Causal neural mechanisms of context-based object recognition

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ABSTRACT

Objects can be recognized based on their intrinsic features, including shape, color, and texture. In daily life, however, such features are often not clearly visible, for example when objects appear in the periphery, in clutter, or at a distance. Interestingly, object recognition can still be highly accurate under these conditions when objects are seen within their typical scene context. What are the neural mechanisms of context-based object recognition? According to parallel processing accounts, context-based object recognition is supported by the parallel processing of object and scene information in separate pathways. Output of these pathways is then combined in downstream regions, leading to contextual benefits in object recognition. Alternatively, according to feedback accounts, context-based object recognition is supported by feedback from scene-selective to object-selective regions. Here, in three pre-registered transcranial magnetic stimulation (TMS) experiments, we tested a key prediction of the feedback hypothesis: that scene-selective cortex causally and selectively supports context-based object recognition before object-selective cortex does. Early visual cortex (EVC), object-selective lateral occipital cortex (LOC), and scene-selective occipital place area (OPA) were stimulated at three time points relative to stimulus onset while participants categorized degraded objects in scenes and intact objects in isolation, in different trials. Results confirmed our predictions: relative to isolated object recognition, context-based object recognition was selectively and causally supported by OPA at 160-200 ms after onset, followed by LOC at 260-300 ms after onset. These results indicate that context-based expectations facilitate object recognition by disambiguating object representations in visual cortex.

INTRODUCTION

Objects are typically seen within a rich, structured, and familiar context, such as cars on a road and chairs in a living room. Decades of behavioral work has shown that context facilitates the recognition of objects (Bar, 2004; Biederman et al., 1982; Oliva & Torralba, 2007). This contextual facilitation is crucial for everyday behavior, allowing us to recognize objects under poor viewing conditions (Figure 1), at a distance, in clutter, and in the periphery where visual resolution is low. Yet despite the pervasive influence of context on object recognition, our knowledge of the neural mechanisms of object recognition almost exclusively comes from studies in which participants view clearly-visible isolated objects without context. These studies have shown that isolated object recognition results from the transformation of local, low-level features into view-invariant object representations along the ventral stream (DiCarlo et al., 2012; Liu et al., 2009; Riesenhuber & Poggio, 1999; Serre et al., 2007). Does a similar local-to-global hierarchy support context-based object recognition?

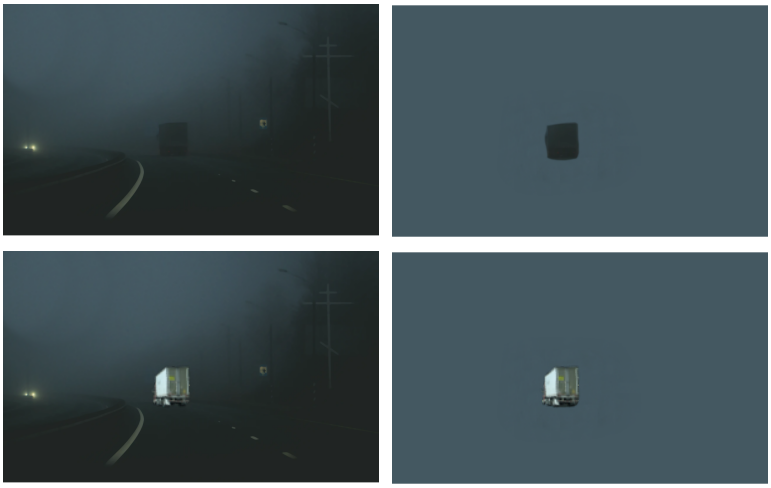

Figure 1. Example of context-based object recognition. *At night (top panels), the truck is easily recognized by participants when placed in context (left) but not when taken out of context (right). With sufficient light (bottom panels), the truck is easily recognized also when presented in isolation.*

One possibility is that context-based object recognition is supported by the parallel feedforward processing of local object information in the ventral stream object pathway and global scene processing in a separate scene pathway (Henderson & Hollingworth, 1999; Park et al., 2011). Output of these pathways may then be combined in downstream decision-making regions, leading to contextual benefits in object recognition. Alternatively, context-based object recognition may be supported by feedback processing, with scene context providing a prior that is integrated with ambiguous object representations in visual cortex (Bar, 2004; Brandman & Peelen, 2017; de Lange et al., 2018). Neuroimaging studies have not been able to distinguish between these possibilities because contextual modulation of neural activity in object-selective cortex (Brandman & Peelen, 2017; Faivre et al., 2019; Gronau et al., 2008; Rémy et al., 2014) could precede but also follow object recognition, for example reflecting post-recognition imagery (Dijkstra et al., 2018; Reddy et al., 2010).

To distinguish between these accounts, we used transcranial magnetic stimulation (TMS) to interfere with processing in right object-selective lateral occipital cortex (LOC (Grill-Spector, 2003; Malach et al., 1995)) and right scene-selective occipital place area (OPA (Dilks et al., 2013; Grill-Spector, 2003)) at three time points relative to stimulus onset. We additionally stimulated early visual cortex (EVC) to investigate the causal contribution of feedback processing in this region during both isolated and context-based object recognition (Camprodon et al., 2010; M. Koivisto et al., 2011; Pascual-Leone & Walsh, 2001; Wokke et al., 2013). The three regions were stimulated in separate pre-registered experiments (N=24 in each experiment; Material and Methods). In all experiments, participants performed an unspeeded 8-alternative forced-choice object recognition task, indicating whether a briefly presented stimulus belonged to one of 8 categories (Figure 2). Participants performed this task for clearly visible isolated objects (*isolated object recognition*) as well as for degraded objects presented within a congruent scene context (*context-based object recognition*). The effectiveness of TMS over each of the regions was ensured by a TMS-based participant assignment procedure involving a separate experimental session (Materials and Methods).

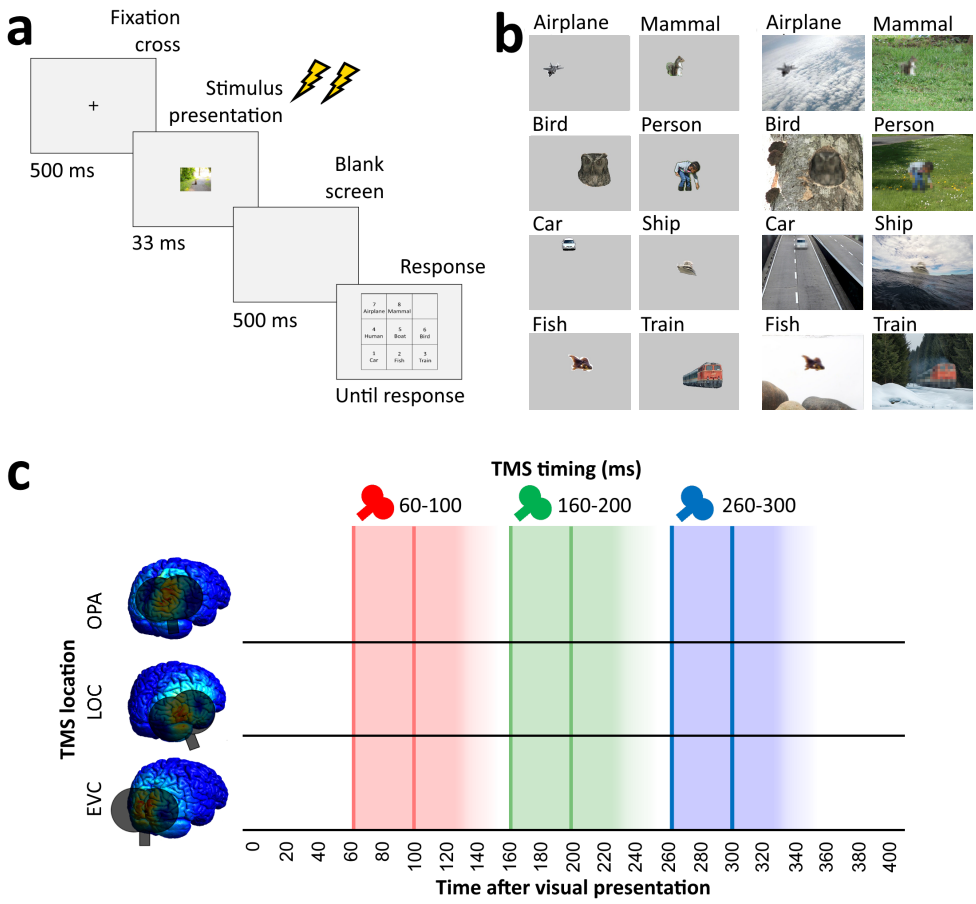

Figure 2. Overview of task and stimulation methods. a) *Schematic overview of a trial. Two TMS pulses (40 ms apart) were delivered on each trial at one of three time windows relative to stimulus onset (60-100 ms, 160-200 ms, 260-300 ms). The three TMS timings occurred in random order within each block.* ***b)*** *examples of each of the 8 categories shown in the experiment, in the isolated object condition (left) and the context-based object condition (right). Note that the local degradation of the objects in the context-based object condition is not clearly visible from these small example images. This degradation strongly reduces object recognition when the degraded objects are presented out of scene context (see Brandman & Peelen, 2017). These conditions were presented in random order and participants performed the same categorization task on all stimuli.* ***c)*** *Overview of the three TMS sites and the three time windows of stimulation. Shaded background colors indicate presumed time windows of inhibition for double-pulse TMS.*

We hypothesized that *isolated object recognition* (Figure 3a, top row) would be causally supported by EVC at 60-100 ms, followed by LOC at 160-200 ms, reflecting feedforward processing of intact object features. Scene-selective OPA was not expected to

contribute to isolated object recognition at any time point (Dilks et al., 2013; Wischnewski & Peelen, 2021). Similar to isolated object recognition, we hypothesized that *context-based object recognition* (Figure 3a, bottom row) would be causally supported by EVC at 60-100 ms and by LOC at 160-200 ms, reflecting feedforward processing. In contrast to isolated object recognition, we hypothesized that OPA would causally support context-based object recognition at 160-200 ms, reflecting scene processing. Crucially, scene-based expectations were hypothesized to feed back to LOC later in time, disambiguating object representations at 260-300 ms (Brandman & Peelen, 2017). TMS over LOC at this time point should thus selectively disrupt context-based object recognition. Finally, EVC was hypothesized to receive feedback from LOC (Camprodon et al., 2010; Koivisto et al., 2011; Murray et al., 2002; Wokke et al., 2013), which we expected to be most important for context-based object recognition, in which the object needs to be segregated from the background scene (Korjoukov et al., 2012; Lamme & Roelfsema, 2000; Scholte et al., 2008).

RESULTS

Across all TMS conditions, objects were equally recognizable when presented in isolation (without degradation; 75.8%) and when presented degraded within a scene (76.7%; main effect of Task: $F(1,71) = 1.22$, $p = 0.27$), replicating previous results showing that scene context can compensate for the loss of object visibility induced by the local degradation (Brandman & Peelen, 2017). Importantly, despite equal performance, recognition in the two tasks was supported by different neural mechanisms in a time-specific manner (3-way interaction between Task (intact object recognition, context-based object recognition), Region (OPA, LOC, EVC), and Time (60-100ms, 160-200ms, 260-300ms); $F(4,138) = 14.37$, $p < 0.001$, $\eta_p^2 = 0.294$; see Supp Fig 1 for RT data). This interaction was followed up by separate analyses for each of the stimulated regions.

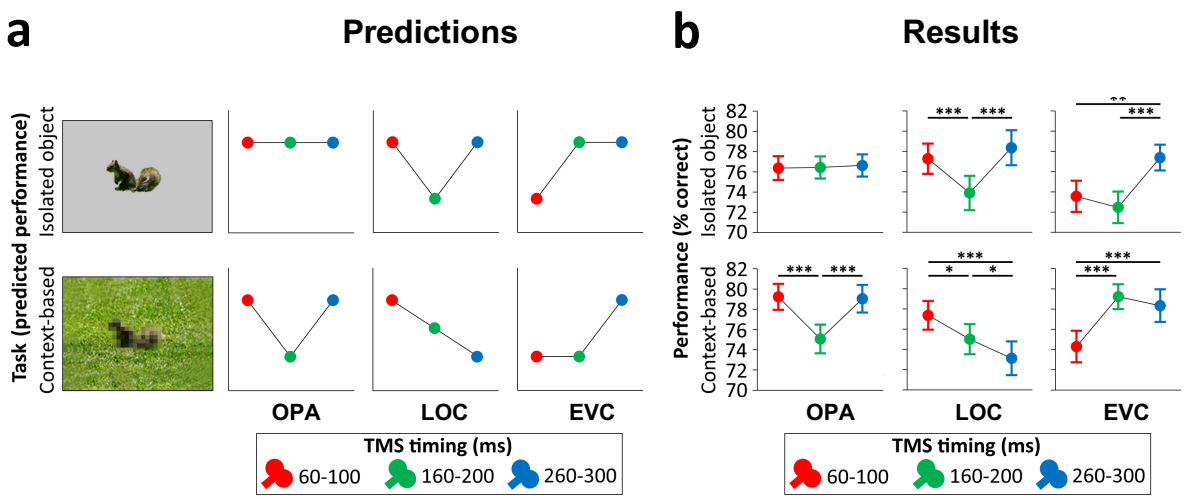

Figure 3. Predictions and results. a) *Preregistered predictions for the isolated object recognition task (top row) and the context-based object recognition task (bottom row).* ***b)*** *Results of three TMS experiments. Predictions were largely confirmed, except for feedback effects in EVC (at 160-200 ms), which were specific to isolated object recognition rather than context-based object recognition. *p<0.05, **p<0.01, ***p<0.001, with error bars reflecting the SEM.*

OPA experiment

Stimulation of scene-selective OPA differentially affected performance in the two tasks (Figure 3b, left panel; Task x Time interaction $F(2,46) = 8.21$, $p < 0.001$, $\eta_p^2 = 0.263$). For *isolated object recognition*, there was no effect of TMS time ($F(2,46) = 0.07$, $p = 0.935$, $\eta_p^2 = 0.003$), indicating that isolated object recognition was not influenced by TMS over OPA. By contrast, *context-based object recognition* was strongly modulated by TMS time ($F(2,46) = 19.54$, $p < 0.001$, $\eta_p^2 = 0.459$). As predicted, TMS selectively impaired context-based object recognition performance when OPA was stimulated 160-200 ms after scene onset, both relative to earlier stimulation ($t(23) = 5.39$, $p < 0.001$, $d = 1.099$) and relative to later stimulation ($t(23) = 5.36$, $p < 0.001$, $d = 1.095$), with no significant difference between early and late stimulation ($t(23) = 0.263$, $p = 0.795$). These results show that OPA, a scene-selective region, is causally and selectively involved in (context-based) object recognition. Results also provide information about the causal time course of OPA's involvement, showing a selective OPA effect at 160-200 ms after stimulus onset.

LOC experiment

Stimulation of object-selective LOC differentially affected performance in the two tasks (Figure 3b, middle panel; Task x Time interaction $F(2,46) = 12.99$, $p < 0.001$, $\eta_p^2 = 0.361$). For *isolated object recognition*, there was a main effect of TMS time ($F(2,46) = 15.50$, $p < 0.001$, $\eta_p^2 = .403$; Figure 3b). As predicted, TMS selectively impaired isolated object recognition performance when LOC was stimulated 160-200 ms after stimulus onset, both relative to earlier stimulation ($t(23) = 4.58$, $p < .001$, $d = 0.936$) and relative to later stimulation ($t(23) = 5.39$, $p < 0.001$, $d = 1.101$), with no significant difference between early and late stimulation ($t(23) = -1.17$, $p = 0.255$). A different temporal profile was observed for *context-based object recognition*. For this task, TMS time also had a significant effect ($F(2,46) = 9.03$, $p < 0.001$, $\eta_p^2 = .282$; Figure 3b). In contrast to the isolated object condition, performance strongly decreased when TMS was applied later in time, at 260-300 ms after stimulus onset, both relative to early stimulation ($t(23) = 4.01$, $p < 0.001$, $d = 0.818$) and relative to middle stimulation ($t(23) = 2.26$, $p = 0.034$, $d = 0.461$). Context-based object recognition accuracy was moderately reduced when TMS was applied at 160-200 ms relative to earlier stimulation ($t(23) = 2.17$, $p = 0.041$, $d = 0.442$). These findings confirm that LOC is causally involved in both isolated and context-based object recognition at 160-200 ms after stimulus onset. Crucially, LOC was causally involved in context-based object recognition at 260-300 ms, confirming our hypothesis that contextual feedback to LOC supports context-based object recognition.

EVC experiment

Finally, stimulation of EVC allowed us to test whether similar feedback effects could be observed earlier in the visual hierarchy. Results showed that the time of EVC stimulation differentially affected performance in the two tasks (Figure 3b, right panel; Task x Time interaction $F(2,46) = 14.42$, $p < 0.001$, $\eta_p^2 = 0.385$). For *isolated object recognition*, there was a main effect of TMS time ($F(2,46) = 13.27$, $p < 0.001$, $\eta_p^2 = 0.366$; Figure 3b). As

predicted, TMS applied early in time impaired recognition performance relative to TMS late in time ($t(23) = 3.44$, $p = 0.002$, $d = 0.701$). Interestingly, and contrary to our prediction, isolated object recognition was also impaired when TMS was applied at 160-200 ms compared to late stimulation ($t(23) = 5.19$, $p < 0.001$, $d = 1.06$). There was no difference in performance between TMS at early and intermediate time windows ($t(23) = 1.163$, $p = 0.257$). For *context-based object recognition*, there was a main effect of TMS time ($F(2,46) = 19.01$, $p < 0.001$, $\eta_p^2 = 0.452$; Figure 3b). As predicted, TMS applied early in time impaired recognition performance relative to TMS late in time ($t(23) = 5.41$, $p < 0.001$, $d = 1.105$). Contrary to our prediction, context-based object recognition performance was not significantly reduced when TMS was applied at the middle time window relative to later stimulation ($t(23) = 0.99$, $p = 0.334$). These findings confirm that EVC is causally involved in initial visual processing, supporting both isolated object recognition and context-based recognition. In the 160-200 ms time window, EVC was causally involved in isolated object recognition but not context-based object recognition.

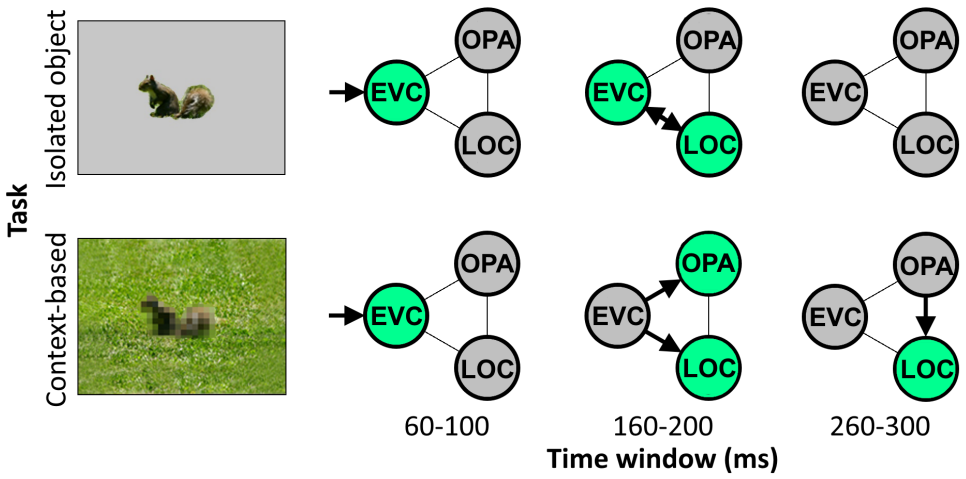

Figure 4. Schematic summarizing results. *Distinct cortical routes causally supported isolated object recognition and context-based object recognition. Isolated object recognition (top row) was supported by EVC early in time (60-100 ms), reflecting initial visual encoding. This was followed by LOC at 160-*

200 ms, reflecting higher-level object processing. At this time window, EVC was still required for isolated object recognition, reflecting feedback processing. Similar to isolated object recognition, context-based object recognition (bottom row) was supported by EVC at 60-100 ms, followed by LOC at 160-200 ms. However, context-based object recognition additionally required OPA at 160-200 ms, reflecting scene processing. Finally, context-based object recognition causally depended on late processing (260-300 ms) in LOC, reflecting contextual disambiguation (Brandman & Peelen, 2017). Note that the arrows do not necessarily reflect direct connections between brain regions.

DISCUSSION

Altogether, these results reveal distinct neural mechanisms underlying object recognition based on local features (isolated object recognition) and based on scene context. During feedforward processing, early visual cortex and object-selective cortex supported both the recognition of objects in scenes and in isolation, while scene-selective cortex was uniquely required for context-based object recognition. Results additionally showed that feedback to early visual cortex causally supported isolated object recognition, while feedback to object-selective cortex causally supported context-based object recognition. Together, these results provide evidence for two routes to object recognition, each characterized by feedforward and feedback processing but involving different brain regions at different time points (Figure 4).

The finding that EVC (for isolated object recognition) and LOC (for context-based object recognition) causally supported object recognition well beyond the feedforward sweep indicate that feedback (or recurrent) processing is required for accurate object recognition. Both these effects may reflect hierarchical perceptual inference (Friston, 2005; Haefner et al., 2016; Lee & Mumford, 2003; Rao & Ballard, 1999), in which a global representation provides a prior that allows for disambiguating relatively more local information. For context-based object recognition, the scene (represented in OPA) is the global element, providing a prior for processing the relatively more local shape of the object (represented in LOC), while

for isolated object recognition object shape is the global element, providing a prior for processing the relatively more local inner object features (e.g., the eyes of a squirrel; represented in EVC). Feedback based on the more global representations thus serves to disambiguate the representation of more local representations. The specific feedback that is useful for a given task – and the brain regions involved – likely depends on the available information in the image together with specific task demands (Hochstein & Ahissar, 2002).

The current results show that context-based object recognition is mediated by feedback to object-selective regions. This mechanism may underlie the behavioral benefits previously observed for object recognition in semantically and syntactically congruent (vs incongruent) scene context (Biederman et al., 1982; Davenport & Potter, 2004; Munneke et al., 2013; Võ & Wolfe, 2013). Our results thus support interactive accounts that propose that contextual facilitation is supported by contextual expectations (Bar, 2004; Davenport & Potter, 2004), with quickly extracted global scene “gist” priming the representation of candidate objects in visual cortex (Bar, 2004; Oliva & Torralba, 2007; Torralba, 2003). Results suggest that OPA is crucial for extracting this global scene information, and that this information is integrated with local object information in LOC shortly afterwards. The current results do not speak to whether OPA-LOC connectivity is direct or indirect, for example involving additional brain regions such as other scene-selective regions or the orbitofrontal cortex (Bar, 2004).

To conclude, the current study provides causal evidence that context-based expectations facilitate object recognition by disambiguating object representations in visual cortex. More generally, results reveal that distinct neural mechanisms support object recognition based on local features and based on global scene context. Future experiments may extend our approach to include other contextual features such as co-occurring objects, temporal context, and input from other modalities.

METHODS

Participants

Prior to experimentation, we decided to test 24 participants in all three experiments. Preregistrations can be found at: https://aspredicted.org/cs4wz.pdf (OPA), https://aspredicted.org/yc969.pdf (LOC), and https://aspredicted.org/cy9fq.pdf (EVC). In total, 72 right handed volunteers (43 females, mean age ± SD = 23.33 ± 3.59, age range = 18-33) with normal or corrected-to-normal vision took part in the experiment, after participating in a TMS localization experiment (Wischnewski & Peelen, 2021). Participants were excluded if they reported to have one of the following: CNS-acting medication, previous neurosurgical treatments, metal implants in the head or neck area, migraine, epilepsy or previous cerebral seizures (also within their family), pacemaker, intracranial metal clips, cochlea implants, or pregnancy. Additionally, participants were asked to refrain from consuming alcohol and recreational drugs 72 hours before the experiment and refrain from consuming coffee 2 hours before the experiment. Participants were divided over three experiments, targeting three cortical areas, based on a previous experiment (see below). All experiments included 24 participants (OPA experiment, 12 females, mean age ± SD = 23.67 ± 3.92; LOC experiment, 14 females, mean age ± SD = 23.50 ± 3.09; EVC experiment, 17 females, mean age ± SD = 22.83 ± 3.81). Prior to the experimental session, participants were informed about the experimental procedures and gave written informed consent. The study procedures were approved by the 'Centrale Commissie voor Mensgebonden Onderzoek (CCMO)' and conducted in accordance with the Declaration of Helsinki.

Participant assignment procedure

There are several reasons for why an individual may or may not show an effect of TMS over a particular brain region, including individual differences in functional coordinates but also skull thickness and subject-specific gyral folding patterns (Opitz et al., 2013). Therefore, we used a TMS-based assignment procedure to ensure the effectiveness of TMS over each of

the three stimulated regions at the individual participant level (van Koningsbruggen et al., 2013). To achieve this, all 72 participants in the current study first underwent a separate TMS session in which the effectiveness of TMS over the three regions was established using different object and scene recognition tasks (Dilks et al., 2013; Wischnewski & Peelen, 2021) and phosphene induction. Only participants who showed reduced scene recognition performance after OPA stimulation were assigned to the OPA experiment (N=24), only participants who showed reduced object recognition performance after LOC stimulation were assigned to the LOC experiment (N=24), and only participants who experienced TMS-induced phosphenes after EVC stimulation were assigned to the EVC experiment (N=24). The large effect sizes and consistency of results across participants in the current study suggest that this procedure may be a powerful and cost-effective alternative to functional localization using fMRI.

Transcranial magnetic stimulation

TMS was applied via a Cool-B65 figure-of-8 coil with an outer diameter of 75 mm, which received input from a Magpro-X-100 magnetic stimulator (MagVenture, Farum, Denmark). Two TMS pulses (biphasic, wavelength: 280 µs) separated by 40 ms (25 Hz) were applied to disrupt visual cortex activity. Given that latency of visual cortex activation varies across participants, a two-pulse TMS design was chosen since it allows for a broader time window of disruption while maintaining relatively good temporal resolution (O'Shea et al., 2004; Pitcher et al., 2007; Wokke et al., 2013). Intensity of stimulation was adjusted to 85% of the individual phosphene threshold (PT). PT was established by increasing stimulator output targeting EVC until 50% of the pulses resulted in the perception of a phosphene while participants fixated on a black screen in a dimly lit room. The TMS coil was placed with the help of an infrared-based neuronavigation system (Localite, Bonn, Germany) using an individually adapted standard brain model over the right LOC, right OPA or EVC. Each stimulation location was identified through Talairach coordinates set in the Localite neuronavigation system. The coordinates were 45, -74, 0 for LOC (Pitcher et al., 2009) and

34, -77, 21 for OPA (Julian et al., 2016). TMS was placed on EVC based on its anatomical location, 2 cm above the inion (Koivisto et al., 2010; Pascual-Leone & Walsh, 2001). We then established the optimal coil position in such a way that phosphenes were reported centrally in the visual field, where the stimuli were presented.

Experimental stimuli

Stimuli consisted of 128 scene photographs with a single object belonging to one of the following 8 categories: airplane, bird, car, fish, human, mammal, ship, and train. For the isolated object recognition task, the object was cropped out of the scene and presented at its original location on a gray background. For the context-based object recognition task, the object was pixelated to remove local features. The experiment additionally included a scene-alone condition, in which the object was cropped out and replaced with background using a content-aware fill tool. In this condition, participants had to guess the object category of the cropped-out object. Performance in this condition was low and not affected by TMS (Supp Figure 2).

To avoid that participants could recognize the degraded objects in scenes based on having seen their intact version, the stimulus set was divided in two halves: for each participant, half the stimuli were used in the context-based object condition, and the other half of the stimuli were used both in the isolated object condition and the scene-alone condition. This assignment was counterbalanced across participants. The scenes spanned a visual angle of 6 x 4.5 degrees.

Main task

Before the experiment, participants received instructions and were presented with an example stimulus (which was not used in the main experiment). This example displayed how each stimulus variation (context-based, isolated object, and scene alone) was derived from an original photograph. For the main task each trial started with a fixation cross (500 ms), followed by a stimulus presented for 33 ms. Next, a blank screen was shown for 500 ms.

After this, participants were asked to respond by pressing one out of eight possible keys according to the object category presented (Figure 2). No limit on response time was given. However, participants were encouraged during the instructions to respond within 3 seconds. The response screen was presented until the participant responded. The next trial started after a 2s inter-trial interval. This relatively long interval was chosen to prevent repetitive TMS effects. TMS was applied at one of three different time points, with randomized order. TMS pulses could be applied at 60 and 100 ms after stimulus onset, 160 and 200 ms after stimulus onset, or 260 and 300 ms after stimulus onset. In two participants out of the 72 (one in the LOC experiment and one in the EVC experiment), each pulse was accidentally delivered 16 ms earlier than described above.

Each stimulus was repeated three times, once for each TMS timing (60-100 ms, 160-200 ms, 260-300 ms). This resulted in a total of 576 trials, which were presented in a random order. To avoid fatigue, the task was divided into 12 blocks of 48 trials, each lasting approximately 4 minutes, with short breaks in between of approximately 1 minute. Thus, completing the task took about 60 minutes. Total duration of the experiment, including preparation and phosphene threshold determination, was approximately 90 minutes.

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AUTHOR CONTRIBUTIONS

Conceptualization, M.V.P.; Methodology, M.W. and M.V.P.; Investigation: M.W.; Writing – Original Draft, M.V.P.; Writing – Review & Editing, M.W. and M.V.P.; Funding Acquisition, M.V.P.

DECLARATION OF INTERESTS

The authors declare no competing interests.

REFERENCES

Bar, M. (2004). Visual objects in context. *Nature Reviews Neuroscience*, *5*(8), 617–629. https://doi.org/10.1038/nrn1476

Biederman, I., Mezzanotte, R. J., & Rabinowitz, J. C. (1982). Scene perception: Detecting and judging objects undergoing relational violations. *Cognitive Psychology*, *14*, 143–177.

Brandman, T., & Peelen, M. V. (2017). Interaction between Scene and Object Processing Revealed by Human fMRI and MEG Decoding. *The Journal of Neuroscience*, *37*(32), 7700–7710. https://doi.org/10.1523/JNEUROSCI.0582-17.2017

Camprodon, J. A., Zohary, E., Brodbeck, V., & Pascual-Leone, A. (2010). Two Phases of V1 Activity for Visual Recognition of Natural Images. *Journal of Cognitive Neuroscience*, *22*(6), 1262–1269. https://doi.org/10.1162/jocn.2009.21253

Davenport, J. L., & Potter, M. C. (2004). Scene Consistency in Object and Background Perception. *Psychological Science*, *15*(8), 559–564. https://doi.org/10.1111/j.0956-7976.2004.00719.x

de Lange, F. P., Heilbron, M., & Kok, P. (2018). How Do Expectations Shape Perception? *Trends in Cognitive Sciences*, *22*(9), 764–779. https://doi.org/10.1016/j.tics.2018.06.002

DiCarlo, J. J., Zoccolan, D., & Rust, N. C. (2012). How Does the Brain Solve Visual Object Recognition? *Neuron*, *73*(3), 415–434. https://doi.org/10.1016/j.neuron.2012.01.010

Dijkstra, N., Mostert, P., de Lange, F. P., Bosch, S., & van Gerven, M. A. (2018). Differential temporal dynamics during visual imagery and perception. *ELife*, *7*, e33904. https://doi.org/10.7554/eLife.33904

Dilks, D. D., Julian, J. B., Paunov, A. M., & Kanwisher, N. (2013). The Occipital Place Area Is Causally and Selectively Involved in Scene Perception. *Journal of Neuroscience*, *33*(4), 1331–1336. https://doi.org/10.1523/JNEUROSCI.4081-12.2013

Faivre, N., Dubois, J., Schwartz, N., & Mudrik, L. (2019). Imaging object-scene relations processing in visible and invisible natural scenes. *Scientific Reports*, *9*(1), 4567. https://doi.org/10.1038/s41598-019-38654-z

Friston, K. (2005). A theory of cortical responses. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *360*(1456), 815–836. https://doi.org/10.1098/rstb.2005.1622

Grill-Spector, K. (2003). The neural basis of object perception. *Current Opinion in Neurobiology*, *13*(2), 159–166. https://doi.org/10.1016/S0959-4388(03)00040-0

Gronau, N., Neta, M., & Bar, M. (2008). Integrated Contextual Representation for Objects' Identities and Their Locations. *Journal of Cognitive Neuroscience*, *20*(3), 371–388.

Haefner, R. M., Berkes, P., & Fiser, J. (2016). Perceptual Decision-Making as Probabilistic Inference by Neural Sampling. *Neuron*, *90*(3), 649–660. https://doi.org/10.1016/j.neuron.2016.03.020

Henderson, J. M., & Hollingworth, A. (1999). High-level scene perception. *Annual Review of Psychology*, *50*(1), 243–271. https://doi.org/10.1146/annurev.psych.50.1.243

Hochstein, S., & Ahissar, M. (2002). View from the Top: Hierarchies and Reverse Hierarchies in the Visual System. *Neuron*, *36*, 791–804.

Julian, J. B., Ryan, J., Hamilton, R. H., & Epstein, R. A. (2016). The Occipital Place Area Is Causally Involved in Representing Environmental Boundaries during Navigation. *Current Biology*, *26*(8), 1104–1109. https://doi.org/10.1016/j.cub.2016.02.066

Koivisto, M., Railo, H., Revonsuo, A., Vanni, S., & Salminen-Vaparanta, N. (2011). Recurrent Processing in V1/V2 Contributes to Categorization of Natural Scenes. *Journal of Neuroscience*, *31*(7), 2488–2492. https://doi.org/10.1523/JNEUROSCI.3074-10.2011

Koivisto, Mika, Mäntylä, T., & Silvanto, J. (2010). The role of early visual cortex (V1/V2) in conscious and unconscious visual perception. *NeuroImage*, *51*(2), 828–834. https://doi.org/10.1016/j.neuroimage.2010.02.042

Korjoukov, I., Jeurissen, D., Kloosterman, N. A., Verhoeven, J. E., Scholte, H. S., & Roelfsema, P. R. (2012). The Time Course of Perceptual Grouping in Natural Scenes. *Psychological Science*, *23*(12), 1482–1489. https://doi.org/10.1177/0956797612443832

Lamme, V. A. F., & Roelfsema, P. R. (2000). The distinct modes of vision offered by feedforward and recurrent processing. *Trends in Neurosciences*, *23*(11), 571–579. https://doi.org/10.1016/S0166-2236(00)01657-X

Lee, T. S., & Mumford, D. (2003). Hierarchical Bayesian inference in the visual cortex. *Journal of the Optical Society of America A*, *20*(7), 1434. https://doi.org/10.1364/JOSAA.20.001434

Liu, H., Agam, Y., Madsen, J. R., & Kreiman, G. (2009). Timing, Timing, Timing: Fast Decoding of Object Information from Intracranial Field Potentials in Human Visual Cortex. *Neuron*, *62*(2), 281–290. https://doi.org/10.1016/j.neuron.2009.02.025

Malach, R., Reppas, J. B., Benson, R. R., Kwong, K. K., Jiang, H., Kennedy, W. A., Ledden, P. J., Brady, T. J., Rosen, B. R., & Tootell, R. B. (1995). Object-related activity revealed by functional magnetic resonance imaging in human occipital cortex. *Proceedings of the National Academy of Sciences*, *92*(18), 8135–8139. https://doi.org/10.1073/pnas.92.18.8135

Munneke, J., Brentari, V., & Peelen, M. V. (2013). The influence of scene context on object recognition is independent of attentional focus. *Frontiers in Psychology*, *4*. https://doi.org/10.3389/fpsyg.2013.00552

Murray, S. O., Kersten, D., Olshausen, B. A., Schrater, P., & Woods, D. L. (2002). Shape perception reduces activity in human primary visual cortex. *Proceedings of the National Academy of Sciences*, *99*(23), 15164–15169. https://doi.org/10.1073/pnas.192579399

Oliva, A., & Torralba, A. (2007). The role of context in object recognition. *Trends in Cognitive Sciences*, *11*(12), 520–527. https://doi.org/10.1016/j.tics.2007.09.009

Opitz, A., Legon, W., Rowlands, A., Bickel, W. K., Paulus, W., & Tyler, W. J. (2013). Physiological observations validate finite element models for estimating subject-specific electric field distributions induced by transcranial magnetic stimulation of the human motor cortex. *NeuroImage*, *81*, 253–264. https://doi.org/10.1016/j.neuroimage.2013.04.067

O'Shea, J., Muggleton, N. G., Cowey, A., & Walsh, V. (2004). Timing of Target Discrimination in Human Frontal Eye Fields. *Journal of Cognitive Neuroscience*, *16*(6), 1060–1067. https://doi.org/10.1162/0898929041502634

Park, S., Brady, T. F., Greene, M. R., & Oliva, A. (2011). Disentangling Scene Content from Spatial Boundary: Complementary Roles for the Parahippocampal Place Area and Lateral Occipital Complex in Representing Real-World Scenes. *Journal of Neuroscience*, *31*(4), 1333–1340. https://doi.org/10.1523/JNEUROSCI.3885-10.2011

Pascual-Leone, A., & Walsh, V. (2001). Fast Backprojections from the Motion to the Primary Visual Area Necessary for Visual Awareness. *Science*, *292*(5516), 510–512. https://doi.org/10.1126/science.1057099

Pitcher, D., Charles, L., Devlin, J. T., Walsh, V., & Duchaine, B. (2009). Triple Dissociation of Faces, Bodies, and Objects in Extrastriate Cortex. *Current Biology*, *19*(4), 319–324. https://doi.org/10.1016/j.cub.2009.01.007

Pitcher, D., Walsh, V., Yovel, G., & Duchaine, B. (2007). TMS Evidence for the Involvement of the Right Occipital Face Area in Early Face Processing. *Current Biology*, *17*(18), 1568–1573. https://doi.org/10.1016/j.cub.2007.07.063

Rao, R. P. N., & Ballard, D. H. (1999). Predictive coding in the visual cortex: A functional interpretation of some extra-classical receptive-field effects. *Nature Neuroscience*, *2*(1), 79–87. https://doi.org/10.1038/4580

Reddy, L., Tsuchiya, N., & Serre, T. (2010). Reading the mind's eye: Decoding category information during mental imagery. *NeuroImage*, *50*(2), 818–825. https://doi.org/10.1016/j.neuroimage.2009.11.084

Rémy, F., Vayssière, N., Pins, D., Boucart, M., & Fabre-Thorpe, M. (2014). Incongruent object/context relationships in visual scenes: Where are they processed in the brain? *Brain and Cognition*, *84*(1), 34–43. https://doi.org/10.1016/j.bandc.2013.10.008

Riesenhuber, M., & Poggio, T. (1999). Hierarchical models of object recognition in cortex. *Nature Neuroscience*, *2*(11), 1019–1025. https://doi.org/10.1038/14819

Scholte, H. S., Jolij, J., Fahrenfort, J. J., & Lamme, V. A. F. (2008). Feedforward and Recurrent Processing in Scene Segmentation: Electroencephalography and Functional Magnetic Resonance Imaging. *Journal of Cognitive Neuroscience*, *20*(11), 2097–2109. https://doi.org/10.1162/jocn.2008.20142

Serre, T., Oliva, A., & Poggio, T. (2007). A feedforward architecture accounts for rapid categorization. *Proceedings of the National Academy of Sciences*, *104*(15), 6424–6429. https://doi.org/10.1073/pnas.0700622104

Torralba, A. (2003). Contextual Priming for Object Detection. *International Journal of Computer Vision*, *53*, 169–191.

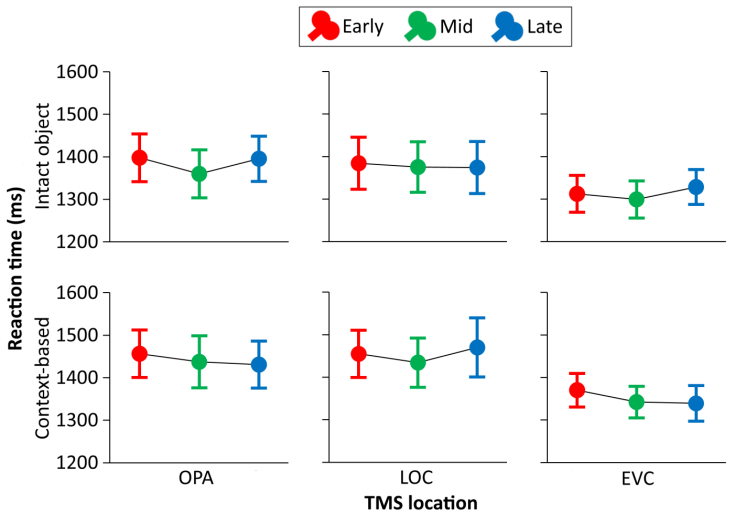
van Koningsbruggen, M. G., Peelen, M. V., & Downing, P. E. (2013). A Causal Role for the Extrastriate Body Area in Detecting People in Real-World Scenes. *Journal of Neuroscience*, *33*(16), 7003–7010. https://doi.org/10.1523/JNEUROSCI.2853-12.2013

Võ, M. L.-H., & Wolfe, J. M. (2013). Differential Electrophysiological Signatures of Semantic and Syntactic Scene Processing. *Psychological Science*, *24*(9), 1816–1823. https://doi.org/10.1177/0956797613476955

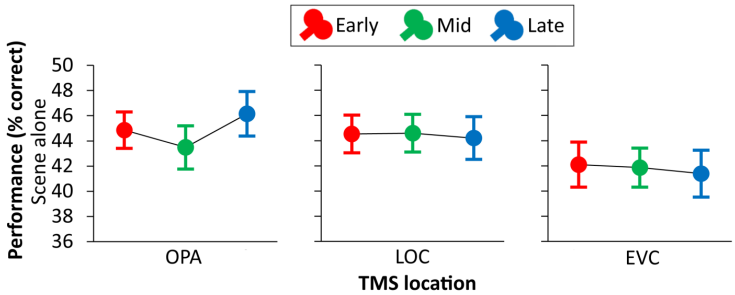
Wischnewski, M., & Peelen, M. V. (2021). Causal Evidence for a Double Dissociation between Object- and Scene-Selective Regions of Visual Cortex: A Preregistered TMS Replication Study. *The Journal of Neuroscience*, *41*(4), 751–756. https://doi.org/10.1523/JNEUROSCI.2162-20.2020

Wokke, M. E., Vandenbroucke, A. R. E., Scholte, H. S., & Lamme, V. A. F. (2013). Confuse Your Illusion: Feedback to Early Visual Cortex Contributes to Perceptual Completion. *Psychological Science*, *24*(1), 63–71. https://doi.org/10.1177/0956797612449175

Supplementary Material



Supplementary Figure 1. *Reaction time (ms) of each experiment for context-based and intact object recognition. TMS did not significantly affect RT, with no interactions involving either TMS timing or TMS region: Timing*Region, F(4,138) = 0.163, p = 0.957; Task*Region, F(2,69) = 0.81, p = 0.450; Timing*Task, F(2,142) = 0.37, p = 0.689; Timing*Region*Task, F(4,138) = 1.153, p = 0.334. There were also no significant main effects of Timing (F(2,142) = 2.88, p = 0.060) or Region (F(2,69) = 0.82, p = 0.447).*



Supplementary Figure 2. *Performance (% correct) for the scene alone task. In this task, participants had to guess the object category of the cropped-out object. Performance was generally low and not significantly affected by TMS (Timing*Region, F(4,138) = 1.77, p = 0.138; Timing, F(2,142) = 0.68, p = 0.509; Region, F(2,69) = 1.05, p = 0.355).*