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Cognitive Brain Research 5 (1996) 123–130

COGNITIVE
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Mental transformations in the motor cortex

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Abstract

The behavioral and neural correlates of processing of motor directional information are described for two visuomotor tasks: mental rotation and context-recall. Psychological studies with human subjects suggested that these two tasks involve different time-consuming processes of 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. In the mental rotation task the patterns of neuronal activity revealed a rotation of the intended direction of movement. In contrast, in the context-recall task the patterns of neural activity identified a switching process of the intended direction of movement.

Keywords: Motor cortex; Movement direction; Cognitive process; Mental rotation; Memory scanning; Context-recall

1. Introduction

The objective of cognitive neuroscience is to unveil the neural mechanisms underlying cognitive processing. A way to address this problem is to record signals that are more or less closely related to neural activity (e.g., activity of neurons, electroencephalogram, regional cerebral blood flow) during the performance of a cognitive task. Then, changes of the variable recorded in a particular brain area are taken to indicate a relation between that area and the task. This approach provides a first level of description that associates cognitive processes with brain processes.

Another approach consists of reconstructing the cognitive process unfolding in time from the neural data. Here the cognitive process is described directly in terms of brain processes. An example of this latter approach is given for two cognitive visuomotor tasks: mental rotation and context-recall. For each task we present psychological and neurophysiological studies.

2. Mental rotation: psychological studies

Shepard and colleagues [18,19] pioneered in a series of experiments supporting the hypothesis of mental rotation of visual images. In the original experiment subjects were shown two perspective drawings of three-dimensional asymmetric objects and were asked to judge whether they represented the same or a mirror-image object [19]. The results indicated that the time it takes for subjects to respond increased as a linear function of the angle between the two portrayed orientations. This suggested that the subjects mentally rotate one object's image into congruence with the other object's image to make their decision. That is, assuming a constant velocity of rotation, the larger the angle, the longer the time of rotation, and therefore the longer the time to respond.

Asymmetric two-dimensional figures like letters, numbers or random shapes were used in other studies [14,18]. Now, only one stimulus was presented for each trial and the subjects had to decide whether it was normal or mirror-image. Again it was found that the response time was a monotonic increasing function of the angle between the stimulus orientation and either the standard upright position with letters and numbers, or the previously learned orientation with random shapes (Fig. 1). These results suggested that the image of the stimulus is mentally rotated to be superimposed on the reference figure for the judgment to be made.

The hypothesis of mental rotation assumes that mental images are transformed continuously passing through representations of intermediate positions. This is also referred to as the analog hypothesis, because it postulates a one-to-one correspondence between the mental transformation

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PII S0926-6410(96)00048-1

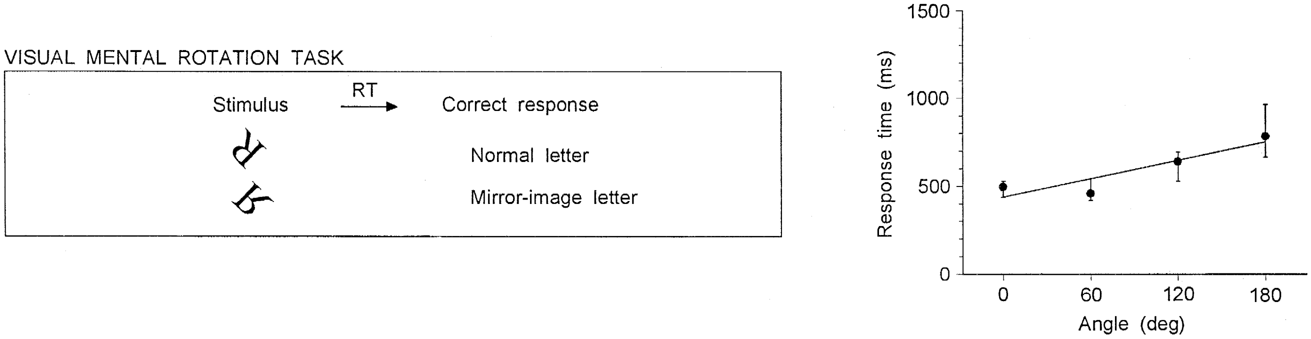


Fig. 1. Left panel: diagram of the visual mental rotation task. A stimulus was presented to the subject who had to decide whether it was a normal or mirror-image letter. Right panel: median response time vs. stimulus angle for one subject. Error bars indicate interquartile ranges. (Reproduced with permission [14].)

and the actual rotation of an object. Despite objections raised to this view in the so-called analog-propositional controversy on mental imagery [e.g., [16]], the mental rotation hypothesis remains well established.

Although the phenomenon of mental rotation is usually considered as limited to perceptual-like processes, it extends to motor processes as well and particularly to representations of the intended direction of movement [10,14]. In these experiments human subjects were asked to make an arm movement on a plane at an instructed angle from the direction of a visual stimulus. The result was that the response time increased linearly with the instructed angle, which is similar to what has been described for mental rotation of visual images (Fig. 2). This finding suggested that subjects mentally rotate the intended direction of movement from the direction of the visual stimulus toward the direction of movement.

Recent experiments with monkeys provided a direct evidence of a mental operation that has analog characteristics [9,13]. These experiments showed that a physiological process in the brain, which represents the intended direction of movement, is continuously transformed during the response time when a movement has to be made at an angle from the stimulus direction. To understand the results of these experiments, it is necessary first to describe how neural activity in the motor cortex can be meaningfully related to the intended direction of movement.

3. Neural coding of movement direction

The relation between direction of movement and single cell activity in the primary motor cortex has been studied in awake monkeys [1,2,5,12,17]. Typically, neuronal activity was recorded in the arm area of the primary motor cortex contralateral to the performing arm, while monkeys moved the hand from a starting position in the direction of a visual target. The direction of movement was varied by varying the direction of the target. The results showed a significant change of cell activity in relation to the direction of movement before its initiation and during its execution.

How much a cell is active depends on the cell and on the direction of the movement. The cell activity is broadly

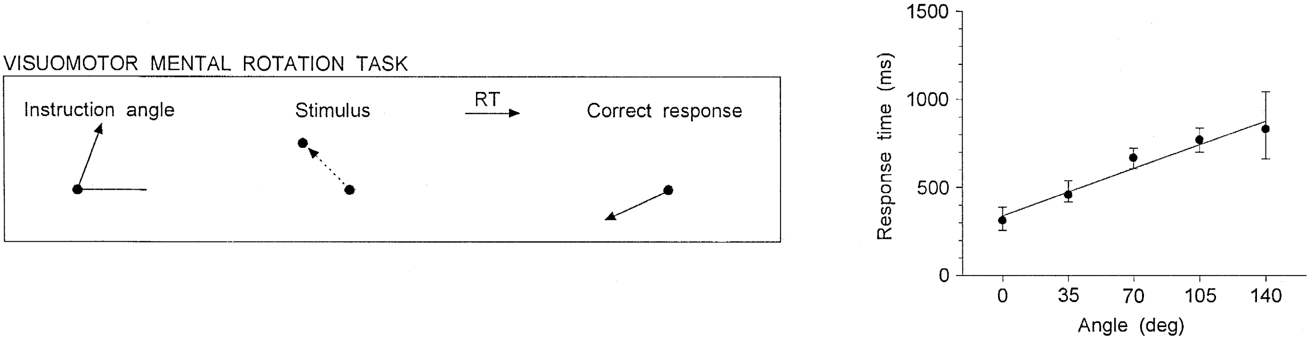


Fig. 2. Left panel: diagram of the visuomotor mental rotation task. The subject had to move the hand at an instructed angle from the direction of the stimulus. Right panel: median response time vs. instruction angle for one subject (same subject as in Fig. 1). Error bars indicate interquartile ranges. (Reproduced with permission [14].)

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 further away from this direction. The direction corresponding to the highest activity 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 involve 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.

A measure of the direction of movement coded by a neuronal population is provided by the neuronal population vector [3,11]. The population of directionally tuned cells is regarded as a population of vectors. A particular vector points in the preferred direction of the cell, and its length is a function of the cell activity associated with a given direction of movement. The vector sum of this population of vectors is the neuronal population vector, which points at or near the direction of the movement. Therefore, information concerning the direction of movement can be unambiguously obtained from the neuronal ensemble.

In addition, the neuronal population vector provides a tool to monitor the processing of directional information in time before the movement is initiated, that is, when the movement is intended [6]. 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 [6,7]; during an instructed delay, that is, when a delay is imposed before the initiation of the movement [4]; and during a memorized delay, that is, when the information about the direction of the movement must be kept in memory [20].

In consequence, it is possible that if monkeys were to perform a mental transformation of the intended direction of movement, and neuronal activity was recorded during that performance, the mental transformation could be visualized in time. An example of such a visualization is given for the mental rotation experiment described in the next section.

4. Mental rotation: neurophysiological studies

Two monkeys were trained to move a handle on a planar surface either toward a visual stimulus (*direct* task) or at 90° counterclockwise from it (*transformation* task) depending on whether the stimulus was dim or bright, respectively [9,13]. 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 [5–7]. The activity of these cells also changed in the *transformation* task. No cells were found that were active exclusively in only one task, which suggests that the representation of the direction of movement involves the same population of motor cortical cells in both tasks.

The patterns of cell activity were frequently different in the two tasks when either the stimulus or the movement were the same. No insight into the process could be gained from the single cell analysis. However, the analysis at the population level by computing the population vector as a function of time after the target onset revealed the process of rotation of the intended direction of movement (Fig. 3).

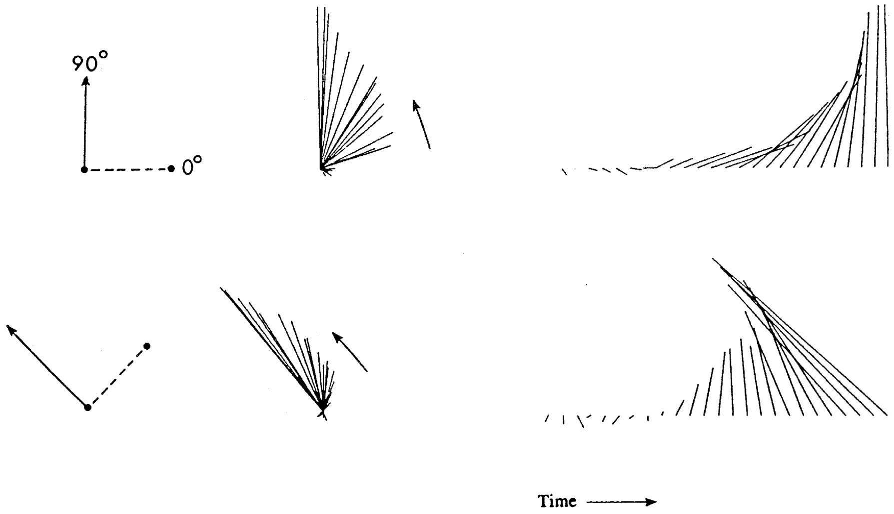


Fig. 3. Neuronal population vector in two conditions of the *transformation* task. Left panel: stimulus (dashed line) and movement (arrow) directions. Right panel: neuronal population vector plotted every 10 ms from the onset of the stimulus until after the onset of the movement. Middle panel: same data 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. (Reproduced with permission [13].)

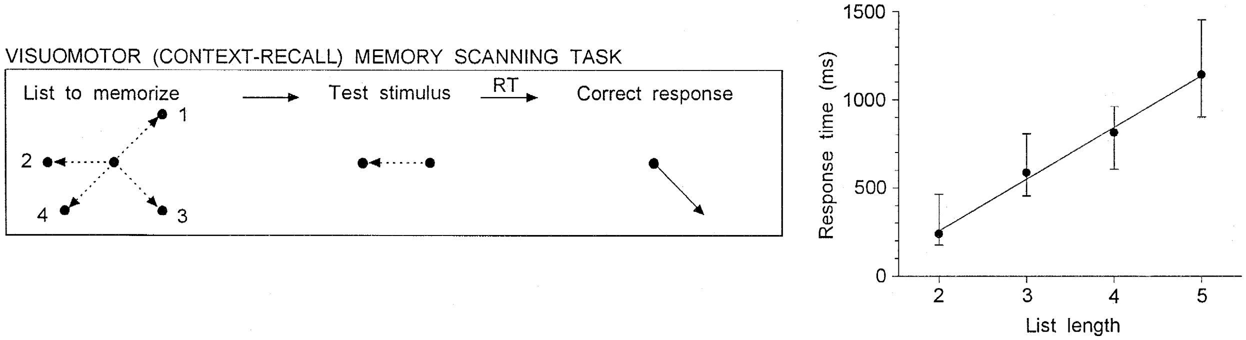


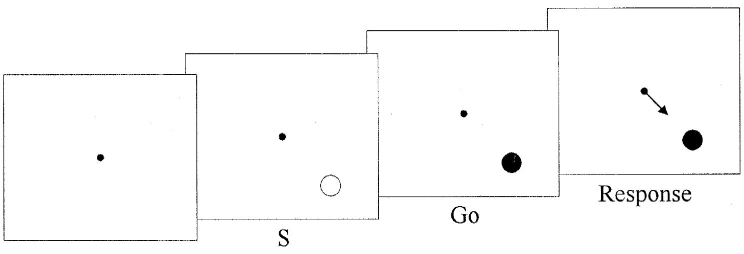
Fig. 4. Left panel: diagram of the visuomotor context-recall task. The subject had to remember the order of presentation of a list of stimulus directions. Then, the subject had to move the hand in the direction of the stimulus that followed the test stimulus in the sequence. Right panel: median response time vs. list length for one subject (same subject as in Figs. 1 and 2). Error bars indicate interquartile ranges. (Reproduced with permission [14].)

During the response time the population vector rotated from the direction of the target counterclockwise through 90° to the direction of the movement. 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 [10,14].

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 [13]. Therefore, these results provided direct evidence for the mental rotation as an analog process.

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 command 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

Control task



Context-recall task

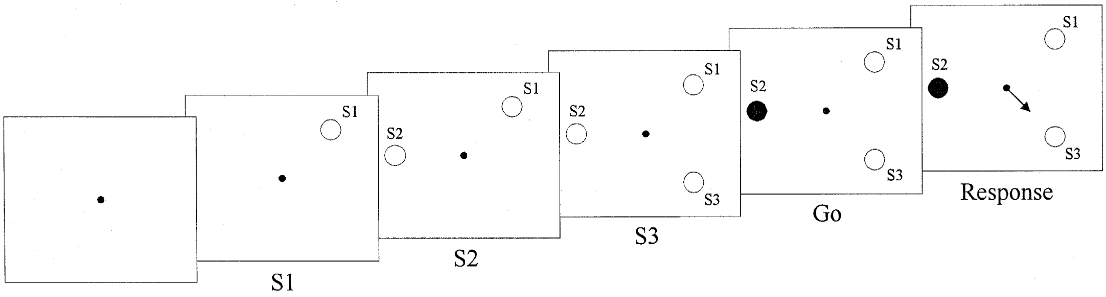


Fig. 5. Diagram of the *control* and *context-recall* tasks. In the *control* task (top), the yellow stimulus S (empty circle) changed to blue (filled circle) after 400 ms, which gave the go signal. The correct motor response was in the direction of the stimulus. In the *context-recall* task (bottom), three yellow stimuli (S1, S2 and S3; empty circles) were presented sequentially at 400 ms intervals and stayed on the screen. In the trial illustrated S2 changed to blue (filled circle), which now dictated a motor response toward S3 [15].

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.

5. Memory scanning: psychological studies

Retrieval of memorized information is an important aspect of cognitive function. Sternberg [21–23] 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 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 in the list presented (positive response) or was not in the list (negative response). 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.

There are two distinct types of scanning processes: a self-terminating scanning, that is, the scanning is interrupted when a match occurs between the test stimulus and a stimulus in the memorized list; and an exhaustive scanning, that is, all the comparisons between test stimulus and stimuli in the list are made whether or not a match exists. If the scanning process were self-terminating, the number of comparisons in trials requiring a positive response would be on average half the one 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, 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 test stimulus was always a member of the list of stimuli to memorize. The subjects had to locate the test stimulus in the list, and 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 with a steeper slope. 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 [8,14]. 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 [8], or to look at them only [14]. 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 (Fig. 4). This suggests that the scanning process here is either exhaustive or self-terminating with a random start within the sequence.

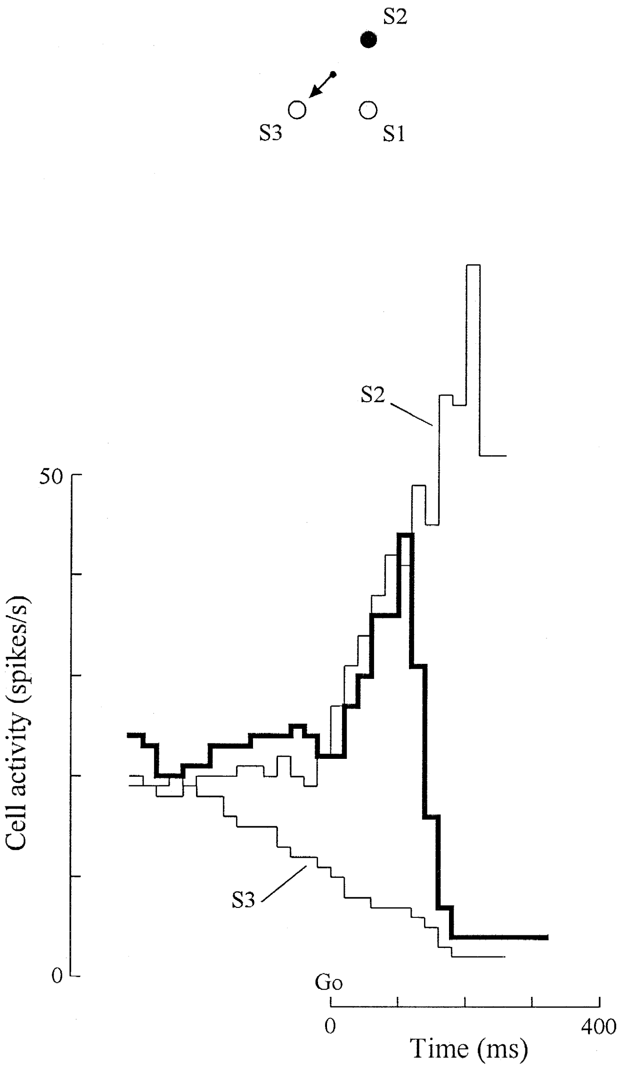


Fig. 6. Peristimulus histograms of activity of a motor cortical cell for two directions in the *control* task, and one condition in the *context-recall* task. The two thin lines represent the activity of the cell in the *control* task for motor responses in the upward-right (S2) and downward-left (S3) 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 toward the test stimulus (S2), and then changed abruptly to the level corresponding to the *control* activity for the direction of the motor response (S3) [15].

6. Mental rotation and memory scanning

Are mental rotations of visual images and of the intended direction of movements associated in some way? To answer this question, we took advantage of the large diversity of rates of rotation among human subjects and compared their performance in the two kinds of mental rotation tasks [14] (Figs. 1 and 2). We found that the processing rates in the two tasks were significantly correlated. This suggested that the two kinds of mental rotation either share a common stage of processing, or are subject to similar processing constraints although performed by separate neural mechanisms.

It is also possible that the correlation between processing rates results from general differences of processing rates among subjects, that is, some subjects may perform generally faster (or slower) than others. To control for this confounding factor, we used a different type of task where a processing rate can also be estimated. We chose the visuomotor memory scanning task (Fig. 4). The processing rates in this task did not correlate with those in the mental rotation tasks [14].

These results suggest that (1) visual mental rotation and visuomotor mental rotation share common processing constraints that cannot be ascribed to general mental processing capacities, (2) mental rotation and memory scanning involve different types of processing mechanisms.

7. Memory scanning: neurophysiological studies

The activity of cells in the motor cortex was recorded recently during a *context-recall* task [15]. A monkey was trained in two tasks (*control* and *context-recall*) to exert a force pulse on a semi-isometric manipulandum in eight directions. A visual force-feedback cursor was displayed on a monitor in front of the monkey. In the *control* task, a yellow stimulus was presented on the monitor in one direction. After 400 ms the stimulus turned blue which 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 yellow stimuli were presented successively (every 400 ms) in different directions and stayed on the screen. Then, after 400 ms either the first or the 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 (Fig. 5).

The patterns of activity of single cells tuned to the direction of the motor response in the *control* task were used to interpret the activity recorded during the *context-recall* task. It was observed that cell activity during the first half of the response time corresponded to the activity associated with a response toward the direction of the second stimulus in the sequence.

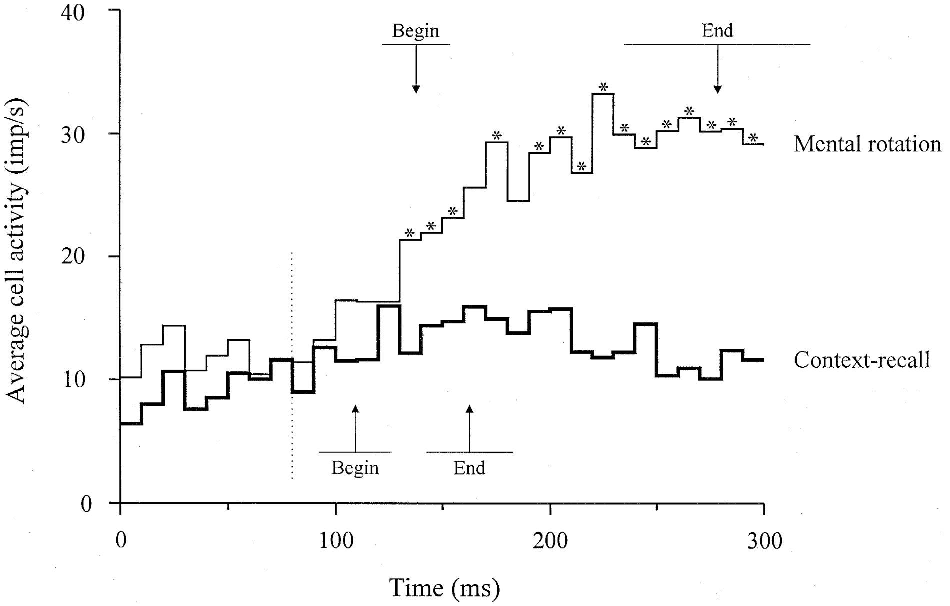


Fig. 7. Peristimulus time histograms (bin width, 10 ms) of the activity of cells with preferred direction at the intermediate direction (±10°) between the stimulus and movement directions in the mental rotation task, and between the test stimulus (S2) and motor response (S3) in the context-recall task. Histograms start at the onset of the go signal (time zero). In the mental rotation task, the activity of such cells (thin line) increased by more than three-fold and was statistically significant (indicated by asterisks), whereas in the context-recall task cell activity remained almost constant (thick line) and was not statistically significantly different, as compared with cell activity during the first 80 ms (dotted line; baseline period). The arrows indicate the average time (±S.D.) at which the population vector began to change direction (begin) and when it attained the direction of the motor response (end) [15].

Then, during the second half of the response time the patterns of cell activity were differentiated according to 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. In contrast, when the test stimulus was the second stimulus 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 (Fig. 6).

The switching process was also 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.

The abrupt change of direction of the population vector observed in this study contrasts with 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 velocity, and (2) cells with preferred directions intermediate between the direction of the test stimulus and the direction of the motor response did not change activity in the middle of the response time, unlike what was observed in the mental rotation experiment (Fig. 7).

8. Conclusions

The experiments presented above give an example of interaction between psychological and neurophysiological studies of cognitive function. Psychological studies suggested that the processing of directional motor information in visuomotor mental rotation and context-recall tasks is of different nature. The relation between neural activity in the motor cortex and the intended direction of movement gives an opportunity 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 define 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 analog 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.

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