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**CHAPTER 13**

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**MOTOR CORTEX: NEURAL AND COMPUTATIONAL STUDIES**

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**ABSTRACT**

The motor cortex can be regarded as a network of neurons processing, *inter alia*, spatial motor information. A basic component of this information is the direction of movement in space. Experimental studies in behaving monkeys have shown that the impulse activity of single motor-cortical cells relates to this component in an orderly fashion, such that the frequency of cell discharge is a sinusoidal function of the direction of movement, with the direction for which cell discharge is highest denoting the "preferred direction" of the cell. The neuronal ensemble of such directionally tuned cells can be regarded as a network in which each cell is represented as a vector pointing in the cell's preferred direction. The network operates to generate a signal in the direction of a desired movement. We regard this operation as the vectorial summation of the cell vectors, weighted by a scalar measure of the intensity of cell activation. The resulting vector sum is called the "neuronal population vector." Analysis of experimental data has shown that the population vector points in the direction of the movement. In addition, the population vector can be calculated as a time-varying signal and, as such, is a robust predictor of the direction of the upcoming movement during the reaction time and during instructed and memorized delays. Finally, it has proven a good tool for monitoring and deciphering directional information when more complex directional operations are performed.

**Introduction**

The motor cortex is located on the lateral and medial surface of the cerebral hemisphere, just in front of the central sulcus, and is the major precentral motor area. Several premotor areas have been identified anterior to the motor cortex. They are interconnected with the motor cortex and, taken together, constitute a highly interactive group of motor areas in the cerebral cortex. This chapter focuses on the coding of directional information by single cells and neuronal populations in the motor cortex. Applications of these analyses are discussed, together with neural-network modeling studies to which the coding scheme has led.

### Directional Tuning of Single Cells

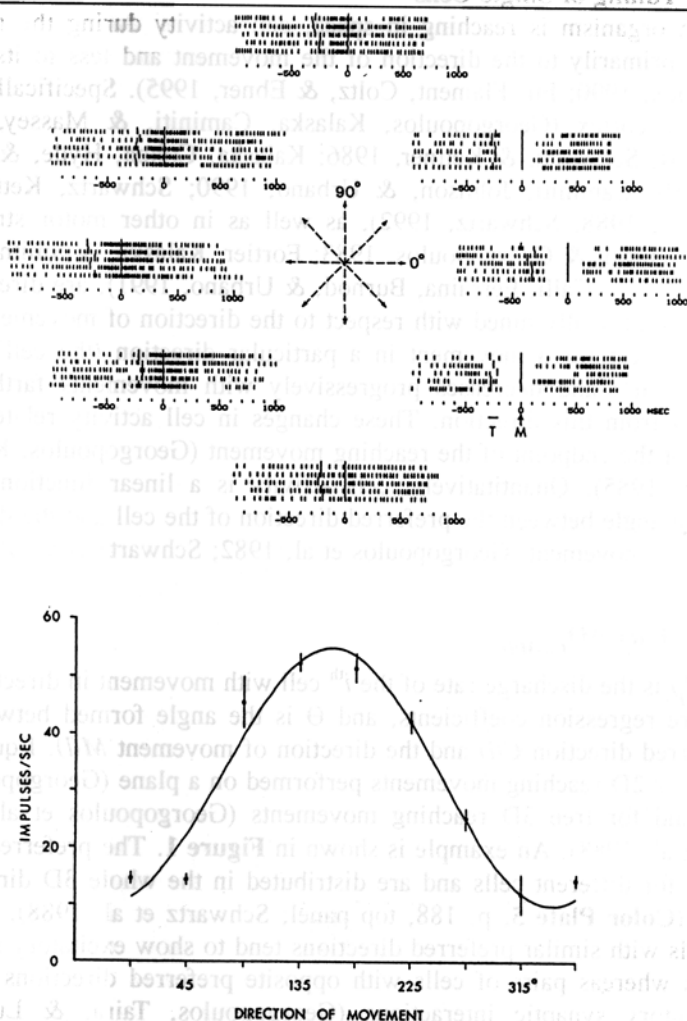
When an organism is reaching in space, cell activity during the reaction time relates primarily to the direction of the movement and less to its extent (Georgopoulos, 1990; Fu, Flament, Coltz, & Ebner, 1995). Specifically, cells in the motor cortex (Georgopoulos, Kalaska, Caminiti, & Massey, 1982; Georgopoulos, Schwartz, & Kettner, 1986; Kalaska, Cohen, Hyde, & Prud'homme, 1989; Caminiti, Johnson, & Urbano, 1990; Schwartz, Kettner, & Georgopoulos, 1988; Schwartz, 1992), as well as in other motor structures (Kalaska, Caminiti, & Georgopoulos, 1983; Fortier, Kalaska, & Smith, 1989; Caminiti, Johnson, Galli, Ferraina, Burnod, & Urbano, 1991), are directionally selective and broadly tuned with respect to the direction of movement. Cell activity is highest for a movement in a particular direction (the cell's "preferred direction") and decreases progressively with movements farther and farther away from this direction. These changes in cell activity relate to the direction, not the endpoint of the reaching movement (Georgopoulos, Kalaska, & Caminiti, 1985). Quantitatively, cell activity is a linear function of the cosine of the angle between the preferred direction of the cell and the direction of a particular movement (Georgopoulos et al, 1982; Schwartz et al, 1988), as follows:

$$d_i(M_j) = b_i + a_i \cos \Theta_{C(i)M(j)} \quad (1)$$

where  $d_i(M_j)$  is the discharge rate of the  $i^{\text{th}}$  cell with movement in direction  $M_j$ ,  $b_i$  and  $a_i$  are regression coefficients, and  $\Theta$  is the angle formed between the cell's preferred direction  $C(i)$  and the direction of movement  $M(j)$ . Equation 1 holds both for 2D reaching movements performed on a plane (Georgopoulos et al, 1982) and for free 3D reaching movements (Georgopoulos et al, 1986; Schwartz et al, 1988). An example is shown in **Figure 1**. The preferred directions differ for different cells and are distributed in the whole 3D directional continuum (**Color Plate 5**, p. 188, top panel; Schwartz et al, 1988). Finally, pairs of cells with similar preferred directions tend to show excitatory synaptic interactions whereas pairs of cells with opposite preferred directions tend to show inhibitory synaptic interactions (Georgopoulos, Taira, & Lukashin, 1993).

### Directional Coding by Neuronal Populations

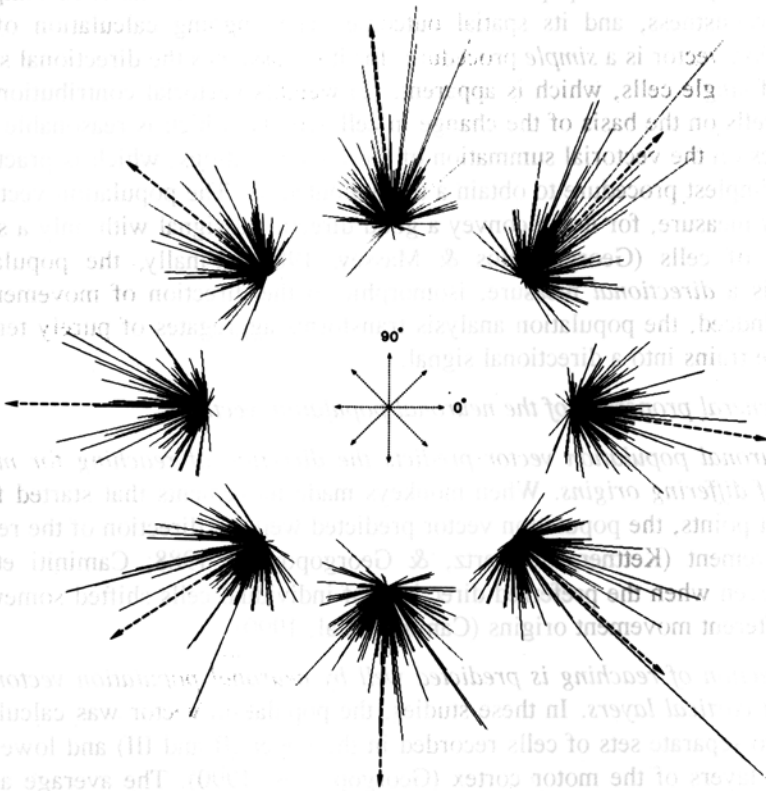
The broad directional tuning indicates that a given cell participates in movements of various directions, and that, conversely, a movement in a particular direction will involve the engagement of a whole population of cells. Therefore, a unique signal for the direction of a movement could reside in the activity of the neuronal ensemble. We proposed a vectorial code for the recovery of this signal from the neuronal ensemble (Georgopoulos, Caminiti, Kalaska, & Massey, 1983; Georgopoulos et al, 1986; Georgopoulos, Kettner, & Schwartz, 1988), as follows: (1) A cell is represented as a vector that points in



**FIGURE 1.** Directional tuning of a cell recorded in the arm area of the motor cortex during 2D reaching. Top: Impulse activity during five trials of reaching in the directions indicated in the drawing at the center. Short vertical bars indicate the occurrence of an action potential. Rasters are aligned to the onset of movement (M). Longer vertical bars preceding the onset of movement indicate the onset of the target (T); those following the movement indicate, successively, the entrance to the target zone and the delivery of reward. Bottom: Average frequency of discharge ( $\pm$  SEM) from the onset of movement. Continuous curve is a cosine function fitted to the data using multiple-regression analysis. (From Georgopoulos et al, 1982; reproduced with permission. Copyright by Society for Neuroscience.)

the cell's preferred direction. (2) Cell vectors are weighted by the (scalar) change in cell activity during a particular movement. (3) The sum of these vectors (i.e., the population vector) provides the unique outcome of the ensemble coding operation. This operation can be expressed as follows:

$$P_i = \sum_i w_{ii} C_i \quad (2)$$



**FIGURE 2.** Neuronal-population coding of the direction of reaching illustrated for a motor-cortical population ( $N = 241$  cells) and 8 movement directions on a 2D working surface. Vectorial contributions of single cells (continuous lines) add to yield the population vector (dotted arrow). Each cluster represents the same population; the movement directions are shown in the diagram at the center. The population vector points in or near the direction of the movement. (From Georgopoulos et al, 1983; reproduced with permission.)

It was found that the population vector points in the direction of the movement (Georgopoulos et al, 1983; Georgopoulos et al, 1986; Georgopoulos et al, 1988; **Figure 2** and **Color Plate 5**, p. 188, middle and bottom panels). The population-vector approach has proved useful not only in studies of motor cortex (Georgopoulos et al, 1983; Georgopoulos et al, 1986; Georgopoulos et al, 1988; Kalaska et al, 1989; Caminiti et al, 1990) but also in studies of other brain areas, including the cerebellum (Fortier et al, 1989), the premotor cortex (Caminiti et al, 1991), area 5 (Kalaska et al, 1983), and area 7 (Steinmetz, Motter, Duffy, & Mountcastle, 1987).

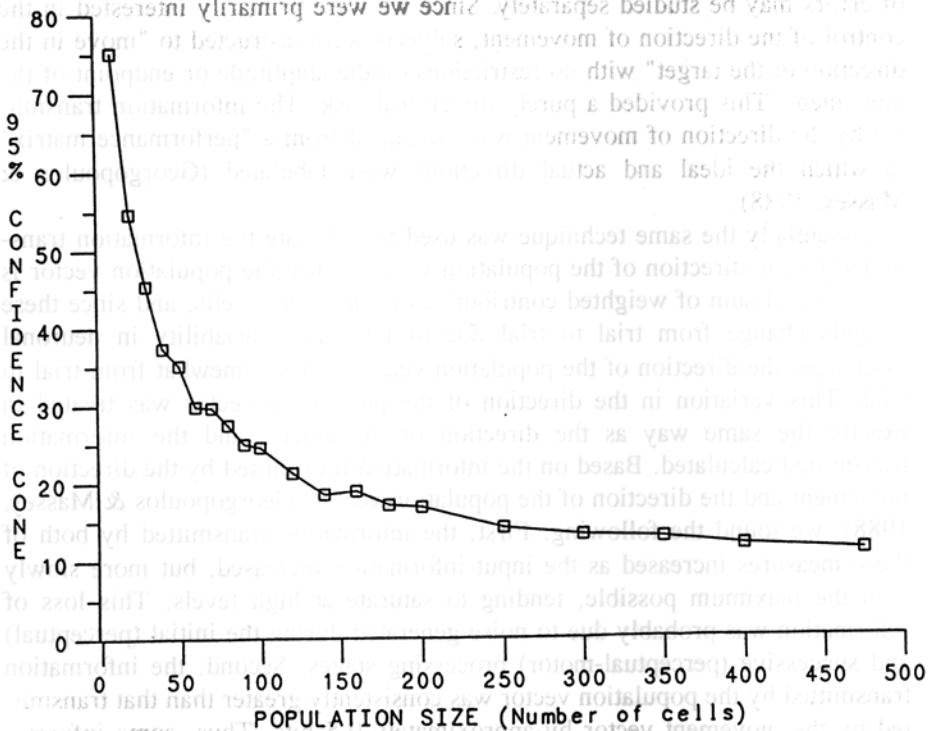
Three aspects of the population-vector analysis are remarkable: its simplicity, its robustness, and its spatial outcome. The ongoing calculation of the population vector is a *simple* procedure, for it (1) assumes the directional selectivity of single cells, which is apparent, (2) weights vectorial contributions 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. The population vector is a *robust* measure, for it can convey a good directional signal with only a small number of cells (Georgopoulos & Massey, 1988). Finally, 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.

#### *Some general properties of the neuronal population vector*

*The neuronal population vector predicts the direction of reaching for movements of differing origins.* When monkeys made movements that started from different points, the population vector predicted well the direction of the reaching movement (Kettner, Schwartz, & Georgopoulos, 1988; Caminiti et al, 1991), even when the preferred directions of individual cells shifted somewhat with different movement origins (Caminiti et al, 1990).

*The direction of reaching is predicted well by neuronal population vectors in different cortical layers.* In these studies, the population vector was calculated from two separate sets of cells recorded in the upper (II and III) and lower (V and VI) layers of the motor cortex (Georgopoulos, 1990). The average absolute angle between the population vector calculated from cells in the upper layers and the direction of movement was  $4.31^\circ$  (SD =  $2.98^\circ$ ) for eight different movement directions, compared to  $2.32^\circ$  (SD =  $2.06^\circ$ ) for the lower layers (Georgopoulos, 1990). This finding suggests that the ensemble operation of the population vector can be realized separately in the upper and lower layers. This is important because information can then be distributed to different structures according to the differential projections from the upper and lower layers (Jones & Wise, 1977).

*The neuronal population coding of the direction of reaching is resistant to loss of cells.* The population coding described above is a distributed code and as such does not depend exclusively on any particular cell. This robustness was evaluated by calculating the population vector from progressively smaller samples of cells randomly selected from the original population (Georgopoulos et al, 1988). It was found that the direction of the population vector can be reliably estimated from as few as 100-150 cells (Figure 3), and from many fewer if optimal algorithms are used (Salinas & Abbott, 1994).



**FIGURE 3.** Directional variability of the population vector (ordinate) plotted against population size (abscissa). Points in the graph are means of eight half-angles of 95% variability cones, one for each of the eight movement directions used. Units on the ordinate are in degrees. (From Georgopoulos et al, 1988; reproduced with permission by the publisher.)

*The neuronal population vector transmits directional information comparable to that transmitted by the direction of movement.* In the standard two-dimensional movement task used in our studies, monkeys (Georgopoulos et al, 1982) and human subjects (Georgopoulos & Massey, 1988) moved a manipu-

landum from the center of a planar working surface to a target on the circumference of a circle. In this case, movement directly toward the target is the ideal direction. If the subject's movements were directly toward the target, performance would be perfect, and the movement could be said to transmit the maximum possible information. However, movements are rarely dead on target, and, therefore, the information transmitted is rarely maximal. The greater the dispersion of the movement endpoint around the target, the less the information transmitted. This dispersion may be parceled into errors in the amplitude of movement and in the direction of movement, and these two types of errors may be studied separately. Since we were primarily interested in the control of the direction of movement, subjects were instructed to "move in the direction of the target" with no restrictions on the amplitude or endpoint of the movement. This provided a purely directional task. The information transmitted by the direction of movement was calculated from a "performance matrix" in which the ideal and actual directions were tabulated (Georgopoulos & Massey, 1988).

Essentially the same technique was used to calculate the information transmitted by the direction of the population vector. Since the population vector is the vectorial sum of weighted contributions of individual cells, and since these weights change from trial to trial due to inter-trial variability in neuronal discharge, the direction of the population vector varies somewhat from trial to trial. This variation in the direction of the population vector was treated in exactly the same way as the direction of movement, and the information transmitted calculated. Based on the information transmitted by the direction of movement and the direction of the population vector (Georgopoulos & Massey, 1988), we found the following. First, the information transmitted by both of these measures increased as the input information increased, but more slowly than the maximum possible, tending to saturate at high levels. This loss of information was probably due to noise generated during the initial (perceptual) and successive (perceptual-motor) processing stages. Second, the information transmitted by the population vector was consistently greater than that transmitted by the movement vector by approximately 0.5 bits. Thus, some information is lost between the motor cortex and the movement. However, this loss differed from that due to noise, for it did not increase with increasing stimulus information but remained constant at about 0.5 bits at all levels of input information. The second form of loss could occur during processing in other motor structures or during the biomechanical implementation of movement.

*The neuronal population vector predicts the direction of dynamic isometric force.* The dynamic relations of cell activity in the motor cortex to the direction of 2D isometric force has been investigated more recently (Georgopoulos, Ashe, Smyrnis, & Taira, 1992). The following experimental arrangement allowed dissociation of the dynamic and static components of the force.

Monkeys produced pure force pulses on an isometric handle in the presence of a constant force bias such that the net force (i.e., the vector sum of the monkey's force and the bias force) was in a visually specified direction. The net force developed over time had to maintain the specified direction and to increase in magnitude until it exceeded a criterion intensity threshold.

The most interesting case occurred when the directions of the net and bias forces differed by being, for example, orthogonal. In order for the task to be performed successfully under these conditions, the animal's force has to change continuously in direction and magnitude. At every moment during force development, the vector sum of the movement force and the bias force had to be in the visually specified direction. This experimental arrangement effectively dissociated the animal's force vector, the direction of which changed continuously in a trial, from the net-force vector, the direction of which remained invariant. Eight net-force directions and eight bias-force directions were employed.

Recordings of neuronal activity in the motor cortex revealed that the activity of single cells was directionally tuned in the absence of bias force, and that this tuning remained invariant when the same net forces were produced in the presence of different directions of bias force. These results demonstrated that cell activity does not relate to the direction of the animal's force, since the net force was equivalent to the dynamic component of the force exerted by the animal after a static component vector (equal and opposite to the force bias) was subtracted. These findings suggest that the motor cortex provides a dynamic force signal during force development with other, possibly subcortical, structures providing the static compensatory signal. This latter signal could be furnished by antigravity neural systems, given that most static loads encountered are gravitational in nature. According to this general view, the force exerted by the subject consists of dynamic and static components, each of which is controlled by different neural systems. These signals converge in the spinal cord and provide an ongoing integrated signal to the motoneuronal pools.

The foregoing results establish that coding of directional information applies to the motor output in general, even in the absence of joint motion. Moreover, the direction specified by the motor cortex is not that of the total force exerted by the animal but of the dynamic component of the force; i.e., the component of the force remaining after subtraction of a constant, static force.

#### *Time-varying properties of the neuronal population vector*

The population vector is a robust predictor of the direction of movement, as shown by the following analyses in which the population vector was calculated as a time-varying signal at short successive intervals (e.g., every 10 or 20 ms). The relation of this signal to an ongoing or a planned movement was assessed.

*The neuronal population vector predicts the movement trajectory in continuous tracing movements* (Schwartz 1993, 1994). In this experiment monkeys smoothly traced sinusoids with their index finger from one end of the display screen to the other. The direction of the population vectors, calculated successively along the trajectory, changed throughout the sinusoidal movement, closely matching the smoothly changing direction of the finger path. Moreover, a neural "image" of the sinusoidal trajectory of the movement was obtained by connecting successive population vectors tip-to-tail (Georgopoulos et al, 1988). This finding suggests that the length of the population vector carries information about the instantaneous velocity of the movement.

*The neuronal population vector predicts the direction of reaching during the reaction time.* This is the simplest case of predicting *in time* the direction of an upcoming movement. Given that changes in cellular activity in the motor cortex precede the onset of movement by 160-180 ms, on the average (Georgopoulos et al, 1982), it is an important finding that the population vector predicts the direction of the upcoming movement during the period when the movement is being planned (Georgopoulos, Kalaska, Crutcher, Caminiti, & Massey, 1984; Georgopoulos et al, 1988). An example is shown in **Figure 4**.

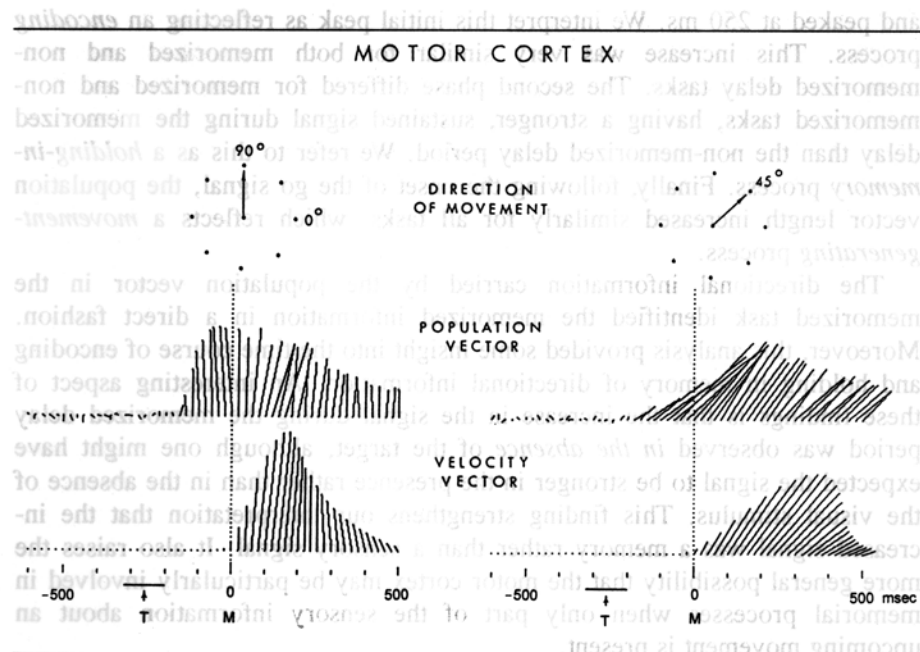
*The neuronal population vector predicts the direction of reaching during an instructed-delay period.* In these experiments monkeys were trained to withhold the movement for a period of time after the onset of a visual cue signal, and then to move in response to a "go" signal. During this instructed delay period, the population vector in the motor cortex (computed every 20 ms) gave a reliable signal specifying the direction of movement that was later triggered for execution (Georgopoulos, Crutcher, & Schwartz, 1989b).

### **The Neuronal Population Vector Deciphers Complex Directional Processing**

The results summarized above underscore the operational usefulness of the neuronal population vector for monitoring in time the directional tendency of the neuronal ensemble. We took advantage of this property and used the population vector *as a probe* to decipher the neural processing of directional information during various cognitive operations.

#### *Memory holding*

In these experiments (Smyrnis, Taira, Ashe, & Georgopoulos, 1992) monkeys were trained to move a handle on a 2D working surface in directions specified by a light on the plane. They first moved the handle to "capture" a light on the center of the plane, and then moved the handle in the direction indicated by a peripheral light (the *cue* signal). A signal to move (the *go* signal) was given by turning off the center light. The following tasks were used. In the *non-delay* task, the peripheral light was turned on at the same time as the center light went off. In the *memorized delay* task, the peripheral light stayed on for 300 ms (cue period) and the center light was turned off 450-750 ms later



**FIGURE 4.** The population vector points in the direction of movement well before the movement begins. Top: The results for two movement directions in 2D space are illustrated. Middle: The population vector was calculated every 20 ms. Bottom: The average instantaneous (20 ms bin) velocity of the movement is also shown. Before target onset (T), the population vector is very small in length and its direction varies from moment to moment. Well before the onset of movement (M), the vector increases in length and points in the direction of the upcoming movement. (From Georgopoulos et al, 1984; reproduced with permission by the publisher.)

(delay period). Finally, in the *non-memorized delay* task the peripheral light stayed on continuously, whereas the center light went off 750-1050 ms after the peripheral light came on.

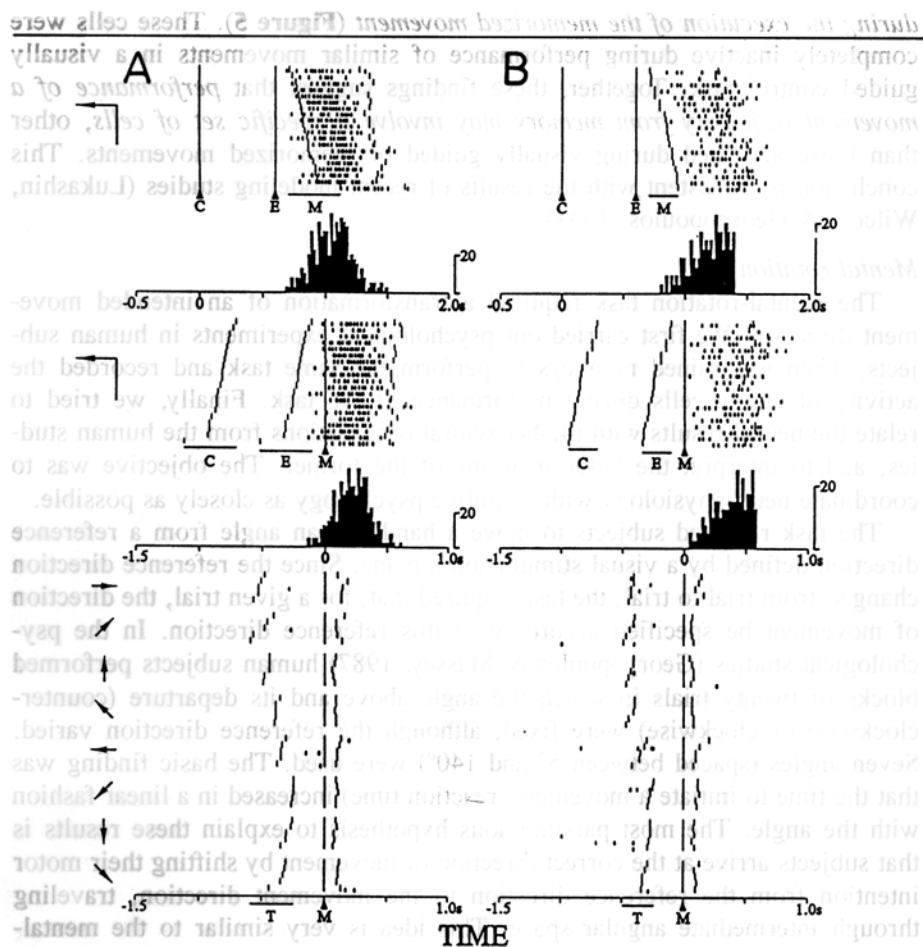
Recordings in the arm area of the motor cortex allowed the population vector to be calculated every 20 ms, following the onset of the peripheral light. We were interested in two aspects of the information carried by the population vector—its direction, which can be interpreted as the directional information carried by the population signal, and its length, which can be regarded as the strength of the directional signal. We found that the direction of the population vector during the memorized delay period was close to the direction of the target. The length of the population vector was similar in the cue period but longer during the memorized than the non-memorized part of the delay. Three phases were distinguishable. First, the population vector showed an initial increase in length that started approximately 100 ms following the cue onset

and peaked at 250 ms. We interpret this initial peak as reflecting an *encoding* process. This increase was very similar for both memorized and non-memorized delay tasks. The second phase differed for memorized and non-memorized tasks, having a stronger, sustained signal during the memorized delay than the non-memorized delay period. We refer to this as a *holding-in-memory* process. Finally, following the onset of the go signal, the population vector length increased similarly for all tasks, which reflects a *movement-generating* process.

The directional information carried by the population vector in the memorized task identified the memorized information in a direct fashion. Moreover, this analysis provided some insight into the time course of encoding and holding in memory of directional information. An interesting aspect of these findings is that the increase in the signal during the memorized delay period was observed *in the absence* of the target, although one might have expected the signal to be stronger in the presence rather than in the absence of the visual stimulus. This finding strengthens our interpretation that the increased signal was a memory rather than a sensory signal. It also raises the more general possibility that the motor cortex may be particularly involved in memorial processes when only part of the sensory information about an upcoming movement is present.

#### *Memorized complex trajectory*

The studies summarized above dealt with motor-cortical activity during a task that required memorization of the direction of a straight movement. A related question concerns the neural mechanisms subserving memorized, *complex* movement trajectories (Hocherman & Wise, 1991). We investigated this problem in a recent study (Ashe, Taira, Smyrnis, Pelizzer, Georgakopoulos, Lurito, & Georgopoulos, 1993) in which monkeys were trained to perform from memory an arm movement requiring an orthogonal bend, up and to the left, following a waiting period. 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. At the time of movement, there were no external signals specifying the time to initiate or the trajectory of the movement. Following 20 trials of the memorized movement trajectory, 40 trials were performed with visually triggered movements in radially arranged directions. The activity of 137 single cells in the motor cortex was recorded extracellularly during performance. A substantial percentage (62.8%) of cells changed activity during the waiting period prior to the beginning of movement. Other cells did not change activity until after the 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*



**FIGURE 5.** Examples of two cells (A and B) that showed changes in activity during the execution of the memorized movement trajectory (top) but not during movements of the visually instructed task (bottom). For each cell, the following are plotted. Top: Twenty trials of impulse activity (short vertical bars) are shown aligned to the onset (C) of the beginning of the delay (i.e., the time that the center light went off). Subsequent longer vertical bars indicate the end (E) of the waiting period, the exit of the handle from the center (M), and the entrance into the endpoint window. The vertical scale in the histogram indicates impulses. Middle: The same data are plotted aligned to the exit of the handle from the center window. Bottom: Five trials of visually triggered movements in the direction shown to the left of the rasters are shown aligned to the exit (M) of the handle from the center window. The longer vertical bar preceding M indicates the onset of the visual target (T). Filled triangles below the horizontal axes indicate fixed events; horizontal bars indicate the range of time for the event indicated below them. (A, cell Pi054u/6; B, cell Pi062u/4). (From Ashe et al, 1993; reproduced with permission by the publisher.)

during the execution of the memorized movement (Figure 5). These cells were completely inactive during performance of similar movements in a visually guided control task. Together, these findings suggest that *performance of a movement trajectory from memory may involve a specific set of cells*, other than those activated during visually guided or memorized movements. This conclusion is consistent with the results of recent modeling studies (Lukashin, Wilcox, & Georgopoulos, 1994).

### *Mental rotation*

The mental-rotation task required a transformation of an intended movement direction. We first carried out psychological experiments in human subjects. Then we trained monkeys to perform the same task and recorded the activity of single cells during performance of the task. Finally, we tried to relate the neural results with the behavioral observations from the human studies, and to interpret the latter in terms of the former. The objective was to coordinate neurophysiology with cognitive psychology as closely as possible.

The task required subjects to move a handle at an angle from a reference direction defined by a visual stimulus on a plane. Since the reference direction changed from trial to trial, the task required that, for a given trial, the direction of movement be specified according to this reference direction. In the psychological studies (Georgopoulos & Massey, 1987) human subjects performed blocks of twenty trials in which the angle above and its departure (counterclockwise or clockwise) were fixed, although the reference direction varied. Seven angles (spaced between  $5^\circ$  and  $140^\circ$ ) were used. The basic finding was that the time to initiate a movement (reaction time) increased in a linear fashion with the angle. The most parsimonious hypothesis to explain these results is that subjects arrive at the correct direction of movement by shifting their motor intention from the reference direction to the movement direction, traveling through intermediate angular space. This idea is very similar to the mental-rotation hypothesis of Shepard and Cooper (1982), which accommodates the monotonic increase of reaction time with orientation angle during a judgment task. The task is to decide whether a given line drawing is the same as, or a mirror image of, a comparison drawing. The subjects are said to rotate a visual image when responding. In fact, the mean rates of rotation and their range among subjects were very similar in the perceptual (Shepard & Cooper, 1982) and motor (Georgopoulos & Massey, 1987) studies. Moreover, when the same subjects performed both perceptual and motor rotation tasks, their processing rates were positively correlated (Pellizzer & Georgopoulos, 1993), which implies similar processing constraints for both tasks.

In the neurophysiological studies (Georgopoulos, Lurito, Petrides, Schwartz, & Massey, 1989a; Lurito, Georgakopoulos, & Georgopoulos, 1991), two rhesus monkeys were trained to move the handle  $90^\circ$  and counterclockwise from the direction of the reference stimulus. These trials were

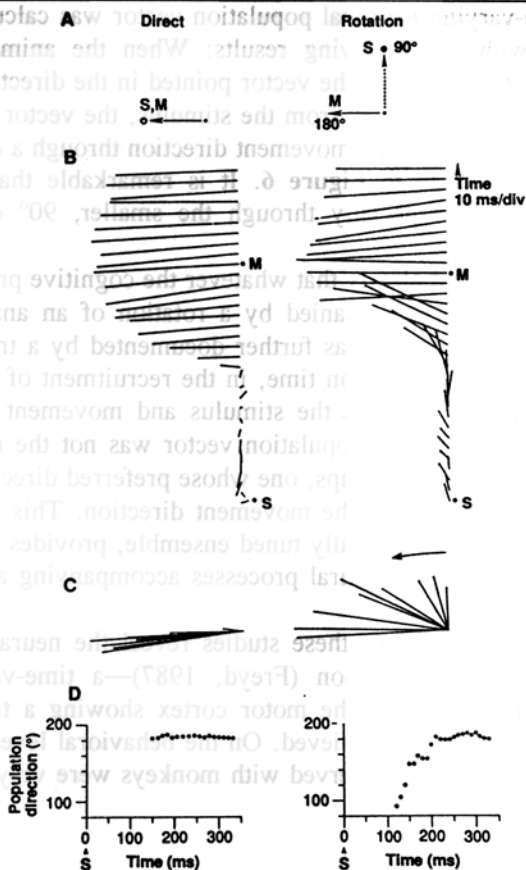
intermixed with others in which the animals moved in the direction of the target. The time-varying neuronal population vector was calculated during the reaction time, with the following results: When the animal's arm moved toward the reference stimulus, the vector pointed in the direction of the stimulus; when the arm moved away from the stimulus, the vector rotated from the direction of the stimulus to the movement direction through a counterclockwise angle. This is illustrated in **Figure 6**. It is remarkable that the population vector rotated at all, especially through the smaller, 90° counterclockwise angle.

These results showed clearly that whatever the cognitive processes involved in the task, they were accompanied by a rotation of an analog signal. The occurrence of a true rotation was further documented by a transient increase, during the middle of the reaction time, in the recruitment of cells whose preferred directions were between the stimulus and movement directions. This indicated that rotation of the population vector was not the result of varying activations of only two cell groups, one whose preferred directions centered on the stimulus and the other on the movement direction. This rotation process, "sweeping" through a directionally tuned ensemble, provides for the first time a direct visualization of the neural processes accompanying a dynamic cognitive process.

In summary, the results of these studies reveal the neural correlates of a dynamic cognitive representation (Freyd, 1987)—a time-varying, dynamic representation of direction in the motor cortex showing a transformation of direction when required and achieved. On the behavioral level, the mean rotation rate and range of rates observed with monkeys were very similar to those obtained with humans.

#### *Context-recall memory scanning*

In the preceding studies, we identified the neural correlates of a mental-rotation process as an orderly rotation of the neuronal population vector from the direction of the stimulus to that of the movement, through successive directions within a specified angle. This rotation paralleled the spatial rule operating in the mental-rotation task, which required the production of a movement at an angle from a stimulus direction. In the present study (Pellizzer, Sargent, & Georgopoulos, 1995) we sought, instead, to determine the neural correlates of a cognitive process that was not based on a spatial constraint but on the serial position of stimuli within a sequence. Given an arbitrary sequence of stimuli on a circle, with one identified as the test stimulus, the criterion response was movement toward the stimulus that followed the test stimulus in the sequence. This task is a visuomotor version (Georgopoulos & Lurito, 1991; Pellizzer & Georgopoulos, 1993) of a context-recall memory scanning task (Sternberg 1969). Previous psychophysical studies (Pellizzer & Georgopoulos, 1993) suggested that the processing mechanisms differed between mental-rotation and



**FIGURE 6.** Results from a direct (left) and a rotation (right) case in a mental-rotation task. **A.** Task description. Unfilled and filled circles indicate the dim and bright lights, respectively. Interrupted and continuous lines with arrows indicate the stimulus (S) and movement (M) directions, respectively. **B.** Neuronal population vectors calculated every 10 ms from the onset of the stimulus (S) at positions shown in A until after the onset of the movement (M). When the population vector lengthens, for the direct case it points in the direction of the movement, whereas for the rotation case it points initially in the direction of the stimulus and then rotates counterclockwise and points in the direction of the movement. **C.** Ten successive population vectors from B are shown in a spatial plot, starting from the first population vector that increased significantly in length. Notice the counterclockwise rotation of the population vector (right). **D.** Scatterplots of the direction of the population vector as a function of time, starting from the first population vector that increased significantly in length following stimulus onset (S). For the direct case, the direction of the population vector is in the direction of the movement ( $\sim 180^\circ$ ); for the rotation case, the population vector rotates counterclockwise from the direction of the stimulus ( $\sim 90^\circ$ ) to the direction of the movement ( $\sim 180^\circ$ ).

context-recall tasks. In order to determine the neural mechanisms in the latter task, we recorded single-cell activity in the motor cortex of a monkey trained to perform a context-recall and, as a control, an instructed-delay task. We also re-analyzed the neural data from the mental-rotation study (Lurito et al, 1991) to provide a comparison to the present context-recall study.

In the control task, a yellow stimulus was presented in one of eight directions and stayed on for 400 ms, after which it turned blue. This provided the go signal for the monkey to exert a force pulse such that a force feedback cursor exceeded a certain threshold. In the context-recall task, three yellow stimuli (list stimuli) were presented successively (every 400 ms) at different positions on the circle, and stayed on the screen. After an additional 400 ms, one of these stimuli (excepting the last) turned blue. This identified the test stimulus, and also served as the go signal. The monkey then moved the cursor in the direction of the stimulus that followed the test stimulus in the sequence. During the response time, the patterns of neural activity in the motor cortex initially resembled those associated with the direction of the second stimulus. When the test stimulus was the first in the sequence, cell activity continued to reflect the direction of the second stimulus which in this case was the appropriate motor response. However, when the test stimulus was the second in the sequence, neural activity changed to reflect the pattern associated with the direction of the third stimulus which was now the appropriate motor response. This switch was abrupt, occurring  $\sim 100$ -150 ms after the go signal, and was evident both in the activity of single cells and in the time-varying neuronal population vector, which changed direction within  $\sim 50$ -60 ms.

These findings reveal neural correlates of a switching process that is different from mental rotation (Lurito et al, 1991). Additional evidence for the differing nature of the two neural processes was provided by an analysis of the directional selectivity of cells that changed activity during the response time. In a rotation process, the set of cells that change activity during the response time should include cells whose preferred directions are intermediate between the stimulus and response directions. Indeed, this is what was observed (see Figure 13 in Lurito et al, 1991). In contrast, a switching process, such as postulated for the context-recall task, should not involve the activation of cells in directions intermediate between the test stimulus ( $S_2$ ) and motor response ( $S_3$ ). And, this was precisely what was observed (see Figure 4 in Pellizzer et al, 1995). The time taken to derive the direction of movement in the mental-rotation task reflects a transformation, whereas time in the context-recall task reflects a selection process. Finally, these studies provide an insight into the neural mechanisms of these processes in a particular brain area, namely the motor cortex. But, it is obvious that other brain areas are likely to be involved. Additional experiments are needed to delineate such areas and elucidate their contributions to performance.

### Neural-Network Modeling of Motor-Cortical Directional Operations

The motor cortex can be essentially regarded as a neural network whose elements are directionally tuned. One of the possible operations of the network may be described as the computation of the neuronal population vector. The broad directional tuning of single cells seems to be a general property of the population operation, and broad tuning has emerged for units in the hidden layer of a three-layer network trained to calculate the population vector (Lukashin, 1990).

The contribution of interactions among cells to the computation of the population vector also requires examination. It is known that there are extensive local interconnections (Huntley & Jones, 1991) among cells in motor cortex and these promote functional neuronal interactions (Stefanis & Jasper, 1964; Asanuma & Brooks, 1965). Our objective was to (1) identify the nature of these interactions among directionally tuned cells in the motor cortex, (2) to study interactions among units in an artificial neural network made of directionally tuned elements with massive interconnections, and (3) to compare the findings obtained from the motor cortex with those from artificial neural networks. We found the following (Georgopoulos et al, 1993). First, in the motor cortex, interactions between cells were more than twice as frequent when they were tuned than when they were not. The interaction between pairs of cells ranged from strongly positive (i.e., excitatory) to strongly negative (i.e., inhibitory) as the angle between the preferred directions of the cells varied from  $0^\circ$  (i.e., same preferred direction) to  $180^\circ$  (i.e., opposite preferred directions). Second, the same trend was found between the directionally tuned elements of a massively interconnected, dynamic artificial network during the computation of the population vector. Third, when computation of the population vector was stable, the strength of the synaptic interactions was low. In the best (i.e., most stable) case, the mean synaptic strength tended toward  $2/N$ , where  $N$  is the number of elements in the network. This is consistent with the finding that cortical cells in an area are extensively but weakly interconnected (Martin, 1988). Such findings tend to validate the correspondence between the motor-cortical and the artificial neural network and open the possibility of using such networks to interpret the cognitive operations involved in mental-rotation and context-recall tasks.

The time-varying directional operations discussed in the preceding sections have recently been modeled using a massively interconnected artificial neural network consisting of directionally tuned neurons. The outcome of this simulation has reproduced the neuronal population vector (Lukashin & Georgopoulos, 1994a,b) and many of the experimental findings. This work has led to a novel hypothesis concerning how the memorized trajectories of complex movements could be stored in the synaptic connections of overlapping neural networks (Lukashin et al, 1994). In brief, there is a general-purpose network that is

involved in all movement, memorized or not, that carries no information about trajectories of specific paths of movement (e.g., circles, ellipses, scribbles, etc.), and that, if activated in isolation, would produce straight-line trajectories. There are also networks that are highly specific for a particular trajectory (e.g., clockwise circle) and that are interconnected with the general-purpose network. When a specific trajectory is to be performed, the appropriate specific network coordinates with the general-purpose network to produce the desired trajectory. Simulations demonstrate that the size of the specific network need be less than 5% of the size of the general-purpose network for the desired trajectory to be stored and reproduced (Lukashin et al, 1994). It is noteworthy that such very specific cells have, in fact, been observed at low proportions in neurophysiological recordings during the performance of memorized trajectories (Hoeherman & Wise, 1991; Ashe et al, 1993).

How specialized are these small networks of cells and how do such networks come about in the first place? As yet, we can only speculate on these issues. With respect to the general-purpose network, it is reasonable to assume that it is present at birth, since it is assumed to subserve all movement. There are several possibilities concerning the specialized networks. One is that there are a number of small-size networks, specific for basic paths of movement (e.g., straight lines, curves, and combinations thereof—"motor-shape primitives"), present at birth. Then, learning other, complex motor acts would consist of adjusting the connection strengths between the general-purpose and specific networks. This idea implies that all of the specialized networks are used routinely, although not as frequently as the general-purpose network. Another 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 required. Under these circumstances, a number of the complex, specialized networks might never be used. Such a situation would be parallel to that encountered in the immune system, in which a potential exists for making a large number of antibodies but only some are actually made, depending on the exposure of the organism to specific antigens. In both cases there is a selection—of a specialized trajectory or of an antibody—from a large ensemble available. Finally, an intermediate possibility would be that we begin with motor-path primitives, but end with more complex trajectories by combining these primitives with the general network to become very specialized and to form other trajectories in novel associations.

### **Concluding Remarks**

The topics reviewed above demonstrate the richness of neurophysiological, behavioral, and neural-network modeling studies of the direction of movement in space. They underline the heuristic value and power of the neuronal population-vector analysis in deciphering directional neuronal operations. And, a

scheme for the possible translation of motor-cortical directional commands to muscle activations via spinal interneuronal systems has been proposed (Georgopoulos, 1988, 1996) and modeled (Lukashin, Amerikian, & Georgopoulos, 1996).

The population-vector analysis provides quite a general scheme. It need not be confined to physical space but may be generalized to arbitrary spaces and dimensions. Indeed, applications have been made successfully to the coding of faces in the inferotemporal cortex of the monkey (Young & Yamane, 1992) and have been suggested for coding combinations of finger movements (Georgopoulos et al., 1993).

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