

Preparation of Movement

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Abstract

It is widely believed that voluntary movements must be prepared before they are executed, but there is so far little consensus on exactly what mechanisms and computations must occur prior to a movement. Here, we argue that movement preparation is most usefully thought of as a process of setting an appropriate state for the motor system that poises it to generate a particular desired movement. This process, which can occur in as little as 50 ms, does not directly trigger movement initiation, nor is it required to initiate a movement. Instead, initiation of movement is determined by a distinct process, independent of the state of movement preparation. We suggest that, during the course of determining a task goal, or making a decision, the prepared state is continually updated as the desired movement changes in light of new evidence and beliefs. This ensures that the motor system is able to generate an appropriate movement as rapidly possible when necessary.

Introduction

How does the brain generate movement? A longstanding idea in neuroscience is that movements must be 'prepared' before they can be executed. This notion is inspired by the fact that the patterns of muscle activation to achieve even simple goals can be extremely complex and, thus must require complex, time-consuming computations. It is also supported by numerous behavioral and physiological observations. Over recent years, however, as our understanding of how movements are generated by the brain has advanced, it has become less and less clear the extent to which movement preparation is truly necessary.

There is in fact surprisingly little consensus on what the term 'preparation' should even mean. The term often collapses together multiple distinct processes that occur prior to movement (e.g. selecting what action to take versus specifying the details of how to execute that action). At other times, the term 'preparation' is used without any explanation of what exactly it may or

may not entail, or whether it even necessarily occurs. A dictionary definition of preparation is “the act of being made ready for use or consideration”. We suggest that this definition aptly applies to movement preparation. It emphasizes several important features of movement preparation: that the act of preparation is distinct from the act of generating a movement, that it happens before we ever need to move, and that it is time-consuming. Furthermore, this definition suggests that preparation pertains to readiness to perform a *specific* action, and we will focus in this chapter on preparation in this sense, rather than in the more generic sense of readiness to transition from being at rest to moving.

In this chapter, we will review conventional assumptions about movement preparation and outline a new emerging perspective. We start by reviewing behavioral studies examining the time course of movement preparation and its relationship to movement initiation. We then consider convergent evidence gained from neurophysiological investigations. Collectively, these lines of evidence point to a reappraisal of movement preparation as a relatively rapid process whereby specified high-level goals are translated into a suitable policy for movement, ready to be invoked when movement initiation is triggered.

Is movement preparation time-consuming?

It has long been argued that preparation is a time-consuming process, based on the general observation that, when participants know beforehand which movement will be required, their reaction times are considerably faster (and movement accuracy is improved) than when the required movement is cued at the same time as a GO cue.

An example of this effect comes from the work of David Rosenbaum (1980) in which human participants were instructed, via a series of letters, which among eight possible targets they may have to move to (e.g. F = forwards, B = backwards). In some instances, certain letters were pre-cued, narrowing down the range of possible targets ahead of the GO cue. Reaction times were significantly faster the more information about the forthcoming movement was disclosed beforehand. The interpretation of these findings, which has dominated much of the thinking about movement preparation and initiation, is that specifying each parameter of the movement is time-consuming. Pre-cuing some aspect of the required movement enables the corresponding parameter to be specified in advance, allowing the movement to then be generated with a shorter reaction time.

As pointed out by Goodman and Kelso (1980), however, a major frailty in this logic is that specifying the movement may not have been the most challenging aspect of this task. Parsing the presented letters into a required movement goal is not straightforward and could well have been sufficiently time-consuming to account for much of the reaction time. Indeed, the reaction times exhibited by participants in tasks such as Rosenbaum’s are relatively long, often around 500-700ms. This is far longer than the typical reaction times of 200-250ms for reaching movements towards a visually-presented target location (Haith, Pakpoor, & Krakauer, 2016). It is unlikely, therefore, that the typical reductions in reaction time afforded by pre-cues are attributable to movement preparation *per se*.

This raises an important point about movement preparation: that it should only encompass processes specific to generating the movement itself, not to deciding which movement to make. Although parsing the stimulus is clearly a prerequisite for making the right movement, it seems unreasonable to class this as *movement* preparation – just as planning your next move in a chess match should not qualify as such.

A more focused definition of movement preparation is as a process that bridges between the high-level goals of a movement (*'what'* you want to do, out of the many alternatives available), and the control policy for executing the movement (*'how'* you will achieve the goal). Only the specification of the policy prescribing the actual movement to be generated, contingent upon a selected goal, should be considered movement preparation. Processes required for specifying goals should not be.

With this in mind, movement preparation is perhaps best studied through tasks in which the required movement is cued by a highly salient, spatial cue, so that deciding what action to take should be trivial (though we discuss preparation in the context of decision making further below). In this case, pre-cuing the target location before a 'go' cue still leads to a reduction in reaction time, consistent with the theory that it enables some time-consuming preparation phase to be completed in advance (Goodman & Kelso, 1980). However, the reduction in reaction time enabled by direct, spatial pre-cues is only of the order of 50-100ms, and can be as little as 30ms in monkeys (Churchland, Yu, Ryu, Santhanam, & Shenoy, 2006). The time consumed by preparation therefore seems to be quite modest, and certainly much shorter than postulated by most classical theories.

Movement Preparation versus Movement Initiation

Approaches to understanding movement preparation based on examining reaction times are inevitably indirect, and rely on strong assumptions about what determines reaction times. In particular, it is commonly assumed that a movement is generated as soon as preparation is complete. As we shall see, this assumption does not withstand closer scrutiny of how we prepare and execute movements.

A more direct approach to characterizing movement preparation was devised by Claude Ghez and colleagues. Rather than treating the reaction time as a dependent variable, they instead employed a method to control the reaction time, and measured the quality of movement as a dependent variable (Ghez et al., 1997). In their *timed-response* paradigm (Figure 1a), participants were required to initiate a movement synchronously with a predictable auditory cue – the fourth tone in a sequence of four equally spaced tones. The allowed reaction time (and consequently time available for movement preparation) could be varied by varying the moment at which the target was presented relative to this fixed time of movement initiation

This approach reveals how movements transition from a default movement generated at very low allowed reaction times, to a movement that is precisely tuned to the presented target at

longer times – with appropriate movements able to be executed within as little as 150ms following presentation of the target (Haith et al., 2016) (Figure 1b). This duration is scarcely longer than the signaling delays that would be necessary for information to travel from the eye, through the cortex and to muscles. Therefore, to the extent that movement preparation does occur, it does not seem to occupy the bulk of the reaction time.

Contrasting the time course of preparation from this timed-response approach with behavior in a more conventional “free” reaction time paradigm (in which participants react as quickly as possible to move towards a presented target), reveals that typical reaction times are much longer than is apparently necessary (Figure 1b). Whereas accurate movements could be reliably generated whenever there was at least 150ms preparation time, typical “free” reaction times were delayed relative to this time by around 80ms – around a third of the reaction time (Haith et al., 2016).

The substantial delay between the inferred timing of movement preparation and the timing of movement initiation suggests distinct mechanisms for these processes. This is perhaps unsurprising – after all, delay paradigms depend on the ability to prepare a movement without initiating it. However, it has also been noted that participants still exhibited a speed–accuracy trade-off even when acting under “free” reaction time conditions (Haith et al., 2016). That is, they committed errors in which they apparently initiated movement before preparation had become complete. This, critically, suggests that movement initiation was independent of, and not contingent on movement preparation having become complete. This also offers a potential explanation as to why there should be a delay between movement preparation and initiation: it serves to minimize the risk of ‘fast errors’ in which a movement is initiated before the correct movement can be selected and prepared.

Movement preparation and freedom from immediacy

An important implication of the independence of movement preparation and initiation is that, regardless of the time a movement is ultimately initiated, there is a transition from being unable to make the correct movement, to being able to do so. This illustrates an important sense in which movements are indeed prepared: the movement is made ready for later execution, and this readied movement can be held in a prepared state until it is executed. Preparation in this sense differs from classical characterizations as a necessary and time-consuming computation, which triggers movement initiation as soon as it is complete (Allen, Kornblum, & Meyer, 1986).

Many of our movements are generated without being held in a readied state prior to their initiation. One trivial example is a stretch reflex, such as the patellar reflex, which might be induced by a doctor tapping on the tendon below your knee cap. This reflex is mediated by a simple monosynaptic circuit within the spinal cord that translates information about muscle length into motor neuron activity that causes the muscle to contract. In this case, movement happens as a direct consequence of the stimulus in a direct *stimulus-response association*, but this movement is not held in any ‘prepared’ state prior to being initiated.

Such immediacy of movement also occurs when an ongoing movement is perturbed. For example, displacing the target of a movement elicits a rapid response that corrects for the effects of the perturbation (Day & Lyon, 2000; Pruszynski, Kurtzer, & Scott, 2008), often with considerable sophistication (Nashed, Crevecoeur, & Scott, 2014; see also Chapter ?? by Weiler and Pruszynski). These corrective movements are involuntary in that they occur even when they conflict with task goals, e.g. an instruction to move in the opposite direction of a target jump.

The ability to prepare a movement without immediately initiating it thus seems critical to the “freedom from immediacy” that is a defining aspect of volitional control. It has long been appreciated, when it comes to internally-generated, self-initiated movements, that decisions about ‘what to do’ occur independently of decisions about ‘when to do it’. It should therefore perhaps not be surprising that voluntary movements cued by an external stimulus follow a similar organization.

Neural mechanisms of movement preparation: activity during delay periods

The behavioral evidence reviewed above suggests that voluntary movements are ‘prepared’ before they are executed in the sense that a movement is made ready for execution. Neurophysiological investigations have yielded more or less the same conclusion.

Experiments seeking to characterize neural mechanisms of movement preparation have also typically employed a pre-cuing approach, enabling preparatory activity to be distinguished from activity related to actually generating the movement. Many neurons active during movement exhibit similar tuning during the delay between a sensory cue and the ultimate initiation of the movement (Crammond & Kalaska, 2000; Kurata, 1989; Riehle & Requin, 1989; Tanji & Evarts, 1976; Weinrich & Wise, 1982) (Figure 2a). This pre-movement activity can also be influenced by the number of possible movement options, information about the timing of movement, and various types of precues (e.g., Bastian, Schöner, & Riehle, 2003; Dekleva, Ramkumar, Wanda, Kording, & Miller, 2016). It has thus been suggested that movement preparation amounts to ‘priming’ movement, by bringing activity in these regions close to, but just below, some threshold level required for generating a movement.

Implicit in such accounts is that individual neurons represent specific aspects of movement, such as the kinematics of the hand or joints, applied forces or torques, or the activity of specific muscles. Perhaps consistent with this view, microstimulation in either premotor cortex or M1 (henceforth PM/M1) can elicit movement of specific body parts (Dum & Strick, 2002; Leyton & Sherrington, 1917). It therefore seems plausible that pre-movement activity might serve to give the specification of these parameters a head start, so that when the movement needs to ultimately be made, it is generated faster and more accurately (Hanes & Schall, 1996).

Recent work, however, challenges the view that movement preparation serves to simply hold movement-related activity in a sub-movement-threshold state. Systematic examination of

delay-period activity in hundreds of neurons in PM/M1 reveals that delay-period activity just as often shows an opposite pattern to activity during movement (see example in Figure 2b), or is entirely unrelated to it (Churchland, Cunningham, Kaufman, Ryu, & Shenoy, 2010).

Movement preparation as state-setting for subsequent movement

What is clear, however, is that pre-movement population activity in PM/M1 reliably converges to a specific state (Figure 2c). For example, the variability in neural firing rates in premotor cortex decreases, whilst mean firing rates remain largely unaffected (Churchland et al., 2006). Similar variability decreases occur in corticospinal excitability in humans before movement (Klein-Flügge, Nobbs, Pitcher, & Bestmann, 2013). This convergence appears to be functionally relevant; disrupting PM/M1 activity prior to movement erases the reaction-time advantage gained by pre-cuing the target location (Churchland & Shenoy, 2007; Schluter, Rushworth, Passingham, & Mills, 1998). Thus, it appears that the overall population of neurons in PM/M1 must be active before movement with a very specific pattern.

Closer examination of neural activity during movement provides clues as to why this may be necessary. The joint population activity of neurons can be visualized and analyzed using dimensionality reduction techniques, which has helped to reveal that pre-movement activity occur in distinct patterns (or, to be more precise, different subspaces) (Elsayed, Lara, Kaufman, Churchland, & Cunningham, 2016; Kaufman, Churchland, Ryu, & Shenoy, 2014). Furthermore, during movement, the population-level activity across PM/M1 exhibits characteristic dynamics in which the future state of the neural population depends largely on its current state (Churchland et al., 2012, 2010). While different movements exhibit different patterns of activity, all movements exhibit stereotypical transitions from one state to another; such structure is not present in downstream EMG activity.

Movement preparation might therefore be conceived as one of attaining a specific state within PM/M1 that seeds the initial state of the dynamical system to generate a specific time-varying pattern of activity that will then drive muscle activity in the required way (Churchland et al., 2012, 2010). In this view, the state of activity of neurons prior in PM/M1 prior to movement encodes the policy for how the subsequent movement will be generated. Indeed, trial-by-trial comparisons show an initially high variability of firing rates for individual neurons at the start of each trial which rapidly diminishes after the target is presented (Churchland et al., 2006). Coupled with distinct changes in mean firing rate for different movements, this suggests a convergence of the population-level activity onto the specific state that is required to generate the desired movement (Churchland et al., 2006).

This perspective accords well with our understanding of movement preparation gained from behavioral investigations. Behaviorally, we determined that movement preparation must be rapid, not requiring more than 50-100ms. Delay-period population activity typically converges to a stable state within around 50-100ms. Behavioral evidence also suggested that movement preparation is more than just a time-consuming process that precedes movement, instead

reflecting an underlying transition from not being able to make the required movement, to being able to do so. This is entirely consistent with the convergence of neural population activity onto a specific state.

One concern with the above proposal is that it is primarily founded on neural activity occurring during an artificially-imposed delay period. It remains unclear to what extent patterns of neural activity in such paradigms can be generalized to more naturalistic scenarios in which action may be required immediately. However, the basic structure of preparatory events seems to be preserved even when no instructed delay is present (Lara, Elsayed, Zimnik, Cunningham, & Churchland, 2018).

Finally, neural data also suggest that movement initiation is distinct from and does not appear to be directly triggered by movement preparation. The state of PM/M1 at the time of the GO cue is predictive of reaction times (though it only accounts for around 20% of their variance) (Afshar et al., 2011). Motor cortical population activity does, however, exhibit a rapid, step-wise change in firing rates which is strongly predictive of reaction time. Unlike most other aspects of activity in PM/M1, this step-wise change occurs regardless of the specific movement being made (Kaufman et al., 2016). This seems compatible with the conclusion, from behavioral investigations, that movement initiation is governed by process that is distinct from processes responsible for movement preparation.

Single versus Parallel plans

One unresolved question that has occupied the field is whether several movements can be prepared in parallel, as opposed to only single movements. One popular view is that the brain prepares multiple potential movements at the same time. For example, Cisek and Kalaska (2005) reported that, if there is more than one potential target during the delay period, then neurons tuned to each of these *specific options* appear to be active during this time. One interpretation of this observation is that multiple movements are prepared in parallel, presumably to allow the reaction time savings secured through advance preparation to be gained for either potential target.

This interpretation, however, is somewhat at odds with the dynamical systems account of movement generation. According to the latter, the pre-movement state of PM/M1 seeds the initial state of a dynamical system, leading to movement. Each possible state is therefore associated with generating a single movement, thus framing PM/M1 as a tuned population of neurons, whose collective state encodes a single movement. This is in stark contrast to the idea underlying parallel preparation, in which different are represented by different sub-populations of neurons; framing PM/M1 as a population of tuned neurons.

How can these conflicting neural accounts of movement preparation be reconciled? One potential explanation is that it is far from clear exactly what observed pre-movement activity actually represents. It is often assumed to reflect specification of a movement or control policy, because it occurs in an ostensibly 'motor' region of the brain. Alternatively, however, this

activity might reflect processes related to the emergence and specification of a movement goal, to be elaborated into a policy elsewhere. Thus, even if the motor system prepares only a single movement, it still may be able to entertain multiple potential *goals* in parallel. Indeed, the timecourse of the delay-period neural dynamics would be compatible with such an interpretation, but less so with the short time that is required for preparation.

A number of lines of research have sought to establish behavioral evidence for the existence of parallel movement plans, based on the following logic: if two similar movement plans are indeed simultaneously activated, they may interfere with one another, leading to a movement that resembles a mixture of the features of the individual movements. For instance, two reaching movements planned to adjacent targets might ultimately give rise to a movement that reflects the average of the two trajectories, falling intermediate between the potential targets. This phenomenon of intermediate movements is indeed well established. Whenever there is ambiguity surrounding the required target location, participants are prone to generate movements between potential targets. This effect is most starkly revealed in “go-before-you-know” experiments that deliberately manipulate this ambiguity by presenting multiple potential targets, and forcing participants to initiate movement before the true target location is disclosed (Chapman et al., 2010).

An alternative explanation for these intermediate movements, however, is that they are quite deliberate, goal-directed movements, and not generated through inadvertent mixing of parallel plans. If the motor system is only able to prepare a single movement given an ambiguous target array, it should prepare the best possible movement for achieving task goals. An intermediate movement between two potential targets brings the hand closer towards both of them - a sensible policy, since it makes it then easier to move towards either target if one emerges as more appealing later in the movement. A number of findings favor this optimization-based view: intermediate movements become less likely as the spatial separation between targets increases (Ghez et al., 1997); participants can avoid intermediate movements if these are penalized (Haith, Huberdeau, & Krakauer, 2015); and fast movements prohibit mid-movement corrections, tipping the balance in favor of moving directly towards one target or the other (Wong & Haith, 2017). Collectively, these results suggest that parallel preparation of multiple movements is at the very least not an essential requirement for action, and lend support to the idea that only a single movement is prepared by the motor system. This conclusion is supported by a recent study using large-scale neural recording in premotor cortex, which found that single and not multiple plans are represented, even when multiple potential targets are present (Dekleva, Kording, & Miller, 2018).

Relationship between Movement Preparation and Decision Making

In many cases, our movements are not unambiguously cued by a salient stimulus and instead we must decide for ourselves what movement to make. The process of making such decisions is well studied. However, what remains less well understood is exactly how this process interacts with the generation of movement required to indicate one’s decision.

A common paradigm for studying decision making is to ask participants to make judgements about a stimulus. For instance, a series of dots may appear and disappear on a screen, resembling 'snow' on a de-tuned television, except that some proportion of the dots move coherently in a particular direction. Participants judge in which direction the coherent dots are moving and the difficulty of this judgement can be altered by varying the proportion of dots that move coherently. When, say, only 5% of the dots are moving coherently, it becomes necessary to observe the stimulus for some time, accumulating evidence from momentary observations, before making a decision as to which way the dots are moving.

A simplistic serial viewpoint might suggest that such a decision is first made on the basis of visual evidence and, after commitment to a particular decision, the required action is prepared. It seems, however, that movements can be continuously modulated by the state of an inchoate decision, speaking against such an interpretation. For instance, in an experiment by Gold and Shadlen (2000), monkeys had to make a saccade in the appropriate direction of a random dot motion stimulus once they had judged the direction the dots were moving in. At times, prior to monkeys having made up their minds about the direction of the dots, an involuntary eye movement would be elicited by stimulating the frontal eye field. Although the monkey had not yet completed its decision, the elicited eye movements deviated in the direction favored by current evidence accumulated so far.

This phenomenon is not restricted to eye movements. In a study by Selen and colleagues (2012), human participants performed a similar task, but had to generate an arm movement indicating the perceived motion direction. After various durations viewing the stimulus, the participant's arm was perturbed and the strength of the low-latency feedback responses were closely tuned to the strength and direction of the evidence provided to participants up to that point.

These findings suggests an overlap between the mechanisms by which a decision is formed, and the mechanisms for representing a movement. At a neural level, the state of a decision (which can typically be inferred from the stimulus, often with the aid of a model) can be clearly decoded from neurons in motor areas (Thura & Cisek, 2014). In fact, the ubiquity with which decision state has been found to be apparently represented in the motor system has even led to the suggestion that movement preparation may play a causal role in influencing the outcome of a decision (Cisek & Kalaska, 2005).

We propose an alternative interpretation. As we have just discussed, current evidence suggests that it is only possible to prepare a single movement at any point in time. During a developing decision, it would make sense for the motor system to specify the movement that corresponds to the best possible course of action, given the current available evidence. If the decision, and, consequently, the goal of movement, is ambiguous, prematurely initiated movements will reflect this ambiguity, and be biased towards the movement corresponding to the current most likely goal. Indeed this account can explain intermediate movements amid uncertainty; in these cases, the optimal course of action among two neighboring targets is to move along an

intermediate movement trajectory, anticipating that more evidence will be available by later in the movement (Haith et al., 2015).

In support of this general view that the motor system may not encode a decision *per se*, but rather a policy associated with the current evidence for one goal or another, a recent paper by Hanks and colleagues found differential tuning for decision-related variables in different brain regions in rats (Hanks et al., 2015). In posterior parietal cortex, neural activity was closely tuned to the current evidence available in their task, varying continuously with the available evidence. In prefrontal cortex, however, neural activity followed a more categorical tuning; population activity fell into one of two specific states depending on which response option was, on current evidence, more likely. As the authors stated, activity in these areas effectively answered the question: “If the go signal came now, which action should I take?”. The response required by the animal in this case is rather more abstract than in the case of a saccade. However, we suggest that the distinction apparent in these data reflects a general principle of the gradient from evidence to action in decision making. Within this gradient, the bulk of the required computations specifies the goals of our actions, whereas their actual preparation and initiation is, comparatively, not time consuming.

Summary

Classical views of movement preparation suggest that it is a time-consuming process entailing computations necessary for movement. However, we have argued that these ideas are difficult to uphold. Instead, a new view of movement preparation has emerged: movement preparation is a process of setting the state of the motor system once an action goal is identified, priming it to generate a single specific required movement. Contrary to traditional views, this process occurs very rapidly, within around 50ms, and does not directly trigger initiation of the movement upon completion.

Figures and Legends

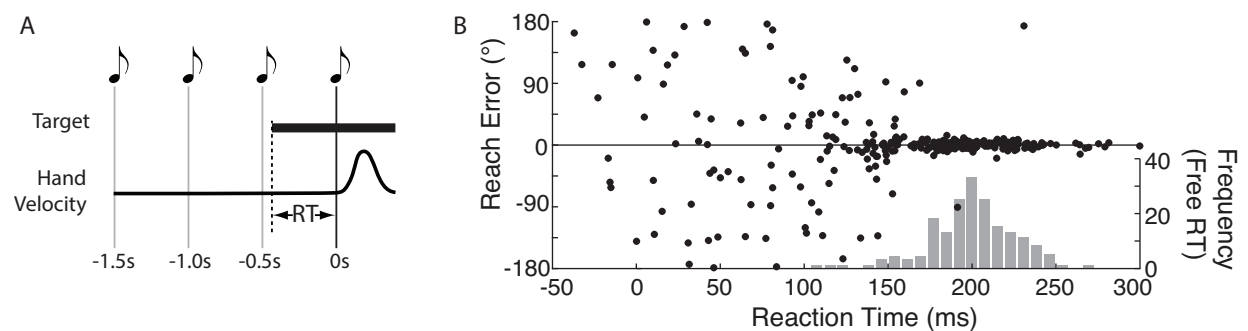


Figure 1. Relative timing of movement preparation versus movement initiation, adapted from (Haith et al., 2016). A) Timed-response paradigm. In each trial, participants must initiate a response (a reach to one of eight possible targets) coincident with the fourth of four predictable tones. The time at which the true target is presented can be varied relative to the

fourth tone to impose a particular reaction time. B) Behavioral results from a representative participant. Blue dots show imposed reaction time and initial directional error for individual trials. This participant could reliably generate accurate response whenever the imposed preparation time was greater than 150ms, indicating that movement preparation was complete by that time. Green histogram shows the distribution of reaction times for the same participant in a ‘free’ reaction time version of the task. Note that, despite perfect performance above imposed reaction times of 150ms, typical free reaction times were around 200ms, and often even longer – illustrating the delay between the time required for preparation, and the time at which movement is initiated.

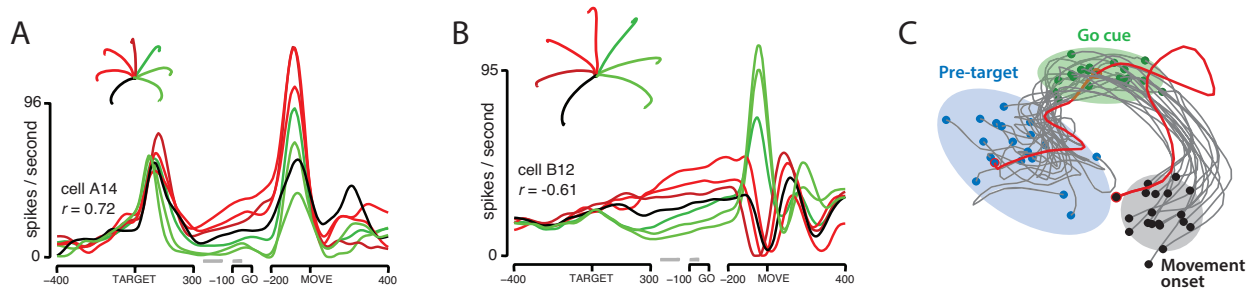


Figure 2. Neural mechanisms of movement preparation. A-B) Preparatory and movement-related activity in two example neurons. Reproduced from (Churchland et al., 2010). Different colors indicate activity for different movements (shown in inset). A) shows a neuron whose preparatory activity (between TARGET and GO) is positively correlated ($r=0.72$) with its activity during movement (MOVE). B) shows a neuron whose analogous correlation is negative ($r=-0.61$). C) At the population level (here, a 2-dimensional view of overall population activity), preparatory neural activity across different trials is initially variable across trials (blue dots), but converges to a specific state by the time of the GO cue (green dots). After the GO cue, neural activity follows a stereotyped activity profile. Red curve indicates data from one outlying trial. Reproduced from (Shenoy, Sahani, & Churchland, 2013).

References

- Afshar, A., Santhanam, G., Yu, B. M., Ryu, S. I., Sahani, M., & Shenoy, K. V. (2011). Single-trial neural correlates of arm movement preparation. *Neuron*, *71*(3), 555–564. <https://doi.org/10.1016/j.neuron.2011.05.047>
- Allen, O., Kornblum, S., & Meyer, D. E. (1986). The point of no return in choice reaction time: Controlled and ballistic stages of response preparation. *Journal of Experimental Psychology*, *12*(3), 243–258.
- Bastian, A., Schönner, G., & Riehle, A. (2003). Preshaping and continuous evolution of motor cortical representations during movement preparation. *European Journal of Neuroscience*, *18*(7), 2047–2058. <https://doi.org/10.1046/j.1460-9568.2003.02906.x>
- Chapman, C. S., Gallivan, J. P., Wood, D. K., Milne, J. L., Culham, J. C., & Goodale, M. A. (2010). Reaching for the unknown: Multiple target encoding and real-time decision-making in a

- rapid reach task. *Cognition*, *116*(2), 168–176.
<https://doi.org/10.1016/j.cognition.2010.04.008>
- Churchland, M. M., Cunningham, J. P., Kaufman, M. T., Foster, J. D., Nuyujukian, P., Ryu, S. I., & Shenoy, K. V. (2012). Neural population dynamics during reaching. *Nature*, *487*(7405), 51–56. <https://doi.org/10.1038/nature11129>
- Churchland, M. M., Cunningham, J. P., Kaufman, M. T., Ryu, S. I., & Shenoy, K. V. (2010). Cortical Preparatory Activity: Representation of Movement or First Cog in a Dynamical Machine? *Neuron*, *68*(3), 387–400. <https://doi.org/10.1016/j.neuron.2010.09.015>
- Churchland, M. M., & Shenoy, K. V. (2007). Delay of Movement Caused by Disruption of Cortical Preparatory Activity. *Journal of Neurophysiology*, *97*(1), 348–359.
<https://doi.org/10.1152/jn.00808.2006>
- Churchland, M. M., Yu, B. M., Ryu, S. I., Santhanam, G., & Shenoy, K. V. (2006). Neural variability in premotor cortex provides a signature of motor preparation. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, *26*(14), 3697–3712.
<https://doi.org/10.1523/JNEUROSCI.3762-05.2006>
- Cisek, P., & Kalaska, J. F. (2005). Neural correlates of reaching decisions in dorsal premotor cortex: specification of multiple direction choices and final selection of action. *Neuron*, *45*(5), 801–814. <https://doi.org/10.1016/j.neuron.2005.01.027>
- Crammond, D. J., & Kalaska, J. F. (2000). Prior Information in Motor and Premotor Cortex: Activity During the Delay Period and Effect on Pre-Movement Activity. *Journal of Neurophysiology*, *84*(2), 986–1005. <https://doi.org/10.1152/jn.2000.84.2.986>
- Day, B. L., & Lyon, I. N. (2000). Voluntary modification of automatic arm movements evoked by motion of a visual target. *Experimental Brain Research*, *130*(2), 159–168.
<https://doi.org/10.1007/s002219900218>
- Dekleva, B. M., Kording, K. P., & Miller, L. E. (2018). Single reach plans in dorsal premotor cortex during a two-target task. *Nature Communications*, *9*(1), 3556.
<https://doi.org/10.1038/s41467-018-05959-y>
- Dekleva, B. M., Ramkumar, P., Wanda, P. A., Kording, K. P., & Miller, L. E. (2016, July 15). Uncertainty leads to persistent effects on reach representations in dorsal premotor cortex. <https://doi.org/10.7554/eLife.14316>
- Dum, R. P., & Strick, P. L. (2002). Motor areas in the frontal lobe of the primate. *Physiology & Behavior*, *77*(4), 677–682. [https://doi.org/10.1016/S0031-9384\(02\)00929-0](https://doi.org/10.1016/S0031-9384(02)00929-0)
- Elsayed, G. F., Lara, A. H., Kaufman, M. T., Churchland, M. M., & Cunningham, J. P. (2016). Reorganization between preparatory and movement population responses in motor cortex. *Nature Communications*, *7*, 13239. <https://doi.org/10.1038/ncomms13239>
- Ghez, C., Favilla, M., Ghilardi, M. F., Gordon, J., Bermejo, R., & Pullman, S. (1997). Discrete and continuous planning of hand movements and isometric force trajectories. *Experimental Brain Research*, *115*(2), 217–233. <https://doi.org/10.1007/PL00005692>
- Gold, J. I., & Shadlen, M. N. (2000). Representation of a perceptual decision in developing oculomotor commands. *Nature*, *404*(6776), 390–394.
<https://doi.org/10.1038/35006062>

- Goodman, D., & Kelso, J. A. (1980). Are movements prepared in parts? Not under compatible (naturalized) conditions. *Journal of Experimental Psychology. General*, *109*(4), 475–495. <https://doi.org/10.1037//0096-3445.109.4.475>
- Haith, A. M., Huberdeau, D. M., & Krakauer, J. W. (2015). Hedging Your Bets: Intermediate Movements as Optimal Behavior in the Context of an Incomplete Decision. *PLOS Computational Biology*, *11*(3), e1004171. <https://doi.org/10.1371/journal.pcbi.1004171>
- Haith, A. M., Pakpoor, J., & Krakauer, J. W. (2016). Independence of Movement Preparation and Movement Initiation. *Journal of Neuroscience*, *36*(10), 3007–3015. <https://doi.org/10.1523/JNEUROSCI.3245-15.2016>
- Hanes, D. P., & Schall, J. D. (1996). Neural Control of Voluntary Movement Initiation. *Science*, *274*(5286), 427–430. <https://doi.org/10.1126/science.274.5286.427>
- Hanks, T. D., Kopec, C. D., Brunton, B. W., Duan, C. A., Erlich, J. C., & Brody, C. D. (2015). Distinct relationships of parietal and prefrontal cortices to evidence accumulation. *Nature*, *520*(7546), 220–223. <https://doi.org/10.1038/nature14066>
- Kaufman, M. T., Churchland, M. M., Ryu, S. I., & Shenoy, K. V. (2014). Cortical activity in the null space: permitting preparation without movement. *Nature Neuroscience*, *17*(3), 440–448. <https://doi.org/10.1038/nn.3643>
- Kaufman, M. T., Seely, J. S., Sussillo, D., Ryu, S. I., Shenoy, K. V., & Churchland, M. M. (2016). The Largest Response Component in the Motor Cortex Reflects Movement Timing but Not Movement Type. *ENeuro*, *3*(4), ENEURO.0085-16.2016. <https://doi.org/10.1523/ENEURO.0085-16.2016>
- Klein-Flügge, M. C., Nobbs, D., Pitcher, J. B., & Bestmann, S. (2013). Variability of Human Corticospinal Excitability Tracks the State of Action Preparation. *Journal of Neuroscience*, *33*(13), 5564–5572. <https://doi.org/10.1523/JNEUROSCI.2448-12.2013>
- Kurata, K. (1989). Distribution of neurons with set- and movement-related activity before hand and foot movements in the premotor cortex of rhesus monkeys. *Experimental Brain Research*, *77*(2), 245–256. <https://doi.org/10.1007/BF00274982>
- Lara, A. H., Elsayed, G. F., Zimnik, A. J., Cunningham, J. P., & Churchland, M. M. (2018). Conservation of preparatory neural events in monkey motor cortex regardless of how movement is initiated. *ELife*. <https://doi.org/10.7554/eLife.31826>
- Leyton, A. S. F., & Sherrington, C. S. (1917). Observations on the Excitable Cortex of the Chimpanzee, Orang-Utan, and Gorilla. *Quarterly Journal of Experimental Physiology*, *11*(2), 135–222. <https://doi.org/10.1113/expphysiol.1917.sp000240>
- Nashed, J. Y., Crevecoeur, F., & Scott, S. H. (2014). Rapid online selection between multiple motor plans. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, *34*(5), 1769–1780. <https://doi.org/10.1523/JNEUROSCI.3063-13.2014>
- Pruszynski, J. A., Kurtzer, I., & Scott, S. H. (2008). Rapid motor responses are appropriately tuned to the metrics of a visuospatial task. *Journal of Neurophysiology*, *100*(1), 224–238. <https://doi.org/10.1152/jn.90262.2008>

- 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. *Journal of Neurophysiology*, *61*(3), 534–549.
- Rosenbaum, D. A. (1980). Human movement initiation: Specification of arm, direction, and extent. *Journal of Experimental Psychology: General*, *109*(4), 444–474. <https://doi.org/10.1037/0096-3445.109.4.444>
- Schluter, N. D., Rushworth, M. F., Passingham, R. E., & Mills, K. R. (1998). Temporary interference in human lateral premotor cortex suggests dominance for the selection of movements. A study using transcranial magnetic stimulation. *Brain*, *121*(5), 785–799. <https://doi.org/10.1093/brain/121.5.785>
- Selen, L. P. J., Shadlen, M. N., & Wolpert, D. M. (2012). Deliberation in the Motor System: Reflex Gains Track Evolving Evidence Leading to a Decision. *The Journal of Neuroscience*, *32*(7), 2276–2286. <https://doi.org/10.1523/JNEUROSCI.5273-11.2012>
- Shenoy, K. V., Sahani, M., & Churchland, M. M. (2013). Cortical Control of Arm Movements: A Dynamical Systems Perspective. *Annual Review of Neuroscience*, *36*(1), 337–359. <https://doi.org/10.1146/annurev-neuro-062111-150509>
- Tanji, J., & Evarts, E. V. (1976). Anticipatory activity of motor cortex neurons in relation to direction of an intended movement. *Journal of Neurophysiology*, *39*(5), 1062–1068. <https://doi.org/10.1152/jn.1976.39.5.1062>
- Thura, D., & Cisek, P. (2014). Deliberation and Commitment in the Premotor and Primary Motor Cortex during Dynamic Decision Making. *Neuron*, *81*(6), 1401–1416. <https://doi.org/10.1016/j.neuron.2014.01.031>
- Weinrich, M., & Wise, S. P. (1982). The premotor cortex of the monkey. *Journal of Neuroscience*, *2*(9), 1329–1345. <https://doi.org/10.1523/JNEUROSCI.02-09-01329.1982>
- Wong, A. L., & Haith, A. M. (2017). Motor planning flexibly optimizes performance under uncertainty about task goals. *Nature Communications*, *8*, 14624. <https://doi.org/10.1038/ncomms14624>