Modern study of the neurophysiology of the cerebral cortex began with Fritsch and Hitzig’s discovery that electrical stimulation of the cortex produces movements. The importance of this discovery was threefold: it was the first demonstration of cortex devoted to motor function, the first indication that the cortex was electrically excitable, and the first evidence of a topographically organized representation in the brain. Fritsch and Hitzig’s basic findings were soon replicated by Ferrier, but there were differences between the two studies in both method and interpretation. These different approaches have continued to reverberate in research on the function of motor cortex from the late 19th century to the present day. NEUROSCIENTIST 9(5):332–342, 2003. DOI: 10.1177/1073858403257037

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One of the most important events in the history of neuroscience was the discovery by Gustav Fritsch and Eduard Hitzig in 1870 that electrical stimulation of the cerebral cortex produces discrete movements. This experiment represented the intersection of several controversies of the time: whether any part of the central nervous system was electrically excitable, whether the cerebral cortex was of functional importance, and the contentious issue of whether functions could be localized in the brain. Fritsch and Hitzig’s remarkable demonstration that the cortex was excitable, that it did in fact have a meaningful function, and that there was a topographical representation of the body in the cortex may be viewed as the beginning of modern neurophysiology.

One aim of this article is to trace the various lines of thought that led to this discovery. A second aim is to outline its subsequent fate. A few years after Fritsch and Hitzig’s (1870) report, David Ferrier (1873) published his own study of electrical stimulation of motor cortex. Although fundamentally a replication of Fritsch and Hitzig’s demonstration of a somatotopically organized motor cortex, Ferrier’s methods, results, and interpretation were somewhat different from theirs. Whereas Fritsch and Hitzig reported that stimulation evoked muscle contractions such as spasms or twitches, Ferrier reported complex movements. The issues that distinguished Fritsch and Hitzig on one hand and Ferrier on the other are still discernable in contemporary research on motor cortex.

The Situation before 1870

The Neural Control of Movement

From the earliest Western medical writings, it was thought that the movement of the body was controlled by the brain. In the Edwin Smith Surgical Papyrus, whose origins lie in the Pyramid Age (about 30th century BCE), there are a number of descriptions of motor dysfunctions after head injury (Breasted 1930). For example, in case 8, the patient “walks shuffling with the sole on the side of him having that injury which is to his skull” (p 210; presumably a contrecoup injury where a blow to one side of the head causes the brain to impact on the inside of the contralateral skull).

The Hippocratic doctors (5th century BCE) wrote extensively on the treatment of head wounds and, unlike the author of the Surgical Papyrus, were well aware that head injuries produce contralateral symptoms. However, they were primarily interested in diagnosis and treatment and had little interest in studying the underlying anatomy or physiology (Hippocrates 1927).

Galen of Pergamon (129-199) was the most important figure in classical medicine and biology and a brilliant experimental physiologist and anatomist. His ideas dominated European medicine for more than 1500 years. This was especially true for his views of brain function and the control of movement. His theories derived from many sources including his training in Alexandria (where human vivisection had been practiced), his clinical experience (especially as physician to a gladiator school), and his experiments on the spinal cord and brain of animals. Galen distinguished between sensory and motor nerves; he thought nerves were hollow and carried “psychic pneuma.” The brain was supposed to act as a pump that moved the psychic pneuma from the sense
organs into the ventricles, then into the motor nerves, and finally into the muscles, causing their contraction by inflation (Gross 1998a, 1998b).

René Descartes (1596-1650) elaborated these ideas by suggesting that the centrally located pineal body directed the pneumatic flow from sense organs into the muscles (Descartes 1972). Several lines of evidence soon refuted this pneumatic theory of movement: Francis Glisson (1597-1677) and, independently, Jan Swammerdamm (1637-1680) demonstrated that contraction of a muscle did not increase its volume, as it should if the pneuma were swelling it (Fearing 1970); Alexander Monroe (1697-1762) showed that ligation of a nerve produced no distal swelling, and nothing flowed from a cut nerve. Having disproved pneuma as a transmitter of nerve activity to muscle, Monroe suggested that, instead, electricity might be the mechanism (Brazier 1959).

Electricity and the Nervous System

The 18th century was a period of great excitement over the new discoveries about electricity. At this time, it was realized that man-made electricity, lightning, and the sting of the electric fish were examples of the same phenomenon. There were a number of attempts to use electricity for therapeutic purposes (including by the French revolutionary Jean-Paul Marat, whose murder in the bathtub was immortalized by the painter Jacques-Louis David) and even studies of electrical stimulation of various brains from frogs to dead humans (Brazier 1959, 1984; Finger 2000).

The modern study of the electrical nature of nervous activity begins with Luigi Galvani’s (1737-1798) demonstration that electrical stimulation of the sciatic nerve in a severed frog leg resulted in contraction of the attached muscle. These findings sparked a fierce debate between Galvani and Volta (1745-1827) concerning the cause of movement: the electricity came from within (“animal electricity”) (Brazier 1984; Finger 2000). Alessandro Volta considered the cause to be the use of dissimilar metals, whereas Galvani was convinced that the electricity came from within (“animal electricity”) (Brazier 1984). Eventually, this debate led, on the one hand, to the development of the electric battery and, on the other hand, to the discovery of the action potential and electroencephalogram. Galvani’s results prompted attempts to stimulate other nervous structures, but the vast majority of experiments on the electrical stimulation of the cerebral cortex were negative, reinforcing the prevailing view that the cortex had no significant functions (Fritsch and Hitzig 1870; Brazier 1984; Finger 2000).

Functions of the Cortex

Until the start of the 18th century, the cerebral cortex was usually dismissed as an insignificant “rind,” which indeed is what the Latin word cortex means. Some thought it a glandular organ and others a network of capillaries nourishing the tissue below (Gross 1998a). However, a few figures did dissent from the near universal dismissal of any functional importance for cortical tissue. The most influential dissenter was Thomas Willis (1621-1675), professor at Oxford, one of the founders of the Royal Society, and author of the first monograph on brain anatomy, physiology, and chemistry as well as clinical neurology (Willis 1684). On the basis of animal and human studies, Willis implicated the “cortical and grey matter of the cerebrum” in memory, will, and voluntary movement. He relegated the control of involuntary movement to the cerebellum. On the basis of the post-mortem examination of paralyzed patients, Willis thought that the motor mechanisms of the cortex acted through the corpus striatum (Gross 1998a).

The other advocate of a role for the cerebral cortex was François Pourfour du Petit (1664-1741), a French army surgeon who studied the effects of lesions on what we now call motor cortex. He carried out a series of experiments on cortical lesions in dogs and related them to his clinicopathological studies of wounded soldiers. From these investigations, he inferred that the cerebral cortex played a critical role in normal movement. He also reported that there was no response when the cortex was touched (Kruger 1963). Although du Petit did not hold an academic post and published his account in an obscure pamphlet, his observation that the cortex was insensitive to touch was repeatedly cited as indicating the nonimportance of the cortex. Unfortunately, du Petit’s lesion work showing the role of the cortex in movement was ignored in his time. This was probably because of the contemporary anticortex ideology, however, rather than because only 200 copies of his pamphlet were printed (Gross 1998a).

Like Willis, du Petit thought that the psychic pneuma mediated movement. However, he believed that it came from the cortex and passed through the corpus striatum on the way to muscles. He had both experimental and clinicopathological evidence for the importance of both the cortex and the corpus striatum for movement. Although the idea of cortical motor functions disappeared until Fritsch and Hitzig, the view of the corpus striatum as a dominant motor center remained influential (Gross 1998a).

A major figure that denied significant functions for the cerebral cortex was Albrecht von Haller (1708-1777), professor at Tübingen and, later, Bern. Using animals, he tested the “sensibility” of various brain structures with mechanical stimuli such as pricking with a scalpel and pinching with forceps as well as with chemical stimuli such as sulfuric acid and alcohol. With these methods, he found the cortex completely insensitive. By contrast, he reported the white matter and subcortical structures to be highly sensitive; their stimulation, he said, produced expressions of pain and movement. He concluded that all parts of the cortex had the same function because they were equally insensitive, and all subcortical regions were also equivalent because their stimulation had equally positive effects. This was the dominant
view until the rise of phrenology at the turn of the 19th century (Neuberger 1981; Gross 1998a).

Gall, Flourens, Broca, and the Localization of Function

The localization of different psychological functions in different regions of the cerebral cortex begins with Franz Joseph Gall (1758-1828) and his collaborator, J. C. Spurzheim (1776-1832). The central idea of their phrenological system was that the cerebral cortex consisted of a set of organs with different functions. Gall and Spurzheim initially postulated 35 affective and intellectual faculties. It was assumed that these were localized in specific cortical organs and that the size of each cortical organ was indicated by the prominence of the overlying skull, that is, by cranial bumps. Their primary method was examining the skulls of a variety of people from lunatics and criminals to the eminent and accomplished. The absurdity of phrenology’s dependence on cranial morphology was quickly recognized, at least in the scientific community. In spite of this, Gall’s ideas about the cortex as a set of psychological organs stimulated investigation of the effects of cortical lesions in humans and animals and of structural variations across different cortical regions. In these ways, phrenology had a lasting influence on the development of modern neuroscience. All the phrenological localizations were of “higher” intellectual and personality traits; the highest sensory functions were still in the thalamus, and the highest motor functions in the corpus striatum (Young 1970; Gross 1987, 1998a).

The cortical localizations of phrenology were attacked by Pierre Flourens (1794-1867). Within the cortex, he found no localization of function; only the size and not the site of the lesion mattered. However, Flourens did find that different major brain regions had different functions. For example, he implicated the cerebral hemispheres in willing, remembering, and perceiving and the cerebellum in movement. Although these results refuted the punctate cortical localizations of Gall, they actually supported both the general idea of localization of function in the brain and the specific importance Gall had given to the cerebral hemispheres in cognition (Young 1970; Gross 1998a).

In 1861, Paul Broca (1824-1880) described several patients with long-standing difficulties speaking, which he attributed to damage to their left frontal lobes. This was the first generally accepted evidence for localization of a specific function in the cerebral cortex. At the time, this was viewed as a general vindication of Gall’s ideas on localization of function in the brain and a specific confirmation of Gall’s localization of language in the frontal lobes (Young 1970; Schiller 1979; Gross 1998a).

Early Suggestions of a Somatotopically Organized Motor Cortex

There were two prescient proposals for the existence of a somatotopically organized motor representation in the cerebral cortex. The first was by a Swedish mystic and had no affect at all. The second was by a leading English neurologist and was a powerful stimulus to the work of Ferrier.

In 1743, the Swedish nobleman and polymath Emanuel Swedenborg began to see and converse with God and angels. His interest in the soul led him to study its housing in the brain, and he wrote a set of extraordinary treatises on brain function. He thought the cortex was the “principal substance of the brain” and both its “sensormus commune” and its “motorium commune voluntarium... [It] imparts... sensation, perception, understanding and will; and it imparts motion” (Gross 1997, p 145). There were “little brains” in the cortex that had nerve fibers connecting them to each other and to the rest of the body. (This was more than 100 years before neuron theory.) He located control of the foot in the dorsal cortex, the trunk in the intermediate cortex, and the face and head in the ventral cortex. It is quite unknown where he got these ideas, but he did pass through Paris in the same year that Pourfour du Petit was carrying out his experiments on the motor cortex of the dog. Although Swedenborg had many religious and philosophical followers, his ideas on the brain were unknown to his contemporaries and were only discovered long after Fritsch and Hitzig’s discovery of motor cortex (Gross 1997).

John Hughlings Jackson (1815-1911) is often called “the father of English neurology” because of his many discoveries in clinical neurology. Heavily influenced by evolutionary ideas, Hughlings Jackson reasoned that the cortex should have basic sensory-motor functions and gathered clinicopathological evidence for this view (Young 1970). In studying epileptic seizures, including those of his wife, he noticed that there was a consistent systematic spread of convulsions from one body part to the next. From this, he inferred that different parts of the cortex must be involved in the control of different muscle groups and that these parts must be arranged in a way to mimic the organization of the body (Hughlings Jackson 1873; Young 1970; Temkin 1971). Hughlings Jackson was a major influence on Ferrier, and, although Fritsch and Hitzig did not mention Jackson in their first paper, Hitzig (1900) later commented that his experiments with Fritsch had only confirmed the conclusions reached by Hughlings Jackson on clinical evidence.

Fritsch and Hitzig on Motor Cortex

Who Were Fritsch and Hitzig?

When Gustav Fritsch (1838-1927) and Eduard Hitzig (1838-1907) carried out their famous experiments (Fritsch and Hitzig 1870), they were young medical Privatdozents (roughly, assistant professors) in Berlin. They had no facilities for animal experimentation, so their experiments were carried out on Frau Fritsch’s dressing table (Kuntz 1953). Previously, Fritsch had carried out anthropological and geographical studies and
worked as a battlefield surgeon in the Franco-Prussian war (Grundfest 1963). Hitzig was a psychiatrist who had tried the therapeutic use of electricity on his patients. After their collaboration, Hitzig continued to work as a psychiatrist and to research on cortical localization in animals (Brazier 1988). His 1874 book is an expansion of his earlier work on motor cortex and a critique of Ferrier's writings on motor cortex. Fritsch returned to his earlier interests in anthropology and was particularly concerned in using studies of the eye and hair to establish the superiority of the white race (Grundfest 1963). (In the course of his studies of the eye, he coined the terms “fovea” and “area centralis”). When the American anatomist C. L. Herrick (founder of the Journal of Comparative Neurology) met Fritsch and Hitzig, he described them as “splendid specimens of physical development and German culture at its best” (Herrick 1892). Hitzig, who came from a distinguished Jewish family, was characterized by one of his biographers as “a stern and forbidding character of incorrigible conceit and vanity complicated by Prussianism” (Kuntz 1953; Finger 2000). Portraits of Fritsch and Hitzig are shown in Figure 1.

**The 1870 Paper on Motor Cortex**

The rise of interest in electricity and the nervous system had led to a number of attempts to electrically stimulate the cerebral cortex. However, the results, including those of such brilliant experimenters as François Magendie and Carlo Matteucci (Fritsch and Hitzig 1870; Brazier 1959) were invariably negative, leading Fritsch and Hitzig to comment in the introduction to their 1870 paper that there “was hardly a question about which opinions agreed so well, and which appeared so completely settled, as the question of excitability of the cerebral hemispheres” (p 17). They did not know about the speculations of Swedenborg, and there is no evidence that they were influenced by Hughlings Jackson’s observations (Young 1970). Why then did they set out to electrically stimulate the cortex of a dog? One reason was that they were intrigued with the paradox that some parts of the nervous system, such as the spinal cord and nerves, were electrically excitable, whereas other parts such as the cortex did not seem to be. Probably more important were observations each of them had made previously. Hitzig had tried electrical stimulation of the human head for therapeutic purposes and had noticed it caused eye movements (Hitzig 1870). He then tried rabbits and also elicited movements. Fritsch, while working as a battlefield surgeon, had apparently noticed that the contralateral limbs twitched while he dressed an open head wound (Walker 1998).

Fritsch and Hitzig’s 1870 motor cortex experiments were fundamentally simple. They exposed the surface of the dog’s cerebral cortex and then applied galvanic stimulation and observed the results. This method of electrical stimulation involved passing a current directly from a battery through electrodes to the surface of the brain, essentially the application of a pulse of direct current. They used brief durations of stimulation, and the usual response was a Zuckung, or muscle twitch. Using this method, Fritsch and Hitzig made three observations that still form part of the basic knowledge about the organization of motor cortex. First, they found that electrical stimulation evoked contralateral movements from some regions of cortex but not from others. (Although the finding of contralateral control was not new, it was important that the findings from electrical stimulation confirmed the effects of lesions in humans and other animals.) Second, they found that stimulation of different parts of cortex activated different groups of muscles. Finally, the excitable sites formed a topographical map of movements of the body that was laid out on the surface of the brain.

Fritsch and Hitzig investigated whether the movements evoked from a particular site matched the movement deficits observed when the site was lesioned. For example, after using stimulation to locate the region of the cortex from which movements of the right foreleg could be evoked, they lesioned that area. Although there was no total paralysis of the leg, the dogs had marked difficulty in controlling it. This incomplete loss of function suggested to them that there were other motor centers that had not been affected by the lesion.

Their overall results led Fritsch and Hitzig (1870) to conclude their paper with a strong statement about localization of function in the cortex:

> It also results from the sum of all our experiments that by no means, as Flourens and most of the others after him believed, is the psyche a kind of total function of the entire cerebrum, whose expression can be removed as a whole but not in its individual parts by mechanical means, but that rather individual mental functions, probably all of them, contribute to the occurrence of the matter in circumscribed centers of the cerebral cortex. (p 27)

**Ferrier on Motor Cortex**

**From West Riding Lunatic Asylum to Knighthood**

At the age of 26, James Crichton-Browne (1840-1938, later Sir) was appointed head of West Riding Lunatic Asylum in the West Riding (or western third) of Yorkshire. His father had been a pioneer in the reform of mental hospitals, and Crichton-Browne actually grew up living on the grounds of one. In addition to transforming West Riding Lunatic Asylum into an enlightened mental hospital, he made it a major center for research on brain anatomy, brain physiology, and brain pathology with laboratories, weekly seminars, visiting lectures, and visiting researchers. He also founded the first journal devoted to brain research, *West Riding Lunatic Asylum Medical Reports*, which published a string of important papers for 7 years (Viets 1938). (He then abandoned it to found, with Hughlings Jackson and Ferrier, the journal Brain.)
Soon after the Fritsch and Hitzig (1870) paper appeared, Crichton-Browne invited his fellow medical student and Scotsman David Ferrier to come to the West Riding hospital and research center to follow up the Germans’ work on motor cortex (Viets 1938). Ferrier had been strongly influenced by John Hughlings Jackson, and when he realized that Fritsch and Hitzig had confirmed Jackson’s ideas, he was eager to study the new cortical phenomenon (Young 1970; Brazier 1988).

During and after his work on motor cortex, discussed in the next two sections, Ferrier studied the effects of stimulating throughout the accessible cortex and cerebellum. In some of these experiments, Ferrier thought that he might be stimulating sensory rather than motor areas. For example, when he stimulated the superior temporal lobe, he elicited ear movements, which he interpreted as suggesting some auditory functions, and stimulating the parietal lobe resulted in eye movements suggesting some visual functions. He then set out to test these possibilities by studying the behavioral effects of lesions of frontal, temporal, parietal, and occipital cortex. These experiments, described in papers (e.g., Ferrier 1875), two editions of his *The Functions of the Brain* (1876, 1886), and his *The Localization of Cerebral Disease* (1878), formed a major contribution to the understanding of the cerebral cortex (Gross 1998a; Finger 1994, 2000). They also resulted in Ferrier being charged under the Cruelty to Animals Act in 1881 (see Box 1) and being knighted in 1912. Ferrier continued his clinical work and is said to have been one of the last physicians to conduct rounds in “the traditional top hat and black tailcoat” (Clarke 1970). A portrait of Ferrier is shown in Figure 2.

**Ferrier’s Experiments on Motor Cortex**

Ferrier’s (1873, 1874a) initial experiments on motor cortex were carried out at West Riding primarily on dogs but also on cats, rabbits, jackals, and other animals. He asked three main questions: Could seizures similar to those observed by Hughlings Jackson be elicited by electrical stimulation? What was the effect of stimulation beyond the limited region explored by Fritsch and Hitzig? Were the effects of stimulation similar in different species?

Ferrier used faradic stimulation, a type of alternating current (see Fig. 3), and he usually stimulated for longer durations than Fritsch and Hitzig. He found he could induce seizures in the variety of animals tested as long as the duration of the electrical stimulus was 5 seconds or more. The seizures, he thought, were strikingly similar to the “marching seizures” observed by Hughlings Jackson.

Ferrier explored the effects of stimulation of much more of the cortical mantle than Fritsch and Hitzig had and indeed much more than is considered motor cortex today (see Fig. 4). Like Fritsch and Hitzig, Ferrier found that he could evoke movements of different body parts from different regions of the cortex. He localized centers related to the movements of the eyelids, face, mouth and tongue, ear, neck, hand, foot, and tail. Furthermore, Ferrier realized how similar the organization of these “centers” was to the map hypothesized by Hughlings Jackson on the basis of his study of human seizures.

In comparing dogs, cats, and rabbits, Ferrier noticed that the overall organization was the same in different species but that some parts of the body had larger representations in the cortex in some species. He suggested that these differences depended “on the habits of the animals” (Ferrier 1873, p 61) This is the first suggestion of a relationship between the organization of the brain and behavioral specializations in a particular species.

In 1874, Ferrier moved to Kings College Hospital in London and expanded his work to monkeys. By doing so, he hoped to understand the organization of the motor centers in the human brain. In fact, his localizations in monkeys were soon transferred to the human brain and used to localize and remove tumors and blood clots from the brains of patients with surprising success and accuracy (Anonymous 1881a; Ferrier 1890; Jefferson 1960). In the monkey brain, he again found that movements of various body parts were localized in different regions of
cortex. In monkeys, Ferrier delineated 19 centers related to different movements such as walking, arm retraction, flexion and extension of the wrist, mouth opening and “protrusion of the tongue,” “snarling expressions of the face,” and eye movements (Ferrier 1874-1875, p 421).

As had Fritsch and Hitzig, Ferrier found that movements that appeared to be represented at a site would be impaired when he destroyed that site. Furthermore, the larger the lesion, the larger the affected part of the body. A lesion of the entire motor area resulted in paralysis of one side of the body; the lesion of a “centre” that, when stimulated, caused movements of the hand and foot, “caused motor paralysis of the same movements and of none other” (Ferrier 1875, p 443); and finally, small lesions of only the “centre for the biceps” caused “the right arm to hang by the right side in a state of flaccid extension. . . . [The monkey] had lost the power of flexing the right arm” (Ferrier 1875, pp 443–444). As described in Box 2, Ferrier initially had some difficulty getting his results published in the Philosophical Transactions of the Royal Society because the referees thought he had not given adequate credit to the prior work of Fritsch and Hitzig (1870).

Differences between the Fritsch-Hitzig and the Ferrier Studies

The basic findings of Fritsch and Hitzig and of Ferrier were very similar. They both found that electrically stimulating the frontal cortex produces discrete contralateral movements. They both found that movements of different body parts could be evoked from different regions of cortex. They both found that when a part of the motor cortex is damaged, the animal appears to be unable to execute the movement that is evoked by stimulation. However, there were some important differences in their results, their methods, and in their interpretations that have influenced the subsequent direction of research on motor cortex.

The chief difference in their results was the type of movements that each evoked, indeed that each aimed to evoke. Fritsch and Hitzig described the movements they
evoked in terms of spasms or twitches (Zuckungen) of a small number of adjacent muscles. By contrast, Ferrier described the movements that he observed in terms of the natural movements they resembled, as in the following examples from different species. In the cat, Ferrier noted that stimulation of a particular site causes “the shoulder to be raised, and the limb to be adducted, exactly as when a cat strikes a ball with its paw” (Ferrier 1873). In the dog, stimulation of the supra-orbital region caused the following sequence of movements: “The animal opens its mouth, retracts the upper lips, and makes a sort of sniffing or snarling noise” (Ferrier 1873, p 53). In the rabbit, during stimulation of the frontal region, “The mouth is drawn to the left, and a munching movement of the left side of the mouth is made, as if the animal is eating” (Ferrier 1873, p 57). And likewise, in the monkey, stimulating of one site causes “flexion with outward rotation of the thigh, rotation inwards of the leg, with flexion of the toes—the action being such as is seen when the monkey makes a grasping movement, or scratches its chest or abdomen with its foot” (Ferrier 1886, p 241). At another site, Ferrier reported that stimulation caused the following movement: “Shoulder raised, forearm firmly flexed, hand clenched and supinated. The hand ultimately raised to the mouth, the angle of which is retracted and elevated” (Ferrier 1874-1875, p 419). Ferrier, on the basis of replications in 12 other monkeys, identified this site as the “centre for the biceps and muscles concerned in bringing the hand to the mouth” (Ferrier 1874-1875, p 419).

In light of recent work on motor cortex, there appear to be two main reasons for the differences between the results of Fritsch and Hitzig and Ferrier, namely, the nature of the electrical stimulus and its duration (Graziano, Taylor, and Moore 2002, Graziano, Taylor, Moore, and Cooke 2002).

Fritsch and Hitzig used primarily galvanic stimulation, whereas Ferrier used primarily faradic stimulation, and both argued for the superiority of their choice. Ferrier (1886) argued that faradic stimulation was critical for evoking complete movements from a motor center and therefore to “properly characterize” that center. Galvanic stimulation, he noted, results in “only a sudden contraction in certain groups of muscles, but fails to call forth the definite purposive combination of muscular contractions, which is the very essence of the reaction and the key to its interpretation” (p 225).

The second major difference between Fritsch and Hitzig and Ferrier was the duration and strength of stimulation. These parameters were critical in determining whether the evoked movements were twitches or resembled purposive movements. Although Fritsch and Hitzig do not explicitly state the duration of stimulation used in their experiments, it is likely that they used stimulation durations that were very short—on the order of a second—causing twitches or spasms that they describe as “fast-passing” (Fritsch and Hitzig 1870). They were aware of the noxious effect that longer durations of galvanic stimulation could have on the cortex and consequently advocated the use of short durations and weak currents. Furthermore, Hitzig (1874) noted the following:

By the use of very weak currents these muscle contractions can be localized to specific narrowly limited mus-
cle groups, with stronger currents, stimulation . . . led to the immediate participation of other muscles or even muscles of the corresponding body half. (p 53 [our translation])

In contrast, Ferrier stressed the importance of longer durations of stimulation, in keeping with his emphasis on producing a complete movement, and consequently producing the participation of other muscles. He realized that longer duration faradic stimulation was less damaging than equally long galvanic stimulation. In his experiments with different durations of stimulation, he found that “a slight stimulus of short duration causes only a part of a complex action, which is manifested in its completeness when the stimulus is of somewhat greater intensity and duration” (Ferrier 1886, p 239).

In addition to differences in the nature of the movements that Fritsch and Hitzig and Ferrier evoked, Ferrier tested a much greater extent of the cortex. Ferrier located motor centers in several cortical regions including eye movement areas now known as the frontal eye fields (area 8) and the lateral intraparietal area. Indeed, he thought that posterior parietal cortex was the visual center because he elicited eye movements from stimulation there (Glickstein 1985; Gross 1998a). In later work, Hitzig (1874) did investigate wider regions of cortex and described an “inexcitable zone” that overlaps with regions that Ferrier claimed to be excitable. Hitzig (1874, 1900) considered this to be due to Ferrier’s general incompetence, for example, his use of too strong a current and failure to replicate his observations sufficiently. Ferrier (1876) thought that Hitzig failed to produce movements from these regions because the currents he used were too weak.

In summary, Fritsch and Hitzig obtained twitches of a few muscles from brief monophasic direct current stimulation, whereas Ferrier obtained complex movements from long duration alternating current stimulation.

Afterword

Both Fritsch and Hitzig’s and Ferrier’s papers on motor cortex were greeted by much skepticism. Their results went against the generally accepted views that the striatum was the highest motor center, the cortex was inexcitable, and functional localization in the cortex was phrenological pseudoscience. The critics usually interpreted the evidence for the localization of motor function in cortex as artifactual due to “spread of current” to the striatum. To overcome these criticisms, Beevor, Horsley, Sherrington, and others began meticulous “punctate” mapping of cortex using the minimum current to elicit the smallest discernable movement (e.g., Horsley and Schäfer 1883, 1888; Beevor and Horsley 1887; Beevor 1887; Brown and Sherrington 1912, 1915). Thus, Ferrier’s search for the full movement became overshadowed by the effort to localize function more and more precisely.
Twitches Versus Movements

For reaching? What was the shift of emphasis of stimulation studies to the motor cortex? Initially, the views of the referees were sent to Ferrier, and he slightly revised and resubmitted the paper (see Fig. 5), but it was still unacceptable for the same reason. They thought, for example, that its “acknowledgement of Hitzig’s claim to priority was so slight . . . that its publication would be . . . unfortunate to English Science (RR.7.302)”

Later that year, Ferrier presented the material in this paper at a meeting of the Royal Society, and a three-page abstract (unrefereed) was published in its Proceedings (Ferrier 1874b). The abstract described the work as a confirmation of Hughlings Jackson’s views and did not mention Fritsch and Hitzig. Ferrier then wrote up the monkey stimulation data in detail, and it was accepted by the Philosophical Proceedings of the Royal Society (Ferrier 1874-1875). Although the paper did not even mention Fritsch and Hitzig, the priority issue must have seemed less critical because Fritsch and Hitzig had only worked on dogs and this paper was exclusively on monkeys. Much of the other material in the previously rejected paper was eventually published in his 1876 book. Ferrier did give Fritsch and Hitzig more credit there, and by 1890 he wrote,

“failed to give justice to them,” in Foster’s words.

The whole aspect of cerebral physiology and pathology was revolutionized by the discovery, first made by Fritsch and Hitzig, that certain definite movements could be excited by the direct application of electrical stimulation to definite regions of the cortex cerebri in dogs. (Ferrier 1890, p 17)

Ferrier’s rejected paper is in the archives of the Royal Society (AP.56.2), as is the correspondence with the referees about it (RR.7.299-305; RR.12.103), MC10.194. 247; Young 1970).

In the century after the first electrical stimulation experiments on motor cortex, it became possible to evoke smaller and smaller movements and therefore to localize motor functions in an even more punctate fashion. By the 1980s, it was possible to record small changes in the electromyographic activity of muscles in response to single pulses of stimulation (Cheney and Fetz 1985). Leyton and Sherrington’s (1917) map of motor cortex in the chimpanzee followed by Penfield’s human motor homunculus (Penfield and Rasmussen 1950) and Woolsey’s (Woolsey and others 1952) maps of monkeys and other animals became the standard picture of motor cortex. One consequence of this effort to localize the effects of stimulation with increasing precision was the shift of emphasis of stimulation studies to the representation of muscles, rather than of movements (Walshe 1943; Fulton 1949; Phillips 1975). It was not clear, however, how these maps were related to movement. Did motor cortex control relatively low-level aspects of movement such as the muscle tensions required for the flexion and extension of individual joints? Or did it control more complex aspects of movement such as the coordinated muscle activity required for reaching?

The two contrasting views that first emerged with Fritsch and Hitzig’s stress on brief muscle twitches and Ferrier’s stress on integrated movements continue to remain issues in the study of motor cortex. Some researchers emphasize the cortical control of small groups of muscles and individual joints (e.g., Asanuma 1975; Scott and Kalaska 1997), whereas others emphasize the cortical control of reaching in specific directions (e.g., Georgopoulos and others 1986, 1992). Recently, Graziano and colleagues (Graziano, Taylor, and Moore 2002; Graziano, Taylor, Moore, and Cooke 2002) have revisited Ferrier’s idea that motor cortex may control complex, highly integrated behavior.

References


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