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The role of lateral occipital face and object areas in the face inversion effect

David Pitcher[a,b,*], Bradley Duchaine[c], Vincent Walsh[b], Galit Yovel[d], Nancy Kanwisher[a]

[a] *McGovern Institute for Brain Research, Massachusetts Institute of Technology, Cambridge, MA 02139, USA*
[b] *Institute of Cognitive Neuroscience, University College London, Alexandra House, 17 Queen Square, London WC1N 3AR, United Kingdom*
[c] *Department of Psychology and Brain Sciences, Dartmouth College, Hanover, NH 03755, USA*
[d] *Department of Psychology, Tel Aviv University, Tel Aviv 69978, Israel*

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ABSTRACT

Stimulus inversion impairs face discrimination to a greater extent than discrimination of other non-face object categories. This finding has led to suggestions that upright faces are represented by mechanisms specialized for upright faces whereas inverted face representation depends on more general object recognition mechanisms. In the present study we tested the causal role of face-selective and object-selective cortical areas for upright and inverted face discrimination by transiently disrupting neural processing using transcranial magnetic stimulation (TMS). Participants matched upright and inverted faces while TMS was delivered over each participant's functionally localized right occipital face area (rOFA) or right lateral occipital area (rLO). TMS delivered over rOFA disrupted the discrimination of upright and inverted faces while TMS delivered over rLO impaired inverted face discrimination only. These results provide causal evidence that upright faces are represented by face-specific mechanisms whereas inverted faces are represented by both face-specific and object-specific mechanisms. The similar sensitivity of the OFA to upright and inverted faces is consistent with the hypothesis that the OFA processes facial features at an early stage of face processing.

1. Introduction

The face inversion effect (FIE) is a classic signature of face perception in which stimulus inversion disrupts face recognition more strongly than object recognition (Farah, Tanaka, & Drain, 1995; McKone, Kanwisher, & Duchaine, 2007; Yin, 1969). The FIE is taken as evidence for the existence of face-specific mechanisms in the brain that are tailored for processing upright faces only (Farah, 2004; Yin, 1969). However this account does not specify which mechanisms contribute to the perception of inverted faces and whether mechanisms that are not face-selective contribute to upright face recognition. Here we tested these questions using transcranial magnetic stimulation (TMS).

1.1. *The neural basis of the face inversion effect*

Neuropsychological studies of patients with impairments in visual processing provide causal evidence that upright and inverted faces are represented using distinct cognitive mechanisms (Farah, 2004; Yin, 1970). Some prosopagnosic patients are impaired (relative to control subjects) in recognizing upright but not inverted faces (Farah, Wilson, Drain, & Tanaka, 1995). The same is true of developmental prosopagnosics, who have lifelong impairments in face recognition despite the absence of any known brain damage (Duchaine, Yovel, & Nakayama, 2007). By contrast, one patient with an object recognition impairment was normal at upright face recognition, but severely impaired in recognizing inverted faces, thus showing a face inversion effect that was many-fold larger in magnitude than that found in normal subjects (Moscovitch & Moscovitch, 2000; Moscovitch, Winocur, & Behrmann, 1997). These findings have been taken to show that inverted faces are processed through the generic object recognition pathway, whereas upright faces are processed in systems specialized for upright faces only.

Functional magnetic resonance imaging (fMRI) studies of neurologically normal participants have also examined how upright and inverted faces are represented in the brain. Several studies have demonstrated that the face-selective fusiform face area (FFA) (Kanwisher, McDermott, & Chun, 1997) exhibits a greater response to images of upright faces than to images of inverted faces (Epstein, Higgins, Parker, Aguirre, & Cooperman, 2006; Kanwisher, Tong, & Nakayama, 1998; Mazard, Schiltz, & Rossion, 2006; Yovel & Kanwisher, 2005; but see Aguirre, Singh, & D'Esposito, 1999; Haxby et al., 1999). By contrast, the scene-selective parahippocampal place area (PPA) (Epstein & Kanwisher, 1998) as well as the object recognition area in the lateral occipital cortex (LO) (Malach et al., 1995) exhibit greater responses to inverted faces than to upright faces (Aguirre et al., 1999; Epstein 2005; Haxby et al., 1999;

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* Corresponding author at: Laboratory of Brain and Cognition, National Institute for Mental Health, Bethesda, MD 20892, USA. Tel.: +1 301 435 4931.
E-mail addresses: pitcherdj@mail.nih.gov, dpitcher@mit.edu (D. Pitcher).

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Yovel & Kanwisher, 2005). These studies further demonstrate that upright and inverted faces are preferentially processed in functionally segregated and spatially distinct cortical areas.

In the present study we investigated the contribution of face-selective and object-selective cortical areas to upright and inverted face discrimination by combining the spatial precision of fMRI with the causal inferences one can draw from the neural disruption induced by transcranial magnetic stimulation (TMS). Participants performed a delayed match-to-sample discrimination task with upright and inverted faces while TMS was delivered over the functionally localized right occipital face area (rOFA) and right LO (rLO). The OFA is believed to play a role in early feature-based stages of face perception (Haxby et al., 1999) and TMS delivered over rOFA has been shown to disrupt discrimination of upright faces but not discrimination of non-face stimuli such as houses, objects, and human bodies (Pitcher, Charles, Devlin, Walsh, & Duchaine, 2009; Pitcher, Garrido, Walsh, & Duchaine, 2008; Pitcher, Walsh, Yovel, & Duchaine, 2007). The OFA has also been shown to exhibit a similar neural response to upright and inverted faces (Yovel & Kanwisher, 2005; but see Mazard et al., 2006) leading us to hypothesize that TMS delivered over the rOFA would disrupt both upright and inverted face discrimination. TMS delivered over rLO disrupts object discrimination (Chouinard, Whitwell, & Goodale, 2009) but not face discrimination (Pitcher et al., 2007, 2009). Based on the neuropsychological, fMRI and previous TMS evidence we predicted that TMS delivered over rLO would disrupt inverted face discrimination but have no effect on upright face discrimination.

2. Materials and methods

2.1. Participants

Ten right-handed participants with normal or corrected-to-normal vision (5 females, aged 19–27) gave informed consent as directed by the Massachusetts Institute of Technology IRB committee. No participants withdrew due to discomfort with TMS stimulation.

2.2. Materials

Closely matched face stimuli in which the component parts were altered were used and similar example stimuli are presented in Fig. 1 (Yovel & Kanwisher, 2004). These stimuli were used in a previous TMS study of the rOFA (Pitcher et al., 2007).

2.3. Procedure

The experiment used a two-by-three design in which participants discriminated upright and inverted faces while rTMS was delivered over rOFA, rLO or no TMS was delivered (the no TMS condition was included as a behavioural baseline). Fig. 2 shows the trial procedure. Stimuli were presented centrally on an SVGA 20 inch monitor (Resolution 1024 by 768, refresh rate 70 Hz). Participants sat 57 cm from the monitor with their heads stabilized in a chin rest and indicated by a right hand key press whether the sample stimulus was the same as the probe stimulus. They were instructed to respond accurately and as quickly as possible.

Face orientation (upright or inverted) was blocked and the order was balanced across participants (half of the participants started with upright faces, the other half with inverted faces). Three blocks of 40 trials (20 same trials, 20 different trials) were presented for each face orientation. During each block, rTMS was delivered over rOFA or rLO or no TMS was delivered. The order of TMS blocks was varied across participants and balanced using a Latin square design. Within each block the trial order was randomized. During the same testing session participants also completed a second TMS discrimination task using different stimuli that tested a different hypothesis.

2.4. Imaging

TMS target sites (rOFA and rLO) were individually identified in all participants using a standard fMRI localizer task (Pitcher, Dilks, Saxe, Triantafyllou, & Kanwisher, 2011). Functional data were acquired over 4 blocked-design functional runs lasting 234 s each. Scanning was performed in a 3.0 T Siemens Trio scanner at the A. A. Martinos Imaging Center at the McGovern Institute for Brain Research at the Massachusetts Institute of Technology. Functional images were acquired with a Siemens 32-channel phased array head-coil and a gradient-echo EPI sequence (32 slices, repetition time (TR) = 2 s, echo time = 30 ms, voxel size = 3 mm × 3 mm × 3 mm, and 0.6 mm interslice gap) providing whole brain coverage (slices were aligned with the anterior/posterior commissure). In addition, a high-resolution T-1 weighted MPRAGE anatomical scan was acquired for anatomically localizing the functional activations. Each functional run contained two sets of five consecutive dynamic stimulus blocks (faces, bodies, scenes, objects or scrambled objects) sandwiched between rest blocks, to make two blocks per stimulus category per run. Each block lasted 18 s and contained stimuli from one of the five stimulus categories.

Data were analyzed with FS-FAST, Freesurfer (http://surfer.nmr.mgh.harvard.edu/) (Dale, Fischl, & Sereno, 1999; Fischl, Sereno, & Dale, 1999). Before statistical analysis, images were motion corrected (Cox & Jesmanowicz, 1999), smoothed (3 mm FWHM Gaussian kernel), detrended, and fit using a gamma function (delta = 2.25 and tau = 1.25). The pre-processing did not involve any spatial normalization of subjects in a common reference space (e.g., Talairach transformations). The functional data of each subject were co-registered with that subject's anatomical image.

Significance maps of the brain were computed using the same statistical threshold for both TMS target sites ($p = 10^{-4}$, uncorrected) (see Fig. 3). The rOFA was identified using a contrast of dynamic faces greater than dynamic objects and was always located on the lateral surface of the occipital lobe posterior to the face-selective rFFA (mean MNI co-ordinates = 43, −79, −11). The rLO was identified using a contrast of dynamic objects greater than scrambled objects and was always located on the lateral surface of the occipital lobe and was superior to the rOFA (mean MNI co-ordinates = 44, −73, −6). The coordinates and strength of the peak responses varied across participants but rOFA and rLO were identified in each participant.

2.5. TMS stimulation and site localization

TMS target sites were individually identified using the Brainsight TMS–MRI co-registration system (Rogue Research, Montreal, Canada), utilizing individual high resolution structural and functional MRI scans for each participant. The rOFA and rLO were localized by overlaying individual activation maps from the fMRI localizer task for the face and object analysis and identifying the voxel exhibiting the greatest activation in each category-selective region. The surface coil locations were then marked on each participant's head. To ensure accurate coil placement during the experiment the position of the coil was tracked and monitored during half of the TMS blocks using the Brainsight system.

TMS was delivered at 10 Hz and 60% of maximal stimulator output, using a Magstim Super Rapid Stimulator (Magstim, UK) and a 70 mm figure-of-eight coil, with the coil handle pointing upwards and parallel to the midline. A single intensity was used on the basis of previous studies (O'Shea, Muggleton, Cowey, & Walsh, 2004; Silvanto, Lavie, & Walsh, 2005) and for ease of comparison with similar studies of the rOFA and rLO (Pitcher et al., 2007, 2009). In TMS blocks, TMS was delivered at a frequency of 10 Hz for 500 ms and its onset coincided with the onset of the test stimulus.

3. Results

Accuracy was measured with d' (Green & Swets, 1966), an unbiased measure of discrimination performance, and the mean data are shown in Fig. 4a. A two-by- three repeated measures analysis of variance (ANOVA) with orientation (upright or inverted) and TMS site (rOFA, rLO, no TMS) as independent factors revealed main effects of orientation [$F(1,9) = 24.6$, $p = 0.001$] and of TMS site [$F(2,18) = 12.1$, $p < 0.0001$]. Importantly there was also a significant interaction between orientation and TMS site [$F(2,18) = 5.6$, $p = 0.013$]. Planned Bonferroni corrected tests revealed that discrimination of upright faces was significantly impaired by TMS delivered over the rOFA compared with TMS delivered over rLO ($p = 0.008$) and the no TMS condition ($p = 0.014$) but there was no significant difference between the rLO and no TMS condition ($p = 0.8$). By contrast discrimination of inverted faces was significantly impaired by TMS delivered over rOFA ($p = 0.044$) and rLO ($p = 0.034$) compared with the no TMS condition.

To further demonstrate that TMS delivered over rOFA disrupted upright and inverted face discrimination while TMS delivered over rLO disrupted inverted face discrimination only we performed additional analyses to separately compare rOFA and rLO performance with the no TMS condition. As predicted, a two-by-two ANOVA examining performance in the rOFA condition with orientation (upright or inverted) and TMS site (rOFA or no TMS) as independent factors revealed a main effect of orientation [$F(1,9) = 7.6$, $p = 0.022$] and TMS site [$F(1,9) = 18.8$, $p = 0.002$] but no significant interaction [$F(1,9) = 1.6$, $p = 0.229$]. By contrast a two-by-two ANOVA examining performance in the rLO condition with

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Fig. 1. Face stimuli were generated from an image of a male face. The two eyes and the mouth were replaced in each of the four faces by eyes and mouths from different faces but the rest of the face was constant.

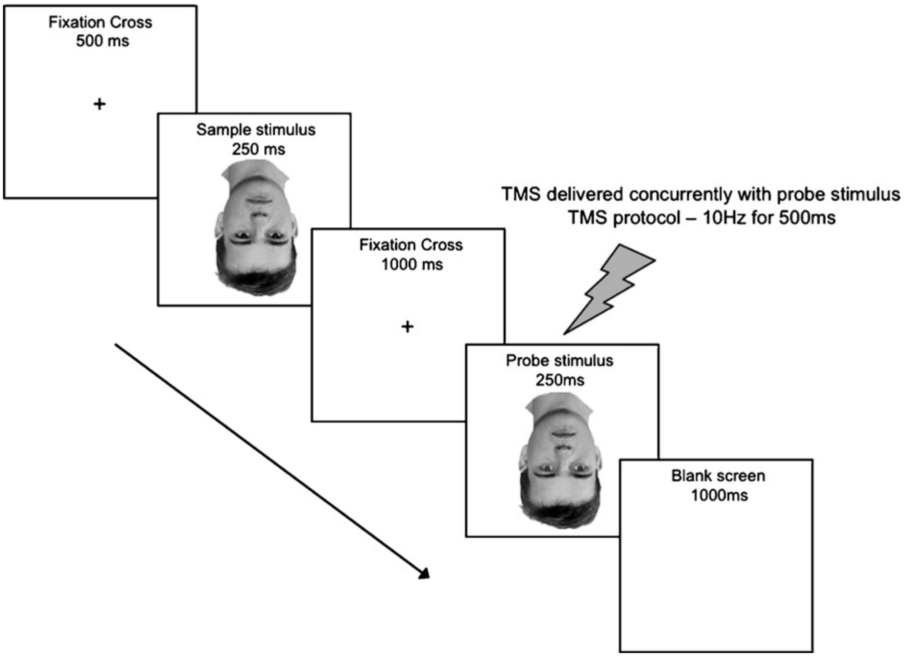

Fig. 2. Timeline of the experimental trial procedure. The first pulse of rTMS coincided with the onset of the probe stimulus. Participants judged whether the probe stimulus was the same or different from the sample stimulus. Although not shown in the figure, the probe stimulus was presented slightly to the left of the sample stimulus.

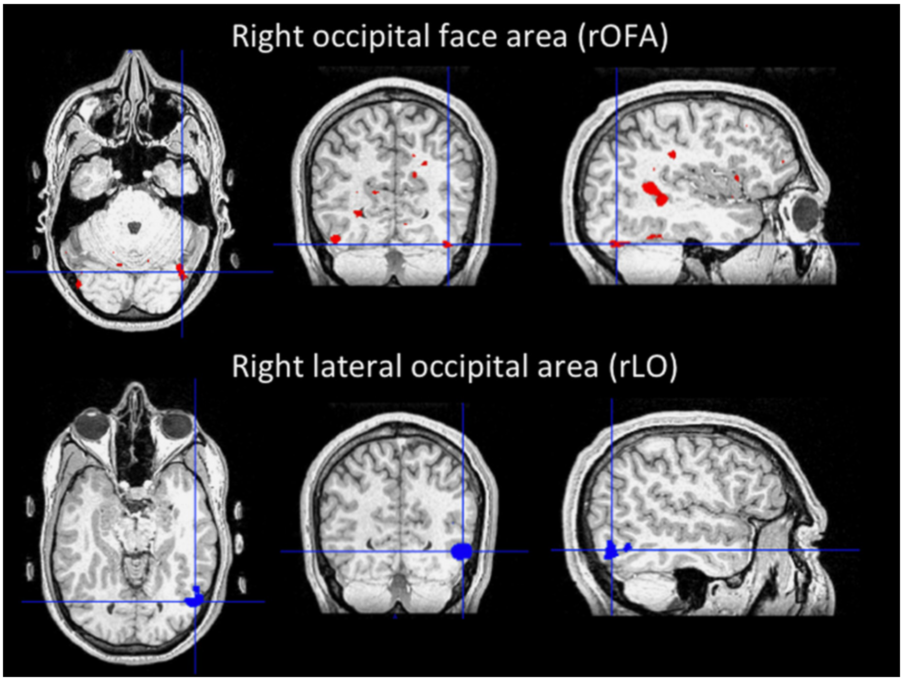

Fig. 3. Locations in one participant of the rOFA in red (faces minus objects) and rLO in blue (objects minus scrambled objects).

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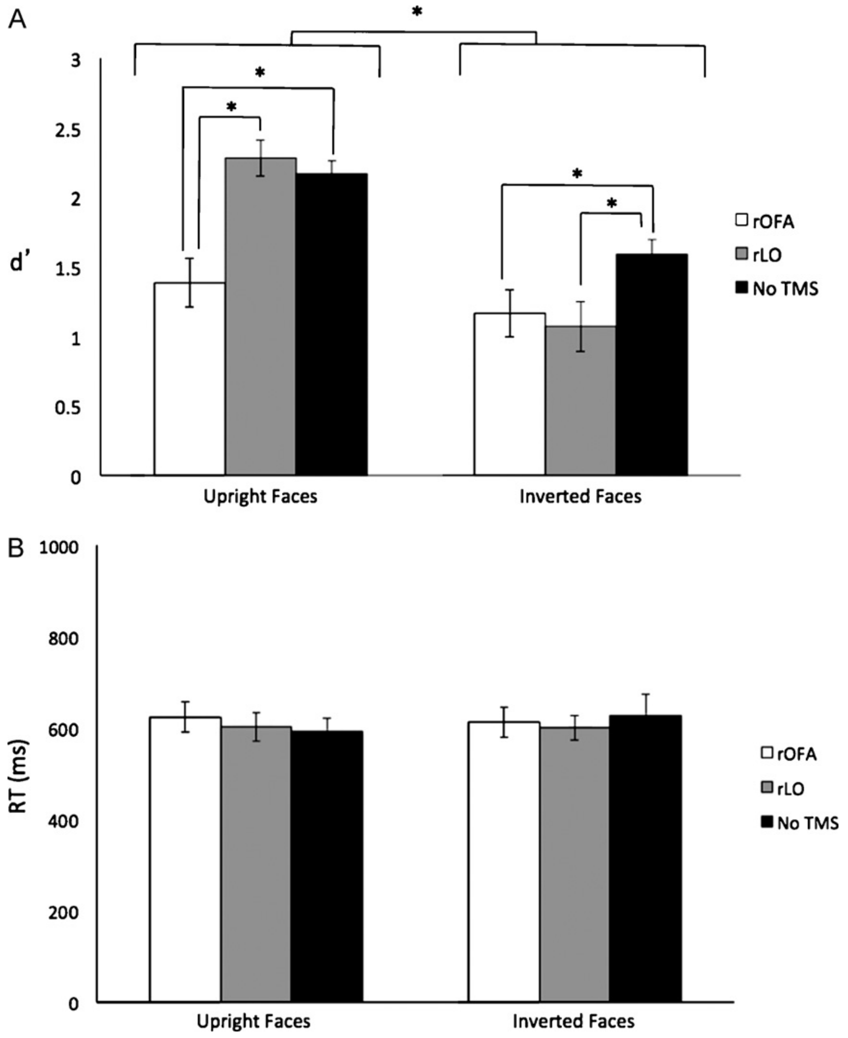

Fig. 4. (a) Mean performance results (accuracy was measured with d'). Overall, participants were more accurate at discriminating upright than inverted faces. rTMS delivered over the rOFA disrupted both upright and inverted discrimination while rTMS delivered over rLO disrupted inverted face discrimination only. Asterisk (*) denotes a significant difference in planned Bonferroni corrected pairwise comparisons. (b) Mean reaction time (RT) performance. Analysis revealed no significant effects.

orientation (upright or inverted) and TMS site (rLO or no TMS) as factors showed a main effect of orientation [$F(1,9) = 39.9$, $p > 0.001$] but not of TMS site [$F(1,9) = 3.5$, $p = 0.092$] and there was a significant interaction [$F(1,9) = 8.7$, $p = 0.016$].

We also compared upright and inverted face discrimination performance separately for each of the three TMS conditions. Pairwise *t*-tests demonstrated that there was no significant difference between upright and inverted face discrimination when TMS was delivered over the rOFA ($p = 0.428$) but that there is a significant difference in the rLO ($p = 0.001$) and no TMS conditions ($p > 0.001$).

A separate-two-by-three ANOVA on the reaction time (RT) data (see Fig. 4b) with orientation (upright or inverted) and TMS site (rOFA, rLO, no TMS) as independent factors revealed no main effects of orientation [$F(1,9) = 0.19$, $p = 0.67$] or of TMS site [$F(2,18) = 1.1$, $p = 0.36$] and there was no significant interaction [$F(2,18) = 1.7$, $p = 0.2$].

4. Discussion

In the present study we used TMS to investigate the causal role of the face-selective rOFA and object-selective rLO in the discrimination of upright and inverted faces. Previous fMRI and neuropsychological studies had suggested that non-face-selective cortical regions play a greater role in the processing of inverted than with upright faces (Epstein et al., 2006; Farah, Wilson, et al., 2005; Goffaux, Rossion, Sorger, Schiltz, & Goebel, 2009; Haxby et al., 1999; Moscovitch et al., 1997; Yovel & Kanwisher, 2005), but no studies have examined the effect that disruption of face and object processing regions has on the discrimination of upright and inverted faces in neurologically normal participants. Our results show that rTMS delivered over rOFA disrupted both upright and inverted face discrimination while rTMS delivered over rLO disrupted inverted face discrimination only.

At the most general level, our results support the hypothesis that upright and inverted faces are differentially processed across different category-selective brain regions. Our finding that the rOFA is causally engaged in the discrimination of both upright and inverted faces accords with prior fMRI results (Yovel & Kanwisher, 2005), and our finding that the object-selective region rLO was causally engaged in the perception of inverted but not upright faces also accords with findings from patients (Moscovitch et al., 1997) and with prior work using fMRI (Aguirre et al., 1999; Epstein et al., 2006; Gilaie-Dotan, Gelbard-Sagiv, & Malach, 2010; Haxby et al., 1999; Yovel & Kanwisher, 2005), especially the finding of a greater response in LO to inverted faces than to upright faces (Aguirre et al., 1999; Epstein, 2005; Yovel & Kanwisher, 2005). The present

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study goes beyond the fMRI evidence by causally demonstrating that transient neural disruption of rLO selectively impairs inverted face discrimination while sparing upright face discrimination. This pattern of results is consistent with recent neuropsychological data from patient P.S., an acquired prosopagnosic with a lesion encompassing her rOFA but with an intact rLO (Rossion et al., 2003). P.S. is severely impaired at upright face discrimination but her inverted face discrimination performance is only slightly impaired compared with controls (Busigny & Rossion, 2010), presumably because her right LO remains intact and contributes to the discrimination of inverted faces.

TMS delivered over rOFA disrupted both upright and inverted face discrimination demonstrating that this region is critical for accurate perception of both upright and inverted faces. Cortical models of face perception propose that the OFA is the earliest face-selective region and that it represents faces prior to sending information to other face-selective regions distributed across cortex (Calder & Young, 2005; Haxby, Hoffman, & Gobbini, 2000). Thus, disruption of the OFA is likely to have disrupted output from the OFA into other face-selective regions, including the FFA. Evidence that the FFA may be a cortical region specialized for the perception of upright but not for inverted faces comes from greater identity-specific adaptation for upright than inverted faces in the rFFA (Mazard et al., 2006; Schiltz & Rossion, 2006; Yovel & Kanwisher, 2005). Furthermore the existence of a cortical region specialized for the perception of upright but not inverted faces is consistent with the classic accounts of the behavioural face inversion effect (Farah, 2004; Moscovitch & Moscovitch, 2000). Although the rFFA is too medial to be disrupted using existing TMS methods, the prediction from these considerations is that if it could be disrupted, the perception of upright faces would be more severely impaired than the perception of inverted faces.

In the present study the faces in a given trial varied only in the appearance of the eyes and the mouth providing further evidence that the rOFA represents the component parts of a face (Liu, Harris, & Kanwisher, 2010; Pitcher et al., 2007). This demonstration that the rOFA processes face parts regardless of face orientation is consistent with an influential cortical model of face perception that proposes that facial features of increasing complexity are represented at progressively higher levels of the visual system (Haxby et al., 2000). This model proposes that the OFA represents face parts, prior to subsequent processing in the fusiform gyrus, where the parts are integrated into a representation of the whole face, a process believed to facilitate accurate identification (Kanwisher & Yovel, 2006; Liu et al., 2010; Pitcher, Walsh, & Duchaine, 2011; Rotshtein, Henson, Treves, Driver, & Dolan, 2005; but see Rossion, 2008).

Given that we used a delayed match-to-sample task with a 1000 ms retention period it is possible that TMS disrupted the visual short-term memory of the sample stimulus, rather than perceptual processing of the probe item. However we consider this hypothesis unlikely because it cannot account for results from two previous studies using the same delayed match to sample design (one of which used the same stimuli as the present study). In those studies, we saw a disruption when double-pulse TMS was delivered 60 and 100 ms after onset of the probe stimulus but no disruption when it was delivered 20 and 60 ms after probe onset (Pitcher et al., 2007, 2008). If TMS was disrupting the memory of the probe stimulus then it should have also done so during the 20 and 60 ms TMS delivery window. Further, in another study (Pitcher et al., in preparation) we found that TMS delivered over the OFA disrupts a 3 alternative forced-choice gaze discrimination task in which only a single stimulus is presented on each trial and no working memory is required. Regardless even if the current results reflected a disruption of visual working memory, rather than a disruption of perceptual processing, this would not change our conclusions about the roles of OFA and LO in upright and inverted face processing.

Finally our findings suggest that not all neural responses or even discriminative responses detected with fMRI reflect an actual causal role in visual perception (Williams, Dang, & Kanwisher, 2007). While LO shows a greater magnitude response to inverted faces than to upright faces it still shows a greater than baseline magnitude response to upright faces (Epstein et al., 2006; Gilaie-Dotan et al., 2010; Haxby et al., 1999; Yovel & Kanwisher, 2005) and a relative sharp tuning for the identity discrimination of upright faces (Gilaie-Dotan et al., 2010). Nevertheless rTMS delivered over rLO had no effect on upright face discrimination (see also Pitcher et al., 2007, 2009). Thus, a discriminative fMRI response in a given brain region does not necessarily imply a causal role for that region in performance of that discrimination task.

In the present study we used TMS to demonstrate that the rOFA is necessary for the accurate discrimination of upright and inverted faces while rLO is necessary for inverted face discrimination only. This result is consistent with prior neuropsychological and fMRI evidence and further demonstrates that upright faces are discriminated using mechanisms localized in specialized and discrete cortical areas. By contrast inverted face discrimination relies on contributions from both face-selective and more general object processing cortical areas.

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