

Combined TMS and fMRI Reveal Dissociable Cortical Pathways for Dynamic and Static Face Perception

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Summary

Faces contain structural information, for identifying individuals, as well as changeable information, which can convey emotion and direct attention. Neuroimaging studies reveal brain regions that exhibit preferential responses to invariant [1, 2] or changeable [3–5] facial aspects but the functional connections between these regions are unknown. We addressed this issue by causally disrupting two face-selective regions with thetaburst transcranial magnetic stimulation (TBS) and measuring the effects of this disruption in local and remote face-selective regions with functional magnetic resonance imaging (fMRI). Participants were scanned, over two sessions, while viewing dynamic or static faces and objects. During these sessions, TBS was delivered over the right occipital face area (rOFA) or right posterior superior temporal sulcus (rpSTS). Disruption of the rOFA reduced the neural response to both static and dynamic faces in the downstream face-selective region in the fusiform gyrus. In contrast, the response to dynamic and static faces was doubly dissociated in the rpSTS. Namely, disruption of the rOFA reduced the response to static but not dynamic faces, while disruption of the rpSTS itself reduced the response to dynamic but not static faces. These results suggest that dynamic and static facial aspects are processed via dissociable cortical pathways that begin in early visual cortex, a conclusion inconsistent with current models of face perception [6–9].

Results

Influential models of face perception [6–8] propose that two functionally distinct cortical pathways process different facial aspects. The ventral pathway, which includes the fusiform face area (FFA) [10], preferentially responds to invariant facial aspects, such as individual identity. The lateral pathway, which includes the posterior superior temporal sulcus (pSTS) [3], preferentially responds to changeable facial aspects, such as emotional expression and eye-gaze direction [4]. Crucially, despite functional differences, both pathways are believed to begin in the same face-selective region, the occipital face area (OFA) [7–9, 11]. In the present study we causally tested the hypothesis that the OFA is the sole gateway for the face perception network using a “virtual” lesion approach.

To examine how face-selective regions are functionally connected, thetaburst transcranial magnetic stimulation (TBS) [12] was used to transiently disrupt the brains of neurologically healthy participants. The effects of this disruption were then measured in local and remote face-selective regions with functional magnetic resonance imaging (fMRI). We reasoned that if the OFA is the sole source of dynamic and static face information for the FFA and pSTS, then disrupting the OFA would reduce the neural response to dynamic *and* static faces in both the FFA and pSTS. However, if a separate pathway conveying only dynamic face information exists to the pSTS, independently of the OFA, then disruption of the OFA would have relatively little impact on the response to dynamic faces in the pSTS (see [Figure 1](#)).

Participants completed two scanning sessions, performed on separate days, while viewing face and object stimuli that were either dynamic or static (see [Figure 2](#)). Scanning was performed before and after TBS was delivered over the functionally localized right OFA (rOFA) or right posterior superior temporal sulcus (rpSTS). We then measured what effect TBS disruption had on the neural response in both the stimulated regions (rOFA and rpSTS), as well as in the right FFA (rFFA), a face-selective region on the ventral cortical surface that cannot be directly stimulated by TBS. The magnitude responses from each face-selective ROI as well as for the right extrastriate body area (rEBA) and right lateral occipital area (rLO) are shown in full in [Figures S1](#) and [S2](#) available online.

ROI Analysis

To understand what effect TBS stimulation had on the three face-selective regions, we calculated the size of the TBS disruptive effect in the rpSTS, rOFA, and rFFA. This was done by subtracting the BOLD responses for each stimulus category (dynamic faces, static faces, dynamic objects, static objects) after TBS stimulation of the rOFA and rpSTS from the pre-TMS baseline response in each ROI (see [Figure 3](#)).

The data were then entered into a 2 (TMS: TBS to rOFA; TBS to rpSTS) by 2 (motion: dynamic, static) by 2 (stimulus: faces, objects) by 3 (ROI: rFFA, rpSTS; rOFA) repeated-measures ANOVA. Results showed a main effect of stimulus ($F(1,14) = 7.3, p = 0.017$) as well as interactions between motion and TMS ($F(1,14) = 4.2, p = 0.048$) and between motion, stimulus, and TMS ($F(1,14) = 3.6, p = 0.041$). Crucially, there was also a significant interaction between ROI, motion, stimulus, and TMS ($F(2,28) = 3, p = 0.043$). No other interactions approached significance.

Separate ANOVAs performed in each of the face-selective ROIs (reported in full in [Supplemental Information](#)) demonstrated that TBS stimulation of the rOFA and rpSTS induced a double dissociation between the response to dynamic and static faces in the rpSTS ([Figure 3](#)). The response to static faces in the rpSTS was reduced by stimulation of the rOFA but not of the rpSTS, while the response to dynamic faces in the rpSTS was reduced by stimulation of the rpSTS but not of the rOFA. This result is consistent with the hypothesis that dynamic face information can reach the rpSTS independently of the rOFA.

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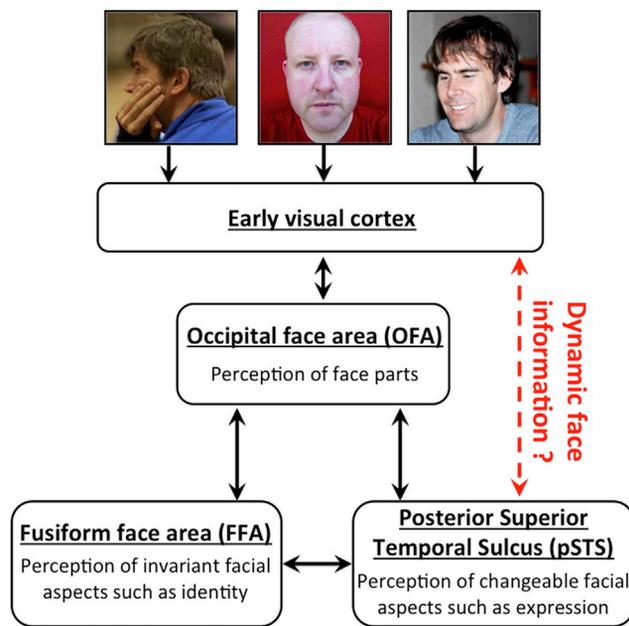


Figure 1. The Cortical Face Perception Network

The present study tests the alternate hypothesis that dynamic face information reaches the pSTS via a cortical pathway that is independent of the OFA (represented by the dotted red line). Adapted from Haxby et al. [7].

TBS to rpSTS Disrupts Facial Motion in the Absence of Facial Expression

The main experiment used dynamic face movies in which actors made a range of different facial expressions while simultaneously moving their heads. We performed an additional control experiment to demonstrate that TBS delivered over the rpSTS could reduce the BOLD response to moving faces in the absence of facial expressions. Participants were scanned before and after TBS was delivered over the rpSTS while viewing dynamic and static stimuli in which actors with neutral facial expressions turned their heads from side to side (see [Supplemental Information](#) and [Figure S3](#)). Results showed that TBS selectively reduced the neural response to dynamic, but not static, faces in the rpSTS but had no effect on the response to dynamic or static faces in the rFFA (see [Figure 4](#)). These results are consistent with the hypothesis that the rpSTS represents facial motion in general and not just facial motion related to facial expression.

Discussion

The role of the posterior superior temporal sulcus (pSTS) in the perception of moving biological stimuli, such as faces and bodies, is well established [4, 13, 14], but the cortical inputs into this region in human cortex are unknown. One likely source of input is the adjacent motion-processing region, V5/MT [15]. Neuroanatomical studies in macaques reporting a cortical projection from V5/MT into the posterior bank of the STS are consistent with this suggestion [16–18]. In humans, the lateral position of V5/MT has led to suggestions that it may be part of a cortical pathway projecting into the superior temporal sulcus (STS) that bypasses the inferior regions of occipital cortex where the OFA is located [19, 20]. Evidence from neuropsychological patients who show neural activation to faces in the pSTS despite having lesions to cortical regions

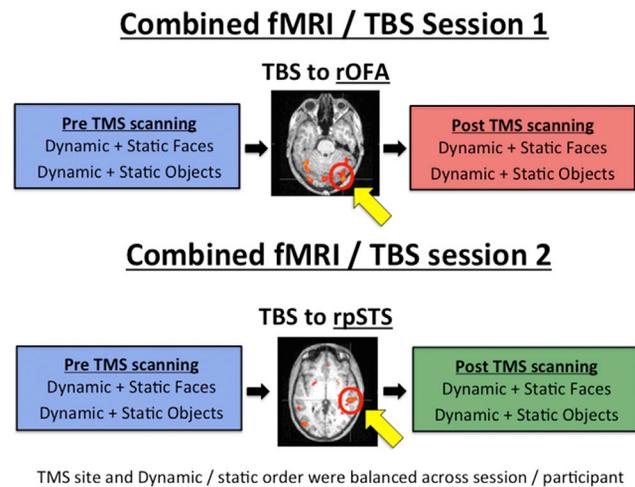


Figure 2. The Experimental Procedure of the Combined Thetaburst TMS and fMRI Scanning Sessions

Participants were scanned using fMRI while viewing dynamic and static face and object stimuli. In the middle of each session, participants exited the scanner and TBS was delivered over the rOFA or the rpSTS. Participants then re-entered the scanner and the post-TMS data were collected.

that would typically encompass the OFA and/or the FFA support this hypothesis [21–23]. In addition, behavioral evidence from two prosopagnosic patients further demonstrates that dynamic and static face discrimination tasks are functionally dissociable [24].

Two independent face cortical pathways, one projecting along the ventral surface that includes the OFA and FFA, the other along the lateral surface that includes the pSTS, were reported in a recent tractography study [25]. However, this prior study found no evidence of connectivity between the ventral and lateral pathways, a result inconsistent with our finding that TBS stimulation of the rpSTS reduced the neural response to dynamic and static faces in the rFFA. Our data support an alternate hypothesis that the rpSTS is connected with at least two functionally distinct pathways. Dynamic face information comes via a direct pathway from early visual cortex (possibly via V5/MT as suggested by nonhuman primate neuroanatomy) while structural face information comes from ventral regions such as the rOFA and rFFA. One potential inconsistency with this hypothesis is neuropsychological and TMS evidence that shows that disruption of V5/MT does not impair discrimination of upright “point-light” figures depicting natural biological motion [26–28]. Perception of these point-light figures is dependent on a region in the posterior STS that is adjacent to the face-selective pSTS region we report here [14]. This discrepancy will need to be addressed in future studies but it seems likely that the perception of form from motion is dependent on information processed across functionally distinct cortical regions that preferentially respond to either form or to motion.

TBS delivered over rOFA reduced the response to both dynamic and static faces in the downstream rFFA, suggesting that the rFFA does not functionally dissociate between dynamic and static faces. A cortical pathway between the OFA and FFA is proposed in models of face perception [6–9] and our data are consistent with this conclusion. Given the posterior location of the OFA in relation to the more anterior FFA and

Dissociable Pathways for Dynamic and Static Faces

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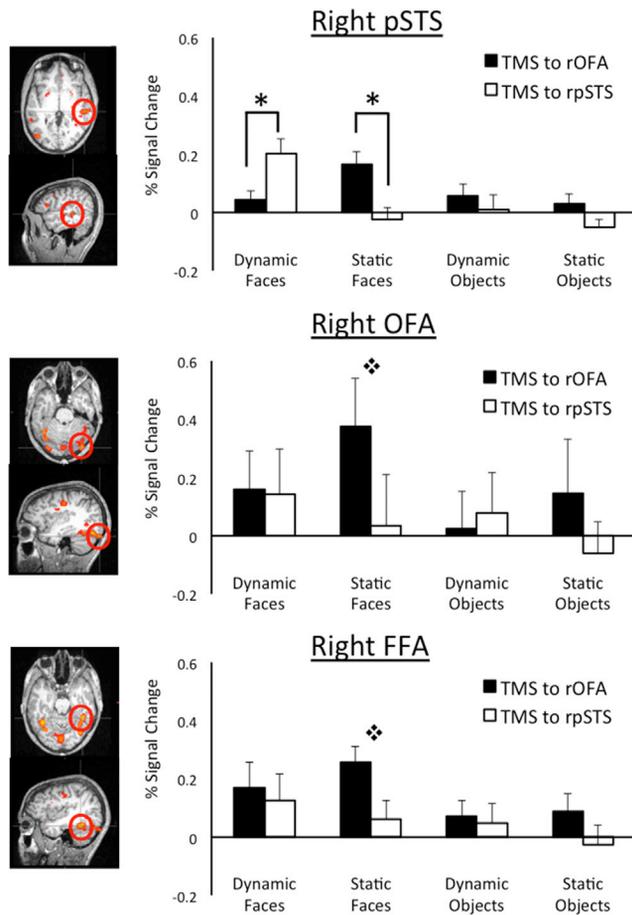


Figure 3. The Size of the TBS Disruptive Effect for All Stimulus Categories in the Three Face-Selective ROIs: rOFA, rFFA, and rpSTS

The TBS disruptive effect was calculated by subtracting the PSC for each stimulus category after TMS stimulation of the rOFA and rpSTS from the pre-TMS baseline. Hence a positive score denotes a TBS-induced reduction in the ROI. In the rpSTS, TBS to rOFA reduced the response to static but not dynamic faces and TBS to the rpSTS itself reduced the response to dynamic but not static faces (asterisk denotes a significant difference in Bonferroni corrected tests). TBS delivered over the rOFA reduced the response to static faces in the rOFA and in the rFFA (diamond denotes a significant difference in Bonferroni corrected tests). Error bars represent SE. The full data set is shown in [Figures S1 and S2](#).

the greater preference for stimuli in the contralateral visual field in OFA than in the FFA [29], it seems likely that the OFA and the FFA are functionally connected as suggested by our earlier TMS studies [30–32].

The present study demonstrated that stimulation of the rOFA and rpSTS produced a double dissociation between the response to dynamic and static faces in the rpSTS. Namely, TBS delivered over the rOFA reduced the response to static but *not* dynamic faces in the rpSTS, while TBS delivered over the rpSTS itself reduced the response to dynamic but *not* static faces. These results suggest that dynamic and static facial aspects are processed via dissociable cortical pathways that originate in early visual cortex, not in the OFA as predicted by existing models of face perception ([6–9]; but see [19]). We argue that this result requires a reassessment of the proposed cortical connections between face-selective regions and consequently of the models that predict how faces are cortically represented (see [Figure 1](#)).

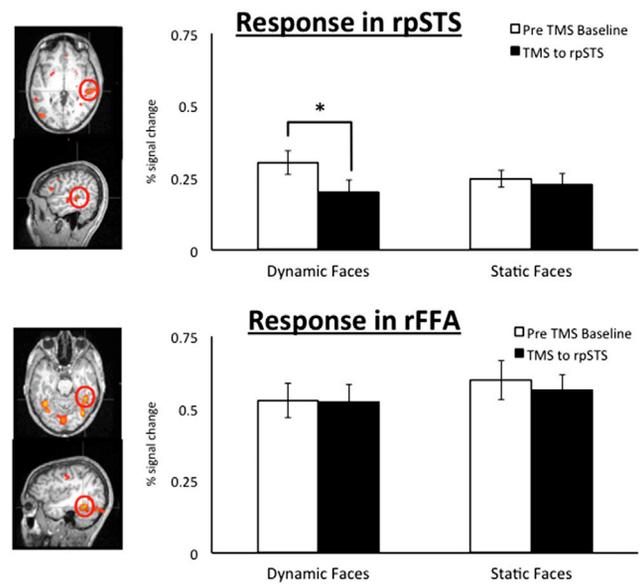


Figure 4. The Results of the Control Experiment

TBS delivered over the rpSTS reduced the response to the dynamic faces in the rpSTS but had no effect on the response to the static faces (as denoted by asterisk). There was no effect on dynamic and static faces in the rFFA. Error bars represent SE. See also [Figure S3](#).

Experimental Procedures

Participants

A total of 15 right-handed participants with normal or corrected-to-normal-level vision gave informed consent as directed by the University College London Ethics committee.

Stimuli

For the independent localizer runs used to identify regions of interest (ROIs), participants viewed dynamic and static stimuli from five different categories (faces, bodies, scenes, objects, and scrambled objects). These stimuli were used in a previous fMRI study of face perception [33]. Separate independent runs were used to collect the experimental data plotted in [Figure 3](#) and in [Figures S1 and S2](#) in which participants viewed the dynamic and static face and object stimuli only.

Dynamic Stimuli

Dynamic stimuli were 3 s movie clips of faces, bodies, scenes, objects, and scrambled objects. There were 60 movie clips for each category in which distinct exemplars appeared multiple times. Movies of faces and bodies were filmed on a black background and framed close-up to reveal only the faces or bodies of seven children as they danced or played with toys or adults (who were out of frame). A total of 15 different moving objects were selected that minimized any suggestion of animacy of the object itself or of a hidden actor pushing the object (these included mobiles, windup toys, toy planes and tractors, and balls rolling down sloped inclines). Within each block, stimuli were randomly selected from within the entire set for that stimulus category. This meant that the same actor or object could appear within the same block.

Static Stimuli

Static stimuli were identical in design to the dynamic stimuli except that in place of each 3 s movie, we presented three different still images taken from the beginning, middle, and end of the corresponding movie clip. Each still image was presented for 1 s with no ISI, to equate the total presentation time with the corresponding dynamic movie clip.

Procedure

Participants completed three separate fMRI sessions, each performed on a different day. The first session was an fMRI experiment designed to individually identify the TMS stimulation sites in each participant. The data collected in this initial session were used for TMS target site identification only. During the two subsequent fMRI sessions, participants were scanned before and after receiving TBS stimulation of either the right

posterior superior temporal sulcus (rpSTS) or the right occipital face area (rOFA). Stimulation site order was balanced across participants. All the data presented in [Figure 3](#) and [Figures S1](#) and [S2](#) (pre-TBS baseline, TBS to rOFA, and TBS to rpSTS) were collected during these two sessions.

Combined fMRI/TBS Sessions

Functional data were acquired over 9 blocked-design functional runs lasting 234 s each (see [Figure 2](#) for an overview of the two fMRI/TBS sessions). Functional runs presented either movie clips of faces and objects (dynamic runs) or sets of static images of faces and objects taken from the same movies (static runs). For the dynamic runs, each 18 s block contained 6 movie clips (each 3 s long) from that category. For the static runs, each 18 s block contained 18 still snapshots (each 1 s long), composed of six triplets of snapshots taken at 1 s intervals from the same movie clip. Participants were instructed to press a button when the subject in the stimuli was repeated (e.g., a repeat of the same actor or object). The order of repeats was randomized and happened at least once per block.

In addition to dynamic and static face and object stimuli, we also included three separate runs designed to independently localize the category-selective regions of interest (ROIs) (see “Data Analysis” section in [Supplemental Information](#)). These localizer runs consisted of two dynamic and one static runs of the functional localizer described in fMRI localizer section.

During each scanning session, participants exited the scanner to receive TBS stimulation of either the rOFA or rpSTS, dividing the session into pre-TBS functional runs and post-TBS functional runs. Functional runs were acquired in the following order. Pre-TBS runs: dynamic faces or objects, static faces or objects, dynamic localizer, static localizer, dynamic localizer. Participants then exited the scanner to receive TBS stimulation. Post-TBS runs: dynamic faces or objects, static faces or objects, dynamic faces or objects, static faces or objects. The order in which the dynamic or static face or object stimuli were presented was balanced across sessions for each participant and across participants. TBS stimulation of the rOFA and rpSTS was balanced across participants.

Supplemental Information

Supplemental Information includes three figures and Supplemental Experimental Procedures and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2014.07.060>.

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