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Investigating the Causal Role of rOFA in Holistic Detection of Mooney Faces and Objects: An fMRI-guided TMS Study

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ABSTRACT

Background: The right occipital face area (rOFA) is known to be involved in face discrimination based on *local featural* information. Whether this region is also involved in *global, holistic* stimulus processing is not known.
Objective: We used fMRI-guided transcranial magnetic stimulation (TMS) to investigate whether rOFA is causally implicated in stimulus detection based on holistic processing, by the use of Mooney stimuli.
Methods: Two studies were carried out: In Experiment 1, participants performed a detection task involving Mooney faces and Mooney objects; Mooney stimuli lack distinguishable local features and can be detected solely via holistic processing (i.e. at a global level) with top-down guidance from previously stored representations. Experiment 2 required participants to detect shapes which are recognized via bottom-up integration of local (collinear) Gabor elements and was performed to control for specificity of rOFA's implication in holistic detection.
Results: In Experiment 1, TMS over rOFA and rLO impaired detection of all stimulus categories, with no category-specific effect. In Experiment 2, shape detection was impaired when TMS was applied over rLO but not over rOFA.
Conclusions: Our results demonstrate that rOFA is causally implicated in the type of top-down holistic detection required by Mooney stimuli and that such role is not face-selective. In contrast, rOFA does not appear to play a causal role in detection of shapes based on bottom-up integration of local components, demonstrating that its involvement in processing non-face stimuli is specific for holistic processing.
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Introduction

The occipital face area (OFA), located in the lateral inferior occipital gyrus, is a key component of the face-processing network (e.g. References 1–5) typically showing a more robust face-response in the right hemisphere [6–8]. In particular, OFA is involved in the encoding of face parts (or so-called facial featural information) such as eyes, nose and mouth (e.g. References 9–11). Accordingly, stimulating right OFA (rOFA) with transcranial magnetic stimulation (TMS) has been found to impair participants' ability in discriminating faces (but not objects) differing by single components (such as the shape of the eyes and the mouth), without affecting the processing of configural information such as the spacing between face parts [12]. These findings suggest that rOFA is important for building up an initial structural representation based on local properties, prior to subsequent processing of more complex aspects occurring in higher-level face areas such as the fusiform face area (FFA) [2,8]. Nonetheless, FFA can be activated even in the absence of input from rOFA, suggesting that OFA may rather respond to re-entrant feedback from higher-level face areas where an initial coarse representation would be constructed [4,13–15]. In line with this, following TMS over rOFA, participants were impaired in face identity discrimination but not in distinguishing intact from scrambled faces [16].

Notwithstanding the important role played by rOFA at different stages of face processing, there is also evidence suggesting that rOFA may be important in processing of non-face stimuli (e.g. References 17–20). Furthermore, prior TMS evidence has shown that

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rOFA plays a causal role in symmetry discrimination, both in faces and in dot patterns [21], raising the possibility that this region is important for extracting global "Gestalt" stimulus properties. Such attributes play an important role in holistic processing, which refers to stimulus detection in which recognition of the "whole" precedes detection of the single elements (e.g. Reference 22). Holistic processing is believed to be based on top-down guidance by previously stored representations (as opposed to bottom-up extraction of local features) (e.g. Reference 23). Such holistic processing is required for the detection of Mooney stimuli [24] which are two-tone (black-and-white) images lacking in distinguishable local facial features and which can be recognized solely on the basis of their global Gestalt [22,25–27].

Whether rOFA is involved in such holistic detection is not known. In the present study, we used online fMRI-guided transcranial magnetic stimulation (cf. Reference 28; for a review, see References 29–31) to investigate this issue. In Experiment 1 we tested three Mooney stimulus categories: faces, guitars and objects. TMS was applied either over the rOFA, the rLO or vertex (control site) while participants performed the Mooney detection task. In a second experiment we used the same TMS parameters but during a shape detection task based on integration of local elements (collinear Gabor patches): this experiment was a direct replication of the experiment reported in Reference 21 and aimed to control for specificity of rOFA involvement in *holistic* processing.

Experiment 1

Materials and methods

Participants

Fifteen students (8 males, mean age = 24.3, SD = 2.07) from Aalto University, Espoo (Finland) took part in Experiment 1. All participants were right-handed [32] and had normal or corrected-to-normal vision. The study was approved by the local ethics committee and participants were treated in accordance with the Declaration of Helsinki. Participants provided a written informed consent and were screened for contraindications to fMRI and TMS. Each participant underwent three sessions: in the first session, the fMRI localization was carried out. The TMS experiments were performed in the remaining two sessions: specifically, Experiment 1 was performed in the second session and Experiment 2 in the third session.

fMRI localization of LO and OFA

A 3T MAGNETOM Skyra whole-body scanner (Siemens Healthcare, Erlangen, Germany) equipped with a 30-channel head–neck coil was used to acquire the functional volumes. The session consisted of 3 runs (one run for LO and two runs for OFA). Stimuli for the LO localizer were gray-scale images of common objects and scrambled objects; for OFA localizers, faces and objects were used. Scrambled objects were obtained by randomly selecting an equal number of square tiles from the original object images and arranging them in a 16×16 grid of the same dimensions as the object images. All stimuli were presented in the middle of the screen on an 18-inch monitor with a display resolution of 1280×1024. Viewing distance was 40 cm. rLO was defined as the activation peak of cluster of voxels that responded more to objects versus scrambled objects (see References 21,33 for similar procedure). Functional images were acquired in a single run lasting 432 sec with gradient echo sequence (23 slices with 3.5 mm slice thickness, RT = 2 s, echo time = 30 ms, voxel size = $3.125 \times 3.125 \times 3$ mm^3, flip angle = 75). rOFA was defined as the activation peak of the cluster of voxels that responded more to faces versus objects. Functional images were collected over 2 runs, each lasting 271.2 sec. Otherwise, the same parameters as for rLO localization were used. For each participant, a high resolution T1 weighted MPRAGE anatomical scan was also collected. Data preprocessing, parameter estimation and visualization were performed with SPM8 MatlabTM toolbox (http://www.fil.ion.ucl.ac.uk/spm, cf. Reference 34). The first four slices of each run were removed to ensure a stable magnetization and subsequent functional images were corrected for slice acquisition order and head movements. During the parameter estimation, the data were high-pass filtered with 128 s cutoff, and noise autocorrelation was modeled with AR(1) model. The data were coregistered with the high-resolution anatomical images. The mean MNI coordinates were: *rOFA*: 39 (SD 4.7), –81 (SD 9.7), –10 (SD 2.8); *rLO*: 46 (SD 3.5), –75 (SD 4.1), –4 (SD 6.7); these coordinates are consistent with those found in prior fMRI-guided TMS studies on rOFA and rLO function (e.g. References 35,36). Fig. 1 shows the rOFA and rLO sites in a representative participant.

TMS stimulation

TMS pulses were delivered through a biphasic figure-of-eight coil connected to a Nexstim stimulator (Nexstim Ltd., Helsinki, Finland). The eXimia NBS neuronavigation system (Nexstim Ltd., Helsinki, Finland), a co-registration software that allows real-time fMRI-guided positioning of the coil (e.g. References 37,38), was used to localize the stimulation sites. In each trial, participants received 3 pulses of TMS at a frequency of 10 Hz and an intensity of 40% of the maximum stimulator output over the stimulation sites, concurrently with visual target onset. These parameters were chosen on the basis of our previous study where we stimulated the same brain regions [21]. This stimulation intensity corresponds to approximately 80% of the phosphene threshold of the early visual cortex, which is in the region of 45–50% with the Nexstim stimulator and has been used in previous work in our laboratory [21,33,39]. A fixed TMS intensity has been used in most prior studies of OFA function (e.g. References 12,21,35). During the stimulation, the coil was held tangentially over the activation peaks obtained from participants' fMRI localizers, with the coil handle pointing upwards and parallel to the midline (e.g. References 36,40). Vertex was identified as the halfway point between the inion and the nasion and equidistant from the left and right intertragal notches [12,41] and was selected as control site to ensure that any TMS effect was not due to somatosensory sensations related to the stimulation (e.g. Cattaneo et al, 2012, 2015; Cattaneo & Silvanto, 2008).

Procedure

Participants performed a detection task with Mooney stimuli. The different Mooney categories (faces, guitars, objects) were tested in separated blocks.

Stimuli. We used 120 two-tone (black and white) Mooney images (40 Mooney faces, 40 Mooney guitars and 40 Mooney objects; see Fig. 2 for an example of each stimulus type). Each stimulus was approximately 15° in height and 10° in width. Mooney faces were drawn from the original set of "Mooney faces" created by Mooney [24]. Mooney guitars were selected from the original set of Castelhano et al. [42]; Mooney objects were selected from the original set of Imamoglu et al. [43] and consisted of pictures of animals, fruits and man-made objects. Mooney guitars are similar to faces in that they are a homogeneous stimulus class exhibiting clear prototypical shapes. Additionally, 40 meaningless images (i.e. non-face/guitar/object stimuli) were created for each of the three stimulus categories by dividing each item into a grid and randomly moving the positions of the squares.

Task. The time line of an experimental trial is shown in Fig. 2E. Stimuli were presented on an 18-inch monitor with a display

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