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# Motor maps and the cortical control of movement

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The brain's cortical maps serve as a macroscopic framework upon which additional levels of detail can be overlaid. Unlike sensory maps generated by measuring the brain's responses to incoming stimuli, motor maps are made by directly stimulating the brain itself. To understand the significance of motor maps and the functions they represent, it is necessary to consider the relationship between the natural operation of the motor system and the pattern of activity evoked in it by artificial stimulation. We review recent findings from the study of the cortical motor system and new insights into the control of movement based on its mapping within cortical space.

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## Introduction

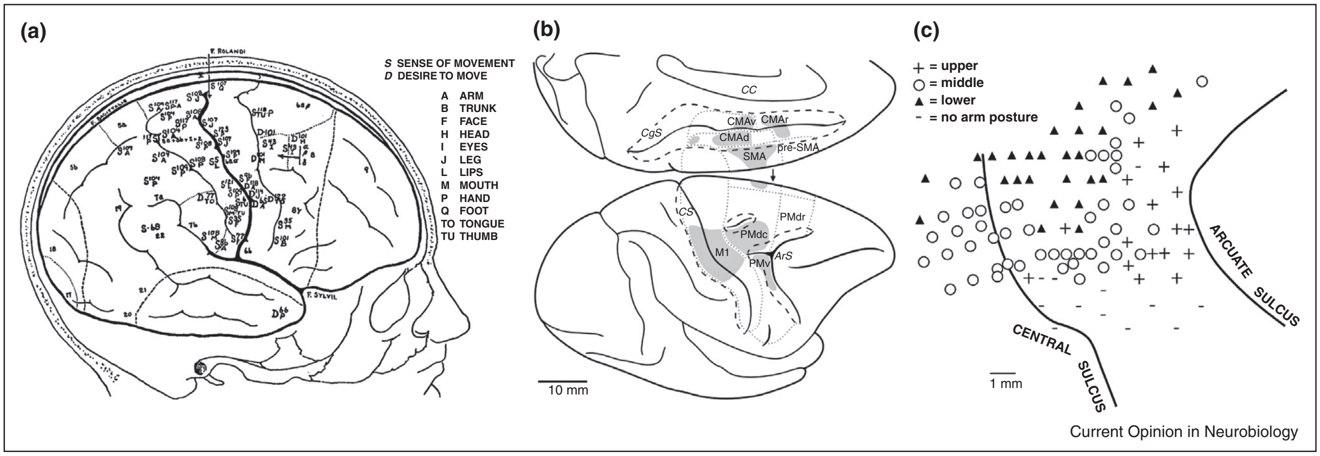
Mapping is a fundamental part of any systematic investigation of the unknown, yet the map of the brain still contains swaths of *terra incognita*. In addition to gross anatomical or cytoarchitectonic parcellation of the brain, physiological details must be added in the form of functionally defined brain regions. Many cortical areas can be surveyed by recording brain activity evoked by specific stimuli delivered to the sensory periphery, but motor maps are unique in the sense that they are created by directly stimulating the brain itself. Meaningful interpretation of a motor map therefore requires an understanding of both the natural flow of activity through the cortical motor system and its reverberation through the same network upon artificial stimulation. Here, we review recent studies of naturally occurring and stimulus-evoked activity in motor cortex in an attempt to strengthen the link between movements and their representation in cortex. The significance of maps for motor control and of their plasticity for recovery from injury is examined. Finally, we discuss new light-based methods for mapping motor cortex.

## What form do motor maps take and what purpose do they serve?

Traditionally, motor maps have been structured according to the correspondence between a cortical point and the muscles that are activated by its stimulation. Early experiments with cortical stimulation in human surgical patients revealed a somatotopic organization of motor cortex, giving rise to the enduring concept of the motor homunculus (Figure 1) [1]. This view progressed to include multiple premotor regions in the cortices of non-human primates [2,3], many of which project directly to the spinal cord [4] (Figure 1). Parameters of movement have also been used as an organizing principle for cortical mapping. In an influential series of experiments in monkeys, the firing rates of individual neurons in motor cortex were found to be related to the direction of forelimb movement by a sinusoidal function, termed cosine tuning [5]. Cells fired most vigorously during forelimb movements in a particular preferred direction; these directions can be weighted by firing rate and summed to produce a population vector that predicts movement direction [6]. This finding has led to the development of brain machine interfaces capable of extracting information from neuronal activity to control prosthetic [7,8] or paralyzed limbs [9]. Complementary experimentation with prolonged electrical stimulation revealed a macroscopic organization of movement categories or postures in motor cortex [10,11]. Similar movement maps have since been described in humans [12,13] and rodents [14–16].

Although the activity of motor cortex appears to be related to movement direction, this could also reflect the contribution of limb biomechanics to a system primarily concerned with the control of the musculature [17••]. For example, motor maps can be interpreted as representing movement endpoints or postures [18] or as the activation of muscle synergies independent of the initial configuration of the limb [19••]. Attempts to identify the movement-related variables encoded by the firing of motor cortex neurons have revealed a bewildering complexity of neuronal tuning [20]. The influence of externally applied loads or initial joint angle varies among neurons [11,21], with multiple forms of tuning reflected at the population level [22]. This complexity may result from a motor control strategy that employs sensory and proprioceptive feedback to optimize movements toward a behavioral goal despite variability and noise in both sensory input and motor output [20,23,24]. The observation that movements evoked by stimulation of a given

**Figure 1**



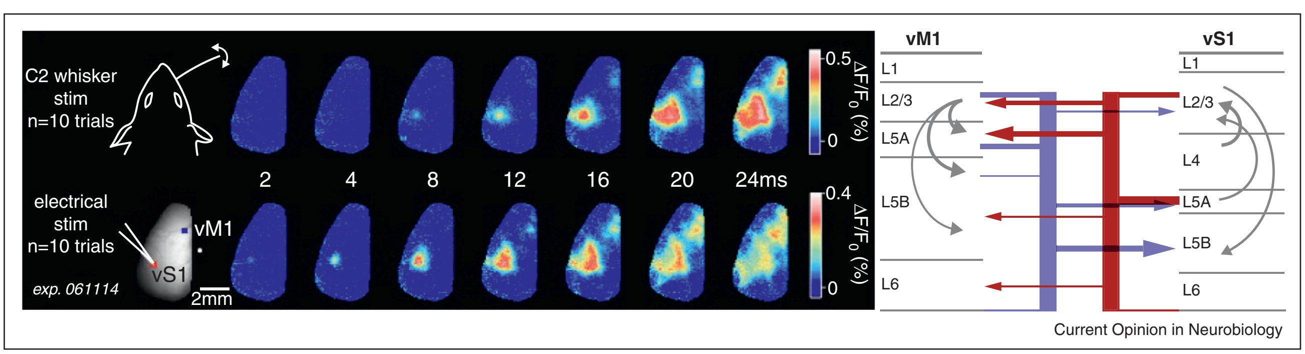

Movement maps in motor cortex. **(a)**, composite map created from data collected in human surgical patients [1]. **(b)** Multiple motor regions in macaque cortex, with areas containing retrogradely labeled corticospinal neurons marked in gray (modified from [4]). **(c)** Magnified view of macaque motor cortex labeled according to the endpoint of arm movement evoked by electrical stimulation [10]. Abbreviations: *ArS*, arcuate sulcus; *CC*, corpus callosum; *CgS*, cingulate sulcus; *CS*, central sulcus; M1, motor cortex; SMA, supplementary motor area; PM, premotor cortex (lower case suffixes denote dorsal, rostral, and/or ventral subregions), CMA, cingulate motor area.

cortical point tend to converge toward a consistent endpoint or posture rather than following an invariant trajectory could be taken as support for this model of cortical motor function.

An additional function of the cortical motor system is the integration of motor acts with sensory feedback. In rodents especially, it may be more correct to speak of the sensorimotor system as a whole given the degree of overlap between sensory and motor representations of the limbs [25,26]. The distinction between movement and sensation is also blurred in cases such as the rodent vibrissal system, where the whiskers must be moved to scan the environment. Though non-overlapping regions of vibrissal sensory and motor cortex exist in mice these areas are closely integrated (Figure 2). Neuronal firing in whisker motor cortex encodes the angular position of vibrissae [27] and modulates somatosensory cortical activity [28], whereas stimulation of sensory cortex drives whisker movements via a direct projection to the brainstem [15]. Sensorimotor integration extends beyond the somatosensory system, with motor activity modulating the function of visual cortex [29,30•].

More fundamentally, one can ask why topographically organized maps should exist at all, rather than a more stochastic ("salt and pepper") arrangement of neurons. Explanations for clustering include the reduced axonal lengths needed to link preferentially interconnected neurons with similar response properties [31]. Another

**Figure 2**




Natural and stimulus-evoked patterns of dynamic cortical activity. At left, voltage-sensitive dye imaging data illustrating the flow of activity through cortex following tactile stimulation (top) and electrical microstimulation of sensory cortex [52]. The flow of natural or evoked activity between whisker sensory (vS1, red dot at lower left) and motor cortex (vM1, blue dot) depends on the connectivity between these regions (right) [49].