

# Probing cortical function with electrical stimulation

TO THE EDITOR—In a recent *News and Views*<sup>1</sup>, Peter Strick comments on our recent finding that microstimulation of motor cortex evokes complex, coordinated behavior<sup>2</sup>. A major concern he raises is that “one might ask whether electrical stimulation of the cortex is capable of revealing its function.” We agree that one should always ask such questions about all experimental methods. However, a large body of recent work successfully probes cortical function using electrical stimulation. For example, stimulation of monkey visual area MT influences the monkey’s perceptual decisions about the direction of motion of visual stimuli<sup>3</sup>. Stimulating primary somatosensory cortex influences the monkey’s perceptual decisions about tactile stimuli<sup>4</sup>, and stimulating the frontal eye fields influences the monkey’s target selection<sup>5</sup>. Many researchers have used electrical stimulation to study functional maps of eye and head movement<sup>6–8</sup>. We took the well-established protocol of stimulating on a behaviorally relevant time scale and applied it to motor cortex. The stimulation durations that we used are within the range of these previous studies, and the current intensities are within the range used in the oculomotor studies. As in previous studies, we evoked meaningful behaviors.

Strick points out that most studies of motor cortex use shorter stimulation trains and lower currents than we did. Early microstimulation studies<sup>9</sup> sought a

stimulation protocol that would activate the most direct pathway from cortex to muscles while avoiding other connected pathways such as to the spinal interneurons, neighboring parts of motor cortex, and other cortical and subcortical structures, many of which also project to the spinal cord. These alternative routes were seen as an experimental nuisance, clouding the study of motor cortex. Unfortunately, further experiments showed that the spread of signal through these alternative routes was inevitable. Even a single pulse of current to motor cortex activates widespread circuits, and longer trains evoke even more transsynaptic signal<sup>10</sup>. Because no stimulation protocol could limit activity to the ‘proper’ descending pathway, the technique fell out of favor and was not explored as fully as in the oculomotor or sensory community.

We believe that a new view of motor cortex is emerging. The motor system, like any other system is a network, not a simple, uni-directional pathway. The transsynaptic spread of signal through this network is hardly an artifact to be avoided, but rather a necessary part of its function. The function of the directly stimulated tissue depends on its connections with, and therefore its influence on, the wider network. Strick suggests that our findings may be partly a function of influencing the spinal interneurons. We agree that stimulation probably recruits interneurons in many

parts of the motor network. This recruitment of interneurons presumably occurs every time we make a movement; it is part of motor function.

Finally, it is not surprising that stimulation of the white matter directly below motor cortex, which connects motor cortex to the rest of the motor network, produces some of the components that we observed on stimulating cortex. It is important to stress the impossibility of studying the function of one small piece of a network, such as a volume of cortex around the tip of the electrode, in isolation of the rest of the network.

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