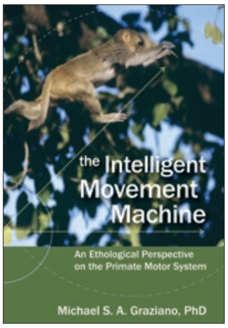
The motor cortex re-imagined



The Intelligent Movement Machine: An Ethological Perspective on the Primate Motor System

by Michael S A Graziano

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Reviewed by Reza Shadmehr

At a time when investigating the functional anatomy of the motor cortex is all but out of fashion in favor of black-box decoders and brain-machine interfaces, it is pure joy to read about a decade of results from a small lab that blazed a lonely trail. Controversial and thought provoking, Michael Graziano's *Intelligent Movement Machine* is a short, but eloquent, argument for a fundamentally different view of the motor cortex. The resulting theory is radical, with elements that make little connection to a large body of established data. However, the book succeeds in shining much needed light from a new angle on the puzzle of the motor cortex.

The book's main hypothesis is that the different frontal motor areas do not represent a hierarchy of motor control. Thus, the term primary motor cortex (M1) is unjustified, as it may be no more primary than the premotor or the supplementary motor areas. Instead, the motor cortex is a two-dimensional map representing statistics of natural movements, which Graziano refers to as an 'action map'. These natural movements are quantified through field studies, producing the surprising observation that reaching constitutes only 3% of natural movement in monkeys, whereas manipulation and hand-to-mouth interactions each constitute about 20%, with the remainder consisting mostly of exploratory gaze. The multiple hand areas that make up parts of M1, ventral premotor and dorsal premotor, for example, arise from the seven or eight ethological categories of movements. Notably, the ethological movements can be generated when the motor cortex is stimulated electrically for half a second or longer using a technique called long-duration stimulation.

The era of long-duration stimulation ended in the late nineteenth century but was revived by Graziano a century later, partly because of the success of the approach in the study of the oculomotor system. "To motor physiologists, [they] seemed out of [their] minds," but Graziano and colleagues found that long-duration stimulation produced convergence of the arm to a specific final joint configuration, regardless of the initial start position. When the final posture was mapped on to the motor cortex, ventral stimulation sites placed the hand in upper regions of the workspace and dorsal sites placed it in lower regions. Anterior stimulation sites placed it in more lateral locations and posterior sites placed it in more medial locations. Alltogether, seven classes of movements were identified through stimulation, ranging from hand placement in specific regions of the workspace to chewing and climbing. The resulting map provides no evidence for a hierarchy in motor cortex, as the movements caused by M1 stimulation are neither simple nor a subset of movements produced by stimulation in premotor cortex or elsewhere.

I suspect that the reader's greatest problem with the proposed theory will be its reconciliation with long-established data from recordings during voluntary movements and anatomical data from axonal track tracing. The book attempts to answer these concerns but leaves several holes. For example, stimulation produces a movement, but the muscle activation patterns lack some of the key characteristics of a voluntary movement. Also, there is much data to support the idea that at least parts of M1 are functionally different from the more anterior motor cortex. Motor cortical cells in the depths of the central sulcus tend to have little, if any, activity during the delay period before a movement starts, whereas cells in more anterior regions, such as premotor, have substantial activity during the period in which the animal is waiting for a 'go' cue to perform the movement. Context (for example, the order of the movements) has a bigger role in modulating the activity of cells in the supplementary motor areas than in M1, where there is greater sensitivity to the specific forces and motions of the movement and less to context. In short, there are big differences in the sensitivity of the various parts of the motor cortex to motor output variables such as forces, postures, spatial kinematics and even choice of limb. This differential sensitivity extends to coding of instructional cues, prior knowledge and conditional response—selection rules that simply do not fit neatly into Graziano's action map. Similar arguments can be made about the distinct anatomical connections of the regions that make up the traditional view of the motor cortex. For example, the cells of M1 within the depths of the sulcus have direct connections to the spinal motor neurons of arm and hand muscles, including fingers, wrist, elbow and shoulder, whereas the cells of M1 on the crown of the gyrus project only to spinal interneurons. It is difficult to dismiss the implications of these results with regard to the hierarchy hypothesis and the 'primacy' of M1.

For the many engineering students who are working on decoding the neuronal activity to predict the intended movement of the animal, the book does not disappoint. Graziano suggests that motor cortical cells primarily encode a desired posture, essentially a set of joint angles. A cell fires less during a movement for which the arm will terminate far from its preferred posture. This is in vivid contrast to the traditional approaches, in which cell activity is fitted to functions of movement direction.

The Intelligent Movement Machine puts forth the first theory of motor cortex organization as viewed from the perspective of stimulation. This controversial theory is driven by data from an uncommon methodology. However, because it attempts to provide a rationale for why we have multiple motor areas, it is an intriguing starting point. ■

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