Cogn Process (2005) 6: 15–24
DOI 10.1007/s10339-004-0046-7

REVIEW

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Neural representations of motor plans, desired trajectories, and controlled objects

Received: 11 November 2004 / Revised: 14 December 2004 / Accepted: 15 December 2004 / Published online: 4 February 2005

Abstract Traditional theories of motor control view it as a serial process of planning and execution situated at the end of a larger serial process of perceptual representation and cognitive decision-making. Here, I examine the assumption that "planning" and "execution" are distinct processes separated by a neural representation of a "desired trajectory". I propose that neural data do not support the existence of a desired trajectory or of any pre-generated plan other than a crude representation of the intended motion of a controlled object. That representation appears to be more strongly involved in decision-making processes than in the control of a specific movement, and it does not appear to be converted into a detailed motor command until after the movement begins, even in well-trained tasks. Thus, one is led to question whether the traditional distinction between decision-making, planning, and motor execution is a useful foundation for interpreting neural data and generating computational theories of motor control.

Keywords Planning · Motor control · Theory

Within the broad field of systems neuroscience, motor control is traditionally viewed as the output end of a long series of perceptual, cognitive, and planning processes. The basic functional architecture of behavior is assumed to consist of separate serial stages: "Perception", which collects information from sensors to construct an internal representation of the world; "Cognition", which uses that representation along with stored representations of past experiences to make judgments about the world and to make decisions about future courses of action; and "Action", which prepares and executes motor plans to accomplish the organism's goals (Newell and Simon 1972). Within that large scheme, the problem of motor control is defined as the problem of how action goals are represented, how motor plans are formulated, and how movements are executed. This standard definition is not only intuitively attractive, but it is also very similar to and compatible with the practices of engineering control theory. As shown in Fig. 1, control theory defines the problem of control in terms of three separate entities: a "planner" which takes high-level representations of goals and task constraints to compute a desired trajectory of the relevant effector; a "controller" which computes the necessary motor command signals to realize that trajectory; and a "plant" which is the effector system being controlled.

A great deal of motor control research has been aimed at addressing questions raised by the conceptual architecture of Fig. 1. For example, one interesting question concerns the extent to which the controller relies on feedback information to fine-tune a movement as it takes place ("feedback" or "closed loop" control) or whether it precisely pre-computes control signals without requiring any sensory contributions ("feedforward" or "open loop" control). There are advantages and disadvantages to each approach. Feedback control is simple and can automatically compensate for perturbations due to the physics of movement or to external forces, but it suffers from serious instabilities if the feedback signals are inaccurate or if they arrive with a significant delay. Feedforward control can operate even with very long transmission delays, but it requires very precise pre-computed command signals and cannot tolerate noise. Other important questions concern the nature of the representations involved, such as the form of the motor plan that is sent to the controller. Some models assume a plan which optimizes nearly every aspect of movement, including the muscular forces required at each moment in time (e.g. Flash and Hogan

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Communicated by Irene Ruspantini and Niels Birbaumer

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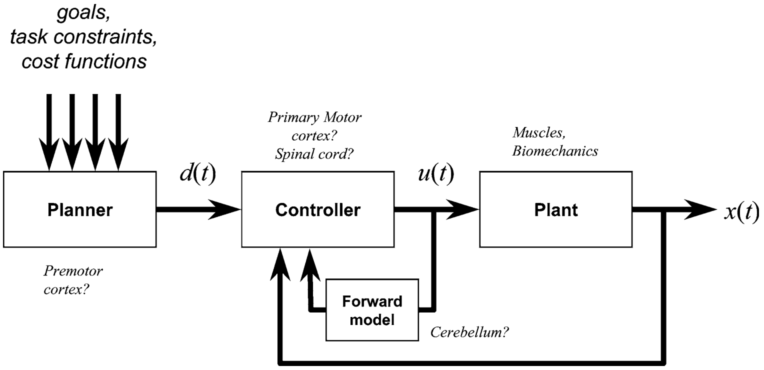

Fig. 1 Control theory architecture. In this view, high-level task goals, constraints, and cost functions are used by a "planner" subsystem to compute a "desired trajectory" $d(t)$ which describes the spatiotemporal features of the movement. This information is transmitted to a "controller" which computes the appropriate command signals $u(t)$ such that the effector "plant" moves the controlled variable $x(t)$ along the desired trajectory. The controller may make use of both overt sensory feedback or predicted feedback provided by a "forward model" that anticipates the consequences of the current motor command

1985; Uno et al. 1989), placing heavy computational burden on the planner. Other models assume purely kinematic plans that only define the spatial path of the relevant effector, letting the controller deal with the problems of movement dynamics and the computation of the specific joint configurations which move the effector along that path (Bullock et al. 1998; Bullock and Grossberg 1988; Cisek et al. 1998). All of these questions can be framed in terms of the underlying neural systems involved in solving the associated problems. Does the primary motor cortex represent the "extrinsic" spatial motion of the end effector (Ashe and Georgopoulos 1994; Georgopoulos 1995; Georgopoulos et al. 1982, 1983, 1988; Schwartz 1992, 1993) or does it represent "intrinsic" aspects of muscle control signals (Ajemian et al. 2000; Cisek et al. 2003; Evarts 1968; Gribble and Scott 2002; Kalaska et al. 1989; Scott et al. 2001; Scott and Kalaska 1997, Sergio and Kalaska 1997, 1998, 2003)? Does the cerebellum step in to solve the problems of dynamics (Albus 1971; Grossberg 1969; Imamizu et al. 2000; Ito 1984; Kawato and Gomi 1992; Marr 1969; Miall and Wolpert 1996; Pellionisz and Llinás 1985; Schweighofer et al. 1998)? Is planning performed by premotor or parietal cortical regions?

Despite the richness of the research programs aimed at addressing such questions, one must also ask whether our working definition of the problem of motor control is in fact accurate. Is it safe to assume that the scheme of Fig. 1 appropriately captures the functional organization that underlies movement control? If not, what aspects are problematic and what are the implications for specific theories of motor control? Here, I will focus on such questions and will specifically examine one of the central assumptions of the control theory view of the organization of the motor system: the distinction between the "planner" and the "controller". Concerns regarding this assumption have been raised by various authors (Alexander et al. 1992; Fetz 1992; Kalaska et al. 1998), but in the absence of an alternative, the scheme of Fig. 1 continues to serve as the major theoretical foundation for motor control research.

In asking the question of whether the planner and controller are separate systems, it is useful to think of the different senses in which two conceptual entities can be separately implemented in the brain. First, there is regional separation, implying that the two functions are performed by anatomically distinct neural structures. For example, it is possible that planning is performed by the premotor cortex while execution is performed by the primary motor cortex and spinal cord. Second, there is temporal separation, which implies that the two functions are performed in some kind of temporal sequence. For example, this would imply that planning processes are completed prior to the onset of movement control processes. Third, there is representational separation, which implies that the functions are performed through the use of distinct representational schemes. For example, planning might make use of extrinsic representations (e.g. of goal states) while execution involves intrinsic representations, and both of these might be distributed throughout the brain. Importantly, one must consider the possibility that these functions are separate in one of these senses while being integrated in other senses. Planning and execution might occur at different times within the same brain regions, or alternatively, in different regions but overlapping in time. While keeping these issues in mind, let us discuss evidence for and against the distinction between planning and execution.

Perhaps the strongest evidence suggesting that planning is separate from control is the phenomenon of "motor equivalence"—that a given high-level goal can be accomplished in a large variety of ways. For example, to grasp an apple you can use either hand, enclosing your fingers around it, scooping it up with your palm, or picking it up by the stem. You can have your arm fully extended or flexed. You can even pick it up with your teeth. In each case the goal is accomplished, even though the specific motor actions taken can be very variable. This suggests that at some level, the goal (picking up an apple) must be specified in a way that is independent of both the effectors and the particular settings of the motor parameters (joint angles, muscle forces) which will be used to accomplish it. Moreover, it has been observed that during many different kinds of reaching movements, the spatial trajectory of the hand is straight even when that is not a requirement of the task (Abend et al. 1982; Atkeson and Hollerbach 1985; Morasso 1981). Not only are the paths straight, but they exhibit a stereotypical temporal pattern of gradual acceleration and deceleration which is remarkably similar across many kinds of movements. This phenomenon is called "kinematic invariance". On the basis of such findings, it has been suggested that the brain computes a "desired trajectory" which is kinematic and extrinsic—that is, a desired spatial path for the hand defined in a coordinate system that is independent of arm geometry (e.g. a Cartesian system with orthogonal x, y, and z axes) and independent of required forces. It is often assumed that a separate system then converts this extrinsic kinematic plan into a sequence of muscle contraction patterns which will produce it. Under this view, planning and execution are separated at the level of a specific internal representation—the "desired trajectory"—in agreement with robotics engineering in which a desired trajectory is computed by a planner and then transmitted to a controller. Thus, this view suggests that there is representational, temporal, and regional separation of planning and execution.

However, while motor equivalence does provide evidence for representational separation of planning and execution, it does not necessarily imply temporal or regional separation. The fact that trajectories tend to be straight does not necessarily imply that the desired trajectory is planned in Cartesian coordinates, or that one even exists at all. Kinematic invariance may simply be a consequence of movement errors being represented in extrinsic space, which is both useful and likely in visually guided reaching tasks where success or failure is determined by spatial accuracy. If one assumes that motor adaptation makes use of an error signal that is primarily based on vision, then one should expect straight trajectories to be produced. No additional assumptions, neither about the existence of a desired trajectory nor its representation in extrinsic coordinates, are necessary.

For example, Todorov and Jordan (2002) show that a feedback system optimized to reduce endpoint error will produce many of the observed features of voluntary reaching movements, even if it contains no internal representation of a desired trajectory. This is based on the "uncontrolled manifold concept" (Scholz and Schöner 1999)—that the motor system minimizes errors along degrees of freedom that are most relevant for task success by allowing variation along the degrees of freedom which are not relevant. Indeed, it has been demonstrated that human movements exhibit the most variability in those degrees of freedom which least affect task success (Domkin et al. 2002; Scholz and Schöner 1999; Scholz et al. 2002), which contradicts the prediction that a desired trajectory is computed and errors minimized equally around it (Scholz and Schoner 1999; Todorov and Jordan 2002). In particular, during reaching, what matters most is that the end effector stops close to the target, and the particular path taken through space or the particular joint angles used to accomplish that feat are not very important. However, because of muscle properties and signal-dependent noise (Harris and Wolpert 1998), it turns out that a straight path with a bell-shaped speed profile is the best way to reduce endpoint error. Assuming that the system uses visually-reported estimates of error to fine-tune its control parameters, one can expect it to converge through adaptation to something which produces straight paths. Todorov and Jordan (2002) propose a computational scheme of how that might occur. In that scheme, a control law is used to generate the motor command online using sensory feedback (However, the control law itself is computed given initial and final states and explicit knowledge of movement duration, which implies a planning process that occurs prior to movement onset, and no attempt has yet been made to express that computation in a biologically realistic manner).

To summarize, motor equivalence argues for at least a representational separation of planning and execution. There is a sense in which a plan (e.g. picking up an apple) can be defined using a representation that has little to do with execution. However, the plan need not necessarily take the form of an explicit "desired trajectory" like what is used in control theory and assumed in many models of motor control (Bhushan and Shadmehr 1999; Bizzi et al. 1984; Flash and Hogan 1985; Uno et al. 1989). Phenomena of kinematic invariance can be produced within feedback systems that have no representation of desired trajectories at all, and involve neither regional nor temporal separation between the processes that plan the trajectory and other processes that execute it.

Nevertheless, it is possible that in addition to a representational separation, there is also regional and/or temporal separation between planning and execution. If that is the case, then it should be possible to find the neural correlates of these processes in movement-related brain regions such as the premotor and motor cortex and the cerebellum. Many neurophysiological experiments have been aimed at precisely that objective. For example, some studies of the primary motor cortex have suggested that cell activity in this region represents the kinematic path of the hand through space, without encoding the details of muscular force (Ashe and Georgopoulos 1994; Georgopoulos 1995; Georgopoulos et al. 1982, 1983, 1988; Schwartz, 1992, 1993). This would suggest that motor cortex resides fairly high in the motor hierarchy, perhaps at the level of the planner, and that downstream systems, such as the spinal cord, take care of the details of force production (Bizzi et al. 2000). However, other studies make a strong case that the primary motor cortex does indeed represent torques and forces at the joints and muscles (Cisek et al. 2003; Evarts 1968; Gribble and Scott 2002; Kalaska et al. 1989; Scott et al. 2001; Scott and Kalaska 1997; Sergio and Kalaska 1997, 1998, 2003), placing it further downstream in the control system. These latter studies suggest that the relation between motor cortical activity and high-level variables such as hand direction is merely a circumstantial correlation due to the strong dependence of that variable on the underlying lower-level motor variables (Ajemian et al. 2000, 2001; Mussa-Ivaldi 1988; Sanger 1994; Scott 2000). While the case for lower-level control signals in primary motor cortex is strong, it raises the question of where the higher-level variables are represented and what form they take.

Assuming the existence of some kind of planning, it makes sense to look for correlates of the plan in the neural activities that exist during an "instructed delay period" in which an animal has been given all the information about the goal of the movement but is not yet allowed to begin moving. Instructed delay period activity has been found in nearly all movement-related regions, including motor and premotor cortices, posterior parietal cortex, and even the spinal cord (Alexander and Crutcher 1990; Andersen 1995; Kalaska and Crammond 1995; Kurata 1993; Prut and Fetz 1999; Riehle and Requin 1989; Wise 1985). To what extent does activity during the instructed delay reflect planning processes that are separate from execution? A recent study by Crammond and Kalaska (2000) examined this very question. These authors compared neural activity in dorsal premotor cortex (PMd) and in both rostral and caudal parts of primary motor cortex (M1r and M1c) during reaching tasks with and without an instructed delay period. It was assumed that in the instructed delay tasks (ID), some processes associated with planning should occur as soon as the instructional information is given, and should not again be repeated after the GO signal. In contrast, during simple reaction time tasks (RT) without delay, all planning processes should occur together after the GO signal. Indeed, some features of neural response appeared to be more closely tied to the arrival of instructional information, while other features seemed to always occur only after the GO signal even during ID tasks. It is possible that those early features reflect planning processes, which can be temporally separated from movement execution using an instructed delay period. Other features, which remain tied to the GO signal even in ID tasks, may be more related to execution processes. In addition to this evidence of temporal separation between planning and execution, Crammond and Kalaska found some evidence of regional specialization. In particular, neural responses related to instructional information were more often found in the rostral regions studied (PMd and M1r), while responses that only occurred after the GO signal were more common in the caudal regions (M1r and M1c). Similar gradients of physiological properties have been found in many studies of the precentral motor regions (e.g. Johnson et al. 1996). Importantly however, regional separation appears far from complete, since both early and late responses are often intermingled within the same cortical region and often are exhibited by the very same individual cells (Cisek et al. 2003; Crammond and Kalaska 2000; Kalaska and Crammond 1992; Shen and Alexander 1997a, 1997b).

Can we therefore conclude that early instruction-related activity in rostral precentral regions reflects planning while later movement-related activity in caudal regions reflects execution? To some extent, the answer may be yes. However, we must be careful what we imply by the term "planning" when we apply it to the interpretation of these results. In particular, if the early activity in rostral regions such as PMd is a neural correlate of a "plan", then that plan appears to be very simple. It does not appear to capture much information on the details of the upcoming movement, and does not appear to exhibit the properties that would be expected of a neural representation of a "desired trajectory". For example, Shen and Alexander (1997b) showed that when the direction of motion of an on-screen cursor is dissociated from the hand movements used to control it, early activity in precentral motor regions is correlated primarily with the direction of cursor motion, not hand motion. Over the course of a trial, especially after movement begins, the activity of individual neurons gradually becomes more hand-related than cursor-related. Other studies have shown that patterns of activity in premotor regions, especially during the early instructed-delay activity, are largely independent of the choice of the arm used to perform the movement (Cisek et al. 2003; Donchin et al. 1998; Hoshi and Tanji 2000, 2002; Tanji et al. 1987, 1988). Again, there is a trend for movement–time activity, even within individual cells, to gradually become more effector dependent (Cisek 2003). Furthermore, PMd activity even appears independent of who performs the movement, and continues to reflect on-screen cursor motion even when a monkey passively observes the task being performed by a third party (Cisek and Kalaska 2004). In other words, when action observation causes a monkey to simply mentally rehearse a learned action without any muscular activity, activity in PMd continues to represent certain abstract aspects of that action such as the specification of possible targets and the selection of one as the correct target for the action (Cisek and Kalaska 2004). These findings suggest that what is represented by the early activity of rostral precentral regions is the motion of a "controlled object" (e.g. the cursor) in the coordinate system that defines task success (e.g. screen coordinates).

All of this raises new questions. If the early activity in premotor regions merely represents the intended motion of the controlled object in an abstract, effector-independent manner, then when and where does that representation get converted into the motor command? Is there another system that uses the premotor command to precompute desired trajectories and muscle contraction patterns *during* the instructed delay period? Or does that conversion not occur anywhere until the movement begins? Several pieces of evidence are relevant for distinguishing these possibilities.

Scott and Kalaska (1997) reported that neural activity in the primary motor cortex is highly sensitive to changes in the posture of the arm, even when the spatial path of the end effector is kept constant. This provides strong evidence that such activity represents movements in an intrinsic coordinate system, rather than in a purely extrinsic spatial one, and is in agreement with numerous studies showing strong relationships between M1 activity and biomechanical details of movement control (Cisek et al. 2003; Evarts 1968; Gribble and Scott 2002; Kalaska et al. 1989; Scott et al. 2001; Scott and Kalaska 1997; Sergio and Kalaska 1997, 1998, 2003). However, while M1 activity during the movement was strongly dependent on posture, the earliest reaction time activity was much less so (Scott and Kalaska 1996). During the earliest post-GO responses, activity in M1 did not appear to take posture into account. It is as if the initial descending command from primary motor cortex is a simple crude approximation which only later becomes more precisely fine-tuned to the details of motor execution. Along similar lines, Sergio and Kalaska (2003) found that the preferred directions of cells in primary motor cortex changed with initial hand position during an isometric task, in a manner appropriate for the geometry of the limb and muscle pulling directions in those positions. However, the earliest post-GO activity did not show this strong postural effect, again suggesting that M1 activity does not take arm geometry fully into account until after the movement starts.

Similar results have been reported at the level of muscle activity and movement kinematics. For example, Karst and Hasan (1991) showed that the initial part of EMG activity does not appear to be ideally suited for a given movement and only becomes fine-tuned only after movement onset. Consequently, the initial trajectory of a reaching movement is not always in the exact direction of the target and appears to be corrupted by the anisotropic inertial properties of the limb (Gordon et al. 1994). Taken together with the neural data discussed above, these findings suggest that the earliest control signals issued by the motor system are somewhat crude and only become more precisely adjusted to biomechanical details after the movement itself begins. This argues against the concept of an internal representation of a desired trajectory that is optimized prior to movement onset. Instead, it suggests that movement planning is relatively simple and crude, even for well-practiced movements, and emphasizes the role of on-line processes (involving both overt sensory feedback and internal "forward models" (Flanagan and Wing 1997; Jordan and Rumelhart 1992; Mehta and Schaal 2002; Miall and Wolpert 1996; Wolpert and Kawato 1998)) to fine-tune the details of execution. Thus, in response to the question posed earlier, it appears that the transformation of a crude motor plan expressed in terms of the motion of a controlled object into a representation of a motor command that takes muscle properties and movement dynamics into account does not occur until the movement begins.

In summary, the results described above do not support the assumption that biological motor control involves a functional architecture resembling that of engineering control theory (Fig. 1). While there appears to be some representational separation of planning and execution, regional and temporal separation between these functions is only partial. The neural representation of a plan does not consist of a desired trajectory or motor program optimized prior to movement onset, but simply represents the desired motion of the controlled object in an effector-independent manner and in the reference frame of whatever defines error in the task. Most of the details of kinematics and kinetics do not emerge until after movement begins, even in very familiar tasks and even when full information about the upcoming movement is provided well ahead of time.

These findings lead us to consider an alternative functional architecture for biological motor control, one in which optimization of the motor command occurs only during the movement itself. In other words, the neural processes which occur during an instructed delay period only represent movement in terms of a "difference vector" between the desired state of the controlled object and its current state (Bullock et al. 1998; Bullock and Grossberg 1988; Buneo et al. 2002; Cisek et al. 1998), expressed in the coordinate system in which errors about the movement are registered. Even for well-practiced movements, the only "plan" computed by the brain prior to movement onset is this simple signal. Once the movement is about to begin, this difference vector is converted into a crude initial motor command which gets the effector moving in the right general direction. At this point, compensatory adjustment signals from a trained forward model (Flanagan and Wing 1997; Jordan and Rumelhart 1992; Mehta and Schaal 2002; Miall and Wolpert 1996; Wolpert and Kawato 1998), as well as overt sensory feedback signals (Desmurget et al. 1999), begin to fine-tune the motor command to take into account all the biomechanical details of the motor plant and the forces that act upon it (Todorov and Jordan 2002).

Other recent studies of movement planning and control go even further to argue against the theoretical scheme described in Fig. 1. Cisek and Kalaska (2002, 2005) found that when a monkey is presented with two mutually-exclusive potential directions for a reaching movement, directional signals corresponding to both of these actions are simultaneously represented in PMd. When a cue is presented that identifies the correct action, PMd activity associated with the selected direction increases while activity associated with the other sharply decreases (Fig. 2), only 110 ms after the decision cue is given. This behavior was observed in the majority of PMd cells with directionally-tuned responses to the onset of spatial cues (127/173, 73%), and was also observed in parietal area 5 (Cisek et al. 2004). Thus, movement-related regions of the cerebral cortex can become active, and can represent multiple possible actions, even before a cognitive decision is made about which action to take. In other words, not only does "motor planning" not appear to involve the computation of desired trajecto-

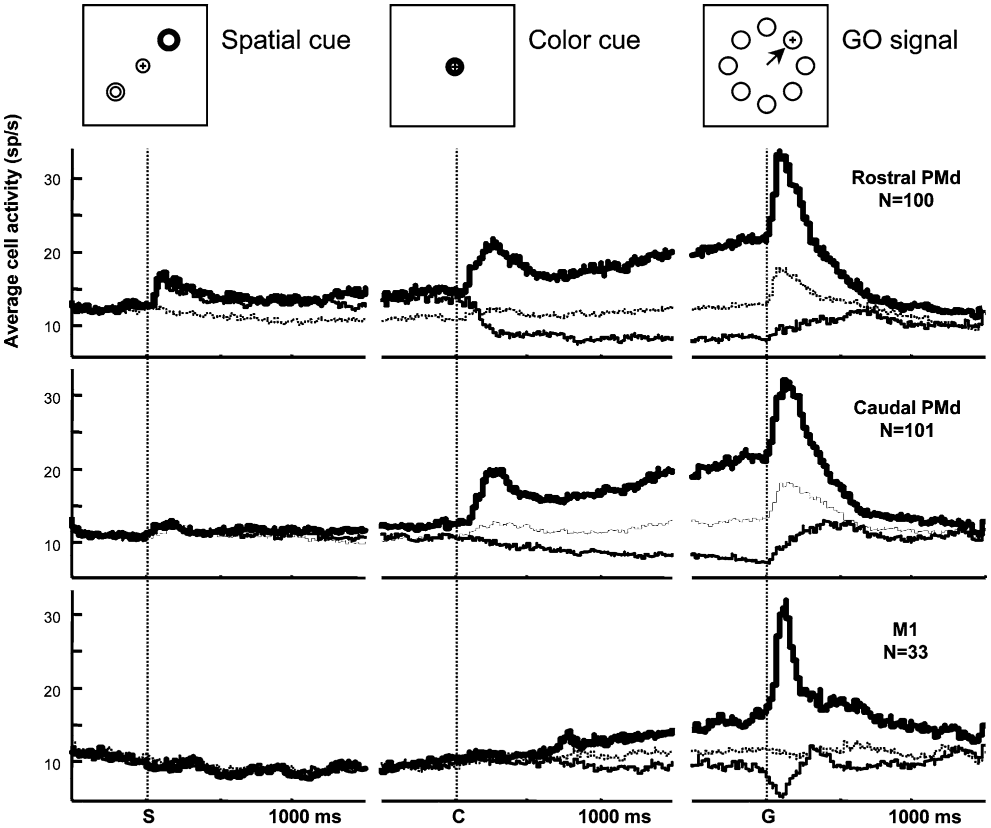

Fig. 2 Population activity in dorsal premotor cortex and primary motor cortex during a reach decision task. In the task (*top*), the monkey begins by holding the cursor (+) in the center circle. Next, two colored potential targets for movement are presented during a spatial cue period and one is later indicated as the correct target with a non-spatial color cue. After an additional delay, a GO signal is given and the monkey must reach to the target where a spatial cue previously appeared whose color matched the color cue. The population histograms show activity in each cell's preferred direction (*thick line*), in the opposite direction (*thin line*), and the average of activities in the orthogonal directions (*dotted line*). The *top row* shows activity from a population of 100 cells in the rostral part of PMd, the *middle row* shows activity of 101 cells in the caudal part of PMd, and the *bottom row* shows activity of 33 cells in primary motor cortex. The *first column* shows activity aligned on the onset of the spatial cue targets (*S*), the *middle column* shows activity aligned on the color cue (*C*), and the *third column* shows activity after the GO signal (G). Note that while two targets are presented during the spatial cue period, two populations of cells are active in PMd, simultaneously generating two directional signals. After the color cue indicates the correct target for movement, one of these populations becomes more active while the other is suppressed. Adapted from Cisek and Klaska (2005)

ries, but it does not even appear to be separate from processes of decision making. What occurs in PMd appears to be less related to the traditional definition of motor control than to what one would be more inclined to describe as a cognitive process.

In conclusion, defining the sub-problems of motor control in terms of a serial process of decision-making, planning, and execution that mimics the schemes traditionally used in engineering control theory does not appear to successfully account for the patterns of neural activity observed in movement-related brain regions. Most notably, one of the central concepts in control theory—the desired trajectory—does not find support either in behavioral or neurophysiological data. Without that concept, the traditional distinction between planning and execution loses much of its meaning, and therefore one need not assume that these processes involve separate neural structures or occur in a strict temporal sequence. Alternative schemes for producing movement have been proposed (Bullock et al. 1998; Cisek et al. 1998; Todorov and Jordan 2002) which do not make use of a pre-computed desired trajectory at all, and in which the only planning that occurs prior to movement initiation is the generation of a difference vector. This does not imply that the motor system's ability to deal with a variety of complex dynamic situations (Krakauer et al. 1999; Lackner and DiZio 1994; Shadmehr and Mussa-Ivaldi 1994) is simply due to feedback control or stabilization around a shifting equilibrium point (Bizzi et al. 1984, 1992; Feldman 1986; Latash and Gottlieb 1991; Polit and Bizzi 1978). In contrast, a great deal of compensation must take place during the movement through the use of predictive signals provided by a forward model that has learned to anticipate the kinds of errors that occur in a given movement context and to provide the appropriate preemptive adjustment of the descending motor command. In a sense, one can view movement control as a set of nested feedback processes that are assisted by feedforward compensatory mechanisms.

Furthermore, not only do neural data cast doubt on the assumption that motor control occurs through a sequence of serial stages such as trajectory planning and execution, but they also cast doubt on the definition of motor control as something that occurs after cognitive processes of decision-making are complete. A growing body of neurophysiological studies at the single-neuron level has shown that the separation between decision-making and motor planning is blurry at best. To date, the neural-level processes of decision-making have been most extensively studied in the oculomotor system (Glimcher 2003). These studies have shown that when multiple potential saccade targets appear, multiple neural populations become active in parietal area LIP (Platt and Glimcher 1997), the frontal eye fields (Schall and Thompson 1999; Thompson et al.1996, 1997) and the superior colliculus (Basso and Wurtz 1998; Glimcher and Sparks 1992), presumably representing those distinct saccade options. As the decision is being made, the activity associated with each option is modulated by various "decision variables" such as prior probability (Basso and Wurtz 1998; Platt and Glimcher 1999) and reward size (Platt and Glimcher 1999; Roesch and Olson 2003, 2004). If a monkey is given ambiguous sensory information on which of two saccadic targets is the correct one, neural activity in several brain regions grows at a rate related to the strength of the evidence for that choice (Gold and Shadlen 2000, 2003; Kim and Shadlen 1999; Mazurek et al. 2003; Ratcliff et al. 2003; Schall and Bichot 1998; Schall and Thompson 1999; Shadlen and Newsome 2001) until some putative decision threshold is reached and the decision is made. What is interesting about these results is that many of the brain areas that have been implicated in saccadic decision-making are also implicated in saccade execution itself, including structures such as the superior colliculus that are only a few synapses away from motor neurons (Basso and Wurtz 1998; Horwitz et al. 2004; Ratcliff et al. 2003). This contradicts the assumption that decisions are made prior to, and by different mechanisms than motor planning. Instead, the neural processes of motor planning appear to be inextricably entwined in the processes of decision-making.

This conclusion holds not only for oculomotor decision making, but for voluntary reaching movements as well. For example, Romo and colleagues (Hernandez et al. 2002; Romo et al. 2004, 2002) found that during tasks in which tactile perceptual decisions are reported by arm movements, correlates of all of the putative sensory discrimination and decision-making processes appear within motor regions such as premotor cortex. As described above, Cisek and Kalaska (2002, 2005) found evidence that neurons in dorsal premotor cortex can encode two distinct reaching movement alternatives before the final decision is made between them (Fig. 2), and that the activity associated with those movements is modulated by estimates of likelihood (Cisek and Kalaska 2001). In summary, even within the neural systems for controlling arm movements, the functional organization does not appear to respect traditional distinctions between sensory, cognitive, and motor processes.

All of these considerations lead one to question the classical architecture that divides behavior into serial stages of perception, cognition, and action. Cognitive neuroscience inherits this architecture from cognitive psychology, a field which was deliberately developed in isolation from neural and physiological data. Furthermore, one may argue (Cisek 1999) that cognitive psychology was forced into embracing that serial architecture by its own roots in early philosophical thought which was strongly dominated by dualism. Given the historical heritage of cognitive psychology, we should be cautious when applying the resulting concepts to the interpretation of brain organization.

I propose that a much better foundation for biologically grounded theories of brain function can come from considerations of evolutionary history. The organization of the vertebrate nervous system has been strongly conserved throughout its phylogenetic history (Holland and Holland 1999; Katz and Harris-Warrick 1999), and even recently-elaborated structures such as the mammalian neocortex have homologues among non mammalian species (Butler and Hodos 1996; Medina and Reiner 2000). Although the idea that brain evolution consists of new structures being added on top of old structures (MacLean 1973) is still popular among non-specialists, it has been rejected by recent comparative neuroanatomical work (Butler and Hodos 1996; Deacon 1990). Brain evolution consists of the differentiation and specialization of existing structures and through shifts in existing axonal projection patterns, not through the addition of new structures. Indeed, the basic anatomical and functional organization of the primate brain reflects an ancient architecture which was well-established by the time of the earliest terrestrial tetrapods. It is safe to assume that this ancient architecture was not designed for cognitive understanding of the external world but for simple, situated interaction with the world. From that perspective, one is tempted to discard the view of behavior as a serial sequence of sensory representation, cognitive decision-making, and motor planning and execution. Instead, behavior may be viewed in terms of parallel processes that specify the potential actions currently made possible by the environment and processes that select of one of those actions for overt execution on the basis of its estimated behavioral payoff (Cisek 2001; Cisek and Turgeon 1999).

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