

Motor Planning

Aaron L. Wong, Adrian M. Haith and John W. Krakauer
Neuroscientist published online 30 June 2014
DOI: 10.1177/1073858414541484

The online version of this article can be found at:
<http://nro.sagepub.com/content/early/2014/06/30/1073858414541484>

Published by:



<http://www.sagepublications.com>

Additional services and information for *The Neuroscientist* can be found at:

Email Alerts: <http://nro.sagepub.com/cgi/alerts>

Subscriptions: <http://nro.sagepub.com/subscriptions>

Reprints: <http://www.sagepub.com/journalsReprints.nav>

Permissions: <http://www.sagepub.com/journalsPermissions.nav>

>> [OnlineFirst Version of Record](#) - Jun 30, 2014

[What is This?](#)

Motor Planning

Aaron L. Wong¹, Adrian M. Haith¹, and John W. Krakauer^{1,2}

The Neuroscientist
1–14
© The Author(s) 2014
Reprints and permissions:
sagepub.com/journalsPermissions.nav
DOI: 10.1177/1073858414541484
nro.sagepub.com



Abstract

Motor planning colloquially refers to any process related to the preparation of a movement that occurs during the reaction time prior to movement onset. However, this broad definition encompasses processes that are not strictly motor-related, such as decision-making about the identity of task-relevant stimuli in the environment. Furthermore, the assumption that all motor-planning processes require processing time, and can therefore be studied behaviorally by measuring changes in the reaction time, needs to be reexamined. In this review, we take a critical look at the processes leading from perception to action and suggest a definition of motor planning that encompasses only those processes necessary for a movement to be executed—that is, processes that are strictly movement related. These processes resolve the ambiguity inherent in an abstract goal by defining a specific movement to achieve it. We propose that the majority of processes that meet this definition can be completed nearly instantaneously, which means that motor planning itself in fact consumes only a small fraction of the reaction time.

Keywords

motor control, reaction time, decision making, optimal control theory, dynamical systems model, attention, motor goal

The time from stimulus onset to the initiation of a motor response—the reaction time (RT)—occurs on the order of 200 ms (e.g., Welford 1980). During this brief time, a series of processes unfold that enable the brain to perceive the surrounding environment, identify a particular object of interest, determine the required action in response to that object, and issue a motor command to implement the desired action. While clearly spanning the domains of perception and movement, it is challenging to define which of these planning processes involve perceptual decision making and which are motor (i.e., “motor planning”). Consider the simple case of reaching to touch a red target amidst a cluster of blue dots. Processing sensory information to identify the location of each dot and its color lies well within the domain of perceptual decision making, while the motor command to reach the target resides within the purview of the motor domain. However, should the attentional allocation to the red stimulus and its identification as the target of interest be part of the motor plan? Or does motor planning begin after that stage, when preparing the actual movement features (e.g., selecting the effector, trajectory shape, kinematics [i.e., the action], and dynamics)? Colloquially, motor planning can refer to any process related to the preparation of a movement that occurs during the RT, but this loose definition could include even the aforementioned detection of sensory information about objects in the environment. In addition, it is unclear which of these processes contribute significantly to the RT. Here we are

particularly concerned with the choice RT, as we are examining decision-making processes about the identity and location of the target and the desired movement to achieve the goal. This review seeks to establish a working definition of motor planning as the set of processes that begin at the juncture between perceptual decision making and movement-related decision-making. We conclude that motor planning, according to our definition, does not require significant amounts of RT; this will have implications for the interpretation of neural activity observed during movement preparation.

All actions revolve around a motor goal, which is an object, location, or motion pattern (e.g., a figure-eight shape) that is selected as the desired outcome of a movement (Passingham and Wise 2012). Recently, Wolpert and Landy (2012) argued that the control of movements is fundamentally about making decisions: deciding upon the motor goal, and deciding how to achieve it. Consistent with this, we have identified six critical processes involved in movement generation: three “what”

¹Department of Neurology, The Johns Hopkins University School of Medicine, Baltimore, MD, USA

²Department of Neuroscience, The Johns Hopkins University School of Medicine, Baltimore, MD, USA

Corresponding Author:

Aaron L. Wong, Johns Hopkins University School of Medicine, 600 North Wolfe Street, Pathology 210, Baltimore, MD 21287, USA.
Email: aaron.wong@jhu.edu

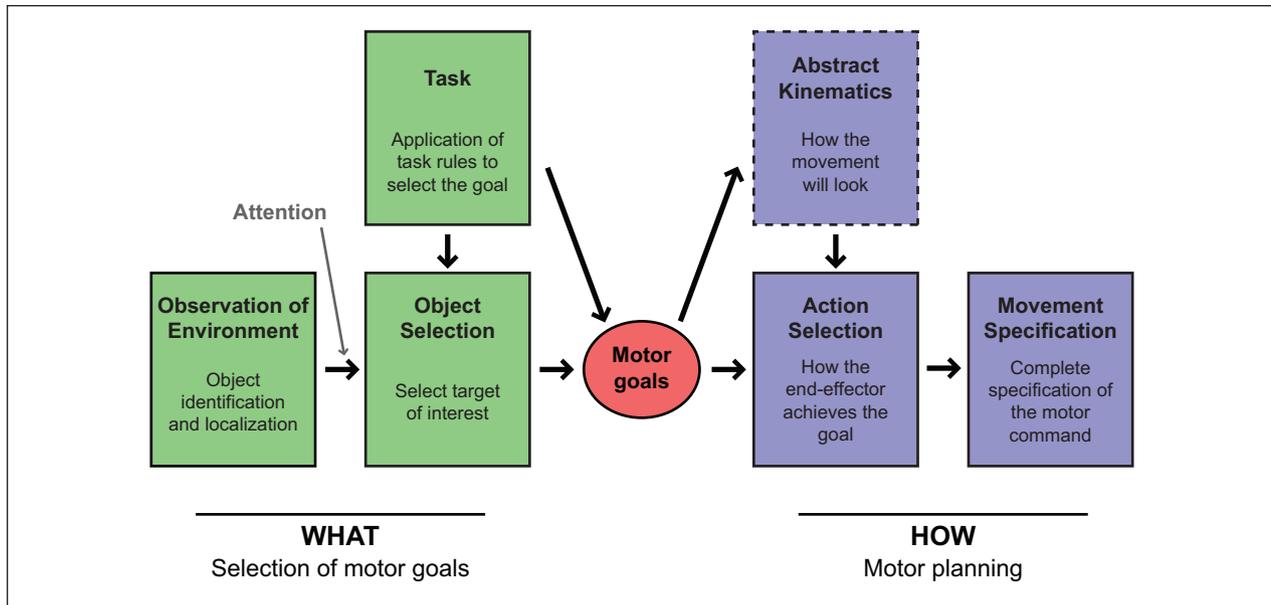


Figure 1. Processes along the pathway from perception to movement. The first of these processes is to observe the environment to identify all potential targets present. Of those targets, the one of interest (the most salient and/or task-relevant) must be selected (“what is the object of interest?”). This selection relies on the use of attention. Additional task rules or constraints (“what should be done to the object?”) may be combined with the identified target to create a motor goal. Once a motor goal has been established, motor planning processes define how the desired movement will be produced. For point-to-point reaches and saccadic eye movements, a motor goal may lead directly to selection of an action of the endpoint effector (“how will the motor goal be attained?,” which may be answered with “move the hand to the object location”). More complex movements may additionally require the specification of a particular trajectory, such as to draw an S-shape or to reach around an obstacle to acquire the target (“how will the overall movement look?”) before the appropriate action can be selected. This optional process contributes more abstract kinematic details that constrain action selection. Finally, the complete set of motor commands necessary to produce the desired movement can be generated (“how should the motor commands to the effector be specified to satisfy the motor goal?”). This framework thus establishes a clear definition of motor planning in the context of the pathway from perception to movement.

processes that together relate to establishment of the goal, and three “how” processes that describe the movement to achieve that goal (Fig. 1). Some of these processes may occur in parallel (see Cisek and Kalaska 2010), but for the organizational purposes of this review we will discuss these processes serially. Nevertheless, the motor goal lies at the boundary between the “what” and “how” processes, and therefore comprises a natural point at which to divide the perception–movement decision pathway. Only processes following the identification of a motor goal – that specifically pertain to describing the features of the movement – are included in our definition of motor planning. That is, motor planning is the set of processes that describe how a motor goal will be achieved.

Formation of Motor Goals: Defining “What”

Identification of a motor goal involves the perception of an object of interest and the determination of what is to be

done to that object. This process includes making decisions about the object’s location in the environment (which involves the deployment of attention), the application of task constraints (i.e., rules) to identify the motor goal, and the choice of whether to initiate the action (go/no-go or countermanding tasks, e.g., Hanes and Carpenter 1999). These perceptual decisions are necessary to produce a motor response, but are not strictly “motor” in that they define the goal rather than the action.

Attention

Following the acquisition of sensory information (observation of the environment, e.g., encompassing the pathway of visual information through occipital cortex and into parietal and temporal cortices), attention is required to select an object of interest to the exclusion of all other parts of the environment (object selection). The deployment of attention is a prerequisite for motor planning, suggested by the challenge of attending elsewhere other than the movement goal while the movement is being

prepared. For instance, subjects asked to discriminate a letter at a particular spatial location while making a saccade in a different direction exhibited a trade-off in performance: they either did well at the discrimination task but generated inaccurate saccades, or could make accurate saccades but had difficulty identifying the letters (Kowler and others 1995). Discrimination thresholds remain consistently better at the location of the saccade goal compared even to conditions in which that task only requires stimulus identification but no subsequent movement (Hoffman and Subramaniam 1995). Furthermore, highly salient distractors that draw attention away from the intended movement goal yield movements that are initially directed erroneously toward the distractor (Theeuwes and others 1998).

In contrast, attention may be deployed without invoking a subsequent orienting movement (i.e., covert attention). Bisley and Goldberg (2003) asked monkeys to make a saccade to a particular location in the context of a go/no-go task in which the orientation of a Landolt C indicated whether or not to perform the requested saccade. When the Landolt C appeared at the same location as the goal of the saccade, discrimination of the Landolt C was improved in a manner consistent with the deployment of attention to the saccade endpoint. However, if a distractor was flashed just prior to the appearance of the cue, the threshold of discrimination was transiently better at the location of the distractor even though the goal of the saccade had not overtly changed. These attentional effects are supported by neural recordings in the lateral intraparietal area (LIP), a region thought to contain a salience map for spatial attention (although others have argued for its role in motor intention instead; for review, see Snyder and others 2000). Notably, during an anti-saccade task, neural activity in LIP reflects the location of the visual target rather than the saccade endpoint even at the time of movement onset (Gottlieb and Goldberg 1999). Thus, attention facilitates the generation of priority maps to describe objects of interest in the environment, aiding in the selection of motor goals.

Decision-making

For simple tasks (e.g., “reach to the target”), the object of interest is the motor goal. More involved tasks, however, may require a decision about which goal to select (e.g., reach to the right or left target) depending on the stimulus appearing at the location of interest. Careful and prolonged observation of the environment at the attended location is necessary when the stimulus is challenging to identify: for example, if the luminance lies at the limit of the detection threshold. Such decision-making processes that slowly accumulate evidence about the nature of the stimulus are formalized in the drift-diffusion model

(Laming 1968; Ratcliff 1978). In this model, evidence in favor of a particular goal gradually accrues as a random walk until it surpasses a threshold, at which time a goal is selected and a movement is generated (Fig. 2A). When more than one goal is possible (or when a countermanding signal appears), evidence in favor of each alternative is accumulated. These diffusion processes “race” against each other until one of them reaches a threshold, at which point the outcome (i.e., the motor goal) is determined by the winning process (Bogacz and others 2006; Ratcliff and McKoon 2008). Evidence that continues to accumulate after movement onset, however, occasionally leads to a mid-movement change of mind (Resulaj and others 2009; Fig. 2).

Drift-diffusion models have prompted a search for neural evidence of a signal that gradually accumulates prior to movement onset, typically during an enforced delay period (Hanes and Schall 1996; Shadlen and Newsome 2001). Gold and Shadlen (2000) located a signature of such a signal for saccadic eye movements in the frontal eye fields (FEFs). Using a motion-discrimination task, monkeys had to detect the direction of net motion in a random dot kinematogram (in which the coherence of motion of a field of moving dots can be varied) and make a saccade in that direction. Stimulation of FEF evoked a movement whose direction was biased in magnitude proportional to the certainty with which the direction of the random dot kinematogram could be ascertained. Thus, taken at face value, neural activity in FEF reflects a decision about a motor goal to guide upcoming actions.

In contrast, these results have also been interpreted as suggesting that there is no separate perceptual decision-making process and that the formulation of motor goals is synonymous with motor planning (Schall 2000). This conclusion is based on the assumption that FEF is analogous to primary motor cortex (M1) in terms of its function for saccadic eye movements, an argument based on its cytoarchitecture (Stanton and others 1989) and the ability to stimulate movements at low latency with relatively low electrical currents (Robinson and Fuchs 1969). However, FEF is not necessary for saccade generation: FEF inactivation only disrupts saccades for which the motor goal must be represented independently of a visual target (e.g., a memory-guided saccade; Sommer and Tehovnik 1997). Since this signal in FEF is not required for all saccadic movements, FEF is unlikely to be strictly a motor area. Neural activity in FEF is therefore unlikely to represent motor planning.

FEF instead appears to be associated with specifying motor goals rather than planning. To understand why this is the case, it is important to first note that FEF is not the only brain region in which the neural signature of an evidence-accumulation process can be found. Such signals can also be observed upstream in LIP (Shadlen and

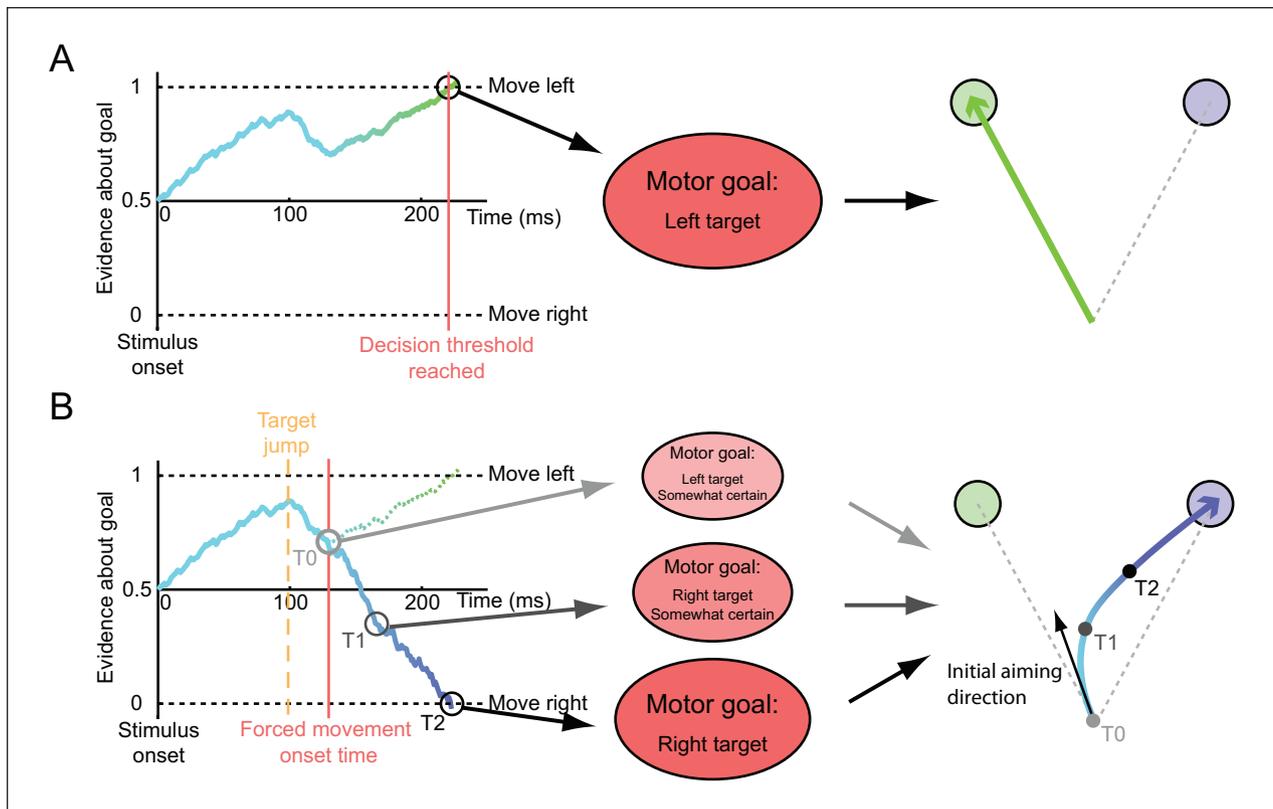


Figure 2. Drift-diffusion model. (A) When a choice about which of two (or more) goals is required based on observation of the environment, evidence in favor of each alternative may be accumulated across time until a threshold is reached. The accumulation of evidence is typically modeled as a random walk, assuming that perception of the sensory information about the environment is noisy and subject to uncertainty. The threshold defines the choice of the motor goal (e.g., to which target the movement should be directed), which in turn is translated via motor planning into a corresponding movement. (B) When the location of the target changes suddenly during the reaction time, evidence begins to accumulate in favor of the alternative movement choice. Under typical circumstances, this often leads to a prolonged reaction time as sufficient evidence must accumulate in favor of the alternative choice. If, however, subjects are forced to move before they are ready, they are likely to choose an initial movement direction that is in line with their certainty about the location of the target at the time of movement initiation (Huberdeau and others 2012). That is, at time T_0 , the subject is somewhat certain that the target is still to the left, and will start to reach leftward although the aiming direction may be intermediate between the two targets (reflecting uncertainty). As time evolves and more evidence in favor of the rightward target is accumulated, the certainty about the motor goal being to the right increases and likewise the subject begins to aim farther to the right, leading to a change-of-mind (Resulaj and others 2009). This change in the online aiming direction is analogous to a situation where the subject simply begins moving at a later time; more evidence in favor of the rightward target being present will lead to a reach that is directed more rightward.

Newsome 2001), where they do not reflect the identity of the upcoming action (Bennur and Gold 2011) but the outcome and certainty of a perceptual decision about the observed visual stimulus (e.g., a decision about the direction of the random-dot kinematogram; Kiani and Shadlen 2009). Additional evidence-accumulation signals can be found downstream of FEF such as in superior colliculus, where neural activity increases to a consistent threshold at which the action outcome is chosen (Ratcliff and others 2003). The dispersion of such neural signatures throughout the brain suggests that downstream brain regions may simply reflect in a near-instantaneous manner the current state of an ongoing decision process

occurring upstream (Selen and others 2012). This might allow movements to be completed immediately once the time-consuming perceptual decision-making processes have finished because motor planning has been occurring concomitantly (Cisek and Kalaska 2010). Alternatively, rather than positing that motor areas are performing time-consuming planning computations in parallel with upstream decision processes, the current state of any perceptual decision might be immediately translated via an RT-inexpensive process into a motor plan for action (Huberdeau and others 2012). Either hypothesis could explain why subjects forced to initiate a movement early (e.g., via the application of a startle

stimulus) make movements that are kinematically identical to those generated with normal reaction times (Carlsen and others 2004; Valls-Sole and others 1999).

Of all the brain regions exhibiting evidence-accumulation activity akin to a drift-diffusion model, only FEF clearly represents the transition from decisions about the stimulus to decisions about the motor action. Neural activity in FEF initially represents several alternative target choices and task-relevant stimulus features, but evolves over time to reflect only the final motor goal (Mante and others 2013; Thompson and others 1996). Gold and Shadlen (2003) used the anti-saccade task in conjunction with their random-dot kinematogram paradigm to argue that this activity indeed represents the selection of the motor goal. FEF stimulation evoked saccades whose direction was biased toward the direction of the anti-saccade, not the location of the visual stimulus; in contrast, attention-related neural activity upstream in LIP reflects the visual stimulus rather than the motor endpoint (Gottlieb and Goldberg 1999). Thus, FEF appears to be a site in which information about the attentionally selected object of interest is transformed—via the application of appropriate task rules—into a goal about the desired location to which a movement should be directed; that is, FEF activity represents the culmination of RT-consuming processes spanning perception of the environment to selection of a motor goal.

Task rules and cognitive influences

Critical to the formation of a motor goal is the application of appropriate task rules. These rules are generally thought to be encoded by prefrontal cortex (PFC; Milner 1963; Wallis and others 2001), and may include any of a wide subset of decisions including which of several potential targets is the object of interest and how features of the selected object translate into the appropriate motor response. PFC represents the association between a specific cue and the goal it indicates (Asaad and others 1998); for example, this association is useful for knowing that Object A indicates a saccade to a rightward target and Object B indicates a saccade to a leftward target. Neuronal activity modulated only when Object A indicated a rightward saccade, as compared with when that same object encoded a leftward saccade or when Object B was used to indicate the same rightward saccade. This implies that PFC encodes the relationship between objects and the goals they specify according to arbitrary task rules. Similarly, PFC may determine whether to proceed with or to inhibit a response to a cued goal, such as during a go/no-go task (Watanabe 1986), as well as describe overall task structure such as to encode the identity and order of a sequence of successive movements (Mushiake and others 2006). These types of high-order decisions are useful in defining a motor goal.

That the selection of motor goals is fundamentally a decision-making process is indicated by the extent to which cognitive processes may bias the outcome of such choices. For example, the observation of a sensory stimulus can facilitate performance of a movement acting on an unrelated but qualitatively similar object. Such sensory priming causes a prior observation of a rectangle to reduce the time required to initiate a grasp of an object oriented in the same manner as the rectangle, in contrast to objects positioned in other orientations (Craighero and others 1996). Goal selection can also be affected by more abstract representations. Song and Nakayama (2008) showed that selecting the location of a motor goal can be influenced by the spatial representation of numeric values on a number line. In that study, subjects determined if a displayed number was greater than, less than, or equal to the number five, and responded by reaching to the right, left, or center target respectively. As numbers approached the value of five, reach trajectories became curved toward the center target, suggesting that the “closeness” of numerical values can introduce a competition between two potential motor goals (e.g., between the leftward target implying “less than five” and the central target implying “equals five”), whose likelihood of being the correct choice become more equal as the numerical value approaches five. Similarly, risk aversion modifies the selection of a goal location; subjects reaching toward an area of high reward located near an area of high risk tended to choose a motor goal that biases their movement endpoints away from the penalty region, seeking to maximize the expected reward across a block of trials even if this increased the number of times they missed the target (Trommershauser and others 2003). Thus, the selection of an (abstract) movement goal arises as the result of a computationally intensive, non-motor (cognitive) decision-making process.

Surprisingly, this decision-making process may even take account of the relative execution difficulty of potential movements, such that motor goals are preferentially selected when the required movement to achieve that goal is biomechanically easier to make (Cos and others 2011). That is, subjects opt to reach to the target for which the required movement path is most closely aligned with the major axis of an ellipse representing the direction of greatest arm mobility (based on joint angles and mass distributions of the arm) and admittance (based on elastic properties of the arm; Hogan 1985a, 1985b). However, this decision does not necessarily require simulation of motor commands to each potential target; instead, such choices could be made with only a general knowledge of which directions are “easier” to reach. This is akin to the way in which a plunger will be grasped lower on the handle when being moved to a higher shelf such that the arm remains in a relatively comfortable position at the

conclusion of the movement (end-state comfort; Rosenbaum and others 1990). It is unlikely that every movement trajectory is evaluated to determine the best grasp location; instead, a general rule (e.g., “grasp the object near the bottom when moving it higher”) is sufficient to determine a reasonable location to grasp. Thus, although such factors as “comfort” and “ease” can influence the selection of a motor goal, this may well occur through the application of implicit task rules rather than requiring a specification about how an action will be generated to achieve that goal—decisions that lie in the domain of motor planning.

Realization of Motor Goals: Motor Planning and Defining “How”

Under typical circumstances, the formulation of a motor goal is critical to gate the onset of motor planning. During motor planning, the specific movement to achieve that goal must then be defined via further processes. These “how” processes are characterized as processes that reduce ambiguity about how the motor goal will be achieved by specifying all remaining details of the movement (e.g., its speed or trajectory). While some of these movement features can be constrained by task goals (e.g., a constraint to move at approximately a certain speed), the precise specification of these movement parameters (e.g., the velocity profile of the entire movement) ultimately resides in the domain of motor planning. That is, motor planning translates the abstract concept of a motor goal into a concrete course of action. Consistent with this view, neural activity in motor cortex increases only following the observation of the first meaningful visual stimulus from which a motor goal can be determined, even if there are additional stimuli presented before or after the informative one (di Pellegrino and Wise 1993). Furthermore, Boussaoud and others (1993) demonstrated that when a series of targets are presented that each provide partial information about the goal (e.g., the target location, then the required action), motor cortex may respond only to the final stimulus that finishes instructing the subject about the motor goal. Although it is clear, then, that motor planning involves processes downstream of the formation of a motor goal, identifying and defining these processes is more challenging.

We propose that the specification of “how” is divided into three processes, one of which may be optional depending on the complexity of the required action. This optional process is quite high-level, and involves decisions about the shape of the trajectory to be produced in an effector-independent manner (abstract kinematics). The other two processes are necessary for motor planning. The first of these is action selection, which involves the choice and a description of the motion of the

end-effector. The end-effector could be a body part, such as the hand or the eye, but it may also include the end-point of a tool; in observing the movements of experienced blacksmiths, Bernstein (1967) noted that the trajectory of the head of the hammer was much more consistently controlled from one movement to the next compared with the variability observed in the joint angles of the arm. Thus, selection of the endpoint effector action is likely separate from the last process, movement specification, when the complete motor command of the limb and any necessary postural adjustments are determined. The distinction between action selection and movement specification is supported by comparing neural activity in ventral premotor cortex (PMv) to that observed in dorsal premotor cortex (PMd) and M1. For movements with identical hand paths but different arm or wrist postures, only neural activity in PMd and M1 modulated with changes in posture (Takei and others 1999, 2001; Scott and Kalaska 1997). PMv activity instead appeared to reflect a more abstract plan that was independent of arm posture. However, even neural activity in M1 does not strictly encode the muscle activity required by each posture; instead, some neurons in M1 consistently represent the common hand path in extrinsic space.

Control Policies

Together, action selection and movement specification rapidly translate a motor goal into a desired movement. In recent years, this has been proposed to occur via the generation or application of a flexible feedback control policy, which determines the complete movement trajectory given the current state of the limb, the desired endpoint (e.g., the motor goal), and a cost associated with the distance between the effector and the endpoint (optimal feedback control [OFC]; Todorov and Jordan 2002). The existence of such a control policy may be argued for by considering tasks in which the motor goal involves reaching to an object while avoiding obstacles. One way to accomplish this task is to plan a curved trajectory that specifies how that obstacle will be circumnavigated (e.g., the arm will pass to the right of the object). However, under conditions in which a sudden and unexpected perturbation during the movement requires rapid compensatory movements, evidence suggests that subjects do not make corrections that will return them to their initial movement path; subjects instead follow a new trajectory that allows them to directly acquire the motor goal from their displaced position (Nashed and others 2012, 2014). The rapid switching between different trajectories suggest that subjects do not generate a new plan. Rather, subjects apply a single control policy that guides the hand either leftward or rightward given its perturbed position. Such control policies may even be cached for rapid reuse

as they can be flexibly reapplied to specify movements to different targets (Liu and Todorov 2007), allowing motor planning to require essentially no computations but instead occur almost as a reflexive response to the motor goal. OFC and similar hypotheses thus concisely explain the production of point-to-point reaches without needing to invoke the concept of a preplanned desired trajectory. Instead, only an abstract motor goal (such as to minimize endpoint error) is necessary.

Using this motor goal, the control policy may be determined by optimizing a combination of accuracy, effort, and time (Haith and others 2012; Shadmehr and others 2010). Control policies do not explicitly specify movement variables such as peak velocity; instead, these kinematics arise indirectly as motor commands are issued according to the control policy. Indeed, pre-cuing a subset of the required parameters of a movement prior to target onset does not change the RT (Goodman and Kelso 1980), suggesting that these parameters are either not explicitly specified or can be specified in very little time. On the other hand, it is possible to intentionally modulate the relative speed of a movement (“faster” or “slower”; Georgopoulos 1986), at least within the limitations specified by the trade-off between movement speed and accuracy (Fitts 1954). While relative speed may be selected as part of the formation of a motor goal, decisions about the complete velocity profile of the limb throughout the course of the movement lie in the purview of motor planning, as mentioned above. That is, action selection and movement specification transform an abstract movement trajectory or a motor goal into a properly scaled and dynamically reasonable movement path (or at least a feedback control policy that implicitly defines one; Fig. 3).

Neural Correlates of Motor Planning

As motor cortex is thought to be the brain region in which motor planning (and movement execution) occurs, much effort has been made to identify neural activity that correlates with the impending movement. Neural activity observed prior to movement onset correlates with movement direction and extent (Alexander and Crutcher 1990; Kurata 1993; Riehle and Requin 1989), speed (Churchland and others 2006a), and curvature (Hoehnerman and Wise 1991). However, the presence of such pre-movement activity in the same regions of motor cortex that directly drive movements, namely PMd and M1, poses a puzzling question: what determines when neural activity in these areas produces a motor response? Initially, it was proposed that planning activity is simply maintained at sub-threshold levels to prevent sending signals downstream. Pre-movement activity is not merely a scaled version of the activity present during movement, however, but instead encodes something qualitatively distinct: not even

a neuron’s preferred movement direction remains constant between the pre-movement and peri-movement periods (Churchland and others 2010; Crammond and Kalaska 2000; Johnson and others 1999). Another proposed explanation is that inhibitory neurons provide a gating mechanism to control the outflow of neural activity to downstream brain regions, but the activity of inhibitory interneurons has been shown to not differ qualitatively between pre-movement and peri-movement activity (Kaufman and others 2013). Hence, an inhibitory gating mechanism is also unlikely.

Instead, Kaufman and others (2013) proposed viewing neural activity across the population as a high-dimensional firing-rate space in which each axis represents the activity of one neuron. In this framework, it is possible to observe that neural activity during motor planning is regulated such that the net population activity remains constant, or at least is constrained to reside only within a specific subset (the “null space”) of that high-dimensional space. In contrast, neural activity extends into many additional dimensions of the firing-rate space during the movement; these excursions from the null space drive muscle activity. Activity in the null space may thus support motor planning by selecting an appropriate position in the high-dimensional space from which the desired motor response unfolds; decomposing the firing-rate space in this manner allows motor planning and execution to reside together in motor cortex.

The existence of a null firing-rate subspace can explain why pre-movement neural activity correlates with parameters of the upcoming movement. Interestingly, the mechanism through which this activity may then be translated into a movement provides an insightful proposal as to how control policies may be implemented by the motor system. A control policy, once planned, guides all future dynamics of a movement by instantaneously issuing the appropriate motor command given the current state of the limb; this instantaneous command may be represented by the current state of motor cortex outside of the null space. Hence, movement of the locus of neural activity through the high-dimensional firing-rate space reflects the changing motor commands issued according to updates by the control policy. Shenoy and others (2013), in observing how consistently the neural activity moves through the firing-rate space across a series of repeated movements, hypothesized that motor cortex should therefore be viewed as a dynamical system for issuing motor commands (dynamical systems model [DSM]), with population-level neural activity reflecting the current state of this system. Since dynamical systems are deterministic and have inherent passive dynamics (i.e., they can evolve over time without requiring continuous external inputs), their initial state largely dictates the state of the system (e.g., the motor command sent to the muscles) for some

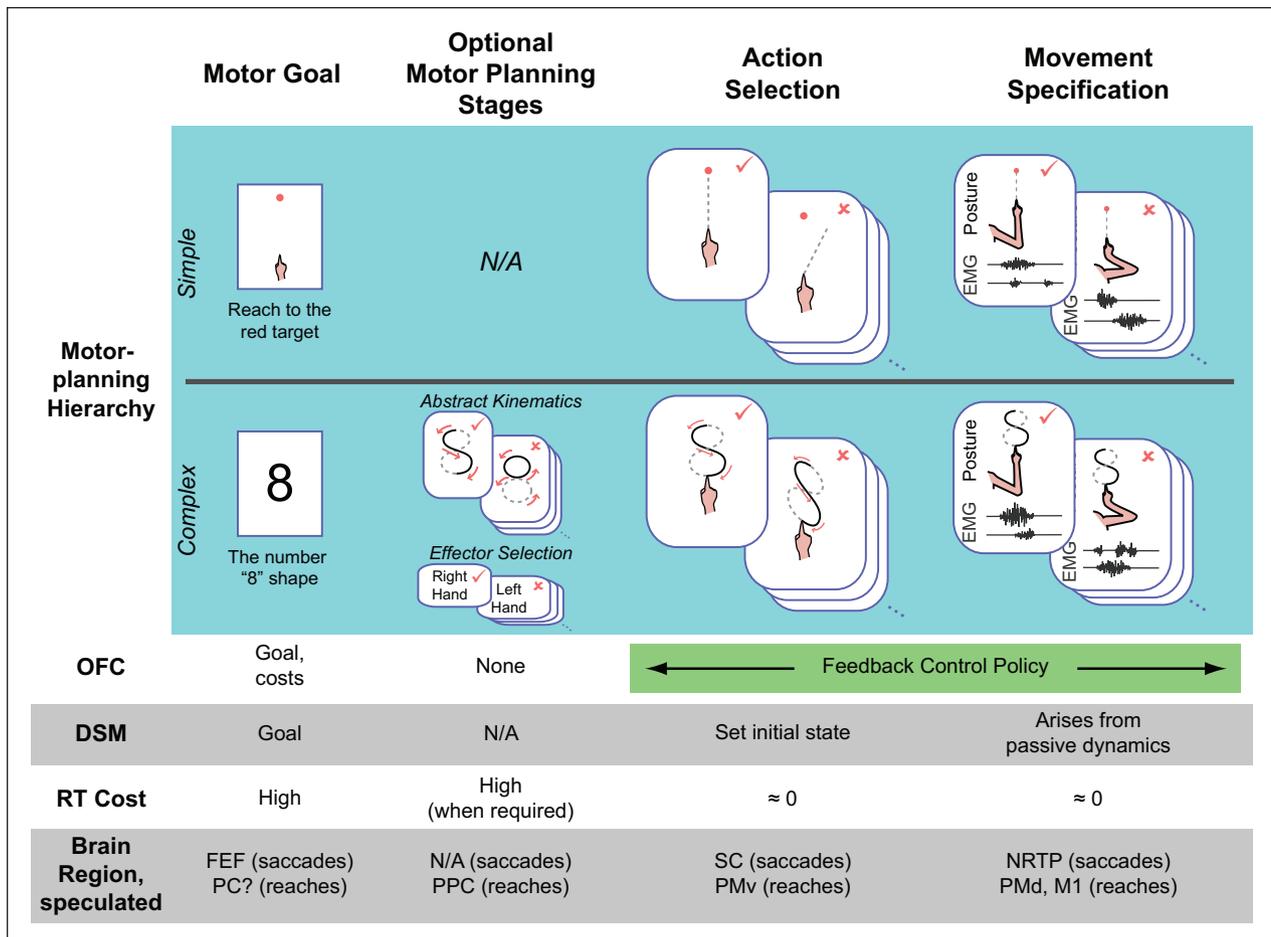


Figure 3. Illustration of the processes involved in motor planning using the hierarchical framework presented in Figure 1, for the example of making a point-to-point reach to a target (simple movement) or writing the number “8” (complex movement). For a simple movement, no additional processes are required, in particular abstract kinematic planning is unnecessary and the movement trajectory arises as a consequence of the control policy. Furthermore, action selection is seemingly trivial but becomes relevant under conditions in which a visual-to-motor mapping (e.g., a visuomotor rotation) is applied, as in motor adaptation paradigms in which the visual workspace has been rotated such that to hit the target, subjects must actually reach at an angle with respect to the target. In contrast, when writing a letter 8, it is necessary to invoke additional cognitive planning processes, such as an abstract kinematic representation in which the desired trajectory of the movement is planned in extrinsic space, as well as a choice of the end-effector of the movement. Action selection then involves an understanding of how the end-effector will move along the desired trajectory. In both cases, movement specification encodes the actual motor commands of the entire limb (and the choice of the appropriate limb posture) that will allow the subject to achieve the motor goal. In the table below, we consider how the optimal feedback control (OFC) model and dynamical systems model (DSM) relate to our proposed framework (see text for details), as well as the anticipated reaction time (RT) costs associated with each process. Finally, we speculate as to the possible brain regions that may be responsible for housing each of these processes, noting that because saccades are point-to-point movements, they necessarily do not require abstract kinematic planning (although certainly additional processes are required to complete saccade planning, such as to satisfy Listing’s law for maintaining appropriate ocular torsion).

time in the future. Neural activity during the RT represents the process of setting the initial state of the system (Churchland and others 2012), and hence indirectly correlates with the movement kinematics that are controlled by the passive system dynamics.

Earlier, we cited evidence for the idea that motor planning occurs as soon as the motor goal is identified, and that this motor plan is reflected in the state of motor

cortex. However, Ames and others (2014) have more recently demonstrated that the neural state in which the system appears to reside during a delay period (i.e., “preparatory” activity) did not need to be attained in order to execute a particular movement. Instead, only the neural state just prior to movement onset (i.e., the initial state of the dynamical system) was required. For example, if the target is switched from left to right at the time of the go

cue, neural activity across the population evolves directly from the leftward preparatory state it reached during the delay period to the rightward initial-movement state without first passing through the corresponding rightward preparatory state (Ames and others 2014). Additionally, if there is no delay period, activity evolves directly to the initial movement state, again bypassing the preparatory delay-period state. Delay-period activity is instead likely to largely reflect inhibitory suppression activity. Therefore, perhaps only neural activity after the go cue—and the decision to initiate a movement—is critical to produce the desired movement and reflects true motor planning processes. In fact, following the go signal there is still a significant RT delay of about 280 ms prior to movement onset; preparatory activity during the delay period only reduces the RT by 30 ms (Churchland and others 2006b). This remaining RT may include the time required for additional perceptual decision-making processes not completed during the delay period (e.g., detection of the go signal) and subsequent motor planning. In agreement with this view, Crammond and Kalaska (2000) observed that while some neural activity occurs just after the appearance of movement instructions (e.g., formulating a motor goal), other patterns of neural activity consistently occur only after the go cue.

Motor Planning and the Reaction Time

Although the RT period is quite long even after a delay period, motor planning appears to consume only a very small fraction of this time. Perfiliev and others (2010) proposed that point-to-point movements are generated simply by selecting and activating an appropriate control policy from an existing preplanned repertoire in a reflex-like fashion, avoiding the need to prepare a new motor command for each movement. They found that the trajectory of the hand, and even the choice of which hand to use, may be decided extremely rapidly in response to a highly salient target (e.g., a rapidly-moving ball to be intercepted). As a result, a movement could be initiated with an RT on the order of 160 ms, which is 90 ms shorter than a movement requiring rule-based cognitive decisions about how to select the hand with which to catch the ball. Additionally, movements that are kinematically identical to voluntary movements can be evoked at low RTs through startle (Carlsen and others 2004; Valls-Sole and others 1999). Such short reaction times are on the same order as the latencies with which transcortical reflex loops can initiate goal-directed feedback corrections (Pruszynski and others 2011), arguing that these feedback loops may mediate the initiation of movements at low RTs. Such reflex loops could thus serve as a mechanism through which cached feedback control policies are stored and implemented. This is analogous to the manner

in which a saccade goal, once identified in cerebral cortex, leads to a rapid cascade of processing stages in the brainstem (extending from superior colliculus to burst-generator circuits) to yield an eye movement (Leigh and Zee 2006).

These observations lead to the surprising conclusion that motor planning, for the most part, only consumes a small portion of the total RT. Given that stimulation of M1 can evoke quite complex goal-directed movements (Graziano and others 2002), motor planning may simply be the act of selecting one of many movements (or control policies) from an existing repertoire to achieve a desired goal. In the OFC framework, small RT demands can be explained by the fact that a single control policy can be reused to produce many different movements, even if the motor goal is updated mid-movement or the effector is perturbed (Nashed and others 2014). This avoids a large RT cost for recomputing a control policy prior to each movement. In the DSM framework, small RT demands are a byproduct of allowing the system to passively evolve to more complex movement states.

Note that the DSM hypothesis, as well as the more general OFC view, does not distinguish between the last two processes of motor planning (Fig. 3). The DSM hypothesis assumes that complete motor commands of the limb are a consequence of the initial state of the dynamical system. Similarly, although OFC hypotheses typically describe feedback control policies in terms of kinematics of the end-effector (i.e., action selection), it is simple to expand the control policy to include the complete motor command of the limb (encompassing both action selection and movement specification). Thus, although there is neural evidence in favor of a separation of these two processes, they are often treated as a single continuous process because action selection and movement specification must both occur during motor planning.

Abstract Kinematic Planning

Under certain circumstances, an additional motor-planning process is required: specification of the abstract kinematics of a movement trajectory. The necessity of such a process is encompassed by the notion of “motor equivalence” (Lashley 1930; see also, Cisek 2005), or the ability to achieve a motor goal in multiple ways because it is represented in a manner independent of any execution-specific parameters such as which arm to use or what type of grasp (e.g., precision or power grip) to apply. A classic example of motor equivalence occurs in writing, in which the characteristic shape and style of a particular letter is effector-invariant: For example, for any individual, the number “8” looks the same whether it is written with the index finger or with the foot (Wing 2000), and

regardless of the scale at which it is written (Kadmon Harpaz and others 2014). This sameness arises from two sources (Fig. 3). The first is the identity of the character itself: the motor goal is to write the glyph of the number eight, which has a particular shape. The second is an abstract representation of the desired movement trajectory required to produce that shape; for example, whether to draw the number using one continuous line, or as a pair of tangent circles. Both movement trajectories are reasonable, commonly employed, and result in achievement of the same motor goal; nevertheless, individuals must make a choice of movement trajectories. Hence, abstract kinematics can serve as a necessary ambiguity-reducing motor-planning decision, although for point-to-point movements it is not required. As this process is likely to be cognitively demanding, it also consumes a significant fraction of the RT unlike action selection and movement specification. Nevertheless, since it resolves a decision about how to achieve the motor goal and moves one step closer to production of the desired movement, this process arguably meets the definition of a motor-planning process.

Inclusion of an abstract desired trajectory in a motor plan is strongly supported by the work of Albert and Ivry (2009), who examined bimanual interference when simultaneously drawing three-sided squares (e.g., a U and a C) with the left and right hand. When the shapes to be drawn were incongruous, subjects found this task challenging. Two things made it simpler: drawing congruous (identical or mirror-image) shapes, and direct cuing such that subjects simply needed to trace the incongruous shapes (akin to Diedrichsen and others 2001). The difficulty of this task therefore lies not at the level of executing two incongruent movement patterns, but in the computational burden of simultaneously representing two distinct abstract motor plans. Abstract trajectory representations also seem necessary to perform other tasks, such as when verbally instructing an individual to generate a movement with a particular characteristic shape. To draw a figure-eight in the air with a fingertip, for example, the required movement trajectory—which is not prompted by the perception of any direct spatial cues—must be represented somewhere in the motor plan to guide its execution. That is, an understanding of how a movement should “look” may be what enables us to immediately perform quite complex actions when given verbal instruction.

A priming effect can be observed for the planning of movement paths, which is thought to reflect the reapplication of an “abstract spatiotemporal form” from one movement to the next (Cohen and Rosenbaum 2004). If on a previous trial the hand moved in a circuitous path to avoid an obstacle, the hand will continue to make gross excursions from a straight-line movement path even after the obstacle is removed (Jax and Rosenbaum 2007) or

when the hand moves to a different target (van der Wel and others 2007). Such priming effects argue that the formulation of abstract kinematic trajectories is a resource-intensive (and RT-consuming) process since priming reduces the computational load associated with formulating new movement trajectories, allowing for faster movement responses. As a consequence, however, occasionally an unnecessarily curved movement trajectory is applied to a task that could easily have been completed using a simpler point-to-point movement.

The representation of abstract trajectories has been suggested to reside in posterior parietal cortex alongside the regions involved in attention (or motor intention). Activity in these regions not only correlates with the intended motor goal, but also with the actual movement path the arm will take (Torres and others 2013). We propose that a curious example of trajectory planning in the parietal cortex can be demonstrated in patients with ideomotor apraxia, who often have a lesion in the left parietal lobe. Although point-to-point movements are generally unimpaired, suggesting a lack of perceptual or execution deficits per se (Ietswaart and others 2006; Mutha and others 2006; Sunderland and Sluman 2000), these patients have difficulty producing complex movement gestures made by imitation or to verbal command (Hermsdorfer and others 1996; Sunderland and Sluman 2000), or demonstrating the use of tools either by pantomiming their function or by selecting an alternative tool that can achieve the same purpose (e.g., using the handle end of a screwdriver to hammer a nail; Goldenberg and Hagmann 1998; Heilman and others 1997). A possible explanation for this puzzling condition is that patients with apraxia have difficulty planning the abstract trajectories necessary to bring about the desired movement outcome with the limb or a tool. Hence, although abstract kinematic planning is not required for point-to-point movements (especially according to the OFC view of the existence of a control policy), under certain conditions such a planning process is critical to resolving abstract motor goals into specific motor actions.

As the abstract kinematics process exemplifies, any movement parameters not explicitly specified by task constraints in the motor goal need to be resolved during motor planning. While the majority of these are specified through the course of action selection and movement specification (e.g., movement speed), others may require an additional planning processes (Fig. 3). For instance, the vast majority of movement tasks generally constrain the choice of effector (e.g., reaches are typically performed with the dominant hand). However when given a choice, selection of the appropriate effector may comprise an additional RT-intensive cognitive decision that contributes to motor planning. Subjects who were allowed to reach to a target with either hand generally selected the hand closest to the target; when the target was placed in an ambiguous

location (e.g., equally distant from either arm), subjects tended to use either hand with equal probability and this hand-selection process required a longer RT (Oliveira and others 2010; but under certain circumstances effector choice may also occur quite reflexively, see Perfiliev and others 2010). Hand preference to these ambiguous targets could be biased by reward history, such that subjects used the arm that successfully acquired the target more often, and would change their preference as this reward probability was artificially manipulated (Stoloff and others 2011). Hence effector selection, like the planning of abstract kinematic trajectories, exemplifies an RT-consuming but optional phase of motor planning.

Motor Planning and the Reaction Time

In this section, we have described the processes of goal selection and motor planning as being strictly serial (e.g., a motor command can only be formed after selection of the motor goal is complete). In fact, it may not be true that such a strict sequence is necessary: for example, a movement may still be produced even if the motor goal has not been fully specified. Subjects who are made to initiate movements early still produce a movement in roughly the appropriate direction even if it is less accurate or its trajectory falls partway between the locations of potential targets (Ghez and others 1997; Hening and others 1988). These intermediate movements have been taken as a signature of disrupted motor planning. Specifically, multiple potential actions to be selected are thought to interfere with one another, leading to an errant intermediate movement. Huberdeau and others (2012) have argued that an intermediate movement instead represents a deliberate action choice that serves to increase the time available to decide on the motor goal. They used a paradigm in which subjects had to initiate their movement at a fixed time relative to the onset of a target. Occasionally, the location of the target jumped just prior to movement, requiring rapid replanning. The authors found that intermediate movements could be eliminated when the targets were widely separated or were discouraged by a virtual barrier; intermediate movements only occurred when initiating a movement midway between the two targets was a beneficial strategy. According to an optimal control model, the initial movement direction should be biased by the certainty with which the target location is known at movement onset. Intermediate movements may thus reflect the current state of an evolving decision-making process regarding the true location of the target (Fig. 2B). According to this hypothesis motor planning is instantaneous, and is continuously updated according to the likelihood of each motor goal and the relative benefit that intermediate movements offer. Thus, while motor planning is an important and

necessary step in the translation of perceptual decisions into movements, the RT predominantly reflects time-consuming perceptual decision-making processes supporting the formation of motor goals and abstract kinematic movement trajectories.

Conclusion

The generation of a movement involves a set of interacting processes that transform the sensation of the environment into an appropriate motor response. Here, we provide a framework with which to operationally parse this process of movement generation into perceptual and motor domains. Three major processes reside firmly in the domain of sensory perceptual decision making and are concerned with identifying the goal of the movement through the selection of an appropriate object in the environment (via attention) and the application of task rules about what to do to that object (e.g., generate an anti-saccade). These processes can be summarized as decision-making steps concerning what the movement should achieve (i.e., they define the motor goal), and consume the majority of the RT. The remaining three processes (abstract kinematic representation, action selection, and movement specification) can be appropriately termed motor planning in that they determine how the motor goal will be achieved—they reduce the ambiguity of the motor goal into a specific desired course of action. Motor planning involves specification of the movement trajectory for the desired action, a description of how the end-effector will produce such an action, and finally a description of the full set of the joint trajectories or muscle activations required to execute the movement. The only RT-expensive portion of motor planning is abstract kinematics, which is unnecessary for many tasks. In contrast, the majority of motor planning is made up of RT-minimal processes such as the use of previously cached control policies or the setting of the initial state of a dynamical system from whose passive dynamics a movement is generated. Together, these six processes form a single unifying framework to describe the pathway from perception to movement.

Acknowledgments

We thank Jing Xu for her helpful comments.

Declaration of Conflicting Interests

The author(s) declared no potential conflicts of interest with respect to the research, authorship, and/or publication of this article.

Funding

The author(s) received no financial support for the research, authorship, and/or publication of this article.

References

- Albert NB, Ivry RB. 2009. The persistence of spatial interference after extended training in a bimanual drawing task. *Cortex* 45(3):377–85.
- Alexander GE, Crutcher MD. 1990. Preparation for movement: neural representations of intended direction in three motor areas of the monkey. *J Neurophysiol* 64(1):133–50.
- Ames KC, Ryu SI, Shenoy KV. 2014. Neural dynamics of reaching following incorrect or absent motor preparation. *Neuron* 81(2):438–51.
- Asaad WF, Rainer G, Miller EK. 1998. Neural activity in the primate prefrontal cortex during associative learning. *Neuron* 21(6):1399–407.
- Bennur S, Gold JI. 2011. Distinct representations of a perceptual decision and the associated oculomotor plan in the monkey lateral intraparietal area. *J Neurosci* 31(3):913–21.
- Bernstein NA. 1967. *The coordination and regulation of movements*. Oxford, England: Pergamon Press.
- Bisley JW, Goldberg ME. 2003. Neuronal activity in the lateral intraparietal area and spatial attention. *Science* 299(5603):81–6.
- Bogacz R, Brown E, Moehlis J, Holmes P, Cohen JD. 2006. The physics of optimal decision making: a formal analysis of models of performance in two-alternative forced-choice tasks. *Psychol Rev* 113(4):700–65.
- Boussaoud D, Barth TM, Wise SP. 1993. Effects of gaze on apparent visual responses of frontal cortex neurons. *Exp Brain Res* 93(3):423–34.
- Carlsen A, Chua R, Inglis JT, Sanderson DJ, Franks IM. 2004. Prepared movements are elicited early by startle. *J Mot Behav* 36(3):253–64.
- Churchland MM, Cunningham JP, Kaufman MT, Foster JD, Nuyujukian P, Ryu SI, and others. 2012. Neural population dynamics during reaching. *Nature* 487(7405):51–6.
- Churchland MM, Cunningham JP, Kaufman MT, Ryu SI, Shenoy KV. 2010. Cortical preparatory activity: representation of movement or first cog in a dynamical machine? *Neuron* 68(3):387–400.
- Churchland MM, Santhanam G, Shenoy KV. 2006a. Preparatory activity in premotor and motor cortex reflects the speed of the upcoming reach. *J Neurophysiol* 96(6):3130–46.
- Churchland MM, Yu BM, Ryu SI, Santhanam G, Shenoy KV. 2006b. Neural variability in premotor cortex provides a signature of motor preparation. *J Neurosci* 26(14):3697–712.
- Cisek P. 2005. Neural representations of motor plans, desired trajectories, and controlled objects. *Cogn Process* 6:15–24.
- Cisek P, Kalaska JF. 2010. Neural mechanisms for interacting with a world full of action choices. *Annu Rev Neurosci* 33:269–98.
- Cohen RG, Rosenbaum DA. 2004. Where grasps are made reveals how grasps are planned: generation and recall of motor plans. *Exp Brain Res* 157(4):486–95.
- Cos I, Belanger N, Cisek P. 2011. The influence of predicted arm biomechanics on decision making. *J Neurophysiol* 105(6):3022–33.
- Craighero L, Fadiga L, Umiltà CA, Rizzolatti G. 1996. Evidence for visuomotor priming effect. *Neuroreport* 8(1):347–9.
- Crammond DJ, Kalaska JF. 2000. Prior information in motor and premotor cortex: activity during the delay period and effect on pre-movement activity. *J Neurophysiol* 84(2):986–1005.
- di Pellegrino G, Wise SP. 1993. Effects of attention on visuo-motor activity in the premotor and prefrontal cortex of a primate. *Somatosens Mot Res* 10(3):245–62.
- Diedrichsen J, Hazeltine E, Kennerley S, Ivry RB. 2001. Moving to directly cued locations abolishes spatial interference during bimanual actions. *Psychol Sci* 12(6):493–8.
- Fitts PM. 1954. The information capacity of the human motor system in controlling the amplitude of movement. *J Exp Psychol* 47(6):381–91.
- Georgopoulos AP. 1986. On reaching. *Annu Rev Neurosci* 9:147–70.
- Ghez C, Favilla M, Ghilardi MF, Gordon J, Bermejo R, Pullman S. 1997. Discrete and continuous planning of hand movements and isometric force trajectories. *Exp Brain Res* 115(2):217–33.
- Gold JI, Shadlen MN. 2000. Representation of a perceptual decision in developing oculomotor commands. *Nature* 404(6776):390–4.
- Gold JI, Shadlen MN. 2003. The influence of behavioral context on the representation of a perceptual decision in developing oculomotor commands. *J Neurosci* 23(2):632–51.
- Goldenberg G, Hagmann S. 1998. Tool use and mechanical problem solving in apraxia. *Neuropsychologia* 36(7):581–589.
- Goodman D, Kelso JA. 1980. Are movements prepared in parts? Not under compatible (naturalized) conditions. *J Exp Psychol Gen* 109(4):475–95.
- Gottlieb J, Goldberg ME. 1999. Activity of neurons in the lateral intraparietal area of the monkey during an antisaccade task. *Nat Neurosci* 2(10):906–12.
- Graziano MS, Taylor CS, Moore T. 2002. Complex movements evoked by microstimulation of precentral cortex. *Neuron* 34(5):841–51.
- Haith AM, Reppert TR, Shadmehr R. 2012. Evidence for hyperbolic temporal discounting of reward in control of movements. *J Neurosci* 32(34):11727–36.
- Hanes DP, Carpenter RH. 1999. Countermanding saccades in humans. *Vision Res* 39(16):2777–91.
- Hanes DP, Schall JD. 1996. Neural control of voluntary movement initiation. *Science* 274(5286):427–30.
- Heilman KM, Maher LM, Greenwald ML, Rothi LJ. 1997. Conceptual apraxia from lateralized lesions. *Neurology* 49(2):457–64.
- Hening W, Favilla M, Ghez C. 1988. Trajectory control in targeted force impulses. V. Gradual specification of response amplitude. *Exp Brain Res* 71(1):116–28.
- Hermesdorfer J, Mai N, Spatt J, Marquardt C, Veltkamp R, Goldenberg G. 1996. Kinematic analysis of movement imitation in apraxia. *Brain* 119(Pt 5):1575–86.
- Hocherman S, Wise SP. 1991. Effects of hand movement path on motor cortical activity in awake, behaving rhesus monkeys. *Exp Brain Res* 83(2):285–302.
- Hoffman JE, Subramaniam B. 1995. The role of visual attention in saccadic eye movements. *Percept Psychophys* 57(6):787–95.
- Hogan N. 1985a. Impedance control: an approach to manipulation: part I—theory. *J Dyn Syst Meas Control* 107(1):1–7.

- Hogan N. 1985b. Impedance control: an approach to manipulation: part II—implementation. *J Dyn Syst Meas Control* 107(1):8–16.
- Huberdeau DM, Haith AM, Krakauer JW. 2012. Continuous and discrete re-planning of reaching movements following abrupt changes to task goals. *Neuroscience 2012 Abstracts (Society for Neuroscience)*; 2012 Oct 13-17; New Orleans, LA. Online.
- Ietswaart M, Carey DP, Della Sala S. 2006. Tapping, grasping and aiming in ideomotor apraxia. *Neuropsychologia* 44(7):1175–84.
- Jax SA, Rosenbaum DA. 2007. Hand path priming in manual obstacle avoidance: evidence that the dorsal stream does not only control visually guided actions in real time. *J Exp Psychol Hum Percept Perform* 33(2):425–41.
- Johnson MT, Coltz JD, Hagen MC, Ebner TJ. 1999. Visuomotor processing as reflected in the directional discharge of premotor and primary motor cortex neurons. *J Neurophysiol* 81(2):875–94.
- Kadmon Harpaz N, Flash T, Dinstein I. 2014. Scale-invariant movement encoding in the human motor system. *Neuron* 81(2):452–62.
- Kakei S, Hoffman DS, Strick PL. 1999. Muscle and movement representations in the primary motor cortex. *Science* 285(5436):2136–9.
- Kakei S, Hoffman DS, Strick PL. 2001. Direction of action is represented in the ventral premotor cortex. *Nat Neurosci* 4(10):1020–5.
- Kaufman MT, Churchland MM, Shenoy KV. 2013. The roles of monkey M1 neuron classes in movement preparation and execution. *J Neurophysiol* 110(4):817–25.
- Kiani R, Shadlen MN. 2009. Representation of confidence associated with a decision by neurons in the parietal cortex. *Science* 324(5928):759–64.
- Kowler E, Anderson E, Doshier B, Blaser E. 1995. The role of attention in the programming of saccades. *Vision Res* 35(13):1897–916.
- Kurata K. 1993. Premotor cortex of monkeys: set- and movement-related activity reflecting amplitude and direction of wrist movements. *J Neurophysiol* 69(1):187–200.
- Laming DRJ. 1968. *Information theory of choice-reaction times*. London, England: Academic Press.
- Lashley KS. 1930. Basic neural mechanisms in behavior. *Psychol Rev* 37:1–24.
- Leigh RJ, Zee DS. 2006. *The neurology of eye movements*. New York, NY: Oxford University Press.
- Liu D, Todorov E. 2007. Evidence for the flexible sensorimotor strategies predicted by optimal feedback control. *J Neurosci* 27(35):9354–68.
- Mante V, Sussillo D, Shenoy KV, Newsome WT. 2013. Context-dependent computation by recurrent dynamics in prefrontal cortex. *Nature* 503(7474):78–84.
- Milner B. 1963. Effects of different brain lesions on card sorting: role of frontal lobes. *Arch Neurol* 9(1):90–100.
- Mushiaki H, Saito N, Sakamoto K, Itoyama Y, Tanji J. 2006. Activity in the lateral prefrontal cortex reflects multiple steps of future events in action plans. *Neuron* 50(4):631–41.
- Mutha PK, Sainburg RL, Haaland KY. 2010. Coordination deficits in ideomotor apraxia during visually targeted reaching reflect impaired visuomotor transformations. *Neuropsychologia* 48(13):3855–67.
- Nashed JY, Crevecoeur F, Scott SH. 2012. Influence of the behavioral goal and environmental obstacles on rapid feedback responses. *J Neurophysiol* 108(4):999–1009.
- Nashed JY, Crevecoeur F, Scott SH. 2014. Rapid online selection between multiple motor plans. *J Neurosci* 34(5):1769–80.
- Oliveira FT, Diedrichsen J, Verstynen T, Duque J, Ivry RB. 2010. Transcranial magnetic stimulation of posterior parietal cortex affects decisions of hand choice. *Proc Natl Acad Sci U S A* 107(41):17751–6.
- Passingham RE, Wise SP. 2012. *The neurobiology of the prefrontal cortex: anatomy, evolution, and the origin of insight*. Oxford, England: Oxford University Press.
- Perfliev S, Isa T, Johnels B, Steg G, Wessberg J. 2010. Reflexive limb selection and control of reach direction to moving targets in cats, monkeys, and humans. *J Neurophysiol* 104(5):2423–32.
- Pruszynski JA, Kurtzer I, Scott SH. 2011. The long-latency reflex is composed of at least two functionally independent processes. *J Neurophysiol* 106(1):449–59.
- Ratcliff R. 1978. Theory of memory retrieval. *Psychol Rev* 85(2):59–108.
- Ratcliff R, Cherian A, Segraves M. 2003. A comparison of macaque behavior and superior colliculus neuronal activity to predictions from models of two-choice decisions. *J Neurophysiol* 90(3):1392–407.
- Ratcliff R, McKoon G. 2008. The diffusion decision model: Theory and data for two-choice decision tasks. *Neural Comput* 20(4):873–922.
- Resulaj A, Kiani R, Wolpert DM, Shadlen MN. 2009. Changes of mind in decision-making. *Nature* 461(7261):263–6.
- Riehle A, Requin J. 1989. Monkey primary motor and premotor cortex: single-cell activity related to prior information about direction and extent of an intended movement. *J Neurophysiol* 61(3):534–49.
- Robinson DA, Fuchs AF. 1969. Eye movements evoked by stimulation of frontal eye fields. *J Neurophysiol* 32(5):637–48.
- Rosenbaum DA, Marchak F, Barnes HJ, Vaughan J, Slotta J, Jorgensen M. 1990. Constraints for action selection: overhand versus underhand grips. In: Jeannerod M, editor. *Attention and performance*. Hillsdale, NJ: Erlbaum. p 321–42.
- Schall JD. 2000. From sensory evidence to a motor command. *Curr Biol* 10(11):R404–6.
- Scott SH, Kalaska JF. 1997. Reaching movements with similar hand paths but different arm orientations. I. Activity of individual cells in motor cortex. *J Neurophysiol* 77(2):826–52.
- Selen LP, Shadlen MN, Wolpert DM. 2012. Deliberation in the motor system: reflex gains track evolving evidence leading to a decision. *J Neurosci* 32(7):2276–86.
- Shadlen MN, Newsome WT. 2001. Neural basis of a perceptual decision in the parietal cortex (area LIP) of the rhesus monkey. *J Neurophysiol* 86(4):1916–36.

- Shadmehr R, Orban de Xivry JJ, Xu-Wilson M, Shih TY. 2010. Temporal discounting of reward and the cost of time in motor control. *J Neurosci* 30(31):10507–16.
- Shenoy KV, Sahani M, Churchland MM. 2013. Cortical control of arm movements: a dynamical systems perspective. *Annu Rev Neurosci* 36:337–59.
- Snyder LH, Batista AP, Andersen RA. 2000. Intention-related activity in the posterior parietal cortex: a review. *Vision Res* 40(10-12):1433–41.
- Sommer MA, Tehovnik EJ. 1997. Reversible inactivation of macaque frontal eye field. *Exp Brain Res* 116(2):229–49.
- Song JH, Nakayama K. 2008. Numeric comparison in a visually-guided manual reaching task. *Cognition* 106(2):994–1003.
- Stanton GB, Deng SY, Goldberg ME, McMullen NT. 1989. Cytoarchitectural characteristic of the frontal eye fields in macaque monkeys. *J Comp Neurol* 282(3):415–27.
- Stoloff RH, Taylor JA, Xu J, Ridderikhoff A, Ivry RB. 2011. Effect of reinforcement history on hand choice in an unconstrained reaching task. *Front Neurosci* 5:41.
- Sunderland A, Sluman SM. 2000. Ideomotor apraxia, visuo-motor control and the explicit representation of posture. *Neuropsychologia* 38(7):923–34.
- Theeuwes J, Kramer AF, Hahn S, Irwin DE. 1998. Our eyes do not always go where we want them to go: Capture of the eyes by new objects. *Psychol Sci* 9(5):379–385.
- Thompson KG, Hanes DP, Bichot NP, Schall JD. 1996. Perceptual and motor processing stages identified in the activity of macaque frontal eye field neurons during visual search. *J Neurophysiol* 76(6):4040–55.
- Todorov E, Jordan MI. 2002. Optimal feedback control as a theory of motor coordination. *Nat Neurosci* 5(11):1226–35.
- Torres EB, Quian Quiroga R, Cui H, Buneo CA. 2013. Neural correlates of learning and trajectory planning in the posterior parietal cortex. *Front Integr Neurosci* 7:39.
- Trommershauser J, Maloney LT, Landy MS. 2003. Statistical decision theory and trade-offs in the control of motor response. *Spat Vis* 16(3-4):255–75.
- Valls-Sole J, Rothwell JC, Goulart F, Cossu G, Munoz E. 1999. Patterned ballistic movements triggered by a startle in healthy humans. *J Physiol* 516(Pt 3):931–8.
- van der Wel RP, Fleckenstein RM, Jax SA, Rosenbaum DA. 2007. Hand path priming in manual obstacle avoidance: evidence for abstract spatiotemporal forms in human motor control. *J Exp Psychol Hum Percept Perform* 33(5):1117–26.
- Wallis JD, Anderson KC, Miller EK. 2001. Single neurons in prefrontal cortex encode abstract rules. *Nature* 411(6840):953–6.
- Watanabe M. 1986. Prefrontal unit activity during delayed conditional Go/No-Go discrimination in the monkey. II. Relation to Go and No-Go responses. *Brain Res* 382(1):15–27.
- Welford AT. 1980. Choice reaction time: basic concepts. In: Welford AT, editor. *Reaction times*. New York, NY: Academic Press. p 73–128.
- Wing AM. 2000. Motor control: Mechanisms of motor equivalence in handwriting. *Curr Biol* 10(6):R245–8.
- Wolpert DM, Landy MS. 2012. Motor control is decision-making. *Curr Opin Neurobiol* 22(6):996–1003.