Visual aspects of reaching represented in primary motor cortex

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Visuomotor skills enrich our behavioural repertoire. In everyday life, visual information is used to guide motor actions. For example, the mouse pointer on a computer screen guides the manipulation of the mouse by hand. The transformation of visual cues into motor actions in this case bears a systematic spatial relationship. The movements of the hand in the horizontal plane translate into vertical movement of the pointer on the screen. Hence the visual and motor aspects of a reaching movement are intricately related to each other. Separating the cognitive aspects pertaining to perception of visual input from the generation of motor information is used to guide motor actions in this case can be critical for understanding the mechanisms underlying reaching movements.

In a recent brain imaging study, Eisenberg et al.\(^1\) designed a clever task to isolate the visual and motor aspects of reaching movements. Their results show that the primary motor cortex represents both visual and motor aspects of reaching movements. However, visual aspects alone, when decoupled from their motor consequences, are not represented in the primary motor cortex.

Brain imaging using functional magnetic resonance imaging (fMRI) allows identifying the functional activation of brain areas while participants are engaged in performing meaningful tasks. In a simple fMRI experiment, a number of three-dimensional brain images are collected in rapid succession, with a temporal resolution of a few seconds per one whole brain volume, while performing a task and during a baseline. Assessment of the functional role of a brain area is typically done by subtracting the average brain responses during the baseline from those while performing the task. This is typically done on a voxel-by-voxel basis, where a voxel refers to a three-dimensional pixel and is referred to as a massive univariate approach. The spatial resolution of fMRI is typically a few millimetres and therefore each voxel encompasses a large number of neurons. This limited spatial resolution of fMRI has proven difficult to replicate the findings from electrophysiological studies from a single neuron. Recent advances using machine learning techniques to analyse fMRI images have demonstrated that it is possible to successfully predict the cognitive states of the brain when a classifier is trained on some exemplars. This technique often referred to as ‘brain reading’, has led to multivariate analysis using information from activity patterns of multiple voxels simultaneously.\(^2\) The key advantage of using multi-voxel pattern analysis (MVPA) is that it is now possible to make inferences below the spatial resolution offered by fMRI. For example, consider the case of neurons in the primary visual cortex (V1) that selectively code for orientation of stimulus. Hence, voxels containing a large number of neurons selective for different orientations would be active for all orientations. However, each voxel has a different number of neurons selective for different orientations, resulting in a weak bias in the voxel activity towards specific orientations. When information from multiple voxels is gleaned together, these weak biases can be used as reliable indicators of orientation selectivity in V1 (refs 3 and 4).

The primary motor cortex (M1) plays a central role in representing movements. Earlier brain imaging studies have confirmed that M1 has a somatotopic representation of different body parts in the contralateral hemisphere,\(^5\) displays high plasticity during motor skill learning, and represents the direction of movement.\(^6\) Neuronal populations in M1 show tuning to the direction of movement.\(^7\) Using MVPA, voxels in M1 have been shown to convey information about hand movement in a centre-out task.\(^7\) The task consisted of moving a joystick to reach out a target from a central location. The targets were placed radially equidistant from the central location. Participants repeated the reaching task in a fast event-related fMRI experiment with 50 trials in each of the five different directions of target location in the range 0° to 180°, in steps of 45°. The trials pertaining to each direction were randomly assigned to two datasets. The activation for each voxel in the region of interest, i.e. M1 was obtained for these two datasets in each direction. This was followed by identifying the correlation matrix between the first and second datasets for each movement direction. The correlation coefficient between the two datasets was found to be highest for movements of the same direction and decreased with increasing absolute angular distance between the two movement directions. For example, consider the four datasets pertaining to two movement directions 45° and 90°. The angular distance between the two datasets with the same movement directions (i.e. 45°–45° and 90°–90°) will be zero. The angular distance between the other two datasets (i.e. 45°–90° and 90°–45°) will be ±45°. The correspondence between correlation coefficients of multi-voxel patterns and angular distance resembled a bell-shaped curve with a maximum at 0° and tailed-off for positively or negatively increasing angular distances. This result suggests that voxels in M1 carried information about the movement direction.

The direction selectivity in the centre-out task is implicitly assumed to be related to the motor aspects of reaching movements. However, this might not be the case and particularly, the visual aspects of the task, such as the target location and the direction of trajectory of the cursor could also influence the direction selectivity. Earlier research has indicated that the visuomotor skills can be represented in visuo-spatial coordinates (such as target location in Cartesian space), or the movement-specific coordinate system such as the joint angles of the various effectors used in the production of the movements (e.g. shoulder, arm, wrist, etc.).\(^8\) Eisenberg et al.\(^1\) modified their earlier centre-out task with two conditions: (1) a baseline condition in which the cursor trajectory and hand movements were in the same direction, and (2) a rotation condition in which the cursor trajectory was rotated 45° in counter-clockwise direction from the hand movement (Figure 1). Thus among the baseline and rotated conditions, the visual target remains the same, but the hand movements are varied (Figure 1). Similarly, the hand movements in the baseline condition of Figure 1a and those in the rotated condition of Figure 1b are similar, although the visual targets and the corresponding cursor movements are different. This clever design allowed dissociating the visual and motor aspects of reaching movements.
The analysis of multi-voxel patterns in M1 was carried out by finding correlation coefficients between the baseline and rotation conditions for each of the five movement directions. High positive correlations were found only when the movement directions matched (and the visual aspects differed), but also when the visual aspects were matched (differing in hand movements). This result shows that M1 voxels carry information about both the visual as well as the motor aspects of reaching movements. This result does not dissociate whether M1 activation was related to the visual or motor aspects of the centre-out task. In a control experiment, participants watched the cursor movements but did not make any hand movements. Hence, the visual aspects were decoupled from the hand movements. There was little evidence for M1 activation in the cursor movement observation paradigm. As a further analysis, half of the M1 voxels that were highly informative about the movement direction were selected and the correlation matrix was recalculated. It was found that the correlations corresponding to motor aspects improved, but not those of the visual aspects. Similarly, when half of the M1 voxels that were highly informative about visual aspects were selected, the correlations of visual aspect improved but not those of the motor aspect. This evidence seems to suggest that the visual and motor representations seem to be independent of one another.

One of the confounding factors in the centre-out task is that the reaching movements are not straight, and the cursor trajectory can sometimes be perturbed and is curved a little bit. Hence spatially adjacent targets can potentially have similar sets of movements. Earlier findings from Eisenberg et al. suggest that the M1 activity patterns separated by 45° are still positively correlated. It is therefore surprising that the paradigm chose rotations of only 45° between the hand movement and cursor trajectory, making the interpretation of the data difficult. However, analysis of angular distances of 45° in spatial and motor aspects revealed that the correlation coefficients were significantly lower than the angular distances of 0°. Overall it appears that M1 neurons are sensitive to both visual and motor aspects with perhaps different sets of voxels having neuronal populations sensitive to these two tightly coupled aspects. The key finding, however, is that the visual aspects of reaching movements are represented in M1 only when they are coupled to a motor consequence.

MVPA as an analysis technique in brain imaging studies has been increasingly used more recently. Eisenberg et al. do not report, for example, whether the motor informative voxels and visual informative voxels overlap. Results of classical fMRI analysis corresponding to the baseline and rotation conditions have not been reported. Other brain areas such as the dorsal premotor cortex and intraparietal sulcus that have been reported to be sensitive to visual aspects of movements were not found by Eisenberg et al. Further extensions of this study can use discrete movement task to overcome variable hand movements and cursor trajectories. In an alternative version, the reaching task can consider greater rotation angles, such as 90° or even 180° resulting in, for example, mirror movements. Eisenberg et al. used only 5 out of 8 possible directions of movement. The fMRI environment imposes a number of limitations of scanning time and possibilities of different movement directions. It remains to be resolved how these findings fit into the neural circuitry of reaching movements and the coordinate system used in these representations.

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