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THE MENTAL AND THE NEURAL: PSYCHOLOGICAL AND NEURAL STUDIES OF MENTAL ROTATION AND MEMORY SCANNING

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Abstract—In this article we review studies pertaining to psychophysical measurements and neural correlates of tasks requiring the processing of directional information in spatial motor tasks. The results of psychological studies in human subjects indicate that time-consuming processes underlie mental rotation and memory scanning. Other studies have suggested that these processes may rely on different basic mechanisms. A direct insight into their neural mechanisms was obtained analyzing the activity of single cells and neuronal populations in the brain of behaving monkeys performing the same tasks. These studies revealed the nature of the neural processes underlying mental rotation and memory scanning and confirmed their different nature.

Key Words: motor cortex; mental rotation; memory scanning; directional processing; spatial transformations.

THE PROBLEM

A basic question in cognitive neuroscience is the elucidation of neural mechanisms underlying cognitive processing. A common strategy to address this problem is to record aspects of neural activity (e.g. impulse activity of neurons, slow potentials, electroencephalogram) or other signals related to it (e.g. regional brain blood flow) during performance of a cognitive task: Then, changes in the relevant variable in a particular brain area during task performance is taken to indicate a relation of that area to the task in question. This approach has resulted in important insights but it falls short of providing a direct description of the cognitive process in terms of a brain process, since it relies essentially on temporal associations alone. Ideally, the neural data should be such that the cognitive process could be constructed from them as it unfolds in time, and be identified and distinguished from other possible processes that could also lead to a successful performance of the particular task. We investigated two cognitive processes with this objective in mind, namely mental rotation and memory scanning.

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Spatial transformations

In a general sense, the tasks used in these experiments required a spatial transformation. A general formulation of these tasks was provided by Duncan [3] who defined a spatial transformation as "an operation which, when applied to the internal representation of a stimulus in a spatial CRT (choice reaction time) task, produces a response bearing some fixed spatial relationship to the stimulus. Hence its use may be described by the equation

$$R = T(S), \tag{1}$$

where R and S can be response and stimulus in a spatial CRT task, and T represents some fixed spatial relationship between them. . . . Transformations as defined here have obvious similarities to those presumably used in tasks such as mental rotation [21]" [3, p. 59]. Duncan correctly pointed out that "the critical property of a transformation, as introduced here, is that it is a rule. It is an operation which will produce a response bearing some fixed relationship to a spatial stimulus. Use of a rule rather than individual S–R (stimulus–response) associations is beneficial when a task is ordered, that is, when S–R relationships are similar in several or all S–R pairs. Under these circumstances the number of rules needed is less than the number of S–R pairs" [3, p. 60]. In the general case, the rule can be the same for all stimuli in a task, or can differ for different stimuli. In fact, it was found that both the kind of rule and the number of possible rules affect the CRT [3].

Mental rotation

Shepard and his colleagues pioneered a series of tasks involving mental rotation of visual images [20, 21]. Typically, subjects are shown two asymmetric figures and are asked to judge whether they are of the same or of mirror image configuration. A salient and consistent finding has been that the reaction time (RT) for a correct judgement is a linear function of the angular difference between the two figures. This suggests that an image of the figure is being mentally rotated to be superimposed on the reference figure for the judgement to be made, a suggestion that has been strengthened by various manipulations of the task (see [20]). The results of these manipulations also indicate that rotating images are passing through intermediate positions in a continuous fashion ('analog' type). Although objections have been raised to this view and alternative explanations proposed (see, e.g. [1] and [19]), the view of mental rotation as an analog process is well established although not definitely proven by the results of psychological studies alone.

A process of mental rotation was inferred to be in operation in another task studied by Georgopoulos and Massey [12]. In this task subjects were required to move a manipulandum in a direction that was at an angle (5, 10°, etc.) and a departure (clockwise [CW] or counterclockwise [CCW]) relative to a reference direction determined by a visual stimulus presented on a planar working surface. Since the position of the stimulus, and therefore the reference direction, changed from trial to trial around the circle, the direction of the movement had to be determined freshly at every trial according to the rules of the task. In this experiment the motor output is the directional outcome of a transformation from a reference to an actual direction. There are many ways by which this problem can be solved. For example, an obvious way would be to form a look-up table which contains the movement directions that correspond to the stimulus directions. Using this strategy, one would simply memorize the corresponding directions in the table and, given a stimulus direction, one would search the table to select the movement direction corresponding to the particular stimulus direction. Of course, one would not have to use numbers, simply imagined directed radii in a unit circle.

A different strategy would be to mentally rotate the stimulus direction in the instructed departure (CCW or CW) by an amount equal to the required angular shift. The look-up table and mental rotation hypotheses lead to different predictions concerning how the reaction time would change, and on this basis they can be distinguished. If the look-up table strategy is followed, the reaction time would increase due to the time taken for the search but this increase should not be greater for larger angles because there is no reason to suppose that searching the table in the case of a large angle should take more time than when searching the table in the case of a small angle. In contrast, the mental rotation hypothesis predicts an increase in the reaction time with the angle because the time taken to rotate a radius through an angle should be proportional to the angle itself. Indeed, the results of the experiments in human subjects [12] showed an increase of the rotation time with the angle and therefore supported the mental rotation hypothesis, as follows.

The angles were 5, 10, 15, 35, 70, 105 and 140°. Nine subjects were instructed to move in the CW departure and 9 to move in either (EI) the clockwise or the CCW departure, as they wished. The RT_θ of movements made at an angle from the stimulus direction showed two kinds of change (Fig. 1): first, a step increase from the RT_0 of movements made in the stimulus direction, and second, superimposed upon it, a linear increase with the amplitude of the angle.

$$\text{CW case}: \mathrm{RT}_\theta - \mathrm{RT}_0\ (\text{msec}) = 155 + 2.37\theta^\circ\ (r^2 = 0.99) \tag{2}$$

$$\text{EI case}: \mathrm{RT}_\theta - \mathrm{RT}_0\ (\text{msec}) = 84 + 2.28\theta^\circ\ (r^2 = 0.98). \tag{3}$$

The slope of the line was similar for the CW (2.37 msec/deg) and the EI case (2.28 msec/deg), but the step increase (y-intercept) for the EI case (84 msec) was substantially less than that of the CW case (155 msec). The linear increase of the RT with angle is compatible with the idea that performance in the task may involve a mental rotation of the imagined movement vector about its origin. The rotation would begin from the stimulus direction and end when the required angle is judged to have been reached; in addition, corrections of this angle at the end of the rotation could be made. The slope of 2.37 msec/deg observed in the CW case corresponds to a rotation rate of 422 deg/sec. Remarkably, this is very close to the value obtained by Shepard and Cooper [20] in experiments of mental rotation of two-dimensional (2-D) visual images. Finally, the finding of a similar rate for the EI case indicates a similarity in strategy with regard to achieving a desired angle. In contrast, the lower intercept observed for the EI case suggests significant savings in processing information which is unconstrained with regard to angular departure.

Fitts' law in mental rotation: the increase in reaction time as a mental movement time

Support for the hypothesis of a mental rotation in our experiments [12] was provided by the results of an analysis of the data based on the assumption that the presumed process of mental rotation involved, indeed, some kind of motion of an imagined movement vector. Assuming this model of internal motion, we analyzed the amplitude–accuracy relations using Fitts' [4] approach to real movements. Specifically, we were interested to find out whether Fitts' law, which holds for real movements, would also hold in the present case.

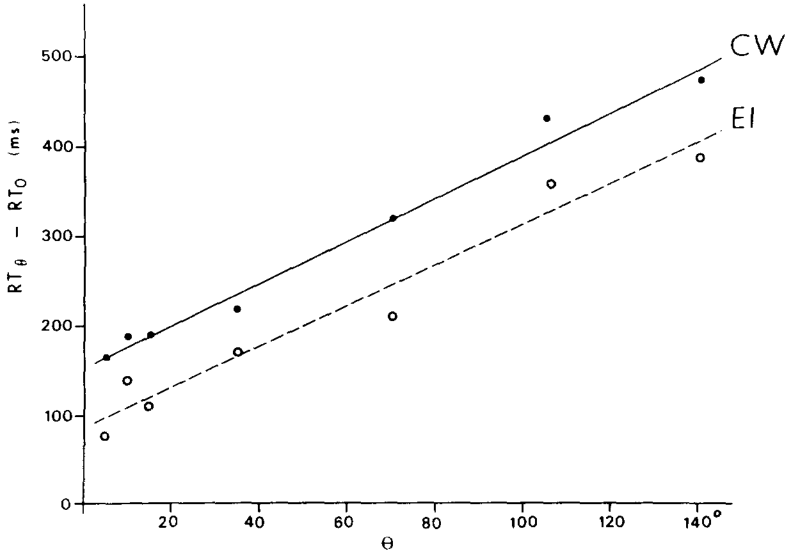

Fig. 1. Changes in RT in CW and EI tasks are plotted versus instruction angle. Each point is the median difference $RT_\theta - RT_0$ ($N = 9$ subjects × 20 trials = 180 trials). See text for details. (Reproduced with permission [12].)

This law relates the movement time, MT, to an informational measure, I_d (index of task difficulty), as follows:

$$\mathrm{MT} = a + bI_d \tag{4}$$

$$I_d \text{ (bits)} = \log_2(2A/W), \tag{5}$$

where A is the amplitude of the movement and W is the target width. This relation has been found to hold in various cases (see [15], for a review of the subject). When the accuracy of the movement is not constrained *a priori*, a measure of dispersion of the movement endpoints can be used as an estimate of W in equation (5). We defined I_d in the present experiments by taking A = achieved angle, and $W = 2s_0$, where s_0 is the circular standard deviation (see Table 1 in [12]). (We limited this analysis to the results of the CW task because the angular variability, s_0, cannot be defined unequivocally in the EI task.) The I_d was calculated from average data obtained from nine subjects [12]; it was found that it increased as a linear function of the instruction angle, as follows (Fig. 2):

$$I_d = 0.46 + 0.015\theta \; (r^2 = 0.98), \tag{6}$$

where θ is the instructed angle (see above).

Finally, the increase in RT was a linear function of I_d (Fig. 3) according to the following equation:

$$\mathrm{RT}_\theta - \mathrm{RT}_0 = 86 + 154I_d \; (r^2 = 0.99). \tag{7}$$

The slope of 154 msec/bit corresponds to an average processing rate of 6.5 bits/sec.

In summary, in accordance with Fitts' law, we found that the increase in RT, considered as a mental movement time, was a linear function of task difficulty which was calculated

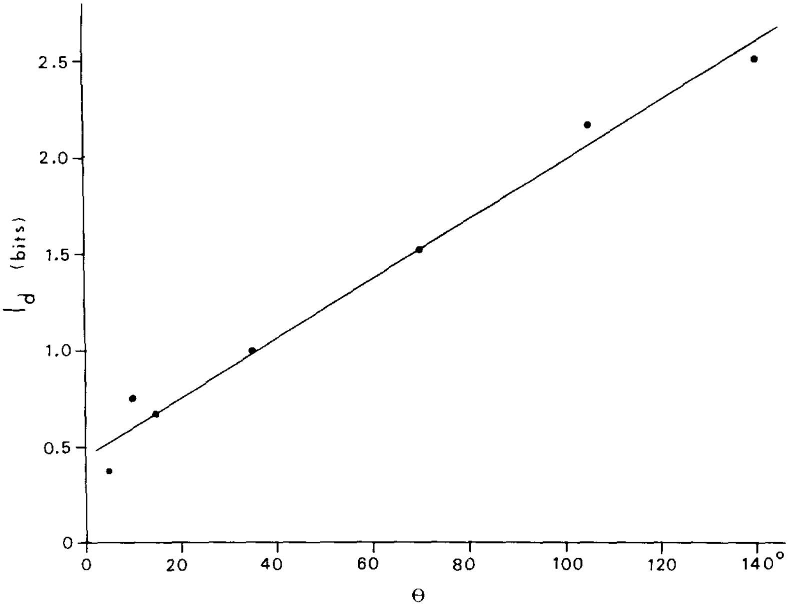

Fig. 2. Index of task difficulty (I_d) is plotted against instruction angle. CW task. (Reproduced with permission [12].)

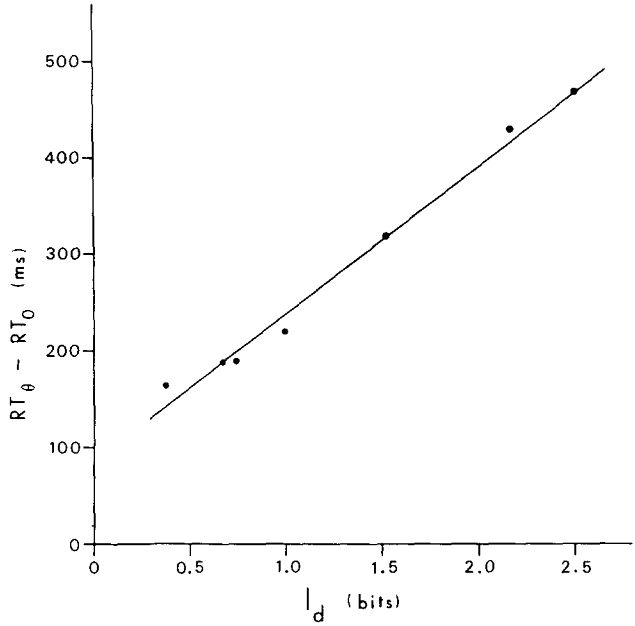

Fig. 3. Changes in RT are plotted against index of task difficulty (I_d). CW task. (Reproduced with permission [12].)

from the angle achieved and its variability. This indicates that Fitts' law holds for the hypothesized rotatory motion of the imagined movement vector, and that both real and imagined movements are governed by similar amplitude–accuracy relations. Indeed, this idea evoked the next series of experiments which exploited recent findings concerning the neural coding of the direction of an *actual* movement to extend them to the case of a *mental* movement, namely mental rotation.

Neural coding of movement direction in space

In the present experiments, the transformation required was an angular deviation from a stimulus direction. The model proposed above to explain the results obtained postulates the rotation in mental space of the image of a movement vector. A visualization of such a vector has been obtained from neurophysiological results of studies of the activity of a population of neurons in the motor cortex of monkeys during the performance of movements in different directions [6, 14]. Individual cells are broadly tuned to the direction of movement, but a weighted vector sum of single cell contributions has provided a measure from the neuronal ensemble ('population vector') that is congruent with the direction of movement (Fig. 4). Moreover, the population vector in the motor cortex predicts accurately the direction of the upcoming movement, when calculated every 20 msec during the reaction time [8], and similarly the direction of movement when the actual movement was withheld for 0.5–3 sec [2], and when it was memorized [22] (Fig. 5).

Three aspects of this analysis are remarkable: its simplicity, its robustness, and its spatial outcome. With respect to *simplicity*, it is noteworthy that the ongoing calculation of the population vector is a simple procedure, for it (i) assumes the directional selectivity of single cells, which is apparent, (ii) involves weighting of vectorial contributions by single cells on the basis of the change in cell activity, which is reasonable, and (iii) relies on the vectorial summation of these contributions, which is practically the simplest procedure to obtain a unique outcome. With respect to *robustness*, the population vector is a robust measure, for it can still convey a good directional signal even with only 100 cells [9]. Finally, it is noteworthy that the population vector is a *spatial* measure, isomorphic in direction with direction in space. Indeed, the population analysis transforms aggregates of purely temporal spike trains into a spatio-temporal population vector. It is this property that makes this measure especially useful, for, through it, the directional tendency of the neuronal ensemble can be monitored in the absence of overt behavior and therefore an insight into the representation of intended movement can be gained in a time-varying and isomorphic fashion. Therefore, it is possible that if monkeys were to perform a mental directional transformation, and recordings of neuronal activity were to be obtained during that performance, the postulated mental rotation of the upcoming movement vector could be visualized in time as a rotating population vector. These experiments are described below.

The neural and the mental: Mental rotation

Two rhesus monkeys were trained to move a handle on a 2-D working surface either towards a visual stimulus ('direct' task) or in a direction orthogonal and CCW from the stimulus direction ('transformation' task), depending on whether the stimulus appeared dim or bright, respectively [11, 16]. Thus the direction of the stimulus (S, in polar coordinates) and the direction of the movement (M) were the same in the direct task but differed in the transformation task, such that $M = S + 90°\mathrm{CCW}$. The task condition ($k = 2$, i.e. direct or transformation) and the direction of the stimulus ($m = 8$, i.e. 8 equally spaced directions on a circle) resulted in 16 combinations ($k \times m = 16$ 'classes') that were varied from trial to trial in a randomized block design. In eight of these combinations the

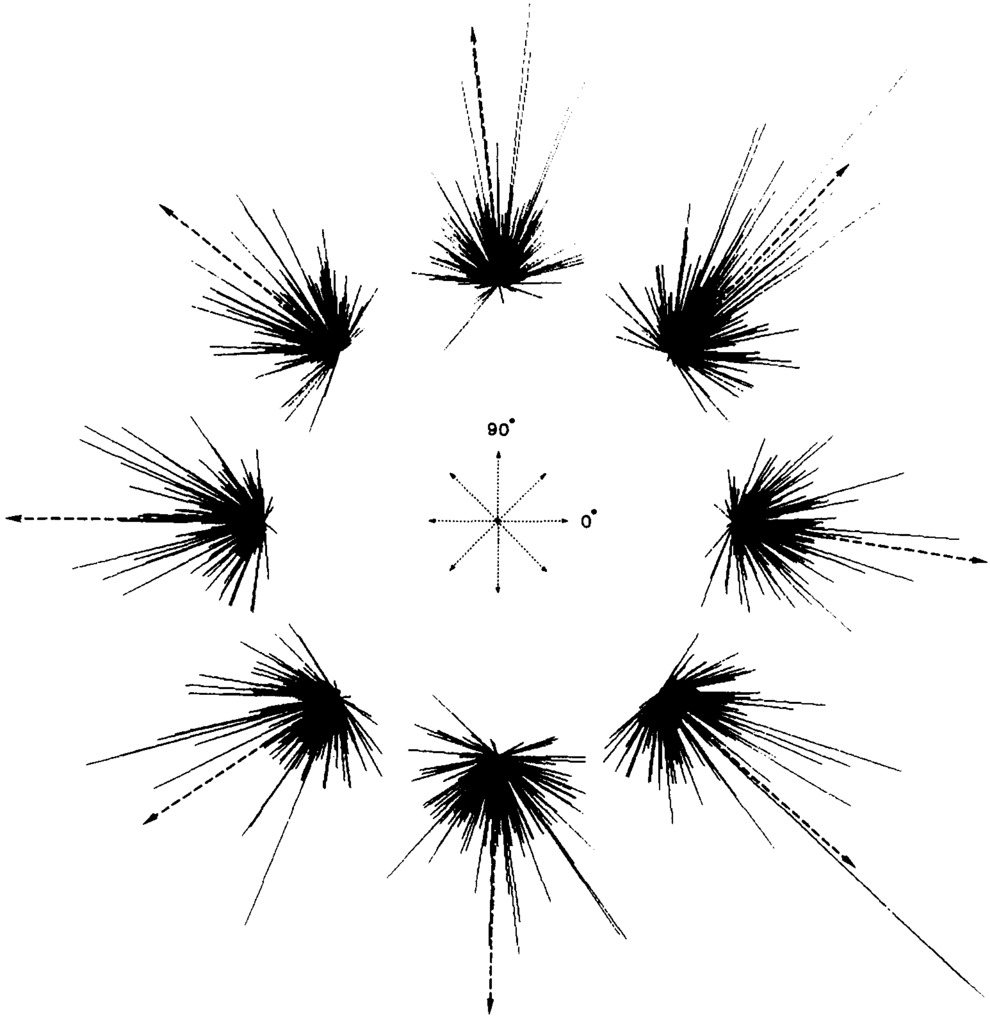

Fig. 4. Vector contributions of 241 directionally tuned motor cortical cells are shown for each of the eight movement directions tested. Notice the spatial congruence between the direction of the vectorial sum (thick interrupted lines in each plot) and the direction of movement (thin interrupted lines at center). (Reproduced with permission [6].)

direction of the stimulus was the same for both tasks, whereas the direction of the movement was the same in the remaining eight cases.

The impulse activity of single neurons was recorded in the arm area of the motor cortex, contralaterally to the performing arm, and the data obtained analyzed at the single cell and neuronal population levels [11, 16]. Individual cells were active in both tasks; no cells were found that were active exclusively in only one of the two tasks. Moreover, the patterns of single cell activity in the transformation task frequently differed from those observed in the direct task when the stimulus or the movement were the same; that is, cells could not be classified reliably as stimulus- or movement-related (for details, see [16], especially Fig. 5 in [16]). However, an analysis of the activity of the neuronal population using the time evolution of the neuronal population vector [8] revealed an orderly rotation

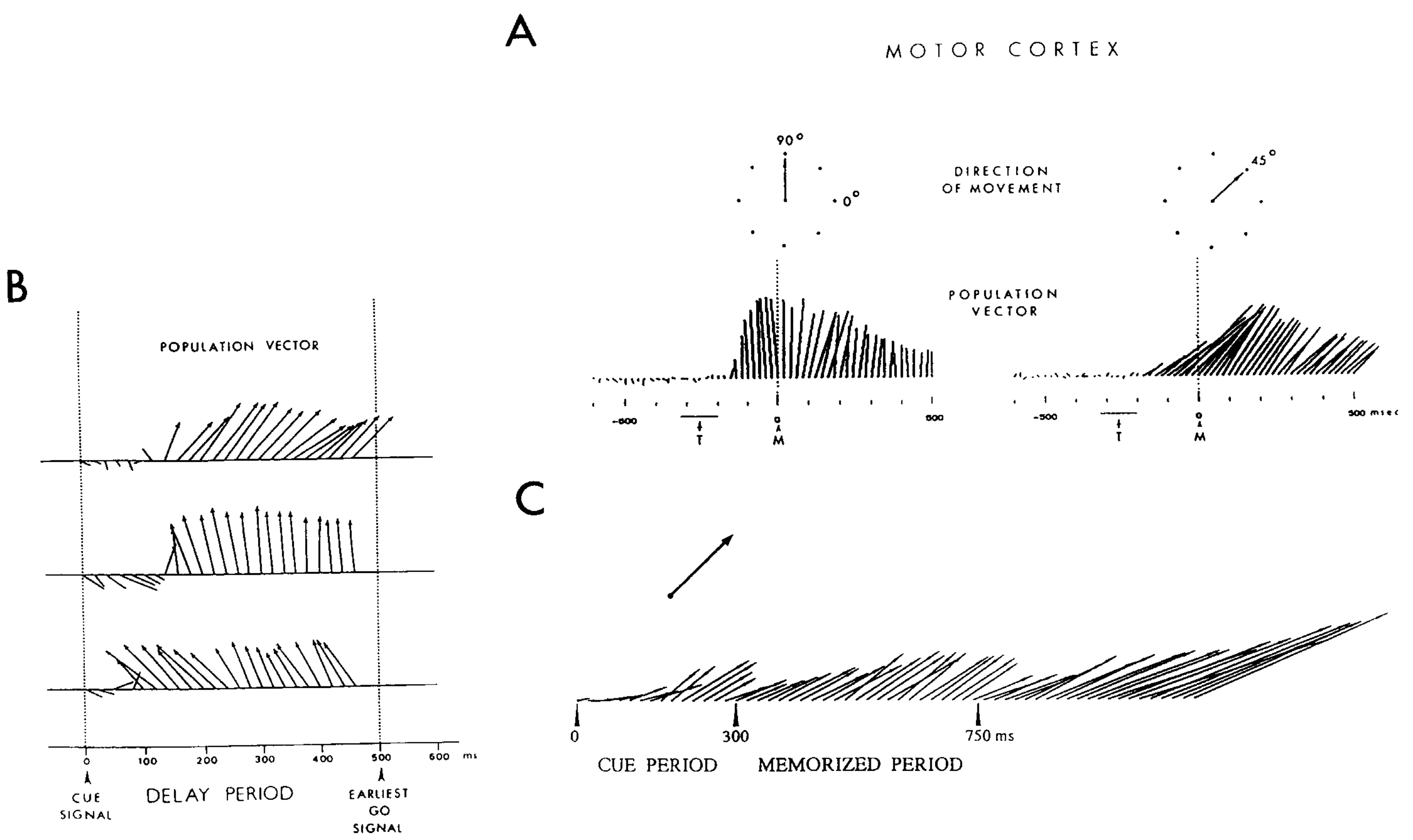

Fig. 5. (A) The population vector during the reaction time points in the direction of movement well before the movement begins. Before the target onset (T), the population vector is very short and its direction varies from moment to moment. Well before the onset of movement (M), it increases in length and its direction points to the direction of the upcoming movement. This finding suggests that even the earliest inputs to the motor cortex are relevant to the direction of the upcoming movement. (Reproduced with permission [8].) (B) Time evolution of the neuronal population vector during an instructed delay period. Three movement directions are illustrated. (Reproduced with permission [7].) (C) Time evolution of population vectors in the memorized delay task. All population vectors 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. (Reproduced with permission [22].)

of the neuronal population vector from the direction of the stimulus towards the direction of the movement through the 90° CCW angle (Fig. 6). The hypothesis was tested that this apparent rotation of the population vector could 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 directions: if cells of the former type were recruited at the beginning of the reaction time, followed by those of the second type, then the vector sum of the two could provide the rotating population vector. However, such a preferential activation of 'stimulus-direction' centered and 'movement-direction' centered cells was not observed. On the other hand, a true rotation of the population vector could be reflected in the engagement of cells with intermediate preferred directions during the middle of the reaction time. Indeed, such a transient increase in the recruitment of cells with intermediate (i.e. between the stimulus and movement) preferred directions during the middle of the reaction time was observed (see Fig. 13 in [16]). This supports the idea of a true rotation of the population signal. Interestingly, the rotation rates (direction of population vector vs time) observed [16] were very similar to the rates (increase in reaction time vs angle) observed in the human studies [12].

In summary, the dynamic processing of a directional transformation was successfully visualized by the neuronal population vector analysis. Moreover, these experiments provided direct neural evidence for a mental rotation and its nature as an analog process.

Neural bases for visuomotor and visual mental rotations

One can hypothesize that there is a common brain structure underlying mental spatial rotation in both visuomotor and visual tasks. However, at the present stage, it is not clear whether such common brain structure exists. Moreover, the assumption that a common brain structure underlies visuomotor and visual mental rotations is not necessary to account for the results obtained. Indeed another hypothesis could be that there are similar neurophysiological constraints when a spatial rotation must be performed, irrespective of the brain structures involved.

As discussed above, information about movement direction resides in the combined activity of the neuronal ensemble, and can be visualized as the neuronal population vector [6, 13, 14]. The studies on visuomotor mental rotation on monkeys reviewed above have clearly showed that mentally rotating an intended movement direction activates an ensemble of neurons in the motor cortex [11, 16]. However no other brain areas have been explored when the animal performed this task, and therefore it is not known whether the motor cortex is the locus of visuomotor mental rotation, whether its activity reflects a transformation that is concurrently generated elsewhere, or whether, and most probably, mental rotation is a distributed brain process involving several areas. Nevertheless the fact that the motor cortex is involved in such a cognitive task is *per se* remarkable, for the motor cortex is not generally considered to be involved in cognitive operations (but see [5]). It is possible that the motor cortex is involved in a mental spatial transformation only when such transformation is a process in the preparation of the movement.

Memory scanning

An important aspect of cognitive function relates to memory operations. A particular kind of such an operation is retrieval of memorized items in a list. Sternberg [23, 24] presented evidence that this operation involved memory scanning. He devised a series of

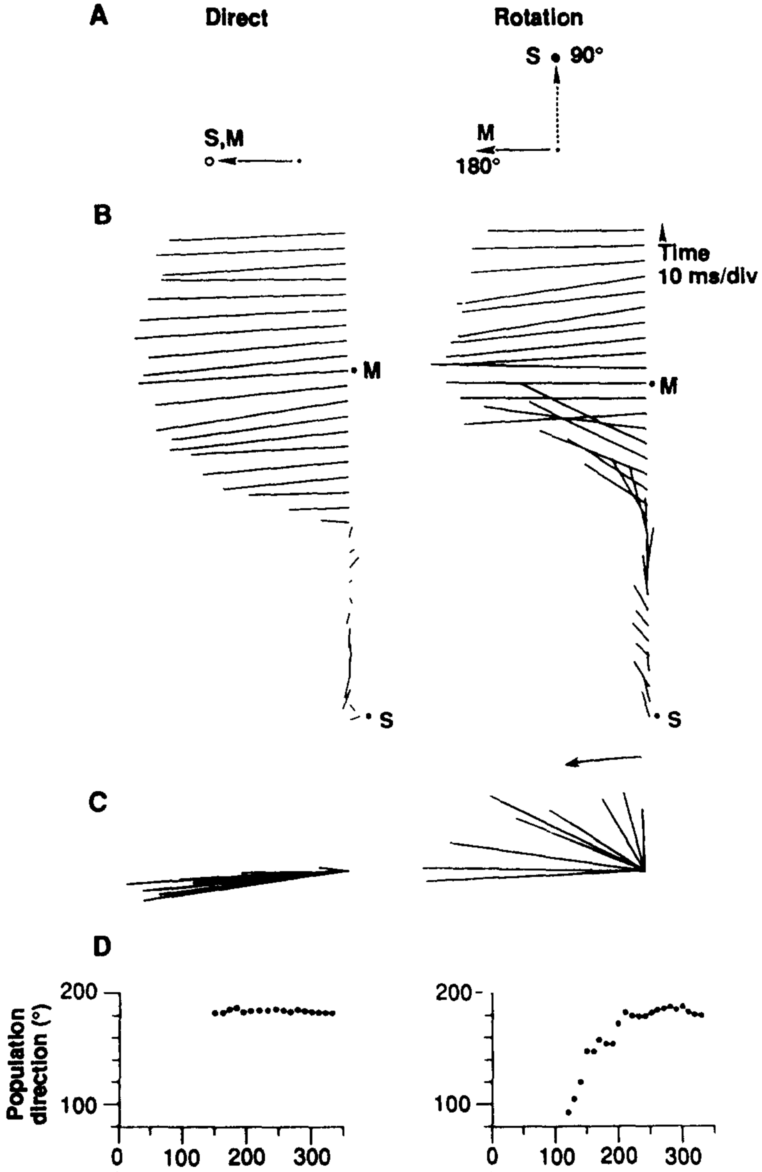

Fig. 6. Results from a direct (left) and rotation (right) movement. (A) Task. Unfilled and filled circles indicate dim and bright light, respectively. Interrupted and continuous lines with arrows indicate stimulus (S) and movement (M) direction, respectively. (B) Neuronal population vectors were calculated every 10 msec from the onset of the stimulus (S) 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 it points initially in the direction of the stimulus and then rotates counterclockwise (from 12 to 9 o'clock) to point 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 after stimulus onset (S). For the direct case (left panel), the direction of the population vector is in the direction of the movement (≈180°); for the rotation case (right panel) the direction of the population vector rotates counterclockwise from the direction of the stimulus (≈90°) to the direction of the movement (≈180°). (Reproduced with permission, copyright by AAAS [11].)

tasks that involve recognition of items in a memorized list. Typically, the stimulus ensemble consists of a list of items. A subset of this list is presented sequentially to the subject, followed by a test stimulus from the stimulus ensemble. Three variants of these tasks were used, each of which required a different response by the subject involving item-recognition, context-recall, or context-recognition. In the *item-recognition* task (scanning-to-recognize) the subject is required to make one response ('positive response') if the test stimulus was contained in the list presented (the 'positive set'), and a different response ('negative response') if the test stimulus was not contained in the positive set. It was found that the RT, from the presentation of the test stimulus to the response, was a linear function of the number of elements in the positive set with a slope of 38 msec/stimulus item [23, 24]. This finding was interpreted as evidence for a process of memory scanning: the list of items in the positive set is scanned and the test item is compared to each item in the list. The higher the number of items in the list, the more time the process takes. Other findings suggested that this memory scanning is exhaustive (i.e. all items in the list are compared) rather than self-terminating (i.e. stop when a positive comparison is found). The increase in the RT with the length of the list is robust and is observed even for well learned lists. Although other hypotheses have been advanced, memory scanning has held its ground adequately [25].

The *context-recall* task requires location of an item in the list ('scanning-to-locate') rather than recognition. A list of items is shown sequentially to a subject followed by a test stimulus selected randomly from the items presented, except the last. The subject is required to identify (e.g. by name) the item that followed the test item in the list. Under these conditions, the RT again increased with the number of items in the memorized list, but the process was self-terminating as evidenced by the increase of the RT with the serial position of the item in the list and the linear increase of RT with both the number of items in the list and their serial position. The slope was 124 msec/item. Assuming that, on the average, one-half of the items on the list were scanned (given a self-terminating process) the slope is effectively approximately 250 msec/item, indicating that 'scanning-to-locate' is about 6–7 times slower than 'scanning-to-recognize'.

Finally, the *context-recognition* task involves recognition of contextual information, that is information concerning serial order of items in the list. Again, a list of items is presented sequentially to a subject but a pair of items in that sequence is presented as the test stimulus. The subject is required to decide whether the left-to-right order of the pair was the same as its temporal order in the list. The RT increased as a linear function of the number of items in the list, and the slope was the same as in the context-recall experiment described above. However, the y-intercept was about 100 msec higher in the present case, reflecting the additional time taken to decide the serial order of the items presented.

In summary, the 'memory scanning' tasks of Sternberg provide a powerful tool by which cognitive operations on memorized lists can be investigated. In the experiments described below [10], we adapted the *context-recall* task for a study of memory-scanning in the motor system in the absence of verbalization. The memorized items were visually guided movements made in 2-D space in the direction of lights turned on sequentially on a planar working surface, and the test stimulus was one of the lights in the previous sequence, except the last: the subject was required to move in the direction that followed, in the sequence, the direction of the test light. We wanted first to define the human capacities in performing the task.

Motor memory scanning: Context recall

Fourteen human subjects performed in this task. First, they made a series of 2–6 movements in different directions from a central point towards peripheral lights on a planar working surface ('list trials'). Then, after a warning signal, one of the previous list stimuli, except the last, was presented again ('test trial'). Subjects were instructed to move in the direction of the stimulus which was presented next in sequence in the list. The mean RT in the test trials increased as a linear function of the number of movements, S, in the list:

$$\text{RT (msec)} = 105 + 205.8S, \quad (2 \leq S \leq 6). \tag{8}$$

This finding suggests that the task involves memory scanning of visuomotor list items.

The tasks used in these experiments required the subjects to make a movement in a direction determined by a series of movement directions ('list directions') immediately preceding the test stimulus. The direction required was the one that followed the direction of the test stimulus when the latter appeared in the series. Successful performance in the task required (a) at least some recall of the list, and (b) generation of a movement direction that depended on the serial position (i.e. context) of the test stimulus in the list. Thus the task closely resembled that used by Sternberg [24] in the context-recall experiments which involved recall of sequentially presented visual items. The main difference between the present experiments and those of Sternberg was that our experiments required a visuomotor response during the list trials, that is the production of movements in the direction of visual stimuli, whereas in Sternberg's case no action was required during the presentation of list items.

A salient finding of this study was the strong and linear dependence of the mean RT on the number of items in the list (Fig. 7). This effect was present in all subjects and was the only statistically significant effect on the RT. The linear increase of RT with list length suggests a memory scanning of list items [24]. It is interesting that this effect was observed

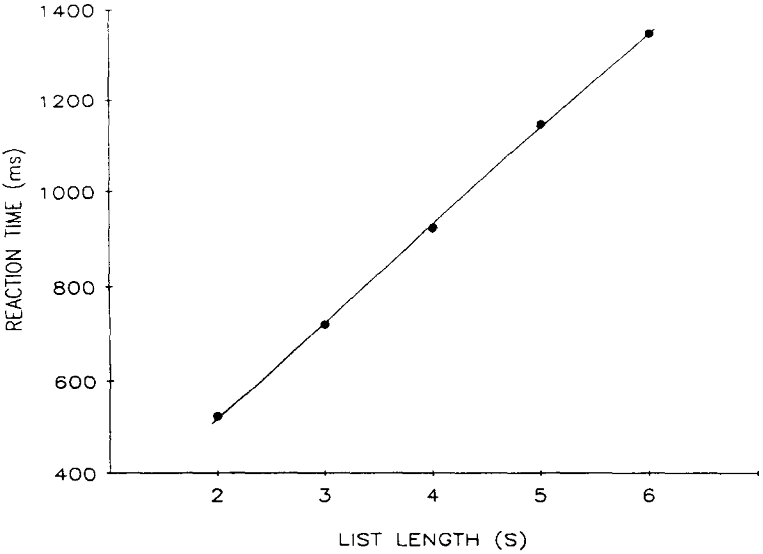

Fig. 7. Mean RT of correct responses is plotted against list length. (Reproduced with permission [10].)

also for directional errors. This suggests that subjects scanned in memory list items even if the response direction was quite variable.

The slope of RT of correct responses vs list length in the present experiments [10] was 205.8 msec/item. This is much higher than that observed by Sternberg [24] which was 124 msec/item. Several factors probably contributed to the higher slope observed in the present experiments. First, the list items in the present experiments were reaction-time movements that were probably more disruptive of memory processes than the passively displayed items presented by Sternberg because a response (i.e. a movement) was required in each trial in the list. Second, the items to be memorized were complex for they comprised stimulus–response elements rather than stimuli alone. Moreover, they could be memorized in different ways which could create a choice situation for the performing subject. For example, one could memorize the location of the list stimulus and the movement towards it or the movement direction alone; also, one could memorize the sequence in a symbolic form (e.g. using numbers, 1, 2, 3, 4, . . .) and associate with a number the position of the light and/or the movement direction. Finally, the time between successive list stimuli was precisely controlled by Sternberg [24] at 1.2 sec per digit, whereas in the present study this time was longer (1.49 sec on the average) and variable (S.D. of 0.91 sec) due to the variability in behavioral times (RT, movement time) and performance (e.g. center hold errors).

It is interesting that the slope was smaller in a motor memory scanning task in which the subjects viewed the list stimuli but did not move to them [10].

$$\mathrm{RT}\ (\mathrm{msec}) = 130 + 163.1S, \quad (2 \leq S \leq 5). \tag{9}$$

The difference in the RT between the two tasks is likely to be due to the longer time that it took for the sequence of the list items in the previous task [10] due to the intervening movement towards them. However, this slope (163.1 msec/list item) is still longer than that obtained by Sternberg [24].

Mental rotation and memory scanning compared

A similarity in the motor rotation [12] and visual rotation [20] studies is that there is appreciable diversity in the rotation rates obtained among different subjects. In fact, we used this feature to test the idea that motor and visual mental rotation processes may be associated: Indeed, a significant correlation was found between the two rotation rates in a group of subjects who performed both tasks [17]. This suggests that the two processes might share a common stage, or that both processes involve constraints that result in the relation obtained. If it be true that visuomotor and visual mental rotations share common processing constraints, then a correlation across subjects should be observed between the processing rates of mentally rotating a movement vector and those for mentally rotating a visual image. However, it is also conceivable that a correlation between processing rates may result from general processing rate differences among subjects, that is, some subjects may perform generally faster (or slower) than others. Thus, a control is needed with a different kind of task where a processing rate can also be estimated. We chose the visuomotor memory scanning task [17] which conforms to these requirements. Consequently, the subjects performed in three different tasks (Fig. 8): (a) A visuomotor mental rotation task [12], in which they were instructed to make a movement at a given angle from a visual stimulus direction; (b) a visual mental rotation task inspired from the

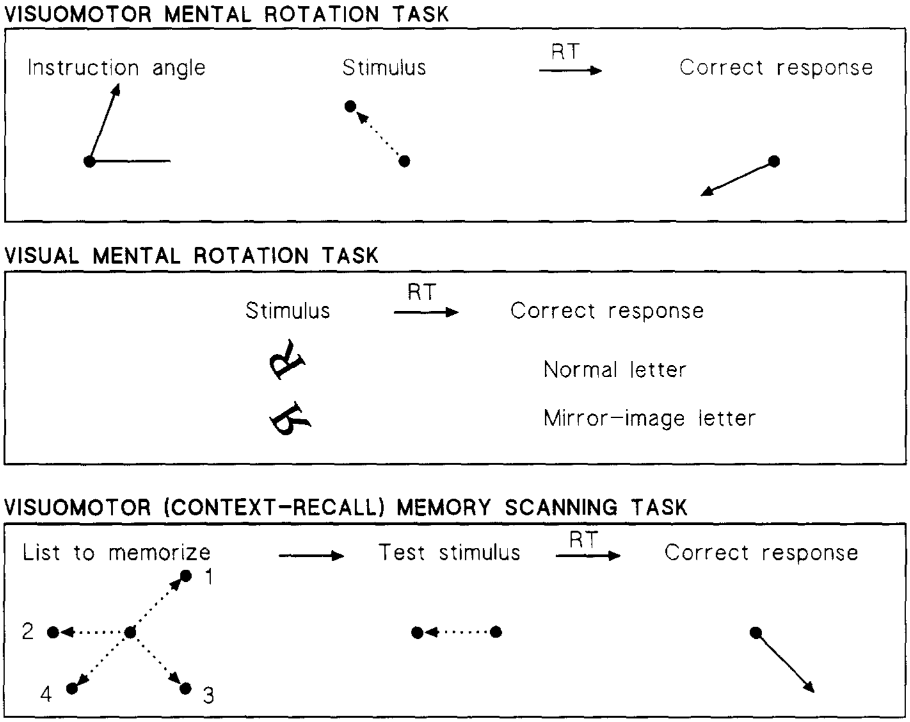

Fig. 8. Schematic diagram of the three tasks used. See text for details. RT, response time. (Reproduced with permission [17].)

Shepard and Cooper letter rotation task [20], in which the subjects had to decide whether the letter displayed was normal or mirror-image regardless of its orientation in the plane of presentation; and (c) a visuomotor context-recall memory scanning task [17], in which a list of 2–5 stimuli directions were presented sequentially. Then, one of the stimuli, except the last one, was displayed again (test stimulus). The subjects were instructed to move in the direction of the stimulus that followed the test stimulus in the previous sequence. The processing rate of each subject in each task was estimated using the inverse of the slope between the RT and the angle (mental rotation tasks) or the list length (memory scanning task). We found that the processing rates in the mental rotation tasks were significantly correlated (Fig. 9) but that neither correlated significantly with the processing rate in the memory scanning task (data not shown). These results suggest that visuomotor and visual mental rotations share common processing constraints that cannot be ascribed to general mental processing capacities. Moreover, we found that the slopes of RT vs angle obtained in the visuomotor mental rotation task were 59% higher than those obtained in the visual mental rotation task. This suggests that mentally rotating an intended movement direction is more time-consuming than for 2-D visual images like letters.

THE NEURAL AND THE MENTAL: MEMORY SCANNING

The neural correlates of visuomotor memory scanning were investigated recently [18]. A monkey was trained to exert a force pulse on a 2-D semi-isometric manipulandum in eight

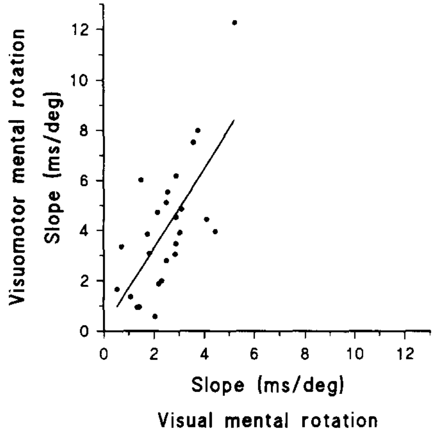

Fig. 9. The individual slopes obtained from the linear regression of median response time on angle for the visuomotor mental rotation task and for the visual mental rotation task are plotted against each other. (Reproduced with permission [17].)

different directions. The force exerted was displayed as a feedback cursor. The memory task can be divided into three parts: (1) A sequential presentation of 3 or 4 yellow stimuli, which stayed on the screen; (2) one of the stimuli, except the last one, changed from yellow to blue which identified it as the test-stimulus, and gave the go signal; (3) the correct response was to the stimulus that succeeded the test-stimulus during the initial presentation. This task required the memorization of the order of presentation of the stimuli, but not of their position in space which was still available. In a control task, one stimulus was presented and the response was made after the go signal. A preliminary analysis of the monkey's eye movements revealed a variety of patterns of saccading towards, and fixating stimuli that did not bear a clear or consistent relation to the hand motor response. For example, although the eyes would ultimately fixate the target of the hand response, prior to that fixation they would move to a different stimulus, or they would move from one stimulus to another in a sequence pattern that differed from one stimulus configuration to another but also for the same stimulus configuration, from trial to trial. Overall, there did not seem to be an obvious correspondence between eye and hand movements. However, the scanning pattern of eye movements need to be analyzed in detail and could potentially provide an insight into the animal's scanning strategy.

The activity of 544 cells in the motor cortex was recorded during performance of the two tasks. The salient finding of the study was that cell activity usually reflected first the direction of the test-stimulus, then switched to reflect the direction of the response, when the test stimulus was the second in the sequence. This was true both for the case of single cells, which showed abrupt changes in activity reflecting the two different directions, as well as for the population vector, which also showed an abrupt shift (within ≈60 msec) from the direction of the test stimulus to that of the motor response. Another finding was that the time for which neural activity reflected the direction of the test stimulus, and, correspondingly, for which population vector stayed in that direction, was approximately 100–150 msec. These results indicate that the neural process that underlies memory scanning is quite different from that which underlies mental rotation: whereas the latter involves an apparently continuous change of direction of the population vector, the memory scanning seems to involve abrupt shifts of the population vector from one direction to another. The explanation, then of the increase of the RT in mental rotation and memory scanning tasks would be different, as follows. In mental rotation, the time taken reflects the finite time to rotate an image, whereas in memory scanning the time taken reflects the aggregate of minimum scanning time required for each list item. In fact, the latter hypothesis is in accord with findings indicating that the distribution of the RT in memory scanning is not uniform but consists of multiple peaks (Pellizzer and Georgopoulos, unpublished observations), which possibly reflect aggregates of elementary scannings.

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