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Report

Triple Dissociation of Faces, Bodies, and Objects in Extrastriate Cortex

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Summary

Neuroscientists have long debated whether focal brain regions perform specific cognitive functions [1–5], and the issue remains central to a current debate about visual object recognition. The distributed view of cortical function suggests that object discrimination depends on dispersed but functionally overlapping representations spread across visual cortex [6–8]. The modular view claims different categories of objects are discriminated in functionally segregated and specialized cortical areas [9–11]. To test these competing theories, we delivered transcranial magnetic stimulation (TMS) over three adjacent functionally localized areas in extrastriate cortex. In three experiments, participants performed discrimination tasks involving faces, bodies, and objects while TMS was delivered over the right occipital face area (rOFA) [12], the right extrastriate body area (rEBA) [13], or the right lateral occipital area (rLO) [14]. All three experiments showed a task selective dissociation with performance impaired only by stimulation at the site selective for that category: TMS over rOFA impaired discrimination of faces but not objects or bodies; TMS over rEBA impaired discrimination of bodies but not faces or objects; TMS over rLO impaired discrimination of objects but not faces or bodies. The results support a modular account in which category-selective areas contribute solely to discrimination of their preferred categories.

Results

To test the predictions of the modular and distributed accounts of visual object discrimination, we compared performance on discrimination tasks involving faces, bodies, or objects when transcranial magnetic stimulation (TMS) was delivered over functionally defined areas selective for faces, bodies, or objects. A no-TMS condition served as a baseline. Functional magnetic resonance imaging (fMRI) localizer results used for TMS site identification were consistent with previous studies (see Figure 1), with peak group responses for faces at 45, −80, −12 (Montreal Neurological Institute; MNI) [15], for bodies at 50, −72, 2 (MNI) [16], and for objects at 44, −75, −6 (MNI) [17]. TMS effects were seen solely as decreases in accuracy for the category of stimuli showing the strongest response in each area (see Figure 2). There were no significant effects of TMS on reaction times (RTs) in any experiment (see Figure S1 available online for the RT data). A separate error analysis performed for both stimulus sets in each experiment revealed that TMS did not selectively impair the same or different experimental trials (see Supplemental Data). Accuracy was measured with d′ [18], an unbiased measure of discrimination performance.

Experiment 1: TMS over rOFA and rLO during Face and Object Discrimination

Face discrimination was impaired when rTMS was delivered over the right occipital face area (rOFA) but not when rTMS was delivered over the right lateral occipital area (rLO). By contrast, object discrimination was impaired by rTMS at rLO but not at rOFA (see Figure 2A). A 3 × 2 repeated-measures analysis of variance (ANOVA) with site (rOFA, rLO, no TMS) and stimuli (faces versus objects) as independent factors showed a main effect of TMS site [$F(2, 28) = 14$, $p < 0.001$] and of stimulus [$F(1, 14) = 14.1$, $p = 0.002$]. TMS site and stimulus also combined in a two-way interaction [$F(2, 28) = 11.7$, $p < 0.001$]. Planned Bonferroni corrected post-hoc comparisons were performed. For face discrimination these revealed a significant performance impairment for rOFA relative to rLO ($p = 0.035$) and for rOFA relative to no TMS ($p = 0.019$). For object discrimination there was a significant impairment for stimulation of rLO relative to rOFA ($p = 0.004$) and for rLO relative to no TMS ($p = 0.014$). Importantly, TMS had no significant effects on the nonpreferred category in each region; performance on faces was equivalent when stimulating rLO or not stimulating at all ($p = 0.6$); and for objects there was no difference between rOFA stimulation and no stimulation ($p = 0.15$).

Experiment 2: TMS over rEBA and rLO during Body and Object Discrimination

Object discrimination was impaired when rTMS was delivered over rLO but not when rTMS was delivered over the right extrastriate body area (rEBA). Conversely, discrimination performance with bodies was impaired by rTMS at rEBA but not at rLO (see Figure 2B). A 3 × 2 ANOVA showed a main effect of TMS site [$F(2, 28) = 5.2$, $p = 0.012$] but not of stimulus [$F(1, 14) = 0.4$, $p = 0.5$]. TMS site and stimulus combined in a two-way interaction [$F(2, 28) = 10.1$, $p < 0.001$]. Planned Bonferroni corrected post-hoc comparisons revealed a significant performance impairment for object discrimination during stimulation of rLO relative to rEBA ($p = 0.023$) and for rLO relative to no TMS ($p = 0.049$). For body discrimination there were significant impairments during stimulation of rEBA relative to rLO ($p = 0.001$) and for rEBA relative to no TMS ($p = 0.004$). Again, these impairments were selective for the preferred category per region. Performance with objects was not significantly different when rEBA and no TMS were compared ($p = 0.9$). Similarly, body discrimination showed no difference between rLO stimulation and no stimulation ($p = 0.2$).

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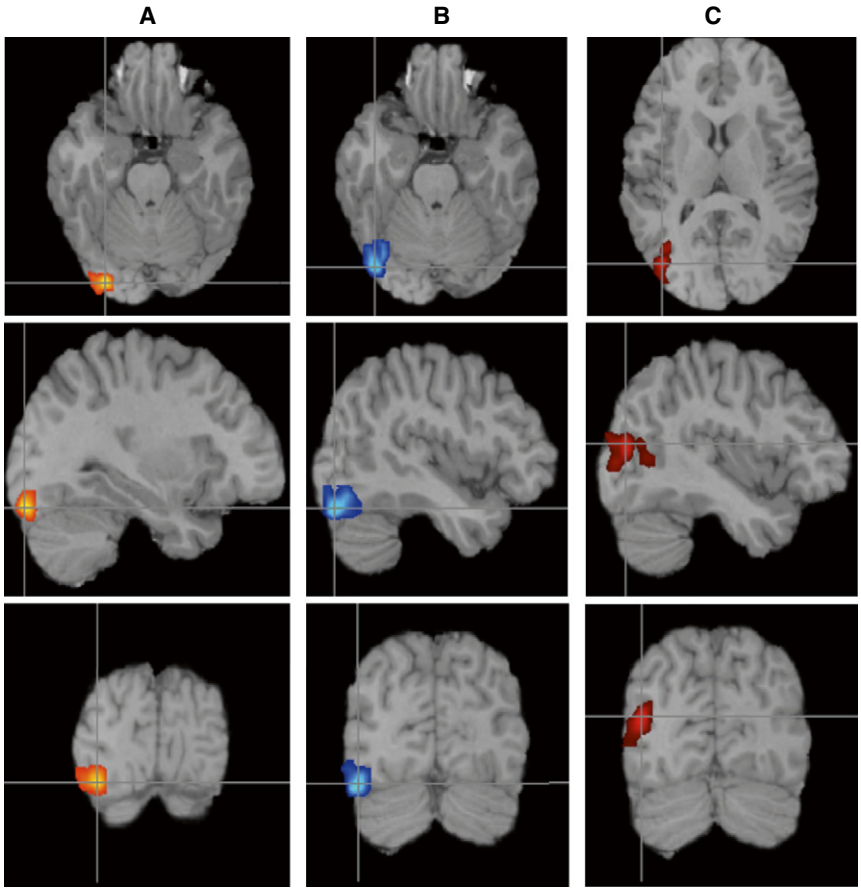

Figure 1. TMS Target Sites

Locations in one participant of (A) the rOFA in yellow (faces minus objects), (B) the rLO in blue (objects minus scrambled objects), and (C) the rEBA in red (bodies minus objects).

Experiment 3: TMS over rOFA and rEBA during Face and Body Discrimination

Face discrimination was impaired when rTMS was delivered over rOFA but not when rTMS was delivered over rEBA. By contrast, discrimination with bodies was impaired by rTMS at rEBA but not at rOFA (see Figure 2C). A 3 × 2 ANOVA showed a main effect of TMS site [$F(2, 28) = 3.5$, $p = 0.05$] and of stimulus [$F(1, 14) = 19$, $p < 0.001$]. TMS site and stimulus combined in a two-way interaction [$F(2, 28) = 10.1$, $p < 0.001$]. Bonferroni corrected post-hoc comparisons revealed a significant impairment for face discrimination during stimulation of rOFA relative to rEBA ($p = 0.036$) and for rOFA relative to no TMS ($p = 0.02$). Body discrimination showed a significant impairment during stimulation of rEBA relative to rOFA ($p = 0.027$) and for rEBA relative to no TMS ($p = 0.049$). As in the previous two experiments, these effects were specific to the regionally preferred categories. For bodies there was no significant difference between rOFA stimulation and no stimulation ($p = 0.8$), whereas for faces there was no difference between rEBA stimulation and no stimulation ($p = 0.9$).

Discussion

Our results clearly demonstrate that the three lateral category-selective visual areas we targeted are much more important for the discrimination of their preferred categories than for other categories. We observed TMS-induced discrimination impairments for the preferred category at each target site, yet TMS to these same sites had no effect on nonpreferred categories.

These findings are consistent with modular views of object recognition in which each functionally defined area represents information about its preferred category [19–21]. According to this account, disrupting processing within a category-selective area should selectively affect that category only and not other categories [9–11, 22], as we observed in all three experiments. These impairments are also consistent with studies of brain-damaged patients who exhibit category-specific recognition problems [23–26] and combined fMRI/single-unit studies that have identified multiple highly selective face patches in macaques [27, 28].

The results are inconsistent with the predictions of the distributed view of visual object representation in the occipitotemporal cortex. According to this view, category-selective areas represent information about preferred and nonpreferred categories [6–8, 29–33] and the apparent preference for one stimulus type is statistical rather than absolute. The distributed view therefore predicts that TMS would affect all category discriminations, though the effects on the preferred category might be the greatest. We did not, however, observe TMS-induced discrimination impairments for nonpreferred categories at any of the three category-selective areas. It remains possible that induced impairments involving nonpreferred categories were too subtle to detect in our tasks, but this seems unlikely because TMS would have stimulated areas containing cells responsive to nonpreferred stimuli equally as much as the preferred category cells according to previous studies [6–8]. However, TMS only affected sensitivity but not RTs because, in part, of RT variability, and it remains logically possible that a different set of performance-matched tasks may reveal that TMS produces graded effects on different categories in the RT domain [34].

Our findings further suggest which aspects of bodies and faces are represented in the rEBA and rOFA. Previous studies that delivered TMS over rEBA demonstrated that isolated body parts [35] and inverted body posture [36] are both represented in this area. In our experiment the body stimuli were presented upright and whole. It is possible that participants discriminated the bodies based on body parts; our results extend earlier findings by showing that rEBA represents bodies in their most common configuration. This role for rEBA is consistent with fMRI studies showing that rEBA responds as strongly or

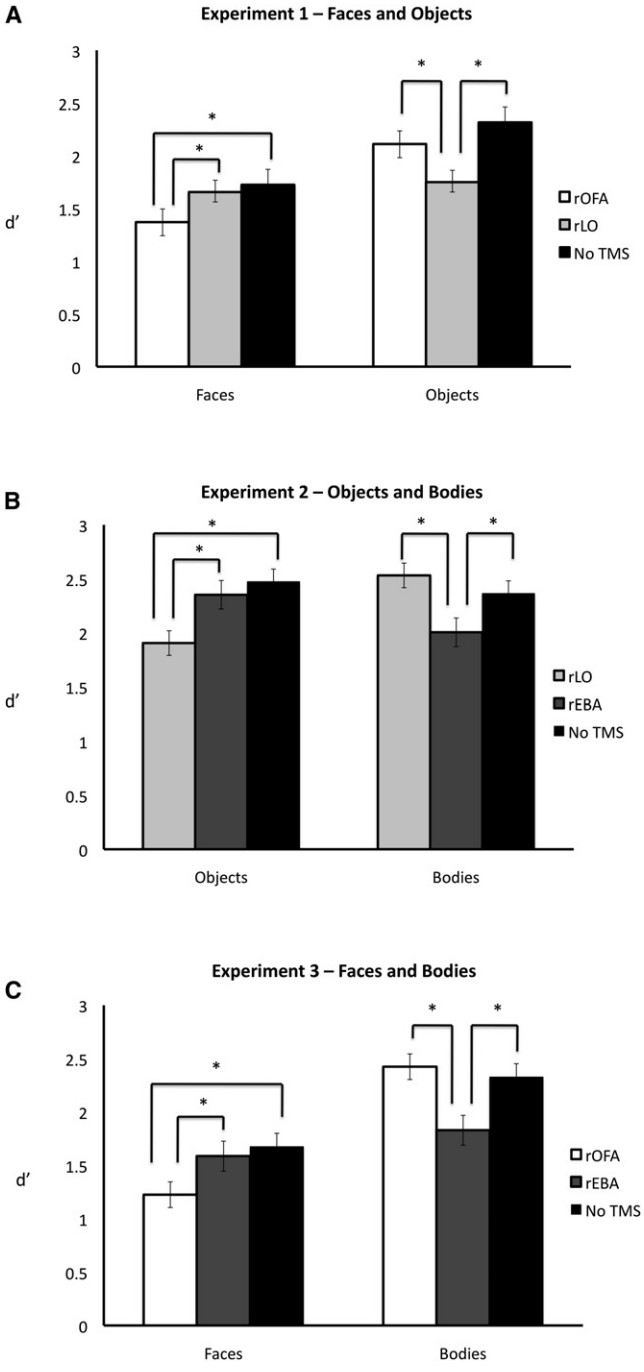

Figure 2. Results from Experiment 1, Experiment 2, and Experiment 3

In each panel, performance on two tasks is compared in three conditions: TMS to a site selective for that category, TMS to a site selective for another category, and no TMS. An asterisk (*) denotes a significant difference in Bonferroni-corrected tests.

(A) Faces and objects. Face task performance was disrupted only by TMS to rOFA, and object task performance was impaired only by TMS to rLO.

(B) Objects and bodies. Object task performance was impaired only by TMS to rLO, whereas performance on the body task was disrupted only by TMS to rEBA.

(C) Faces and bodies. Performance on the face task was impaired only by TMS to rOFA, and body task performance was disrupted only by TMS to rEBA. (Error bars represent standard errors.)

even more strongly to upright whole bodies than to isolated body parts [37].

Previous studies showing a TMS induced impairment for faces at rOFA have suggested that rOFA represents the shape of the internal face parts (e.g., the eyes and the mouth). In the first paper to target rOFA, discrimination of face parts was disrupted by TMS, but discrimination of the spacing between face parts was unaffected [38]. Another study that showed that TMS disrupted facial expression discrimination but not facial identity discrimination is also consistent with rOFA representation of the shape of face parts [39]. We suggested discrimination of facial expressions was disrupted because face part shape was critical to expression identification. In contrast, reliance on part shape for the identity discriminations would not have been an effective strategy because the sample and probe faces always differed in their expressions and hence in the shape of their face parts. In the current study, however, the faces all had neutral expressions, so face part shape differences could contribute to the discrimination task and were thus susceptible to TMS disruption.

The results in the current study do not demonstrate whether the impairments result from disruption to the analysis of the probe stimulus or a memory representation of the sample stimulus. Previous results relevant to this issue are mixed. Two experiments at rOFA in which TMS delivery time was varied suggest that TMS to rOFA disrupts analysis of the probe but has no effect on the memory representation [38, 39]. In these studies double-pulse TMS delivered at 20 and 60 ms after probe presentation had no effect on face discrimination, whereas double-pulse TMS delivered at 60 and 100 ms impaired performance. However in previous studies in which TMS delivered over rEBA disrupted body discrimination [35, 36], double-pulse TMS was delivered during the 500 ms interval between the sample and probe stimuli (pulses were delivered 150 and 250 ms after sample offset and hence 350 and 250 ms before probe onset). This suggests that rEBA may be important for maintaining a short-term visual storage of body information. Future studies will be necessary to more precisely determine what role these category-selective areas perform for visual memory.

To date, the studies that have examined whether visual objects are represented in specialized modules or by more-distributed mechanisms spread across visual cortex have used fMRI [6–11] or computational modeling [29–32] to address the issue. This study is the first to use TMS to systematically investigate this question, and from the causal inferences that can be drawn from induced neural disruptions, we conclude that faces, bodies, and objects are functionally segregated in the human occipitotemporal lobe. The fMRI response in category-selective regions contains information about stimuli from a nonselective category [6, 7, 19, 21], and recent discussion has been concerned with whether this information contributes to recognizing and discriminating non-preferred stimuli [6, 7, 10, 11]. The category-selective triple dissociation between faces, objects, and bodies in extrastriate cortex reported here suggests that this information does not contribute to such recognition.

Experimental Procedures

Participants

Sixteen neurologically normal participants (8 males and 8 females aged 18–34 years, mean age: 24 years) were scanned. One male participant withdrew after the first TMS experiment due to discomfort with TMS stimulation of

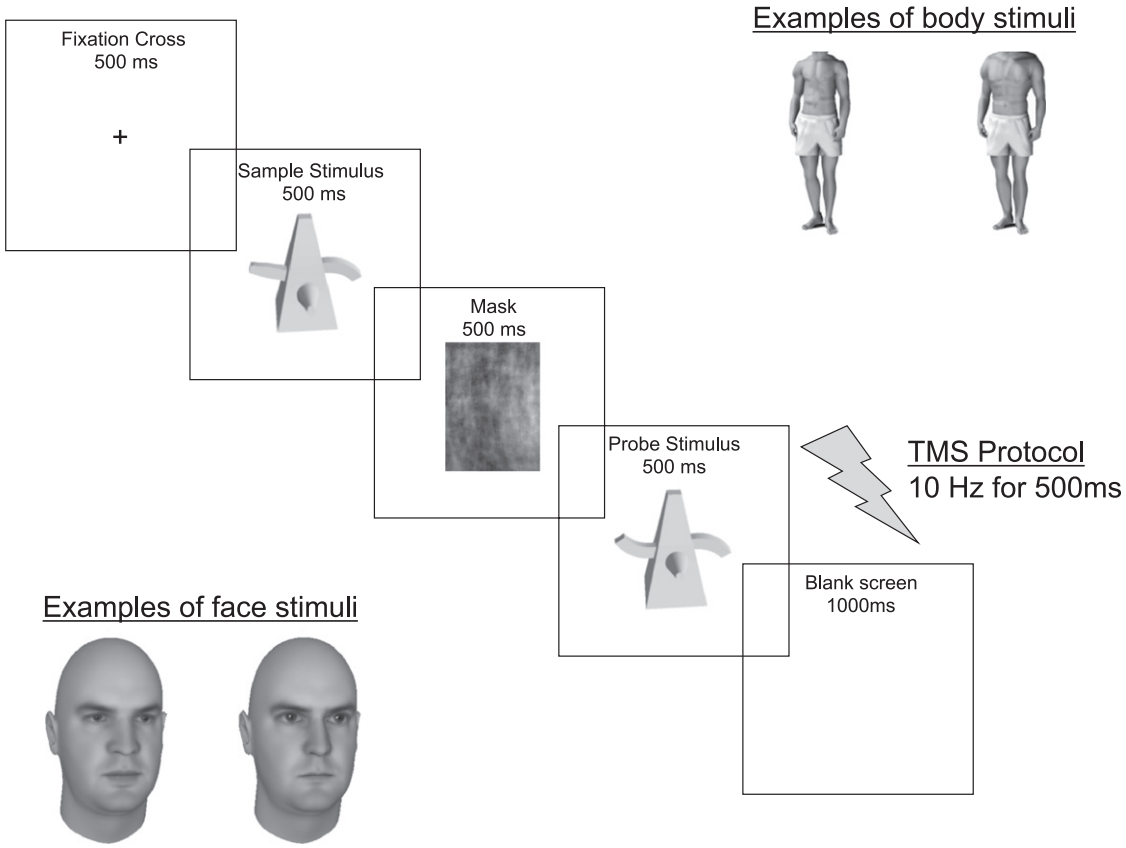

Figure 3. Timeline of the Experimental Trial Procedure and Examples of the Face, Body, and Object Stimuli

The first pulse of rTMS coincided with the onset of the sample stimulus. Participants judged whether the probe stimulus was the same or different from the sample stimulus. Although not shown in the figure, the second stimulus was presented below and to the left or right of the match stimulus.

rOFA. The remaining 15 participants completed all three experiments and were naive to the aims of the study. All were right-handed, had normal or corrected-to-normal vision, and gave informed consent. The experiments were approved by the local research ethics committee of University College London.

Imaging

Whole-brain imaging was performed on a Siemens 1.5 Tesla MR scanner at the Birkbeck-UCL Neuroimaging Centre (BUCNI). Functional data were acquired in a single 11 min run with a gradient-echo EPI sequence (TR = 2500 ms; TE = 50 ms, FOV = 192 × 192, matrix = 64 × 64), giving a notion resolution of 3 × 3 × 3 mm. In addition, a high-resolution anatomical scan was acquired (T1-weighted FLASH, TR = 12 ms, TE = 5.6 ms, 1 mm^3 resolution) for anatomically localizing activations and to accurately target TMS stimulation sites in each individual using a frameless stereotaxic system (BrainSight; Rogue Research, Montreal, Canada).

The functional localizer scan used a one-back paradigm to focus attention on the four categories of visual stimuli: faces, headless bodies, household objects, and scrambled images of the household objects. Each image was presented for 200 ms with an 800 ms blank interval between images. Participants were instructed to press a key whenever they detected two images repeated in a row (one-back task). This happened twice per block and ensured participants were alert and attentive. Stimuli were presented in blocks of 16 items from within a category, and each block was preceded by a centrally presented 16 s fixation dot. Within each set of four blocks, the serial position of the categories was varied and all blocks were repeated eight times, using a total of 80 different images per category.

Functional imaging data were analyzed using FSL (http://www.fmrib.ox.ac.uk/fsl/). After deleting the first two volumes of each run to allow for T1 equilibrium, the functional images were realigned to correct for small head movements [40]. The images were then smoothed with a 5 mm full-width half-maximum Gaussian filter and prewhitened to remove temporal autocorrelation [41]. The resulting images were entered into a subject-specific general linear model with four conditions of interest corresponding to the four categories of visual stimuli. Blocks were convolved with a double-gamma canonical hemodynamic response function [42] to generate the main regressors. In addition, the estimated motion parameters were entered in as covariates of no interest, to reduce structured noise due to minor head motion. Linear contrasts were used to identify the three TMS target sites within each subject: rOFA by contrasting faces to objects, rLO by contrasting objects to scrambled objects, and rEBA by contrasting headless bodies to objects. The functional images were then registered to each participant's individual structural scan using a 12 DoF affine transformation [40] to identify three TMS target sites (rOFA, rLO, and rEBA) in the right cerebral hemisphere. Each TMS target site was individually identified in each participant by selecting the peak activation (minimum required zstat value was 2.3) for that category in the lateral occipital cortical region. The coordinates and strength of the peak responses in the 15 participants varied, but rOFA, rEBA, and rLO were identified in each participant (see Table S1 for individual participant localizer results).

Experimental Stimuli

All stimuli were presented centrally on an SVGA 17 inch monitor set at 1024 × 768 resolution and a refresh rate of 100 Hz. FantaMorph software (Abrosoft; http://www.abrosoft.com/) was used to make a morph series between the 10 pairs of each stimulus category: faces, objects, and bodies (30 in total). Each morph series was composed of ten images with a 10% difference between each image. These morph-series images were then used to create 80 unique experimental trials (40 same, 40 different) comprised of eight trials per morph-series pair.

Faces

Ten faces (varied in gender and viewing angle) were created using FaceGen software (Singular Inversions; Toronto, ON, Canada), and the component parts of these faces (eyes, mouth, and nose) were then individually altered

to create a second face. Each face pair was then used to create a morph series. For the different trials, the percentage morph difference between the two images was 50% (10 trials), 80% (20 trials), or 100% (10 trials).

Objects

A set of novel objects was downloaded from Michael Tarr's website (http://titan.cog.brown.edu:8080/TarrLab/author/tarr). Each pair used for morphing was comprised of two visually similar objects seen from the same viewing angle that had the same overall shape but which varied in local details. For different trials the percentage difference between the two images was 20% (three trials), 30% (14 trials), 50% (six trials), 80% (seven trials), or 100% (ten trials).

Bodies

Ten pairs of male bodies (varied in corpulence and muscle tone) wearing white shorts and seen from different viewing angles were created using Poser software (Smith Micro, Inc.; Watsonville, CA). Adobe Photoshop was used to remove the head. Body pose was the same for both images in each trial. For different trials the percentage difference between the two images was 50% (10 trials), 80% (20 trials), or 100% (10 trials).

TMS Stimulation and Site Localization

A Magstim Super Rapid stimulator (Magstim; Whitland, UK) was used to deliver the TMS via a figure-eight coil with a wing diameter of 70 mm. TMS was delivered at 10 Hz and 60% of maximal stimulator output, with the coil handle pointing upwards and parallel to the midline. A single intensity was used for all subjects on the basis of previous studies [38, 39, 43–45]. On blocks of trials with TMS, test stimuli were presented during 500 ms rTMS with rTMS onset concurrent with the onset of the target visual stimulus.

TMS sites were located with the Brainsight TMS-MRI coregistration system (Rogue Research), utilizing individual high-resolution MRI scans for each participant. The rOFA, rLO, and rEBA were localized by overlaying individual activation maps from the fMRI localizer task for the face and object analysis, and the proper coil locations were marked on each participant's head. The target area was identified by selecting the voxel exhibiting the peak activation in each functionally defined area.

Procedure

Each participant was tested across three sessions run on different days. In experiment 1, rTMS was targeted at either rOFA or rLO while participants performed two blocks of 80 trials each for both categories (faces and objects). A no-TMS block for each category was also included as a behavioral baseline. Category order was alternated during the testing session. The order of TMS stimulation blocks was counterbalanced between participants. The no-TMS blocks were interspersed at the beginning, middle, or end of each testing session, and the order was counterbalanced between participants.

Figure 3 displays the trial procedure. Participants were required to judge whether the sample stimulus was the same as the probe stimulus. Each image was presented for 500 ms. Within each block, the trial order was randomized. Participants made keyboard responses using the right hand while seated with their heads stabilized on a chinrest 57 cm from the computer screen. They were instructed to respond as accurately and as quickly as possible.

Experiment 2 followed the same procedure as experiment 1. Participants were presented with two sequential discrimination tasks (objects and bodies) while rTMS was delivered over rLO and rEBA. A no-TMS block was again included for each task.

Experiment 3 followed the same procedure as experiments 1 and 2 except that faces and bodies were used and TMS was delivered over rOFA and rEBA.

Supplemental Data

Supplemental Data include eight figures and Supplemental Experimental Procedures and can be found with this article online at http://www.current-biology.com/supplemental/S0960-9822(09)00543-0.

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