Somesthesis and the Neurobiology of the Somatosensory Cortex
O. Franzén, R. Johansson and L. Terenius (eds.)

Changing the intended direction of movement

Giuseppe Pellizzer

Department of Physiology, University of Minnesota Medical School, Minneapolis, MN 55455, USA, and Brain Sciences Center, Veterans Affairs Medical Center, Minneapolis, MN 55417, USA

Summary. The behavioral and neural correlates of processing of motor directional information are described for two different visuomotor tasks: mental rotation and context-recall. Psychological studies in human subjects suggested that these two tasks may involve different mechanisms processing directional information. Analyses of the activity of single cells and neuronal populations in the motor cortex of behaving monkeys performing in the same tasks provided direct insight into the neural mechanisms involved, and confirmed their different nature.

Introduction

The objective of cognitive neuroscience is to define the neural mechanisms underlying cognitive processing. The strategy usually followed in experimental studies is to record neural events (e.g., activity of neurons, electroencephalogram) during the performance of a cognitive task. Two levels of analysis of the data can be performed. A first level of understanding of the cognitive processes consists of describing the association of neural events to relevant variables of the task. This provides a first degree of insight into the processes, but has usually little explanatory power. A second level of analysis is to model the cognitive processes and its development in time from the neural data. Only this second level of analysis provides a potential explanation of the neural mechanisms of the cognitive processes. Two examples of cognitive processing in visuomotor tasks are described in the following sections: mental rotation and context-recall. For each one, behavioral experiments and neural mechanisms as observed in the motor cortex are presented. However, to understand the results of these experiments, it is necessary first to describe how neural activity in the motor cortex can be related to directional motor information.

Neural coding of direction of movement

The relation between direction of movement and single cell activity in the primary motor cortex was studied in awake monkeys (e.g., Georgopoulos et al., 1982; Schwartz et al., 1988). In these studies, neuronal activity was recorded in the arm area of the primary motor cortex contralateral to the performing arm, while the monkey moved the hand from a starting position in the direction of a visual target. Significant change of activity in relation to the direction of movement was observed before the initiation of movement and during its execution. How much a cell is active depends on the cell and on the direction of movement. Cell's activity is broadly tuned with respect to the direction of movement; that is, the activity is highest for movements in a particular direction, and decreases progressively for movements made farther away from this direction. The direction of movement corresponding to the highest activity of the cell is called the preferred direction of the cell. The preferred directions vary from cell to cell, and are distributed in all directions. These results indicate (1) that a given cell contributes in movements in various directions, (2) that movements in a particular direction involves the contribution of a large population of cells, and (3) that the direction of movement is uniquely defined only at the level of a population of cells.

One hypothesis about the population coding of direction of movement is to regard the directionally tuned cells as an ensemble of vectors (Georgopoulos et al., 1983, 1986). Each vector represents the contribution of a directionally tuned cell. A particular vector points in the direction of the cell's preferred direction, and its length is a function of the cell activity for a given direction of movement. The vector sum of this ensemble of vectors is called the neuronal population vector, and points at or near the direction of movement. These results indicate that information concerning the direction of movement can be extracted unambiguously from the neuronal ensemble. What is most important for the next sections of this chapter is that the neuronal population vector provides a tool to monitor the processing of directional information in time before the initiation of movement, that is, when the movement is intended. For example, it was observed that the neuronal population vector computed in time points in the direction of the upcoming movement during the response time, that is, after the visual target is presented and before the movement is initiated (Figure 1; Georgopoulos et al., 1984, 1988); during an instructed delay, that is, when a delay is imposed before the initiation of the movement (Georgopoulos et al., 1989a); and during a memorized delay, that is, when the information about the direction of the movement must be kept in memory (Smyrnis et al., 1992).

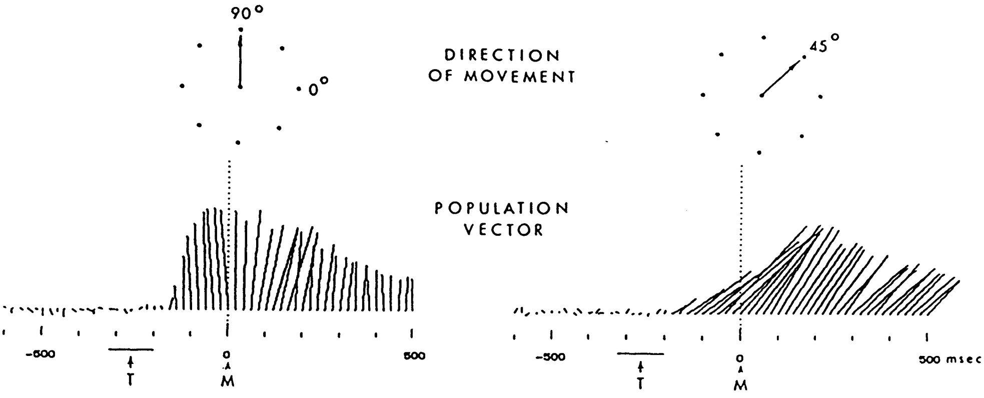

Figure 1. Time course of population vector for movements at 90° and 45°. The population vector was calculated every 20 ms. After the target onset (T) and before the begining of the movement (M) the population vector increases in length and its direction points toward the direction of the upcoming movement. (Georgopoulos et al., 1984; reproduced with permission).

Mental rotation

Shepard and colleagues (Shepard and Metzler, 1971; Shepard and Cooper, 1982) reported a series of experiments that supports the hypothesis of a mental rotation of visual images. Typically, subjects have to judge whether two figures are the same or are mirror images of each other. The finding was that the response time increased as a linear function of the angular difference between the orientation of the two figures. This suggested that subjects mentally rotate the image of one figure into congruence with the other to make their judgment.

The process of mental rotation is not limited to perceptual type of tasks, but can be also inferred in visuomotor tasks (Georgopoulos and Massey, 1987; Pellizzer and Georgopoulos, 1993). In these tasks, human subjects were asked to make a planar arm movement in a direction that was at a specified angle away from the direction of a visual stimulus. The results were that the response time increased as a linear function of the angle. These results are similar to those described for mental rotation of visual images and are compatible with the hypothesis that subjects mentally rotate their intended direction of movement from the direction of the visual stimulus toward the direction of movement.

The hypothesis of mental rotation assumes that there is a neurophysiological variable that represents the orientation of an imagined object, or the direction of the intended movement, and that this variable undergoes a continuous transformation during mental rotation passing through values that represent intermediate directions. Direct evidence for such a process was obtained in an experiment with monkeys that were trained to move a handle on a planar surface either toward a visual stimulus (*direct* task) or 90 degrees counterclockwise from it (*transformation* task) depending on whether the stimulus was dim or bright, respectively (Georgopoulos et al., 1989b; Lurito et al., 1991).

The activity of cells in the arm area of the motor cortex contralateral to the performing arm was recorded extracellularly. The changes of cell activity after the visual stimulus appeared in the *direct* task were as described previously (Georgopoulos et al., 1982, 1984, 1988). The activity of these cells also changed in the *transformation* task. There were no cells the activity of which changed only in one task, which suggests that the representation of the direction of movement involves the same population of motor cortical cells in both tasks. The analysis of the population vector as a function of time after the target onset revealed the process of rotation of the intended direction of movement. During the response time the population vector rotated from the direction of the target counterclockwise through 90 degrees to the direction of the movement (Figure 2). The rates of rotation of the population vector (about 400 deg/s) were within the range of those obtained with human subjects in the same task (Georgopoulos and Massey, 1987; Pellizzer and Georgopoulos, 1993). In addition, it was found that cells with preferred directions intermediate between the direction of the stimulus and the direction of the movement were transiently recruited in the middle of the response time, which supports the hypothesis of a true rotation of the population signal (Lurito et al., 1991).

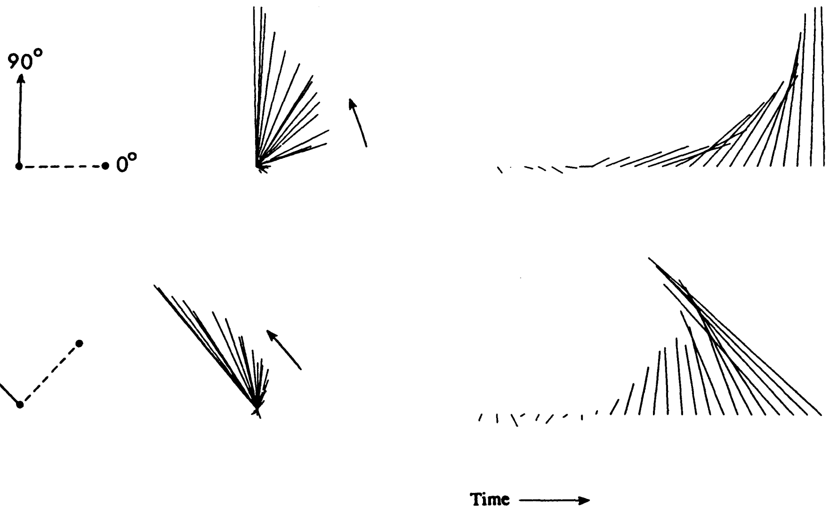

Figure 2. Neuronal population vector in two conditions of the transformation task. Left panel: Stimulus (dashed line) and movement (arrow) directions. Right panel: Neuronal population vector plotted every 10 ms from the onset of the stimulus until after the onset of the movement. Middle panel: Same data as in right panel but plotted in polar fashion. When the population vector lengthens it points initially in the direction of the stimulus and then rotates counterclockwise and points in the direction of the movement. (Lurito et al., 1991; reproduced with permission).

These results have several remarkable points: (1) There was no a priori reason to expect that the population vector would point to any direction other than the direction of movement, on the simple hypothesis that the motor cortex is only involved in the production of movement. The interpretation that the population vector indicates the intended direction of movement suggests that, in the transformation task, the intention of movement spans a range of directions during the response time. (2) There was no a priori reason to expect the direction of the population vector to shift gradually counterclockwise, for no explicit instruction was given to the animal about how to accomplish the transformation task. This strategy may minimize time and computational load to solve the transformation required.

Mental rotation and memory scanning

Are visual mental rotation and visuomotor mental rotation associated in some way? To answer this question we took advantage of the large diversity of rates of rotation between subjects (Pellizzer and Georgopoulos, 1993). We found a significant correlation of the rates of rotation in human subjects performing in the two tasks. This suggested that the two types of mental rotation either share a common stage of processing, or are the object of similar constraints although performed by separate neural mechanisms. It is also possible that the correlation between processing rates results from general processing rates differences between subjects, that is, some subjects may perform generally faster (or slower) than others. To control for this, we needed a different type of task where a processing rate can also be estimated. We chose a visuomotor memory scanning task (Georgopoulos and Lurito, 1991). In this task, a list of two to five visual stimuli directions were presented sequentially. Then, one of them, except the last one, was displayed again as test stimulus. The subjects had to make an arm movement in the direction of the stimulus that followed the test stimulus in the sequence. The processing rates in this task did not correlate with those in either mental rotation tasks. These results suggested that (1) visual mental rotation and visuomotor mental rotation share common processing constraints that cannot be ascribed to general mental processing capacities; (2) that mental rotation and memory scanning involve different types of processing mechanisms.

Memory scanning

An important aspect of cognitive function relates to retrieval of memorized information. Sternberg (1966, 1967, 1969) devised a series of tasks that requires to find an information among items in a memorized list. Two of these tasks (*item-recognition* and *context recall*) are briefly described here. Typically, subjects were presented with a list of items to memorize, followed with a test stimulus. In the *item-recognition* task, the subjects had to decide whether the test stimulus was contained in the list presented, or was not in the list. The results were that the response time for positive and negative responses increased as a linear function of the number of items contained in the list. This suggested that the task involves a scanning process, that is, a serial comparison of the test stimulus with the memorized items. If the scanning process were self-terminating, the number of comparisons in trials requiring a positive response would be on average half those in trials requiring a negative response, therefore the slope of the response time versus the number of items for the positive responses should be half the one for the negative responses. Instead, if the scanning process is exhaustive, that is, all items are scanned even when a match had occurred, the two slopes should be equal. The results fit the latter pattern, which supports the hypothesis that the *scanning to recognize* is exhaustive.

In the *context-recall* task, the subjects had to locate the test stimulus in the list. Then they had to name the item that followed the test stimulus in the list. Like in the previous task, the response time increased with the number of items in the list, but at a slower rate. Moreover, the response time increased also with the serial position of the test stimulus in the list. Therefore, these results suggest that the retrieval of contextual information, viz. the *scanning to locate*, is a self-terminating scanning process.

These paradigms provide a way to investigate cognitive operations on memorized items. The *context-recall* task was adapted to test memory scanning in the motor system (Georgopoulos and Lurito, 1991; Pellizzer and Georgopoulos, 1993). In these experiments, a sequence of visual stimuli directions was presented to the subjects. They had either to move the hand toward them when they were presented (Georgopoulos and Lurito, 1991), or only to look at them (Pellizzer and Georgopoulos, 1993). Then one of the stimuli, except the last one, was presented again as test stimulus. The subjects had to make a movement in the direction of the stimulus that followed the test stimulus in the sequence. The results showed that the response time increased with the number of stimuli in the list, but not with the serial position of the test stimulus. This suggests that the scanning process in this case is either exhaustive, or self-terminating with a random start within the sequence.

The activity of cells in the motor cortex was recorded recently during a *context-recall* task (Pellizzer et al., 1995). A monkey was trained in two tasks (*control* and *context-recall*) to exert a force pulse on a semi-isometric manipulandum in eight directions. The force exerted was displayed as a feedback cursor. In the *control* task, a yellow stimulus was presented in one direction and stayed on the screen, then after a delay it turned blue. This provided the go signal for the monkey to exert a force pulse such that the feedback cursor crossed the position of the stimulus. In the *context-recall* task, three different stimuli were presented successively and stayed on the screen. Then, the first or second stimulus turned blue. This identified the test stimulus and gave the go signal. The monkey had to move the cursor in the direction of the stimulus that followed the test stimulus in the sequence.

The activity of single cells tuned to the direction of the motor response in the *control* task served as markers to interpret the activity recorded during the *context-recall* task. It was observed that cell activity during the first half of the response time matched the activity associated with a response toward the direction of the second stimulus. Then, what happened to the cell activity during the second half of the response time depended on the serial position of the test stimulus. When the test stimulus was the first stimulus in the sequence, cell activity continued to match the activity associated with a response toward the second stimulus, which was the correct direction of response. However, when the test stimulus was the second in the sequence, cell activity changed abruptly to correspond to the activity associated with the direction of the third stimulus, which was in this condition the correct direction of response (Figure 3). The switching process was visualized at the ensemble level using the neuronal population vector computed in time. When the anticipated response did not have to change, the population vector pointed in the appropriate direction throughout the response time. In contrast, when the response had to be changed, the population vector changed abruptly from the direction of the test stimulus to the direction of the motor response.

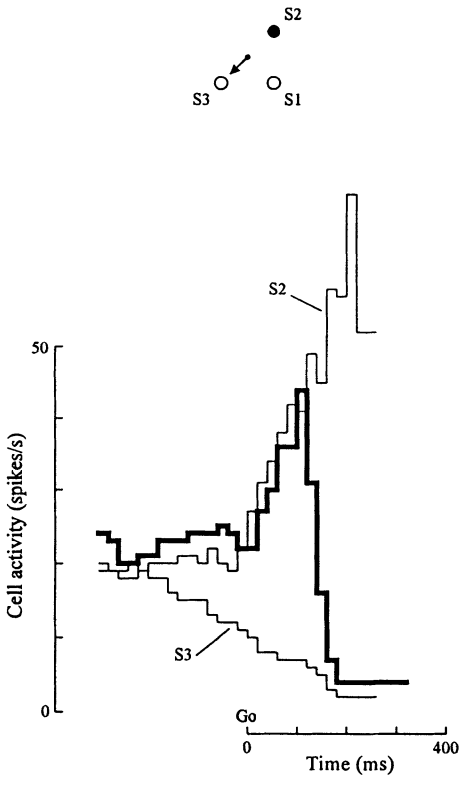

Figure 3. Peristimulus histograms of activity of a motor cortical cell for two directions in the control task, and one condition in the context-recall task. The two thin lines represent the activity of the cell in the control task for motor responses in the upward-right (S2) and downward-left (S3) directions. The thick line represents the activity of the cell in the condition of the context-recall task illustrated at the top. After the go signal, cell activity initially increased in the same way as in the control case for the direction towards the test stimulus (S2) and then changed abruptly to the level corresponding to the control activity.

The abrupt change in the direction of the population vector observed in this study is quite different from the slow rotation observed in the mental rotation experiment. Additional evidence for the different nature of the two processes was that (1) the duration of change of direction of the neuronal population vector did not vary with the angle between the test stimulus and the direction of the response, unlike what would be expected if the transformation were a rotation at a constant speed; (2) cells with preferred directions intermediate between the direction of the test stimulus and the direction of the motor response were not recruited in the middle of the response time, unlike what was observed in the mental rotation experiment.

Conclusions

The experiments presented in this chapter provide an example of interaction between psychological and neurophysiological studies of cognitive function. Psychological studies suggested that the neural mechanisms underlying the processing of directional motor information in visuomotor mental rotation and context-recall tasks are of different nature. The relation between neural activity in the motor cortex and the intended direction of movement gives a tool to investigate the neural mechanisms underlying the processing of directional motor information in both tasks. Obviously other brain areas than motor cortex are likely to be involved, but additional studies are needed to identify them, and to elucidate their relative contributions during these tasks. Neurophysiological studies provided direct insight into the neural mechanisms of changing the direction of the intended direction of movement during mental rotation and context-recall tasks. The analyses of neural activity in the motor cortex showed that during the mental rotation task, the direction of the intended direction of movement is slowly and gradually transformed from the direction of the stimulus toward the direction of the response. Instead, during the context-recall task when a change of the intended direction of movement is required, this direction switches abruptly. Therefore it seems that the time spent to derive the direction of the motor response in the mental rotation task reflects an analogue transformation process, instead in the context-recall task it reflects a selection process.

Acknowledgements

This work was supported by United States Public Health Service grant NS17413.

References

Georgopoulos, A.P., Caminiti, R., Kalaska, J.F., and Massey, J.T. (1983) Spatial coding of movement: A hypothesis concerning the coding of movement direction by motor cortical populations. *Experimental Brain Research Supplement* 7: 327-336.

Georgopoulos, A.P., Crutcher, M.D. and Schwartz, A.B. (1989a) Cognitive spatial-motor processes: 3. Motor cortical prediction of movement direction during an instructed delay period. *Experimental Brain Research* 75: 183-194.

Georgopoulos, A.P., Kalaska, J.F., Caminiti, R. and Massey, J.T. (1982) On the relations between the direction of two-dimensional arm movement and cell discharge in primate motor cortex. *Journal of Neuroscience* 2: 1527-1537.

Georgopoulos, A.P., Kalaska, J.F., Crutcher, R., Caminiti, R. and Massey, J.T. (1984) The representation of movement direction in the motor cortex: Single cell and population studies. *In:* G.M. Edelman, W.E. Gall and W.M. Cowan (eds.): *Dynamic Aspects of Neocortical Functions*, Wiley, New York, pp. 501-524.

Georgopoulos, A.P., Kettner, R.E. and Schwartz, A.B., (1988) 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.

Georgopoulos, A.P. and Lurito, J.T. (1991) Cognitive spatial-motor processes. 6. Visuomotor memory scanning. *Experimental Brain Research* 83: 453-458.

Georgopoulos, A.P., Lurito, J.T., Petrides, M., Schwartz, A.B. and Massey, J.T. (1989b) Mental rotation of the neuronal population vector. *Science* 243: 234-236.

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

Georgopoulos, A.P., Schwartz, A.B. and Kettner, R.E. (1986) Neuronal population coding of movement direction. *Science* 233:, 1416-1419.

Lurito, J.T., Georgakopoulos, T. and Georgopoulos, A.P. (1991) 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.

Pellizzer, G. and Georgopoulos, A.P. (1993) Common processing constraints for visuomotor and visual mental rotation. *Experimental Brain Research* 93: 165-172.

Pellizzer, G., Sargent, P. and Georgopoulos, A.P. (1995) Motor cortical activity in a context-recall task. *Science* 269: 702-705.

Schwartz, A.B., Kettner, R.E. and Georgopoulos, A.P. (1988) 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.

Shepard, R.N. and Cooper, L.A. (1982) *Mental Images and their Transformations.* MIT Press, Cambridge, MA.

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

Smyrnis, N., Taira, M., Ashe, J. and Georgopoulos, A.P. (1992) Motor cortical activity in a memorized delay task. *Experimental Brain Research* 92: 139-151.

Sternberg, S. (1966) High-speed scanning in human memory. *Science* 153: 652-654.

Sternberg, S. (1967) Retrieval of contextual information from memory. *Psychonomic Science* 8: 55-56.

Sternberg, S. (1969) Memory-scanning: Mental processes revealed by reaction-time experiments. *American Scientist* 57: 421-457.