

Disrupting Parietal Function Prolongs Dominance Durations in Binocular Rivalry

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Summary

Human brain imaging studies of bistable perceptual phenomena revealed that frontal and parietal areas are activated during perceptual switches between the two conflicting percepts [1–3]. However, these studies do not provide information about causality, i.e., whether activity reports a consequence or a cause of the perceptual change. Here we used functional magnetic resonance imaging to individually localize four parietal regions involved in perceptual switches during binocular rivalry in 15 subjects and subsequently disturbed their neural processing and that of a control site using 2 Hz repetitive transcranial magnetic stimulation (TMS) during binocular rivalry. We found that TMS over one of the sites, the right intraparietal sulcus (IPS), prolonged the periods of stable percepts. Additionally, the more lateralized the blood oxygen level-dependent signal was in IPS, the more lateralized the TMS effects were. Lateralization varied considerably across subjects, with a right-hemispheric bias. Control replay experiments rule out nonspecific effects of TMS on task performance, reaction times, or eye blinks. Our results thus demonstrate a causal, destabilizing, and individually lateralized effect of normal IPS function on perceptual continuity in rivalry. This is in accord with a role of IPS in perceptual selection, relating its role in rivalrous perception to that in attention [4–6].

Results

Binocular rivalry occurs when two distinct stimuli are presented to each eye, leading to perceptual alternations between them. These perceptual alternations result from competition at a multitude of processing stages, and there is evidence that some executive regions involved in rivalry are shared with those involved in shifting attention and perceptual selection [1, 2, 7–9].

In binocular rivalry, two entirely distinct stimuli compete from the level of monocular channels up to high-level representations [8–11]. The channels related to the eye of origin have been shown to play a relatively strong role in determining perception in binocular rivalry [12–14], with additional competition occurring between representations of the stimulus features, the latter having been suggested to be common to binocular rivalry and other types of bistable perception [8, 9].

It has been questioned whether binocular rivalry and other types of bistable perception share the same neural resources that mediate voluntary top-down control, which is thought to be exerted by parietal sites, because bistable perception appeared more accessible to cognitive attentional selection compared to rivalry [15].

If there is a parietal contribution to both bistable perception and binocular rivalry, one may expect its function to be similar in both. During the submission stage of this manuscript, one study reported a correlation between gray-matter density in parietal cortex and the duration of percepts during viewing of a bistable structure-from-motion stimulus [6]. An inhibitory repetitive transcranial magnetic stimulation (TMS) protocol applied to the single parietal site identified there (which was equidistant to the two sites stimulated in our study) subsequently lengthened periods of perceptual stability. However, a correspondence published during the reviewing stage of our study reported the opposite effect of parietal transcranial stimulation during binocular rivalry compared to the effect observed during bistable perception [16].

All of the above points make it particularly interesting to examine carefully whether parietal sites are causally involved in modulating perceptual stability in binocular rivalry, whether this involvement is of a stabilizing or destabilizing nature, and whether distinct anatomical sites differ in their contribution.

Localization of TMS Stimulation Sites Using an fMRI Rivalry Experiment

First, we performed a functional magnetic resonance imaging (fMRI) experiment to identify cortical responses related to perceptual switches during binocular rivalry and during a replay condition. During rivalry, subjects viewed dichoptically presented face and house stimuli for a duration of 4 min while reporting their percepts via button presses; during replay, the reported percepts of the preceding rivalry period were physically replayed to the subjects (see [Supplemental Experimental Procedures](#) available online for details). Consistent with previous findings, we found higher blood oxygen level-dependent (BOLD) activity during rivalry switches compared to replay switches in extrastriate visual areas, in motor cortex, and in a predominantly right lateralized frontoparietal network [1, 2] (see [Figure 1A](#); [Table S1](#) lists activated clusters).

Two anatomically distinct parietal regions were apparent in most individual subjects and in the group analysis (see [Figure 1A](#)). These were the superior parietal lobule (SPL_{right}) and the anterior intraparietal sulcus (IPS_{right}). Even though the right hemisphere achieved higher significance in the group analysis in this study as well as in previous ones [1], this was not the case for every subject. [Figure 1B](#) plots the sorted lateralization indices (LI: right – left fMRI signal [t value] related to perceptual switches in rivalry divided by their mean; see [Experimental Procedures](#)) for every subject. Nine subjects tended toward a right-lateralized fMRI response and six toward a left-lateralized response.

TMS

For the subsequent TMS experiments, the stimulation sites were planned for each subject according to their individual

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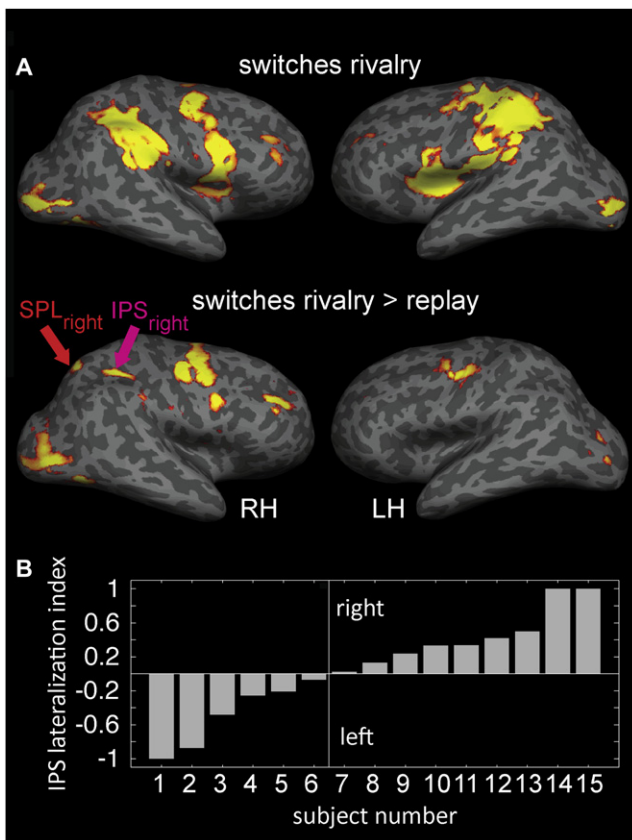


Figure 1. Results of the fMRI Localizer Experiment

(A) Group random-effects analysis across 15 subjects. Top row: significantly activated regions during perceptual switches in binocular rivalry ($p < 0.001$, uncorrected). Dominance times were 3.23 ± 0.30 s (median \pm standard error of mean [SEM]). Bottom row: regions that were significantly more activated during perceptual switches in the rivalry condition compared to the replay condition (same threshold). See Table S1 for coordinates of all clusters. Note that during rivalry, the left parietal cortex also showed robust blood oxygen level-dependent (BOLD) signal during switches, but this tended to cancel out in most subjects in the contrast rivalry versus replay. The arrows indicate the sites chosen for subsequent TMS testing.

(B) Lateralization indices (LIs) of IPS activity during switches in the rivalry condition, shown sorted across all subjects. LI was defined as the difference between right and left mean t value in the individual regions of interest, divided by the sum of the absolute mean right and left t values.

fMRI activation at both of the above sites in each hemisphere. The highest point on the head (vertex) served as a control, leading to a total of five tested sites in each subject. The arrows in Figure 2A indicate the mean locations of the stimulated sites (see Table S2 for coordinates). Subjects were stimulated using 2 Hz continuous TMS in order to disrupt processing at the stimulated site while they viewed the rivalrous display. The order of stimulation sites was randomized within and across sessions in every subject, because durations of perceptual dominance can systematically vary over time [17]. Eye movements and blinks were also monitored throughout all sessions. We first examined dominance durations obtained during stimulation of left and right parietal test sites and of the vertex. A random-effects (RFX) group analysis ($n = 15$) revealed a highly significant effect of TMS (in comparison to vertex stimulation) on the right IPS (signed rank test: $W = 8$, $p = 0.0015$, remaining significant after Bonferroni correction), with a trend in right SPL ($W = 27$, $p = 0.064$) (see Figure 2B;

Table S3 lists statistics for all tested sites). Note that right SPL and right IPS are relatively close in Montreal Neurological Institute volume (~ 20 mm), and represented linked activation clusters in some subjects, which may account for the observed trend. Still, TMS over right IPS had significantly stronger effects than over right SPL ($W = 6$, $p = 0.0068$). There was no significant effect for stimulation of the left parietal sites. The effects of TMS on the right IPS were neither percept specific (i.e., house versus face; two-way percept by site interaction $F(1,14) = 0$, $p = 0.95$) nor eye specific (two-way eye by site interaction $F(1,14) = 0.05$, $p = 0.82$).

We can exclude that the effects in the right IPS are due to blinks, because the analysis of the electrooculography (EOG) data did not reveal any significant difference in blinks between right IPS and vertex ($W = 48$, $p = 0.524$; see Table S3 for all sites). Similarly, we can exclude that the results were due to a change in the subject's criterion to report a percept, because there was no change in the median blend duration between TMS on right IPS compared to vertex ($W = 34.5$, $p = 0.275$).

Given that TMS on parietal cortex has been shown to affect task performance, such as the ability to report perceptual changes and reaction times, we performed a rivalry replay experiment while applying TMS to right IPS or to vertex to examine whether the observed effect can be explained by TMS affecting general task performance. This was clearly not the case, because we observed no differences in mean reaction times at the physical onset of the stimulus during replay (i.e., press and hold a corresponding button; $W = 42$, $p = 0.330$), no differences in reaction times at the physical offset of the stimulus (i.e., release the button; $W = 45$, $p = 0.421$), no difference in reported median percept duration ($W = 35$, $p = 0.169$), and no differences in EOG during replay ($W = 58$, $p = 0.923$).

Relations between Perceptual TMS Effects and BOLD Signal Strength at the Stimulated Site

The finding of lateralized BOLD activity as well as that of a lateralization of the TMS effects suggests that the two may be related. Indeed, if this is the case, the above grouping of the TMS effects according to the anatomical side (i.e., left versus right) might not be optimal, given that some (6 of 15) subjects had opposite BOLD signal lateralization. To test this, we labeled IPS sites according to fMRI lateralization (i.e., more versus less active IPS for rivalry switches in each brain) and not according to the hemisphere (i.e., left versus right) and analyzed the perceptual effect size of TMS over each group. Figure 2C shows that TMS effects for the IPS with the higher BOLD activity (consisting of nine right and six left hemispheres) differed significantly from vertex ($W = 4$, $p = 0.0004$) and from the less active IPS ($W = 20$, $p = 0.041$), whereas the less active IPS did not differ from vertex ($W = 42$, $p = 0.33$). Again, this result could not be explained by differences in EOG. We next performed a direct test between the amount of BOLD signal lateralization and that of TMS effect lateralization by correlating the two measures across subjects. This revealed a significant positive correlation for IPS (Spearman's $\rho = 0.58$, $p = 0.024$; see Figure S1). The equivalent analysis conducted with data from SPL showed no correlation ($\rho = -0.099$, $p = 0.72$).

Discussion

We have shown that disrupting activity in the right parietal cortex has a stabilizing effect on binocular rivalry and that

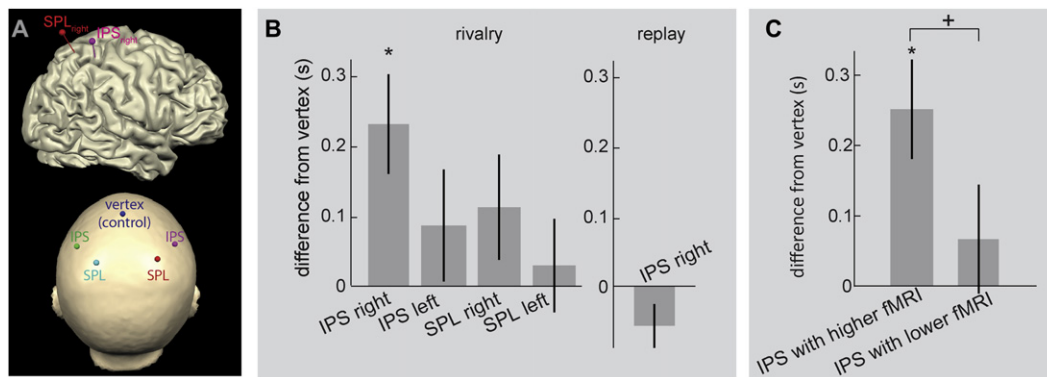


Figure 2. Effect of TMS over Parietal Areas on Dominance Durations during Rivalry

(A) Mean location of the individual TMS coil positions, shown on the right hemisphere of one of the subjects and on a posterior view of the head surface of the same subject, showing both left- and right-hemispheric stimulation sites (approximate position of vertex is shown in blue). See Table S2 for mean coordinates.

(B) Group results of TMS effects on dominance durations for each parietal site relative to vertex stimulation. Shown are the mean difference of the dominance durations for each parietal stimulation site and vertex \pm SEM, separately for SPL and IPS. Dominance times during vertex stimulation were 2.57 ± 0.28 s (median \pm SEM). * $p \leq 0.0015$ (<0.01 Bonferroni corrected, paired signed-rank test, $n = 15$ subjects).

(C) As in (B), but with IPS data sorted according to the BOLD signal lateralization, $+p < 0.05$, uncorrected. See Figure S1 for a scatter plot of the fMRI and TMS lateralization indices that were significantly correlated ($r = 0.58$, $p = 0.024$).

this causal effect is anatomically specific to one of four subject-specific functionally activated sites. Our findings additionally suggest that lateralization of parietal function varies from individual to individual and that BOLD signal lateralization is predictive of that of the TMS effect on perceptual stability. Additional control replay experiments during stimulation of vertex and parietal cortex showed that these effects indeed affected perceptual alternation rates of rivalry and cannot be explained by unspecific effects such as affecting the subject's ability to report perceptual changes or by affecting their reaction times. Our results thus provide causal evidence for a destabilizing influence of a higher-level executive region on perceptual stability in binocular rivalry, which has been a much-discussed topic in the literature [1–5, 18, 19]. Our results therefore fall in line with those of Kanai et al. [6], obtained using bistable structure-from-motion stimuli, who reported that cortical thickness in parietal cortex correlates negatively with percept duration and that inhibitory rTMS applied to parietal cortex lengthens percepts. Thus, even though the type of rivalry, the stimuli, and the TMS approach differed from ours (offline versus online), the results of both studies suggest a causal role of parietal cortex that leads to a shortening of percept durations. Impairing this function therefore lengthens stable dominance times of a given percept both in bistable perception and in binocular rivalry.

Our results are in line with recent studies exploiting the high temporal resolution of electroencephalography, suggesting that parietal activity precedes, instead of follows, perceptual switches both in rivalry and in bistable perception [19]. Our additional finding of a correlation between parietal switch-related fMRI activity and switch-reducing TMS effects also speaks in favor of the fMRI activity reflecting a cause rather than a consequence of perceptual switches. Also, patient studies support this hypothesis: neglect patients with right hemispheric lesions in posterior parietal cortex (PPC) experience longer dominance times during binocular rivalry, speaking for a destabilizing role of normal function in parietal cortex [20]. The finding by Kanai et al. [6] that cortical thickness correlates negatively with percept durations in bistable

perception again confirms this point, this time for normal subjects—the more neural resources are available in parietal cortex, the shorter perceptual times are. This may also explain slowing down of perceptual reversal rates with increasing age or in bipolar disorder, both of which are associated with thinning of parietal cortex [6].

Furthermore, given the functional and anatomical similarities of attention and rivalry and given the fact that both involve the selection of one alternative and the suppression of others, partially shared mechanisms of the two appear likely [1, 18]. Shared mechanisms may also explain why the distributions of spontaneous acts of perceptual selection—expressed as saccade rates, which are also thought to be controlled by the parietofrontal system—share distributions that are similar to those of perceptual alternation rates in all forms of bistable percepts [21]. Our more medially located SPL site (without significant TMS effects) is nearer visual-sensory regions responsive to visual motion cues and may thus be active as a consequence rather than cause of perceptual switches. The IPS site, however, overlaps attention-related activity, and TMS applied to it has been shown to affect various attention-related tasks [22], notably including the detection of stimulus change [23]. TMS applied to IPS has also been shown to modulate early visual cortical activity, also with stronger effects of right parietal TMS [24], similar to top-down attention [25]. Note that in contrast to our parietal stimulation, TMS applied directly to early visual areas increases (rather than decreases) the probability of perceptual switches during rivalry [26].

One reasonable interpretation of our results (and those of Kanai et al. [6]) is thus that TMS removes attentional resources from the parietofrontal system, thus making it less likely to re-select new interpretations of the ambiguous or dichoptic input, which leads to the observed lengthening of dominance times during TMS. Indeed, if TMS of parietal cortex is equivalent to removing attention from the stimulus, psychophysics has pre-empted our findings: directing attention away from rivalrous (and bistable) stimuli prolongs perceptual dominance durations [4, 5]. Because reducing attention is equivalent to

reducing visual contrast (and, with it, neural adaptation, thought to underlie some aspects of rivalry), this may equally account for the lengthened dominance periods [4, 27].

However, labeling parietal function as “stabilizing” or “destabilizing” and the mutual exclusion this entails may not embrace the full complexity of the problem. Not only removing attention from rivalrous stimuli but also performing a demanding task on the dominant stimulus can lengthen dominance periods (see e.g. [28]). Therefore, there is apparently a fine line between withdrawing attention, baseline perception, and focusing attention, with both extremes paradoxically leading to the same effect of lengthening dominance periods. Perhaps it is even simply directing focused attention per se that lengthened dominance in both cases. Interestingly, a recent study by Carmel et al. [16] also applied an inhibitory rTMS protocol over the parietal cortex before measuring perceptual stability in binocular rivalry but reported an opposite effect, i.e., shortening of dominance times as a result of TMS. Those findings were interpreted as showing that normal parietal function stabilizes the percept in rivalry, arguing that the parietal activation typically observed during perceptual transitions [1, 2] occurs as a consequence of the perceptual switch, stabilizing the new percept. Thus, impairing that activity would shorten stable dominance times [16].

Given the considerations outlined above, the scenario proposed by Carmel et al. [16] seems unlikely, especially because generic attention directed onto rivalrous stimuli (without a demanding task) has generally little stabilizing influence on dominance, in particular for rivaling grating stimuli (see e.g. [15, 29]). Therefore, there would be little room for disrupting such a weak hypothetical stabilizing function. The stimulation site used by Carmel et al. was within 3 mm of our mean right IPS site, so its location is an unlikely cause for this surprising divergence. However, it cannot be ruled out that other methodological differences underlie this discrepancy, such as the TMS approaches used (online 2 Hz disruption in our study and 40 s of offline inhibitory theta-burst TMS in Kanai et al. [6], versus 30 min of offline inhibitory 1 Hz rTMS in Carmel et al. [16]), or differences in visual stimuli. A possible scenario is that the specific TMS protocol used in Carmel et al. had the opposite effect of that intended and interpreted by the authors of that study: a recent study has shown that the same protocol can enhance functional connectivity between the stimulated cortex and remote brain areas, thereby improving rather than disrupting behavioral performance associated to the targeted area [30]. This account would reconcile the findings of Carmel et al. [16] with ours and those of Kanai et al. [6] in ways compatible with the above view of parietal cortex function.

Regardless of this, the sample size used in Carmel et al. [16] ($n = 6$) does not allow for strong conclusions, and the lack of vertex stimulation to control for unspecific TMS effects (see e.g. Figure 5 in Kanai et al. [6]) makes their baseline of no TMS difficult to interpret. For example, it does not allow the complete exclusion of alternative explanations, including nonspecific TMS-induced changes in arousal (see e.g. [31]) that in turn can lead to shortened dominance times [4, 5, 32].

Nevertheless, parietal function should perhaps not be dichotomized into either stabilizing percepts or selecting new ones. Instead, it could be seen as optimizing our perceptual input: seeking and maintaining access to important information. In baseline perception (i.e., without particular behavioral interests), new, potentially interesting interpretations are being reselected. This process may have been disrupted in our study

and in Kanai et al. [6], similar in effect to withdrawing attention [4, 5]. However, when an important target is in sight (e.g., during task performance on the rivaling stimuli), parietal function stabilizes the percept [28]. There are a multitude of mechanisms that could mediate this parietal selection process, none of which is so far established. A plausible one may involve changing the effective contrast of stimuli, thus tilting the ongoing competition in visual cortex between the stimulus representations in favor of one [4, 5, 28], but other mechanisms are also possible, such as changing neural noise or adaptation properties in visual stimulus representations [7–9, 27].

Most, if not all, prior studies involving rivalry have reported a lateralized involvement of parietal cortex during or preceding perceptual alternations [1, 2, 18, 19]. Our study confirms this across the group of 15 (right-handed) subjects but additionally suggests that the relative contribution of left and right parietal function in affecting perceptual switches is not lateralized in an absolute sense but varies considerably from subject to subject, which we confirmed using TMS. These findings lead us to propose a direct link to other lateralized parietal functions and neglect symptoms, for which a considerable individual variation, also with a right-hemispheric bias, have been reported [33, 34].

In sum, the present findings, in accord with those of Kanai et al. [6], clearly reveal a destabilizing role of parietal cortex during rivalrous perception. These results may reflect a default mode of parietal function, which may be reversed depending on the behavioral relevance of the stimuli. Our results suggest that the right PPC might be a part of general machinery regulating disambiguation, perceptual selection, and access to awareness and that it therefore likely plays a causal role in a variety of rivalrous or bistable settings. Our findings additionally reveal that this function is lateralized with a considerable degree of individual variability, as evidenced in fMRI signal strength as well as in TMS effects. It will thus be a challenge for future studies to dissect the potentially distinct modes and the underlying mechanisms of parietal and frontal functions in selecting a new percept versus maintaining a behaviorally relevant one, and also to clarify the mechanisms that appear to initiate perceptual reversals regardless of such higher-level influences.

Experimental Procedures

Participants

A total of 15 right-handed subjects (age 22–30 years, eight females, seven males) participated in this study. All had normal or corrected-to-normal vision, had prior experience with binocular rivalry experiments, and had well-balanced eye dominances. All subjects gave written informed consent prior to participation. The study was approved by the local ethics committee of the Medical Faculty of the University of Tübingen.

TMS Experiment: Stimulation Sites

Our localizer results had shown increased activation in several parietal subregions in the contrast “switches rivalry versus switches replay,” especially in the right hemisphere (see Figure 1A). We therefore defined two consistently activated regions in the right and left PPC located along the dorsal-ventral axis to be tested using TMS (Figure 2A; Table S2). These regions were visible in most subjects and had an average distance of ~2 cm. Initially, a third region located more ventrally was also planned, but in the first seven tested subjects, a mild but consistent side effect (facial muscle twitching) occurred during the stimulation. We therefore concentrated on the two more dorsal sites, where TMS was well tolerated by all subjects. Vertex stimulation served as the control condition. The individual stimulation sites were chosen within a distance of 15 mm of the group activation for “switches rivalry versus switches replay” (unwarped to the individual space). If no individual peak ($p < 0.01$) was present for the contrast

“switches rivalry versus switches replay,” then an individual site significantly responding to the much more robust contrast “switches rivalry” and overlapping with the group activity was chosen. In rare cases where none of the above applied, the anatomically mirrored site of the contralateral hemisphere was used. This procedure ensured consistency across subjects while ensuring subject-specific stimulation.

TMS Experiment: Setup and Procedures

Subjects were seated in a comfortable chair with their chin on a chin rest. A CRT monitor (refresh rate 120 Hz) with shutter glasses (StereoGraphics/REAL D, Beverly Hills, CA) was used for dichoptic stimulus presentation. The stimuli were identical to those used in the fMRI localizer session and had the same size of 1.8°. Prior to the TMS sessions, subjects performed several 3 min runs in which the stimulus contrast was adjusted to obtain a mean dominance duration of ~2–3 s, leading to a mean root-mean-square contrast of 10.10 cd/m² (standard deviation [SD] = 1.27). Subjects were asked to report their percepts by pressing and holding one of the two corresponding buttons with their right hand. The face stimulus was shown to the left eye and the house stimulus to the right eye in seven subjects. In the other eight subjects, the stimuli were exchanged. Biphasic magnetic pulses were delivered by a figure-eight coil (MC-B70) connected to a MagPro X100 stimulator (MagVenture, Farum, Denmark). Subjects wore earplugs throughout the stimulation period. The coil position was controlled online using a neuro-navigation system based on optical tracking (BrainView, Fraunhofer IPA, Stuttgart, Germany). The coil was held manually by a trained investigator, keeping the coil position at a range of 2 mm or less from the preplanned stimulation sites acquired from the fMRI localizer session. Runs were repeated whenever the distance of the coil to a stimulation site exceeded 2 mm. In order to control for potential eye blinks related to the TMS stimulation, the EOG was recorded from two bipolar channels using cup electrodes placed above and below the left and right eyes (ground electrode on the forehead). The electrodes were connected to the AD converter (DAQ2205, sampling rate 10 kHz; Adlink Technology, Taiwan) of a computer via an amplifier (Psychlab, band-pass filter of 1–400 Hz; Contact Precision Instruments, London) and recorded using a custom-written MATLAB program.

Each subject underwent 1–2 TMS sessions, separated by at least one week. After the preparatory phase, 9–15 runs followed during which 2 Hz repetitive TMS was delivered at 120% of the individual resting motor threshold to continuously interfere with the neural activity in the targeted area during the 3 min of dichoptic stimulus presentation. The 2 Hz protocol was chosen because continuous rTMS applied online during task execution in a block design has been shown to efficiently impair behavioral performance, accompanied by a decrease in task-related brain activity [35]. Because our aim was to use rTMS to constantly interfere with processing in the targeted area (rather than to persistently condition its excitability), a repetition rate of 2 Hz was chosen. This lies between the classical inhibitory 1 Hz rTMS and the facilitatory protocols typically using repetition rates of 5 Hz or higher and is rather inefficient in robustly modulating cortical excitability [36]. Taken together, each region (including the vertex control site) was tested three times, with the order of stimulation being pseudorandomized within each session. In order to avoid potential TMS aftereffects and to obey the TMS safety limits, a break of >3 min was introduced between runs. This resulted in an average time between retesting the same site of 39.69 min (SD = 16.71).

Finally, to confirm that the results obtained during rivalry were specific to rivalry and not caused by unspecific site-dependent effects such as TMS-induced changes in ability to perform the task, we conducted an additional set of control “replay” experiments. In these experiments, the subjects’ individual percepts acquired during vertex TMS in previous rivalry experiments were replayed to them binocularly forward or backward, while TMS was applied to either right IPS or vertex (IPS was chosen because its stimulation led to the most significant effects compared to vertex during rivalry; see Results for details). The order of stimulation sites and replay direction were randomized across subjects. To imitate rivalry as close as possible in appearance and task difficulty during replay, we showed a semitransparent blend of face and house stimuli during blend periods. Transitions from replayed dominance to blends (or vice versa) were implemented as a linear change of transparency from 0% to 50% (or vice versa) of the dominant stimulus, lasting 200 ms. All other experimental conditions and tasks were the same as during the rivalry experiment.

TMS Experiment: Data Analysis

Based on the subjects’ button presses, dominance periods of each of the two percepts and blend periods were determined. Data from different

runs of the same stimulation site were pooled for each subject, and a median dominance duration of each site was calculated. TMS effects between each parietal site and vertex were determined via random-effects Wilcoxon signed-rank test ($n = 15$). Data from the subsequent replay experiments were analyzed in the same way, with additional calculation of mean reaction times within 80–1000 ms after the physical onset and offset of each stimulus.

In order to relate fMRI activations to the perceptual effects of TMS over the same sites, for each subject, a cylindrical mask (radius 5 mm, height 3 cm) was applied beneath the TMS coil center at each parietal stimulation site to get its mean t value of an fMRI activity (unsmoothed data) during switches in the rivalry condition. Cortex of the postcentral sulcus and postcentral gyrus, which could possibly be contaminated by motor-related activity, was excluded in every subject using individual anatomy. fMRI lateralization index was computed as a difference between right and left mean t value divided by a sum of the absolute mean right and left t values. TMS lateralization index was computed in the same manner using the median dominance duration during the right and left IPS stimulation.

In order to determine whether our results were biased by TMS-induced eye blinks, the EOG data were analyzed within periods from 18 to 200 ms after the magnetic pulses. The first 18 ms after the pulses contained TMS-induced artifacts and was therefore excluded. A blink was defined as the absolute difference between the minimal and maximal EOG amplitude in this time period exceeding 0.2 mV. The mean number of blinks was determined for each stimulation site and analyzed in the same way as TMS effects.

Supplemental Information

Supplemental Information includes one figure, three tables, and Supplemental Experimental Procedures and can be found with this article online at doi:10.1016/j.cub.2010.10.046.

Acknowledgments

This work was funded by the Max Planck Society and by the Centre for Integrative Neuroscience, Tübingen.

Received: September 10, 2010

Revised: October 18, 2010

Accepted: October 20, 2010

Published online: November 18, 2010

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