Laying the Ghost of 'Muscles Versus Movements'

C. G. PHILLIPS

An invited lecture given to the Tenth Canadian Congress of Neurological Science, London, Canada, June 1975. Dr. Phillips was the distinguished guest speaker of the congress for 1975.

Deux fois je l'ai vu, mille fois je l'ai senti.

M. R. JAMES *(Canon Alberic's Scrap-Book)*

INTRODUCTION OF DR. CHARLES PHILLIPS

HERBERT H. JASPER

It is certainly a mark of great wisdom to the organizer of this meeting to have chosen Charles Phillips as our Guest Lecturer for this meeting.

Whilst I am grateful for this opportunity of saying a few words of introduction, I am sure it can be said of Charles Phillips that very little introduction is necessary, since we meet him at the most important meetings in Neurophysiology around the world. Any meeting on the motor system, of course, is not complete without the participation of Dr. Phillips. However, some of the less old-timers than myself, and the students, might be interested in the beginnings of Dr. Phillips' career in neurophysiology and to know that he was first a clinical neurologist beginning his medical studies in Oxford just before the war, where he came under the influence of Sir Charles Sherrington with Jack Eccles as his tutor. Following his medical studies he went to St. Bartholomews for training in clinical neurology where he came under the influence of Sir Hugh Cairns, Sir Charles Symonds and Dr. Riddoch. During the war, Dr. Phillips participated in the Head Injury team, studying the effects of acute head injuries. After the war, he returned to Oxford and has been Professor of Neurophysiology there ever since. He has recently been appointed to the Chair of Neuroanatomy at Oxford. Dr. Phillips was one of the pioneers in the cellular physiology of the nervous system making use of intracellular microelectrodes to study relations between cerebral cortex and spinal motor neurones beginning, I believe, about 1953. Thanks to his clinical training and scholarship, Dr. Phillips has been able to relate his microphysiological studies to behavior and to clinical neurology in a most meaningful manner, as shown particularly in his Ferrier Lecture before the Royal Society in 1969, and in the Hughlings Jackson lecture delivered before the Royal Society of Medicine in 1973.

Dr. Phillips' address on "Laying the Ghost of Muscles Versus Movements" provides a fitting introduction to the symposium which will follow on "Mechanisms of Motor Control".

The ghost I am raising is the ghost of what I think should never have been regarded as a live issue: whether 'muscles' or 'movements' are 'represented' in the sensorimotor cortex. It walked the corridors of neurology in the nineteen-thirties and -forties and then seemed, in the nineteen-sixties, to be fading quietly away, losing its hold over a new generation of microanatomical and microphysiological researchers who were busying themselves with details of corticospinal connectivity. Evarts' thoughtful paper, 'Representation of Movements and Muscles by Pyramidal Tract Neurons of the Precentral Motor Cortex' (1967), shed altogether too much daylight for the ghost's comfort. It had depended all along for its influence on spreading the false belief that a man called Hughlings Jackson had formulated alternative propositions, 'muscles' or 'movements', A or B; and on suggesting that one or other of these propositions could, in principle, be demolished by a suitable experiment: one involving electrical stimulation of the cortex. Jackson had, in fact, propounded no such alternatives (Phillips 1966; Evarts 1967). It

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seems, nevertheless, that we may now have to beware of a fresh series of Appearances, and to prepare ourselves to make renewed efforts to lay this ghost.

The ghost has always respected those who have chosen their words carefully. 'Since the time of Hughlings Jackson (1834-1911) it has been taught that the motor cortex is organized to yield movements. This is sometimes picturesquely stated by saying that the motor cortex "thinks in terms of movements, not muscles" ' (Ruch, 1951). The inverted commas and the 'picturesquely' should have ensured peaceful nights. 'One of the questions imposed on this series of experiments was "whether the motor cortex thinks in terms of movements or muscles?" The answer obtained was "the motor cortex thinks in terms of muscles" ' (Asanuma 1973). Again, the inverted commas should be keeping the ghost at bay. But in order to re-establish its former influence it has only to blind the readers of such passages to the 'picturesquelys' and to the inverted commas. The more elegant the experiments (and those of Asanuma and his colleagues are some of the most elegant that have been performed on the cerebral cortex) the easier its task. In their admiration for the experimental achievement, the readers can be helped to overlook the inverted commas completely. And since readers include writers of textbooks and reviews, the ghost is likely to have a whole new generation of students in thrall.

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From the very outset of his clinical studies of the control of movements by the human brain, Hughlings Jackson had been made aware of the difficulty of making his ideas intelligible to his neurological readers, experimental as well as clinical (Phillips, 1973). His posthumous readers must often have been tempted to give up the unequal struggle. 'As to his language, this was in part that of his period, but candour compels the admission that in general he is a very untidy writer. Many of his papers give the impression of being first drafts . . . Instead of polishing his presentation, he appends, perhaps out of that impatience of delay he showed in certain of his ways of life, a long footnote purporting to clarify what he allows to be an obscure passage' (Walshe 1961). It was natural, therefore, that his readers should fasten gratefully on any passage whose meaning seemed immediately obvious. Of these, one of the most famous is the following. 'Here I may best remark on the differences between muscles and movements, a matter of vast importance. To speak figuratively, the central nervous system knows nothing of muscles, it only knows movements. I have already stated the speculation that all muscles of the skeleton are represented in the cerebrum in one set of movements, and all in the cerebellum in another set. I here give another illustration simplifying it in several ways. There are, we shall say, thirty muscles of the hand; these are represented in the nervous centres in thousands of different combinations — that is, as very many movements; it is just as many chords, musical expressions and tunes can be made out of a few notes' (II,400).

He was trying hard to help: unfortunately, his 'to speak figuratively' was soon forgotten or ignored. Thus, Beevor (1904), in his Croonian Lectures on Muscular Movements, stated: 'Dr. Hughlings Jackson has laid down the dictum that "nervous centres know nothing of muscles, they only know movements." This in other words means that the ordinary individual has no power to make any one muscle contract by itself; he can only order a movement; he cannot pick out one muscle from a group and order that to contract; he can, on requiring to attain a certain object, order a certain movement.... Throughout these lectures I have used the word "movement" to denote the change of position in a joint brought about by the muscles taking part in the movement, while keeping the word "action" for the individual muscles, the resultant of whose actions is the movement'. So far so good; but Beevor went further. The individual can 'order a certain movement, but the mechanism by which that movement is produced and the muscles which are required to perform that movement, and the order in which they act, is not known to the brain; the order for a movement is given and the movement is performed.'

Jackson was still alive, and I do not know if he actually criticized this statement; he might well have done so, for it is at variance with the letter as well as with the spirit of much of what he wrote about 'movements'. As a dualist who tried to avoid mixing physiological and psychological language, he would certainly have objected to the words 'not known to the brain'. Beevor might have replied that he was 'speaking figuratively', and that by 'the brain' he only meant 'the ordinary individual'. That would have been the end of the matter. But suppose he had insisted that by 'the brain' he meant 'the brain'. Jackson would then have protested that his whole conception of 'movements' was in terms of 'localized processes representing movements' in the brain (I,38), and that Beevor's 'mechanism by which that movement is produced and the muscles which are required to perform that movement, and the order in which they act' is just what 'processes representing movements' is all about. The 'processes' are 'physical' not psychical. 'When I actually move my arm (say that it is what is popularly called a "voluntary movement") there is a process from highest motor centres, through lower centres, then by nerves to some muscles, which are discharged in a particular way. This is a purely physical process and we have no ideas of any part of it. No doubt there are activities of sensory[1] elements from skin, joints and muscles, back, so to say, to highest sensory centres. But this also is a purely physical process and we have no ideas of any part of it. I would put it that we have a vivid psychical state concomitant with activities of the

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[1] 'It is a most unfortunate thing that the word "sensation," the name of a state of consciousness, is of the same derivation as "sensory," the name given to afferent nerves and to centres to which afferent nerves go; it fosters the confusion that a physical state in a sensory centre is a sensation' (I, 140).

motor and sensory elements of the highest motor and sensory centres engaged in the double physical process described' (II,95). 'I carry the doctrine of sensorimotor constitution of the nervous system further than anyone else, so far as I know, since I urge that the highest cerebral centres (the "organ of mind" or anatomical substrata of consciousness) represent parts of the body as certainly as that of the lumbar enlargement does' (II,399). Believing that the brain obeys the laws of reflex action, he defined the sensorimotor 'unit of constitution of the nervous system' as 'the skin impression, the sensory nerve, the centre, the motor nerve, the sensory nerves from moving muscles, and from tracts of the skin stretched or relaxed by the movement' (II,235).

Jackson wrote about 'sensorimotor processes', 'processes representing movements' and 'processes for movements' (Phillips 1973) and illustrated his ideas in various ways. 'Harmony of movements is space coordination — the coordination of simultaneous movements; melody of movements in time coordination — the coordination of movements in succession' (I,272). All this was inaccessible to experimenters in his day, but is the subject of much neural modelling in ours. Has he, perhaps, a better chance of being understood nowadays, when terms like 'executive programmes', 'sub-routines', 'closed-loop operation' etc. are on every tongue?

One must remember always that in Jackson's writings 'the term "movement" is used in an unusually extended sense, to cover not only effects produced by nerve centres on muscles (including arterial coats, muscular fibres of intestine, etc.), but on glands and effects by inhibitory nerves' (I,136). He was greatly interested in the autonomic manifestations of epilepsy (e.g. I,47, 137).

But although so much of what he wrote is about the hierarchical organization of 'sensorimotor processes' representing 'movements' at 'highest', 'middle' and 'lowest' levels, he cannot be accused of neglecting connexions from the brain to muscles. Thus, in distinguishing muscles which commonly act bilaterally from those which commonly act unilaterally, he writes that the former 'are represented in each side of the brain nearly equally in quantity of fibres and cells' whereas 'the unilateral of both sides are represented *in* each side of the brain very unequally in quantity of fibres and cells' (I,29).

We come now to the sensorimotor cortex, Jackson's 'middle level', and to the structure of its projection to the spinal segments ('lowest level'). Jackson rejected Ferrier's belief that the cortical sub-areas for arm, leg, face, trunk and head-and-eyes are 'as completely differentiated from one another as the limbs themselves' (Ferrier 1890). For this error, as he saw it, he used his own term, 'abrupt localization'. He believed in 'minute localization' within overlapping areas (Phillips, 1966). He held that each sub-area of 'Hitzig and Ferrier's region' has its 'leading representation', related to a specific periphery, but that it also contains commingled 'subordinate representations' related to other peripheries (Phillips 1973). He almost certainly believed that minimal stimulation of any sub-area revealed only its 'leading representation' and not its 'subordinate representations'. Horsley (1909), to whose experiments Jackson had appealed as seeming 'to be in great disaccord with the current doctrine of localization' (II,385), stated explicitly that 'a minimal stimulus may only be adequate for one item of several represented in one portion of the cortex'. Jackson's own interpretation of the 'march of spasm' in focal epilepsy was that it was due to continuing activity within the sub-area first exploded, e.g. the leg area, involving, successively, its 'subordinate representations,' including those of the arm; but he admitted that he could not disprove 'the current hypothesis' that the discharge had 'spread from the leg centre to the arm centre' (I,444).

In support of overlapping 'minute localization' he cited Sherrington's discovery of degenerating fibres descending into the lumbar cord from a small lesion confined within the arm area (I,444) — an experiment whose repetition has always given the same result (Leyton & Sherrington 1917, Glees & Cole 1950, Barnard & Woolsey 1956).

Much clinical evidence, painstakingly and accurately garnered from cases of 'destroying' and 'discharging' lesions, obliged Jackson to distinguish between 'muscles' and 'movements of muscles'; but I cannot find that he anywhere formulated, or implied, any *antithesis*. The distinction 'is exceedingly important all over the field of neurology; I think the current doctrine of "abrupt" localization would not be so much in favour if it were made. The occurrence of convulsion in a muscular region which is already imperfectly and yet permanently paralysed is unintelligible without that distinction. And without it we shall not understand how it can happen that there is loss of some movements of a muscular region without obvious disability in that region' (I,421).

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Consider the nature of the responses evoked by minimal 'faradic' stimulation of the cortical surface, with inspection and palpation of the intact limbs, myography or electromyography of one or more muscles as detector.

One can assert a *priori* that such stimulation is unlikely to activate 'processes for movements' within the cortex. Populations of neurones which would have to engage in patterned activity to produce 'movements' would be driven in abnormal 'hypersynchrony' (Jasper's excellent term) by the trains of electrical pulses. In conscious man, 'the effect of the electrode is to interfere with the patient's ability to make voluntary employment of the cortex near the electrode. He may be able to move the foot and the face at will, but he cannot direct the movement of the hand while hand cortex is being stimulated. Sometimes the electrode produces no movement and then this interference is the only effect of the stimulating current. When it does produce movement, it is by virtue of conduction of impulses from cortex to ganglionic areas of the cerebrospinal axis' (Penfield 1958). In this, it is comparable to 'faradic' stimulation of an afferent nerve, which sends impulses in abnormal spatio-temporal patterns into the spinal cord. That both inputs, corticospinal and peripheral, can evoke coordinated movement of a limb is due to the organization of the segmental apparatus.

Thus Ferrier (1876) could suppose that the responses he evoked had 'evidently a purposive or volitional character,' and Jackson could agree: 'The artificial movements I have seen Ferrier produce by locally applied faradic currents to limited spots on the surface of the cerebral hemisphere of a monkey simulate the movements of health . . .' (I,39). But Sherrington later showed that the responses to stimulation of cortex, of skin and of afferent nerve resemble one another. 'Movements regularly and widely elicitable as local reflexes are liberally represented in the motor cortex . . . The local reflex movements obtainable from the bulbo-spinal animal and the reactions elicitable from the motor cortex of the narcotized animal fall into line as similar series' (details in Phillips 1973). It would be more correct to say 'liberally represented *in the spinal cord*'. This formulation would have disarmed nineteenth century critics who objected that 'there is no more significance in the statement that movements are represented in the cortex than there is in the statement that movements are represented in the skin' (Bates 1957).

By prolonging the length of trains of 'faradic' stimulation Leyton & Sherrington (1917) could evoke from the cortex of anthropoids 'combinational sequences' which were, 'so to say, eloquent of purpose in most instances'. But the main object of their experiments was '"localization" of the primary movement.' Such movements, 'elicited by somewhat minutely localized stimulations, are, broadly speaking, fractional, in the sense that each, though coordinately executed, forms, so to say, but a unitary part of some more complex act, that would, to attain it purpose, involve combination of that unitary movement with others to make up a useful whole. . . . It is the isolated and restricted character of the primary movements elicited by punctate stimulation of the cortex, or, to repeat the term introduced above, their fractional character, which makes so equivocal any purpose that an observer, who would interpret their purpose, can assign to them.' 'This discrete "representation" of small local items of movement' is 'more evident in cat and dog than in rabbit, more evident in the macaque than in cat or dog, in baboon than in macaque, in gibbon than in baboon, and in the chimpanzee, orang, and gorilla than in gibbon.' Leyton & Sherrington thus conceived the motor cortex as a 'synthetic organ for motor acts', building up from the coordinately executed local items, 'larger combinations varied in character and serviceable for purposes of different and varied kind.' 'It would seem that in order to preserve the possibility of being interchangeably compounded in a variety of ways, successive or simultaneous, these movements must lie, as more or less discrete and separable elements, within the grasp of the organ which has the varied compounding of them.' They also conceived it as an analytic organ, capable of breaking up 'compounds already constructed by lower centres.'

It is natural to think of 'compounds already constructed by lower centres' as parts of built-in postural and locomotor patterns involving fairly stereotyped reciprocal relationships, particularly between muscles working antagonistically at hinge joints. Jackson would have classified these as 'more automatic' movements and placed them low on his hierarchical scale. Hering and Sherrington's experiments on reciprocal inhibition from the monkey's cortex (Sherrington 1906) were concerned with such muscles, which they called 'true' antagonists. In the suspended lightly-etherized monkey, hip and elbow were held in flexed postures. Stimulation of the elbow-extensor 'point' caused palpable relaxation of biceps as well as palpable contraction of triceps. Such 'true' antagonists could never be made to contract together. Their reciprocal responses were elicited equally from the internal capsule after removal of the cortex, and were therefore organized at the lowest level, and were 'not chiefly or at all due to an interaction of cortical neurones one with another'. Hering found that cortical stimulation evoked co-contraction of wrist extensors and finger flexors. He called these 'pseudoantagonists'. Following Beevor we would call the wrist extensors 'fixators' and the finger flexors 'prime movers'. Every neurologist is familiar with this stereotyped pattern, which survives in patients with cortical or capsular lesions who cannot use the wrist extensors to voluntarily dorsiflex their wrists.

In 'voluntary' use, the primate's forelimb shows a remarkable range of mobility. The movements involve many muscles which act across more than one joint. In the organization of 'voluntary' movements ('less automatic' — high in Jackson's hierarchy), the reciprocal relationships between muscles would need to be labile: one can imagine that the relationship between a muscle-pair could shift from reciprocal action to co-contraction during the 'melody' of a complex movement. Leyton & Sherrington's later emphasis was on the synthesis of new combinations by selection of 'fractional' cortical outputs, and on the breaking-up (by selective inhibition?) of 'compounds already constructed by lower centres.'

Melody and harmony of movements? Today, when thinking of 'the organ which has the varied compounding' of the 'local items', we look to other cortical areas as well as to the 'motor' cortex; to their projections to the basal ganglia and cerebellum, converging thence on to ventrolateral thalamus and thence back to the sensorimotor cortex (Kemp & Powell 1971). We do not know the capabilities of the neuropil of the sensorimotor cortex itself in the process of 'compounding'. Leyton & Sherrington's 'facilitations', 'deviations' and 'reversals' gave glimpses of 'horizontal' connectivity, intracortical or corticocortical, but the mode of stimulation was too crude to lead to more significant insights. And there we must leave Jackson's 'processes for movements' to future research.

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In 1949 Fulton was enjoying a controversy with Walshe (1943) about whether the minimal reaction that could be evoked by stimulation of the motor cortex was 'an organized pattern of response involving reciprocal innervation of opposing muscle groups' or whether it was 'merely the reaction of a single muscle or part of a muscle.' This is a question of fact which ought to be settled by experiment, and could not be settled, as Fulton rightly said, by 'philosophical reflection.' But he headed this passage *Representation of muscles versus movements* (without inverted commas). The ghost! What was it saying? 'Perform the experiment. If (A) the response is confined to a single muscle, then the Jackson-Walshe hypothesis is demolished and Fulton's hypothesis survives. If (B) nothing less than "an organized pattern of response" can be elicited, then Fulton's hypothesis is demolished and the Jackson-Walshe hypothesis survives.' First, the experiment; then the problems of interpretation.

Hines (1944) had concluded, from great experience of cortical stimulation, that weak stimulation 'permits restriction of responses to single muscles.' In their classical experiments, Chang, Ruch & Ward (1947) recorded simultaneous myograms from eight muscles acting across the monkey's ankle joint, and explored the leg area with pulses at 60Hz in trains lasting 4 s. 'Solitary responses' of single muscles were 'by no means the typical response to cortical stimulation; they appeared only under favorable conditions', usually in the distal muscles EDL and EHL. When, as was usual, there was co-contraction of several muscles, some gave more tension than others, and some responded more promptly than others, when different points were stimulated: these criteria were used to map the best cortical area for each muscle. All the muscles were not 'equally available to cortical stimulation': gastrocnemius, soleus, FDL, FHL and tibialis posterior responded rarely, peroneus longus not at all. The maps were interpreted in terms of overlapping fields of Betz cells for each muscle, each with a denser focus and a more diffuse fringe, and the conclusion was that 'the representation of muscles stands midway between a strict mosaic pattern and diffuse representation.'

Thus the 'single muscle' hypothesis did not receive unqualified support from these fine experiments. The 'organized pattern' hypothesis was not actually tested by them. Crucial testing would have required that some of the eight muscles should have exhibited some background tonus, recorded by their myographs. If a 'solitary response' of an agonist muscle had been separable from relaxation of its antagonist, the 'organized pattern' hypothesis could have been rejected. If contraction of the agonist had been inseparable from relaxation of the antagonist, the 'single-muscle' hypothesis could have been rejected. (Would 'solitary inhibition' ever have occurred?). Evidence of inhibition there was, but only with stronger stimuli: thus, a weak stimulus activated EHL and FDL equally, but a stronger stimulus to the same point gave a larger response of EHL and no response from FDL. 'The failure of the flexor point to yield a response to strong stimulation may mean an inhibition of the flexor motor neurons by the surrounding extensor points which are activated by the spread of excitation from the flexor point.' Reciprocal inhibition: but not a crucial result, because not part of a liminal response.

Suppose, however, that a decisive result had been obtained one way or the other, in heroic experiments in which every muscle in a monkey's limb had been wired for electromyography, and recordings made under conditions in which reciprocal relaxation of antagonists would have shown up equally with excitation of agonists; and in which every effect had been evoked by liminal cortical stimulation. What bearing would this have had on the ghost's 'issue'?

Confinement of the responses to excitation of single muscles would not have falsified Jackson's hypothesis about 'minute' versus 'abrupt localization'. The stimulated area would project to its 'leading part': why should not a threshold stimulus activate one only of the muscles of that part? Hines (1944) had concluded that a particular muscle need not be the only one 'represented at a specific cortical point, but that it is the one predominantly represented there.' Nor could the 'single muscle' result have falsified Jackson's hypothesis about function: that in the waking brain, 'processes representing movements' could select the cortical outputs to muscles in 'thousands of different combinations — that is, as very many movements.' Equally, the 'organized pattern' result could not have falsified Fulton's hypothesis: his muscle 'representations' might occupy cortical territories so small that it would have been impossible to stimulate them separately by electrodes applied to the cortical surface. And if these territories were juxtaposed in appropriate 'functional' patterns, this would have explained the 'organized pattern of response,' at least in respect of excitatory synergies (his hypothesis said nothing about a possible cortical projection of inhibition to 'single muscles').

I have allowed myself to waste just enough time on this line of argument to show that it is leading not to decision between definable alternatives, but rather towards inconclusive 'philosophical reflection', which is something the ghost has always encouraged. The 'issue' was a mix-up of function and structure. The experimental methods were incapable in principle of analyzing cortical function, and were too limited in their resolving power to answer the straightforward questions we can ask about cortical output structure. Thus, no-one knew the extent of the area of cortex across which stimulation at 60Hz for 4 s has to spread, physically and physiologically, before it can evoke a minimal muscular response. Such prolonged trains of stimuli would have had ample time to activate subcortical areas interposed between the motor cortex and the 'lowest level' (e.g. cortico-rubro-spinal, cortico-reticulo-spinal, cortico-cerebello-corticospinal projections) as well as the corticospinal projection itself. And since muscle was used as the detector of corticofugal action, extensive imposition of subliminal excitation and inhibition on different classes of interneurons and motoneurons would have gone undetected.

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The most straightforward questions one can ask about structure are questions about the localization in the motor cortex of clusters of corticospinal neurons which project excitation and inhibition, directly or indirectly, to motoneurons of different muscles. Modern microanatomical and electroanatomical methods are bringing these questions within sight of answers. Intracellular recording in particular can detect subliminal synaptic excitation and synaptic inhibition evoked in interneurons and motoneurons by one or a few corticospinal volleys, discharged from circumscribed areas of cortex by stimuli which are well below threshold for motor response. The very important corticospinal projections to the sensory mechanisms of the dorsal horn, and the all-important inputs which 'drive' the motor cortex, are considered elsewhere (Phillips 1973). Put in a more interesting way, the questions can be summed up thus: what output channels are available for selection by intracortical input-output processes 'in thousands of different combinations — that is, as very many movements'?

In the nineteen-fifties the new Nauta method made it possible for the first time to trace degenerating axons reliably as far as their terminations. Chambers and Liu (1957) made lesions in the cat's motor cortex and traced the corticospinal projection into the dorsal horn and intermediate region of the grey matter of the opposite side of the cord. These are the regions which Lloyd (1941), in his classical analysis of the cat's corticospinal mechanism, had probed with microelectrodes and discovered the interneurons that are thrown into activity by pure pyramidal volleys; some of these were driven to fire one impulse in response to each volley, and a few were inhibited. Three volleys at least (at about 400 Hz) were needed to exert any subliminal effect on the motoneurons. The effect was detected by an increase in excitability of the motoneurons, as tested by the segmental monosynaptic reflex. Thus there is no direct connexion between corticospinal axons and motoneurons in the cat. Some of the interposed interneurons are shared with reflex arcs (Lundberg 1964), others are specific propriospinal interneurons (Kostyuk 1974). Their effect is to distribute excitation to flexor and inhibition to extensor motoneurons (Lundberg 1964).

In primates, corticospinal axons make monosynaptic connexions with motoneurons, especially those of the hand and foot (Bernhard & Bohm 1954, Kuypers 1964, Phillips 1968). There is also disynaptic inhibition, mediated by the 1a inhibitory interneurons (Jankowska & Tanaka 1974), as well as plentiful polysynaptic excitation and inhibition, which is distributed between flexors and extensors as in the cat. Except at the elbow: in the cat, the elbow flexors receive polysynaptic excitation and the extensors inhibition; in the baboon this relationship is reversed, possibly in 'the transition from quadruped to biped posture' (Preston, Shende & Uemura 1967).

The cortico-motoneuronal projection in primates is evidently the most elemental type of cortical localization that can exist. One can investigate the localization of the colonies of cortico-spinal neurons which project to sampled motoneurons of hand (Landgren, Phillips & Porter 1962) or foot (Jankowska, Padel & Tanaka, 1975b), and measure the maximum quantity of monosynaptic excitation commanded by each colony by intracellular recording from its target motoneuron. The colonies belonging to motoneurons of the baboon's hand command larger quantities of monosynaptic excitation than do those belonging to the motoneurons of proximal muscle groups. This is the explanation of the preferential accessibility of hand and foot to those cortical stimuli (a few pulses at 500Hz, or a single pulse of 5.0 ms duration) which discharge a few corticospinal volleys at high frequency. The monosynaptic cortico-motoneuronal pathway bypasses the segmental apparatus and puts the cortex directly in touch with the motoneurons which constitute the Final Common Path. It is as if these motoneurons had been transplanted into the cortex — as if the dendrites of the corticospinal pyramids could act vicariously for the dendrites of the motoneurons as antennae sensitive to intracortical synaptic activities (Phillips 1968), especially those controlling the very varied, 'least automatic' performances of the hand. The density of corticomotoneuronal endings in the ventral horn increases as one ascends the primate scale from monkey to man (Kuypers 1964). There is also a tightly-coupled cortico-fusimotor projection in baboons, partly monosynaptic (Grigg & Preston 1971; Clough, Phillips & Sheridan 1971), which one would expect to be even better developed in man, and which would be instrumental in initiating and maintaining the afferent discharges from the spindles of human finger muscles which would otherwise by silenced by unloading when the muscles shortened (Vallbo 1970).

Unifocal surface-anodal pulses selectively excite those corticospinal pyramidal neurons that are located on the convexity of the precentral gyrus, and are useful for mapping the cortical territories occupied by cortico-motoneuronal colonies, especially in the leg area of monkeys where the Rolandic fissure is shallow or non-existent (Jankowska et al., 1975b), but also in the part of the arm and hand area that comes closest to the convexity in baboons (Landgren, Phillips & Porter 1962). It has been shown that different relative quantities of monosynaptic excitation and disynaptic inhibition are projected to target motoneurons from different 'best points' on the cortex; but no sequestered reciprocal areas could be found for biceps and triceps colonies (Phillips & Porter 1964). These colonies were overlapped by colonies projecting to motoneurons of distal muscles, about half of which occupied cortical territories measuring several mm along the precentral gyrus. In the leg area, also, the colonies overlap extensively (Jankowska et al., 1975b).

Independent evidence for overlap comes from experiments of another sort. Evarts (1967) found that most of the antidromically-identified pyramidal-tract neurons encountered in a single micro-electrode track in the precentral arm area of freely-moving monkeys tended to fire in relation to movements at a particular joint. Pairs of PTN recorded from the same point along the track must have been very close together. Such pairs generally exhibited highly variable mutual firing patterns: for example, one pair fired in phase when the monkey was grooming hairs, but out of phase when it was scratching itself. Evarts argued that mutually-invariant behaviour would have been expected if both PTN had projected to motoneurons of the same muscle. Such adjacent PTN were therefore probably members of colonies belonging to different muscles, and it is absurd to suppose that all such pairs should have happened to lie on opposite sides of hair-sharp boundaries between 'abruptly-localized' colonies.

The elegant and powerful new method of intracortical microstimulation, introduced by Asanuma & Sakata in 1967, has made possible important advances in the description of 'cortical efferent zones', first in cats, later in capuchin monkeys (Asanuma 1973) and baboons (Andersen, Hagan, Phillips & Powell 1975).

In cats, as Lloyd's experiments first proved, there is no direct pathway to the motoneurons, and at least three pyramidal tract volleys at 400Hz are needed to produce enough interneuronal firing to evoke any excitatory depolarization of the motoneurons, detected by facilitation of the segmental monosynaptic reflex. Asanuma & Sakata (1967) used 11 pulses at 400Hz for intracortical stimulation; Asanuma (1973) has calculated that at a strength of 10μA, which was usually well above threshold, neurons within a sphere of radius 90μm would have been discharged. The resulting action on the motoneurons of different muscle groups was detected by facilitation (39 examples) or inhibition (18 examples) of the monosynaptic reflexes evoked by single afferent volleys in the different muscle nerves. The 'efferent zones' measured 0.5mm to a few mm across, 'and the fringes overlapped' (Asanuma & Sakata 1967). Since it would be virtually impossible to record monosynaptic reflexes from every muscle in the limb, the full extent of overlap of 'efferent zones' is likely to remain unknown. The combinations of overlapping foci for excitation and inhibition of groups of muscles showed no 'meaningful correlation between the overlappings and the functions of the muscles.' Such foci would be available for varied 'compounding' by intracortical 'processes for movements.'

When working with a projection involving spinal interneurons it is necessary to use repetitive corticospinal volleys, and this may complicate the interpretation of results. To discover in the cortex what we might call a "hot spot" is not to prove that the entire corticofugal discharge arises within a sphere of cortex of radius 90μm. Stoney, Thompson & Asanuma (1968) investigated the actions of a single microstimulus on single PTN. They found that PTN could be fired not only by the direct electrical action of a nearby microstimulus, but also indirectly, and from as far as 0.5mm distant, by excitatory synaptic action (mediated by intracortical axons or by U-fibres?). Jankowska et al., (1975a) find that the lowest-threshold effect is the trans-synaptic one, and that the extent of horizontal spread is increased by repetitive stimulation. Thus, repetitive stimulation of a "hot spot" cannot fail to recruit PTN contained within a wider 'efferent zone' whose fringes may be more or less remote from the "hot spot:" the breakthrough to the spinal motoneurons may require temporo-spatial facilitation in the cortex as well as temporal facilitation in the cord. These considerations apply with even greater force to the experiments of Asanuma & Ward (Asanuma 1973). Instead of using 11 pulses to elicit facilitation or inhibition of monosynaptic reflexes, they used 60 pulses (at 300Hz) to evoke actual contractions of antagonistic muscles, namely extensor digitorum communis and palmaris longus, whose tendons were attached to myographs. The responses that were selected for study had latencies < 100ms (minimum 40ms). The experiments proved their point, that co-contraction of antagonists can be evoked by intracortical stimulation, in contrast with the reciproval innervation which is all that can be evoked by surface stimulation (Asanuma 1973). Indeed, careful examination of the forelimb showed that other muscles which were not attached to myographs (biceps, triceps, distal forearm muscles) were also responding feebly.

Interpretation is less complicated, although not entirely simplified, when microstimulation is applied to the motor cortex of primates. Asanuma & Rosén (Asanuma 1973) chose New World Cebus monkeys, which, like the Old World baboons, possess direct cortico-motoneuronal projections to the cervical enlargement, particularly to motoneurons of distal muscles (Petras 1968). The responses were recorded by electromyography and by stroboscopic photography of the digits. The muscles of the hand were preferentially accessible to microstimulation, and there was frequent overlap between the 'efferent zones' projecting to antagonist muscles. Although we are here dealing with outputs projecting directly to motoneurons, and do not have to consider the complications that are introduced when spinal interneurons are interposed in the pathway, we still need a brief high-frequency repetitive burst to make the motoneurons discharge an impulse. A single volley is ineffective: presynaptic facilitation of corticomotoneuronal synapses is needed to depolarize the motoneurons to their firing level. Thus the risk of some trans-synaptic intracortical recruitment of output neurons from the fringes of the "hot spots", though much reduced, is not altogether absent. Unfortunately it has not yet been found feasible to record intracellularly from motoneurons while exploring the motor cortex by microstimulation. Nothing less would enable the quantities of EPSP and IPSP projected from the "hot spots" and from different parts of the fringes of the cortical 'efferent zones' to be measured exactly.

In baboons, Andersen, Hagan, Phillips & Powell (1975) investigated the architecture of the 'efferent zones' projecting to three of the most preferentially-accessible muscles of the hand, chosen because their motoneurons receive, on average, the largest quantities of monosynaptic excitation from their cortical colonies (cf. Phillips 1968): EDC, first dorsal interosseus, and adductor-flexor brevis-opponens-pollicis group of the thenar mass. The number of possible combinations of these muscles in 'least automatic' movements seems likely to be very large. A combination of surface-positive stimulation and microstimulation was employed, and the responses of single motor units or small groups of motor units were recorded electromyographically. The colonies and aggregations of colonies occupied 'efferent zones' which measured not less than 6.0 x 5.5mm (EDC), 7.0 x 3.5mm (thenar group) and 6.0 x 2.5mm (interosseus). They overlapped extensively and contained more than one "hot spot".

Not all of the very large number of neurons which project from these extensive 'efferent zones' are corticospinal; the number of neurons belonging to the corticomotoneuronal colonies of these distal muscles is likely nevertheless to be large (Andersen et al., 1975). We ought not therefore to be surprised if the contribution to movement of a single corticospinal neuron turned out to be negligible. Indeed, Evarts (1967) commented that the high-frequency injury discharges of antidromically-identified PTN had no visible effect on the conscious monkey's limbs, and Jankowska et al., (1975b) found that the EPSPs evoked in spinal motoneurons by threshold stimulation of the cortical surface are very small. Recruitment of PTN would be necessary for movement (Porter and Lewis, 1975). The responses of single PTN are invaluable as a sample of cortical output in monkeys making movements for reward, and have added and are adding enormously to our understanding of motor control. The intracortical recruiting mechanism must have fantastic selectivity, since, given appropriate visual and auditory monitoring of its output, a monkey can learn to discharge a PTN whose firing is normally positively correlated with arm flexion, and at the same time to reduce the electrical activity in a flexor muscle (Fetz & Finocchio 1972).

Asanuma (1973) writes of 'columnar cortical efferent zones', and says that 'the existence of a columnar organization within the motor cortex in the cats and monkeys was based on the observation that stimulation within a given column produced contraction of the same muscle'. There seems to be a real danger that the motor cortex will come to be misdescribed, by careless reviewers of these beautiful experiments, as a mosaic of cylindrical columns, diameter 1.0 mm, one for every muscle in the body. Andersen et al., while accepting that the input-output organization of the cortex is essentially radial, did not wish to apply the term 'colunnar' to the whole of the 'efferent zone' which contains the aggregation of corticomotoneuronal colonies belonging to a particular muscle. The evidence that the overlapping 'efferent zones' may be built up of sets of narrower radial columns which can be differentiated on the basis of their specific afferent inputs lies outside the scope of this lecture.

CONCLUSION

Hughlings Jackson's clinical investigations of movement were primarily concerned with its organization in hierarchical levels of function, and with the cerebral localization of 'sensorimotor processes representing movements'; but he was also interested in the anatomy of the outputs from the sensorimotor cortex (his 'middle level'), which connected his 'processes' to the 'lowest level', and thence to the muscles. His conclusion was that the cortical localization of outputs is minute and overlapping, muscles and 'processes for movements' of all parts of the body being 'represented', though in very varying porportions, in every sub-area of 'Hitzig and Ferrier's region'. Each sub-area would have its 'leading representation', related to a specific periphery, with commingled 'subordinate representations' related to other peripheries. He thus rejected what he called 'abrupt localization', which he saw gaining ground all around him as the (as he saw it) incorrect interpretation of the results of experimental faradic stimulation of the monkey's cortex.

Unfortunately, his famous statement that 'the central nervous system knows nothing of muscles, it only knows movements' has so often been quoted without its essential qualification 'to speak figuratively' that his real position has been all but universally misunderstood. The ghost I am raising, and am hoping to help to lay, is the false belief that Jackson's clinical studies had led him to formulate alternative propositions, A or B, muscles or movements, such that A or B could be refuted by experiment.

With increasing refinement, particularly in the hands of Sherrington, liminal faradic stimulation of the motor cortex revealed (1) a large repertory of 'local items of movement', e.g. of single digits, and (2) more prolonged sequences of response, involving several joints, which Sherrington believed to be due to activation of those patterns of spinal reflex organization which were also accessible to faradic stimulation of skin or of peripheral nerves.

From the nineteen-thirties until the nineteen-fifties there was controversy over whether the minimal muscular response that could be elicited from the motor cortex was a 'local item of movement', that is, a coordinated process involving reciprocal innervation, or whether it was the response of a single muscle or part of a muscle. The experimental goal was the correct description of the result of liminal faradic stimulation. But the problems of interpretation were never clearly formulated. Reciprocal patterns are built into the spinal segments: are these addressed by liminal corticofugal volleys, or are they by-passed and are the pools of motoneurons addressed directly? And if the latter, are the outputs to the motoneurons of antagonistic muscles reciprocally interlinked within the cortex? At threshold, does 'hypersynchronizing' stimulation of the cortical surface engage such linkages, or is it able to discriminate between, and to excite separately, the elemental outputs? Are there elemental inhibitory as well as excitatory outputs? Are all these outputs intermingled in the cortex, or are they 'abruptly' segregated from one another? Restated in modern terms, Jackson's theory regarded these outputs as the efferent limbs of cerebral input-output systems: 'sensorimotor processes representing movements.' In the controversies the afferent inputs got left out. In the prevailing confusion, the ghost would have seen to it that any demonstration of a response that was limited to a single muscle or part of a muscle would have been generally accepted as the experimental demolition of Jackson's theory of 'movements'.

To establish that the response evoked by a circumscribed corticofugal discharge is limited to a single muscle, it is necessary not only to prove that no other muscle in the body has contracted: it is also necessary to show that the motoneurons of other muscles have not been excited subliminally, and that those of yet other muscles have not been inhibited. Clearly, many uncertainties of interpretation are introduced when the output of a reciprocally-organized segmental apparatus (the 'lowest level'), which is itself capable of elaborating stereotyped 'movements', is used as the detector of circumscribed corticofugal discharge. There is a practical need to disentangle the problems of corticospinal connectivity, which can readily be solved by contemporary microanatomical and electroanatomical techniques, from the problems of 'movements', which will be much more difficult.

The working-out of corticospinal connectivity, inhibitory as well as excitatory, is now proceeding by a combination of stimulation of the cortical surface and intracortical stimulation, by detecting the synaptic potentials evoked in spinal motoneurones by cortical stimuli that are too weak to discharge them, and by detecting the discharges of motor units at the very threshold of minimal muscular response. In primates, the monosynaptic excitatory projections to motoneurones of different muscles of the hand and foot have already been proved to arise from overlapping cortical territories within the 'hand' and 'foot' areas respectively.

Now that we are so busy with the detailed working-out of the 'minute localization' of the motor cortical outputs that are available for selection and 'compounding' by cerebro-cerebellar 'sensorimotor processes', and are thinking in terms of the programmes, subroutines and feedback loops of movement, is it, perhaps, not too much to hope that the hoary ghost of 'muscles VERSUS movements' may now be laid?

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