with the usual *F* test for the difference between two linear models. This study would require large samples with broad ranges of ability for the statistical test to have sufficient statistical power. Using .02, the usual increment to *g* found in our studies, and specifying $p < .05$, the minimum sample required to detect the .02 increment with 80% power is about 320. Only when studies such as this are done can we know the relationships among tacit knowledge, *g*, and job performance.

It should also be remembered that g has been studied for many decades, and its correlations with many other human characteristics are well documented. For example, Brand, whose quotation provides the title for this article, documents more than three dozen correlates of *g*, including creativity, achievement motivation, health and fitness variables, leadership, and social skills. Insofar as these variables are correlated with g, selection on one yields selection on the others *per force*. Put another way, when you select on *g*, you also select on creativity, achievement motivation, health and fitness, leadership, and social skills.

McClelland (this issue) suggests that social class is responsible for much prediction of job performance but stops short of calling for using social class in personnel selection. No doubt *g* and social class are related, but restricted samples and their attendant estimation bias again distort the true predictiveness of *g*. Brand[6] provides an insightful discussion of the fallacy of partialing out variables highly related to g and interpreting the predictiveness of only the remaining *g* variance. Further, McClelland picks one study with low values as an example of the average magnitude of the validity of g and avoids meta-analytic studies with large numbers of validation correlations, which average much higher.[7]

Calfee (this issue) interjects several topics that are irrelevant to the research findings on the prediction of job performance. Although the origin of intelligence testing, teaspoons and gallons of smarts, tracking in schools, and anecdotes about Colorado River boat trips may be important, they do not address the root issue. Further, he suggests that the generality of the measurement of intelligence should not be trusted, but presents no evidence contrary to the findings presented in our original article. In fact, Ceci, whom Calfee cites, noted that intelligence has "ubiquitous significance as a predictor of real-world academic, social, and occupational accomplishments."[8]

Notes

1. Title taken from C. Brand, The importance of general intelligence, in *Arthur Jensen: Consensus and Controversy*, S. Modgil and C. Modgil, Eds. (Falmer Press, New York, 1987).
2. M.J. Ree and J.A. Earles, Intelligence is the best predictor of job performance, *Current Directions in Psychological Science, 1*, 86–89 (1992).
3. R.K. Wagner and R.J. Sternberg, Practical intelligence in real-world pursuits: The role of tacit knowledge, *Journal of Personality and Social Psychology, 49*, 436–458 (1985). See also R.K. Wagner, Tacit knowledge in everyday intelligent behavior, *Journal of Personality and Social Psychology, 52*, 1236–1247 (1987). These two articles and the test manual (see note 5) provide the supporting evidence for the efficacy of tacit knowledge and are the basis for Wagner and Sternberg's claims about intelligence and tacit knowledge.
4. J.E. Hunter, Cognitive ability, cognitive aptitudes, job knowledge, and job performance, *Journal of Vocational Behavior, 29*, 340–362 (1986). See also J.J. McHenry, L.M. Hough, J.L. Toquam, M.A. Hanson, and S. Ashworth, Project A validity results: The relationship between predictor and criterion domains, *Personnel Psychology, 43*, 335–354 (1990).
5. R.K. Wagner and R.J. Sternberg, *TKIM The Common Sense Manager, Tacit Knowledge Inventory for Managers, Users Manual* (Psychological Corp., San Antonio, TX, 1991).
6. See note 1.
7. See Hunter, note 4, for a review including supervisory ratings.
8. S.J. Ceci, How much does schooling influence general intelligence and its cognitive components? A reassessment of the evidence, *Developmental Psychology, 27*, 703 (1991).

Mental Rotation of the Intended Direction of Movement

Giuseppe Pellizzer and Apostolos P. Georgopoulos

Giuseppe Pellizzer is Assistant Professor at the Department of Physiology of the University of Minnesota Medical School. **Apostolos P. Georgopoulos** is Director of the Brain Sciences Center of the Veterans Affairs Medical Center, Minneapolis, MN, and Professor of Physiology and Neurology at the University of Minnesota Medical School. Address correspondence to Apostolos P. Georgopoulos, Brain Sciences Center, Veterans Affairs Medical Center, One Veterans Dr., Minneapolis, MN 55417; e-mail: georgo@georgo.mve.hscs.umn.edu.

In the three-dimensional (3-D) world, a person continuously experiences spatial transformation of the objects and of the global frame of reference (e.g., horizon, mountains) that surround him or her. For example, when driving a car, a person's perspective view of everything that forms the outside environment (buildings, trees, cars, etc.) changes progressively. In a smaller scale, handling an object changes its perspective view in relation to the manipulations. Because people continuously face these spatial transformations, it is adaptively relevant to be able to anticipate their effects. For example, the "sudden insight" (described in apes and infants[1]) to use a nearby stick to catch

Published by Cambridge University Press

a desired object or a fruit, or any problem solving involving detours or use of tools, typically requires mental spatial operations before the action. These past 20 years, a renewed interest in mental operations, and particularly in mental spatial operations, was generated by studies measuring response times.[2] Among the latter, we focus on the so-called mental rotation studies.

STUDIES OF MENTAL ROTATION

In 1971, Shepard and Metzler[3] first reported that the time it takes for subjects to judge whether two 2-D perspective drawings represent the same 3-D object or two mirror-image objects increases as a linear function of the angle between the two portrayed orientations. This finding suggested that the subjects mentally rotate the image of one object into congruence with the other to make their decision. A different set of studies was carried out using asymmetric 2-D figures, like letters, numbers, or random shapes; subjects had to decide whether the stimulus presented was normal or mirror-image.[4] Again it was found that the reaction time (RT) was a monotonic increasing function of the angle between the stimulus orientation and the standard upright position for letters and numbers and between the stimulus orientation and the previously learned orientation for random shapes.

Although the mental rotation phenomenon is usually considered as confined to perceptuallike processes, it extends to motor processes as well, and particularly to representations of the intended direction of movement. In a recent experiment,[5] human subjects were asked to make an arm movement on a plane at a specified angle away from the direction of a visual stimulus. The main finding was that RT increased as a linear function of the angle (see Fig. 1). This result is similar to that described for mental rotation of visual images and is compatible with the idea that the subjects mentally rotate their intended direction of movement from the direction of the visual stimulus toward the final direction of movement.

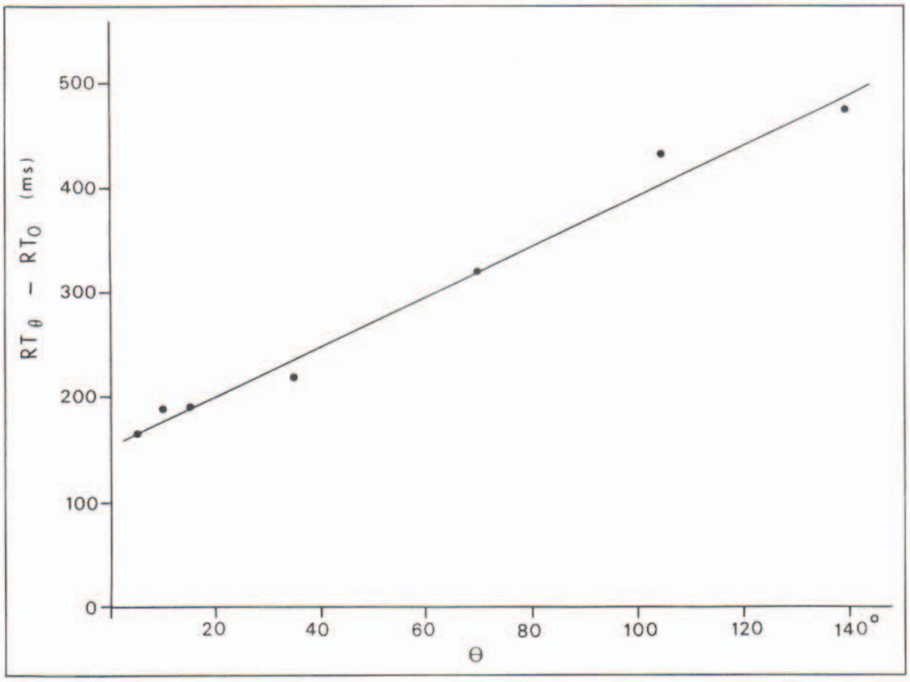

Fig. 1. Results of a study in which subjects were asked to make an arm movement at a specified angle (Θ) away from the direction of a visual stimulus. Each point plots the median difference between the RT for the movement at angle Θ (RT_Θ) and the RT for the movement in the direction of the stimulus (R_0). From Georgopoulos and Massey.[5] Reproduced with permission.

Shepard and colleagues[4] suggested that the process of mental rotation has analog properties in which the ongoing mental transformation has a one-to-one correspondence with the intermediate stages of the external rotation of an object. In other words, the analog hypothesis makes the assumption that there is some physiological variable in the brain that represents the orientation of the imagined object (or the intended movement) and that this variable undergoes a continuous transformation during the mental rotation, passing through values that represent intermediate directions. This point of view was challenged, though, producing the so-called analog-propositional controversy of mental imagery.[6] For example, this mental transformation could be implemented by the application of formal rules on symbolic representations.

Recent experiments[7] with monkeys have provided direct evidence of a mental operation that has analog characteristics. These experiments have shown that a representation in the brain of the intended direction of movement is continuously transformed during the RT when a movement has to be made at an angle from the stimulus direction. However, to understand the results of these experiments, it is necessary to understand how neural activity in the brain can be meaningfully related to the intended direction of movement.

NEURAL CODING OF DIRECTION OF MOVEMENT

Several studies in awake monkeys have been devoted to the relation between direction of movement and single-cell discharge in the motor cortex.[8] Typically, neuronal activity is recorded while monkeys perform a task that requires them to move the hand from a starting position in the direction of a visual target. The direction of the movement is varied by varying the direction of the target. The results show a significant change of activity of cells in the motor cortex in relation to the direction of movement before the initiation of the movement and during the movement itself. How much a cell is active depends on the cell and on the direction of the movement. A cell's activity is broadly tuned with respect to the direction of movement; that is, a cell's activity is most intense for movement in a particular direction (the cell's *preferred direction*) and decreases progressively for movements made farther away from this direction (see Fig. 2). The preferred directions differ from cell to cell and are distributed in the whole 3-D directional continuum. These results indicate that a given cell fires during movements in various directions; conversely, movement in a particular direction is accompanied by the firing of a large population of cells.

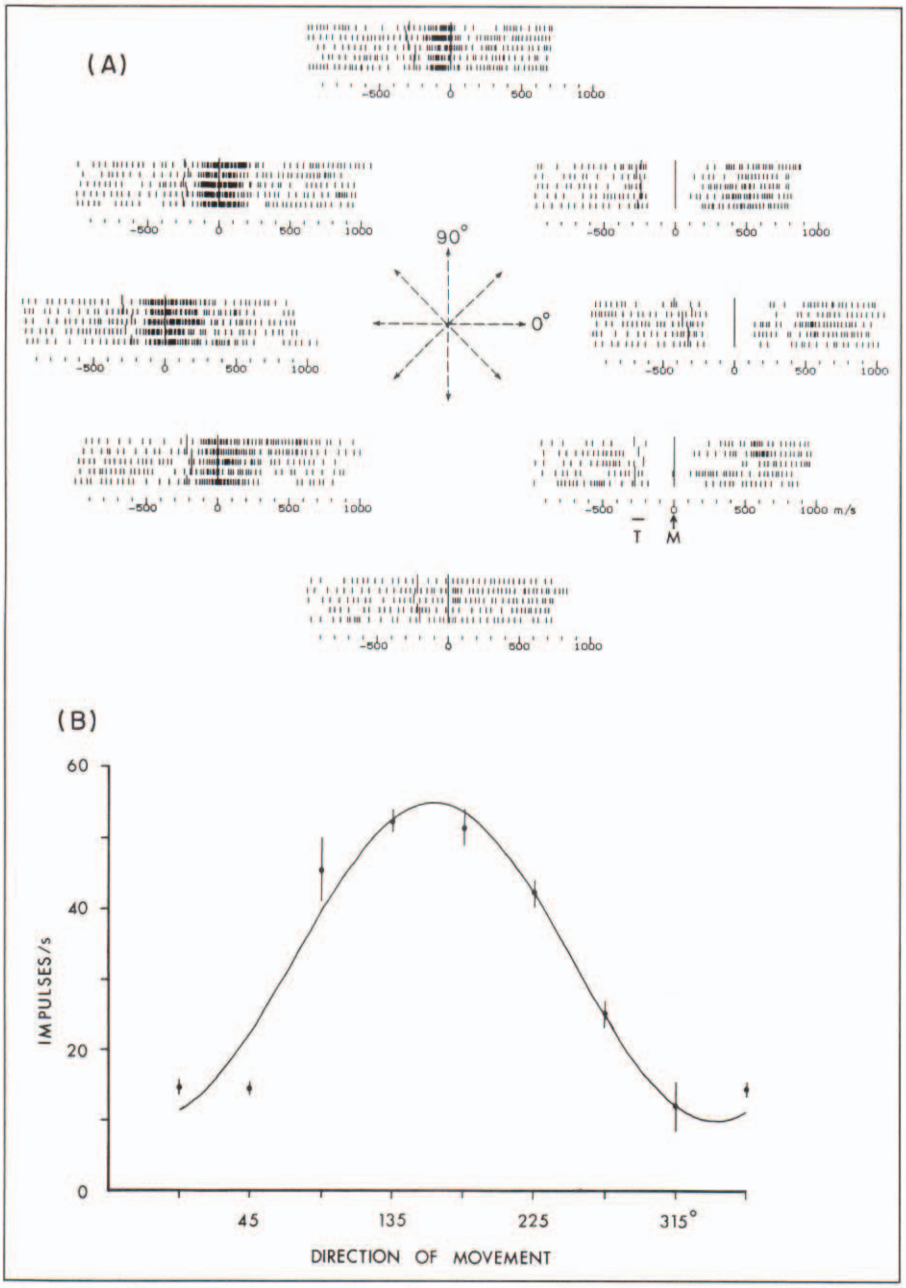

Fig. 2. Broad directional tuning of a cell in the arm area of the motor cortex. (a) Impulse activity (firing) during movements in the planar (2-D) directions indicated by the drawing at the center (five trials per movement direction). The short vertical marks in each record indicate action potentials. The five records for a given direction are aligned to the onset of the movement (M). The slightly longer vertical mark in each record indicates the onset of the target (T) specifying the required direction of movement. Note vigorous firing during movements in the 135° direction and the absence of firing during movements in the opposite direction (315°). (b) Tuning curve derived from the above data. Average firing frequency over the interval from the appearance of the target until the hand entered the target window is plotted against direction of movement. From Georgopoulos, Kalaska, Caminiti, and Massey.[8] Reproduced with permission.

How, then, is the direction of movement represented in a unique fashion in a population of neurons each of which is directionally broadly tuned? One hypothesis is that the motor cortical command for a given direction of reaching can be regarded as an ensemble of vectors.[9] Each vector represents the contribution of a directionally tuned cell. A particular vector points in the cell's preferred direction and has length proportional to the change in cell activity associated with the given direction of movement. The vector sum of these weighted cell vectors (the *neuronal population vector*) points at or near the direction of the movement (see Fig. 3). Therefore, information concerning the direction of movement can be obtained unambiguously from the neuronal ensemble. The neuronal population vector hypothesis provides the tool by which to monitor the processing of directional information in time, that is, when the movement is *intended*.

There are several aspects of intending a movement. The common-

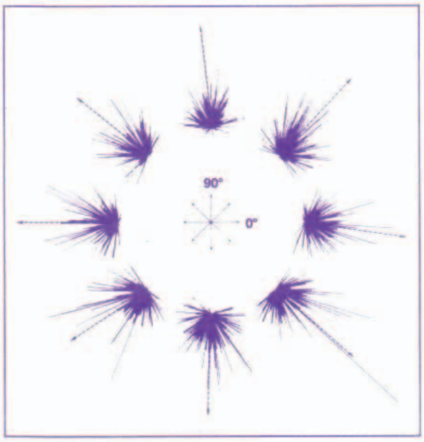

Fig. 3. Neuronal population vectors (thick dashed lines with arrows) calculated for movements in the directions indicated in the drawing at the center. All clusters are formed by the same neuronal population (N = 241 cells). Each cell's vectorial contribution is represented by a thin line along the axis of its preferred direction. The length of the thin line is proportional to the change in the cell's activity from its average activity observed during the eight movement directions. Notice the spatial congruence between the direction of the neuronal population vector and the direction of the movement. From Georgopoulos, Caminiti, Kalaska, and Massey.[9] Reproduced with permission.

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

In all three cases, the representation of information about the intended movement can be studied under different conditions that impose different processing constraints. It would be interesting to know whether this representation could be identified and visualized during the RT, the instructed delay, and the memorized delay periods. Because the information assumed to be represented is about direction, the neuronal population vector could be a useful tool by which to identify this representation. Computing the population vector every 20 ms during these three periods produced clear results: In all these cases, the population vector pointed in the direction of the intended movement.[10] These findings underscore the usefulness of population vector analysis as a tool for visualizing representations of the intended movement and show that in the presence or absence of an immediate motor output, as well as when the directional information has to be kept in memory, the direction of the intended movement is represented in a dynamic form at the ensemble level.

NEURAL ACTIVITY DURING A MENTAL TRANSFORMATION OF THE INTENDED DIRECTION OF MOVEMENT

Knowing how to relate neural activity to the intended direction of movement allows studying conditions in which a mental operation, such as mental rotation, must be performed before the movement is produced. In experiments of this kind,[7] monkeys were trained to move a handle on a 2-D working surface either toward a visual stimulus (*direct task*) or 90° counterclockwise from the stimulus (*transformation task*), depending on whether the stimulus appeared dim or bright, respectively. The cell activity in the arm area of the motor cortex (contralateral to the performing arm) was recorded extracellularly. The neural activity was analyzed at the single-cell and neuronal population levels.

The changes in the activity of single cells after the visual stimulus was presented in the direct task were as described previously.[8] The activities of these cells also changed in the transformation task. There were no cells whose activity changed only in the transformation task, from which we infer that the representation of direction of movement during the transformation task does not involve a separate neuronal population at the level of the motor cortex. (The population of recorded cells is not, and cannot be, exhaustive, but we believe that it is representative.) An analysis of the population vector as a function of the time since target onset revealed an orderly rotation of the population vector from the direction of the target counterclockwise through 90° to the direction of the movement[7] (Fig. 4). Interestingly, the rates of rotation of the population vector (about 400 °/s) were in the range of the rates of mental rotation obtained in human subjects.[5]

There are several surprising points in these results. First, there was no a priori reason to expect that the population vector would point to any direction other than the direction of the movement, on the simple hypothesis that the motor cortex is involved only in the production of movement. The interpretation of the population vector as showing the direction of motor intention suggests that in the transformation task, the motor intention is not restricted to the direction of movement but occupies intermediate directions during the RT. Second, there was no a priori reason to expect that the population vector would shift in an orderly fashion in the counterclockwise direction, for no explicit instruction was given to the animals to that effect. The results obtained suggest that the population vector spanned the smallest angle. This strategy could, presumably, minimize the time and computational load involved in the transformation required.

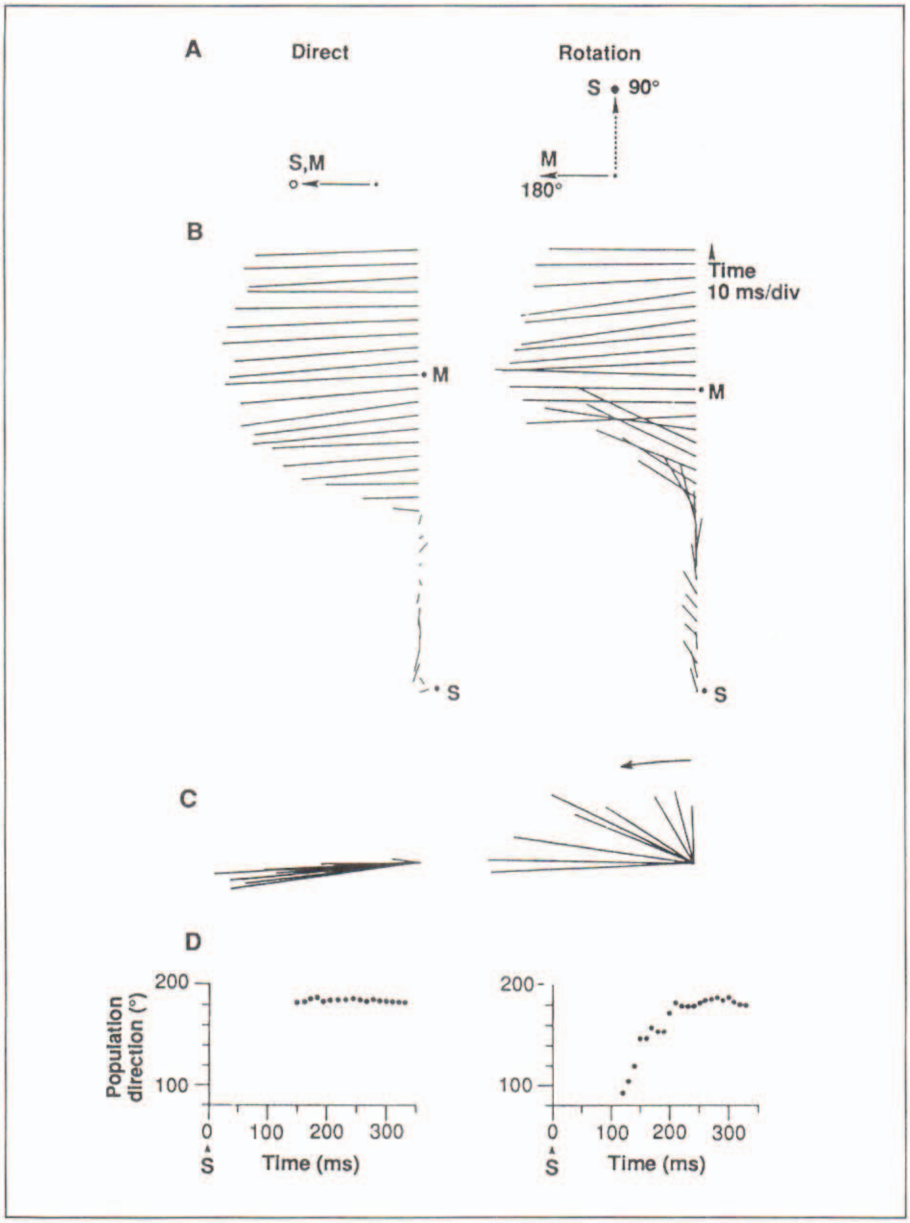

Fig. 4. Results from direct (left panel) and transformation (right panel) tasks. (a) Task. Unfilled and filled circles indicate dim and bright stimulus, respectively. Interrupted and continuous lines with arrows indicate the stimulus (S) and movement (M) directions, respectively. (b) Neuronal population vectors calculated every 10 ms from the onset of the stimulus (S) at the positions shown in (a) until after the onset of the movement (M). For the direct task, when the population vector lengthens, it points in the direction of the movement; in contrast, for the transformation task, when the population vector lengthens, 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 with the first population vector that increased significantly in length. Notice the counterclockwise rotation of the population vector in the right panel. (d) Scatter plots of the direction of the population vector as a function of time, starting with the first population vector that increased significantly in length after stimulus onset (S). For the direct task, the direction of the population vector is in the direction of the movement (~180°); for the transformation task, the direction of the population vector rotates counterclockwise from the direction of the stimulus (~90°) to the direction of the movement (~180°). From Georgopoulos, Lurito, Petrides, Schwartz, and Massey.[7] Copyright 1989 by the American Association for the Advancement of Science. Reproduced with permission.

Could the apparent rotation of the population vector be the result of activation of two subsets of cells, one with preferred directions at or near the stimulus direction and the other with preferred directions at or near the movement direction? If cells of the former type were recruited at the beginning of the RT, followed by those of the latter type, then the vector sum of the two subsets could provide the rotating population vector. However, in an experimental test of this hypothesis, such a pattern of activation was not observed.[7]

A true rotation of the population vector could be reflected in the engagement of cells with intermediate preferred directions during the middle of the RT. Indeed, such a transient increase in the recruitment of these cells was observed.[7] This finding supports the idea of a true rotation of the population signal.

SIMILARITIES BETWEEN MENTAL ROTATION OF DIRECTION OF MOVEMENT AND MENTAL IMAGES

Do the mental rotation of the intended movement direction and of mental images share something in common, or are they totally independent processes? To answer this question, we compared the performances of human subjects in a visuomotor mental rotation task and a visual mental rotation task.[11] We found that the processing rates in both tasks were correlated, but neither rate correlated significantly with the processing rate in a visuomotor memory scanning task. These results suggest that visuomotor and visual mental rotations possess common processing constraints that cannot be ascribed to general processing rate performances.

It is possible that there is a common brain structure underlying mental spatial rotation in both visuomotor and visual tasks. An alternative hypothesis is that there are similar neurophysiological constraints when a mental spatial rotation must be performed, regardless of the brain structures involved. No brain areas other than motor cortex have been explored during the transformation task; therefore, it is uncertain whether the motor cortex is the locus of visuomotor mental rotation or, more probably, whether changes in cell activity occur in parallel in various brain areas. Nevertheless, the fact that the motor cortex is involved in such a cognitive task is remarkable, for the motor cortex is not generally considered to be involved in cognitive operations.

Studies of mental rotation of visual images with brain-damaged human subjects and studies measuring evoked potentials and regional cerebral blood flow in normal human subjects performing a rotation task have documented involvement of structures in the parietal region and primarily in the right cerebral hemisphere.[12] It is not clear what neurophysiological mechanisms underlie the visual mental rotation. However, the neuronal population vector analysis has already been applied successfully to relate neural activity in different brain areas to attributes of visual stimuli,[13] and could be a useful tool to visualize possible mental rotation of images in these areas.

Acknowledgments—This work was supported by U.S. Public Health Service Grants NS17413 and PSMH48185 and Office of Naval Research Contract N00014-88-K0751. G. Pellizzer was supported by a postdoctoral fellowship of the Swiss National Science Foundation.

Notes

1. This type of problem solving has been classically regarded as a landmark for intelligent behavior; see, e.g., W. Köhler, *The Mentality of Apes* (Routledge and Kegan Paul, London, 1925); J. Piaget, *The Origins of Intelligence in Children* (International Universities Press, New York, 1952).

2. S.M. Kosslyn, *Image and Mind* (Harvard University Press, Cambridge, MA, 1980); R.N. Shepard and L.A. Cooper, *Mental Images and Their Transformations* (MIT Press, Cambridge, MA, 1982).

3. R.N. Shepard and J. Metzler, Mental rotation of three-dimensional objects, *Science, 171,* 701–703 (1971).

4. Most of the publications of R.N. Shepard and colleagues concerning mental rotation experiments, as well as other experiments, were reproduced together in Shepard and Cooper, note 2. For a nontechnical presentation of these experiments, see L.A. Cooper and R.N. Shepard, Turning something over in the mind, *Scientific American, 251*(6), 106–114 (1984).

5. A.P. Georgopoulos and J.T. Massey, Cognitive spatial-motor processes: 1. The making of movements at various angles from a stimulus direction, *Experimental Brain Research, 65,* 361–370 (1987).

6. For an account of different opinions in this debate, see, e.g., J.R. Anderson, Arguments concerning representations for mental imagery, *Psychological Review, 85,* 249–277 (1978); Z.W. Pylyshyn, The imagery debate: Analogue media versus tacit knowledge, *Psychological Review, 88,* 16–45 (1981); S.M. Kosslyn, The medium and the message in mental imagery: A theory, *Psychological Review, 88,* 46–66 (1981).

7. A.P. Georgopoulos, J.T. Lurito, M. Petrides, A.B. Schwartz, and J.T. Massey, Mental rotation of the neuronal population vector, *Science, 243,* 234–236 (1989); J.T. Lurito, T. Georgakopoulos, and A.P. Georgopoulos, Cognitive spatial-motor processes: 7. The making of movements at an angle from a stimulus direction: Studies of motor cortical activity at the single cell and population levels, *Experimental Brain Research, 87,* 562–580 (1991).

8. A.P. Georgopoulos, J.F. Kalaska, R. Caminiti, and J.T. Massey, On the relations between the direction of two-dimensional arm movements and cell discharge in primate motor cortex, *Journal of Neuroscience, 2,* 1527–1537 (1982); A.B. Schwartz, R.E. Kettner, and A.P. Georgopoulos, Primate motor cortex and free arm movements to visual targets in three-dimensional space: I. Relations between single cell discharge and direction of movement, *Journal of Neuroscience, 8,* 2913–2927 (1988).

9. A.P. Georgopoulos, R. Caminiti, J.F. Kalaska, and J.T. Massey, Spatial coding of movement: A hypothesis concerning the coding of movement direction by motor cortical populations, *Experimental Brain Research Supplement, 7,* 327–336 (1983); A.P. Georgopoulos, A.B. Schwartz, and R.E. Kettner, Neuronal population coding of movement direction, *Science, 233,* 1416–1419 (1986).

10. A.P. Georgopoulos, J.F. Kalaska, M.D. Crutcher, R. Caminiti, and J.T. Massey, The representation of movement direction in the motor cortex: Single cell and population studies, in *Dynamic Aspects of Neocortical Function,* G.M. Edelman, W.E. Gall, and W.M. Cowan, Eds. (Wiley, New York, 1984); A.P. Georgopoulos, R.E. Kettner, and A.B. Schwartz, Primate motor cortex and free arm movements to visual targets in three-dimensional space: II. Coding of the direction of movement by a neuronal population, *Journal of Neuroscience, 8,* 2928–2937 (1988); A.P. Georgopoulos, M.D. Crutcher, and A.B. Schwartz, Cognitive spatial motor processes: 3. Motor cortical prediction of movement direction during an instructed delay period, *Experimental Brain Research, 75,* 183–194 (1989); N. Smyrnis, M. Taira, J. Ashe, and A.P. Georgopoulos, Motor cortical activity in a memorized delay task, *Experimental Brain Research* (in press).

11. G. Pellizzer and A.P. Georgopoulos, Common processing constraints for visuomotor and visual mental rotations, *Experimental Brain Research* (in press).

12. For reviews, see S.M. Kosslyn, Aspects of a cognitive neuroscience of mental imagery, *Science, 240,* 1621–1626 (1988); M.J. Farah, The neural basis of mental imagery, *Trends in Neuroscience, 12,* 395–399 (1989).

13. M.A. Steinmetz, B.C. Motter, C.J. Duffy, and V.B. Mountcastle, Functional properties of parietal visual neurons: Radial organization of directionalities within the visual field, *Journal of Neuroscience, 7,* 177–191 (1987); M.P. Young and S. Yamane, Sparse population coding of faces in the inferotemporal cortex, *Science, 256,* 1327–1331 (1992).