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You Can Observe a Lot by Watching: Hughlings Jackson's Underappreciated and Prescient Ideas about Brain Control of Movement

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Abstract

John Hughlings Jackson, the 19th-century British neurologist, first described what are today called Jacksonian seizures. He is generally associated with somatotopy, the idea that neighboring brain regions control neighboring body parts, as later represented pictorially in Wilder Penfield's "homunculus," or little man in the brain. Jackson's own views, however, were quite different, though this is seldom appreciated. In an 1870 article, Jackson advanced the hypotheses that each region of the cerebrum controls movements of multiple body parts, but to different degrees, and that the "march" of movements that typically occurs during Jacksonian seizures is caused by the downstream connections of the overactive neurons at the seizure focus, rather than a somatotopic organization of the cerebrum. Jackson's hypotheses, which were based almost entirely on his careful observations of movements during seizures, are well within the range of current hypotheses about how the frontal lobe is organized to control movements and thus deserve renewed attention.

Keywords

Hughlings Jackson, motor cortex, somatotopy, homunculus, distributed coding

> You can observe a lot by watching.
>
> —Yogi Berra

Introduction

John Hughlings Jackson (Fig. 1), the 19th-century British neurologist, did not poke electrodes into brains or use functional magnetic resonance imaging, electroencephalography, transcranial direct current stimulation, optogenetics, or any other technically sophisticated method. For the most part, he simply watched patients having seizures, or listened to the details of those seizures as described by patients' family members. Yet, just by paying close attention to the movement details and thinking about their likely causes, he was not only able to describe for the first time the consistent "march" of movements during one type of seizure (later named Jacksonian seizures) but also able to hypothesize how the brain is organized to control movements normally.

Jackson chronicled the sequence of movements he observed during the seizures (then called "convulsions") of individual patients. For example, in one seizure he witnessed in his office, Jackson described in detail how the movements began with flexion of the right index finger and thumb and continued with movements of the whole right arm, then the right side of the face (Jackson 1870).

At the time, Paul Broca, an esteemed French physician and scientist, had recently added the weight of his reputation in support of the idea that different parts of the cerebrum have distinct functions (Broca 1861). Both Broca and, even earlier, Jean-Baptiste Bouillaud (Bouillaud 1825; Finger 1994, 2000), also a French physician and scientist, had correlated language deficits with damage to the cerebral frontal lobe in human patients. Their findings supported the hypothesis that there is some localization of function in the cerebrum, a hypothesis previously asserted by the German-Austrian physician and anatomist, Franz Joseph Gall, who used bumps on skulls as

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Figure 1. John Hughlings Jackson. From Wellcome Images, CC BY 4.0.

evidence (Finger 1994, 2000; Gall and Spurtzheim 1810-1819).

Building on the idea of cerebral localization of functions, most readers of the time as well as today apparently drew from Jackson's articles the idea that the brain is organized somatotopically, with neighboring brain regions controlling movements of neighboring body parts (Graziano 2009). This idea presaged maps of body movements within the brain (Sherrington and Grunbaum 1902) and eventually the iconic representation of cerebral organization known as the "homunculus," devised by American-Canadian neurosurgeon Wilder Penfield and his colleague Edwin Boldrey to summarize their data (Fig. 2) (Penfield and Boldrey 1937), versions of which now adorn the pages of many neuroscience and physiology textbooks (Bear and others 2016; Boron and Boulpaep 2003; Fox 2008; Guyton and Hall 1996; Johnson 1998; Kandel and others 2013; Marieb 1998; Martini 1998; Nicholls and others 2001; Purves and others 2001; Shepherd 1994; Sherwood 2010; Stanfield 2017; Striedter 2016; Widmaier and others 2008).

Jackson is today closely linked to the idea of somatotopy. Jackson's own ideas about how the brain is organized to control movements, however, were actually more complex than somatotopy or a homunculus and foreshadowed current debates about how the motor cortex is organized to control movements of different body parts. His own hypotheses are laid out in certain passages of his 1870 article, "A Study of Convulsions" (Jackson 1870), that have largely been forgotten or misunderstood.

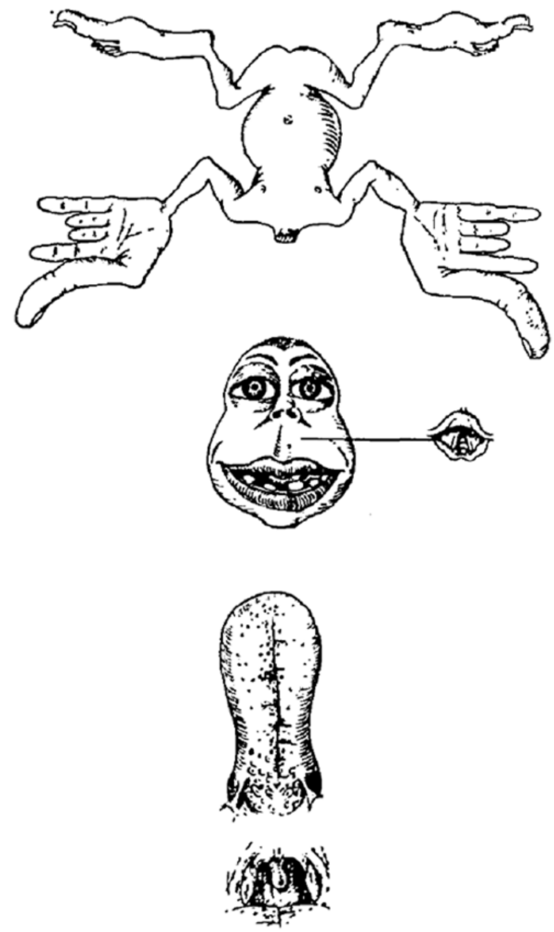

Figure 2. The original sensory and motor homunculus, indicating the relative positions and sizes of human postcentral and precentral cortical regions in which electrical stimulation evoked responses from different body parts. From Penfield and Boldrey (1937) by permission of Oxford University Press.

Cerebral Organization of Movement Control

Jackson summarized the movements occurring during what are now called Jacksonian seizures thus:

> The point of significance is that the spasmodic movements are not contemporaneous, but follow a distinct march, and a different march according as the spasm begins in the hand or in the foot. The sequence is, however, not simple. The spasm does not affect the arm, then cease, next affect the face, etc.

> It is a *compound* sequence. For instance, the face begins to be affected before the spasm of the arm ceases. (Jackson 1870)

From these observations, Jackson speculated about how the brain might be organized that would account for the sequences of movements during such seizures:

> Then it may be said that one convolution [cerebral gyrus] will represent only the movements of the arm, another only those of speech, another only those of the leg, and so on. The facts above stated show that this is not the plan of structure of the nervous system. Thus, to take an illustration, the external parts, x, y, and z, are each represented by units of the corpus striatum. But the plan of representation is not that some units contain x largely only, as x_3, others y largely only, as y_3, but that each unit contains x, y, and z—some, let us say, as x_3, y_2, z, others as x_2, y_3, z, etc. (Jackson 1870)

This is a challenging passage to decipher, but worth the effort. In his algebraic-like formulation, Jackson uses the letters, x, y, and z, to stand for body parts, such as the arm, face, and leg, respectively. He uses subscript numbers to indicate the quantitative extent to which each brain region controls each body part. For example, a "unit" or region of the brain labeled x_3 would control only the arm, while a region labeled x_3, y_2, z would control mostly the arm, but to a lesser extent the face, and to a still lesser extent the leg. A region labeled x_2, y_3, z would control mostly the face, but to a lesser extent the arm, and to a still lesser extent the leg.

Thus, what Jackson argues in this passage is that brain organization is *not* strictly somatotopic. Instead, he supports a kind of compromise between French scientist Marie-Jean-Pierre Flourens's idea that all parts of the cerebrum (but not all parts of the brain) contribute equally to each function (Flourens 1824) and Broca's (and earlier Bouillaud's) idea that each part of the cerebrum has a distinct function (Bouillaud 1825; Broca 1861; Finger 1994). Note that in the above passage Jackson was proposing an organization of the "corpus striatum"—the term at that time for part of the basal ganglia—but he also suggested in the same article that the cerebrum is similarly organized. Jackson was proposing a weighted distribution of function, in which each "unit" controls multiple body parts but controls some more than others. This idea also overlaps somewhat with psychologist and neuroscientist Karl Lashley's later conclusion from his own lesion experiments that while some cortical regions have specialized functions, others are largely "equipotential" for higher order functions (Lashley 1930).

According to Jackson's proposal, ablation of one region of the cerebrum should not prevent movement of any body part, and stimulation of just one movement-control region should trigger movements of multiple body parts. As he put it:

> When we come to the still higher evolution of the cerebrum, we can easily understand that, if the same plan be carried out, a square inch of convolution *may be wanting* [missing], without palsy [paralysis] of the face, arm, and leg, as x, y, and z are represented in other convolutions; and we can also easily understand that discharge of a square inch of convolution must put in excessive movement the whole region, for it contains processes representing x, y, and z, with grey matter in exact proportion to the degree of complexity. (Jackson 1870)

Thus, in current language, Jackson was arguing that the cerebrum has a distributed and redundant organization for movement control.

Brain Control of Movement Sequences

The above passage provides Jackson's opinion on how seizures start: excessive neural activity at one cerebral location triggers movement of multiple body parts, though some more than others, and which body part moves most is determined by the location in the cerebrum (i.e., the epileptic focus). But why should seizure movement "march" from one body part to another? Even if brain organization is strictly somatotopic (which, as we have seen, Jackson did not suggest), one would not necessarily predict that seizure movements would shift systematically from each body part to its neighbor. One would only suppose this if one assumed that the excessive neural activity diffused gradually outward from the site at which it began, affecting all nearby neurons first and more distant neurons progressively later. Such a supposition does not fit well with our current knowledge of how neurons are linked to one another, often at some distance from their cell bodies, via axons and synaptic connections. Although some nearby neurons may be activated quickly via local axon collaterals, this is not the whole story, as the downstream effects depend on the cells' sets of synaptic connections. But did Jackson simply assume that neural activity diffuses locally within the brain?

It turns out that Jackson did not make this assumption. He and others of the time were well aware of the bundles of axons ("fibers") that mediate connections among parts of the central nervous system and he took these connections into account in his hypotheses. Jackson suggested that the sequence of movements during seizures (and normally) is determined independently from the combination of body parts that moves at any one moment:

> Co-ordination in Space—the power of using several muscles together for one purpose—is brought about by groupings of fibres. Co-ordination in Time—the process by which one movement follows another—is brought about by relations betwixt ganglion cells [neuronal cell bodies] . . . There must

> in health be fixed orders of simultaneous movements, and fixed orders of successions of movements.

He added in a footnote, "No doubt there are series of centres betwixt the convolutions and the muscles they move"(Jackson 1870).

Precisely what Jackson meant here is not entirely clear. But he certainly stated that a sequence of movements is caused by "relations betwixt ganglion cells," or, in current language, circuits. The cell bodies of the neurons that trigger the first movement in a sequence need not be near the cell bodies of the neurons that trigger the next movement; they might be far away, as long as there are axonal pathways and connections between them. This would be true both during a seizure and during normal movement sequences. If this is the case, then not only would each cortical region control movement of multiple body parts (to different degrees), but there need be no topographic map of the body at all, that is, no somatotopy, not even a coarse one. Instead, it would be the neural pathways and connections from the seizure focus that determine the sequence of movements.

Jackson's emphasis on pathways and circuits that mediate movement sequences anticipated studies of movement sequences elicited by electrical stimulation of the cerebrum. At the time Jackson published this article, it was generally believed that the cerebrum was electrically inexcitable. However, in the same year that Jackson published this article, German anatomist Gustav Fritsch and psychiatrist Eduard Hitzig published their own findings that weak and brief electrical stimulation of certain regions within a dog's frontal lobe could consistently trigger contractions of "narrowly limited muscle groups" (Fritsch and Hitzig 1870). Fritsch and Hitzig's work has sometimes been interpreted to indicate that each cortical region activates just one muscle.

Fritsch and Hitzig's own interpretation of their findings, however, appears to have been more nuanced than this and in some ways more like Jackson's hypothesis. In addition to triggering contractions of small sets of muscles by brief electrical stimulation of the frontal lobe, they also removed a small portion of the frontal lobe ("the piece was not as big as a small lentil"), where they had previously evoked movement of the right front leg by electrical stimulation and observed the dogs' behavior following this lesion. The dogs still ran, but used the right forepaw "wrongly." They summarized, "No movement was completely gone, however, the right leg was adducted less," adding, "it is certain that a lesion of this center only changes, but does not abolish the voluntary movement of the member [the forepaw] which is certainly in some way dependent from it, that the motor impulse must have still other centers and pathways to originate and to run to the muscles of that leg" (Fritsch and Hitzig 1870), essentially in agreement with Jackson's hypothesis of distributed and redundant cortical control of movement.

Other researchers soon jumped on the cortical stimulation bandwagon and some, in contrast to Fritsch and Hitzig, used long stimulations and were able to trigger sequential movements that were complex, involved multiple body parts, and looked more like natural movement sequences. David Ferrier, a Scottish neurologist and a colleague of Jackson's in a London hospital, stimulated cerebral cortical locations in monkeys and described such resulting movements (Ferrier 1874-1875). For example, one site of stimulation triggered a movement sequence that was "just such as when a monkey scratches its abdomen with its hind leg." At another site: "Long-continued stimulation brings the hand up to the mouth, and at the same time the angle of the mouth is retracted and elevated . . . These uniform results point very clearly to this as the centre for the biceps and muscles concerned in bringing the hand up to the mouth." At still another site, Ferrier found "a centre for the facial muscles concerned in the production of that expressional action so frequently exhibited by monkeys under the influence of fear or anger, viz. the exposure of the canine teeth."

Much later, and using more sophisticated techniques, Michael Graziano et al. evoked movement sequences in monkeys that were very similar to Ferrier's, using 500-ms stimulus trains to the frontal lobe (Graziano and others 2002). These movement sequences, like Ferrier's, included the hand moving to the mouth while the mouth opens (Fig. 3A), as well as (at different sites) a facial expression that involved baring the teeth. Similar results were later found with intracortical microstimulation in other primates (Kaas and others 2013), humans (Desmurget and others 2014), and rodents (Graziano 2016).

To some extent, even though he did not stimulate the brain, Jackson's 1870 article also anticipated the natural-appearing movement sequences elicited by Ferrier and by recent authors. For example, Jackson observed during one seizure: "The same side of the face is drawn, and the head is drawn toward the arm, which is raised to meet it. The patient's remark is, 'it seemed as if it wanted to draw the arm into the head.'" (Jackson 1870) It may be that the epileptic focus in this case was at a location similar to those later electrically stimulated by Ferrier, Graziano et al., Kaas et al., and Desmurget et al. and thus produced movements akin to bringing the hand to the mouth.

Jackson's Hypotheses and Contemporary Hypotheses

Jackson's scheme of weighted distribution of movement control regions in the cerebrum more generally presaged debates that have continued to the present day about how the cerebrum is organized to control movements. Since studies of single-neuron activity in behaving

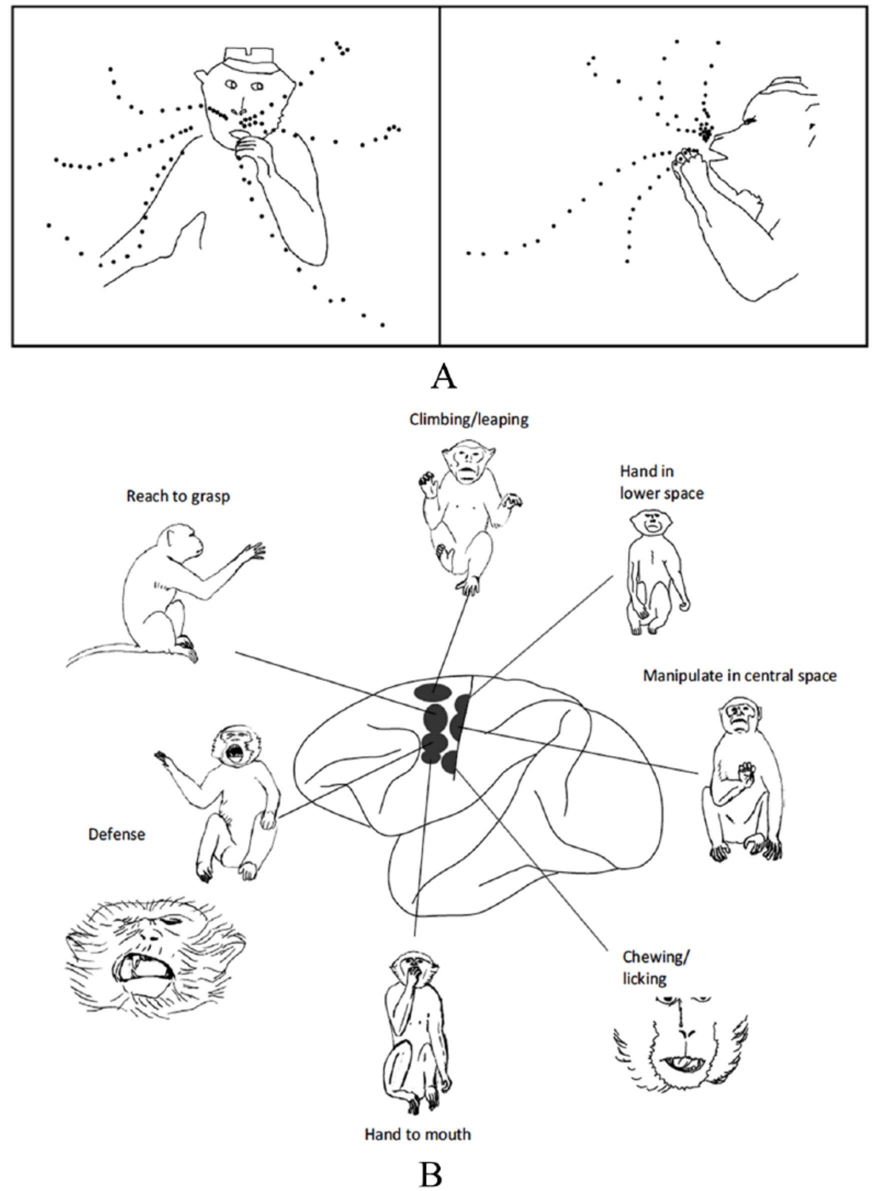

Figure 3. A 500-ms series of electrical stimuli to a monkey's cerebrum triggered coordinated movements of multiple body parts in which (A) the hand reached toward the opening mouth (dots indicate sequential hand positions) for one site of stimulation and (B) the cerebrum forms a map of ethologically relevant actions, including final hand positions in space, triggered by such electrical stimuli. Figure (A) reprinted from Graziano and others (2002), with permission from Elsevier. Figure (B) reprinted from Graziano (2016), with permission from Elsevier.

monkeys began in the 1960s, a variety of hypotheses have been advanced, each supported by some evidence, including cortical neuron control of individual muscles, muscle synergies, forces or torques, limb trajectories, limb endpoints, or sequences of naturalistic movements (Capaday and others 2013; Georgopoulos and Carpenter 2015; Giszter 2015; Graziano 2009, 2016; Harrison and Murphy 2014; Omrani and others 2017; Schwartz 2016; Shenoy and others 2013). W. Thomas Thach summarized the findings of one of his own studies of the monkey motor cortex by stating, "all the types of neuron that were looked for were found, in nearly equal numbers." (Thach 1978) Neurons correlated with various kinds of movement components have been suggested to be loosely embedded within a coarse somatotopic map containing a leg region, an arm region, and a head

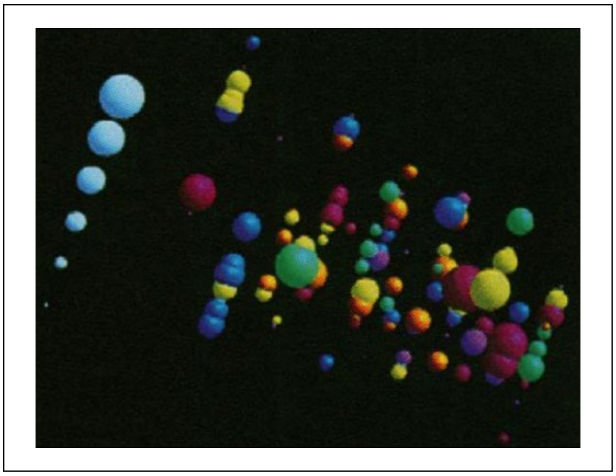

Figure 4. Single-neuron recordings from a monkey's frontal lobe showed that neurons that are most strongly activated just before movements of different fingers (shown here as differently colored circles, with the diameters indicating their movement-related increases in firing rate) are intermingled within the motor cortex hand region. Red, orange, yellow, green, blue, and violet represent digits 1-5 (1 is thumb) and the wrist, respectively. Left is medial; right is lateral. Reprinted from Schieber and Hibbard (1993), with permission from the American Association for the Advancement of Science (AAAS).

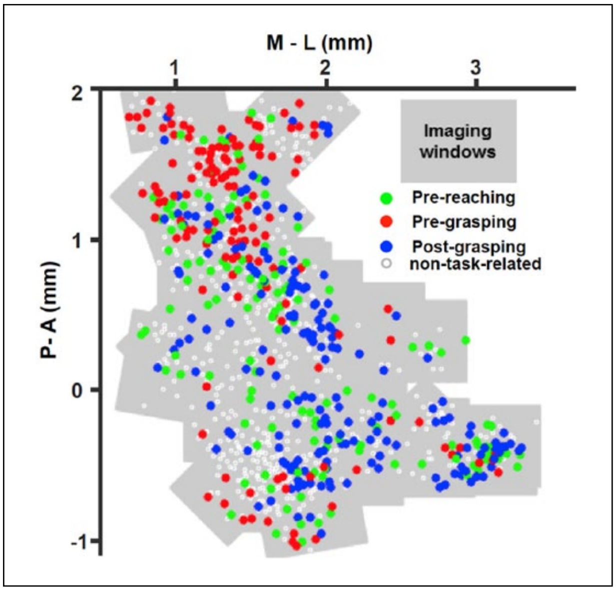

Figure 5. Calcium imaging of mouse corticospinal neurons showed that neurons that were most depolarized during particular segments of a reaching and grasping movement sequence were largely intermingled within the frontal lobe (including both primary and secondary motor cortex). Reprinted from Wang and others (2017), with permission from Elsevier.

region, within the precentral gyrus of the frontal lobe. It has also been suggested, however, that a larger region of the frontal lobe instead encompasses a map of ethologically relevant actions, including final body postures, which can be achieved via a variety of movements of multiple body parts, depending on the initial body posture (Fig. 3B) (Graziano 2009, 2016; Graziano and others 2002). This debate has not yet been resolved, though it may be that these two kinds of maps coexist in the frontal lobe and can be revealed using different stimulation parameters (Graziano 2009, 2016; Graziano and others 2002).

In this context, Jackson's 1870 formulation perhaps deserves renewed attention. Although he published his article just before successful cortical microstimulation experiments had been reported, one prediction of his hypothesis is that weak electrical stimulation of one cortical location should trigger movements mostly of one body part, but to a lesser extent of other parts. This prediction is consistent with much of the data later obtained.

Although Jackson's article appeared decades before cortical single-neuron recording became possible, a second prediction of his hypothesis is that individual cortical neurons should be activated just prior to a range of movements, but some more than others. As Jackson (1870) said, "discharge of a square inch of convolution must put in excessive movement the whole region, for it contains processes representing *x, y*, and *z*." Jackson was thus speculating that focal cortical neuronal discharge (i.e., activity) causes both seizure movements and normal movements of multiple body parts. The prediction that neurons in one cortical region discharge prior to a range of normal movements was essentially confirmed by Marc Schieber and Lyndon Hibbard (Fig. 4) (Schieber and Hibbard 1993).

Note that while Jackson hypothesized that each location controls multiple body parts, to differing extents, he did not stipulate that there need be a somatotopic organization; adjacent brain regions could be weighted toward movements of body parts that are far from each other. Such a scenario is consistent with recent findings using calcium imaging of mouse corticospinal neurons, showing considerable intermingling of frontal lobe neurons activated at different times during a sequence of reaching and grasping movements (Fig. 5) (Wang and others 2017). Neurons best correlated with either distal or proximal muscle activity and either flexion or extension were also intermingled to some extent, though neurons rostral to the precentral gyrus were more often activated during distal, flexion, and grasping movements than corticospinal neurons within the precentral gyrus.

Remarkably, then, modern approaches have not left Jackson's early hypotheses in their dust. Instead, his weighted and redundant distributed coding scheme remains relevant and within the range of current hypotheses for motor cortical organization that are based on modern methods. Students in training today would be well advised to read Jackson's 1870 article and to consider its implications for cerebral organization, as well as Jackson's astounding ability to deduce the likely organization of the brain just by watching movements.

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