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Neural mechanisms of movement planning: motor cortex and beyond

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Neurons in motor cortex and connected brain regions fire in anticipation of specific movements, long before movement occurs. This neural activity reflects internal processes by which the brain plans and executes volitional movements. The study of motor planning offers an opportunity to understand how the structure and dynamics of neural circuits support persistent internal states and how these states influence behavior. Recent advances in large-scale neural recordings are beginning to decipher the relationship of the dynamics of populations of neurons during motor planning and movements. New behavioral tasks in rodents, together with quantified perturbations, link dynamics in specific nodes of neural circuits to behavior. These studies reveal a neural network distributed across multiple brain regions that collectively supports motor planning. We review recent advances and highlight areas where further work is needed to achieve a deeper understanding of the mechanisms underlying motor planning and related cognitive processes.

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Introduction

During perceptual decision-making, behavior-related information flows from sensory to motor areas. Decisions occur in parts of the brain where correlations between neural activity and future actions first emerge. These correlations are also signatures of 'motor planning' (also referred to as 'movement preparation'). Motor planning has been studied extensively in tasks in which a sensory stimulus instructs an action after an imposed delay. During the delay, neurons in frontal and parietal cortex and connected structures show persistent and ramping activity related to specific movements, long before movement onset (Figure 1a–d). This neural correlate of future movement is referred to as 'preparatory activity' (or 'anticipatory activity', 'build-up activity').

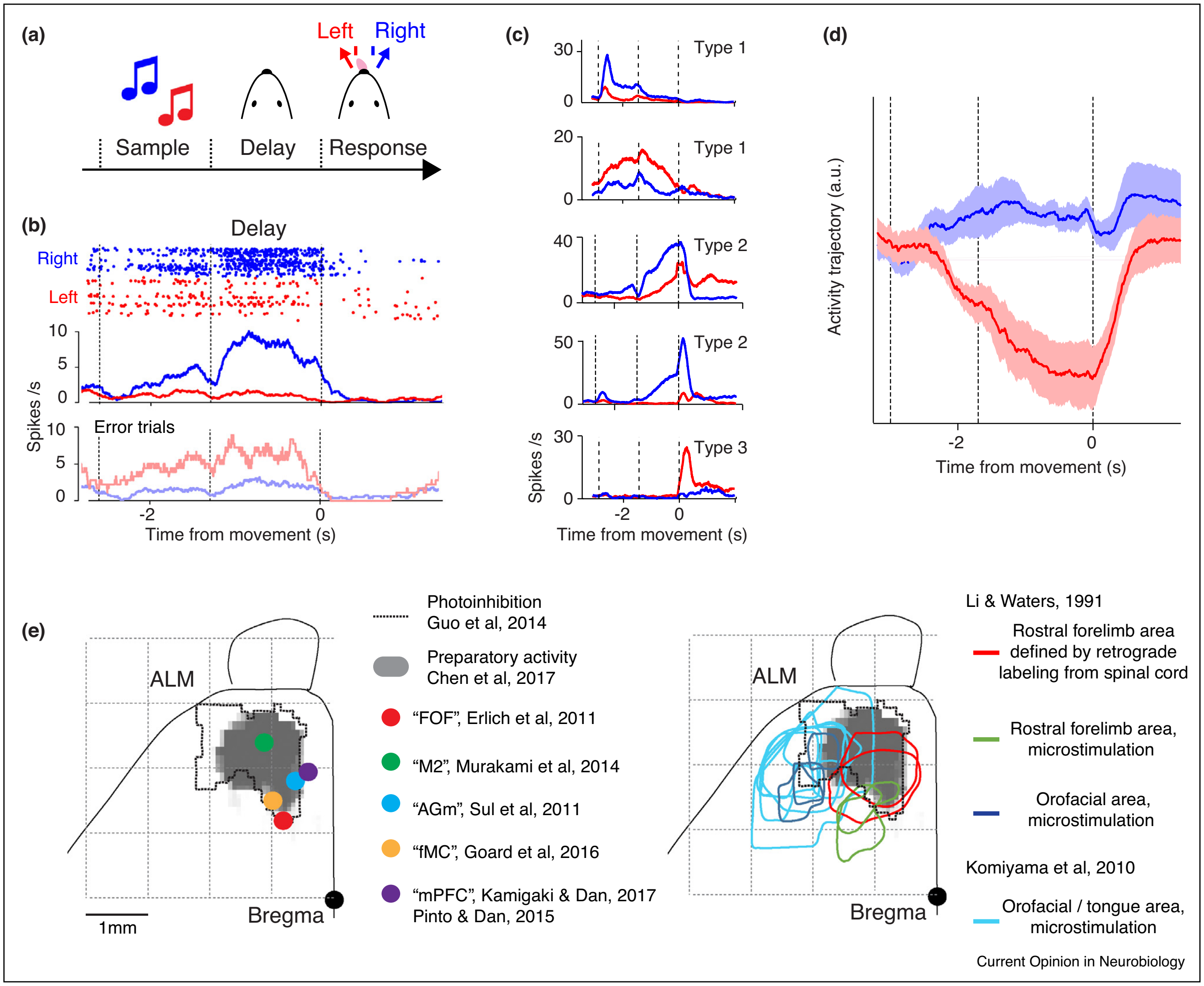
Motor planning and preparatory activity appear in systems neuroscience in three contexts. First, preparatory activity has been studied as part of motor control. Volitional movements are programmed to achieve a specific goal. Many movements are too rapid for online corrections. Movements are therefore preceded by periods of planning, during which parameters are set for specific upcoming movements. Evidence for motor planning comes from behavioral experiments: movements are faster and more accurate when subjects are given time to prepare specific movements [1–3].

Second, motor planning is a link between decision-making and action [4]. In the context of perceptual decision-making, selective ramping activity before a behavioral report (a movement) is often interpreted as a signature of accumulation of evidence [5,6•,7]. However, persistent and ramping activity are typically seen in structures that are also associated with motor control [8], and under conditions where evidence accumulation does not occur [9,10]. Conversely, in evidence accumulation tasks, 'perceptual evidence' is expressed in motor parameters, which can even be read out in muscle tension [11]. In many cases, perceptual decision-making and motor planning thus appear to be one process [12,13] (but see [14]).

Third, motor planning is a prospective form of short-term memory (STM) that links past events and future movements. STM is often represented by 'persistent' changes in spike rates, or slow dynamics in spike rates, that can be maintained internally, in the absence of sensory input [15–18,19•,20]. Preparatory activity is an example of such a memory trace. The mechanisms underlying preparatory activity are therefore of broad significance.

Recent years have seen progress in understanding the neural mechanisms underlying preparatory activity and its role in controlling movements in trained behaviors. These advances are driven in part by large-scale neural recordings during behavior, and, in rodent studies, calibrated optogenetic manipulations. Discoveries made about neural dynamics in non-human primates have now been replicated in detail in the rodent brain. Conversely, analyses of neural mechanisms performed in

Figure 1



Preparatory activity in the mouse brain. **(a)** Delayed response task. **(b)** Example neuron. Top, raster plot, correct trials. Each dot corresponds to an action potential. Bottom, average spike rates for different trial types, including error trials. Note that on error trials the activity still predicts movement direction. **(c)** Additional example neurons. **(d)** Population activity projected onto the direction in activity space that best discriminates movements. **(e)** Regions in the motor cortex with various recording locations (left) and microstimulation locations (right) superposed. The outline corresponds to the standard mouse brain from the Allen Mouse Common Coordinate Framework. Note that studies on rats (FOF, M2) were scaled based on Ref. [79] to account for differences in brain size (scaling factor, 1.6, rat:mouse). Data from Refs. [19•,35•,36•,40–43,80–82].

rodents are now stimulating research in primates. Here we review recent work on motor planning with an emphasis on studies that probe how preparatory activity is related to movement and how preparatory activity is generated and maintained.

Localization of preparatory activity

As a neural correlate of motor planning, preparatory activity has to meet three criteria [21]. First, changes in neural spike rate must precede movement initiation. Second, neural activity must be selective for specific movements, such as saccade location, or movement direction of the hand, wrist or tongue. Third, details of the neural activity predict aspects of the subsequent movement execution, such as reaction time.

Neural activity consistent with motor planning was first recorded in non-human primates [22]. Monkeys were instructed to pull or push a lever, but only after a delayed go cue. A subset of neurons in the primary motor cortex increased their activity seconds before the go cue. This activity was selective for the movement. On error trials the activity still reflected the future movement rather than the instruction, a key signature of preparatory activity.