

Superior parietal cortices and varieties of mental rotation

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Mental rotation is the most distinctly specialized operation of the imagination, one characterized precisely enough psychophysically for parametric study, thereby making it an optimal prospect for isolating and modeling its neural mechanisms. New human brain mapping studies using direct cortical stimulation and repetitive transcranial magnetic stimulation isolate an area in right superior parietal cortex that appears to be crucial for the mental rotation of objects, but not to the mental rotation of one's body.

Imagine your body rotating forward so it is upside down, hold it, and then continue the rotation through to upright. Steady yourself. Now, select an object in front of you and imagine it rotating upside down. Forget about it. Next, imagine reaching your right hand around the far side of your left knee to touch the erogenous bit underneath. Finally, imagine rotating your viewpoint on that object in front of you so that you can see its far side. You have just exercised four primary varieties of mental rotation. On introspection, these acts of imagination are distinct because different objects are spatially transformed with respect to different frames of reference, although they have in common mentally representing an orientation change. Indeed, studies have documented that the time to imagine each transformation is usually proportional to the orientation change, but each variety is associated with differences in rotation rate, accuracy, effort and phenomenology, among other characteristics [1–4]. A new study confirms that these cognitive distinctions are reflected in distinct functional brain organization. In the first study of direct cortical stimulation mapping of mental rotation, Zacks, Gilliam and Ojemann [5] have shown that a region of right superior parietal cortex (Brodmann area 7) has an important supportive role for the mental rotation of objects, but not for the mental rotation of one's body.

Triangulating techniques, tasks and subjects

The Zacks *et al.* results fit neatly with a contemporaneous study using repetitive transcranial magnetic stimulation (rTMS) on healthy humans, by Harris and Miniussi [6]. These independent studies localize approximately the same area for the mental rotation of objects (Figure 1). Moreover, key differences in experimental techniques and designs of the two studies reinforce each other to increase confidence in the shared conclusion. Zacks *et al.* used a chronically implanted electrode grid placed on the right

parietal and temporal cortices in an epileptic patient undergoing pre-operative surgical mapping. By contrast, Harris and Miniussi applied rTMS to a single location, near the inferior parietal sulcus, but in both right and left superior parietal cortices. This site was selected on the basis of published neuroimaging data (see later). As it turned out, Zacks *et al.* probed 14 regions in right parietal cortex and just one region disrupted mental rotation consistently, whereas Harris and Miniussi probed only a single region of left and right superior parietal lobe and only on the right side was it found to disrupt mental rotation performance, and exclusively at one time period (stimulation at 400–600 ms after stimulus onset).

Of equal interest, Zacks *et al.* examined two varieties of mental rotation: (i) imagining the rotation of one's own body into the orientation of a presented picture of a body, and (ii) imagining the rotation of one picture of a body into the orientation of another, which was shown upright. Harris and Miniussi studied the mental rotation to upright of a letter or digit (or their mirror-reversed forms). Both studies elicited and confirmed mental rotation by asking their subjects to discriminate objects similar in appearance but in different handed forms and presented at different orientations from one another. For the body-picture task used in the Zacks *et al.* study, the discrimination was based on whether the left or right arm was outstretched. For the task in which Zacks *et al.*'s patient imagined rotating his own body, as well as for the letter/digit task, only a single stimulus was presented and it was compared with a memory of a familiar object (e.g. the upright letter). In the Zacks *et al.* study, the stimulation of the right superior parietal cortex failed to disrupt the imagined rotation of one's body (an 'egocentric' spatial transformation) but effectively disrupted the mental rotation of a body stimulus (an object transformation

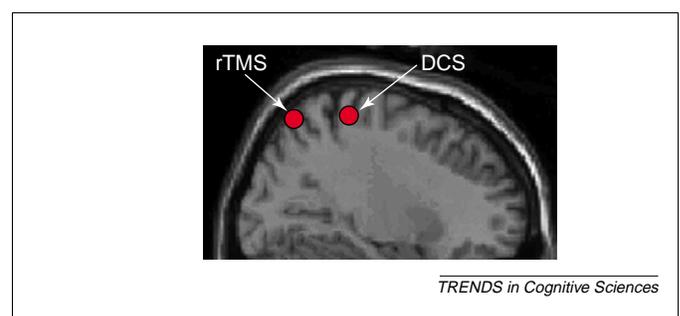


Figure 1. The approximate stimulation sites in right superior parietal cortex for the direct cortical stimulation (DCS) study by Zacks *et al.* [5] and for the rTMS study of Harris and Miniussi [6], as reconstructed by the author.

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without an egocentric transformation). This result is in agreement with the disruption of the mental rotation of a letter or digit caused by rTMS stimulation to approximately the same region in the Harris and Miniussi study.

It is also significant and helpful that the two studies used different stimulation techniques, as well as enlisting subjects in different quantity and neurological condition. The neurological history of head injury and epilepsy in a single patient could diminish the validity or generality of the data acquired from that study. Then too, there is the fact that makes us wish we had gone into rocket science instead: after a focal resection of the epileptogenic brain area, which included the area where stimulation disrupted object mental rotation, the patient's performance on object mental rotation was comparable to his pre-surgical, unstimulated performance. This is where the group data from fifteen neurologically healthy volunteers yielding similar localizations (with rTMS) helps to reinforce the single patient data. And working the other way, the direct cortical stimulation mapping data back up the rTMS data, which are potentially plagued by uncertainties in targeting (targeting accuracy was not confirmed via neuroimaging) and in physiological effects.

Probing activation maps

These stimulation data also begin to clarify activation maps from PET and fMRI studies of mental rotations. Experiments on mental rotation of objects (not one's body) report rotation-specific activations in superior parietal cortex, as well as in occipital and temporal cortices, among several other areas [7–9]. The superior parietal activations appeared on left, right or both sides, suggesting that relatively small differences in stimuli, tasks or strategies across studies influenced which mechanisms became engaged in performance. By probing whether mental rotation directly depends on activated areas in superior parietal cortex, the stimulation studies begin to refine our interpretations of the maps from neuroimaging studies, which are incapable of indicating how dependent task performance is on the activated regions. Certain activated regions must be directly involved in a performance like mental rotation, but others probably have indirect supportive functions [10].

Neuroimaging studies of the mental rotation of one's own body [11,12] do not typically reveal rotation-specific activations in the right parietal and temporal cortices, in agreement with the Zacks *et al.* stimulation mapping study; rather, they detect predominantly left-sided activations [13]. By contrast, imagining moving one's hand (or arm) elicits activations specific to spatial transformations in lateralized somato-motor cortical areas (supplementary motor area, premotor, opercular and primary motor cortices, insula, cerebellum), as well as in occipital, temporal, and (superior and inferior) parietal cortices [14–17]. These differences between activation patterns for imagining rotation of one's body, one's hand, and other objects, brings into relief how the cognitive distinctions described earlier are reflected in functional brain organization.

How parietal cortex might support object mental rotation

The tasks eliciting mental rotations in these two stimulation studies require between one and two seconds of sustained effort, and have 5 major, approximately sequential, stages: (1) perceptually representing the stimulus; (2) analyzing the orientation difference between the to-be-rotated and target objects and using it to plan a rotation; (3) imagining the rotation until object and target are close enough to judge the match or mismatch in shape; (4) comparing the shapes to make the judgment; (5) making a response.

The information processing at each stage is distinct enough to encourage the expectation that such a mental rotation task is subserved by a distributed set of activated areas, specific areas coming into play at different stages. This prediction appears to be confirmed by recent research [7–9,11–17].

In the present case, the rTMS stimulation of the right superior parietal area disrupted the mental rotation of letters and digits specifically at 400–600 ms after stimulus onset, a time period after the initial perceptual registration, but before the completion of the mental rotation, shape comparison judgment, and response [3]. Therefore, it is likely that this area of superior parietal cortex is involved in aspects of spatial-visual processing that relate the object to viewer-based or scene-based frames of reference. Neither study reports introspections by subjects about the experience of mental rotation during the interruption by the stimulation, so this data cannot yet inform ideas about function. Nevertheless, the foregoing functional interpretation is in good agreement with event-related potential (ERP) studies of mental rotation that consistently report orientation-sensitive negativities over parietal regions within this time frame and often on the right side [18–21]. This conclusion is also in broad agreement with accumulated evidence suggesting that different regions of right superior parietal cortex support distinct mechanisms involved in spatial cognition, multimodal association, and scene-based reference frames [13,22–23].

Localizing more accurately the brain region that can interrupt object mental rotation is a significant achievement. It sharpens the basis for characterizing the dynamic interactions among distributed functional areas underlying mental rotation, and it assists in deciphering the complex mosaic of parietal functions. From here, we can look far ahead to the ultimate goal of forming a biologically realistic computational model of this area's activity, one integrating vertically across molecules, cells, distributed circuitry and psychophysics.

References

- 1 Parsons, L.M. (1987) Imagined spatial transformation of one's body. *J. Exp. Psychol. Gen.* 116, 172–191
- 2 Parsons, L.M. (1987) Imagined spatial transformation of one's hands and feet. *Cogn. Psychol.* 19, 178–241
- 3 Shepard, R.N. and Cooper, L.A. (1982) *Mental Images and their Transformations*, MIT Press
- 4 Wraga, M. *et al.* (2000) Updating displays after imagined object and viewer rotations. *J. Exp. Psychol. Learn. Mem. Cogn.* 26, 151–168
- 5 Zacks, J.M. Gilliam, F. and Ojemann, J.G. (2003) Selective disturbance

- of mental rotation by cortical stimulation. *Neuropsychologia* 41, 1659–1667
- 6 Harris, I.M. and Miniussi, C. (2003) Parietal lobe contribution to mental rotation demonstrated with rTMS. *J. Cogn. Neurosci.* 15, 315–323
 - 7 Jordan, K. *et al.* (2001) Cortical activations during the mental rotations of different visual objects. *Neuroimage* 13, 143–152
 - 8 Carpenter, P.A. *et al.* (1999) Graded functional activation in the visuospatial system with the amount of task demand. *J. Cogn. Neurosci.* 11, 9–24
 - 9 Richter, W. *et al.* (1997) Time-resolved fMRI of mental rotation. *Neuroreport* 8, 3697–3702
 - 10 Bower, J.M. and Parsons, L.M. (2003) Rethinking the lesser brain. *Sci. Am.* 289, 50–57
 - 11 Bonda, E. *et al.* (1995) Neural correlates of mental transformations of the body-in-space. *Proc. Natl. Acad. Sci. U. S. A.* 92, 11180–11184
 - 12 Creem, S.H. *et al.* (2001) An fMRI study of imagined self-rotation. *Cogn. Affect. Behav. Neurosci.* 1, 239–249
 - 13 Vogeley, K. and Fink, G. (2003) Neural correlates of the first-person perspective. *Trends Cogn. Sci.* 7, 38–42
 - 14 Parsons, L.M. *et al.* (1995) Use of implicit motor imagery for visual shape discrimination as revealed by PET. *Nature* 375, 54–59
 - 15 Parsons, L.M. *et al.* (1998) Cerebrally-lateralized mental representations of hand shape and movement. *J. Neurosci.* 18, 6539–6548
 - 16 Porro, C.A. *et al.* (1996) Primary motor and sensory cortex activation during motor performance and motor imagery: a functional magnetic resonance imaging study. *J. Neurosci.* 16, 7688–7698
 - 17 Sirigu, A. *et al.* (1996) The mental representation of hand movements after parietal cortex damage. *Science* 273, 1564–1568
 - 18 Peronnet, F. and Farah, M.J. (1989) Mental rotation: an event-related potential study with a validated mental rotation task. *Brain Cogn.* 9, 279–288
 - 19 Desrocher, M.E. *et al.* (1995) Stimulus and sex differences in performance of mental rotation: evidence from event-related potentials. *Brain Cogn.* 28, 14–38
 - 20 Heil, M. *et al.* (1996) Event-related potentials during mental rotation: disentangling the contributions of character classification and image transformation. *Int. J. Psychophysiol.* 10, 326–335
 - 21 Yoshino, A. *et al.* (2000) A topographical electrophysiological study of mental rotation. *Brain Res. Cogn. Brain Res.* 9, 121–124
 - 22 Stein, J.F. (1991) Space and the parietal association areas. In *The Brain and Space* (Pallard, J., ed.), pp. 185–222, Oxford University Press
 - 23 Behrmann, M. (1999) Spatial reference frames and hemispatial neglect. In *The New Cognitive Neurosciences* (Gazzaniga, M., ed.), pp. 651–666, MIT Press

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Neural representations in human spatial memory

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Ekstrom *et al.* report the responses of single neurons recorded from the brains of human subjects performing a spatial navigation task in virtual reality. They found cells encoding the subject's current location, view and destination. These data, and related findings in animals, directly reveal some of the representations underlying spatial cognition. They highlight the potential for cognitive psychology and systems neuroscience to combine to provide a neuronal-level understanding of human behaviour.

In a recent paper Ekstrom and colleagues [1] report the first single-unit investigation of the neural representations supporting human navigation. Extra-cellular recordings were made from single neurons in the hippocampus, amygdala, parahippocampal and prefrontal cortices of seven patients with pharmacologically intractable epilepsy. Although the use of intra-cranial EEG depth electrodes for localizing epileptic foci in such patients is widespread, the use of single-unit recording is currently very rare and offers a unique insight into the mechanisms of human cognition. In addition, Ekstrom and colleagues made use of another recent technological advance, virtual reality (VR), to investigate large-scale spatial behaviour in a controlled situation (see also studies reviewed in [2]). The recordings were made while the subjects were playing the

part of a taxi driver in a small town who searched for passengers and took them to their destinations. The towns consisted of 9 buildings in a grid, 3 of them shops, each with the same distinctive shop-front on all sides. The shops served as destinations.

Experimental findings

Cellular activity was correlated with the subject's location in the town (their 'place'), what they could see (their 'view') and where they were trying to get to (their 'goal'). A 'place' response was one where the cell fired whenever the subject was in a given location in the town irrespective of his or her orientation i.e. independent of the actual view of the subject. A 'view' response was a response to a particular view e.g. looking at a particular shop-front in the town (note that similar responses were not evoked by shop-front patterns presented alone in 2D). View responses could be location specific or not. A 'goal' response was an increase in firing rate whenever the subject was searching for a specific destination (when delivering a passenger) or, in some cases, whenever the subject was searching for the next passenger.

279 neurons were subjected to analysis of variance in terms of the three factors: 26% showed a main effect of place, 12% of view, and 21% of goal. Sixteen percent of cells showed interaction effects only. More selective criteria revealed that 11% of cells responded purely to spatial location independent of view, i.e. showing no effects of view

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