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Research report

# On the translation of directional motor cortical commands to activation of muscles via spinal interneuronal systems

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## Abstract

I discuss in this paper some of the neural mechanisms by which directional motor cortical commands could be potentially translated into multi-muscle activations to generate a directed force (and initial movement) in space. Specifically, I review the results of recent studies in the motor cortex of monkeys and the spinal cord of the frog, and propose a possible mechanism by which these results could be formally connected. It is suggested that spinal mechanisms of the kind described in the spinal frog could serve as substrates for the operation of directionally tuned motor cortical activity to produce an appropriately directed motor output by the limb.

*Keywords:* Motor cortex; Spinal cord; Direction in space; Monkey; Frog; Force

## 1. Introduction

Much effort has been expended during the past thirty-odd years in investigating the relations between single cell activity in the motor cortex and static force exerted by behaving animals about single joints [23]. In contrast, the relations between motor cortical cell activity and changes in force have been studied only occasionally, and usually within studies of the relations to static force. Most of the studies addressing the cortical mechanisms of dynamic motor function have been focused on movements as experimental paradigms [6,7]. Similarly, there is a wealth of information on the relations between spinal mechanisms and movements in locomotion [15]. Studies in monkeys [8] and frogs [14] have addressed questions relating to the development of dynamic force under isometric conditions. These studies used very different methods: the work in monkeys used recording of the activity of single cells in the behaving animal, whereas the work in frogs used microstimulation in spinalized preparations. However, both sets of studies addressed the question of how a change in

force could be generated. These studies also shared another common aspect, namely that the force monitored was exerted in a two-dimensional (2D) space by the distal end of the limb. Although there are substantial differences in species and methods used, it may nevertheless be useful to speculate on how the results of these two kinds of studies could be related. Indeed, that what follows is an initial attempt to connect speculatively these two disparate sets of studies. I summarize first the relevant data and then develop the ideas concerning their interaction.

## 2. Motor cortical commands for directed, dynamic, isometric force

### 2.1. Directional tuning of single cells

The activity of single cells in the motor cortex is directionally tuned with respect to movement [13] or dynamic isometric force [8], in that cell activity is highest for a given direction ('preferred direction') of movement (or isometric force) and decreases gradually with directions farther and farther away from the preferred one. The tuning is broad and usually unimodal. Typically, the frequency of cell discharge is a linear function of the cosine of the angle formed between the direction of a particular movement (or force) and the cell's preferred direction.

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## 2.2. Directional coding by neuronal populations

The population vector hypothesis [9] allows for the calculation of an unambiguous signal by a population of broadly tuned neurons. It was first applied to the coding of the direction of arm movements [9,11,12], and was subsequently extended to the coding of the direction of dynamic isometric force [8]. The calculation is a vectorial summa-

tion of a population of cell vectors pointing in their preferred direction with a strength proportional to the change in their firing rate, for a particular case. This weighted vector sum of the neuronal contributions is the 'population vector':

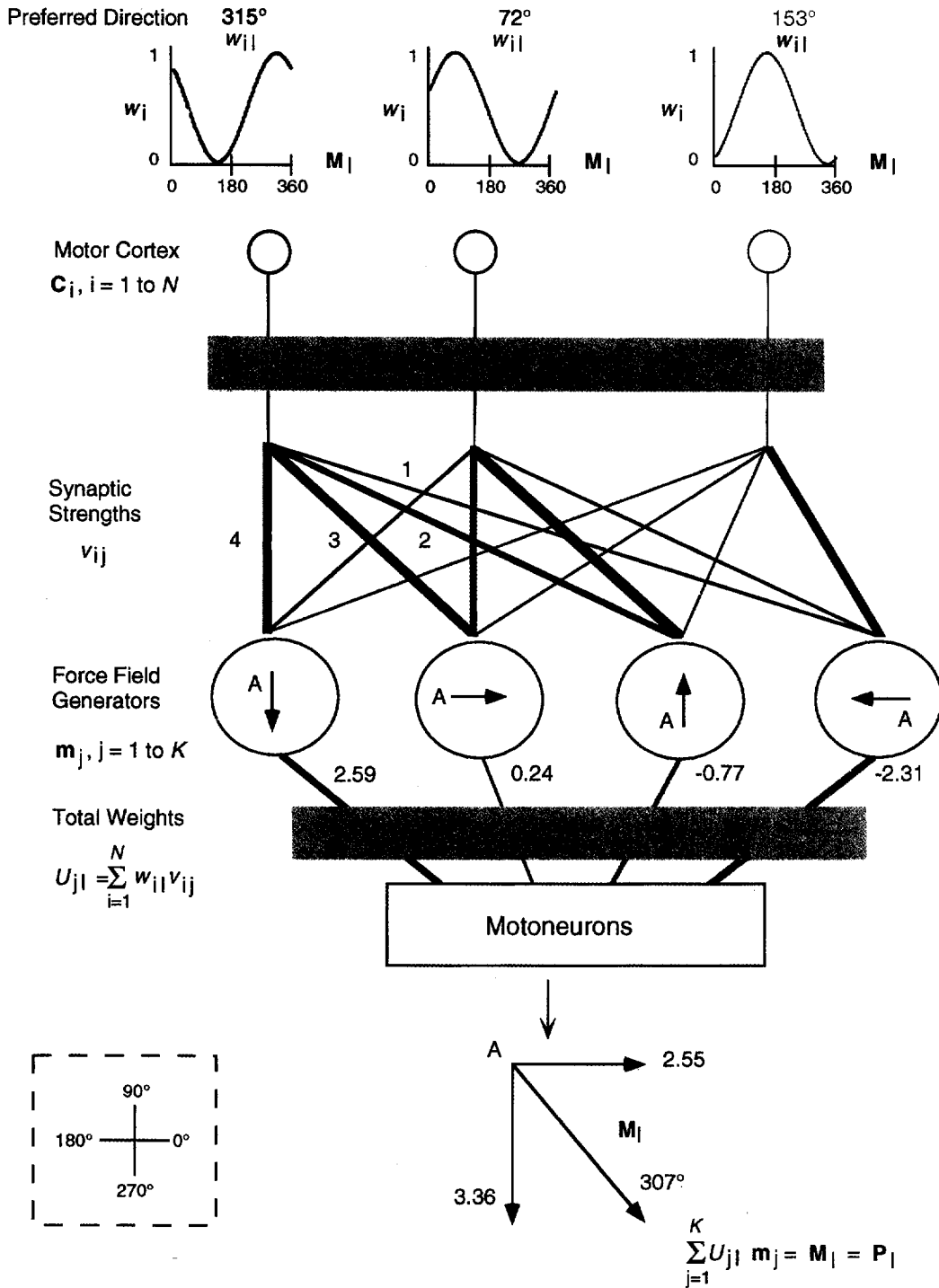$$P_l = \sum_i^N w_{il} C_i \qquad (1)$$



Fig. 1. A hypothetical scheme for the translation of directionally tuned motor cortical command to the activation of muscles by spinal interneuronal systems. See text for explanation.

where $P_l$ is the population vector for movement direction $l$, $w_{il}$ is the weight for the $i^{th}$ cell and $l$ movement, and $C_i$ is the preferred direction of the $i^{th}$ cell. The population vector has been found to point in the direction of movement [9,11,12] and dynamic isometric force [8].

## 3. Spinal cord studies of isometric force production

In general, the neural signals from the motor cortex do not activate muscles directly but ultimately influence the activity of motoneurons through the spinal cord. In certain cases, the corticospinal axons terminate within the motor nuclei, as is the case, for example, for the motoneurons innervating distal muscles of the limb in adult primates [23], but in the vast majority of cases the influence on the motoneuronal pools is exerted through intercalated interneurons. These interneurons are found at the segmental level as well as at upper cervical (C3–C4) levels. The latter system has been investigated extensively in the cat and its intricate inputs from central and peripheral sources partially elucidated [18].

A detailed analysis of how spinal interneuronal systems can influence the spinal motor output in space has been carried out recently in the spinal frog [2,14,21]. In these studies, the technique of microstimulation was used to determine the effects of activation of interneuronal populations on the direction and magnitude of the force in space developed by the limb of the spinalized frog. There were three major findings of these studies. First, microstimulation at a particular interneuronal zone in the spinal cord elicited the development of force by the limb, the direction and magnitude of which differed depending on the position of the limb in space. The set of these forces define a 'force field'. In the absence of microstimulation, there were passive forces due to the resistance to stretch of the tissues of the limb; during microstimulation, active forces were developed which, when added to the passive ones, resulted in the total force exerted by the limb. In the experiment, the total and the passive forces were measured, and the passive subtracted from the total to obtain the 'active' force field. It was found that microstimulation in a given area resulted in an active force field in which the force vectors converged on a particular point in space at which the force developed was zero; this was called the 'equilibrium point' of that field. In many cases, the force field predicted the limb motion when the limb was allowed to move; therefore, these fields can be regarded as underlying movement primitives [14]. The second finding was that only a few (3–4) clusters of equilibrium points were found by a detailed and systematic microstimulation of extensive areas of the spinal cord; each equilibrium point was represented at different locations in the spinal cord. Finally, concomitant microstimulation at any two sites produced a new force field which was the result of a point-by-point linear summation of the force field produced at each of the

two stimulation sites; thus new equilibrium points were created [21]. These findings suggest possible mechanisms by which supraspinal commands could be translated into motor action as follows.

## 4. Translation of supraspinal commands

First, since microstimulation will activate an appreciable number of neurons [22], these intrinsic spinal motor mechanisms involve populations of neurons and summation of influences from potentially separate neuronal ensembles. Second, it is likely that these ensembles are the targets of supraspinal influences. For example, a common characteristic of pyramidal tract axons is their appreciable divergence in the spinal cord with collaterals to various spinal segments [23]. Although spinal microstimulation studies have not been performed in primates, it is reasonable to hypothesize a similar plan of spinal organization. Then this divergence of the pyramidal tract axons would enable central motor commands to address concomitantly a number of the spinal populations associated with different force fields, that is with different movement primitives. Third, this organization could provide the background for the translation of the motor cortical command, as understood at the single cell and neuronal population level, to motoneuronal activation (see [5]). This is illustrated in Fig. 1. Consider movement $M_l$ in direction $l$, starting from point $A$. When the hand is in position $A$, various force fields can act on it, depending on the spinal interneuronal population activated. Let us assume that there are four force fields ($K = 4$) potentially acting on the hand at position $A$ and producing movement primitives $m_j$ ($j = 1$ to $K$) with magnitudes $U_{jl}$, that are proportional to the intensity of activation of the underlying spinal neuronal ensemble, appropriate for movement $M_l$. Assuming that the directions of the force fields are fixed for a given position of the hand, then movement direction $M_l$ should be the result of adjusting the magnitudes $U_{jl}$ so that

$$M_l = \sum_j^K U_{jl} m_j \qquad (2)$$

We assume that $N$ motor cortical cells converge on all $m_j$'s, and that for $M_l$ the influence of the $i^{th}$ cell on the $j^{th}$ $m$ is composed of two parts: one ($v_{ij}$) reflects the hard-wired connection strengths, and the other ($w_{il}$) reflects the activation of the cell during movement $M_l$. Then $U_{jl}$ can be re-expressed as:

$$U_{jl} = \sum_i^N w_{il} v_{ij} \qquad (3)$$

Substituting in Eq. (2) we get:

$$M_l = \sum_j^K \left( \sum_i^N w_{il} v_{ij} \right) m_j \qquad (4)$$

and by rearranging:

$$M_l = \sum_i^N w_{il} \left( \sum_j^K v_{ij} m_j \right) \qquad (5)$$

As discussed above, the population vector $P_1$ (equation 1) points in the direction of movement $M_1$ (equation 5); therefore:

$$\sum_i^N w_{ij} C_i = \sum_i^N w_{il} \left( \sum_j^K v_{ij} m_j \right) \qquad (6)$$

and

$$C_i = \sum_j^K v_{ij} m_j \qquad (7)$$

Equation 7 connects the concept of the preferred direction $C_i$ of the $i^{th}$ cell to that of the movement primitive generator $m_j$, as mentioned above; the weights $v_{ij}$ can be regarded as the hardwired connection strengths of the $i^{th}$ cell on the ensemble of movement primitive generators $m_j$, and then the vector sum of these influences will point at the cell's preferred direction.

Equation 3 implies two important assumptions: namely, (i) that there exist hardwired connections ($v_{ij}$) between motor cortical cells and spinal neurons, and (ii) that the activity of a motor cortical cell ($w_{il}$) can vary independently of its spinal connectivity pattern. Both of these assumptions are supported by the results of experimental studies of corticospinal influences, investigated by using the technique of postspike facilitation (see [23] for a review). Especially important is the observation that for different motor tasks, the cell activity can vary but the pattern of postspike facilitation remains the same [20]. Although these observations are for putative monosynaptic projections of motor cortical cells to motoneurons, it is reasonable to extend them to the more general case in which the effect is mediated, as in intercalated interneurons such as those making up the movement primitive generator $m_j$.

## 5. Concluding remarks: control of the limb as a whole

The results of the studies reviewed above suggest that spinal and supraspinal motor structures regard the limb as a functional whole. Recent studies [3] indicate that afferent systems may do the same. In these experiments single cell activity was recorded in the Clarke's column, the nucleus of origin of the dorsal spinocerebellar tract. Cells were antidromically identified as projecting to the cerebellum and their activity recorded during peripheral stimulation of the hindlimb in anesthetized cats. Although single cells received mono- and polysynaptic convergent inputs from various kinds of receptors and parts of the limb, their activity varied in an orderly fashion with the orientation of

the limb in space and with the direction of limb movement in space, when the limb was moved passively. This shows that the converging information onto single cells can meaningfully reflect spatial aspects of the status of the limb as a whole. Convergence of peripheral inputs on spinal interneurons has been described in several cases, including the C3–C4 propriospinal interneurons mediating central commands to proximal motoneurons [16]. It would be interesting to know whether the activity of these neurons similarly reflects spatial aspects of limb posture and/or movement.

Additional support for the idea that the limb may be controlled as a multijoint unit comes from the results of recent studies in which microstimulation or ablation of central nervous structures were used. First, microstimulation of the motor cortex in the monkey elicited concomitant activation of various muscles [4]. Second, reversible inactivation of the motor cortex in the cat affected multijoint, reaching movements of the limb but not single joint movements about the elbow [19]. And third, lesion of the dentate nucleus in the monkey also differentially affected reaching but not single joint movements [17]. These findings are in accord with the suggestion of the original single cell recording studies [10] that the motor cortex controls reaching movements. The close interaction between the motor cortex and the cerebellum [1] suggests that both of these structures may share this common feature of whole-limb motor control.

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