

Muscles or Movements? Representation in the Nascent Brain Sciences

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Abstract: The idea that the brain is a representational organ has roots in the nineteenth century, when neurologists began drawing conclusions about what the brain represents from clinical and experimental studies. One of the earliest controversies surrounding representation in the brain was the “muscles versus movements” debate, which concerned whether the motor cortex represents complex movements or rather fractional components of movement. Prominent thinkers weighed in on each side: neurologists John Hughlings Jackson and F.M.R. Walshe in favor of complex movements, neurophysiologist Charles Sherrington and neurosurgeon Wilder Penfield in favor of movement components. This essay examines these and other brain scientists’ evolving notions of representation during the first eighty years of the muscles versus movements debate (c. 1873-1954). Although participants agreed about many of the superficial features of representation, their inferences reveal deep-seated disagreements about its inferential role. Divergent epistemological commitments stoked conflicting conceptions of what representational attributions imply and what evidence supports them.

Keywords: representation; muscles versus movements; motor cortex; scientific concepts; John Hughlings Jackson

“Since the days of Jackson we use the term ‘representation’: but again, what representation of parts of the body really means, nobody knows.”

Riese (1950), *Principles of Neurology*, p. 109

Introduction

Following a colleague’s presentation in 1964, neurosurgeon Wilder Penfield exclaimed: “I know ‘representation’ is a poorly chosen word! We must hope to discover what the true function of the motor cortex is, what it adds to the stream of potentials as they come through on the way to the voluntary muscles. When we learn that, it will be possible to choose a better word.” Penfield was responding to a paper presented by neurophysiologist Charles Phillips at the Pontifical Academy of Sciences’ Study Week on Brain and Conscious Experience. Organized by John Eccles, the symposium brought together many of the world’s leading physiologists (Eccles 1965). Phillips’s presentation had aimed to summarize what was known about the brain’s precentral motor area. He had disparaged the “black box” notion of representation and questioned the value of cortical stimulation, whose use in

humans Penfield pioneered (Phillips 1965). Impatient with these critiques, Penfield distanced himself from the term “representation,” declaring it to be a temporary placeholder.¹

Penfield’s apparent willingness to jettison the concept of representation belies its ubiquity in his own work as well as in twenty-first century neuroscience. It is now banal to observe that, from the cellular to the systems level, neuroscientists regularly appeal to what the brain represents. Despite its importance to the recent brain sciences, the concept of representation has captured the interest of philosophers far more than historians. While many philosophical theories of representation have been proposed, there has been little historical work on why the concept was applied to the nervous system or how it developed over time.

A useful starting point for tackling such questions is the so-called “muscles versus movements debate” (Miller 1965, Evarts 1967, Phillips 1975), a controversy in which Penfield and Phillips both participated. The debate was about what the brain’s motor cortex represents. Some argued that it represents complex, ecological movements, while others claimed it represents single muscles or partial movements. The advocates of complex movements were for the most part classical neurologists, who drew evidence from clinical encounters with patients and whose thinking was inflected with holism. The advocates of muscles tended to be neurophysiologists and neurosurgeons, who pursued a more reductive, experimental approach to the nervous system. The muscles versus movements debate heated up just as neurologists and neurosurgeons were struggling for professional dominance in the decades after World War I (Gavrus 2011). It was thus fueled by and reflective of competing visions for the future of the brain sciences.

As one of the earliest controversies surrounding representation in the brain, the muscles versus movements debate offers a unique window into how neurologists and physiologists used the term “representation” in the late nineteenth and early twentieth centuries. This essay will examine brain scientists’ evolving notions of representation during the first eighty or so years of the debate (1873-1954). For most of that time, the concept of representation was frequently invoked but not directly interrogated. Rather than looking at what was said about representation directly, then, the present investigation aims to historicize the concept of representation by exploring the meanings implicit in its early use. Although participants in the muscles versus movements debate largely agreed about the surface-level features of cortical representations, they held drastically different views about what representational attributions imply and what evidence supports them.

Since the most prominent participants in the debate were English and North American, my focus is on its trajectory in the anglophone world. I draw primarily on participants’ lectures, papers, and books. As science is a social endeavor grounded in interpersonal critique (Merton 1973, Longino 1990), the reasons scientists offer to one another and the ways in which they deploy concepts in public venues have a special significance. Scientific controversies are also essentially public: a private

¹ Despite such discussions, Eccles had been discouraged from entertaining philosophical themes at the symposium. He recounts the following anecdote: “Early in the planning I was instructed by the Chancellor that ‘the Academy by its constitution has for aim to promote the study and progress of the physical, mathematical, and natural sciences and their history. Thus the discussion of philosophical questions is excluded.’ I replied, ‘...[T]o me all sciences have a philosophical basis and it is generally agreed that there is a philosophy of science which is in fact basic to all scientific investigations and discussions. Certainly when one comes to a Study Week devoted to brain and mind it is not possible to exclude relations with philosophy...’ (Eccles 1965, pp. vii-viii).

disagreement between researchers only becomes a true controversy when it is aired publicly, enabling others to participate (McMullin 1987, Dietrich 2020). While I therefore draw mainly on published sources, the essay should be seen as an invitation to those who would explore the muscles versus movements debate from other historiographical perspectives.²

Setting the Stage: Movement and the Cerebral Cortex

The debate arose in the wake of two major developments in neurology and neurophysiology during the nineteenth century.³ The first was increasing acceptance of the view that the cerebral cortex is involved not just in higher mental functions, but also in bodily movement. In the early nineteenth century, most physiologists believed that the cortex, as the seat of the mind, is not involved in lower functions (Smith 1973, Harrington 2009). Theories of the reflex arc held that reflex action is produced by the spinal cord and brainstem, not the cerebral hemispheres. Moreover, despite the best efforts of physiologists, the cortex appeared to be inexcitable: unlike other parts of the nervous system, experimenters found it impervious to mechanical, chemical, or electrical stimulation. Nevertheless, the orthodox view of the cortex as exclusively serving mental functions gradually eroded as, for instance, German physiologist Johannes Müller extended the reflex arc to higher nervous centers and English physician Thomas Laycock argued that cerebral reflexes could explain diseases of the brain.

The second crucial development was the ascent of localization theories of the brain. Despite the popular success of phrenology in the early nineteenth century, it was never widely accepted among physiologists (Young 1970). Instead, thanks in large part to Pierre Flourens, the cortex was seen as functionally homogeneous until the 1860s or 1870s. This equipotentiality doctrine was ultimately undermined by an accumulation of clinical evidence for localization. Physicians drew attention to the association of speech deficits with frontal lobe lesions, culminating in Pierre Paul Broca's identification of a left frontal region specialized for articulate language. Broca's findings led to widespread (though not universal) recognition that some functions are served by specific cortical areas.

The view that the cerebral cortex contains localized centers specialized for movement – the synthesis of these two major nineteenth-century developments – was confirmed by Berlin physicians Gustav Fritsch and Eduard Hitzig in 1870. After decades of others' failed attempts, Fritsch and Hitzig were finally able to elicit muscle twitches by applying galvanic current to the cortical surface of dogs. In their watershed report, they concluded that the cortex is excitable, that it contains a region specialized for movement, and that this region is somatotopically organized, meaning that its organization roughly mirrors the arrangement of the body (Gross 2007). English physiologist David Ferrier also succeeded in stimulating the cortex shortly thereafter, but whereas the Germans had

² Mendelsohn (1987) suggests that scientific controversies are a particularly useful site for analyzing the interplay between social and conceptual factors in science. While I do here discuss professional tensions within the brain sciences, there is much interesting work yet to be done situating the debate with respect to other cultural and political currents (Pauly 1983, Harrington 1987).

³ This section draws on Clarke and Jacyna's (1987) *Nineteenth-Century Origins of Neuroscientific Concepts*, Chapters 4 and 6; Harrington's (1987) *Medicine, Mind, and the Double Brain*; and Young's (1970) *Mind, Brain and Adaptation in the Nineteenth Century*.

observed muscle twitches, Ferrier saw complex movements (Ferrier 1876, 1890; see also Beevor and Horsley 1890). As we will see, these divergent results were a portent: controversy about the character of electrically elicited movements would come to fuel competing claims about what the brain represents.

Physiologists soon zeroed in on the Rolandic cortex, the area surrounding the Rolandic or central sulcus, as an area of particular importance to movement (Figure 1). At first there was uncertainty about whether the Rolandic cortex is motor, sensory, or both. Around the turn of the twentieth century, researchers converged on the view that the region anterior to the central sulcus is primarily motor, and the posterior region primarily sensory, though discussion continued about the exact degree of specialization of each region. The anterior motor region, whose names include the precentral gyrus, Area 4, primary motor cortex, and M1, would become the primary focus of the muscles versus movements debate.

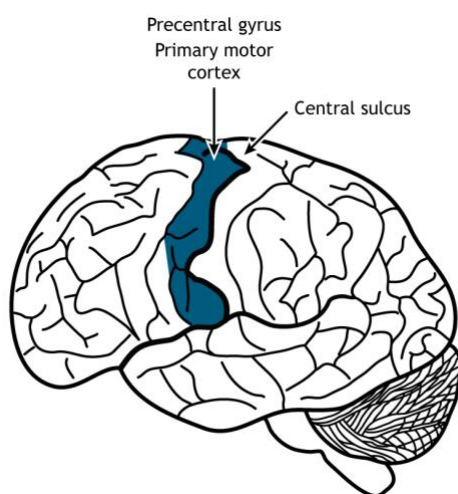


Figure 1. The human primary motor cortex, or precentral gyrus, is located anterior to the central sulcus. This region was the focus of the muscles versus movements debate.

The Debate's Jacksonian Origins

Just as the role of the cortex in motor control was gaining recognition, English neurologist John Hughlings Jackson launched the opening salvo in the muscles versus movements debate. In an 1873 *Lancet* article he declared: “nervous centres do not represent muscles, but very complex movements” (Hughlings Jackson 1873, p. 14). A “great systematizer” with a philosophical streak (Harrington 1987, p. 234), Hughlings Jackson integrated his clinical experience with ideas from associationist psychology and Spencerian evolution (Jacyna 2011, Smith 2012). Following his teacher Thomas Laycock, he embraced the view that the cerebral cortex is involved in reflex action, going as far as to argue that sensorimotor processes underlie all complex mental functions (Greenblatt 1965, Young 1970). The nervous system is a unified “sensori-motor machine,” he thought, in which “even the centres ‘for mind’...are sensory or motor, or both” (Hughlings Jackson 1882, pp. 29, 41).

Hughlings Jackson is often celebrated for anticipating Fritsch and Hitzig's experimental findings on entirely clinical grounds (Ferrier 1876; Walshe 1943, 1961; Clarke and O'Malley 1968; cf. Young 1970, ch. 6). Observation of his patients' convulsions, plus post mortem examinations of their brains, led him to conclude that movements are coordinated in particular parts of the brain in a roughly predictable order. He is also sometimes credited with introducing representation-talk to the brain sciences (Goody 1957, Thomson and Piccinini 2018). Although this priority claim is doubtful,⁴ his theory of the nervous system did make central use of the concept of representation, furthering its spread among English-speaking neurologists and physiologists.

Hughlings Jackson's theory of motor organization posited a three-level motor hierarchy within the nervous system, with levels distinguished by representational character. The lowest level, comprising the anterior horn of the spinal cord and motor cranial nerves, represents simple movements. The Rolandic cortex and corpus striatum, which constitute the middle level, contain representations that combine simple movements from the lowest centers: "these same muscles are represented (re-represented) in still more numerous different combinations, as complex and special movements" (Hughlings Jackson 1889, p. 400). Finally, the highest motor centers, found in the prefrontal cortex, are "re-re-representative," representing even more complex and sophisticated movements (Hughlings Jackson 1882, p. 42). In voluntary movement, activity in the highest motor centers spreads to the middle centers, and then to the lowest centers, leading finally to the contraction of muscles and the execution of movement.

On this account, Hughlings Jackson emphasized, "nervous centres represent movements, not muscles" (1882, p. 29). Or, as he later put it in a passage made famous by the muscles versus movements debate: "to speak figuratively, the central nervous system knows nothing of muscles, it only knows of movements" (Hughlings Jackson 1889, p. 400). By this he meant that there is no single brain region representing just the arm, a region representing just the leg, and so on. Instead, each nervous center corresponds to a broad swath of the body, and each "unit" within the center represents "a different movement of the whole [bodily] region" (Hughlings Jackson 1882, p. 38). He illustrated these ideas with an example: consider a nervous center corresponding to a bodily region with three muscles. The center might "represent seven different movements, in every one of which all the three muscles serve, but...in each of the seven movements the three muscles serve differently" (Hughlings Jackson 1882, p. 31). One unit of the nervous center could represent simultaneous flexion in muscle A, fixation in B, and extension in C, for example; another unit might represent flexion in A and B followed by extension in C. In this case, "our hypothetical centre does not represent three muscles, but seven movements, or we may say it represents muscles which have yielded their individuality into seven different movements" (Hughlings Jackson 1882, p. 31).

Some authors have seized on passages like this one to argue that Hughlings Jackson did not intend an antithesis between the representation of movements and the representation of muscles (Evarts 1967, Phillips 1975, Lemon 1988). They correctly point out that he often spoke of muscles or body parts being represented by the brain. Such language, however, should be understood as an

⁴ Walshe (1961) traces modern representation-talk back to Müller in the 1830s. Hughlings Jackson's contemporary, Vienna psychiatrist Theodor Meynert, also proposed a physiological theory involving distinct *Vorstellungen* (sometimes translated "representations") in different cortical cells (Guenther 2015).

expository convenience, for he repeatedly clarified that muscles are only represented *in* or *as* movements. For instance, he explained that nervous centers “do not represent muscles but, or except as, movements” (Hughlings Jackson 1882, p. 38). He dismissed the cortical representation of muscles via an analogy with language: “it [is] as misleading an expression to say that the convolutions represent muscles directly, as it is to say that language is made up of letters” (Hughlings Jackson 1875, p. xviii). Language is made up of larger units like sentences or words, which are merely comprised of letters; similarly, the brain’s convolutions represent movements, in which muscles merely “serve” (Hughlings Jackson 1875, p. 14).

Hughlings Jackson’s view that the cortex represents complex movements was adopted by many of his fellow neurologists, including Charles Beevor (Beevor 1903, 1909; Beevor and Horsley 1890). Indeed, Beevor was such a strong champion that the dictum, “the brain does not know muscles, only movements” is sometimes mistakenly attributed to him. The view resonated with neurologists’ holistic approach and broad conception of the nervous system (Gavrus 2011). Soon, however, the rise of experimental physiology would animate an opposing view.

Stimulation Frenzy and the Rise of Muscles

The decades around the turn of the twentieth century were “a period of great momentum” in neurophysiology (de Barenne 1933, p. 894), in large part because Fritsch and Hitzig had opened the floodgates to stimulation studies of the motor cortex (Ferrier 1876, Beevor and Horsley 1890, Cushing 1909, Vogt and Vogt 1926). During this heyday of cortical stimulation, dogs, rabbits, non-human primates, and eventually humans were all experimental subjects. In a typical stimulation study, the investigator opened up a portion of the subject’s skull and locally removed the protective layers around the brain. Using galvanic (direct) or faradic (alternating) current, they touched an electrode to the cortical surface and observed which body parts moved as a result. Most studies used “minimal” or “at-threshold” stimulation, meaning that experimenters applied the smallest amount of current that would yield visible movement.

Stimulation studies led to a proliferation of “maps” of the motor cortex, containing labels for different body parts (Figure 2). These maps not only illustrated the results of stimulation; they were also meant to convey the arrangement of cortical *representations*. Stimulation studies therefore crystallized a view of cortical organization that competed with Hughlings Jackson’s. Sometimes called “punctate localization theory” by its opponents, this view held that individual muscles, muscle groups, or minute movements are represented in different regions of the motor cortex. Voluntary movements recruit various combinations of these fractional representations.

A pioneer of cortical stimulation was English histologist and physiologist Charles Sherrington. Like Hughlings Jackson, Sherrington made his mark as a systematizer, proposing an influential account of how the nervous system “integrates” an organism’s needs and behavior (Swazey 1968, Smith 2000). Sherrington’s methodological approach was bottom-up: he spent his early career on the “boring” task of tracing spinal cord reflex pathways in order to understand the basic anatomical principles of motor organization (Swazey 1968, p. 61). In the next stage of his career, however, he was a pioneer of cortical mapping (Grünbaum and Sherrington 1902, Brown and Sherrington 1912). Leyton and Sherrington’s

(1917) classic stimulation study involved numerous experiments on gorillas, chimpanzees, and orangutans. Since their aim was “to ‘localise’ the motor function of each cortical point yielding motor responses,” they applied just enough faradic current to the animals’ cortical surface to elicit visible movements (Leyton and Sherrington 1917, p. 138). The motor responses they observed were fractional: “each [movement], though co-ordinately executed, forms, so to say, but a unitary part of some more complex act, that would, to attain its purpose, involve combination of that unitary movement with others to make up a useful whole” (Leyton and Sherrington 1917, p. 177). Leyton and Sherrington’s paper summarizes their results and describes the size and location of “representations” of different body parts in the brain. The motor cortex, they argue, is a “synthetic organ” that combines a large number of small movements into coherent movement complexes (Leyton and Sherrington 1917, p. 179).

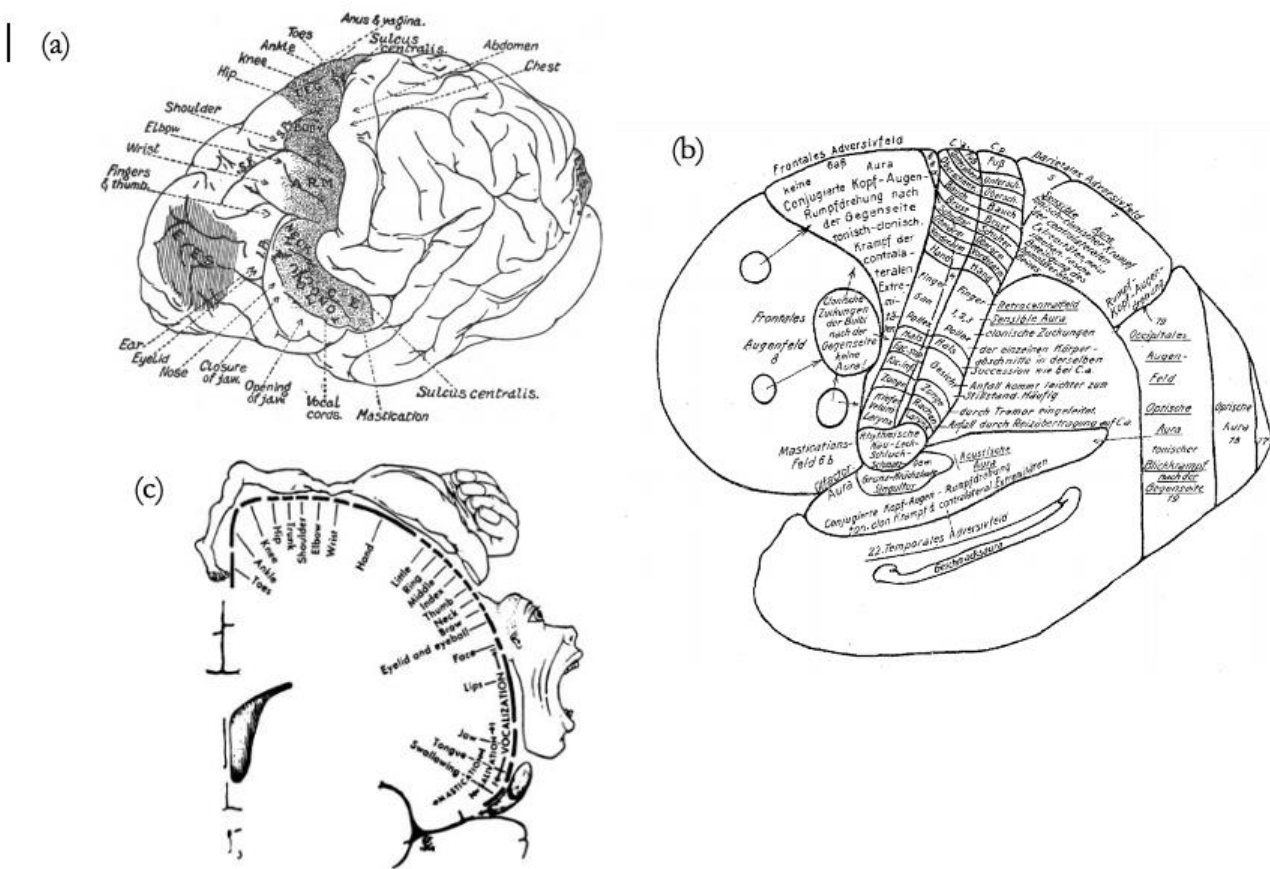


Figure 2. A Sampling of Cortical Maps. (a) Chimpanzee motor map from Grünbaum and Sherrington (1902), reprinted in Sherrington (1906). (b) Human cortical map from Foerster (1926). (c) Motor homunculus from Penfield and Rasmussen (1950).

Sherrington occupies a somewhat ambiguous place in the muscles versus movement debate. Some see him as an ally of Hughlings Jackson (Hines 1944, Walshe 1961, Asanuma 1973), while others take him to offer a competing view (Chang et al. 1947, Walshe 1953, Bates 1957, Humphrey 1986).

The latter assessment is most apt. Sherrington held that ordinary movements are assembled from a mosaic of cortical representations of locally restricted movements. This view denies Hughlings Jackson's contention that ordinary movements are themselves directly represented in the motor cortex. Moreover, later Jacksonians explicitly argued that neither muscles *nor fractional movements* are cortically represented, rejecting the view that the motor cortex represents "elementary co-ordinated components out of which the range of combinations and sequences of purposive movement is made" (Walshe 1953, p. 26). This remark took aim at Sherrington, who often used the phrase "elementary movement" to describe the representations in the motor cortex (Leyton and Sherrington 1917, p. 178).

Strictly speaking, then, the muscles versus movements debate was about whether the motor cortex represents small units of movement (be they individual muscles, muscle groups, or fractional movements) or rather ordinary movements in all their complexity and wide bodily scope:

Theoretically, the matter may be looked at in either of two ways: if the cortex represents only elementary units of movement, then a normal purposive movement complex results from a 'making up' of units. If, on the other hand, we suppose such movement-complexes to be laid down as such in the cortex, then the item of movement we evoke by a brief electrical stimulus results from a 'breaking up' of this representation. (Walshe 1943, p. 121)

Thus, "muscles versus movements" turns out to be something of a misnomer. At root, the controversy was about whether representations in the motor cortex are fractional or not. With this as the primary fault line in the muscles versus movements debate, Sherrington belongs in the former camp. (In what remains, references to muscles proponents should accordingly be understood as shorthand, referring to those who endorse the representation of fractional movements, body parts, individual muscles, or muscle groups.)

While Sherrington was an expert on cortical stimulation in primates, his student Wilder Penfield pushed the technique further. Following in the footsteps of surgeons Harvey Cushing (1909) and Otrid Foerster (1926), with whom he trained, Penfield embarked on a program of intraoperative stimulation in humans. Beginning in the late 1920s, he pioneered the surgical excision of epileptic foci in patients with severe focal epilepsy. Cortical stimulation was used to locate the place in the brain that was triggering a patient's seizures and determine how to remove the area with as little disruption as possible. Like others before him, Penfield stimulated the cortical surface with a sub-threshold stimulus and increased the current until he observed a response. Although he reported that, "in general, stimulation was only carried out in any operation when there was therapeutic justification for it" (Penfield and Boldrey 1937, p. 396), cortical mapping became increasingly important to Penfield for its purely scientific value (Guenther 2015, ch. 6).

A major milestone in Penfield's research was his (1937) paper with Edwin Boldrey, which analyzed cortical responses from 126 neurosurgeries and introduced the first of Penfield's famous homunculi (Snyder and Whitaker 2013, Guenther 2015, Gandhoke et al. 2019; see Figure 2c for a later version). The paper's many cortical maps indicated where on the cortical surface movement and sensation in particular body parts were elicited by stimulation.⁵ Penfield and Boldrey characterized the

⁵ Unlike most previous researchers, Penfield was also able to directly study sensory responses to stimulation, since his human patients, being only locally anesthetized, were able to verbally report what they felt. See Elder (2015) for an account of how patients acted as surveyors in Penfield's cortical cartography project.

elicited movements as “crude” and not “dexterous” rather than complex or purposive (1937, p. 441). From their results, they inferred the size and location of various body parts’ representations in the cerebral cortex. Acknowledging individual differences, they nevertheless emphasized that the sequence of representations in the primary motor cortex is “almost invariable” across subjects (Penfield and Boldrey 1937, p. 430). Occasionally they observed an aberrant response – a hand movement elicited by stimulation far away from the “hand area,” for instance – but they suggested that such responses were due to epileptic spread or atypical brain morphology. Topographical representation of body parts is the organizing principle of the motor cortex, with deviations explained away by abnormalities in the patient population.

Later in his career, Penfield argued that the function of the precentral gyrus is to “transmit, and no doubt transmute, the impulses which reach it” from the brainstem’s “centrencephalic system” (1954, p. 15). A controversial posit of Penfield’s own devising, the centrencephalic system is a hypothetical brainstem structure involved in consciousness that integrates memory, reason, and sensory information to determine the organism’s next movement (Gavrus 2006, Prkachin 2021). Penfield held that the centrencephalic system “plays upon” the precentral gyrus, making the motor cortex a mere “way-station in the stream of volitional impulses” (1954, pp. 14-15). Penfield’s account implied that Hughlings Jackson was mistaken: skilled movements have no “true representation” in the precentral gyrus (1954, p. 12).

Muscles, Movements, and Professional Identity

Penfield’s contributions to the muscles versus movements debate show how its divisions were increasingly drawn along the lines of professional specialization. Those who favored the representation of muscles were for the most part neurophysiologists or neurosurgeons, while advocates of the representation of movements were primarily clinical neurologists. Gavrus (2011) has shown that, beginning in the 1920s, these two groups were frequently at odds over the “jurisdictional boundaries” of their respective fields (Weisz 2006). The institutional ascent of neurosurgery after World War I inspired a sense of crisis in clinical neurologists. They were suspicious of medical specialization and viewed neurosurgeons as “unthoughtful m[e]n of action” who sometimes subjected patients to unnecessary operations (Gavrus 2011, p. 62; Casper 2014). Neurosurgeons, meanwhile, looked down on neurology as therapeutically ineffectual. Their decades-long “fierce exchange” was fueled by competition for patients, funding, and professional appointments (Gavrus 2011, p. 57).

Each group had distinctive epistemological commitments which manifested in the muscles versus movements debate. Since the origins of “physiological surgery” in the late nineteenth century, neurosurgery had been closely aligned with experimental science. For early surgeons, experimentation was an “epistemic and practical alternative to the traditional medical logic of individual experience and judgment” (Schlich 2017, p. 65). Neurosurgeons like Penfield, Cushing, and Victor Horsley argued that clinical practice should be firmly grounded in physiology (as well as histology and neuropathology). Rather than just hunting for treatments that seemed to work, they pursued a reductive approach that sought theoretical justification for clinical interventions (Gavrus 2017). Clinical neurologists hewed closer to the traditional medical ideal which held practical experience and

clinical judgment in high esteem. They resisted technological changes, preferring the art of bedside examination to the science afforded by new experimental tools (Walshe 1933, Casper 2014). Some were highly skeptical of the reductionist ethos of the physiologist, advocating a holistic approach to nervous system function and dysfunction (Harrington 1987, 1990).

The muscles versus movements debate became a proxy war between experimentally-minded neurophysiologists and neurosurgeons and clinically-oriented classical neurologists. No participant typified this dynamic as well as pugnacious English neurologist F.M.R. Walshe. As professional jockeying between brain scientists increased in the 1930s and 1940s, Walshe led a sustained challenge against both the encroachment of neurosurgery on neurology and punctate localization theory. Walshe shared his field's anxieties about the decline of clinical neurology, condemning neurosurgeons' reductionist tendencies and inadequate clinical training (Walshe 1933, Gavrus 2011, Guenther 2015). He saw Hughlings Jackson, widely lauded as the "father of British neurology," as a hero of the underappreciated clinical approach (Walshe 1947, 1961).

In publications spanning several decades, Walshe used his "legendary caustic wit" to ridicule the cortical representation of muscles (Gavrus 2006, p. 73; Walshe 1943, 1947, 1953, 1961). On his view, "what the motor cortex represents... is not a vast collection of elementary units, waiting to be assembled *ad hoc* into those complex combinations and sequences that we know normal voluntary movements to be, but a field in which all possible movements – all the movements the individual has ever learned – have their own separate representations" (Walshe 1947, p. 23). Walshe argued that the evidence in favor of this view was decisive. The many weaknesses of punctate localization theory simply went unnoticed by somnambulant experimentalists. In public lectures and in private correspondence (Guenther 2015, ch. 6), Walshe was especially critical of experimentalists' cortical maps, which he took to be highly misleading.

Walshe hoped to reverse the momentum that the muscles view had been accruing from stimulation studies since the beginning of the century (see also Clark 1948, Gellhorn 1950). He was not alone in thinking he was swimming against the current. Reflecting, perhaps, both neurologists' and neurosurgeons' unease about their professional status during this period, participants on both sides of the muscles versus movements debate tended to see themselves as an embattled minority. Mid-century advocates of the representation of movements said they were challenging "widespread acceptance" of punctate localization theory (Murphy and Gellhorn 1945, p. 256; Walshe 1943; cf. Miller 1965), while proponents of the representation of muscles grumbled that Hughlings Jackson had inspired a "unique convergence of thought" that persisted for half a century or more (Bates 1947, p. 333; Asanuma 1973). This shared sense of underdog status reflected common anxieties about professional recognition and the future direction of the brain sciences.

Representation: Conceptual Common Ground

As more voices joined the muscles versus movements debate, arguments in support of one side or the other proliferated. These arguments provide a valuable window into brain scientists' concepts of representation around the turn of the twentieth century. The remainder of the essay will explore these representation concepts. It is important to keep in mind that how someone explicitly

characterizes a concept may not line up with how they actually use it. Haslanger (2012) calls the former a “manifest” concept, and the latter, an “operative” concept. My primary focus will be on brain scientists’ operative concepts of representation emerging from their practices of use during the muscles versus movements debate.

Despite the epistemological disagreements that existed between neurologists, neurophysiologists, and neurosurgeons, all parties to the debate shared several operative assumptions about representation. Most notably, participants on both sides acknowledged that representations come in degrees and may overlap with one another. Indeed, the idea that the motor cortex contains a “fabric of interwoven and graded representations” had been present since the very beginning of the debate (Walshe 1943, p. 111). Hughlings Jackson frequently distinguished between the “leading representation” and “subordinate representations” within a nervous center, and spoke of certain movements being “more” or “more strongly” represented than others (e.g., 1875, p. 11; 1882, p. 30). These ways of thinking about representation were strongly influenced by the clinical phenomena he devoted his career to studying. In a type of seizure now called a “Jacksonian march,” convulsions spread predictably from one part of the body to another: the physician observes “spasm of the forearm, then more spasm of that and spasm of the face also, then more spasm of these two and spasm of the leg also” (Hughlings Jackson 1882, p. 34). Hughlings Jackson hypothesized that such seizures occur when there is excessive discharge of the movement representations in a nervous center. As more of the representations are activated, convulsions of new body parts are added to the convulsions already occurring, while the latter increase in intensity. This is known as “compound spread.” He speculated that spasms may spread physically as the cortical discharge intensifies even if the discharge does not move to new areas of the cortex (Walshe 1943, pp. 129-30), because multiple movements are represented in the same place, just with different thresholds for discharge. (For a different explanation of Jacksonian marches in terms of cortical representations of movement *components*, see Penfield and Jasper 1954, pp. 359-60.)

Proponents of the representation of muscles also acknowledged that each point in the motor cortex can represent multiple things, and that representations are not all-or-nothing. In a word of warning about cortical maps, for instance, Sherrington cautioned the reader to “never forget the unspeakable complexity of the reactions thus rudely symbolized and spatially indicated” ([1906] 1920, p. 270). By this he meant, in part, that although cortical maps present representations as occupying separate areas of the cortex, in reality they overlap. As Grünbaum and Sherrington explain, “there exists much overlapping of the areas and of their sub-divisions which the diagram [our Figure 2a] does not attempt to indicate” (1902, p. 208). Penfield, too, argued that a limitation of cortical maps was that they did not convey the fact that “one representation is not sharply demarcated from adjacent representations” (Penfield and Jasper 1954, p. 63). Sherrington’s term for this graded notion of representation, a label taken up by others, was “preponderant representation” ([1906] 1920, p. 269).

The idea that representations of different strengths can overlap in the motor cortex was thus accepted by virtually all debate participants. There was some confusion on this point, stoked by a widespread musical metaphor used to describe the muscles view (Walshe 1943, Jefferson 1950, Penfield and Jasper 1954; see also Schieber 2001). The cortex, some argued, is like a piano keyboard: just as the keys on a piano represent different pitches, and chords can be played by selecting different

combinations of keys, so too do regions in the motor cortex represent different muscles or partial movements, and ordinary movements are produced by activating different combinations of regions. Cortical stimulation is analogous to playing a single piano key. As Penfield and Jasper put it, “the succession of motor units in the Rolandic cortex is like a keyboard. Each key is connected to a different peripheral resounding wire [nerve fiber]. Music results only when the keyboard is played upon according to a pattern that has its localization elsewhere in the central nervous system” (1954, pp. 65-6).⁶ The piano metaphor invited misunderstanding of the conceptual commitments of those who favored the cortical representation of muscles. The keys on a piano perfectly tile the keyboard without overlap. At any point on the keyboard, a single pitch is “represented.” In light of the foregoing discussion, however, we see that this falls under the metaphor’s negative analogy (Hesse 1966, Bartha 2010). That is, non-overlap is a feature of the source system (the piano) that proponents of muscle representation, like Sherrington and Penfield, did not intend to impute to the target system (the brain). All parties to the debate recognized gradation and overlap in cortical representation.

Another general feature of representation-talk in the muscles versus movements debate was the intertwining of what is represented with the nervous structure that represents it. In contemporary terms, this amounts to the entanglement of representational content (that which is represented) with representational vehicle (the physical bearer of the content). Those who maintained that the fractional components of movement are cortically represented often also held that the representations are limited in their spatial scope. That is, they claimed that representations are fractional in two senses: they represent partial movements (or muscles), and they physically occupy fractions of the cortex. The piano metaphor reflects this blended notion of representation. It simultaneously conveys fractionation of the cortical surface (a piano’s keyboard is physically comprised of dozens of keys) and fractionation of the represented movements (a piano partitions the space of pitches). This intertwining of content with its physical basis marked thinking about representation in the first half of the twentieth century.⁷

Representation from Stimulation?

Despite the relative novelty of representational attributions to the nervous system, we have now seen that partisans on each side of the muscles versus movements debate made a number of common assumptions about the nature of representation, indicating resemblances among their operative concepts. It may seem, then, that neurologists, neurophysiologists, and neurosurgeons had

⁶ This musical metaphor has an interesting precursor in Müller’s *Elements of Physiology, Vol. II*: “The fibres of all the motor, cerebral and spinal nerves may be imagined as spread out in the medulla oblongata, and exposed to the influence of the will like the keys of a piano-forte” (1842, p. 934; trans. Baly). Here, in accordance with the earlier orthodoxy that motor control does not involve the cortex, the medulla oblongata (in the brainstem) is taken to be the “source of all the voluntary movements,” and the pianist is imagined to be the will, rather than other parts of the nervous system (Müller 1842, p. 934). I do not know if this image influenced the later one.

⁷ Chirimuuta (2019) makes a related observation about Hughlings Jackson’s concept of representation: “unlike the computational notions prevalent today, it has none of the connotation of representations being ‘disembodied’ or abstracted from their biological basis, as software is from hardware” (p. 41). As far as I am aware, the first contributor to the muscles versus movement debate to make a clear vehicle/content distinction was Clark (1948).

converged reasonably quickly on ground rules for representation-talk applied to the brain. This section and the next, however, will show that this appearance is illusory: agreement about the surface-level features of representations obscures major disagreements about representation's inferential role.

A concept's inferential role is roughly the part it plays in reasoning and inference (and perhaps also action and perception; Brandom 1994, Brigandt 2010). For example, consider the concept of *violin*. It is a part of the inferential role of violin that the sentence "George owns a violin" implies that "George owns a string instrument"; that sounds of a particular timbre warrant application of the concept of violin; and that it is appropriate to conclude that a violin is missing when one learns that the concertmaster's instrument is missing. These sorts of inferential transitions constitute violin's inferential role. Likewise, to understand the inferential role of the concept of representation, one must look to the circumstances in which the notion of representation is applied and the consequences that follow from claims about what is represented. As we do this, we will see that brain scientists implicitly held different views about what is implied by the claim that the motor cortex represents muscles or movements. These differences in scientists' operative concepts of representation generated intractable disagreements about which clinical and experimental findings constituted evidence in the muscles versus movements debate.

A primary locus of such disagreement was cortical stimulation. Stimulation results were a central pillar of the case for the representation of muscles. Neurophysiologists took it to be highly significant that single body parts, muscles, or muscle groups could be electrically stimulated in isolation (Foerster 1931). Since stimulation is capable of producing small, localized muscle contractions, they inferred that muscles or fractional movements must be separately represented in the motor cortex (Leyton and Sherrington 1917, Penfield and Boldrey 1937). Experimentalists and neurosurgeons were also constantly striving to refine their stimulation methods so as to elicit ever more limited motor responses. They presumed that representational ascriptions should be as fine-grained as elicited motor responses would allow. To indulge in some sloganeering: they assumed that independence in stimulation implies independence in representation. This inference, which was rarely made explicit, partly constituted the inferential role of representation for proponents of muscles. Its clearest expression is found in cortical maps that purported to reveal the results of stimulation and the brain's representational plan simultaneously (Figure 2).

Proponents of the representation of movements, however, flatly denied that stimulation and representation were so tightly connected. Early reservations about the evidential import of stimulation were articulated by Victor Horsley, a surgeon and sometime practitioner of cortical stimulation, in his Linacre Lecture:

It should not, in my opinion, be assumed that the effect of a minimal stimulus, evoking, as it often does, but a single movement of one segment of a limb, is a criterion of all that is represented...in that portion of the cortex cerebri... [A] minimal stimulus may only be adequate for one item of several represented in one portion of the cortex. It also must not be forgotten that, physiologically considered, an electrical stimulus is a crude method of exciting a nerve centre. (Horsley 1909, p. 126)

Horsley's cautions about what can be inferred from stimulation became key talking points for movements advocates in the decades that followed. Horsley's first worry in the above passage is that stimulation does not indicate all that is represented at a cortical point. Even if stimulation at a point

elicits a small movement, there may be additional movements represented there. In the 1940s, clinical neurologists went on the offensive against the standardized stimulation protocol (Walshe 1943, Murphy and Gellhorn 1945, Clark 1948). In addition to using “minimal” (i.e., at-threshold) stimuli, researchers standardly employed a number of methods for isolating cortical responses, including waiting several minutes between stimuli and drying the cortical surface. Critics of the representation of muscles argued that such procedures stacked the deck in favor of finding fractional motor responses: “th[e] standardized procedure will produce a minimum complexity of response *regardless of the character of representation*” (Clark 1948, p. 322; my italics). In other words, the procedure guarantees that stimulation will evoke isolated twitches, even if the brain does in fact represent complex movements. If different movements are represented in the same location with different excitability thresholds, applying just enough current to evoke a single movement will not elicit represented movements with higher thresholds (Walshe 1943).

Horsley’s second worry, that electrical stimulation is nothing like ordinary cortical excitation, was also a focus of later proponents of movement representation (Clark 1948; Walshe 1943, 1953; Phillips 1965). Even neurophysiologists conceded that stimulation is “at best a crude method for understanding function” (Hines 1944, p. 468; see also Sherrington [1906] 1920, p. 307; Penfield 1954, p. 15). But while they believed stimulation was still a useful tool, many clinical neurologists held that it reveals precious little about the brain’s representational organization. Critics argued that standard stimulation methods do not reveal what the brain represents under biologically normal conditions because of their artificiality. Hence, participants on each side of the debate fundamentally disagreed about whether stimulation was relevant to representational attributions, and thus about the conditions under which it is appropriate to apply the concept of representation, part of its inferential role. This disagreement, rooted in divergent epistemological views about the value of controlled experimentation, drastically restricted the shared evidential basis for assessing competing representational claims.

Injury and Instability: The Case for Movements

Other differences in participants’ operative concepts of representation emerge if we turn our attention to arguments offered in favor of the cortical representation of movements. In keeping with classical neurologists’ training and theoretical orientation, clinical findings took center stage. One clinical phenomenon that Hughlings Jackson and his allies took to be highly significant was “imperfect” or “partial” paralysis (Hughlings Jackson 1882, 1889; Beevor 1903, 1909; Walshe 1947). Partial paralysis occurs when damage to a patient’s brain causes certain muscles to become paralyzed in the context of one movement but not another. For instance, a patient may be capable of rotating his trunk in one direction but not the other, even though both movements require many of the same muscles. Beevor (1903, 1909) reported several examples of this phenomenon from his clinical practice. He argued that partial paralysis “makes it very difficult, if not impossible, to explain how individual muscles could be represented in the cortex” (Beevor 1909, p. 884). Since brain lesions impair particular movements and not particular muscles, the brain must represent movements (Beevor 1903, p. 14). Walshe offered a memorable recapitulation of this argument: “if muscles were directly represented, it

would be a matter of ‘paralysed in one movement, paralysed in all’” (1947, p. 19). But clinical experience shows that it is not.

This argument rests on a reasoning pattern that we may call “lesion logic” applied to representation. Lesion logic holds that one can discover what a part of the nervous system does by removing or disabling it. The resulting deficits indicate the part’s ordinary contribution. Which inferences in lesion logic are warranted and how it may go awry have been hotly debated in physiology and neuropsychology for centuries (Young 1970, Caramazza 1986, Gamboa 2020). Proponents of movements treated the brain’s representations as amenable to lesion logic. On their view, partial paralysis is revealing because the behavioral deficits that follow injury to a brain region indicate what that region represents. As lesion patients sometimes lose the ability to initiate complex movements rather than losing the ability to control particular body parts, movements must be cortically represented. This argument reveals that, for clinical neurologists, lesion logic played a central role in the inferential role of representation.

Some neurologists also took patterns of recovery following injury to favor the representation of movements. Hughlings Jackson claimed that when part of the motor cortex is destroyed, a patient will never regain all previous function. The patient can only partially compensate by deploying cortical representations of movements similar to the representations they have lost. The cortical regions that remain following injury do not “take on duties they never had before, but...having more or less closely similar duties, they serve – not as well, but only – next as well as those destroyed” (Hughlings Jackson 1882, p. 26; see also Walshe 1943). Lost movement representations are not restored, but their absence is disguised by the deployment of related representations. Walshe also argued that proponents of muscles representation could not explain the fact that some recovery does occur: “if the movements of such a part as the thumb and index are wholly and exclusively represented within a sharply limited cortical focus, no recovery of their movements could occur after the ablation of that focus” (1947, p. 22). Were the motor cortex like a keyboard, in other words, then just as the removal of a piano key deprives the pianist of a particular pitch, cortical damage should be followed by permanent motor loss.⁸

Proponents of muscle representation did not often comment on such clinical arguments in favor of movement representation. Neurophysiologists too tended to assume that representation conformed to lesion logic, though their focus was less on “naturally” occurring clinical lesions and more on experimentally-induced ablations. They would have rejected Walshe’s claim that recovery can only be accounted for by the representation of complex movements. For one thing, their work contained extensive documentation of the recovery that occurs after injury (e.g., Leyton and Sherrington 1917, Penfield and Jasper 1954). For another, where a muscle or body part is represented might well change as undamaged brain regions take over lost functions (Harrington 1990).

Penfield’s (1954) discussion of recovery following injury involves his controversial centrencephalic system. He observes that, even after part of an adult’s precentral gyrus is removed, over time she can recover some coarse movements of the corresponding body part. Penfield takes this to mean that there must be other nervous centers, besides the primary motor cortex, that can be

⁸ The possibility of recovery following brain injury was often taken to be a significant challenge for any attempt to localize functions in the brain (Harrington 1987, pp. 262-4).

used for less “skillful” voluntary movement. He suggests that the centrencephalic system contains such nervous centers: it can direct (“infant-like”) movements in the absence of an intact precentral gyrus. Even in healthy individuals, then, the precentral gyrus must be just a “way-station” for motor signals originating in the centrencephalic system (Penfield 1954, p. 14). Whereas Walshe believed recovery to be inexplicable on the view that the primary motor cortex represents muscles, Penfield concluded that recovery indicates that it must only represent muscles. The primary motor cortex, containing representations of movement fragments, is merely “play[ed] upon” by the independent centrencephalic system (Penfield 1954, p. 15). Participants in the muscles versus movements debate therefore appealed to some of the very same clinical phenomena in conflicting inferences about what motor cortex represents.

Despite their vocal criticism of stimulation studies, clinical neurologists also claimed some experimental support for the representation of movements. Their focus was cortical instability (de Barenne 1933). Instability is an umbrella term for three related phenomena that occur when a cortical point is stimulated multiple times: facilitation, which is when the motor response increases in intensity; reversal, when the response is inverted (e.g., from flexion to extension); and deviation, when the response changes character entirely. In classic work on these phenomena, Brown and Sherrington (1912) and Leyton and Sherrington (1917) showed that instability can be induced by changes in blood supply, temperature, stimulation intensity, depth of anesthesia, and the application of “precurrent” to the cortical surface.

Proponents of movements saw instability as decisive evidence in their favor. They argued that if muscles were cortically represented, then stimulation of a particular cortical point should always yield the same motor response (Clark 1948). Evoking the musical metaphor, they claimed that instability shows that “the motor cortex [is] not like a pianoforte where pressure on one key invariably produces the same note” (Jefferson 1950, p. 335). Proponents of the representation of muscles, it was argued, had no resources to account for “the apparent shifting of the localization of units of movement from point to point” (Walshe 1943, p. 115; Clark 1948). By contrast, Hughlings Jackson’s view provides a tidy explanation: since multiple complex movements are represented in a single cortical point, but with different excitability thresholds, it is no surprise that different movements are elicited when the point is stimulated under different experimental conditions.

Again, however, neurophysiologists and neurosurgeons did not seem to see instability as a challenge to the representation of muscles. Brown and Sherrington downplayed the instability they uncovered, cautioning that, “we would not be understood as impugning the general regularity of the results which such cortical points yield when appropriately examined. The same cortical point, returned to after a period of quiescence, will usually, time after time, yield approximately the same result” (1912, p. 277). Others embraced widespread instability but did not take it to undermine muscle representation. Neurophysiologist John Farquhar Fulton, for instance, trumpeted the representation of muscles in the precentral gyrus in his highly successful textbook *Physiology of the Nervous System* (1949, 8). Then, on the very next page, he launched into a lengthy discussion of the many sources of cortical instability. Fulton apparently saw no contradiction between cortical instability and the representation of muscles (see also Penfield and Jasper 1954). Muscles proponents’ indifference to much of the evidence celebrated by their opponents shows once again that they did not agree about which

observations support particular representation attributions, marking further differences in the two sides' understanding of the inferential role of representation.

A Mid-Century Impasse and Dueling Stimulation Studies

The back-and-forth between pro-muscles neurophysiologists and neurosurgeons and pro-movements clinical neurologists in the first few decades of the century thus lays bare a number of differences in their operative concepts of representation. There was considerable disagreement about representation's inferential role, with participants at odds about whether the representation of muscles or movements was supported by various clinical and experimental findings. A central point of contention, discussed above, concerned the proper experimental protocol for investigating cortical representation. Neurologists argued that at-threshold stimulation virtually guaranteed fractional motor responses and did not reflect normal functioning. Neurophysiologists defended the standardized procedure, countering that only at-threshold stimulation could separate distinct cortical representations. These competing understandings of representation in relation to experiment came to a head during a series of contrasting stimulation studies in the late 1940s. Partisans on each side, using their own preferred methodologies, got results they took to support their own views.

Advocates of movements, no longer content to rely only on clinical findings and the reinterpretation of others' experimental results, sought new evidence in the laboratory (Murphy and Gellhorn 1945, Bosma and Gellhorn 1947, Gellhorn 1950).⁹ In doing so, however, they abandoned standard stimulation protocols (see also Graziano et al. 2002). Because they thought that only above-threshold stimuli would reveal the full range of movements represented at a cortical point, they stimulated with strong, sustained currents. By “evok[ing] as much as possible rather than as little as possible,” their experiments aimed to create physiologically realistic conditions and reveal the “full potentialities” of the motor cortex (Murphy and Gellhorn 1945, p. 257). Murphy and Gellhorn (1945) stimulated the cortices of rabbits, cats, and monkeys with large currents for ten seconds and observed the resulting movements of the face and extremities. They found that many of the movements elicited from above-threshold stimulation, far from being fractional, were complex and purposive. To establish that their results were not merely due to the spread of current to other cortical areas, they isolated cortical regions by transcerebral section. After making an island of the points to be stimulated, they continued to observe complex movements. Soon, advances in electromyography (EMG) permitted the direct measurement of muscular responses to stimulation. Using above-threshold stimulation plus EMG, Bosma and Gellhorn (1947) confirmed the findings of Murphy and Gellhorn (1945): “a considerable number of muscles of one extremity is activated from a single cortical focus” (Bosma and Gellhorn 1947, p. 140).

⁹ Even though most advocates of the representation of movements were clinical neurologists, this effort to gather experimental support for movements seems to have been led by neurophysiologist Ernst Gellhorn. With little existing scholarship on Gellhorn, it is difficult to figure out his place in our narrative. By mid-century, neurosurgeons had largely triumphed over neurologists in their struggle for professional dominance (Gavrus 2011). Perhaps the fizzling out of professional conflict removed the impetus for aligning one's position in the muscles versus movements debate with one's professional interests. Gellhorn's experimental work may herald the beginning of this breakdown.

Gellhorn and his collaborators argued that their results showed that “the motor cortex does not consist of a great number of mutually exclusive and independently operative ‘tiles’ of gray matter, the whole forming a mosaic of individual muscular representation” (Murphy and Gellhorn 1945, p. 270). Instead, it contains multiple, overlapping representations of movements. This conclusion reflected the view that representational attributions must reflect ordinary functioning, in conjunction with the assumption that strong, sustained currents were a closer imitation of normal excitation than at-threshold stimulation. In light of such background assumptions, proponents of the cortical representation of movements took Gellhorn and colleagues’ work to be “the most striking and, so far, the most complete confirmation of the Jacksonian hypothesis” (Walshe 1947, p. 25; see also Clark 1948).

Advocates of the representation of muscles disagreed. On their view, at-threshold stimulation and other techniques for reducing cortical excitability served the essential purpose of isolating individual representations. Using above-threshold stimulation only made it harder to observe the true boundaries between representations. This perspective fueled a contrasting stimulation study by Chinese neurophysiologist Hsiang-Tung Chang and his colleagues at Yale University. In their classic paper, Chang et al. hypothesized that the motor cortex contains a “highly organized topographical representation of body musculature” that had been obscured by experimental challenges (1947, p. 40). Their aim was to stimulate with weak current in order to “map the mosaic” in the motor cortex in fine-grained detail (Chang et al. 1947, p. 40). Like Bosma and Gellhorn (1947), Chang and colleagues made pioneering use of EMG, measuring the strength and contraction of muscles in the ankle joint as they systematically stimulated macaque precentral gyrus millimeter by millimeter. Their key result was the observation of so-called “solitary responses”: activity in just one muscle following stimulation. However, solitary responses were not typical. When stimulation led to activity in multiple muscles, as was common, Chang et al. calculated the ratios of muscular tension. They argued that these tension-ratios revealed a topographical plan of representation: “only one focus for each muscle is found and the focus of representation of two muscles in no case falls at exactly the same locus” (Chang et al. 1947, p. 52). Although multiple muscles may be represented at a single cortical point, one muscle predominates. Chang and colleagues concluded that ordinary movements are “compounded” from muscle representations in the motor cortex (Chang et al. 1947, p. 55).

The study became a touchstone for proponents of the cortical representation of muscles, who claimed that it settled the debate (Hines 1944, 1947; Fulton 1949). Committed as they were to the implicit principle that independence in stimulation implies independence in representation, proponents of muscle representation took solitary responses as proof that representations in the motor cortex are fractional in character. They likewise put little stock in Gellhorn and colleagues’ above-threshold studies. Gellhorn (1950), in reply, endeavored to show that even at-threshold stimulation supported the representation of movements. Using EMG to record activity in the leg muscles of monkeys, he found that at-threshold stimulation usually produced activity in multiple muscles too. Movement representation, he thought, had been vindicated.

These dueling stimulation studies present a puzzle: although participants on each side of the debate claimed that their results decisively supported their view of cortical representation, there was arguably little direct conflict between their findings. Despite highlighting the typical complexity of

elicited movements, Bosma and Gellhorn (1947) admitted to finding *some* solitary responses. And even though they placed great weight on the existence of solitary responses, Chang et al. (1947) acknowledged that at-threshold stimulation at *many* cortical points produced responses in multiple joints. The studies were therefore not as conflicting as their rhetoric would suggest. What explains the fact that participants arrived at such different theoretical views despite the broad compatibility of their findings? The answer lies in their conflicting understandings of representation's inferential role, which were in turn rooted in their divergent epistemological commitments. Muscles proponents held that simplified, tightly controlled stimulation studies revealed cortical representations. Movements proponents thought representation could be illuminated by emulating the complexity of ordinary functioning. These different conceptions of the experimental conditions under which it is appropriate to apply the concept of representation led participants to different conclusions from a largely consistent body of evidence.

Facing Representation Head-On: Participants' Manifest Concepts and the Debate Recast

Such conceptual gridlock increasingly led participants in the muscles versus movements debate to examine the notion of representation directly, as can be seen in the opening vignette from Eccles' Study Week at the Pontifical Academy of Sciences. We have thus far focused on the inferential role of participants' operative concepts of representation, illuminated by their practices of use. By mid-century, however, a few participants were explicitly discussing the notion of representation, shedding light on the manifest concepts they took themselves to be applying (Haslanger 2012).¹⁰

In his Study Week clash with Phillips, Penfield disavowed representation, declaring it to be a placeholder for the functional contribution of the motor cortex. Although one may suspect Penfield of understating his commitment to representation to make peace with Phillips, his remarks were at least consistent with earlier work in which he treated representation as a functional notion (Penfield and Boldrey 1937). Elsewhere, however, Penfield gestures at a *structural* notion of representation, which he sometimes calls "anatomical representation" (Penfield and Jasper 1954, p. 828). In the legend for a figure depicting the precentral gyrus, Penfield explains, "Representation signifies the connexions of gyrus with contralateral anterior horn formation of spinal cord and medulla" (1954, p. 6). The part of the motor cortex that represents the hand, on this understanding, is the region that sends efferent projections to spinal cord segments controlling the hand. It is "in this sense only" that "movements

¹⁰ In the debate's early years, Hughlings Jackson had, in fact, made a handful of oblique comments about his use of the term "representation," though his remarks are hardly clarifying. He claims, for instance, that the "[m]ethod of representation and localisation are only different names for one thing" (Hughlings Jackson 1882, p. 33) and "representation and co-ordination are the same thing" (Hughlings Jackson 1884, p. 83). Presumably this means that a brain region represents a particular movement when it coordinates that movement, or the movement is localized there, though this is hardly satisfying as an explication of representation. Chirimuuta (2019) has recently offered a detailed analysis of Hughlings Jackson's elusive notion of representation, arguing that it combines reductive and holistic strands of thought. The result, she concludes, is a uniquely "integrative" concept on which cortical representations "somehow holographically represent the entire region of the body relevant to the movement...while at the same time co-ordinating or controlling more local parts" (Chirimuuta 2019, p. 41).

of different portions of the body are represented” in the precentral gyrus (Penfield 1954, p. 15). In nearly the same breath, however, Penfield also claims that “mechanisms” and processes like vocalization are cortically represented, expressions that are difficult to square with a purely structural understanding of representation (1954, p. 15).

Of all the debate participants, Walshe devoted the most direct attention to the notion of representation. He expressed concern that representation meant different things to different people, sowing confusion in neurology (Walshe 1953). So, he tried to define it: “representation,” he claimed, refers to “all those processes in the cortex by which visible [motor performances] are brought about” (Walshe 1943, p. 108). (Note that this characterization is tailored to the present debate, since it applies only to motor, not sensory, representation.) According to Walshe, representation abstracts away from the neurophysiological details of movement production, such as nerve conduction and synaptic transmission. As such, it “answers none of [the physiologist’s] questions,” since physiology is concerned with *how* the motor cortex enables movement (Walshe 1943, p. 108).¹¹

Walshe wielded representation as a weapon, molding a manifest concept to buoy his Jacksonian view. First, he argued that the concept itself ruled out the representation of muscles or body parts. It is an “ontological absurdity,” he claimed, to think that the content of a representation could be a structure rather than a process (Walshe 1947, p. 20). The motor cortex must represent “performances” rather than “performing parts” (Walshe 1943, p. 107). Walshe thereby centered activity in his conception of representation: representational content reflects what a brain structure does, not what its object is. Second, Walshe claimed that representation requires a degree of fixity. To make sense of cortical instability, he argued, a proponent of the representation of muscles must hold that “a given representation actually changes its location from place to place and moment to moment, and that cortical representation is in a perpetual flux” (Walshe 1947, p. 23). He saw such shifts in representation as untenable. Once one admits “a perpetual flux of representation, the idea of fixed representation is gone, and to call the cortex labile or unstable gives us nothing in its place” (Walshe 1943, p. 9). In claiming that it “gives us nothing” to posit representational volatility, Walshe is suggesting that representations necessarily possess a certain degree of fixity. And representational fixity, he thought, was incompatible with the muscles hypothesis.

Walshe’s attempts to dismiss the cortical representation of muscles by conceptual fiat were not successful. But others soon came to share his frustration with the concept of representation (Goody 1957, Phillips 1975). In the decades after 1954, this frustration fueled a determined push by several researchers to put the muscles versus movements debate to rest. Charles Phillips, Penfield’s Study Week foil, led the charge. Phillips held that the debate should never have been a live issue, in part because Hughlings Jackson had not intended an antithesis between the representation of muscles and movements (a claim I disputed above). The debate led to “inconclusive ‘philosophical reflection,’” Phillips argued, because stimulation studies were unable to falsify either position (1975, p. 213). He proposed that neurophysiologists shelve questions of representation and try instead to determine

¹¹ Walshe also declared that representations can be distributed, or “spread out widely throughout the motor cortex” (1943, p. 111). For decades, participants in the debate had closely associated representation with localization, assuming that representations occupy restricted areas of the cortex. Walshe drove a wedge between representation and localization by claiming that cortical representations are “widely localized” (1943, p. 111).

where exactly efferent projections from the motor cortex end up. Several others shared Phillips's (1965, 1975) deflationary attitude, or his preference for substituting structural questions in place of functional ones (Woolsey 1947, Goody 1957, Evarts 1967, Lemon 1988).

Despite the pleas of Phillips and his allies, however, the muscles versus movements debate has been transformed but not abandoned. Technological advances for stimulating and recording from ever-smaller units of the nervous system shifted discussion to whether *single neurons* represent muscles or movements (Evarts 1967, Asanuma 1973). This transposition of the debate to a smaller spatial scale was also accompanied by a replacement of the muscles/movements dichotomy with a contrast between kinematics and kinetics. Kinematic variables characterize the “spatiotemporal form of a movement,” while kinetic variables concern a movement’s “underlying causal forces and muscle activity” (Kalaska 2009, p. 142). Today, discussion continues about whether the motor cortex represents kinetics or kinematics, a controversy taken to be continuous with the muscles versus movements debate (Humphrey 1986, Kakei et al. 1999, Ebner et al. 2009, Kalaska 2009, Oby et al. 2013).

Historicizing Representation

The debate’s transformation in the second half of the twentieth century deserves much more consideration than can be given it here. Suffice it to say that at mid-century, resolution of the debate was far from reach. This will come as no surprise to Engelhardt and Kaplan, who claim that “[t]he final resolution of a scientific controversy, if such is to be available at all, often requires the resolution of philosophical problems” (1987, p. 7). Unresolved philosophical problems about representation were indeed central to the muscles versus movements debate. Engelhardt and Kaplan also observe that scientific controversies resist closure when stakeholders belong to different scientific communities with different understandings of the evidence. Here too we find their analysis well-suited to the current case, which divided brain scientists largely along professional lines: clinical neurologists favoring the representation of movements, neurophysiologists and neurosurgeons supporting muscles.

Both professional divisions and the slipperiness of the concept of representation contributed to the debate’s persistence in the first half of the twentieth century. Indeed, these two factors were intertwined: epistemological disagreements between professional groups generated discrepancies among participants’ operative concepts of representation. Representation-talk had gained steam in neurology and physiology, and participants in the debate agreed that cortical representations were graded and overlapping. But those with different training and investigative commitments held different views about what evidence supported representational attributions. Neurologists privileged clinical arguments in favor of movements, while neurophysiologists were most impressed by reductive experimental results supporting muscles. Experimental results that one side took to be decisive, including the presence of cortical instability and solitary responses, were ignored or dismissed by the other. In the clinic, too, participants drew opposing conclusions from patterns of deficit and recovery

following injury. Disagreement about what the motor cortex represents therefore persisted despite broad agreement about many basic observational and experimental findings.¹²

Divergent understandings of what representational attributions imply, and what counts as evidence for them, amount to differing conceptions of the inferential role of representation. If one adopts an inferentialist semantics, the analysis provided here suggests that the debate's intransigence was partly rooted in disagreement about the very meaning of the term "representation." According to inferentialism, a concept's meaning is related to its role in inferences. On Brandom's (1994) development of the view, the content of a term is determined by its inferential role, which Brandom construes broadly to include both the circumstances in which it is appropriate to apply the concept and the inferences and actions that its application licenses. (Or as he later put it, a concept's inferential role encompasses "language-language moves," "language entry moves," and "language exit moves" [Brandom 2010, p. 171]). Brandom rejects the idea that only some inferences are meaning-constitutive (cf. Fodor and Lepore 2001), opting instead for the holist view that all of the inferences in which a concept figures contribute to its meaning (2010, pp. 166-74). On this semantic picture, brain scientists' disagreements about what follows from claims about what the motor cortex represents take on special significance. Since drastically different understandings of a concept's inferential role correspond to different meanings, early brain scientists were at loggerheads about just what "representation" *meant*. This inferentialist understanding of the debate resonates with Freudenthal's contention that divergent meanings of concepts are an "essential feature" of scientific controversies (2000, p. 130).¹³

One need not endorse inferentialism, however, to accept the story told here: that the muscles versus movements debate defied resolution in part because it pitted an upstart surgical and experimental epistemology against a traditional clinical epistemology. Each side possessed distinct ideas about the sources of reliable knowledge, ideas which were channeled into contrasting inferences regarding cortical representation. This analysis shows that examining the inferential role played by a concept in a scientific controversy can offer a useful window into the epistemologies of the conflicting parties. Contested scientific concepts often reflect the assumptions and aspirations of those who deploy them. By analyzing the inferences in which a concept is deployed, the historian of science can gain insight into the epistemological commitments of individual researchers and scientific groups.

¹² McMullin (1987) suggests that a difference between scientific and moral controversies is that there is usually consensus about the proper means of resolving the former but not the latter. In scientific controversies, unlike moral ones, participants "agree (at least in broad outline) on what would count as relevant considerations on either side of the case" (p. 55). The muscles versus movements debate shows this is unreasonably optimistic. Because participants did not share a common understanding of representation, there was little agreement about what would constitute decisive evidence for one side or the other.

¹³ This brief discussion of inferentialism elides many nuances. For one thing, the inferences that Brandom holds determine a concept's meaning are *correct* inferences: "the ones people ought to make, rather than the ones they are actually disposed to make" (2010, p. 163). For another, Brandom recognizes that the inferential significance of a concept depends on auxiliary hypotheses, or what he calls "collateral commitments" (1994, p. 92). Perhaps the disagreements between brain scientists discussed here can be traced back to differing collateral commitments. An objector might claim that the meaning of "representation" was shared among scientists, even if they were led to endorse different inferences by different auxiliaries. A more careful articulation of the inferentialist argument suggested here would need to address these complexities.

Such analyses also raise normative questions about how we should think about scientific concepts that are contested or vague. Some have claimed that conceptual flexibility can in fact be serviceable for researchers. Rheinberger suggests as much with respect to the gene (Rheinberger 2010, Rheinberger and Müller-Wille 2017). He argues that it is precisely because of the gene concept's malleability that it has been a useful tool for translating between different domains and “reach[ing] out into the realm of what we do not yet know” (Rheinberger 2010, p. 223). Boundary objects and concepts like the gene not only defy definition, attempting to pin them down is counterproductive: “as long as the objects of research are in flux, the corresponding concepts must remain in flux, too” (Rheinberger 2010, p. 221; see also Elkana 1970). One might wonder whether representation is a boundary concept amenable to such an analysis. On this view, the muscles versus movements debate reveals a constructive mutability in the notion of representation, one which facilitates linkages between different practices and domains. Far from being cause for concern, disagreement about representation's inferential role was simply a symptom of its centrality in the early brain sciences.

But a more critical perspective is available as well. While the debate may have inspired new research, it is reasonable to see participants' divergent understandings of representation as an obstacle to theoretical advancement. The controversy's heated rhetoric belied widespread agreement about many key scientific findings. Lacking a common understanding of the implications of representational attributions, researchers had no shared evidence base for adjudicating competing theoretical claims about the motor cortex. The flexibility of representation, a critic might contend, was therefore a hindrance to scientific consensus building, deepening unproductive disputes between competing professional groups. Something like this view animated later commentators who urged the abandonment of the debate (Phillips 1975, Lemon 1988).¹⁴

Far from being a purely historical matter, these two perspectives carry significant contemporary relevance. Representation-talk has exploded in the brain sciences since the time of Hughlings Jackson. Rare is the present-day neuroscientist today who never talks of what cells, regions, systems, or networks represent. One wonders whether neuroscientists have converged on a shared understanding of what such representational attributions imply, or whether the disagreements present in the muscles versus movements debate persist to the present day. Recent work has begun investigating this question (Vilarroya 2017, Favela and Machery ms). Much more remains to be done to determine if the conceptual ambiguity that exists is a boon or a detriment to neuroscience. Such work will shape how we look back on the muscles versus movements debate, as either a scientific relic or harbinger of the role of representation in the contemporary brain sciences.

¹⁴ Criticism of the concept of representation can be found in other literatures that are more or less related to the present discussion of representation in the brain. For instance, science studies scholars have debated the utility of the notion of representation (Lynch and Woolgar 1990, Lynch 1994), and the “representation wars” in cognitive science have pitted representationalist against dynamicist models of cognitive processes (Constant et al. 2021).

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