CORTICAL MOTOR REPRESENTATION IN VIEW OF RECENT EXPERIMENTS ON CORTICO-SPINAL RELATIONS

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Abstract. The results of recent experiments using either intracortical stimulation or stimulation of the surface of the motor cortex were reviewed from the point of view of "muscle" and "movement" cortical representation. It has been concluded that there is no satisfactory evidence for location of the pyramidal tract (PT) cells which project directly (monosynaptically) to motoneurones of one muscle in primates within small and separate cortical areas; such evidence is even weaker for PT cells which exert their effects via polysynaptic pathways in other species. The available evidence shows in contrast a very pronounced overlap of cortical areas of projection to different motor nuclei.

The organization of the motor cortex and the way it might control motor activity have been extensively discussed in a number of recent reviews, e.g., by Asanuma (1), Brooks and Stoney (8), Phillips (33) and Porter (35). Only some aspects of the cortical motor representation will therefore be considered in the following.

The electrical stimulation of the motor cortex may evoke two kinds of motor responses: movements involving activation of several muscles in one or more joints, or contractions of single muscles. This fact together with a number of other observations (see 31, 33) raised the problem of the nature of the cortical motor representation. One alternative was that the motor cortex constitutes a kind of a mosaic of separate areas, each controlling contractions of single muscles; movements would result...
from a concomittant activation of a number of such areas. According to another alternative, first proposed by Jackson (16, see 11, 31, 33), movements, i.e., contractions of various combinations of muscles, would be unit responses evoked from the cortex, different ones from different cortical areas; contractions of individual muscles would be initiated in parallel with contractions of other muscles and from several cortical areas if they take part in different movements.

In terms of cell physiology (see, for example, in 1 and 11) the two alternatives would refer to relations between discrete cortical areas and spinal motoneurones which innervate different muscles. However, cortical effects on motoneurones are exerted via polysynaptic pathways in most animal species and via both polysynaptic and direct cortico-motoneuronal connexions in primates (7, 36). The polysynaptic pathways have relays both at a spinal and a supraspinal (via cortico-subcortico-spinal pathways, see, e.g., in 13) levels and are likely to mediate much wider-spread effects than those evoked monosynaptically. In consequence the cortico-motoneuronal relations and the "muscle" or "movement" cortical representation should be considered separately for these two kinds of pathways.

In the case of the polysynaptic cortico-motoneuronal effects it is rather difficult to imagine that they could ever be limited to only one motor nucleus. It appeared, namely, that these polysynaptic effects are mediated via the same spinal interneurones (17, 28, see, however, 39) which are interposed in segmental reflex paths to motoneurones from various afferents: tendon organ, cutaneous and high threshold muscle and joint afferents (27, 28) as well as group Ia muscle spindle afferents as shown recently (15, 20). Hardly any effects mediated by these interneurones would involve only one motor nucleus because of the patterned character of spinal reflexes. Even in the case of the simplest reflexes, the monosynaptic reflexes, the sensory impulses which give rise to them excite motoneurones to several agonist muscles (10) and in addition disynaptically inhibit motoneurones to their antagonists. Polysynaptic reflexes involve even more complex patterns of effects, ipsilateral as well as bilateral and often including several parts of the body. In consequence any cortical effects mediated by interneurones of spinal reflex pathways should be considered in relation to different reflex patterns and movements and not single muscle activity.

The results of experiments designed to analyse types of movements evoked from the cortex, or location of cortical areas from which different movements are initiated (e.g., 3, 6, 9, 40), give fairly limited information on the extent of any concomittant actions. These experiments reveal
only such cortical excitatory effects which are potent enough to fire impulses in the motoneurones and leave undetected all those which are subthreshold for spike generation. The latter may consist of relatively weak excitatory postsynaptic potentials as well as of potentials which could fire the motoneurones if not counteracted by simultaneously evoked inhibitory postsynaptic potentials. A subthreshold excitation of motoneurones or their inhibition can be revealed with the technique of conditioning monosynaptic reflexes (e.g., in 5 and 28). However, mixed excitatory-inhibitory cortical effects might remain undetected even then and their analysis would require intracellular recording from motoneurones. So far intracellular recording has been used only in studies in which the whole pyramidal tract or the whole motor cortex were stimulated in the cat (28) and the pattern of polysynaptic effects of different fractions of pyramidal tract cells at a cellular level still awaits its analysis.

In the studies of the monosynaptic cortico-motoneuronal effects the technique of intracellular recording from motoneurones has been used very extensively (12, 19, 22, 23, 34). This technique allows the detection of even very weak postsynaptic potentials evoked from the cortex. The main problem in establishing the origin of these potentials was thus to define the location of pyramidal tract (PT) cells responsible for them. Two techniques of activation of PT cells have been used, stimulation of the surface of the cortex and intracortical stimulation, but neither of them turned out to be fully adequate for revealing the detailed organization of cortical projections.

Surface stimulation has the advantage of activating PT cells directly (18, 22, 30). Its disadvantage is that its effects are evoked from within a considerable radius (23, 34). In the most favourable situation, when the stimulated PT cells are located in a layer parallel to the surface within the convexity of the precentral gyrus, the threshold for their activation is about 0.2–0.3 ma (12, 34). With stimulus strength of 0.3–0.4 ma the PT cells would be excited within about 1.0 mm² (34). The accuracy in establishing areas of location of PT cells responsible for EPSPs evoked in motoneurones by cortical stimulation with this intensity would thus be of the same order. It would be much lower for effects evoked by PT cells located in the depth of the central sulcus and requiring stronger stimuli.

In the case of intracortical stimulation PT cells can be activated by stimuli 100 times weaker than those applied to the surface of the cortex, which largely reduces the complications produced by physical spread of current. The technique seemed thus very well suited for exploring effects of PT cells located within limited cortical zones. Unfortunately,
it turned out that even the weakest intracortical stimuli activate PT cells not only directly but also (4, 38) or predominantly (18) indirectly. The indirect or transsynaptic activation of PT cells will be due to the electrical excitation of fibres or nerve terminals in the vicinity of the stimulating electrodes; the nerve impulses evoked in them might, however, be conducted both ortho- and antidromically over unknown distances and influence all the PT cells on which any of their collaterals terminate. Di- and polysynaptic effects on PT cells via other cells can then be also produced. Our knowledge of the network of short and particularly of long intracortical connexions and of the distribution of their terminal branches is still very limited. It has been shown, however, that at least some of the fibres with monosynaptic connexions with PT cells, those originating in VL may bifurcate (2, 37) before they reach the motor cortex, or within it, and terminate in several separate (3-4 mm apart) cortical areas (2). Stimulation of such fibres might thus have widespread effects on PT cells in spite of very local direct effects of the electrical current. EPSPs evoked in motoneurones by intracortical stimulation may thus be due to directly excited PT cells located close to the electrode tip, as well as to PT cells activated indirectly and with an unknown location.

The conclusions on location of PT cells responsible for muscle contractions evoked from the motor cortex must be associated with even more serious errors. Thresholds for evoking muscle contractions by surface stimulation are higher than for activation of single PT cells; they are rarely below 0.5 ma (40) and most often between 1.0 and 2.0 ma (24, 25, 40). With the latter stimulus strength one can activate PT cells directly more than 5 mm away (23, 34) and in addition indirectly (30) within an unknown distance. Both in the case of surface and of intracortical stimulation repetitive activation of PT cells is necessary, by either short repetitive or single long pulses (24, 25), and such stimulation may well activate polysynaptic cortico-motoneuronal pathways even if only monosynaptic potentials are evoked in motoneurones by single stimuli of the same intensity. Furthermore repetitive intracortical stimuli may excite much greater proportion of PT cells indirectly (18).

The studies of direct effects evoked in motoneurones of primates by surface stimulation have shown that monosynaptic EPSPs can be evoked in individual neurones from surprisingly large cortical areas and that the areas of projection to different motor nuclei largely overlap. This was reported both in the case of projections to forelimb (12, 22, 23, for more recent references see 32, 33) and to hindlimb (19) motoneurones, when relatively strong stimuli were used (23, see also 33) as well
as when the stimulus strength (0.3–0.4 ma) was near threshold for activation of PT cells (12, 19, 22). The comparison of cortical areas from which EPSPs were evoked in single motoneurones under conditions of minimal spread of current (19) revealed the following. (i) The size of these areas differed considerably (from 1 to 14 mm²). (ii) The areas of projection to various motoneurones of the same nucleus only partly overlapped and the total areas of projection to motoneurones innervating one muscle were much larger. (iii) In the case of different location of areas of projection to various motoneurones of the same muscle, these areas often overlapped with areas of projection to different other motor nuclei. (iv) In several individual motoneurones EPSPs could be evoked from two or three separate cortical areas, each of which overlapped with areas of projection to different other motor nuclei.

These observations indicate that individual motoneurones of the same motor nucleus which innervate the same muscle may be excited from somewhat different cortical areas and in parallel with motoneurones to different other muscles.

The fact that monosynaptic EPSPs are evoked in parallel in motoneurones of different motor nuclei from one cortical area may be due: (i) to a grouping of PT cells, each of which projects to different species of motoneurones, or (ii) to projections of single PT cells to not only one but to several motor nuclei (11). If PT cells have only one species of motoneurones as their target, and if those which project to a given motor nucleus are spread over large cortical areas and mixed with PT cells to other motor nuclei, a very complex system of intracortical connexions might be necessary for selection of proper combinations of cells involved in different movements and for routing of cortical output. The role of PT cells would on the other hand be reduced to that of very simple relays and somewhat difficult to fit with their involvement in complicated feedback systems at different levels of the neuraxis (see, e.g., 1, 8, 11, 35). It might thus be important to pay more attention to the possibility of a functional differentiation and specialization of PT cells. Such a differentiation would mean that individual PT cells had connexions with various combinations of motoneurones (11, 19) as well as with spinal interneurones or cells in different brain centres. The PT cells with one kind of target motoneurones in common might constitute a conglomerate of several subgroups of PT cells, each with multiple projections to various combinations of their other target cells. Such an arrangement would be fully compatible with the extensive overlap of the cortical areas of projection to different motor nuclei which has been found experimentally. It might also require a much simpler system of intracortical connexions to a relatively small number of PT cells which project to a needed
combination of motor nuclei and cells in different neuronal circuits instead of a much larger number of PT cells with only one kind of target cells. Multiple projections of PT cells would well correspond to multiple projections of other cells involved in regulation of nervous activity (e.g., some spinal interneurones, see 17). Their functional differentiation might also represent a similar kind of differentiation as that occurring in various sensory systems. A high degree of cellular specialization has been found both at the cortical level, where it was studied in most detail in case of cells processing a visual information (14) and for cells of the spinal ascending tracts. For instance in case of cells of origin of the ventral spino-cerebellar tract (26, 29) it has been reported that “one cell hardly resembles another” as far as their input and the information they carry are taken into account. Such a specialization became also of great interest in the context of different problems of learning and much attention has been given, to the so-called gnostic units (21).

If and how the hypothesis of multiple projections and of a functional differentiation of PT cells can be experimentally verified is a separate problem. However, if it turns out to be true, the idea of a mosaic-like organization of cortico-motoneuronal projections would be untenable even at single cell output level.

REFERENCES


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