POPULATION ACTIVITY IN THE CONTROL OF MOVEMENT

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This review summarizes key observations and concepts concerning the role of neuronal populations in specification and control of the direction of movement and isometric force. Large populations of neurons in the motor cortex are engaged with reaching movements. This engagement is fairly early, starting approximately 60 msec following target onset. Single cells are directionally broadly tuned, but the neuronal population carries an unambiguous directional signal. The outcome of this population code can be visualized as a vector that points in the direction of the upcoming movement during the reaction time, during an instructed delay period, and during a memorized delay period. Moreover, when a mental transformation is required for the generation of a reaching movement in a different direction from a reference direction, the population vector provides a direct insight into the nature of the cognitive process by which the required transformation is achieved.

The problem we are investigating concerns the neural mechanisms of spatially directed motor output, including reaching movements and isometric forces exerted by the arm. For this purpose, we have trained rhesus monkeys to operate three devices to produce motor outputs in various directions in space. The first device allows movements in two-dimensional space (Fig. 1); the monkey moves an articulated manipulandum from one point to another on a planar working surface (Georgopoulos *et al.,* 1981, 1982). The second device allows reaching movements in three-dimensional space (Fig. 2); the monkey pushes buttons placed at various points in three-dimensional space (Georgopoulos *et al.,* 1986; Schwartz *et al.,* 1988). Finally, an isometric force device allows exertion of two-dimensional isometric forces on a rigid handle (Georgopoulos *et al.,* 1992). In all three paradigms, we focused on the neural coding of the direction of the motor output, be it movement or isometric force. The salient finding of these studies has been that the activity of single cells in the motor cortex is broadly tuned with respect to the direction of the motor output (Georgopoulos *et al.,* 1982, 1992; Schwartz *et al.,* 1988). In general, the intensity of cell discharge varied as a cosine function of this direction (Figs. 3 and 4). The peak of this function is the direction for which the cell activity is most intense; this is the cell's

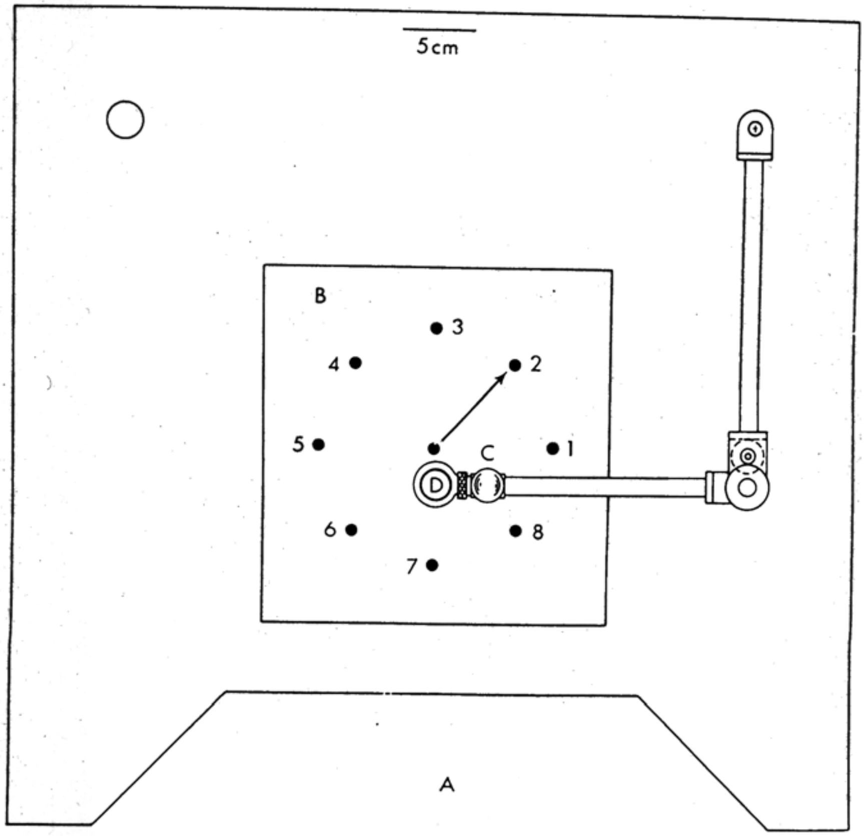


FIG. 1. Schematic drawing of the two-dimensional apparatus used to study two-dimensional movements of monkeys. The monkey sat at A, in front of the working surface, B. The numbered light-emitting diodes (LEDs) were placed on a circle of 8 cm radius. The monkey held the articulated manipulandum at its distal end (C) and captured a lighted LED within a transparent plexiglass circle (D). The arrow indicates the direction of one movement. The x–y motion of the center of that circle was monitored every 10 msec with a resolution of 0.125 mm. (Modified from Georgopoulos *et al.*, 1981; reproduced with permission.)

preferred direction. The preferred directions ranged throughout the directional continuum without any particular tendency to cluster (Fig. 5). The similarity of the directional tuning in two- and three-dimensional movements, and in two-dimensional isometric forces, provides a common background on the problem of how motor direction could be specified in a unique fashion within the neuronal population, as follows.

The broad directional tuning indicates that a given cell participates

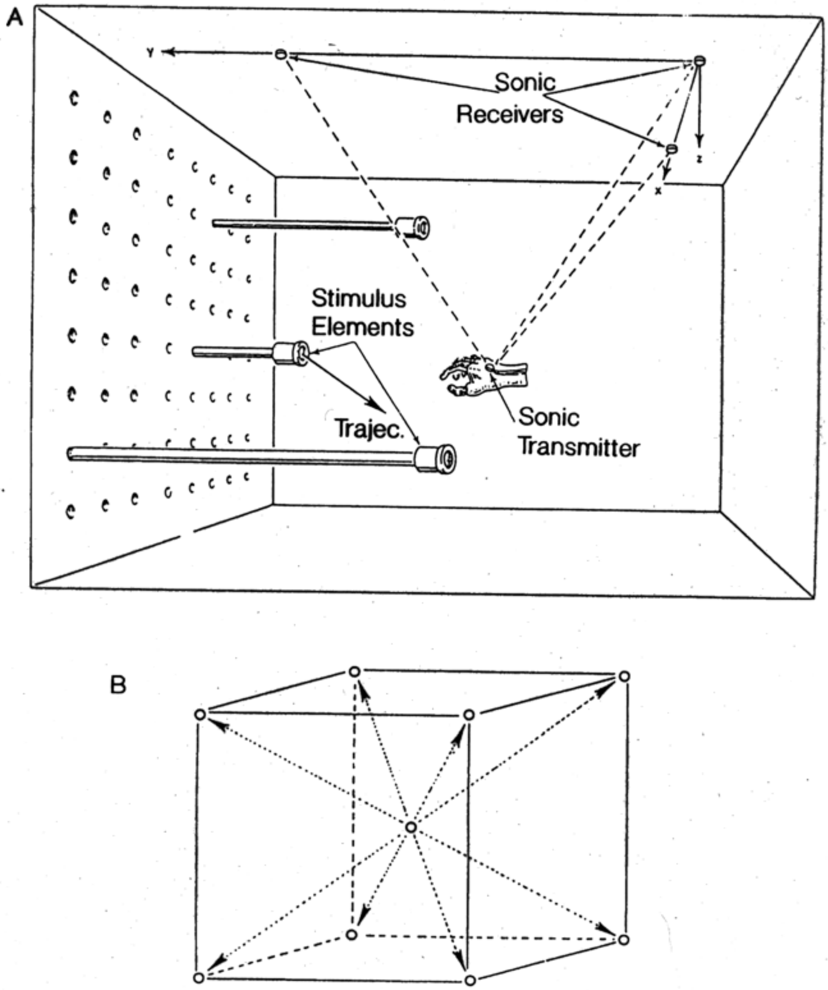


FIG. 2. Schematic drawing of the apparatus used to study free reaching movements in three-dimensional space. (A) The monkey reached toward and pushed lighted buttons mounted at the end of metal rods threaded through a heavy metal plate. The movement trajectory was monitored using an ultrasonic system. (B) Schematic diagram of the location of the nine buttons used. Dotted lines indicate directions of movements. (From Schwartz *et al.*, 1988; reproduced with permission. Copyright by Society for Neuroscience.)

in movements of various directions, and that a movement in a particular direction will involve the activation of a whole population of cells. Given that single cells are directionally tuned, we proposed a vectorial neuronal population code for the direction of reaching (Georgopoulos *et al.*, 1983, 1986, 1988, 1992): (1) a particular cell vector represents the contribution

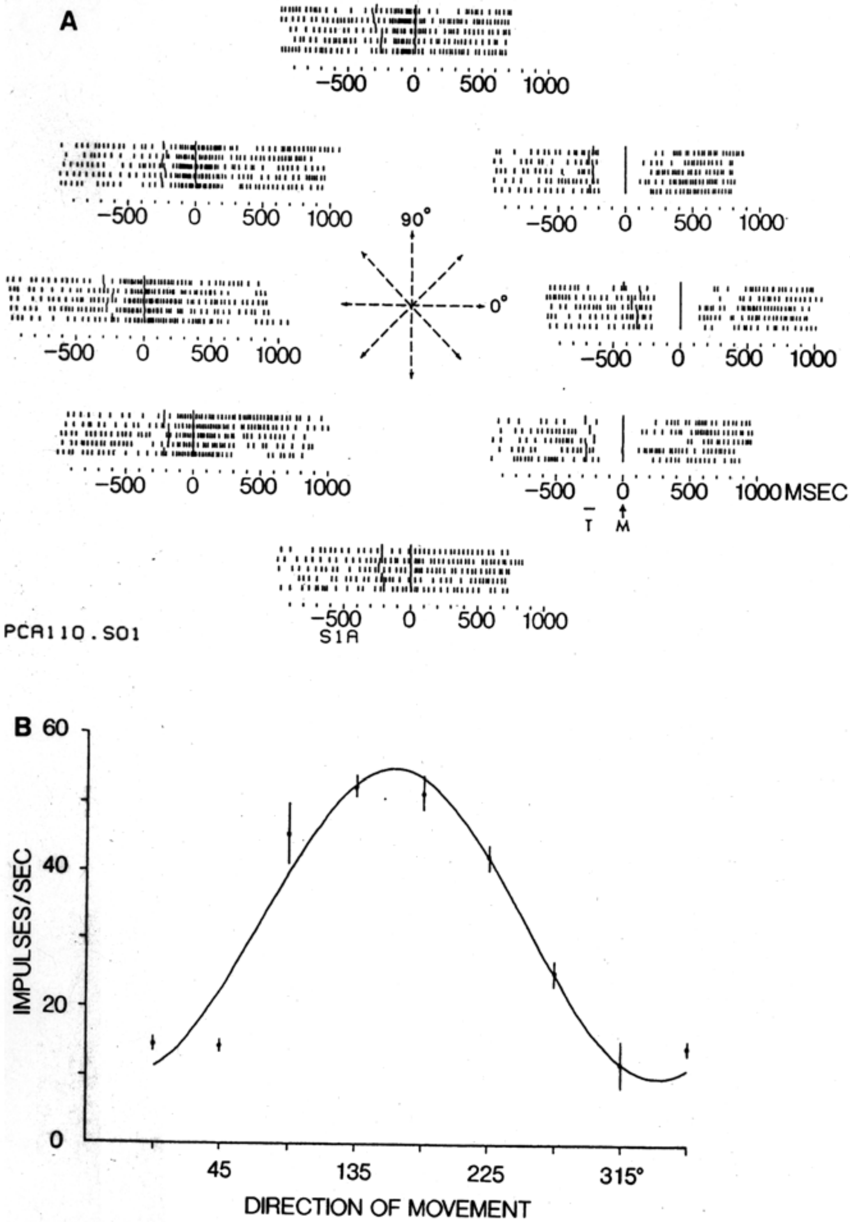


FIG. 3. Broad directional tuning in two-dimensional space of a cell recorded in the arm area of the motor cortex. (A) Impulse activity during five trials with movements in the directions indicated in the drawing at the center. Short vertical bars indicate the occurrence of an action potential. Rasters are aligned to the onset of movement (M). Longer vertical bars preceding the onset of movement indicate the onset of the target (T). (B) Average frequency of discharge (±SEM) from the onset of the stimulus until the entry to the target window are plotted against the direction 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.)

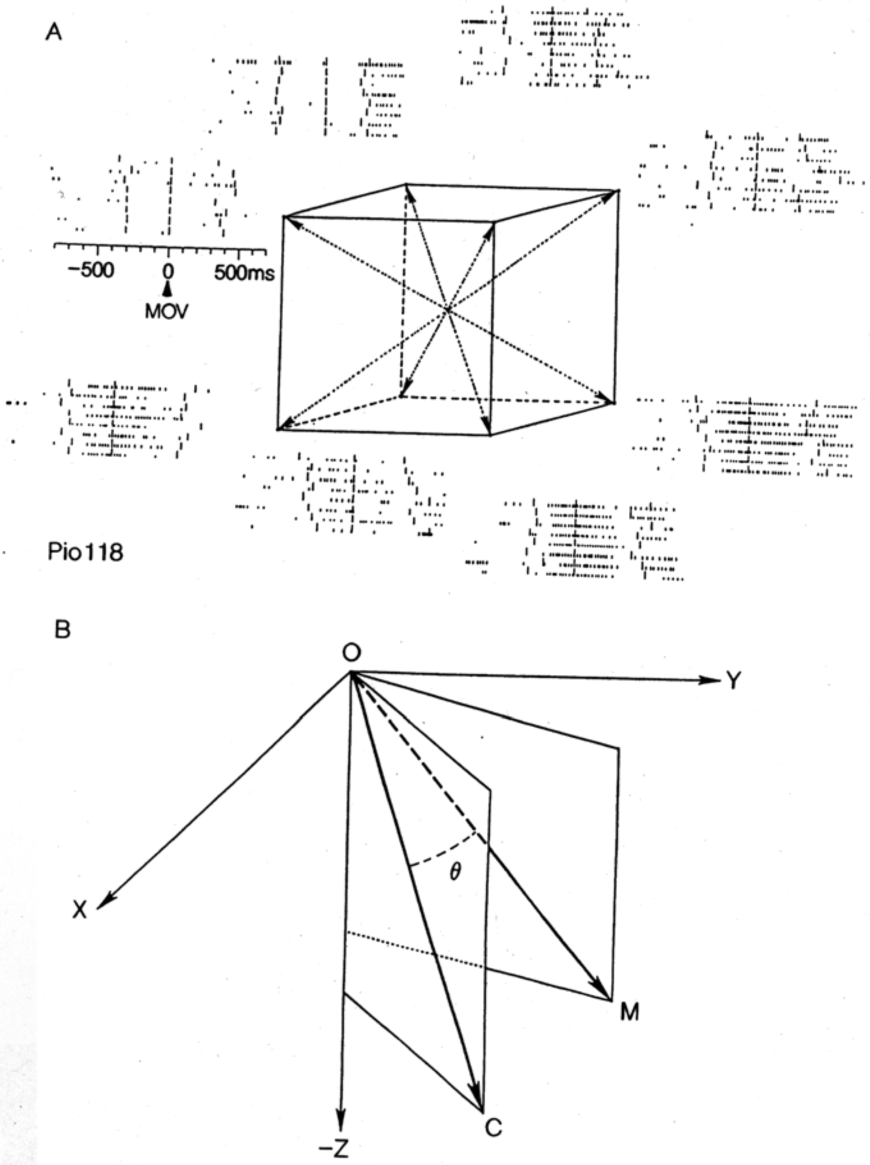


FIG. 4. Broad directional tuning in three-dimensional space of a motor cortical cell. (A) Impulse activity is shown in raster form for eight trials in eight movement directions indicated in the drawing at center. MOV, Onset of movement. (B) Principle of directional tuning: C is the preferred direction of the cell whose rasters are shown in A; M is the direction of a movement; θ is the angle between C and M. The cell activity varies in a linear fashion with $\cos(\theta)$. (Adapted from Georgopoulos *et al.*, 1986; reproduced with permission. Copyright by AAAS, 1986.)

of a directionally tuned cell and points in the cell's preferred direction; (2) cell vectors are weighted by the change in cell activity during a particular movement; and (3) the sum of these vectors (i.e., the population vector) provides the unique outcome of the ensemble coding operation. We found that the population vector points in the direction of movement for two-dimensional movements (Fig. 6; Georgopoulos *et al.,* 1983), and three-dimensional movements (Fig. 7; Georgopoulos *et al.,* 1986, 1988), and in the direction of net force for two-dimensional isometric forces (Georgopoulos *et al.,* 1992).

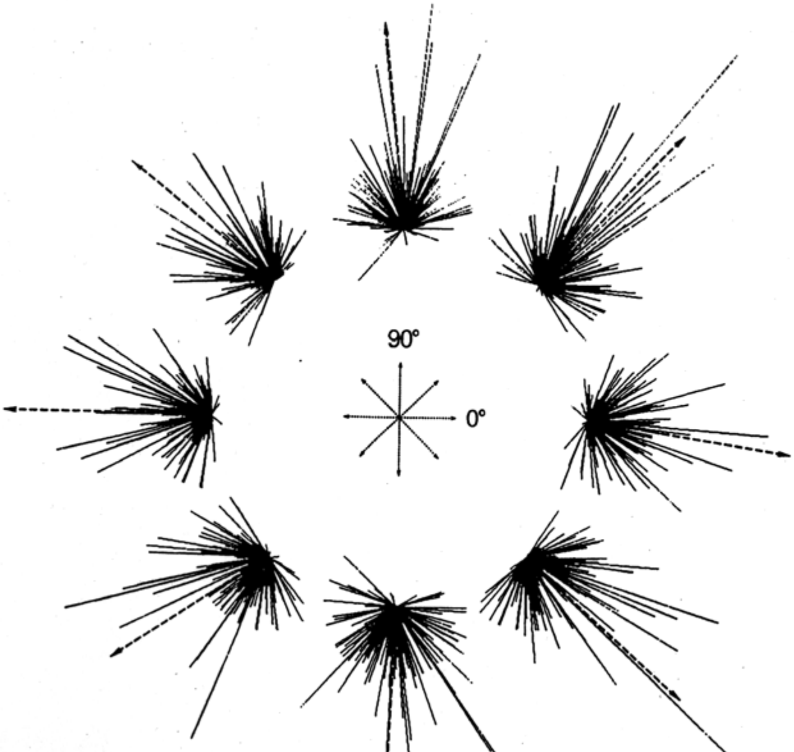


FIG. 6. Neuronal population coding of the direction of two-dimensional reaching movements. Vectorial contributions of single cells (continuous lines, $N = 241$) add to yield the population vector (interrupted line). Each cluster represents the same population; the movement directions are shown in the diagram at the center. The population vector points in or near the direction of the movement. (From Georgopoulos *et al.,* 1983; reproduced with permission.)

What do we gain and lose with this coding scheme? First, we gain a unique spatial measure. It is remarkable that we start with purely *temporal* spike trains, and through their tuning and the interpretation of this tuning in a vectorial fashion, we end up with a unique *spatial* outcome that is isomorphic in space with the direction of the movement. Second, we gain a continuous coding of directions by the same ensemble without depending on specific cells to code uniquely for specific directions. And third, this kind of coding is resistant to cell loss (Georgopoulos *et al.*, 1988). The main drawback of this coding scheme is that it is energetically inefficient, because the whole ensemble is engaged for any particular movement. We could have devised another scheme by which only a small number of cells, very specific for a particular direction, would be activated, and this would have been energetically inexpensive. Be that as it may, our code is a distributed one and involves the whole population.

The next step in our investigation was to find out whether we could get useful information *in time*, that is, whether we can use the population vector to acquire information during the reaction time about the upcoming movement direction. And indeed, this was the case (Georgopoulos *et al.*, 1984, 1988). Figure 8 illustrates two examples in which the movement was instructed to be in two different directions. We calculated the population of vector every 20 msec during the reaction time. It can be

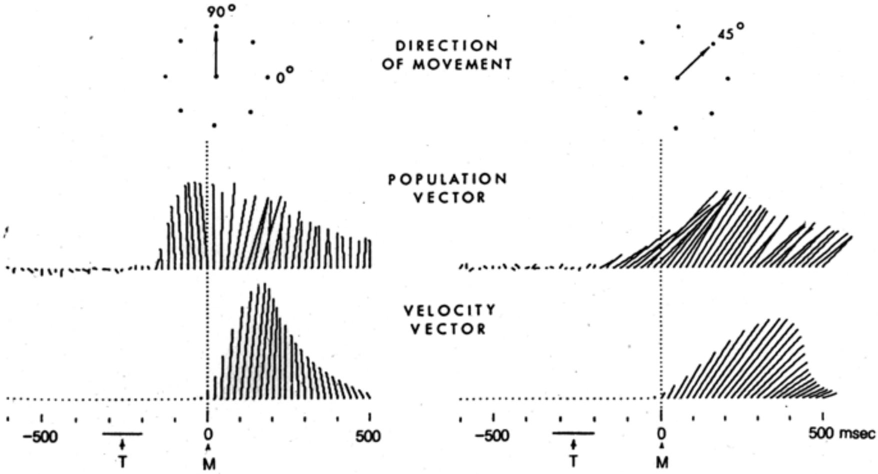


FIG. 8. Population vectors computed every 20 msec for movements in two different directions. Instantaneous velocity vectors are also shown. Notice that the population vector lengthens well before the movement begins and points in the approximate direction of the upcoming movement. M, Onset of movement; T, target. (From Georgopoulos *et al.*, 1984; reproduced with permission.)

seen that after the stimulus was given and approximately 180 msec before the onset of the movement, the population vector lengthens and points in the direction of the upcoming movement. The same also held for three-dimensional movements (Georgopoulos *et al.,* 1988) and isometric forces (Georgopoulos *et al.,* 1992).

These findings provided us with the tools for probing time-varying, directional processes involved in cognitive function. The diagram in Fig. 9 is from Edelman's book (Edelman, 1992). The connection between neuroscience and psychology is a crucial one, and it was on this connection that we focused our research during the past several years. Our strategy to attack this problem is shown in Table I. First, we have to select a cognitive process for study. Second, we need a variable on which this process will operate. Third, we need to understand the neural coding of the variable outside the process. Finally, we design an experiment and look at the neural representation of the process, having understood the coding for the variable on which the process operates.

The variable of interest in our case is the direction of the motor output, and the population vector provides the neural coding of that variable. The next question is how can we use the population vector as a *probe* to decipher brain events underlying a cognitive process. If we formulate a problem properly and devise an appropriate task, we can then record the activity of cells during a task, and use the population

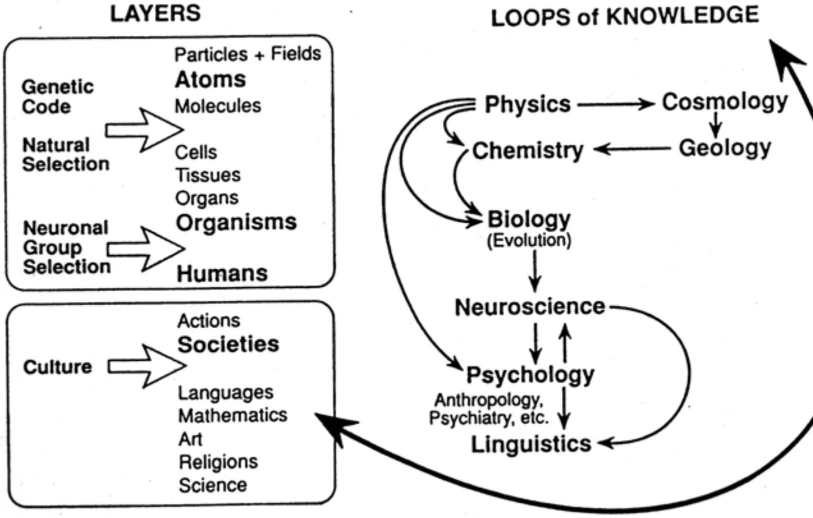


FIG. 9. Layers of biological organization and loops of knowledge. (From Figure 14-1 from "Bright Air, Brilliant Fire" by Gerald Edelman. Copyright © 1992 by Basic Books, Inc. Reprinted by permission of Basic Books, a division of Harper Collins Publishers, Inc.)

TABLE I
STEPS IN DECIPHERING BRAIN MECHANISMS OF COGNITIVE PROCESSES

1. Select a variable of interest
2. Find the neural coding of the variable outside the cognitive process
3. Select a cognitive process operating on the variable of interest
4. Record brain activity during cognitive processing and infer how the variable is operated on

vector as a probe to elucidate how the motor cortex deals with a cognitive directional process.

As a first step in that direction, we investigated the changes in cell activity in the motor cortex during two delay tasks that involved either an instructed delay, during which the target was continuously present, or a memorized delay, during which information about the direction of movement had to be kept in mind before a go signal was given. In the latter task, the target light was presented for 300 msec and was turned off, and, after a memorized delay, the *go* signal was given for the monkey to move its arm in the direction of the target that disappeared (Smyrnis *et al.,* 1992). Making the correct movement depended on keeping in mind the position of that target. In contrast, in the nonmemorized delay task, the target came on and stayed on until the *go* signal was given. During this delay period there was information available all the time about the direction of the upcoming movement.

Tanji and Evarts (1976) had shown previously that motor cortical cells can be activated during imposed delays, in the absence of an immediate motor output. We confirmed that approximately one-half of the cells in the motor cortex changed activity during the delay periods in our tasks (Georgopoulos *et al.,* 1989; Smyrnis *et al.,* 1992). However, the simple knowledge that cells change activity during a task does not provide the crucial information concerning the *content* of the process in which a cell participates. We gained valuable insight in this problem by the population vector analysis. The population vector during the nonmemorized (Georgopoulos *et al.,* 1989) or the memorized (Fig. 10; Smyrnis *et al.,* 1992) delay period pointed in the direction of the upcoming movement. Therefore, the directional information carried by the population vector in these tasks identified the content of the process in a direct fashion.

Another interesting point concerns the strength of the signal. Figure 11 plots the length of the population vector over time in the memorized and nonmemorized delay tasks. There are two phases in this time course. First, the population vector increases shortly after the cue onset, and

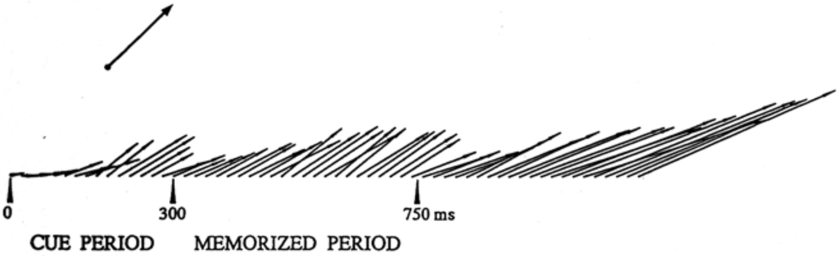


FIG. 10. Population vectors in the memorized delay task for the direction indicated are plotted every 20 msec. The arrow on top indicates the direction of the cue signal present during the first 300 msec of the delay period. (From Smyrnis *et al.*, 1992; reproduced with permission.)

then decreases at the end of the cue period. This phase is almost the same in both tasks. However, during the memorized delay period, there is a sustained, longer population vector in the memorized compared to the nonmemorized delay task (Fig. 11; stippled area). It is intriguing that there is a stronger signal in the absence of the target stimulus, which may reflect the higher demand for keeping information in mind. This brings us to a peculiar hypothesis about the motor cortex; namely, that this structure may be more active when there is lack of external information and the information has to be constructed from memory, rather than when everything is given for a particular movement.

We now move to the third and central part of this psychology–neuro-

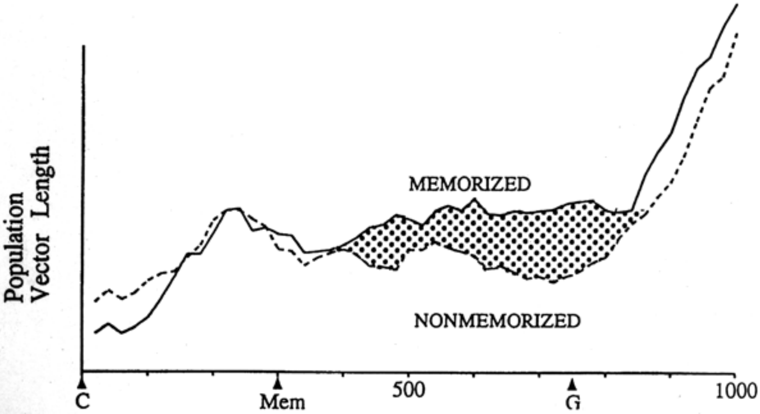


FIG. 11. Length of mean resultant of the population vector is plotted against time for the two delay tasks. C, Cue onset; G, minimum time of onset of the *go* signal. (From Smyrnis *et al.*, 1992; reproduced with permission.)

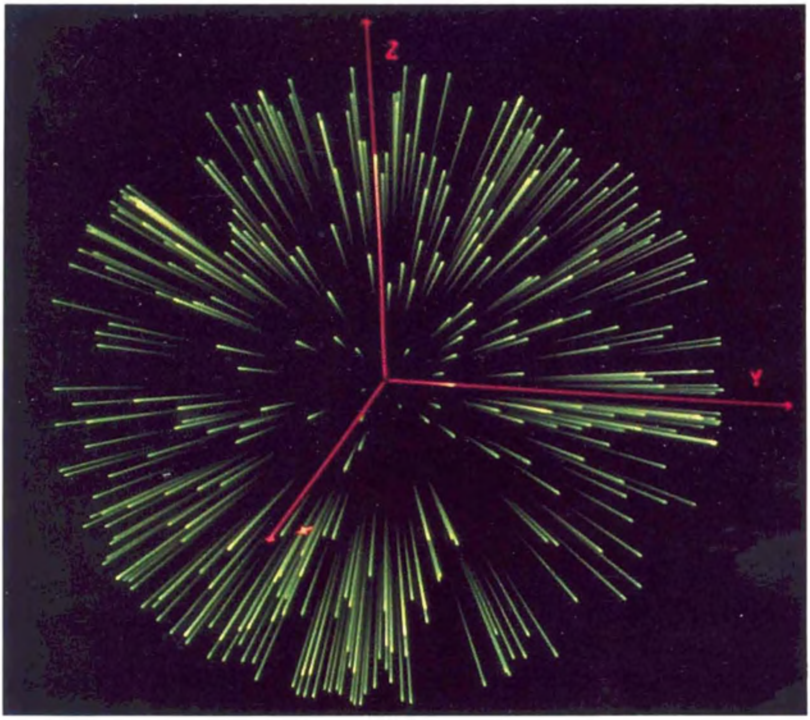


FIG. 5. Preferred directions of 475 directionally tuned cells recorded during a three-dimensional reaching task. Lines are vectors of unit length. (From Schwartz et al., 1988; reproduced with permission. Copyright by the Society for Neuroscience.)

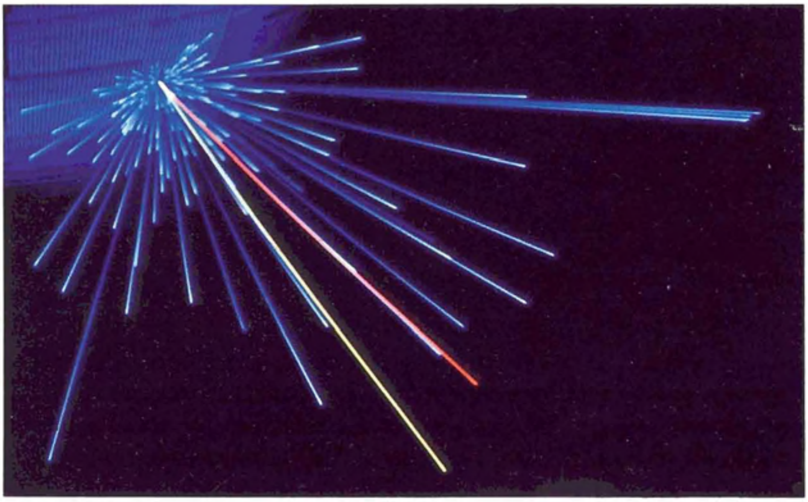


FIG. 7. Neuronal population coding of the direction of three-dimensional reaching movements. Vectorial contributions of single cells (light blue lines) add to the yield of the population vector (orange), the direction of which is close to the direction of the movement (yellow). (From Georgopoulos et al., 1988; reproduced with permission. Copyright by the Society for Neuroscience.)

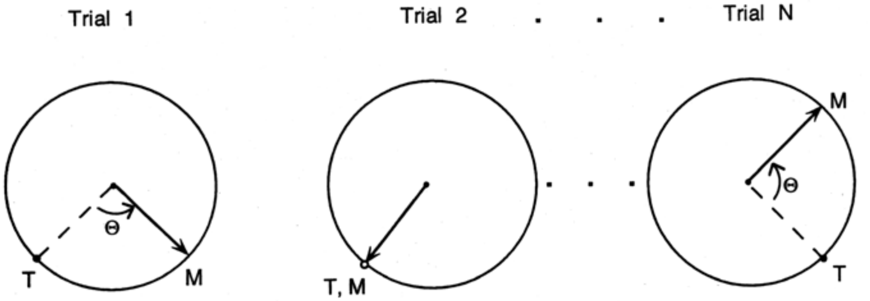


FIG. 12. Schematic directional transformation experiment. Three typical trials are shown. T, Stimulus; M, movement. Open and filled circles indicate trials of direct and transformation tasks, respectively.

science interplay. We first studied human subjects, to learn how they perform and solve a particular problem. From the results of these studies we formulated hypotheses about the psychological process(es) underlying the solution of the problem. Then, we trained monkeys to solve the same

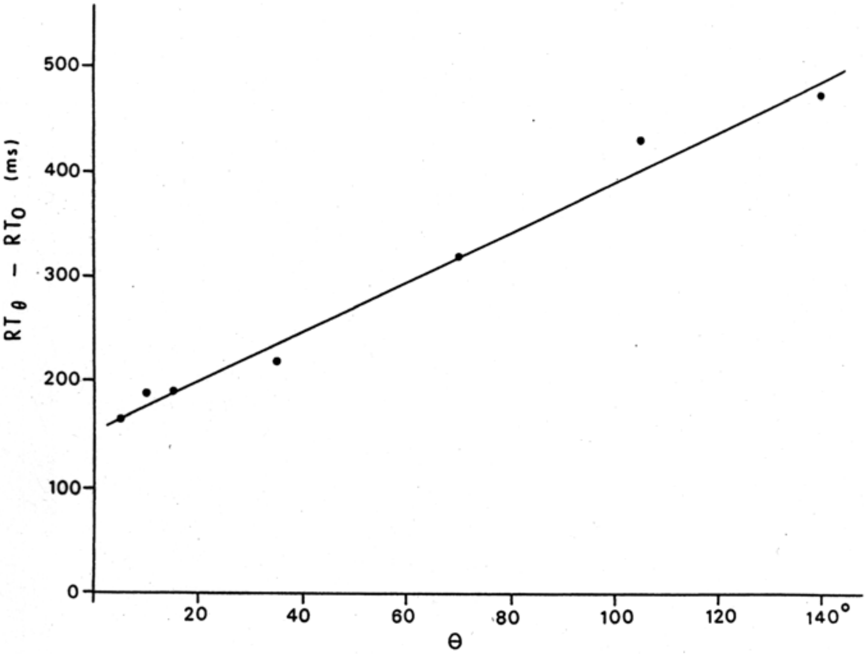


FIG. 13. Increase of reaction time with instructed transformation angle (see text). (From Georgopoulos and Massey, 1987; reproduced with permission.)

problem and recorded the activity of cells in the motor cortex, trying to interpret the results of the psychological experiments on the basis of the results of the neurophysiological studies.

The problem we studied is illustrated in Fig. 12. Subjects were trained to start from the center of the plane in the two-dimensional device. But when the target shifted to a peripheral location, the light would be either dim or bright. The brightness level gave the subject the clue to either move the handle in the direction of the light (*direct* task) or away from the light at an instructed angle, clockwise or counterclockwise (*transformation* task). These trials were randomized in terms of the stimulus position and the condition of brightness. This task is quite difficult. The problem can be solved in different ways (Georgopoulos and Massey, 1987), which makes the studies interesting. For example, subjects can form a lookup table in their mind to associate specific stimuli with specific movements, given the particular instructions: they look at their table to determine which is which. But for any given trial, and however the subjects solve the problem, they have to derive the direction of their movements on the basis of the stimulus direction. The basic finding from the human studies is shown in Fig. 13: it takes more time to generate movements when the subject is instructed to move away from the target for a given angle, and the increasing reaction time is a linear function of the angle that the subject is instructed to move away from the stimulus direction.

This finding cannot be explained by the above hypothesis involving a lookup table, because in that case we would have to suppose that it takes more time to search for one angle than for another; and there is no *a priori* reason for that supposition. We might expect longer reaction times but not a dependence of the increase of the reaction time on the angle. The most parsimonious explanation for these findings is shown

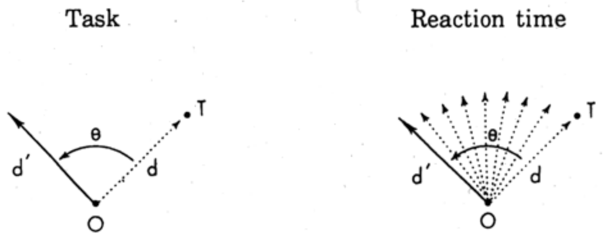
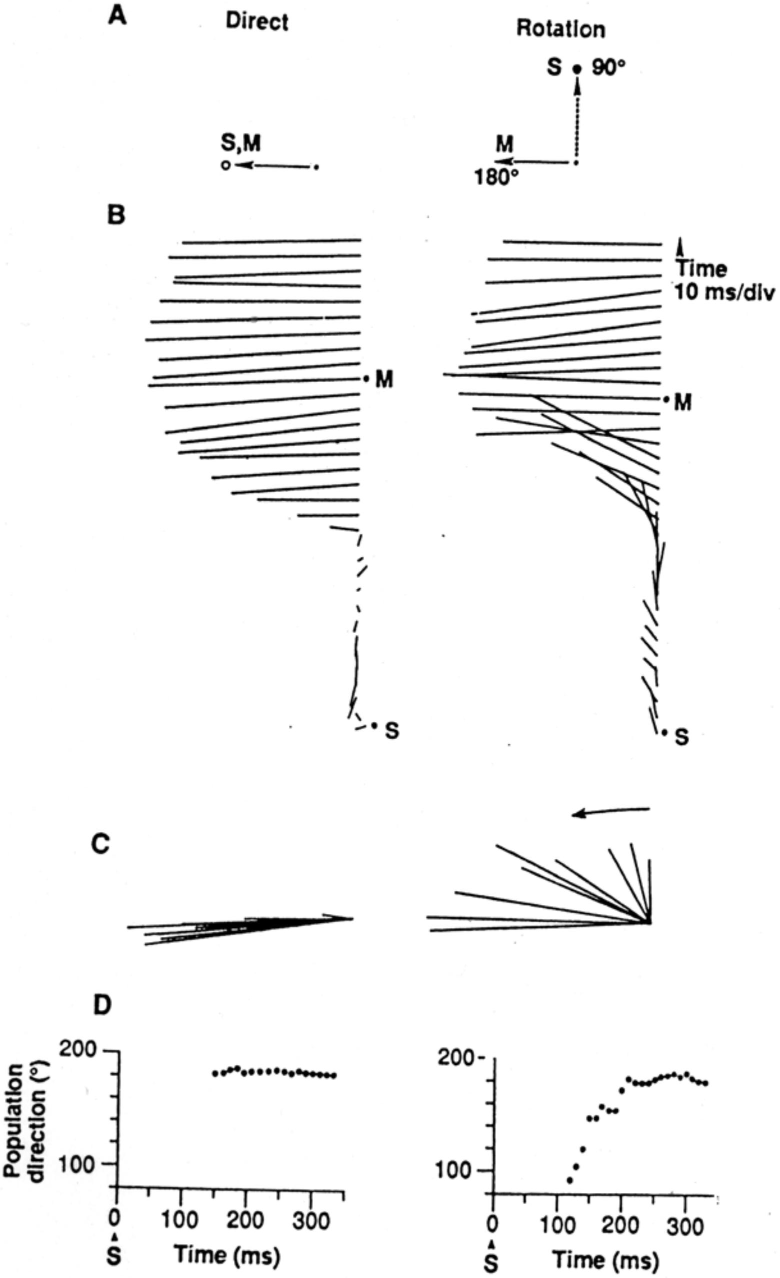


FIG. 14. O, Movement origin; T, stimulus location; d, stimulus direction; d′, movement direction; θ, transformation angle. Dotted lines indicate hypothesized rotation of imagined movement direction.

in Fig. 14. If the task is to move away from a stimulus direction at a given angle, then our results would be explained by the idea that the subject rotates a representation of the motor intention from the stimulus direction toward the movement direction. If the instruction is for a short angle, then the process would take less time. However, more time would be needed for a larger angle because the subject has to go through the intermediate directions. This idea is very similar to the mental rotation hypothesis advanced by Shepard and Cooper (1982) to explain the monotonic increase of the reaction time with orientation angle, when a judgment has to be made whether a visual image is normal or mirror image. In both cases a mental rotation is postulated. We thought that we could identify the neural representation of the motor intention by the population vector, and we were curious to see if the population vector would rotate in this task. The null hypothesis was that the motor cortex is involved only in the generation of movement and therefore the population vector would just point in the direction of the upcoming movement.

To our surprise, we found that the population vector rotated over time. In these experiments, the animals were trained to move, in the transformation trials, at 90° counterclockwise from the stimulus direction. An example is shown in Fig. 15. The movement was the same as for the above experiment, but was made in the direct task (left panel) or the transformation task (right panel). In the latter, the movement had to be 90° counterclockwise from the stimulus direction. It can be seen that in the direct task the population vector points in the direction of the upcoming movement, whereas in the transformation task it rotates counterclockwise from the stimulus direction to the movement direction. An interesting question is whether one would see a moving wave across the cortex during the rotation period. We believe that we would not, because the cells are distributed within the arm area of the motor cortex and the cells' latencies are very similar within that area. Therefore we would not expect to see a spatial movement of the population but we cannot test this idea at the moment.

It could be argued that the population vector rotation does not necessarily imply a rotation per se. For example, there could be two subsets of neurons, one pointing in the stimulus direction and the other in the movement direction. If their intensity changes accordingly, their vector sum would seem to be rotating without a "true" rotation, that is, without involving cells with a preferred direction intermediate between the stimulus and movement directions. This idea is a strong prediction of a "true rotation," namely, during the reaction time, there is a preferential recruit-


A
Direct
Rotation
S 90°
S,M
M
180°
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Time
10 ms/div
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S
M
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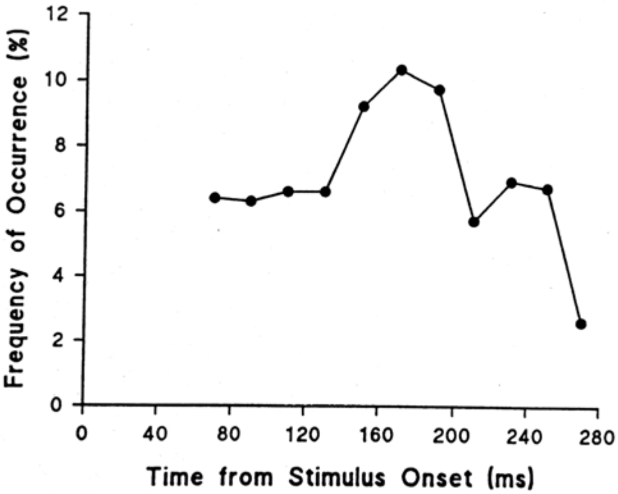

FIG. 16. Percentage of cells recruited at times indicated with preferred directions at or near the intermediate direction. Data points are centered on the middle of 20-msec bins. See text for explanation. (N = 94, 119, 150, 91, 185, 203, 104, 122, 71, 90, and 78 for the 20-msec time bins used, from 60–80 to 260–280 msec.) (From Lurito *et al.*, 1991; reproduced with permission.)

ment of cells with preferred directions intermediate between those of the stimulus and those of the movement. Figure 16 shows that cells of preferred directions within 20° in the intermediate direction (between

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FIG. 15. Results from direct and rotation movements. (A) Task. Open and filled circles indicate dim and bright light, respectively. Interrupted and continuous lines with arrowheads indicate stimulus (S) and movement (M) direction, respectively. (B) Neuronal population vectors calculated every 10 msec 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 (left) it points in the direction of the movement, whereas for the rotation case (right) it points initially in the direction of the stimulus and then rotates counterclockwise (from 12 o'clock to 9 o'clock) 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 panel). (D) Scatter plots 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 (left), the direction of the population vector is in the direction of the movement (~180°); for the rotation case (right) the direction of the population vector rotates counterclockwise from the direction of the stimulus (~90°) to the direction of the movement (~180°). (From Georgopoulos *et al.*, 1989; reproduced with permission. Copyright by AAAS, 1989.)

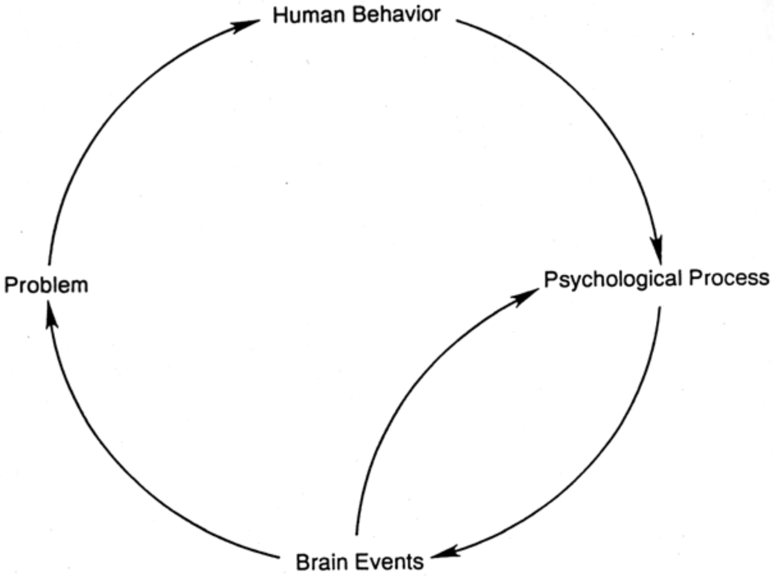

FIG. 17. Cognitive neuroscience conceptual loop. Links between studies probing the relation between psychology and neuroscience.

stimulus and movement) were preferentially engaged during the middle of the reaction time, as predicted by the rotation hypothesis. Therefore, we are dealing with a dynamic cognitive process evolving in time (Freyd, 1987). Interestingly, the mean rotation rate (about 400°/second (Lurito *et al.*, 1991) and the range of rates observed for different stimulus directions were very similar to those obtained in the human studies.

And these studies, in a way, close the circle (Fig. 17). We started with the problem of spatial transformation, and obtained the linear increase of the reaction time with the angle. On the basis of these findings, we hypothesized the rotation of an internal representation of the directional motor intention and then, with the same task, we directly visualized the hypothesized rotation in the rotation of the population vector. And so we closed the loop in the circle.

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