Published in final edited form as:
Cortex. 2010 February ; 46(2): 270–271. doi:10.1016/j.cortex.2008.07.005.

Columnar Organization in the Motor Cortex

Nicholas G. Hatsopoulos
Dept. of Organismal Biology and Anatomy and Committees on Computational Neuroscience and Neurobiology, University of Chicago, Chicago, IL 60637

Despite many attempts to find spatial structure in the functional properties of neurons within the primary motor cortex (MI), there is still no compelling evidence for such structure despite the anatomical similarities between motor cortex and other neocortical areas. This is a longstanding puzzle in motor cortical physiology because topographic structure of function is a hallmark of primary sensory cortices including the visual, somatosensory, and auditory cortices. In particular, experimental evidence has supported the idea of vertical columns perpendicular to the cortical surface which contain neurons that share similar sensory tuning properties. Moreover, horizontal spatial structure has been observed in sensory cortices, most elegantly manifested by the pinwheel structure of orientation tuning across V1 (Bonhoeffer and Grinvald, 1991). Although early work by Asanuma provided some evidence for somatotopic, columnar organization in MI using intracortical microstimulation (Asanuma, 1975), further research by many others did not support this perspective but rather suggested distributed and overlapping representations of body parts. Namely, nearby sites in motor cortex could represent or evoke very different muscles and joints, and multiple, spatially-distributed sites could represent very similar body parts (Donoghue, Leibovic et al., 1992; Schieber and Hibbard, 1993; Sanes, Donoghue et al., 1995). By focusing on movement parameters instead of body parts, recent studies have provided evidence that a topographic organization of directional tuning does exist within the motor cortex (Amirikian and Georgopoulos, 2003; Georgopoulos, Merchant et al., 2007). However, it still remains controversial as to which movement parameters, if any, are truly encoded in single MI neurons.

Stark and colleagues (Stark, Drori et al., in press) attempt to tackle the problem of encoding as well as its possible local spatial organization within MI by addressing a fundamental problem that is faced in motor physiology. The problem is that natural movement is characterized by movement parameters that are highly correlated with each other. For example, in the classic center-out task used by many physiologists to study directional tuning in MI, the direction of movement is correlated with the position of the hand. When the hand moves to the right, the hand spends all of its time in the right portion of the workspace. Likewise, speed and position are correlated such that the hand is moving slowly at the center and at the periphery while it is moving more quickly in between. Stark and Abeles attempted to alleviate the problem of correlations by having monkeys perform two tasks: a scribbling task and a path-tracking task. In both tasks, the monkey moved its hand in a non-stereotyped fashion throughout the workspace. These tasks have two advantages over

Correspondence should be addressed to Nicholas G. Hatsopoulos: University of Chicago 1027 E 57th Street, Room 202 Chicago IL, 60637 (nicho@uchicago.edu).

previous stereotyped behavioral paradigms: 1) many of the parametric correlations at zero time-lag are removed, and 2) the hand visits larger portions of the parametric space and workspace. However, as the authors pointed out, there remain time-lagged correlations between position and its derivatives.

To account for these remaining correlations, the authors approached the problem in a very clever way. The authors developed encoding models that included all three primary kinematic parameters: position, velocity (speed and direction), and acceleration (acceleration magnitude and direction). They then systematically varied the temporal lags of all three parameters and computed the "contribution" (i.e. the percentage of variance accounted for) of each parameter over all possible time lags. They searched for fixed time-lag planes of significant contribution in which one parameter contributed significantly regardless of the time-lags of the other two parameters. These fixed time-lag planes of contribution could not be explained by time-lagged parametric correlations because the significant contributions of the one parameter occurred at all relative time-lags between that parameter and the other two. The authors found that two thirds of MI neurons exhibited single planes of significant contribution for only one parameter indicating that they encoded a single movement parameter. Among these neurons, the vast majority encoded velocity while a minority encoded either position or acceleration.

Having identified neurons that encoded a single kinematic parameter, the authors proceeded to compare the encoding similarity between neurons recorded within the same electrode tract (i.e. site) or electrode. They found that pairs of these neurons encoded the same kinematic parameter (i.e. position, velocity, or acceleration) more often than chance when they were recorded on the same site or electrode. Moreover, as others had found for directional tuning (Ben-Shaul, Stark et al., 2003; Amirikian and Georgopoulos, 2003; Georgopoulos, Merchant et al., 2007), these authors found that neurons shared similar preferred kinematic values within the same electrode site and particularly within the same electrode. More interestingly, the authors went one step further and compared single-unit (SU) and multi-unit (MU) encoding on the same electrode and also found that they shared the same parametric encoding more often than randomly chosen SU/MU pairs and among those pairs that encoded the same parameter, they shared similar preferred tuning values. These results applied for both raw MU activity as well as so-called "de-spiked" MU activity in which they removed the SU spikes from the voltage trace. Because MU activity corresponds to the aggregate spiking of multiple neurons within a region of 200 microns, these results provide some of the strongest support to date that the motor cortex possesses functional clusters composed of perhaps hundreds of neurons encoding a single common parameter with similar preferred tuning.

Despite this evidence supporting functioning clustering within motor cortex, the authors do acknowledge results which are difficult to reconcile with a columnar structure. First, the similarity in kinematic encoding between neurons recorded on the same site or electrode was rather weak, and there were cases where nearby neurons were tuned to different kinematic parameters or, if they shared common parametric tuning, they had very large differences in preferred tuning. In addition, there remained one third of recorded neurons that encoded more than one kinematic parameter suggesting a more complex functional architecture. Although beyond the scope of this study, a perhaps more general and fundamental issue which will require further research is to what extent individual neurons truly encode any single movement parameter. Although the authors demonstrate very elegantly a correlation between MI activity and single kinematic parameters, it still remains to be seen whether individual MI neurons invariantly specify a given parameter regardless of context, a hallmark of genuine encoding (Hatsopoulos, Saleh et al., in press). Previous attempts to characterize the encoding properties of MI neurons have failed to show invariant

specification across different portions of the workspace (Caminiti, Johnson et al., 1990), different postural states (Scott and Kalaska, 1995), different task paradigms (isometric versus isotonic) (Sergio and Kalaska, 1998), and even across time (Sergio and Kalaska, 1998; Johnson, Coltz et al., 1999; Sergio, Hamel-Paquet et al., 2005; Hatsopoulos, Xu et al., 2007).

References

Amirikian B, Georgopoulos AP. Modular organization of directionally tuned cells in the motor cortex: Is there a short-range order? Proc Natl Acad Sci U S A. 2003; 100:12474–9. [PubMed: 14523235]

Asanuma H. Recent developments in the study of the columnar arrangement of neurons within the motor cortex. Physiological Reviews. 1975; 55:143–156. [PubMed: 806927]

Ben-Shaul Y, Stark E, Asher I, Drori R, Nadasdy Z, Abeles M. Dynamical organization of directional tuning in the primate premotor and primary motor cortex. J Neurophysiol. 2003; 89:1136–42. [PubMed: 12574486]

Bonhoeffer T, Grinvald A. Iso-orientation domains in cat visual cortex are arranged in pinwheel-like patterns. Nature. 1991; 353:429–31. [PubMed: 1896085]

Caminiti R, Johnson PB, Urbano A. Making arm movements within different parts of space: Dynamic aspects in the primate motor cortex. Journal of Neuroscience. 1990; 10:2039–2058. [PubMed: 2376768]

Donoghue, JP.; Leibovic, S.; Sanes, JN. Organization of the forelimb area in squirrel monkey motor cortex: Representation of digit, wrist, and elbow muscles; 1992. p. 1-19.

Georgopoulos AP, Merchant H, Naselaris T, Amirikian B. Mapping of the preferred direction in the motor cortex. Proc Natl Acad Sci U S A. 2007; 104:11068–72. [PubMed: 17569784]

Hatsopoulos, NG.; Saleh, M.; Mattiello, JA. Encoding and beyond in the motor cortex. In: Platt, ML.; Ghazanfur, AA., editors. Primate neuroethology. Oxford University Press; Oxford: in press

Hatsopoulos NG, Xu Q, Amit Y. Encoding of movement fragments in the motor cortex. J Neurosci. 2007; 27:5105–14. [PubMed: 17494696]

Johnson MT, Coltz JD, Hagen MC, Ebner TJ. Visuomotor processing as reflected in the directional discharge of premotor and primary motor cortex neurons. J Neurophysiol. 1999; 81:875–94. [PubMed: 10036299]

Sanes JN, Donoghue JP, Thangaraj V, Edelman RR, Warach S. Shared neural substrates controlling hand movements in human motor cortex. Science. 1995; 268:1775–1777. [PubMed: 7792606]

Schieber MH, Hibbard LS. How somatotopic is the motor cortex hand area? Science. 1993; 261:489–92. [PubMed: 8332915]

Scott SH, Kalaska JF. Changes in motor cortex activity during reaching movements with similar hand paths but different arm postures. Journal of Neurophysiology. 1995; 73:2563–2567. [PubMed: 7666162]

Sergio LE, Hamel-Paquet C, Kalaska JF. Motor cortex neural correlates of output kinematics and kinetics during isometric-force and arm-reaching tasks. J Neurophysiol. 2005; 94:2353–78. [PubMed: 15888522]

Sergio LE, Kalaska JF. Changes in the temporal pattern of primary motor cortex activity in a directional isometric force versus limb movement task. J Neurophysiol. 1998; 80:1577–83. [PubMed: 9744964]

Stark E, Drori R, Abeles M. Cortex. in press.