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Current issues in directional motor control

Apostolos P. Georgopoulos

Many studies during the past 15 years have shown that the direction of motor output (movement or isometric force) is an important factor for neuronal activity in the motor cortex, both at the level of single cells and at the level of neuronal populations. Recent studies have investigated several new aspects of this problem including the effect of posture, the relations to time-varying movement parameters (for example, position, velocity and acceleration) and the cortical representation of memorized simple movements and complex-movement trajectories. Furthermore, the neural correlates of directional operations, such as mental rotation and memory-scanning of visuomotor directions, have also been investigated. In addition, neural networks have been used to model dynamic, time-varying, spatial motor trajectories.

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RESEARCH INTO THE ROLE of brain structures in the control of motor output in behaving animals was focused initially (from around 1965 to 1980) on the control of the magnitude of force, usually within the framework of a single joint or a precision grip (for review, see Ref. 1). There were two notable exceptions during that period. First, one study documented the sequential (that is, proximal-to-distal) activation of arm-related motor-cortical cells during reaching towards and manipulating an object[2], and this was amplified in a later study[3]. Second, Mountcastle and colleagues[4] suggested that reaching movements could be coded in the patterns of cell activity in the CNS and proposed a major role for the posterior parietal cortex in 'command functions for operations within extrapersonal space'. However, an investigation of motor-cortical activity in relation to joint motion and muscle activity during reaching did not yield clear cut results[5].

A reaching movement is a vector in space that can be described fully by its direction and amplitude. Studies on the neural coding of these parameters were initiated in the early 1980s (for review, see Ref. 6). In 1982, the first systematic study of the relationship of the activity of motor-cortical cells to the direction of reaching was published[7], and this was complemented 11 years later by a comprehensive investigation of the relationship of cell activity to the amplitude of movement[8,9].

Directional tuning of motor cortical cells

The activity of single cells is tuned directionally; cell activity is highest for a given direction ('preferred direction') of movement (for review, see Ref. 10) or isometric force[11,12], and decreases gradually as the direction becomes farther away from the preferred one. Typically, the frequency of cell discharge is a linear function of the direction cosines of the movement vector (relative to its origin), or, equivalently, of the cosine of the angle formed between the direction of a particular movement and the preferred direction of the cell. These relationships have been documented for planar pointing movements[7,13], free pointing movements in three-dimensional (3D) space[14,15], continuous planar movements[16] and isometric force pulses[11]. Changes in cell activity relate to the direction but not to the endpoint of the movement[17]. Directional tuning is observed for cells with different types of resting firing patterns, including cells with low-rate, regular-spike trains, cells with bursting patterns and cells with high frequency of discharge[18]. Preferred directions differ for different cells and are uniformly distributed in 3D space[14,15]. They are represented many times on the cortical surface and tend to cluster in columns[19]. The preferred direction is very similar for movements of different amplitudes[8], although it can change when the origin of the movement[15] or the posture of the arm[20] change. Finally, cells with similar preferred directions tend to have excitatory synaptic interactions, whereas cells with opposite preferred directions tend to have inhibitory interactions[10].

Relationship between cell activity and movement parameters

An analysis of the timecourse of cell activity[21] was used to assess the relationship of ongoing single-cell activity to evolving movement parameters, including position, velocity and acceleration, and to the direction of the target[22]. It was found that cell activity was related to all of these parameters, but that target direction and movement velocity were the most important determinants of cell activity. The importance of the signal provided by ongoing movement velocity was also indicated by neural studies of continuous movements[16]. It is reasonable to suppose that these effects reflect motor-control signals as well as the effects of peripheral inputs. A contribution of feedback is supported by the known inputs to the motor cortex from the somatic periphery (for review, see Ref. 23). A feedforward signal could relate to the length- tension state of the muscles[24], in which case this signal could be tailored to the current states of the muscles to be controlled.

This combination of afferent and efferent signals could be quite complex, given the appreciable divergence of corticospinal axons at the spinal level[23], the wide distribution of motor-cortical output signals to various cortical and subcortical structures, and the convergence of peripheral inputs to cortical areas (for example, areas 2 and 5) that provide major inputs to the motor cortex. If one adds the known inputs from subcortical structures (basal ganglia and cerebellum) and considers the large divergence[25] and convergence[26] of the thalamic projections to the motor cortex, then a picture emerges in which the motor cortex occupies a nodal point at the cross-section of many interacting circuits. The pattern of convergence of local and distant projections determines the complexity of the structure. This complexity is reflected in the fact that several other factors have been shown to be important for the activity of motor cortical cells, including the direction of an upcoming movement[27], the direction of a visual target[28], joint stabilization[29], instructed delay[30], memorized delay[31], memorized complex-movement trajectory[32], and specific task conditions (for example, see Ref. 33). With respect to movement co-ordination, motor-cortical activity seems to be involved in muscle selection and co-ordination during accurate, visually guided locomotor movements (for review, see Ref. 34), rather than during just an increase in muscle activity[35].

Control of visually guided reaching movements

Visually guided reaching movements and visually guided locomotor movements share several common features[36]. For example, they involve drastic changes in arm posture and musculoskeletal conditions during their execution and are usually aimed accurately at targets in space. Moreover, they are under continuous visual control and can change direction very quickly when their target changes[37]. In addition, their trajectory can be influenced by subtle factors (for example, repetition of the same movement[38] and cognitive loads[39]). Therefore, it comes as no surprise that reaching movements are associated with a high activation of the motor cortex. However, it is remarkable that discharge of motor-cortical cells varies in such an orderly fashion with the direction of movement in space (or the direction of multidimensional isometric force). This suggests that direction comprises a multitude of factors and that motor-cortical cells, in turn, provide a simplified representation of a number of visuomotor variables through an orderly relation to a single variable, namely direction. This might enable other structures involved in motor control to address motor cortex through that representation, thus simplifying the overall problem of control.

This idea is analogous to the different levels of control of computer hardware through the use of computer languages of varying complexity. For example, actual instructions at the lowest level can be given in assembly (machine) language, but higher-order computer languages enable the execution of a number of such instructions through a single statement. Continuing the analogy, if the peripheral hardware changes, then a particular higher-order language might no longer be appropriate, or might need to be modified to accommodate the new situation. Similarly, if conditions within the motor system undergo drastic changes (for example, microgravity or strange posture), a period of motor learning might be necessary to re-code for the new conditions so that efficient motor control can be restored.

This example illustrates how a 'higher-order' motor-cortical 'language' might operate with respect to a 'lower-order' musculoskeletal system. In fact, the results of a recent study showed that the ability of a monkey to make wrist movements in a direction (higher-order 'directional language') that requires the coactivation of different muscles (lower-order 'muscle machine language') is permanently lost after a lesion of the contralateral-arm area of the motor cortex[40]. This result demonstrates the critical role of the motor cortex in directional motor control; it selects and co-ordinates muscle activity[41,42] rather than controlling single muscles alone. A scheme for the translation of directional motor-cortical commands to multi-muscle activation has been described elsewhere[42,43].

Directional coding by neuronal populations

An unambiguous signal from a population of neurons that are tuned broadly can be defined by the 'population-vector' hypothesis[44]. The population vector is a vectorial summation 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 movement. This weighted vector sum has been found to point in the direction of movement[15,44–47], and in subsets of cells recorded in the upper or lower cortical layers[6]. It has been shown that the population vector will point in the direction of movement if the following conditions apply: (1) the directional tuning is symmetric; (2) the preferred directions are uniformly distributed; and (3) there is no statistically significant association between the amplitude of tuning and the preferred direction[46]. Although the second condition is quite robust, and a variety of distributions will enable correct prediction by the population vector, it does not apply when there is a bimodal distribution of the preferred directions[48].

Advantages of the population-vector analysis

Three aspects of the population-vector analysis are remarkable. First, the ongoing calculation of the population vector is a simple procedure since it (1) assumes the directional selectivity of single cells, which is apparent, (2) involves weighting of vectorial contributions by single cells on the basis of the change in cell activity, which is reasonable, and (3) relies on the vectorial summation of these contributions, which is practically the simplest procedure to obtain a unique outcome. Second, the population vector is a robust measure, for it can still convey a good directional signal with only 100 cells[46], or much fewer[49,50]. Third, the population vector is a directional measure, isomorphic to the direction of movement in space. Indeed, the population analysis transforms aggregates of purely temporal spike trains into a directional signal. Furthermore, the population-vector analysis is quite general, and can be applied to other problems beyond the motor system. Indeed, it was applied recently with success to the coding of faces in the inferotemporal cortex[51].

Effect of posture

The effect of posture on the population vector is still under investigation. It has been observed previously that the population vector is a good and unbiased predictor of movement direction even for movements of different origin in space[47,52], that is, for movements associated with different arm postures. In all of these cases, monkeys moved their arm freely in 3D space and in a natural, unconstrained posture.

Further evidence for this robustness has been provided by a recent preliminary study in which a monkey was forced to abduct its arm by 80° in order to move a handle in eight directions on a plane (from the center to eight targets on a circle); control movements were also made with the natural posture of the arm[20]. The population vector was calculated from the average cell activity during the reaction and movement time and plotted together with plots of the movement trajectories for both control and abducted postures (see Fig. 2 of Ref. 20). To compare the directions of the population vectors obtained for different movement directions in the two postures, we measured the directions (polar angles) of the 16 population vectors directly from this figure. These directions are plotted against each other in Fig. 1, which demonstrates that the two sets of population-vector directions are highly correlated. Moreover, the slope does not differ significantly from unity (Student's t test, $P > 0.2$). Hence, the directions of the population vectors are very similar and do not differ significantly as a group between the two postures. This conclusion was confirmed by the results of a paired Student's t test, which showed that the directions of the population vectors did not differ significantly between the two groups ($t = -0.15$, $P = 0.88$).

Finally, a qualitative observation added further weight to the hypothesis that the population vector predicts the direction of the movement. The observation pertains to the systematic change observed in the direction of two movement trajectories under the abducted posture. In the lower panel of Fig. 2 of Ref. 20, the trajectories in the upper-right and upper-left directions are both observed to shift in the abducted posture towards 12 o'clock; remarkably, the directions of the two corresponding population vectors also shifted towards the 12 o'clock direction.

These simple quantitative and qualitative analyses show that the population vector remains a robust predictor of the direction of movement even under conditions in which 'the intrinsic kinematics and kinetics of the movement were dramatically different'[20].

Monitoring directional information in time

The population vector can be calculated at short time intervals (for example, 10 or 20 ms) as a time-varying signal[19]. In this mode, it has served as a useful monitor of the directional tendency of the neuronal ensemble under various experimental conditions. There have been two main fields of application of this analysis.

The first series of applications deals with the representation of trajectories of ongoing, continuous tracing movements[54,55]: the time-varying population vectors are strung tip-to-tail and provide a 'neural' trajectory[46]. It was determined that this neural representation of the trajectory is very similar to the trajectory of movement, and that it conforms to the '2/3 power law'[55], which describes the relationship between speed and curvature in continuous, curved movements[56].

The second series of applications deals with the processing of directional information during operations that unfold for a period of time in the absence of an immediate motor output. The time-varying population vector has been observed to point in the direction of the upcoming movement during the reaction time[19,46], during an instructed delay period[30] and during a memorized delay period[31]. In all of these periods, the changes in neural activity precede the execution of the movement, and, therefore, the population vector provides a temporally predictive directional signal.

In other tasks, the population vector identified the nature of dynamic processes that operate on central representations of direction, namely mental rotation[57,58] and context-recall memory-scanning[59]. The first case involved a directional transformation by requiring the generation of a movement in a direction orthogonal and counterclockwise from a stimulus direction: the population vector rotated counterclockwise during the reaction time, from an initial direction close to the direction of the stimulus to the direction of the movement[57,58]. The second case involved the selection of a movement direction out of a set, on the basis of the serial position of a stimulus on a list: after three stimuli were presented successively at different positions on a circle, one of them (not the last) changed color (test stimulus); this required the monkey to move in the direction of the stimulus that followed the test one in the sequence. It was observed that the population vector changed direction very abruptly (within 40–60 ms) from the direction of the stimulus anticipated to the direction of the ensuing movement[59]. Thus, two very different processes were visualized, one of which involved a continuous transformation of direction whereas the other involved a discrete selection of a direction from a set. This hypothesis was supported further by the observation that cells with preferred directions that are intermediate between the direction of the stimulus and that of the response were activated in the mental rotation[57–59] but not in the context-recall[59] task.

Memorized trajectories of complex movements

The studies summarized above dealt with motor-cortical activity during tasks requiring a directional transformation[57,58] or selection[59], or during memorization of simple pointing movements[31]. A different question concerns the neural mechanisms subserving memorized trajectories of complex movements. This problem was investigated in a recent study in which two monkeys were trained to perform from memory an arm movement with an orthogonal bend, up and to the left, following a waiting period[32]. They held a 2D manipulandum over a spot of light at the center of a planar working surface. When this light went off, the animals were required to hold the manipulandum there for 600–700 ms and then move the handle up and to the left to receive a liquid reward. There were no external signals concerning the go time or the trajectory of the memorized movement.

Following 20 trials of the memorized movement trajectory, 40 trials of visually triggered movements in radially arranged directions were performed. The activity of 137 single cells in the motor cortex was recorded extracellularly during performance of the task. A high percentage (62.8%) of cells changed activity during the waiting period. Other cells did not change activity until after the 600 ms minimum waiting time was over, and, occasionally, cell activity changed almost exactly at 600 ms after the center light was turned off. However, the most interesting observation was that a few cells changed activity exclusively during the execution of the memorized movement; these cells were completely inactive during performance of similar movements in the visually guided control task. These findings suggest that performance of a movement trajectory from memory might involve a specific set of cells, in addition to the cells activated during both visually guided and memorized movements.

Neural-network modeling of dynamic directional operations

The time-varying directional operations summarized above have been modeled recently using a massively interconnected artificial neural network that consists of neurons that are tuned directionally and produces the neuronal population vector as the final outcome[10,60,61]. This network has reproduced many of the experimental findings accurately, and has led to a novel hypothesis on how memorized trajectories of complex movements could be stored in the synaptic connections of overlapping neural networks[62].

It is proposed that there is a general-purpose network that is involved in all kinds of movements, both memorized and not memorized; it does not carry any information about memorized trajectories of specific shapes (for example, circles, ellipses and scribbles) and, if activated alone, it would produce straight-line trajectories. It is now hypothesized that there are also networks highly specific for a particular trajectory (for example, clockwise circle) that are interconnected with the general-purpose network: when a specific trajectory needs to be performed, the appropriate specific network fuses with the general-purpose network and, as one network, produces the desired trajectory. The specific network need only be less than 5% of the size of the general-purpose network for the desired trajectory to be stored and reproduced effectively[62]. This is in accord with the low proportions of very specific cells that have been observed in neurophysiological recordings during performance of memorized trajectories[32], as discussed above.

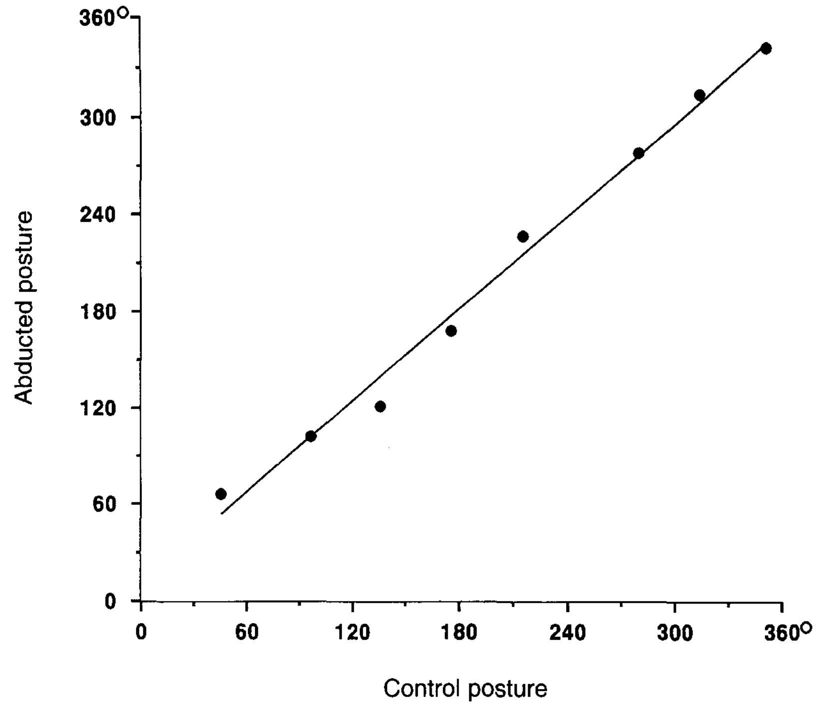

Fig. 1. ***The directions of population vectors obtained for control and abducted arm postures.*** *Data were measured from the graph of Fig. 2 A and B of Ref. 20, and are polar angles with 0° pointing towards 3 o'clock and the angle increasing counterclockwise ($n = 8$ movement directions). The linear correlation coefficient in the data plotted is $r = 0.995$ ($P < 0.00005$); the circular correlation coefficient[53] is $\hat{\rho}_T = 0.979$ ($P < 0.00005$; bootstrap sample size = 1 million).*

The idea of the existence of very specialized networks raises the question of the degree of specialization and of how such networks are created in the first place. We can only speculate on these issues. It is reasonable to assume that the general-purpose network is present at birth, since it is assumed to subserve all movements. There are several possibilities concerning the specialized networks.

First, a number of small-size networks that are specific for basic shapes (for example, straight lines, curves and some combinations thereof ('motor shape primitives')] might be present at birth; motor learning for complex motor acts would then consist of adjusting the strengths of connections between the general-purpose and specific networks. This idea implies that all of the specialized primitives are used routinely, although not as frequently as the general-purpose network.

A second possibility is that innate specific networks code for more complicated shapes and are large in number. The mechanism of motor learning would then be similar to that described above, but only a small number of the specialized networks would be used. This means that a number of the complex, specialized networks might never be used. This situation would be analogous to that encountered in the immune system in which there is potential for making a large number of antibodies, but only certain antibodies are made, depending on the exposure of the organism to specific antigens. In both cases there is a selection: selection of a specialized trajectory or selection of an antibody, both from a large ensemble available.

Finally, an intermediate hypothesis suggests that we start with networks for motor shape primitives, but that the more complex trajectories resulting from the combination of these primitives with the general-purpose network become themselves very specialized and behave as such in the formation of other trajectories in novel associations.

Note added in proof

In a recent study[63], the population vector was calculated every 10 ms in the premotor cortex during a task in which a movement was made either in the direction of an attended stimulus ('compatible condition') or in a constant direction irrespective of the direction of the attended stimulus ('incompatible condition'). In the compatible condition, the population vector pointed in the direction of the attended stimulus, which was the same as the direction of the movement. However, in the incompatible condition, the population vector rotated from an initial direction near the stimulus to the direction of the movement. This rotation and the initial offset in the direction of the population vector were remarkably similar to those observed in the mental rotation task described above[58]. Moreover, the rotation of the population vector was observed for the various stimulus–response angles used, including ±45, ±90, ±135 and 180°.

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