Correspondence

Right parietal TMS shortens dominance durations in binocular rivalry

David Carmel[1,2,3]*, Vincent Walsh[1], Nilli Lavie[1], and Geraint Rees[1,2]

Binocular rivalry occurs when dissimilar images are presented to each eye. Rather than a combined picture being perceived, each monocular image competes for perceptual dominance, becoming visible for a few seconds while the other is suppressed. Stable visual input thus leads to alternations in conscious perception, dissociating stimulation from awareness. This makes rivalry particularly useful for elucidating the neural processes underlying consciousness [1]. Retinotopic visual cortex [2] and lateral geniculate nucleus [3] activity are modulated by such alternating perception, implying an early locus for rivaling neural representations. However, higher cortical regions, including right superior parietal cortex, exhibit activity that is time-locked to perceptual transitions [4]. Though this implies the involvement of top-down processes in rivalry, the correlational nature of neuroimaging precludes the attribution of a causal role to such activity, which may instead simply reflect orientating attention to the transition. Here we distinguish these two hypotheses by showing that repetitive transcranial magnetic stimulation (rTMS) over right superior parietal cortex shortened binocular rivalry dominance durations. This suggests that right parietal cortex maintains the current perceptual state during rivalry.

We employed rTMS parameters known to induce prolonged neural inhibition at stimulated loci (1 Hz for 30 minutes, at 90% motor threshold), specifically targeting the region in right parietal cortex previously implicated in rivalry transitions (Figure 1A). Immediately following stimulation, participants viewed a rivalry display (Figure 1B) and reported their percepts continuously for ten minutes by key-presses. We compared dominance durations following right parietal stimulation with two control conditions: after rTMS to the homologous region of left parietal cortex, and no TMS (see online Supplemental Information). To avoid any carry-over effects of TMS, the experiment was carried out over three consecutive days, with each condition on a different day. The order of conditions was counterbalanced across participants. As a result of the skewed distribution of dominance durations in rivalry, the median durations under each condition were taken as the main dependent measure.

We found that stimulating right superior parietal cortex significantly shortened dominance durations compared to both control conditions (Figure 1C; see Supplemental Information for detailed results and statistics). The frequency histogram of dominance durations in binocular rivalry is approximated by a gamma distribution [1]. Here, right TMS decreased the central tendency measures and variance of the best-fit gamma function compared to left and no TMS (Figure 1D). Importantly, non-specific effects of TMS were ruled out by the different effects of left and right TMS. But could right TMS have induced a response bias, whereby participants adopted a more stringent criterion for reporting dominance? This account would predict that right TMS would also lead to longer-duration reports of the mixed percepts that occur

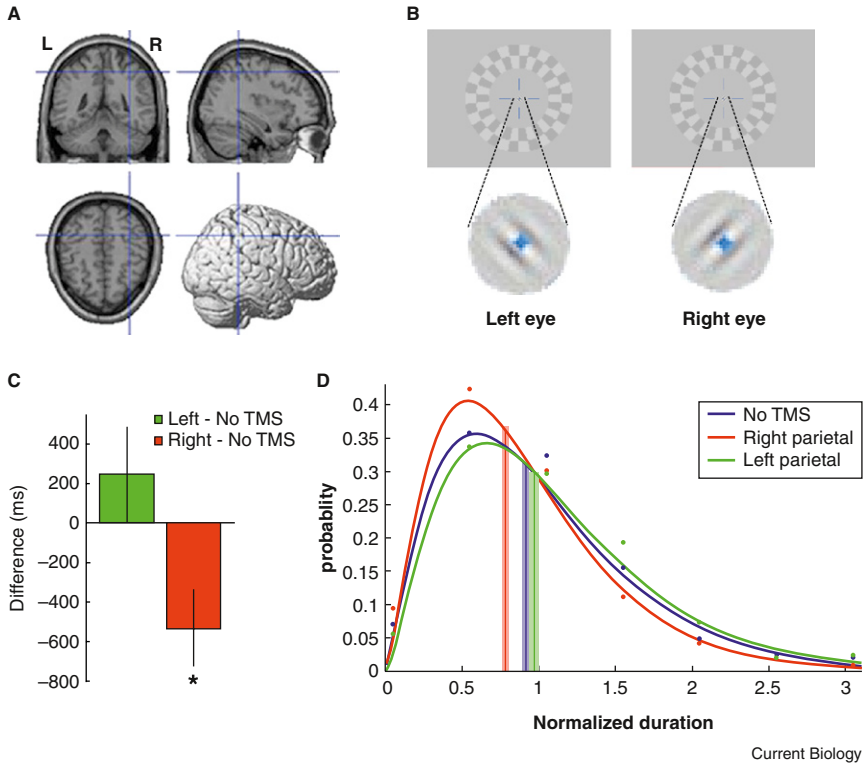

Figure 1. TMS site, binocular rivalry stimulus and results.

(A) TMS site in right parietal cortex. Crosshairs show the site in coronal, sagittal and horizontal views of a single participant's brain and on a rendered three-dimensional brain (MNI coordinates x = 36, y = –45, z = 51). The homologous site (x = –36) was stimulated in the left hemisphere. L: Left; R: Right. (B) The binocular rivalry stimulus. Each eye was presented with a moving grating (shown here enlarged from the centre of the screen). Fixation dots, lines around fixation and dartboard rings helped maintain stable alignment of the eyes. (C) Results: mean differences of dominance duration medians for left and right TMS versus no TMS. Positive values indicate longer durations compared with no TMS; negative values indicate shorter dominance durations compared with no TMS. Error bars: ±1 SEM. Asterisk: $p < 0.05$. (D) Best-fit gamma functions for the distribution of normalized dominance durations. Each participant's dominance durations were normalized to their mean and pooled. Vertical lines represent medians; shaded regions represent SEMs. Under right TMS, the gamma function (red) has a smaller median and variance than under no (blue) or left (green) TMS. (See also Table S1.)

occasionally between dominance phases in rivalry, and that the effects of right TMS on dominance and on mixed percept durations would be negatively correlated (shorter dominance durations would be associated with longer mixed percepts). However, mixed percept durations did not significantly differ between conditions. Despite a weak trend for longer mixed percepts after right TMS, the effects of right (versus no) TMS on dominance and mixed-percept durations were uncorrelated (Figure S1). Finally, a response bias account predicts that dominance durations followed by mixed percepts would be shorter than those that were not, but there was no such difference (see Supplemental Information). Taken together, these results rule out a response bias account for the results.

Two previous studies have examined the effects of TMS on rivalry. In one [5], single-pulse TMS to occipital cortex during rivalry increased the probability of a perceptual transition, which is consistent with early visual cortex involvement in rivalry. This, however, does not shed light on the role brain regions outside retinotopic cortex play in rivalry. In another study [6], single-pulse TMS was applied to left temporo-parietal cortex, time-locked to the onset of reported perceptual transitions, causing their reversal (i.e. very short dominance phases) for one of the two eyes. These effects could result from neural activity bursts following TMS pulses. In contrast, we applied rTMS to superior parietal cortex before participants viewed binocular rivalry, disrupting parietal function continuously throughout the task.

Our results have potentially important implications for understanding the involvement of high-level brain regions in binocular rivalry. Disrupting the activity of right (but not left) superior parietal cortex altered the temporal dynamics of rivalry, establishing a causal role for this region in the control of rivalry. The specific effect found critically constrains the interpretation of this role: A temporary deficit in right parietal activity would lead to longer dominance durations if such activity initiated perceptual transitions, but to shorter dominance durations (and possibly longer mixed-percept durations, though this would be hard to distinguish from response bias) if such activity was necessary for maintaining the current perceptual state during rivalry. The present results clearly favor the latter possibility.

What is the nature of the perceptual maintenance our results suggest? Neuroimaging studies employing various tasks have associated activity in the superior parietal regions stimulated here with both awareness and voluntary attention [7]. Indeed, attending to features of one image in binocular rivalry prolongs that image's dominance [8]. Furthermore, TMS to right superior parietal cortex increases 'change blindness' in change detection tasks [9], which are assumed to require efficient allocation of attention; similar stimulation also causes perceptual fading of peripheral stimuli [10], consistent with evidence that conscious visual perception depends on top-down feedback from parietal cortex to early visual areas representing sensory data. Disrupting parietal activity may thus impair attentional allocation and conscious perceptual representations — leading to fading of a single percept [10], and reduced dominance durations in visual competition, as we find here for binocular rivalry. Note that rivalrous competition itself need not occur in parietal cortex; top-down parietal influences may indirectly affect perceptual representations elsewhere in the visual hierarchy. This account suggests a possible reconciliation of the present results with neuroimaging findings [4] associating right parietal activity with perceptual transitions. One explanation, in light of the correlative nature and low temporal resolution of imaging, is that parietal activity maintains and stabilizes the new dominant percept following (rather than preceding) transitions. Impairing this activity leads to a weaker top-down signal, making it easier for the suppressed image to become dominant. By elucidating the causal involvement of right parietal cortex in rivalry, our study therefore contributes to an emerging understanding of this region's critical role in awareness.

Supplemental Information

Supplemental Information includes one figure, one table and Supplemental Experimental Procedures and can be found with this article online at doi:10.1016/j.cub.2010.07.036

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[1]Institute of Cognitive Neuroscience, University College London, Alexandra House, 17 Queen Square, London WC1N 3AR, UK. [2]Wellcome Trust Centre for Neuroimaging, University College London, London WC1N 3BG, UK. [3]Current address: Department of Psychology and Centre for Neural Science, New York University, 6 Washington Place, New York, NY 10003, USA.
*E-mail: davecarmel@nyu.edu