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Motor Cortex: A Changing Perspective

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The study of the motor cortex in the full-blown behavioral context of voluntary movement was introduced by Evarts (1966, 1968, 1969). Indeed, this is the only appropriate way to study the initiation of voluntary movement. The possibility of studying single cell activity in the behaving animal (Ricci et al. 1957) has opened new avenues and has changed the way in which we look at the neural bases of motor behavior , especially since motor mechanisms can be studied not only within narrowly defined motor conditions but also within a wide variety of behavioral contexts. Some of the changes that have gradually occurred during the past 25 years or so are outlined and briefly discussed below.

Changes in the way we use motor parameters as experimental tools

A major change has occurred with respect to how motor parameters are used as experimental tools; namely, from a restricted approach to a rich variety. Good examples are provided by the use of isometric force and movements for this purpose.

Isometric force

In the original (Evarts 1968) and later (Evarts et al. 1983) work of Evarts and his colleagues, and in subsequent work by others (e.g. Thach 1978; Cheney and Fetz 1980) force was restricted to one joint and to the activation of reciprocal groups of muscles. These studies were extended to the use of precision grip as an experimental tool (Smith et al. 1975; Hepp-Reymond and Diener 1983; Hepp-Reymond et al. 1978). The precision grip involves the simultaneous activation of a large number of muscles (Smith 1981; Maier et al. 1990a) and yet requires accurate control of force levels as an output motor parameter. Although earlier results on the relations between motor cortical cell activity and isometric force in a single joint could be interpreted in a simple fashion (Fromm 1983), these relations in the precision grip cases cannot be as easily interpreted, given that desired force levels can be attained by various combinations of muscle activations and that the amount of activation of a particular muscle may not vary in a simple fashion with the amount of force exerted (Maier et al. 1990a). Moreover, motor cortical cells with postspike facilitation effects of hand muscles may show both positive and negative correlations with precision grip force (Maier et al. 1990b).

A different level of complexity in the use of isometric force as a motor parameter was added when force was varied over time in a sinusoidal fashion at different frequencies (Humphrey and Reed 1983). At low frequencies of force change flexor and extensor muscles contracted reciprocally, but at high frequencies the joint was stabilized by the co-contraction of flexors and extensors which increased the mechanical stiffness of the joint. This paradigm revealed the existence of a subset of cells in the motor cortex that became active only at higher frequencies of force change. This finding suggested that these cells might relate to the control of joint stiffness.

Movement

A similar extension from simple to complex has occurred with regard to movements. Several studies were focused on one-dimensional movements made about one joint (e.g. Evarts 1968; Thach 1978; Alexander and Crutcher 1990a,b). Even when a joint with more than one degrees of freedom was used (e.g the wrist), the experimental design restricted the use of the joint in one dimension (e.g. flexion-extension - see, for example, Evarts 1968; Thach 1978). Recordings in the motor cortex during two- and three-dimensional arm movements revealed orderly relations of cell activity to spatial aspects of the movements in the workspace, especially to the direction of movement in space (Georgopoulos et al. 1982; Schwartz et al. 1988). The introduction of additional complexities in the planning of a spatial movement trajectory revealed additional complexities in motor cortical activity (Hocherman and Wise 1991).

In subsequent work (Caminiti et al. 1990; and this volume) the study of the motor cortical mechanisms underlying reaching movements was extended from movements made within a limited part of space to movements in the whole peri-personal space. These studies revealed a systematic variation of a higher order functional cell property, namely the cell preferred direction, with the part of space in which the movements are made. Thus an additional spatial enrichment of the experimental paradigm led to interesting changes of functional cell properties.

Finally, an important extension was the change from pointing movements to stationary targets to continuous, tracing movements (Schwartz 1988; Schwartz and Anderson 1989). Recordings in the motor cortex under these conditions revealed the lawful activation of cells according to their directional selectivity and meaningful "neuronal images" derived from population analyses. These observations form part of the neural substrate for continuous movements that underlie, for example, tracing movements and handwriting.

Changes in the way we look at and interpret neural activity

The major change in this aspect has been the realization that single cells provide only the building elements of the neural construct underlying movement generation and control: this construct invariably involves populations of neurons. The idea and use of neuronal populations in this context is different from common statistical measures of populations, such as averages, variances and frequency distributions of cell properties. Instead, the idea is that any single neuron carries only partial information about a movement parameter which is therefore uniquely represented only in the whole neuronal ensemble. Although this idea of distributed coding in the arm motor system was first elaborated in the neural coding of the direction of 2-dimensional movements in the motor cortex (Georgopoulos et al. 1983), it has much wider applicability. First, it has been confirmed in the motor cortex for free three- dimensional reaching movements (Georgopoulos et al. 1986, 1988; Caminiti et al. 1990, and this volume), and in the presence of static loads (Kalaska et al. 1989). Second, it has been identified as a time-varying directional population signal (Georgopoulos et al. 1984, 1988, 1989a). Third, it has been extended to other motor structures, including the premotor cortex (Caminiti et al. 1991) and the cerebellar cortex and nuclei (Fortier et al. 1989). Fourth, it has been applied successfully to the coding of arm movement direction in parietal area 5 (Kalaska et al. 1983; Kalaska 1988). And fifth, it has been used successfully to predict the direction of a moving visual stimulus from the activity of a population of cells recorded in area 7 of the parietal cortex (Steinmetz et al. 1987). Finally, excellent examples of neural network modeling of the directional population coding are presented by Burnod et al. (this volume).

Thinking along population lines in general is now supported by the results of studies concerning (a) the interaction of the motor cortex with input (e.g., thalamus, other cortical areas) and output (e.g., spinal cord) structures and (b) the representation of muscles and/or joints in the motor cortex. Concerning the first point, studies over the past two decades using anatomical techniques (intra-axonal injections of single fibers) and/or physiological recordings (spike triggered averaging) have shown a substantial divergence of the inputs to the motor cortex from the thalamus (Shinoda and Kakei 1989; Shinoda, this volume) and somatosensory cortex (DeFelipe et al. 1986), and of the outputs from the motor cortex to the spinal cord (Shinoda et al. 1979,1981; Fetz and Cheney 1980; Lemon et al. 1986). Concerning the second point, electrical stimulation studies have shown that muscles are multiply represented in the motor cortex in a weighted fashion (Donoghue et al. 1989), as are joints (Humphrey and Mitz 1989). Therefore, one cannot but consider motor cortical activity along the lines of distributed population systems both within the motor cortex itself and in its interactions with its inputs and outputs. The fact that input structures to the motor cortex such as cerebellum (Fortier et al. 1989), premotor cortex (Caminiti et al. 1991) and area 5 (Kalaska et al. 1983; Kalaska 1988) follow distributed population coding, and that the reaching movements themselves involve the activation of several muscles and therefore activity in the spinal cord spread over several segments, underscore the importance of population coding in the planning and execution of these movements. In fact excellent examples of formal treatment of this principle as applied to motor control are given in this volume (see articles by Burnod et al., Caminiti et al., Miller et al., and Hoff and Arbib).

The importance of behavioral conditions for motor cortical activity

The close association of motor cortex to output motor function, exemplified by its more or less direct connections to the spinal cord, had led for many years to a restricted view of the role of the motor cortex as practically nothing but a muscle controller. However, the process of movement generation, be it a self-initiated or a stimulus-evoked movement, is quite complex, and probably comprises several stages relating to the specification of its parameters (Favilla et al. 1989). On the other hand, other aspects of a motor act, relating, for example, to the stimulus conditions leading to movement initiation, the required precision, and the context of its implementation are additional factors that are relevant in a consideration of planning in motor control. A major change in the field has been that the motor cortex is a legitimate place in which these more complicated planning aspects are manifested. This was the result of positive findings that cell activity in the motor cortex can be shown to relate to these aspects, but also of negative findings that the simplistic view that cell activity in the motor cortex is related only to muscles is untenable.

The importance of task conditions for motor cortical cell activity has been shown clearly by the results of several studies. Indeed, as early as 1976 Tanji and Evarts (1976) showed that the activity of pyramidal tract cells was influenced by the instruction to the animal about the impending movement, during a waiting period in the absence of movement or muscle contraction. Changes in motor cortical cell activity during an instructed delay period have since then been described in several studies (Kubota and Hamada 1979; Wise et al. 1986; Lecas et al. 1986; Georgopoulos et al. 1989a). Moreover, such changes were recently observed during a preparatory period preceding movements in memorized directions (Alexander and Crutcher 1990a,b). These findings indicate that information regarding upcoming motor events or instructions for them can be represented in the motor cortex in the absence of immediate movement.

A different aspect of task condition shown to be important for motor cortical cell activity is the independent use of fingers. In particular, it was shown that single cells in the motor cortex can be active during a precision grip but not during a power grip, even when the two grips involve similar amounts of muscle activity (Muir and Lemon 1983). It is interesting that in that case the relation between cells and motoneurons seem to remain invariant, as evidenced by the similar postspike facilitation observed in the two conditions (Muir and Lemon 1983). This shows clearly that the intensity of muscle activation is not the sole, and probably not the most important, determinant of cell activity in the motor cortex.

The results of these studies showed that motor cortical cells can be preferentially active during a precision grip but they also showed that the intensity of activation of these cells can be dissociated from that of their target motoneurons, even in the presence of postspike facilitation, that is when monosynaptic connections to motoneurons are probably present. In fact, a dissociation of motor cortical cell activity from the activity of muscles has been well documented by the results of studies in which movements were made in the presence of loads of various directions. Thus in the study of Thach (1978) the activity of only one-third of motor cortical cells seemed to relate to muscle activity, and comparable results were obtained in a recent study of Alexander and Crutcher (1990a). Other variables, dissociated from the muscle pattern, seem to be important in determining motor cortical cell activity, including the direction of movement (Thach 1978; Alexander and Crutcher 1990a,b) and the position of the joint (Thach 1978). Therefore, it seems reasonable to suppose that during movements in which direction, position and muscle activity covary, the activity of cells in the motor cortex relates to all of these parameters with variable strength.

It is remarkable that relations of motor cortical cell activity have been observed in the context of more complex tasks that require a more abstract processing of information. For example, when the direction of movement was dissociated from that of a visual stimulus, the activity of a number of cells in the motor cortex reflected the change in the visual stimulus (Alexander and Crutcher 1990b). In another study, information about the direction of an upcoming movement was provided for a period of time preceding the movement-triggering signal (Riehle and Requin 1989); it was found that the changes in activity of motor cortical cells reflected the information gained by this prior knowledge of the direction of movement. Finally, the neural correlates of a process requiring a 90° transformation of a stimulus direction to a movement direction were studied in the motor cortex (Georgopoulos et al. 1989b); it was found that cell activity changed in such a way that the directional tendency of the neuronal ensemble (the neuronal population vector, see Georgopoulos et al. 1983, 1986; and Caminiti et al., this volume) changed in an orderly fashion during the reaction time from the stimulus direction to the movement direction. The findings of the above studies underscore the fact that changes in cell activity in the motor cortex can be as complex as the behavioral tasks that the animals perform.

The main take-home message from the studies summarized above is that motor cortex is complex! Any simplistic notion of this structure as nothing but a muscle controller is untenable. Therefore, it is more appropriate, and more useful, to incorporate this structure in the whole behavioral-motor repertoire than to pigeonhole it to a muscle function (Mussa- Ivaldi 1988). The behavioral aspects are as important as the motor aspects in determining the activity of cells in the motor cortex and therefore should be incorporated in any modeling of motor cortical function.

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