

ity that arise from the different solutions may provide an adaptive advantage.

An intriguing implication of the Schummers et al. findings is that the precise mechanisms that generate orientation selectivity could be different at different locations in cortex—there is not just one way in which orientation selectivity is generated. This notion challenges the conventional view of visual cortex as a more-or-less crystalline structure in which the same circuit iterates the same function across the cortical surface, with each module varying only with respect to the portion of the visual field represented. If the relationships between local circuits and function vary across the cortical surface, then the challenge for linking circuits to function becomes even greater than assumed. These findings therefore underscore the need for the development of increasingly sophisticated methods to more directly link neural circuits to function. Rather than extrapolating between one set of studies which reveals circuits and another that reveals function, further progress will likely benefit from more directly correlating the circuitry of single cortical neurons or identified cell types to their functional properties *in vivo*. These new findings should provide a much-needed push in that direction.

Edward M. Callaway

The Salk Institute for Biological Studies
Systems Neurobiology Laboratories
10010 North Torrey Pines Road
La Jolla, California 92037

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A Hidden Sensory Function for Motor Cortex

Sensory perception has traditionally been attributed to the activation of sensory cortices. However, by inducing an illusory perception of movement, Naito and colleagues show in this issue of *Neuron* that the illusory perception of movement is related to activation of primary motor cortex.

Which patterns of neuronal activity are related to kinesthesia—that is, with the sense of our own corporal movements? It is not easy to tackle this question, because a number of factors come into play in this perceptual process. When a voluntary movement is made, in addition to the neuronal activity associated with kinesthesia, there is also cortical activity related to the intention of movement (Roland et al., 1980), to the motor commands themselves (Georgopoulos et al., 1982) and to the sensory information fed back into the cortex by proprioceptors (Dietz, 2002). To study kinesthesia, then, what is required is an experimental paradigm that allows the neuronal activity associated with this phenomenon to be isolated from the neuronal activity of other processes that naturally occur simultaneously with it.

By taking advantage of an interesting sensory illusion, Naito and colleagues (2002) inquired into the neural basis of the sense of kinesthesia in human subjects. They were able to produce an illusory perception of movement in either one of the hands through a vibratory stimulus (80 Hz) applied to the tendon of the *carpi ulnaris extensor* muscle of the wrist. The illusion of movement is produced as the vibration in the tendon activates the muscle spindles in a similar way to when the muscle actually stretches.

In principle, this illusion should allow us to study the patterns of neural activity associated with kinesthesia in the absence of movement, but the problem is how to eliminate the cortical activity arising in the muscle spindles activated by the vibratory stimulus? Naito and colleagues resolved this problem elegantly by *transferring* the illusion of movement to the nonstimulated hand. The transference of the illusion occurs when both hands come into skin contact (palm to palm or palm to back of hand). Upon detecting that the vibrated hand is moving and that both hands are in contact, the brain—after an interval of a few seconds (4–12)—interprets this information as if both hands were moving.

Since the subjects were not asked to generate any motor action, the hemisphere controlling the nonstimulated hand was free of any activity related to the intention of movement, to motor commands, and to the sensory information that motion would have been generated. It can be assumed that a pure sensory percept of kinesthesia exists in the hemisphere controlling the hand with the transferred illusion. The perception of the illusion of movement in the nonstimulated hand thus constitutes an ideal phenomenon for studying the neuronal basis of kinesthesia.

What is the pattern of neural activity related to the illusory perception of movement? By recording neuronal activity through fMRI, Naito and colleagues obtained an unexpected and surprising result: when the image of cortical activity during a control condition (stimulus vibration with separated hands) was subtracted from the image of cortical activity during the perception of the illusion (stimulus vibration with hands in contact), the only area that remained active—that can be related exclusively to the perception of the transferred illusion—was the area 4p in the primary motor cortex (MI). This result is surprising because, as the authors themselves mention, the sense of kinesthesia has traditionally been associated with the somatosensory cortex.

Such an extraordinary result required incisive tests,

and Naito and colleagues produced them. To probe that MI is exclusively activated during the perception of movement, they used transcranial magnetic stimulation (TMS) to stimulate area 4p in the cortical hemisphere that controls the hand with the transferred illusion and recorded the amplitude and latency of the motor evoked potentials (MEPs) thus generated. The results demonstrate that amplitude of the MEPs increases and latency decreases only at the end of a 4–12 s period, the time required for the illusion to transfer to the nonstimulated hand. These results show that facilitation of MI occurs and is restricted only to the period of time when the subjects are feeling the illusion. Moreover, the authors found that the magnitude of the angle of movement experienced by subjects was directly correlated to amplitude and inversely correlated to latency of the MEPs.

What do the results obtained by Naito and colleagues mean? A direct interpretation of their results suggests that MI, in addition to its traditional assumed function in controlling the output of motor commands, also participates in the analysis of sensory information coming from the muscles (Fetz et al., 1980). This view is congruent with previous electrophysiological evidence showing that neuronal subpopulations in MI can participate in processes of decision making concerning sensory information (Salinas and Romo, 1998).

One crucial question emerges from these results: is the activity of neuronal populations in MI *sufficient* to generate the perception of corporal movement? Or, to put it more generally: can neuronal activity in a specific cortical area generate sensory percepts? To answer this question, a significant portion of research on the neuronal correlates of perception has attempted to test two hypotheses, not necessarily contradictory (Lamme et al., 2000; Pascual-Leone and Walsh, 2001; Romo et al., 1998). (A) Perception is related to the activity of exclusive and clearly localized cortical areas; or (B) perception emerges from the conjoined pattern of activity of many areas, including subcortical structures. Though it was not the purpose of Naito's study to tackle this question, the distribution of cortical activity shown in their fMRI images favors the second hypothesis. This shows that when the subjects perceive the illusion of movement, in addition to the activity of MI, there is cortical activity in the two supplementary motor areas, the two frontal opercular areas, the right dorsal premotor area, the right area 8, the right cytoarchitectonic area 2, and the right supramarginal gyrus. This distribution of activity suggests that, although activation of MI is crucial for the perception of movement, the conjoined activity of all these areas is necessary for the subjects to experience the sensation of limb motion.

As suggested by a growing body of evidence and now by the remarkable results of Naito and colleagues, our vision of the specialization of cortical areas as a paradigm of cerebral function should be widened to consider the perception process as a phenomenon that requires the activity of several brain areas, activated in a simultaneous, recurrent, and resonant way.

Victor de Lafuente and Ranulfo Romo
Instituto de Fisiología Celular

Universidad Nacional Autónoma de México
04510 México, D.F.
México

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