Cortical Representation of Intended Movements

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Abstract

The neural representation of reaching movements in the motor cortex of the monkey is discussed with respect to the coding of the direction of movement in the activity of single cells and neuronal populations. This code is then used to monitor the processing of directional information in various contexts involving delayed movements or directional transformations. Finally, some implications of these findings for the role of the motor cortex in planning and execution of reaching movements are discussed.

1 Introduction

The study of neural mechanisms underlying intended movements was made possible by the development of a technique which allowed the monitoring of the activity of single cells in the brain of behaving animals: it is obvious that *intended* movements can be studied only in a state permitting intention, namely in an awake, behaving animal. Although studies in anesthetized animals can provide a wealth of information concerning the connections and functional organization of brain structures participating in motor control, they cannot be used to study intended movements; for these, one needs an awake, behaving animal. The technique for recording single cell activity in behaving primates was originally developed by Jasper and his colleagues

(Ricci et al. 1957) and then perfected and popularized by Evarts (1966). This technique has a fine grain for studying neural activity and has been used successfully during the past 25 odd years to study the neural mechanisms underlying voluntary movement, perception and memory. In that what follows I summarize the results of our studies of cell activity in the motor cortex preceding the initiation of intended arm movements.

2 Reaching movements

Arm movements typically involve well coordinated and tightly coupled motions at the shoulder and elbow joints (Soechting and Lacquaniti, 1981), and are usually directed to visual targets. The main function of arm movements is to position the hand at a desired position within reaching space. The hand movement can be regarded as a vector possessing direction and distance. The expression of arm movement in this way is justified by the results of experiments that have shown (a) that pointing errors differ in the direction and distance domains (Soechting & Flanders 1989), (b) that precueing the direction or distance differentially affects the reaction time (Rosenbaum, 1980), and (c) that the processes of specifying direction and distance are dissociable (Favilla et al., 1989). Moreover, it seems now that reaching movements are specified and controlled by the brain as organized, multi-joint movements rather than as aggregates of single-joint movements. It was commonly believed in the past that the neural control of arm movements was operating on a single joint basis and that the multi-joint movement was the outcome of stringing together, so to speak, of individually controlled single joint elements. In fact, a major research effort has been expended studying neural activity in cortical and subcortical structures with respect to "simple", single joint movements see (Evarts, 1981, for a review). An alternative idea was that reaching movements could be specified and controlled as wholes (Mountcastle et al., 1975). Indeed, we used this idea successfully to describe the relations between the direction of reaching and cell activity in the motor (Georgopoulos et al., 1982; Schwartz et al., 1988) and parietal

(Kalaska et al., 1983) cortex. Similar relations have been found now in the cerebellum (Fortier et al., 1989) and the premotor cortex (Caminiti et al., 1991), and the results of other studies (Gibson et al., 1985) have produced evidence that the controlled unit in arm movements may be a complex multi-joint pattern. Finally, evidence for a separate control of multi-joint movements has come from studies using reversible lesions which showed that such lesions of the cerebellum (Kane et al., 1989) and motor cortex (Cooper et al., 1989) disrupt reaching but not single-joint movements.

In summary, reaching movements can be legitimately treated as behavioral units and studied at the behavioral and neural level with respect to their behavioral goal, namely hand movement in space.

3 Coding of directional information

The main aspect of reaching to which neural activity has been found to relate to is direction in space (Georgopoulos et al., 1982; Schwartz et al., 1988; Caminiti et al., 1990); in contrast, the relations of neural activity to distance have been elusive (Schwartz and Georgopoulos, 1987; Georgopoulos, 1990; Park et al., 1987,1988; Karluk and Ebner, 1989). The investigation of the relations of neural activity to direction is complicated by the fact that direction is not a linear variable but a closed circular (or spherical) variable. There can be basically two ways to represent direction: one is to allocate specific cells to represent specific directions and the other is to represent direction in an ensemble of cells. In the first case, reaching in the intended direction would be initiated by recruiting cells possessing the appropriate directionality, whereas in the second case the whole ensemble would be engaged in such a way that direction would be represented unambiguously in the ensemble. The results of experimental studies (Georgopoulos et al., 1982; Schwartz et al., 1988) proved the second idea to be correct, both with negative and positive findings. On the negative side, cells that are very sharply tuned to direction are very rare, if they exist; therefore, the hypothesis that intended movements are represented as ensembles of cells uniquely related only to these movements can be rejected. On the positive side, most cells are active with movements in different directions which means that for a movement in a particular direction a whole neuronal population is engaged; therefore, the direction of an intended movement is represented in the population. The question then is what is the nature of this representation and whether it is unambiguous and operationally useful.

A clue for the solution of this problem came from the directional tuning function of single cell activity. This function has three basic characteristics: (a) it is broad, which means that cell activity varies throughout the range of directions, in both 2D (Georgopoulos et al., 1982; Kalaska et al., 1989) and 3D (Schwartz et al., 1988; Caminiti et al., 1990) space; (b) it is orderly and can be described well by a cosine function (Georgopoulos et al., 1982; Schwartz et al., 1988); and (c) it is symmetric and unimodal, which means that there is a direction for which cell activity will be highest (the cell's "preferred direction"); the preferred directions differ for different cells and range throughout the whole directional continuum (Schwartz et al., 1988). It follows from these characteristics of the directional tuning curve that, except at the peak, the directional information provided by cell activity is ambiguous, for the same discharge rate can correspond to two different directions.

The broad directional tuning of single cell activity indicates that a given cell participates in movements of various directions; and from this it follows that, conversely, a movement in a particular direction will involve the activation of a whole population of cells: how, then, is the direction of reaching represented in a unique fashion in a population of neurons each of which is directionally broadly tuned? An unambiguous population code was proposed (Georgopoulos et al., 1983, 1986, 1988) which regarded the motor cortical command for the direction of reaching as an ensemble of vectors. Each vector represents the contribution of a directionally tuned cell. A particular vector points in the cell's preferred direction and has length proportional to the change in cell activity associated with a particular movement direction: then the vector sum of these weighted cell vectors (the "neuronal population vector") points at or near the direction of the movement (Georgopoulos et al. 1983, 1986, 1988). Therefore, information concerning the direction of movement can be unambiguously obtained from the neuronal ensemble. This then provides the tool by which to monitor the processing of directional information in time, that is when the movement is *intended*.

4 Processing of directional information in time

There are several aspects of *intending* a movement. (a) The commonest case is when a movement is produced as soon as a stimulus appears: then some time intervenes between the occurrence of the stimulus and the beginning of the movement which is the traditional reaction time. This time varies depending on the sensory modality of the stimulus and any imposed constraints on the movement but it usually takes 200-300 ms. The reaction time then can be regarded as a time during which the movement is *intended*. (b) In other cases a delay can be imposed so that the movement will be initiated after a period of waiting, while the stimulus is still present. These *instructed delay paradigms* probe a step further the representation of intended movements, in the sense that there is not an immediate motor output while the representation is being kept active. (c) A specific case of delayed tasks involves movements that have to be produced on the basis of information kept in *memory*. The difference from the instructed delay task is that now the stimulus defining the direction of the movement is turned off after a short period of presentation and the movement is triggered after a delay by a separate "go" signal. Thus information concerning the intended movement has to be retained during the memorized delay.

In all three cases above the representation of information about the intended movement can be studied under different conditions which impose different constraints on the system. It would interesting to know whether this representation could be identified and visualized during the reaction time, the instructed delay and the memorized delay periods. Since the information assumed to be represented is about direction, the neuronal population vector could be a useful tool by which to identify this representation. For that purpose we computed the population vector every 20 ms (a) during the reaction time (Georgopoulos et al., 1984, 1988), (b) during an instructed delay period (Georgopoulos et al., 1989), and (c) during a memorized delay period (Smyrnis et al., 1991). The results were clear: in all these cases the population vector pointed in the direction of the intended movement during the above time periods. These findings (a) underscore the usefulness of the population vector analysis as a tool for visualizing representations of the intended movement, and (b) show that in the presence or absence of an immediate motor output, as well as when the directional information has to be kept in memory, the direction of the intended movement is represented in a dynamic form at the ensemble level. These results also document the involvement of the motor cortex in the representation of intended movements under various behavioral conditions.

5 Processing a directional transformation

In the delayed tasks described above the movement to be made is unequivocally defined in the sense that its direction is determined by the location of a stimulus relative to the starting point. In that situation the visual information concerning direction is used to generate the appropriate motor command to implement a movement in that direction; truly, this movement direction has to be generated and kept available during the delay period but it is defined from the beginning; therefore, the direction of the intended movement is the same throughout the various times considered above. A very different situation was created in an experiment (Georgopoulos and Massey, 1987) in which the direction of the movement to be made had to be determined freshly at every trial according to a certain rule, namely that the movement direction be at an angle (counterclockwise, CCW, or clockwise, CW) from the stimulus direction. This experiment takes us away from the case of a *fixed* motor intention: instead, this intention has now to be derived as the solution to the problem. In fact, there are many ways by which this problem can be solved (discussed in Georgopoulos and Massey, 1987). An obvious way would be to form a look-up table which contains the movement directions that correspond to the stimulus directions. Using this strategy, one would simply memorize the corresponding directions in the table and, given a stimulus direction, one would search the table to select the movement direction corresponding to the particular stimulus direction. Of course, one would not have to use numbers, simply imagined directed radii in a unit circle.

A different strategy would be to mentally rotate the stimulus direction in the instructed departure (CCW or CW) by an amount equal to the required angular shift. The look-up table and mental rotation hypotheses lead to different predictions concerning how the reaction time would change, and on this basis they can be distinguished. If the look-up table strategy is followed, the reaction time would increase due to the time taken for the search but this increase should not be greater for larger angles because there is no reason to suppose that searching the table in the case of a large angle should take more time than when searching the table in the case of a small angle. In contrast, the mental rotation hypothesis predicts an increase of the reaction time with the angle because the time to be taken to rotate a radius through an angle should be proportional to the angle itself. Indeed, the results of the experiments in human subjects (Georgopoulos and Massey, 1987) showed an increase of the reaction time with the angle and therefore supported the mental rotation hypothesis. The average rate of the hypothesized rotation was approximately 400^o/s. Remarkably, this is very close to the value obtained by Shepard and Cooper (1982) in experiments of mental rotation of visual images. Another similarity in the motor rotation (Georgopoulos and Massey, 1987) and visual rotation (Shepard and Cooper, 1982) studies is that there is appreciable diversity in the rotation rates obtained among different subjects. In fact, we used this feature to test the idea that motor and visual mental rotation processes may be associated: indeed, a significant correlation was found between the two rotation rates in a group of subjects who performed both tasks (Pellizzer et al., 1991). This suggests that the two processes might share a common stage, or that both processes involve constraints that result in the relation obtained.

The neural mechanisms underlying the process of mental rotation in the movement domain were investigated by training monkeys to perform a task in which they made a movement in a direction 90^0 CCW from a stimulus direction. We supposed that if a mental rotation of an imagined vector was taking place, the neuronal population vector could reveal it. Indeed, the population vector rotated during the reaction time from the stimulus to the movement direction through the 90^0 CCW angle (Georgopoulos et al., 1989b; Lurito et al., 1992). Interestingly, the rotation rates (direction of population vector vs. time) observed (Lurito et al., 1992) were very similar to the rates (increase in reaction time vs. angle) observed in the human studies (Georgopoulos and Massey, 1987). Thus, the dynamic processing of a directional transformation was successfully visualized using the neuronal population vector analysis. The crucial aspect of this analysis is the consideration of neuronal populations as the meaningful level of synthesis of motor cortical events. Indeed, the population vector approach has proved useful not only in studies of motor cortex (Georgopoulos et al., 1983, 1986, 1988; Kalaska et al., 1989; Caminiti et al., 1990; Smyrnis et al., 1991; Taira et al., 1991) but also in studies of other areas, including the cerebellum (Fortier et al., 1989), the premotor cortex (Caminiti et al., 1991), and parietal area 5 (Kalaska et al., 1983; Kalaska, 1988) and area 7 (Steinmetz et al., 1987). Three aspects of this analysis are remarkable: (a) its simplicity, (b) its robustness, and (c) its spatial outcome. With respect to *simplicity*, it is noteworthy that the ongoing calculation of the population vector is a simple procedure, for it (i) assumes the directional selectivity of single cells, which is apparent, (ii) involves weighting of vectorial contributions by single cells on the basis of the change in cell activity, which is reasonable, and (iii) relies on the vectorial summation of these contributions, which is practically the simplest procedure to obtain a unique outcome. With respect to *robustness*, the population vector is a robust measure, for it can still convey a good directional signal even with only 100 cells (Georgopoulos et al., 1988). Finally, it is noteworthy that the population vector is a *spatial* measure, isomorphic in direction with direction in space. Indeed, the population analysis transforms aggregates of purely temporal spike trains into a spatio-temporal population vector.

It is this property that makes this measure especially useful, for, through it, the directional tendency of the neuronal ensemble can be monitored in the absence of overt behavior and therefore an insight into the representation of intended movement can be gained in a time-varying and isomorphic fashion.

6 Concluding remarks

The results of the experiments discussed above raise several points concerning the representation of intended movements in the motor cortex. (a) The *first* point is that this representation is not obligatorily connected with the production of movement, that is its presence does not necessarily lead to motor output. This has been shown by the results of previous studies (Tanji and Evarts, 1976) and of the delay studies (Georgopoulos et al., 1989a) summarized above. This is in accord with findings of psychophysical studies that movement planning and movement triggering are different processes (Hening et al., 1988). It is interesting that when a delay is introduced, there seem to be at least two different subsets of cells: one that is active during the delay and becomes further active following the movement triggering signal, and another that is not active during the delay but becomes engaged after the "go" signal (Georgopoulos et al., 1989a). Therefore, it seems that both the planning and the triggering processes involve the motor cortex. Concerning downstream points where motor cortical activity could be gated, segmental and propriospinal (Lundberg, 1979) levels in the spinal cord are good candidates, given the extensive convergence of several supraspinal inputs on these interneuronal systems. Therefore, engagement of the motor cortex is not a sufficient condition for triggering the movement. On the other hand, motor cortical activation seems to be necessary for appropriate planning of the movement, as suggested by the disturbed reaching movements produced by reversible inactivation of the motor cortex (Cooper et al., 1989). (b) The *second* point concerns the nature of information that is represented. It may not be appropriate to assign all of this information to the upcoming movement for it may very well reflect procceses subserving the translation of visual or memorized information to motor output. The complexity of potential explanatory factors for motor cortical activity in behavioral tasks is suggested by the results of studies where such factors were dissociated (Thach, 1978; Alexander and Crutcher, 1990a,b) but also by the results of the directional transformation study (Georgopoulos et al., 1989) discussed above which showed that motor cortical activity does reflect a process involved in mental rotation. (c) The *third* point concerns the place of motor cortex among other motor structures. In this context, it is important to realize that unlike primary sensory cortices, motor cortex is the site of convergence from a large number of other areas, both cortical and subcortical. For example, the large extent of the convergence on the motor cortex, in distinction to that on the somatosensory cortex, can be appreciated from the results of recent studies of the thalamocortical projections to small motor cortical areas (Darian-Smith et al., 1990). Therefore, the discharge patterns of motor cortical cells are generated through this convergence rather than being the outcome of a faithful transmission through sensory lines. It seems then that although both primary somatosensory and motor cortices are close to somatic periphery, the analogy (Fetz, 1984) is misleading. On the other hand, the motor cortex is not the "final" motor path from the cerebral cortex. It has been shown now conclusively that several premotor areas possess direct and dense projections to the spinal cord (Dum and Strick, 1991). It seems that the motor cortex and premotor areas might be concerned with different but overlapping aspects of motor control (Tanji and Kurata, 1985; Alexander and Crutcher, 1990a,b; Chen et al., 1991) and that a particular movement might be the result of this parallel processing. These findings have an important implication, among others, and that is that the spinal motor mechanisms involved in the production of voluntary movement can be properly understood only if one takes into account (a) the convergent pattern of influences from the motor and premotor cortical areas, (b) influences from subcortical structures such as the red nucleus and the reticular formation, and (c) the organization and dynamic interplay of spinal interneuronal circuits involved in the transmission of central commands (Lundberg, 1979), the generation of stereotypic motor patterns (Grillner et al., 1988; Gelfand et al., 1988), and the control of afferent input from the moving limb (Rudomin, 1990a,b). The intricacy of the latter can be appreciated from the elucidation of the mechanisms involved in presynaptic inhibition (Rudomin 1990a,b) and its differential control by supraspinal structures (Rudomin et al., 1986), including the motor cortex (Eguibar et al., 1991). Conversely, the patterns of activity of precentral corticospinal corticospinal neurons will have to understood in the light of their influences on the spinal mechanisms. In that respect, most of the attention in behaving primates has been focused on those motor cortical neurons that are presumably monosynaptically projecting onto motoneurons (Cheney and Fetz, 1980; Lemon et al., 1986), and practically no attention has been paid to the cortical influences on spinal interneuronal mechanisms, in spite of the fact that it is through the latter that a major, and indeed exclusive in some species (e.g. the cat), cortical effect is exerted. There is little doubt that understanding the interactions among the various motor areas, and in particular those between the motor cortex and the spinal cord (Georgopoulos and Grillner, 1989), is now the biggest challenge in deciphering the "natural intelligence" of the motor system.

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