Causal evidence for a double dissociation between object- and scene-selective regions of visual cortex: A pre-registered TMS replication study

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Abstract

Background: Daily-life scenes contain both global layout information as well as local object information. Accordingly, functional neuroimaging research has identified regions in visual cortex that represent either global scene layout or local object properties. Specifically, fMRI activity patterns in scene-selective regions, including the occipital place area (OPA), carry information about the layout of the scene, but not about object content. Conversely, fMRI activity patterns in object-selective regions, including the lateral occipital complex (LOC), carry information about object content, but not about scene layout. However, causal evidence for a double dissociation between OPA and LOC in representing scenes and objects, respectively, is currently limited.

Objective: One TMS experiment, conducted in a small sample (N=13), reported a double dissociation between OPA and LOC in scene and object recognition tasks [1]. In the current study, we present a high-powered (N=72) pre-registered replication of Dilks et al. [1], testing for a double dissociation between OPA and LOC.

Results: Our findings fully replicate the original report, providing even more convincing evidence showing that TMS over OPA selectively impairs the recognition of scenes, while TMS over LOC selectively impairs the recognition of objects. Furthermore, we found that these effects were stable over time and consistent across individual objects and scenes.

Conclusions: We conclude that OPA and LOC can be reliably targeted with TMS, selectively disrupting either scene or object processing. The selective interference of scene and object processing allows future TMS studies to address new questions, including about how scene and object processing interact during naturalistic vision.

Keywords

Object recognition, Scene recognition, Lateral occipital complex, Occipital place area,

Transcranial magnetic stimulation

Introduction

Our daily life visual environments, such as city streets, forests, and kitchens, are characterized by both local object content (cars, trees, refrigerators) and global spatial layout [2,3]. These sources of information are to some extent independent, with many scenes being identifiable without requiring individual object recognition, and most objects being identifiable without a background scene. Accordingly, cognitive neuroscience research has revealed distinct pathways in visual cortex that are primarily involved in either scene or object recognition.

In humans, functional magnetic resonance imaging (fMRI) research has shown that viewing objects (vs scrambled controls) selectively activates regions in lateral occipital cortex (LOC) and posterior fusiform gyrus [4,5]. By contrast, viewing scenes (vs objects) activates three scene-selective regions [6]: the parahippocampal place area (PPA), the retrosplenial complex (RSC) and the transverse occipital sulcus / occipital place area (OPA). Studies using multivariate pattern analysis have shown that these scene- and object-selective regions represent distinct aspects of a scene, with scene-selective regions representing spatial layout (e.g., open vs closed) and object-selective regions representing object properties (e.g., object shape [7-9]).

While the neuroimaging evidence for a functional distinction between scene- and object-selective regions is convincing, the evidence for these regions being causally involved in selectively processing their preferred category is much weaker. A number of studies have used transcranial magnetic stimulation (TMS) to interfere with activity in one of these regions to demonstrate impaired object or scene recognition. These studies showed that TMS over LOC impaired object recognition performance [1,10-12]. Due to physical limitations of TMS reaching deeper structures, studies investigating scene recognition have targeted the OPA, rather than PPA

and RSC. These studies found that OPA is causally involved in scene processing by showing that scene categorization is impaired when OPA is stimulated [1,13].

Importantly, however, to our knowledge only one TMS study has provided causal evidence for a double dissociation between object-selective LOC and scene-selective OPA (Experiment 2 in Dilks et al. [1]). Such a double dissociation is important in ruling out alternative explanations for impaired performance, such as TMS-related artifacts and differences in sensitivity to such artifacts across tasks. In this experiment, thirteen participants performed two four-alternative forced-choice (4AFC) categorization tasks, one involving scenes (beach, forest, city, kitchen) and one involving objects (camera, chair, car, shoes). In different blocks, TMS was applied over right LOC, right OPA, or vertex. Results showed a double dissociation: TMS over LOC selectively impaired object recognition, while TMS over OPA selectively impaired scene recognition.

Considering the importance of this experiment for our understanding of object and scene processing in visual cortex, the aim of the current study was to replicate this experiment in a large sample of participants (N=72) using a pre-registered protocol.

Methods

The pre-registration is available at this website: https://aspredicted.org/jm6ey.pdf.

Participants

Seventy-two volunteers (mean age ± SEM = 23.30 ± 0.42, range 18-33 years, 43 female) participated in the study. All volunteers had normal or corrected-to-normal vision and were right handed. Exclusion criteria were: (i) History of epileptic seizures, (ii) a nuclear family member

afflicted with epilepsy, (iii) history of psychiatric or neurological diseases, (iv) metallic objects in the head, (v) implanted devices (e.g., pacemaker, cochlear implant), and (vi) having used psycho-active medication or recreational drugs less than 48 h before the experiment. The protocol was approved by the medical ethical committee of the Commissie Mensgebonden Onderzoek, Arnhem-Nijmegen and carried out in accordance with the Declaration of Helsinki (Fortaleza amendments).

Behavioral task

Participants performed a 4AFC task, identical to the task used by Dilks et al. [1] In a blocked design, participants were either presented with an object, which could be a camera, car, chair or shoes, or with a scene, which could be a beach, city, forest, or kitchen. For all stimuli, grayscale images from the SUN Database [14] were used, which were further degraded by blending the image with 8x8 grid of tiles. For scenes, these tiles were grayscale with random intensity. For objects, a scrambled version at 60% transparency was used as tiles and overlaid on the image.

The experiment consisted of two parts. The first part of the experiment determined the optimal stimulus presentation duration by using a thresholding procedure that leads to an average score of ~63% for each category. For this a QUEST staircase procedure was used (number of trials = 32; beta = 3.5; delta = 0.01; gamma = 0.5; grain = 2) in two runs of 256 stimuli (i.e. 128 stimuli for objects as well as for scenes, equaling 32 stimuli per category). The range of stimulus presentation was fixed between 64-128 ms per category. The lower (shorter presentation time) threshold value of the two runs for each category was selected for the second part of the experiment. The stimulus presentation times on average were: camera 91.6 ms, car 74.9 ms,

chair 114.0 ms, shoes 110.5 ms, beach 80.8 ms, city 93.3 ms, forest 86.9 ms, and kitchen 116.1 ms. Each stimulus was followed by a mask, which was presented for 500 ms. The mask was made of a 4x4 grid of tiles containing a scramble of 8 randomly selected image parts. For scenes, undegraded images were used, whereas for objects, degraded images were used to make the mask.

The second experimental part consisted of six runs of 64 stimuli (i.e. 32 stimuli for objects as well as for scenes, equaling 8 stimuli per category). During this part participants were stimulated with TMS, which started at stimulus onset. Stimulation site, that is, rLOC, rOPA, or vertex, was changed each run and followed a pseudorandom, counterbalanced palindromic design.

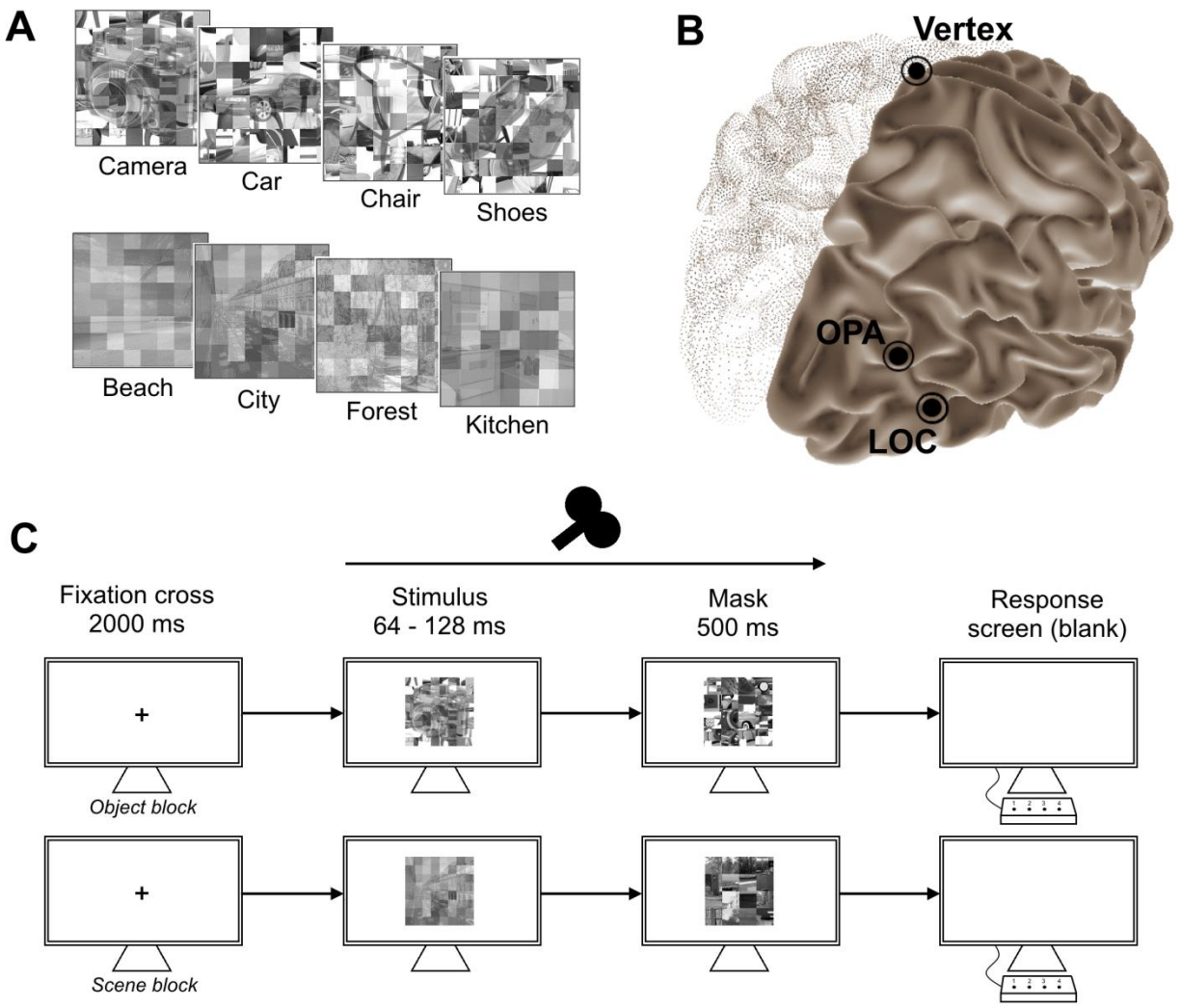

Figure 1. A) Examples of stimuli for each category. B) TMS sites used in the present study. OPA and LOC were based on fMRI coordinates from previous studies, i.e. for the LOC Talairach 45,-74,0 [10] and for the OPA Talairach 34,-77,21 [15]. C) Example trial of the 4AFC object/scene recognition task. Five TMS pulses at a rate of 10 Hz were delivered at the onset of the stimulus.

Transcranial magnetic stimulation and site localization

A MagVenture MagPro X100 was used to deliver TMS with a Cool B-65 figure-of-eight coil. Note that this is different from [1], who used a MagStim Super Rapid^2 stimulator.

At the onset of each object or scene stimulus a train of 5 pulses was applied at 10 Hz (i.e., 500 ms total duration of a single train) at 60% of maximum stimulator output (MSO). TMS was delivered over rLOC, rOPA and vertex, with a posterior-to-anterior magnetic field orientation [10]. The correct location during stimulation was monitored using a Localite neuronavigation system. The size and shape of a participant's head was modelled by marking left and right tragus of the ear, left and right canthi of the eyes, nasal bridge, inion and vertex. Subsequently, a standard MNI brain was fit, based on those points. MRI coordinates were used to identify the peak activation voxel of the rLOC, that is Talairach 45,-74,0 [10], and of the rOPA, that is Talairach 34,-77,21 [15]. Note that Dilks et al [1] used individual fMRI coordinates. The location of the vertex was determined as the midpoint between both tragi, on top of the head. For all stimulation sites, coil location was monitored using the Localite system and was kept constant within a range of 2 mm displacement.

Before the start of the task, the phosphene threshold (PT) of each participant was determined using the 'method of constant stimuli' [16]. On average, PT was 60.43 ± 1.45% of MSO ranging between 38 and 100 MSO. After PT determination the 5 pulse, 10 Hz stimulation, as during the experiment, was shortly applied to each experimental region for participants to acclimatize to the feeling of TMS. No adverse events were reported.

Statistical analysis

Similar to Dilks and colleagues (2013), for the main analysis a 3x2 GLM repeated measures ANOVA was performed with percentage correct as dependent variable, following our pre-registration. TMS site (rLOC, rOPA and vertex) and category (object and scene) acted as independent variable. A significant main and interaction effects were followed by post hoc t-

tests. In addition, Bayes factors (BF_{10}) are reported for post hoc analysis. Values larger than 1 indicate evidence that the alternative hypothesis (i.e., performance in the active TMS condition is different from vertex TMS) is true, with larger values suggesting stronger evidence. Values smaller than 1 indicate evidence for the null hypothesis (i.e., performance does not differ between active and vertex TMS) with values closer to 0 suggesting stronger evidence. Data was further explored by comparing the LOC effect (percentage correct during vertex – LOC stimulation during object recognition) and OPA effect (percentage correct during vertex – OPA stimulation during scene recognition) between first and second half of the experiment. A paired samples t-test was used to test for differences between halves and one sample t-tests with zero as test value was used to investigate whether the effect was larger than zero. Finally, repeated measures ANOVAs were used to test for differences between categories for the LOC and OPA effect as well as a one-sample t-test to indicated whether the effect is larger than zero. All analyses were performed using SPSS 25.0 (ANOVA and post hoc tests) and JASP 0.12.2 (Bayes factors).

Results

Main results: Replication of Dilks et al (2013)

A 3 (TMS site: rOPA, rLOC, vertex) x 2 (Category: objects, scenes) ANOVA revealed a significant interaction ($F(2,142) = 7.09$, $p = 0.001$), indicating that TMS site differentially affected performance (% correct) in the two tasks. To test whether object and scene recognition performance was impaired following stimulation, we followed up this interaction by separate one-way ANOVAs for each category.

For the object recognition task, a significant main effect of TMS site indicated that object recognition was affected by TMS ($F(2,142) = 8.38$, $p < 0.001$, Figure 2A). Post hoc t-tests showed that performance was reduced during LOC TMS compared to vertex TMS ($t(71) = 4.05$, $p < 0.001$, $d = 0.48$, $BF_{10} = 269.65$, Figure 2B) and compared to OPA TMS ($t(71) = 2.55$, $p = 0.013$, $d = 0.30$, $BF_{10} = 3.81$). OPA TMS did not impair object recognition performance compared to vertex TMS ($t(71) = 1.42$, $p = 0.159$, $d = 0.17$, $BF_{10} = 0.31$).

For the scene recognition task, we similarly found a main effect of TMS site ($F(2,142) = 11.97$, $p < 0.001$, Figure 2A). In this case, performance was reduced during OPA TMS compared to vertex TMS ($t(71) = 4.91$, $p < 0.001$, $d = 0.58$, $BF_{10} = 5753.48$, Figure 2B) and compared to LOC TMS ($t(71) = 3.08$, $p = 0.003$, $d = 0.36$, $BF_{10} = 5.39$). LOC TMS did not impair scene recognition performance compared to vertex TMS ($t(71) = 1.51$, $p = 0.135$, $d = 0.18$, $BF_{10} = 0.687$).

These results replicate the results of Dilks et al [1], providing convincing causal evidence for a double dissociation between scene- and object-selective regions in the recognition of scenes and objects. The overall pattern of results of the two studies was nearly identical, with statistically stronger evidence in the current study due to the larger sample size (Figure 2B).

Individual differences and consistency across time

Although overall TMS was effective in altering scene and object recognition performance, there is a notable amount of individual variability in response to TMS. To get an idea of this variability, the responder rate was calculated. 37.5% of participants showed both an effect of TMS over LOC (object recognition performance vertex – LOC > 0) and OPA (scene recognition performance vertex – OPA > 0), 18.1% of participants showed an effect of LOC but

not OPA TMS, and 25.0% of participants showed an effect of OPA but not LOC TMS (Figure 2C). This means that the susceptibility to TMS over LOC and OPA was 55.6% and 62.5%, respectively. Although these rates are lower than those of Dilks and colleagues (69.2% and 84.6%, respectively), chi-square tests indicated no significant difference between these percentages ($X^2 = 0.84$, $p = 0.358$, and $X^2 = 2.40$, $p = 0.122$, respectively). The susceptibility rates found here are in agreement with susceptibility rates of previous studies targeting visual areas, such as Van Koningsbruggen et al [17], who showed a susceptibility rate of 54% for TMS over the extrastriate body area (EBA), located near the LOC.

Individual differences in the excitability of the stimulated cortex, skull thickness, neuronal and axonal orientation as well as metabolic factors may impact the susceptibility to TMS. One way to control for this variability is to take into account the phosphene threshold. We found that phosphene threshold was not significantly correlated with the LOC TMS effect ($r = 0.04$, $p = 0.739$), nor with the OPA TMS effect on performance ($r = 0.13$, $p = 0.269$). This suggests that the above-mentioned physiological differences between participants, to the extent that these are captured by phosphene threshold, did not significantly mediate our effects.

Since all TMS sites were stimulated twice in a palindromic design it was possible to investigate the consistency of the effects over time by comparing the TMS-induced LOC effect (% correct object recognition, vertex – LOC) and OPA effect (% correct scene recognition, vertex – OPA) in the first half to the second half of the task. The LOC effect was significant for both the first (4.60 ± 1.15%, $t_0(71) = 3.90$, $p < 0.001$, $d = 0.47$) and second half (4.04 ± 1.40%, $t_0(71) = 2.88$, $p = 0.005$, $d = 0.34$), with no significant difference between the two halves ($t(71) = 0.36$, $p = 0.724$, $d = 0.04$, $BF_{10} = 0.138$, Figure 2D). Similarly, the OPA effect was significant in the first (4.69 ± 1.12%, $t_0(71) = 4.18$, $p < 0.001$, $d = 0.49$) and second half (3.13 ± 0.99%, $t_0(71)$

= 2.89, p = 0.005, d = 0.37) of the experiment, with no difference between halves (t(71) = 1.05, p = 0.300, d = 0.12, BF_{10} = 0.219, Figure 2D). These results indicate that the TMS effects of LOC and OPA were robust over time.

Furthermore, to ensure that the results were not driven by specific features of one or a few objects or scenes, the LOC and OPA effects were compared between categories. There were no significant differences between the individual objects and scenes for the LOC effect (F(3,213) = 0.23, p = 0.859) or for the OPA effect (F(3,213) = 0.85, p = 0.465). Furthermore, all categories showed the effect in the expected direction (Figure 2E), although it did not reach significance for all individual categories tested separately (LOC effect: camera: p = 0.006, car: p = 0.084, chair: p = 0.048, shoes: p = 0.08; OPA effect: beach: p = 0.289, city: p = 0.064, forest: p = 0.008, kitchen: p = 0.006). This is likely a consequence of increased variability by selecting a subset of trials, which consequently reduces statistical power.

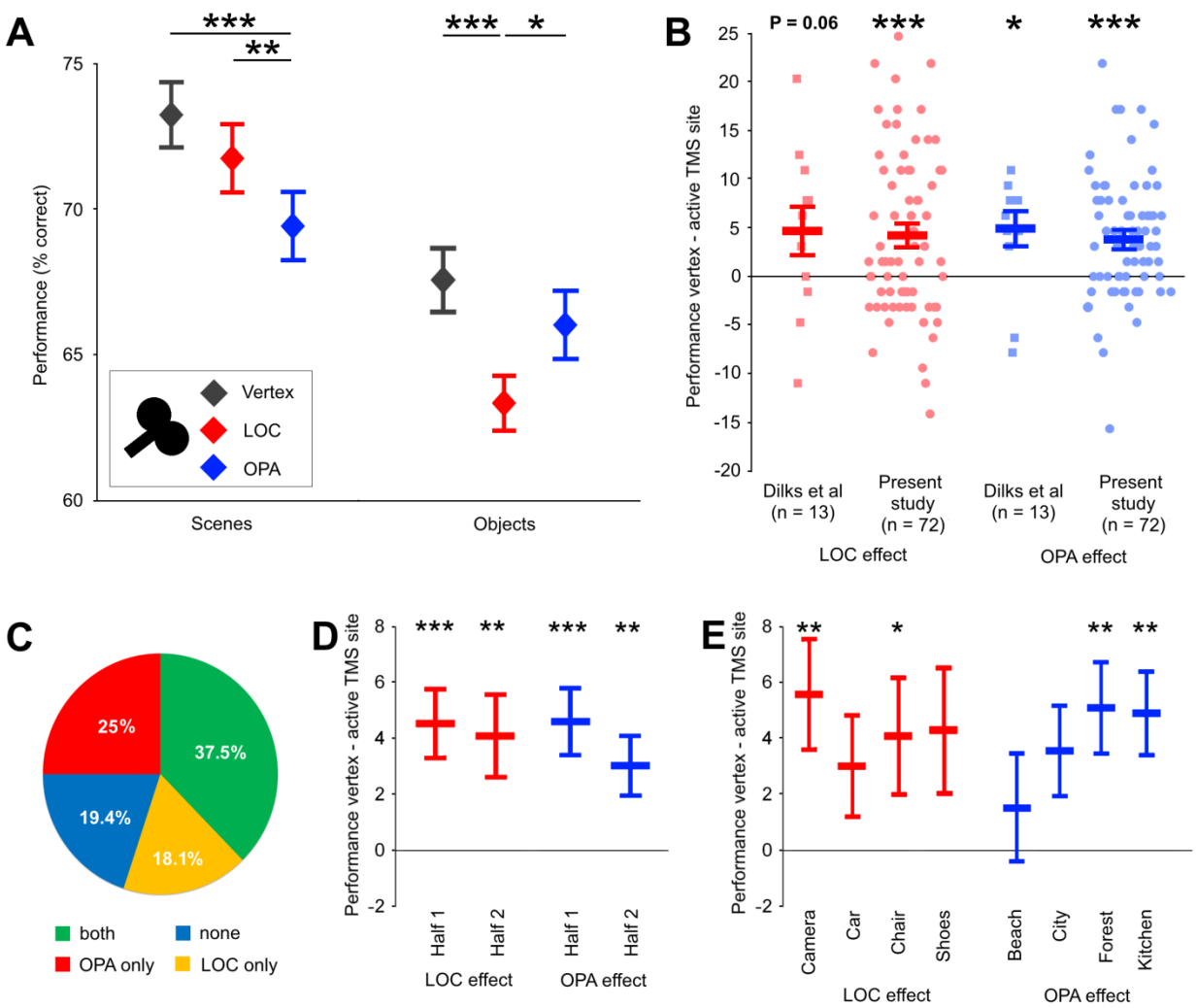

Figure 2. A) Results of the present study (N = 72). The findings are similar to Dilks et al [1] showing decreased performance for scene recognition during TMS over OPA (compared to vertex) and decreased performance for object recognition during TMS over LOC (compared to vertex). B) Average and individual data of the LOC effect (% performance difference vertex – LOC during object recognition) and OPA effect (% performance difference vertex – OPA during scene recognition) for both the present study and Dilks et al [1]. C) Percentages of participants susceptible to TMS over OPA, LOC, both or neither. D) LOC (red) and OPA (blue) effect for the first half and second half of the experiment. E) LOC (red) and OPA (blue) effect per category. In all graphs: * $p < .05$, ** $p < .01$, *** $p < .001$, with error bars reflecting the SEM.

Finally, to exclude speed-accuracy trade-offs, we analyzed reaction time (RT) data. A 3x2 repeated measures ANOVA revealed no significant main effect of TMS site ($F(2,142) = 0.839$, $p = 0.394$) or category ($F(1,71) = 3.28$, $p = 0.074$), and no significant interaction of TMS

site*category ($F(2,142) = 0.11$, $p = 0.893$). This indicates that RT did not differ between TMS conditions, neither for object nor scene stimuli, excluding speed-accuracy trade-offs.

Discussion

The current pre-registered TMS replication study provides strong causal evidence for a double dissociation between object-selective LOC and scene-selective OPA. In the same group of participants (N = 72), LOC was causally involved in object recognition (but not scene recognition) and OPA was causally involved in scene recognition (but not object recognition). The results could not be explained by a speed-accuracy trade-off, and were consistent across time and individual object and scene stimuli. Altogether, these findings provide a successful replication of Dilks et al [1].

We aimed to reproduce all methodological aspects of Dilks et al [1], and hence we used the same behavioral task, stimuli, procedure, and TMS timing. However, two differences between the two studies should be highlighted. First, the present study used a MagPro X100 TMS stimulator with a 75 mm diameter coil, whereas Dilks and colleagues employed a MagStim Super Rapid² with a 70 mm diameter coil. Differences in induced voltage, pulse width, pulse form, and focality may affect the brain in distinctive ways. Second, rather than using individual fMRI coordinates per participant, here we used average coordinates from previous research. This may implicate less spatial specificity in the present study, potentially decreasing the effect magnitude and number of participants susceptible to TMS.

Despite these differences, the present results are remarkably similar to those of Dilks et al [1]. In addition to the main results replicating, the effect sizes and variability are also quite comparable. LOC TMS induced a 4.7% decrease in object recognition performance (standard

deviation 8.0%) in the study by Dilks et al (Cohen's d = 0.59), whereas here LOC TMS reduced performance by 3.9% (standard deviation 8.3%; Cohen's d = 0.47). OPA TMS reduced scene recognition performance by 4.9% (standard deviation 5.7%) in the Dilks et al study (Cohen's d = 0.86), while here scene recognition performance was reduced by 3.8% (standard deviation 6.4%; Cohen's d = 0.59). The marginally smaller effect sizes in the current study may be related to the above mentioned differences between the studies, or may reflect a regression to the mean. However, overall the data was replicated well, providing clear causal evidence for the involvement of LOC in object recognition and OPA in scene recognition.

The results of the present study show that LOC and OPA can be targeted reliably based on average fMRI coordinates, providing an easy and cost-effective way to investigate the LOC and OPA when an fMRI scan is not feasible. Nevertheless, the effects observed in the present study are likely to be optimized when using individual fMRI coordinates. Additionally, following Dilks and colleagues, the same TMS intensity was used for all participants (60% MSO). Yet, individualizing stimulation intensity may improve the effects of TMS. It should be noted, however, that the effects of TMS on performance in our study were not correlated with phosphene threshold.

Furthermore, TMS timing in the current study was rather aspecific with a window of 500 ms and a frequency of 10 Hz. Several studies have suggested that the LOC represents object category between 120 and 200 ms after stimulus onset [12,18-21]. Similarly, the OPA represents scene layout around the same time window [22]. Based on these values, TMS timings could be optimized to disrupt object and scene recognition, with a narrower window and a higher frequency, for example TMS between 100 and 300 ms after stimulus onset, with a frequency of 20 Hz. Alternatively, single- or double-pulse TMS at specific latencies can be used to test the

time point at which these regions are causally involved in the recognition of objects and scenes [12,23].

In summary, the current study provides causal evidence for a double dissociation between LOC and OPA, successfully replicating Dilks et al [1]. By showing that these regions can be reliably targeted with TMS, even when using group-average fMRI coordinates, we can now address new questions regarding the functionality of these regions. One interesting avenue for future research is to move beyond the classical division of object and scene processing and test the causal involvement of LOC and OPA during naturalistic situations, in which scene and object processing interact and mutually inform each other [24,25].

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