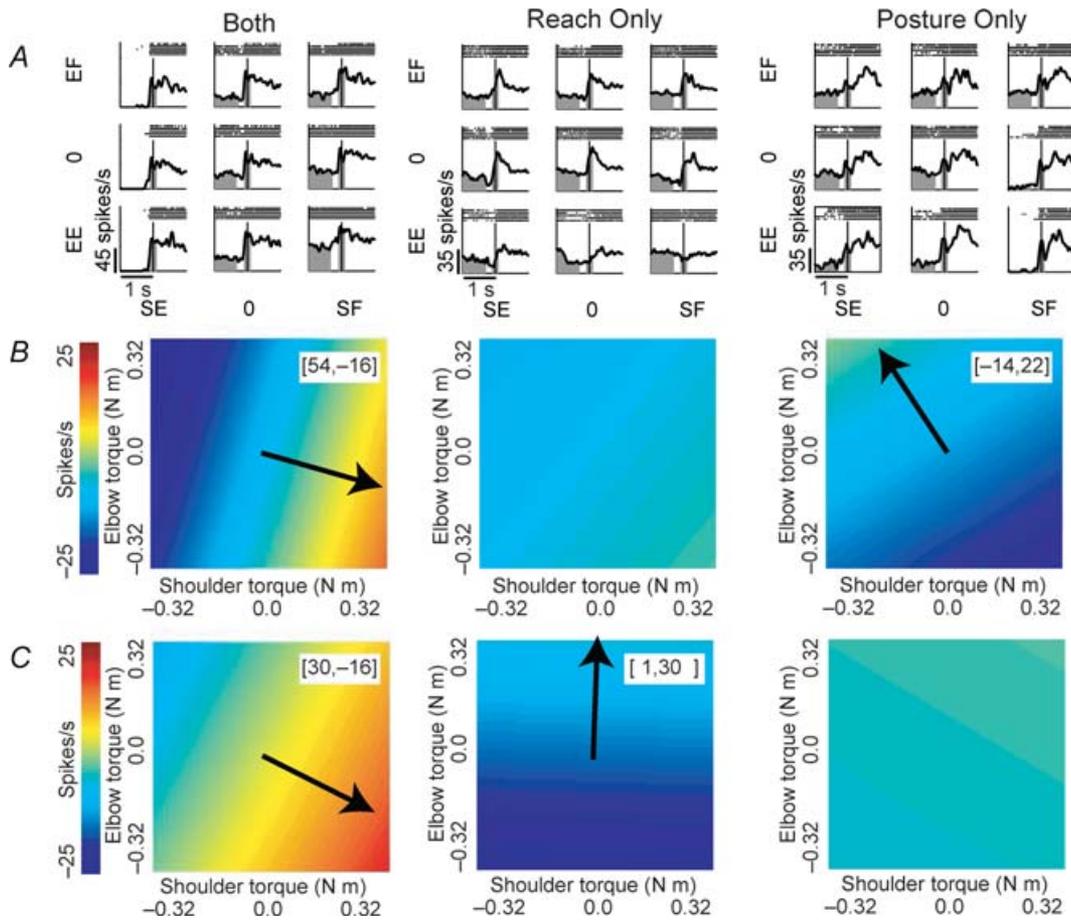
Figure 4. Load-related activity across posture and reaching periods with constant-magnitude load
A–C, vertical columns indicate exemplar neurons expressing load-related activity during both posture and reaching time periods, only during the reaching period, and only during the posture period. *A*, spike rasters and mean instantaneous firing rate under the nine load conditions in a muscle-torque coordinate frame, shoulder extensor (SE) and flexor (SF) torques *versus* elbow extensor (EE) and flexor (FF) torques. 0, no muscular torque. Vertical lines indicate movement onset; shaded regions denote posture and movement epochs used for plane fits displayed in subsequent panels. *B*, plane fits of change in neural activity to change in muscle torque during the posture time period. Neuron's response gain and direction are indicated by strength and direction of the plane's colour gradient; arrows and plane coefficients clarify and denote significant plane fit (*P* < 0.01). *C*, plane fits of change in neural activity to change in muscle torque during reaching time period. Reproduced from Kurtzer *et al.* (2005).

mathematics of optimal feedback controller is certainly not performed by the brain leading to several important avenues of research to explore how near-optimal control can be generated from a hierarchically organized system like the central nervous system (Todorov *et al.* 2005) and how artificial neural networks can generate near-optimal control. However, if OFC is a good description of motor behaviour, then certain aspects of this controller should be evident at the single-cell level. In this regard, OFC can be an important conceptual model for interpreting neural processing in MI (Scott, 2004). Importantly, this conceptual framework resolves or is consistent with many aspects of neural processing in MI.

First, the observation that neural activity correlates with high-level and low-level parameters of movement is not surprising and is expected from a region involved in using feedback for control. Afferent feedback from vision will correlate with high-level features of movement, whereas proprioceptive or cutaneous feedback will correlate with low-level features of the motor task. The motor system does not need to create a single common coordination frame to integrate all sensory information. Therefore, simple convergence can generate neural representations that reflect either visual signals or a portion of the motor periphery that may include one or more spanned joints (Herter *et al.* 2007).

Second, an optimal feedback controller is designed based on the goals of a task. If the task changes, the feedback gains will be modified accordingly. This feature of OFC emphasizes the importance of the motor task on neural processing and thus it should not be surprising to observe that the response of neurons to applied loads can abruptly change in the transition from posture to movement control (Kurtzer *et al.* 2005).

Finally, the principles of OFC explain how smooth hand trajectories can be generated without explicitly coding this parameter in the brain. The behavioural goal, reach to a spatial target, can be mapped directly into feedback control policies. Hand trajectory is an emergent property that comes from the interplay between feedback and noise/errors in the system (Liu & Todorov, 2007). This view of the volitional motor system is more in-line with other biological control systems such as locomotion in cats and lampreys or simple invertebrate nervous systems. Therefore, OFC is potentially a useful general description of not only volitional reaching in primates, but also other motor functions (Kuo, 1995) and other animal species (Loeb *et al.* 1990; Lockhart & Ting, 2007; Tresch, 2007).

How optimal feedback control can guide experiments on the neural basis of volitional motor control

The most important aspect of a formal scientific model is not that it is right or wrong; they are all wrong. Rather, a key value of a model or concept is its ability to generate ideas for experimentation. Searching for state variables used by the CNS would simply be a continuation of the present search for the holy grail of coordinate frames. Instead, OFC highlights the neural process and not the neural codes as the problem we need to address experimentally.

Perhaps the most important implication of OFC is emphasizing the importance and flexibility of sensory feedback for volitional control. Motor reflexes are typically seen as a separate weaker cousin to volitional control, and visualized as the flinching motion generated by a tap of a muscle's tendon in a basic medical exam. OFC provides a very different perspective on reflexes and volitional control processes.

In particular, our general hypothesis is that there is an intimate relationship between long latency reflexes associated with the transcortical pathway and volitional motor control (Scott, 2004). Both share similar neural
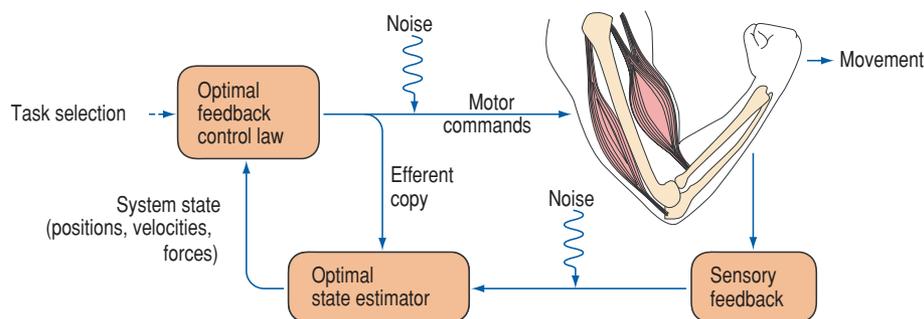
Figure 5. Optimal feedback control
Feedback control laws convert state variables into motor commands. A key difference between servo-control and optimal feedback control is that all state variables related to the body (joint position, velocities, force, etc.) can influence motor commands to each muscle (multiple input, multiple output). Delays in sensory feedback from the periphery can be overcome by using efference copy of motor commands to help estimate present state variables. Reproduced from Scott (2002).

circuits, notably primary motor cortex, as well as other cerebral cortical and subcortical regions. The volitional motor system can appropriately scale motor commands based on movement direction, distance, speed and environmental loads, and can rapidly learn either novel loads or complex sensorimotor associations. We predict that long latency reflexes are will share many of these complex capabilities. Our preliminary human studies illustrate that long, but not short, latency reflexes have knowledge of the limb (Kurtzer *et al.* 2007) and can scale motor responses based on spatial target location (Pruszynski *et al.* 2007). How regions of the brain create and learn these smart reflexes remains an important avenue of study.

The first 20 years (mid 1960s to mid 1980s) of research examining MI activity in awake, non-human primates created a cycle of research with two phases, an initial phase that examined which parameters, muscles *versus* movements, were coded in MI, and then a second phase that examined how MI and other brain regions behaved like a servo-controller. The shift to whole-limb movements and the use of sensorimotor transformations represented the start of a second cycle that first returned to the problem of movement parameters and coding. It is proposed here that it is time to shift to the second part of this cycle, this time based on the ideas of OFC, that captures many of the sophisticated features of volitional behaviour.

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