PERSPECTIVES

Cables *vs.* networks: old and new views on the function of motor cortex

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Early in the physiological study of the motor cortex, one experimental question began to dominate the research. How are points in cortex connected to muscles? The question fosters a simplistic, feed-forward view of motor cortex in which its intrinsic processing is ignored and its function is assumed to be defined almost entirely by the cables that run down to the spinal cord, relay onto motor neurons, and thus cause muscle contraction. This perspective still pervades almost all modern thinking about the motor cortex. As a result, a more realistic view of motor cortex as a control network has been hindered. The study by Capaday *et al.* (2011) in this issue of *The Journal of Physiology*, examining the lateral interactions among neurons in motor cortex, represents an important step beyond the limited muscle-map conception and toward a better understanding of the processing network within the cortex itself.

The distinction between the simplistic cables view and the more sophisticated network view emerged more than 100 years ago. Fritsch & Hitzig (1870) discovered motor cortex in the dog brain. They saw motor cortex as comprising a set of cortical centres, each centre a sophisticated processor of sensory and motor information that coordinated among the muscles and joints of a particular body part to produce movement. Fritsch and Hitzig proposed nothing like the simplistic cables view of motor cortex.

Among the many early physiologists to study the motor cortex, Beevor & Horsley (1890) performed an experiment in which they dissected away the cortex itself and electrically stimulated the severed fibres of the pyramidal tract, obtaining for the first time a clean map of the body's musculature. This experiment was arguably the unintentional beginning of the view of motor cortex as a muscle map whose intrinsic processing could be largely ignored and whose functionality was defined by descending connectivity from cortex to the motor neurons in the spinal cord.

Through more than 100 years surprisingly little is to be found on the specifics of network interactions in motor cortex. Sherrington (1939) provided one of the few counterexamples, concluding that a major part of motor cortex function was the lateral linking of different cortical sites to obtain a rich repertoire of motor output.

In modern research on motor cortex, a major category of study emphasizes the mapping from motor cortex to muscles. Most of these studies indicate that the muscle map is extensively overlapped and topologically complex. These studies include anatomical tracing and stimulus triggered averaging (e.g. Park *et al.* 2004; Rathelot & Strick, 2006). While such studies are important, they continue to focus on one question, fostering the idea of a motor cortex whose function is defined by its map.

In this context, the work of Capaday and colleagues is a welcome departure from the usual. It represents one of the few lines of research to address the question of lateral interactions in the motor cortex (e.g. Schneider *et al.* 2002; Capaday *et al.* 2011). Capaday and colleagues find that activity originating at one site in motor cortex can drive a relatively large cortical neighbourhood of about 7 mm^2. Because of this large zone of influence, the concept of a muscle representation breaks down. Each cortical site is part of a cortical network rather than merely the head of a cable. The activity of a cortical neuron presumably spreads in a complex, context-dependent fashion through the network and has a causal effect on movement via many paths, some more direct and some less direct. Focusing on only the most direct path limits our understanding of the system. The study helps to establish a fundamentally different, more realistic view of motor cortex function.

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