

An alternative interpretation of population vector rotation in macaque motor cortex

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Abstract

Neural recordings from the primary motor cortex of monkeys performing movements at an angle to a cue stimulus have yielded two main results: (A) the population vector rotates from the direction of the cue to the direction of movement, and (B) cells with intermediate preferred directions are recruited during the middle of this rotation. These results have been interpreted as the neural correlates of a process of 'mental rotation'. Here we propose that results A and B are also consistent with an alternate hypothesis of 'response substitution', given four well known features of cortical neurophysiology. © 1999 Elsevier Science Ireland Ltd. All rights reserved.

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Several studies have recorded neural activity in primary motor cortex (MC) during tasks which dissociate the spatial direction of a visual cue from the direction of the movement which it specifies [1,2,5,9,12,16,17]. Prominent among these is a study by Georgopoulos and colleagues [5,9] in which monkeys performed center-out movements in a plane under two conditions: a 'direct' task, where movements were made directly toward the cue stimulus; and a 'transformation' task, where movements were made in a direction 90° counter-clockwise (CCW) to the cue stimulus.

The monkeys may have used various strategies to perform the transformation task. The first, called 'mental rotation', involves the rotation of an intended movement direction vector from the cue stimulus counter-clockwise through 90°, arriving at the required movement direction. Lurito et al. [9] present two pieces of evidence for this hypothesis: (A) the population vector (PV) from MC rotates from the stimulus direction to the movement direction during the reaction time (RT); (B) cells with preferred directions (PDs) intermediate between the stimulus and movement directions are recruited during the middle of the RT, suggesting a sequential recruitment of cells by a rotating input signal.

Below, we illustrate that results A and B are also consistent with a second hypothesis, which we call 'response substitution', where the transformation task is solved using a learned association between a cue stimulus and the rewarded movement direction. Because the cue is a target in the direct task, its presentation during the transformation task initially elicits a default movement intention directed toward it (a response with high 'stimulus-response compatibility' [3]). Shortly thereafter, this default response is aborted and replaced by the learned response in the 90° CCW direction. Below, we propose that such a replacement of signals, together with well known properties of movement-related neural activity, is sufficient to produce the results of Lurito et al. [9].

Our proposal rests on four premises: (1) cells have broad directional tuning [4]; (2) cells are recruited at different times during the reaction and movement times of a task [14]; (3) the magnitude and onset times of movement-related cell activities are weakly coupled [4,11], (4) during the RT, the earliest neural activity covaries with the direction of the instructional signal, while later activity covaries with the direction of the final intended movement [1,2,12,16,17].

We demonstrate our point by implementing these four premises in a simple model of cell activity and simulating the direct and transformation tasks. However, it must be noted that our goal is not to propose a new computational

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model of cortical activity, but merely to demonstrate that results A and B follow from premises (1)–(4). A variety of formalisms may be employed to this end, as we verified in another set of simulations (not shown) using a different kind of model (a cascade of ‘integrate-and-fire’ neurons).

We describe cortical neurons using the following equations

$$\frac{dx_i}{dt} = \kappa(-x_i + g_i E_i) \quad (1)$$

$$y_i = [x_i - \Gamma_i]^+ + b_i \quad (2)$$

where y_i represents the activity of a primary motor cortical neuron and x_i represents the processed input to neuron i . The parameter κ is a time constant ($\kappa = 13$), g_i is a gain (normal distribution with mean 1.2 and standard deviation (SD) 0.5), Γ_i is a threshold (mean 0.4 and SD 0.2), b_i is a baseline activity (set to zero since the analyses of interest focus only on changes of activity) and $[w]^+ = \max(w, 0)$. The rate of activity growth dx_i/dt is dependent on the magnitude of excitatory input E_i (see Eq. (3)). This rate determines both the time at which the threshold is crossed and the final level of activity, resulting in a coupling of onset time and magnitude. When the strength of this coupling is reduced to levels estimated physiologically [11] by randomly shifting the onset time of cells during movements in different directions, the main results still hold (data not shown).

Cells were presented with directional inputs each with direction ϕ_j and magnitude a_j . To simulate the broad directional tuning of cells we used the following excitation function:

$$E_i = \sum_j a_j [\cos(\theta_i - \phi_j) + s_j]^+ \quad (3)$$

where θ_i is the preferred direction of neuron i (uniform distribution from 0 to 2π), and s_j is an offset parameter controlling the breadth of that neuron’s tuning function (normal distribution with mean 0.0 and standard deviation 0.3). Finally, to produce recruitment curves similar to those reported for MC during the direct task [9,14], each cell’s input was withheld for a random delay of 0.05–0.2 s.

Using these parameters, we reproduced many features of the cell activities seen in MC during a direct reaching task, including broad cosine-tuning, recruitment curves, and coupling of onset time and magnitude. When modeling the transformation task, we used the following input schedule. For the first 100 ms, the magnitude of the stimulus-direction signal was 1 and the magnitude of the movement-direction signal was zero. During the next 250 ms, these two magnitudes switched in a linear manner, with the SD signal decaying to zero while the MD signal grew to 1. The two signals then remained at constant values for the final 150 ms of the simulation.

Eqs. (1)–(3) describe the model. To analyze the model’s behavior during both direct and transformation tasks, activities y_i were summed together into a population vector (PV)

at intervals of 20 ms for 500 ms. The PV was computed as

$$\vec{P} = \sum_i \vec{p}_i (y_i - b_i)$$

where \vec{p}_i is a unit vector in each cell’s preferred direction as obtained from the direct task. In all simulations, 300 neurons were used. Direct and transformation movements were simulated to each of eight targets spaced evenly around 360° to mimic the paradigm used by Lurito et al. [9].

Fig. 1A illustrates the time-varying PV computed for movements away from the monkey in the transformation task. During the transformation task, the PV grows gradually and rotates from the stimulus direction to the movement direction. During the direct task, the vector simply grows in the movement direction (not shown). The model also exhibited a systematic variation in onset times dependent on each cell’s PD. Fig. 1B shows the cumulative histograms of onset times for three groups of cells: those whose PD fell within 10° of the stimulus direction (SD cells); those whose PD fell within 10° of the movement direction (MD cells), and those whose PD fell within 10° of the direction intermediate between stimulus and movement directions (ID cells). These groups were collected across eight movement directions after they were normalized with respect to the stimulus. As is clear from the cumulative histograms, SD cells tended to be recruited before ID cells which in turn were recruited before MD cells. Fig. 1C shows the percentage of cells in each group recruited during three epochs: 50–110 ms after the start, 130–190 ms, and 210–270 ms. As in Fig. 12 of Lurito et al. [9], the ID cells were most often recruited during the middle epoch. (Note: There are some differences between this histogram and the experimental data [9]. However, because our results on Fig. 1C look even more like a rotation process than does the data, this difference cannot be used to support a hypothesis of rotation.)

Fig. 2 illustrates two related phenomena reproduced by the model. Fig. 2A shows results resembling the modest RT differences observed by di Pellegrino and Wise [2] in monkeys performing a transformation task with different angular offsets between stimulus and movement directions. Since movement initiation may be related to the crossing of a threshold of activity [7], we estimated the movement onset as the time at which the length of the PV exceeded an arbitrary threshold. This threshold was crossed earliest when stimulus and movement directions were aligned, and the RT showed a systematic relationship with the angular difference between them. This relationship was produced in the model because the growth of activity in MD cells was hastened when the SD input fell close enough to their PD to contribute to their excitation.

A second auxiliary result concerns a consistent deviation of the PV at the beginning of the RT [9]. During transformation tasks, the PV started 30° CCW from the stimulus direction and rotated counterclockwise to the movement direction. During direct tasks, the PV also started CCW from the stimulus direction but rotated clockwise toward

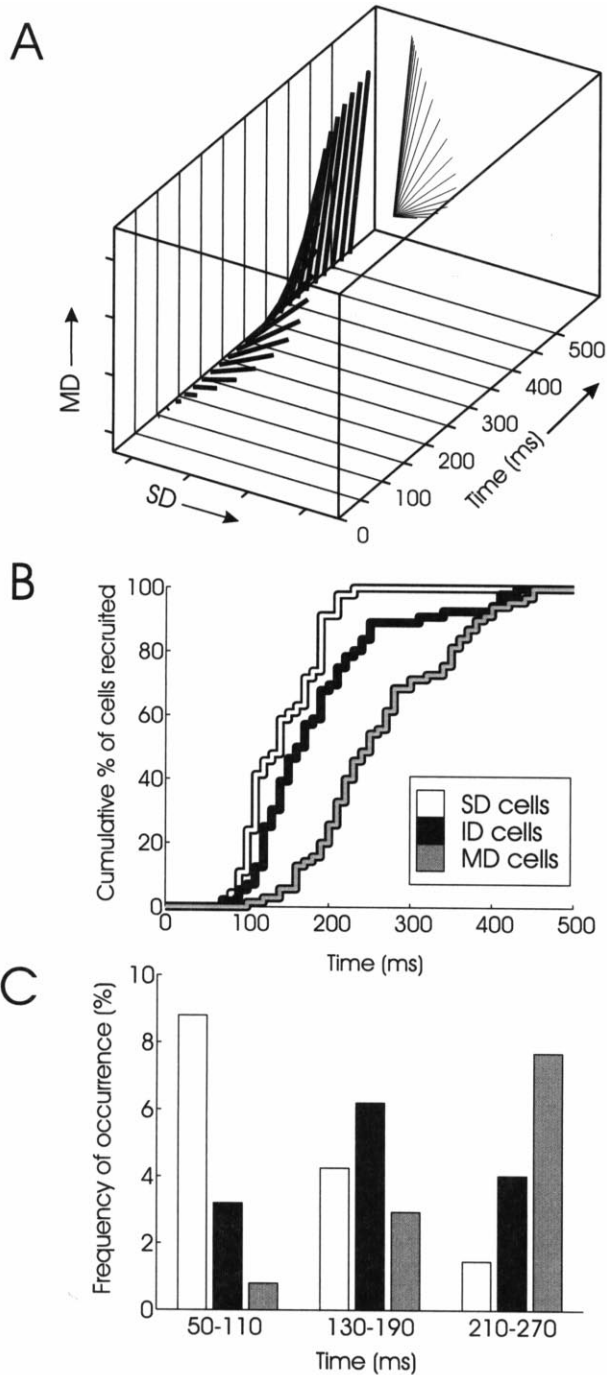


Fig. 1. (A) Time sequence of the population vector (plotted at 20 ms intervals) during the transformation task. (B) Cumulative histograms of recruitment times for cells with PDs near the stimulus direction (SD), intermediate direction (ID), and movement direction (MD). (C) Histogram showing, for each of three epochs, the percentage of recruited cells that were SD, ID, or MD cells.

the stimulus. Both these effects were reproduced by the model under the assumption that the cue stimulus elicits two independent directional input signals – one at the stimulus direction and a weaker one at the 90° CCW direction.

Such multiple inputs may occur because the monkey is initially unsure of which movement to make, and both potential responses are represented in its motor cortical activity. With these two input signals, the initial direction of the PV falls between the two input directions. In the transformation task, the 90° CCW direction is selected as the target for movement, and therefore the input signal in that direction grows while the SD signal decays. The result is counterclockwise rotation. Conversely, in the direct task, the stimulus direction signal grows while the 90° CCW direction signal decays, causing a slower and smaller clockwise rotation (Fig. 2B). A similar combination of input signals could be used to explain the consistent deviation of the initial premotor PV from the stimulus location in the study by di Pellegrino and Wise [2] (see also Ref. [16]).

The original motivation for the concept of mental rotation came from human studies which showed increases in RT with increasing angular deviation between two objects that were to be compared [13] or the angle between stimulus and movement directions [6]. In the monkey experiments of

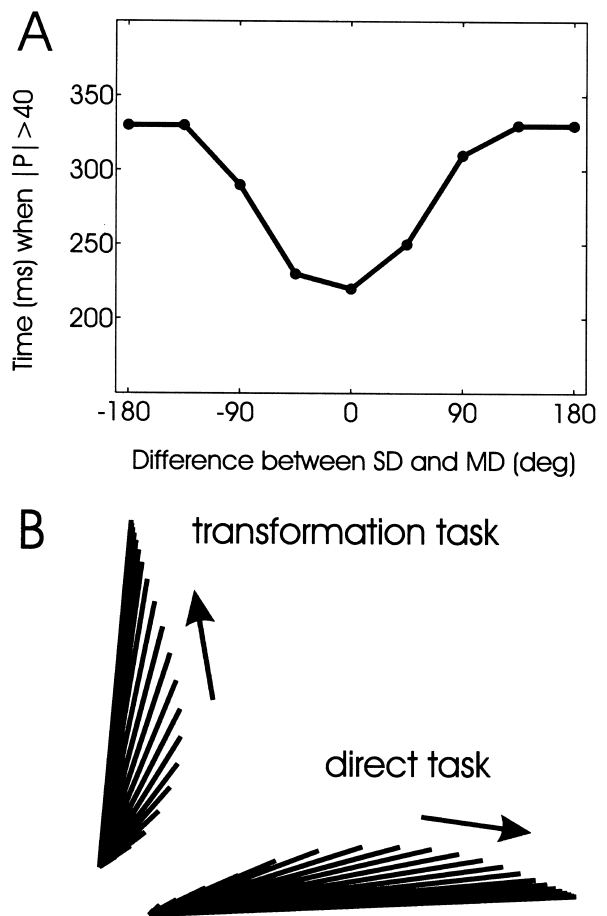


Fig. 2. (A) Simulated ‘reaction times’ for tasks with different angles between stimulus and movement directions. Plotted are the times (in ms) at which the length of the population vector $|\vec{P}|$ exceeded an arbitrary threshold of 40. (B) Population vector rotations generated with two initial input signals (see text) during transformation and direct tasks.

Lurito et al. [9], such increases in RT accounted for only 1.6% of total reaction time. In a related study, Wise and colleagues found a relationship between increases in RT and angular deviations between stimulus and movement directions [2,16], but these increases were not of the order seen in human subjects [6]. It is possible that the small RT differences in the monkey experiments may be due to overtraining [9], since RT differences are known to decrease with practice. However, since the PV, even from the highly trained animals, required about 140 ms to rotate during the transformation task, it is unclear why this rotation time should not produce a matching increase in RT. As illustrated by the simulation in Fig. 2A, performance of movements at an angle to a cue stimulus may incur a time cost unrelated to a process of mental rotation.

Another relevant experimental result concerns motor cortical activity during a context-recall task [10], in which a monkey was trained to make isometric movements to a target determined by its serial placement in a sequence of targets. In that task, there was an abrupt change in the direction of the PV and no recruitment of cells with PDs intermediate between the two possible response directions (S2 or S3, see Ref. [10]), suggesting a process of response replacement. The difference between these results and those of Lurito et al. [9] may be due to differences in the task design, in particular, to the fact that in [10] the monkeys have 400 ms to prepare their potential responses, whereas in [9] they made the movement immediately after the stimulus appeared. Thus, in [10], the two potential movements can be prepared well ahead of the end of the instructed delay period and then quickly exchanged when the target identifying signal is given, resulting in a rapid exchange of directional signals in MC.

We are aware of two other proposals which reach similar conclusions through a somewhat different set of premises [8,15]. Our hypothesis is similar to both in that it involves the gradual replacement of one directional signal with another. Unlike ours, however, these previous models relied upon specific interactions among cells to explain the rotation data. We extend these arguments by showing that the rotation results can be explained without any theory of cell-to-cell interactions but are simply consequences of well known features of cortical neurophysiology.

Our fourth premise concerns the nature of the stimulus-direction and movement-direction signals that have been observed in motor cortex. That stimulus-related signals precede movement-related signals has been interpreted as evidence that motor cortex may be involved in the transformation of extrinsic visuospatial information into appropriate motor commands [12,17]. An alternate hypothesis is that the initial activity reflects an early 'default' intention of movement directed toward the stimulus which is later quenched and replaced by a new movement intention reflecting more complex S-R associations [1,3]. Our argument here has been

presented with reference to the latter interpretation, but it is in fact compatible with both.

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