

Event-related Repetitive TMS Reveals Distinct, Critical Roles for Right OFA and Bilateral Posterior STS in Judging the Sex and Trustworthiness of Faces

Milena P. Dzhelyova¹, Amanda Ellison², and Anthony P. Atkinson²

Abstract

■ Judging the sex of faces relies on cues related to facial morphology and spatial relations between features, whereas judging the trustworthiness of faces relies on both structural and expressive cues that signal affective valence. The right occipital face area (OFA) processes structural cues and has been associated with sex judgments, whereas the posterior STS processes changeable facial cues related to muscle movements and is activated when observers judge trustworthiness. It is commonly supposed that the STS receives inputs from the OFA, yet it is unknown whether these regions have functionally dissociable, critical roles in sex and trustworthiness judgments. We addressed this issue using event-related, fMRI-guided repetitive transcranial magnetic stimulation (rTMS). Twelve healthy volunteers judged the sex of individually

presented faces and, in a separate session, whether those same faces were trustworthy or not. Relative to sham stimulation, RTs were significantly longer for sex judgments when rTMS was delivered over the right OFA but not the right or left STS, and for trustworthiness judgments on male but not female faces when rTMS was delivered over the right STS or left STS but not the right OFA. Nonetheless, an analysis of the RT distributions revealed a possible critical role also for the right OFA in trustworthiness judgments, limited to faces with longer RTs, perhaps reflecting the later, ancillary use of structural cues related to the sex of the face. On the whole, our findings provide evidence that evaluations of the trustworthiness and sex of faces rely on functionally dissociable cortical regions. ■

INTRODUCTION

Humans are adept at judging whether visually presented faces are male or female, even in the absence of hair, make-up, or facial hair (e.g., Atkinson, Tipples, Burt, & Young, 2005; Brown & Perrett, 1993; Bruce et al., 1993). The ability to judge the sex of faces relies principally on cues related to facial morphology (e.g., Calder, Burton, Miller, Young, & Akamatsu, 2001; Brown & Perrett, 1993; Bruce et al., 1993). These structural cues include the shape and size of the face, the spatial relations between features (e.g., the distance between the eyebrows and eyelids), and three-dimensional information (e.g., brow and chin protuberance). Other cues to the sex of faces include superficial properties such as skin texture and complexion.

In contrast, the ability to judge whether a face is trustworthy or untrustworthy relies on expressive cues as well as on a set of structural cues that mostly differ from those involved in the determination of a face's sex (e.g., Oosterhof & Todorov, 2009; Said, Sebe, & Todorov, 2009; Todorov, 2008; Krumhuber et al., 2007). For example, by manipulating a large number of shape components of realistic computer-generated faces, Oosterhof and Todorov (2008) and Todorov, Baron, and Oosterhof (2008) created a set of faces that varied systematically in their rated trustworthiness. The image manipulations included changes equiva-

lent to movements of the facial muscles, as well as more structural transformations. With respect to structural cues, more trustworthy faces had pronounced rather than shallow cheekbones, wide rather than thin chins, and shallow rather than deep nose sellions. Differences in expressive cues related most obviously to changes in the shape of facial features: More trustworthy faces had more \wedge -shaped eyebrows and more \cup -shaped mouths, whereas more untrustworthy faces had more \vee -shaped eyebrows and more \cap -shaped mouths (Todorov et al., 2008). That the judged trustworthiness of emotionally neutral faces is highly correlated with the valence of their judged emotion (see also Richell et al., 2005; Winston, Strange, O'Doherty, & Dolan, 2002) suggests that trustworthiness judgments are based on subtle facial cues that resemble expressions signaling whether the person should be avoided or can be approached (Oosterhof & Todorov, 2009; Todorov, 2008).

Two cortical regions identified by their functional selectivity for faces are prime candidates for having critical roles in sex and trustworthiness judgments. The occipital face area (OFA) processes cues related mostly to the invariant structure of faces, and may thus play a critical role in sex judgments. Regions in and surrounding the STS process cues related to changeable properties of faces, and may thus play a critical role in trustworthiness judgments.

The OFA is a region typically located in the lateral portions of the inferior and middle occipital gyri that is functionally

¹University of St. Andrews, UK, ²Durham University, UK

defined by its selectivity for faces over nonface objects in neuroimaging studies (for a review, see Kanwisher & Yovel, 2006). This face-selective activity in the lateral occipital gyri reflects the processing of the shape and features of faces (e.g., Fox, Moon, Iaria, & Barton, 2009; Haxby, Hoffman, & Gobbini, 2000). There is also evidence that the inferior occipital gyrus or OFA, as well as the fusiform gyrus, processes second-order relational or configural cues (the metric distances between features) (Rhodes, Michie, Hughes, & Byatt, 2009; Rotshtein, Geng, Driver, & Dolan, 2007), but not first-order configural cues (which encode the relative positions of facial features) (Liu, Harris, & Kanwisher, 2010). Studies using TMS have confirmed a critical role for the right (but not left) OFA in the discrimination of faces based on differences in individual features alone (Pitcher, Walsh, Yovel, & Duchaine, 2007) or in both featural and structural cues (Pitcher, Charles, Devlin, Walsh, & Duchaine, 2009). Nonetheless, one of these studies found that the right OFA was not critically involved in the discrimination of faces on the basis of the spacing between features (Pitcher et al., 2007). These partly conflicting findings may be reconciled by recent evidence indicating that the occipital and fusiform face areas, which are closely functionally interlinked (e.g., Rotshtein et al., 2007; Kim et al., 2006), may process either or both featural and configural cues, depending on the task demands (Cohen Kadosh, Henson, Cohen Kadosh, Johnson, & Dick, 2010).

Regions of superior temporal cortex, especially in the posterior STS, are also selective for faces (for a review, see Kanwisher & Yovel, 2006). As with the OFA, in the majority of subjects, this face-selective activity is evident principally or only in the right hemisphere. In an influential model of face processing (Haxby et al., 2000), superior temporal cortex represents changeable properties of faces, such as what occur with changes in expression and eye gaze, whereas more invariant properties of faces related to the shape of the face, its features and their spatial relations, are represented in inferior occipito-temporal cortex (principally the fusiform and occipital face areas). A different view, but nevertheless consistent with the reasoning stated here, is that the STS's involvement in face perception reflects a more general role in integrating motion, form, and auditory cues related to changeable social signals (Calder & Young, 2005).

Existing studies suggest distinct roles for the OFA and posterior STS in sex and trustworthiness judgments, respectively, but it is not yet known whether, in neurologically intact individuals, these regions are critically involved in evaluations of sex and trustworthiness. An early positron emission tomography study found right inferior occipital gyrus activation when participants judged the sex of faces, compared to when they judged the orientation of gratings (Sergent, Ohta, & MacDonald, 1992). Yet judging the sex of faces typically does not elicit occipital gyrus activation when contrasted with other face-processing tasks, such as emotion judgments (e.g., Winston, O'Doherty, & Dolan, 2003). An individual (D. F.) with lesions encompassing lat-

eral occipital cortex in both hemispheres showed no face-selective activation in the regions that normally correspond to the OFA, yet she showed the typical face-selective activity in the bilateral fusiform gyrus and bilateral STS (Steeves et al., 2006). Importantly, although D. F. could differentiate faces from nonface objects, principally on the basis of configural cues, she could not discriminate faces on the basis of sex, emotion, or identity. Two fMRI studies revealed posterior STS activation for judgments of trustworthiness as compared to judgments of the age of faces. This activation was in the right hemisphere for healthy volunteers (Pinkham, Hopfinger, Pelphrey, Piven, & Penn, 2008; Winston et al., 2002) and for individuals with nonparanoid schizophrenia (Pinkham et al., 2008), but in the left hemisphere for adults with autism and in both hemispheres for individuals with paranoid schizophrenia (Pinkham et al., 2008).

Our reasoning, so far, has assumed that the OFA and the face-selective posterior STS are functionally independent. However, in Haxby et al.'s (2000) model of face processing, the OFA (or IOG more generally) is the principal and common source of input for the STS and the fusiform gyrus. The question therefore arises as to whether the contributions of the OFA and the posterior STS to sex and trustworthiness judgments can be functionally dissociated. We addressed this question using event-related, fMRI-guided repetitive TMS (rTMS). We predicted that rTMS delivered over the right OFA would impair the ability to distinguish female from male faces and that rTMS delivered over the right STS would impair the ability to distinguish trustworthy from untrustworthy faces. Given the inconclusiveness of existing fMRI findings, we had no firm predictions as to the effect on trustworthiness judgments of rTMS applied over the left STS. Given that the STS is downstream of the OFA and that judging the sex of faces relies little, if at all, on the processing of expressive cues, we predicted that sex judgments would not be impaired by rTMS over the right or left STS. It was an open question whether rTMS over the right OFA would impair trustworthiness judgments.

METHODS

Participants

Twelve healthy volunteers (3 men), aged 25–49 years (mean age = 32 years, $SD = 8$), all with normal or corrected-to-normal vision, took part in the study. All participants had previously participated in one or the other of two fMRI studies investigating face perception (Cavina-Pratesi, Kentridge, Heywood, & Milner, 2010; Atkinson et al., unpublished data) and were selected in accordance with the current safety guidelines for TMS research (Wassermann, 1998). All participants gave their signed, informed consent in accordance with the Declaration of Helsinki and with the approval of Durham University Psychology Department's Ethics Sub-Committee.

Stimuli and Apparatus

The stimuli were selected from a set of realistic computer-generated, male and female white faces developed by Oosterhof and Todorov (2008) and Todorov et al. (2008) using the FaceGen software (www.facegen.com). These face images were specifically created to vary in equal steps of judged trustworthiness (expressed in *SD* units ranging from -8 to $+8$). Oosterhof and Todorov achieved this by obtaining the best linear fit of the mean trustworthiness judgments of a larger number of raters as a function of 50 shape components and then exaggerating the features that contributed to those judgments.

We conducted an initial experiment in order to select a subset of the Oosterhof and Todorov (2008) face images for the present TMS study. Our aim was to select a set of 80 female and 80 male faces whose sex and trustworthiness could be reliably discriminated in two-alternative forced-response tasks, but such that the difficulty of the two tasks, as assessed with accuracy and RT measures, was approximately matched. Eighteen participants (12 women, aged 19–33 years, mean age = 23.1 years) viewed color images of 39 facial identities at each of 17 levels of trustworthiness (663 stimuli in total; due to a technical error, 2 of these images were not presented). As the complexion of the original male and female faces differed, this color was matched across the male and female face sets using Adobe Photoshop, to avoid participants discriminating the sex of the face on the basis of complexion. Participants made speeded judgments about the trustworthiness (trustworthy or not trustworthy) or sex (female or not female) of each individually presented face. All faces were presented in each task, in

a different random order for each task and participant. The order of tasks was counterbalanced across participants. Based on the results of this experiment, an item-by-item procedure for selecting the faces was employed: Images for which the mean accuracy and response latencies across the two tasks differed the least were selected, with greater weight given to response latencies (as this was the main measure of interest in the TMS experiment). Examples of the selected stimuli are shown in Figure 1. The distribution of the predetermined levels of trustworthiness across the male and female faces in the final selected set of 160 images is shown in Table 1. For the final selected set of faces, RTs did not differ significantly between tasks for trustworthy or untrustworthy male or female faces (all $ps > .09$); accuracy did not differ between tasks for either trustworthy female or trustworthy male faces (both $ps > .65$), but accuracy was significantly greater for sex judgments than for trustworthiness judgments of untrustworthy female and untrustworthy male faces (both $ps < .001$).

The 160 selected faces were presented on a 16-in. CRT monitor with a 1024×768 resolution and a 60-Hz refresh rate. Stimulus presentation and response recording were controlled with PsyScope X software (<http://psy.ck.sissa.it>). A button box (ioLab Systems, UK) was used for recording responses and for triggering the TMS pulses (synchronized with stimulus onset). The participants were seated directly in front of the monitor with their head position controlled by a chinrest positioned 57.5 cm from the monitor screen. At this viewing distance, the faces subtended 11° (width) \times 14° (height) of visual angle. All faces were presented in color against a black background. During the experiment, the room lights were dimmed.

Figure 1. Examples of face images used in the main experiment, adapted from Oosterhof and Todorov (2008): highly untrustworthy (left) and highly trustworthy (right) versions of the same female (top row) and male (bottom row) identities. In the experiment, all images were presented individually, in color.



Table 1. The Numbers of Female and Male Face Images for Each of the Predetermined Levels of Trustworthiness in the Set of 160 Stimuli Used in the Present Study

	<i>Trustworthiness Level</i>													
	-8	-7	-6	-5	-4	-3	+1	+2	+3	+4	+5	+6	+7	+8
Female	15	8	10	4	2	1	5	4	5	5	5	8	6	2
Male	14	12	7	4	1	2	3	4	7	7	4	4	6	5

The levels of rated trustworthiness were determined by Oosterhof and Todorov (2008), and in their original, larger stimulus set, ranged in equal steps from -8 (highly untrustworthy) to +8 (highly trustworthy). For the present study, a pilot experiment was conducted to select faces from this larger set (see Methods). We avoided selecting faces from the middle of the scale in order to lessen the difficulty of making the required two-alternative forced-response (trustworthy/untrustworthy) judgment.

Transcranial Magnetic Stimulation and Localization

A Magstim super rapid stimulator (Magstim, Whitland, UK) was used to deliver rTMS pulses via a 70-mm figure-of-eight coil. Five pulses at 10 Hz were delivered from visual stimulus onset at 65% of the stimulator's maximum power (approximately 1.3 Tesla). The handle pointed backward, parallel to the horizontal and midsagittal plane. In each case, the TMS coil was held in place by the experimenter. When any head movements occurred, the coil was repositioned manually. Four different TMS conditions were used: three sites of stimulation (the left and right STS and the right OFA) plus sham stimulation. In the sham condition, a nondischarging coil was placed over the area of interest, and a discharging coil was placed in close proximity to the participant. The participants therefore still heard the same noise associated with the TMS pulses and had the same feeling of a coil placed on the head, but no pulse was administered into the brain.

Each TMS target site was individually localized for every participant. For each participant, a functional activation map obtained from one of two prior fMRI studies (Cavina-Pratesi et al., 2010; Atkinson et al., unpublished data) was overlaid onto that participant's native structural MRI scan. A face versus object contrast was used in order to define the face-selective areas within the inferior-mid occipital and superior posterior temporal regions (see Figure 2 and Table 2). All MR image processing and statistical analyses were carried out using SPM5 (Wellcome Trust Centre for Neuroimaging), with the same basic settings for all participants. Prior to statistical analyses, the functional images were spatially realigned to the first volume by rigid-body transformation (after spatial smoothing with an isotropic 5 mm full width at half maximum Gaussian kernel) and resliced to correct for head motion. Boxcar regressors for the relevant stimulus blocks were convolved with a canonical hemodynamic response function. Additional regressors of no interest were used to capture residual movement-related artifacts from the six realignment param-

eters determined from initial spatial registration. To remove low-frequency drifts from the data, a high-pass filter was applied using a standard cutoff frequency of 128 sec (0.008 Hz).

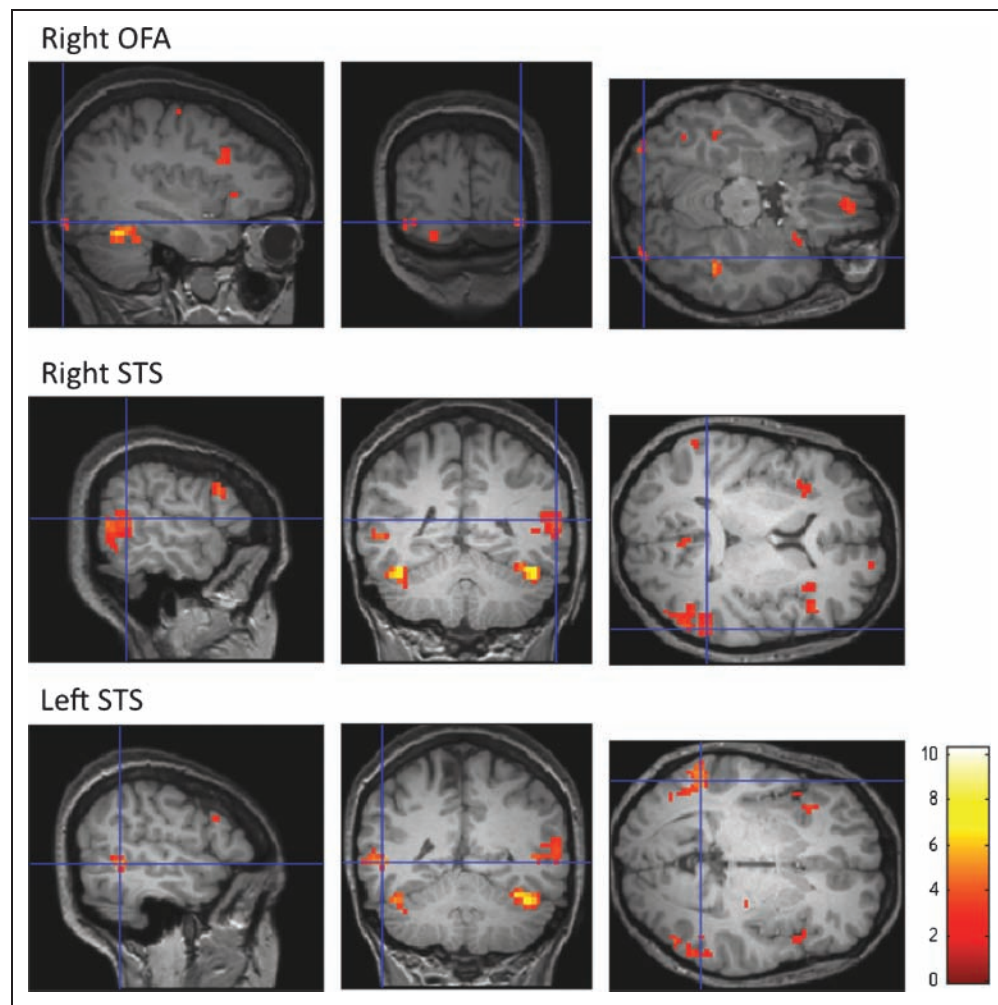
For the present study, the site defined as the right posterior STS was identified on the basis of face-selective activation within the posterior STS, extending into either or both of the middle and superior temporal gyri. Where possible, the left posterior STS site was identified on the basis of face-specific activation at or very near the corresponding region in the left hemisphere; for 4 of the 12 participants, such face-specific activity was not evident even at a liberal threshold ($p < .05$, uncorrected), in which cases the left posterior STS site was chosen on the basis of a location in the left STS that corresponded to the face-selective cluster in the right STS. Table 2 shows the MNI coordinates for the peak face-selective voxel for each region of interest in each participant. A Polaris (Northern Digital, Ontario, Canada) infrared tracking device was used to measure the position of each participant's head, and theBrainsight frameless stereotaxic software (Rogue Research, Montreal, Canada) was used to co-register the participant's head with the participant's MRI scan. This co-registration system was then used to determine the scalp positions corresponding to the three brain regions of interest (determined by the face-selective activations, as described above), which were marked on a swimmer's cap worn by the participant. Halfway through each experimental session, the scalp position of each TMS site marker was checked using the co-registration system, and their locations were adjusted if necessary.

Procedure

The participants completed two different tasks on the same set of faces. In one task, the participants judged singly presented faces as either trustworthy or not trustworthy. In the other task, the participants categorized the sex of the same individually presented faces (they were instructed to judge them as female or not female, in order to increase the correspondence between the two tasks). The two tasks were performed separately in two sessions at least several days apart. The order of tasks/sessions was counterbalanced across participants.

For each task, the participants were asked to respond as quickly as possible without sacrificing accuracy. Each session started with five practice trials, consisting of faces not presented in the main experiment. The main experiment consisted of eight blocks (4 TMS conditions, repeated once in the same order) of 40 images, resulting in 320 trials overall. The order of the stimulation sites was randomized across participants with the restriction that the second round of blocks for each participant had the same order as the first four blocks. The 40 images were presented randomly within a block. The first four blocks displayed uniquely the 160 images, whereas the second four blocks

Figure 2. The three face-selective regions of interest (ROIs) for a single participant in the TMS experiment (right OFA, right STS, left STS), as defined by a faces > objects functional localizer in a separate fMRI experiment (unsmoothed data; $p < .01$, uncorrected; cluster size > 5 voxels). As illustrated here, the functional scan for each participant was overlaid on that person's native structural MR scan. TMS sites at the locations on the skull corresponding to these ROIs were confirmed using frameless stereotaxy. Five of the 12 participants did not show face-selective activity in the left STS. (See main text for further details.) Scale: t -values.



repeated the images with the constraint that none of the images was repeated across the two blocks associated with each stimulation site. The participants were allowed to take breaks between every block. Every trial started with a fixation cross, presented for 500 msec, followed by the stimulus presented for 500 msec. After the stimulus presentation, varying intertrial intervals (ITIs) of 3500, 3750, 4000, and 4250 msec were used, during which participants made their response. The ITI duration was varied in order to diminish expectation effects and automation of responses. The ITIs were relatively long in order to ensure that the durations between repeated applications of TMS were well within the safety guidelines for rTMS (Wassermann, 1998), and to allow enough time for the neural regions to recover from stimulation and return to baseline level. Participants responded using the two middle buttons on the response box; the left one was mapped to trustworthy/female judgments and the right one to not trustworthy/not female judgments. (Possible learned stimulus–response mappings were very unlikely given the delay between experimental sessions.)

After the second TMS session, each participant completed an additional, computer-based task in which they

were asked to judge the trustworthiness of all the 160 face stimuli used in the TMS sessions. This time, the participants were again presented each face once, one after the other in random order, and, without any time pressure, were required to judge whether each face was trustworthy or not trustworthy. Because trait assessment is a more subjective judgment than determining the sex of a face, this final task was used in order to obtain a representative measure of each participant's judgment under unconstrained conditions.

RESULTS

Incorrect responses, which were excluded from analyses of RT, accounted for 6.9% of the trials overall when accuracy for the trustworthiness judgments was based on the predetermined classification of trustworthiness from Oosterhof and Todorov (2008), and 7.9% of the trials when accuracy for the trustworthiness judgments was based on our participants' own post-TMS judgments. Analyses of the accuracy data indicated that there were no speed–accuracy tradeoffs (see below). Missed responses and excessively

Table 2. MNI Coordinates of the Peak Face-selective Voxel for Each Region of Interest in Each Participant

Participant	Right OFA			Right STS			Left STS		
	<i>x</i>	<i>y</i>	<i>z</i>	<i>x</i>	<i>y</i>	<i>z</i>	<i>x</i>	<i>y</i>	<i>z</i>
1	50	-74	-12	56	-66	18	-58	-65	10*
2	34	-94	-12	54	-46	10	-60	-50	6
3	48	-74	-14	54	-42	2	-52	-40	4
4	42	-74	-16	42	-58	12	-60	-48	6
5	44	-72	-12	50	-64	12	-52	-66	4
6	36	-90	-8	58	-48	10	-54	-46	6*
7	40	-64	-16	48	-40	12	-46	-50	6
8	32	-88	-8	52	-46	4	-56	-52	2*
9	32	-96	-12	52	-44	4	-54	-56	10
10	42	-84	-6	56	-44	22	-60	-48	14
11	38	-86	-12	44	-38	8	-54	-42	10*
12	46	-78	-12	60	-44	10	-52	-58	8
Mean (<i>SD</i>)	40 (6)	-81 (10)	-12 (3)	52 (6)	-48 (10)	10 (6)	-55 (4)	-52 (8)	7 (3)

The data presented here are for the normalized images; TMS sites were located by overlaying the nonnormalized functional images onto individual structural scans in native space. OFA = occipital face area; STS = superior temporal sulcus.

*ROIs in left STS for which no face-selective clusters of activation were evident, in which case the reported coordinates are for the left STS location approximately corresponding to the cluster in right STS for that participant.

long RTs (≥ 3500 msec, the shortest of the ITIs) accounted for 1.16% of the total trials and, because of their low number, were not analyzed further.

The mean error rates on the trustworthiness task calculated according to the two estimates of accuracy differed significantly when averaged across conditions for each participant [$t(11) = 2.85, p < .05$, two-tailed; predetermined trustworthiness criterion: $M = 3.12\%$, $SD = 1.62$; self-judgment criterion: $M = 3.67\%$, $SD = 1.45$]. For the trustworthiness task, the results of the statistical analyses are therefore presented for both the data based on the predetermined classification of trustworthiness (indexed with a subscript of 1) and the data based on our participants' own post-TMS judgments (indexed with a subscript of 2).

Prior to analysis, RTs were inverse-transformed and mean proportion correct scores were arcsine-transformed to reduce the impact of deviations from the normal distribution. (A log transformation of the RTs produced a similar pattern of statistical effects as those reported below, although unlike the inverse transformation, it did not reduce the skewness and kurtosis for all conditions to acceptable levels, i.e., such that their Z -scores $< 1.96, \alpha = .05$). For all analyses, the criterion for statistical significance, α , was set at .05. All post hoc pairwise or planned comparisons were Bonferroni corrected for multiple comparisons. Effect sizes are reported using partial eta squared (η_p^2) for analyses of variance (ANOVAs) and Pearson's correlation coefficient (r) for t tests. Statistically significant interactions were

followed up with separate ANOVAs at each level of the most theoretically relevant factor.

Analyses of Reaction Times

Mean RTs for correct responses are presented in Figure 3. Inverse-transformed RTs for correct responses were analyzed in an ANOVA with four repeated measures: task (trustworthiness, sex), TMS condition (right OFA, right STS, left STS, sham), trustworthiness of the face (trustworthy, untrustworthy), and sex of the face (female, male). Sex of the face was included as a factor given previous findings that the sex and trustworthiness of faces are not entirely independent dimensions (Oosterhof & Todorov, 2008; Buckingham et al., 2006; Perrett et al., 1998), a relationship that has yet to be tested in an RT task. There were significant main effects of task [$F_1(1, 11) = 27.72, p < .0005, \eta_p^2 = .72; F_2(1, 11) = 27.16, p < .0005, \eta_p^2 = .71$], trustworthiness [$F_1(1, 11) = 12.34, p < .005, \eta_p^2 = .53; F_2(1, 11) = 11.93, p < .01, \eta_p^2 = .52$], and TMS condition [$F_1(3, 33) = 3.97, p < .05, \eta_p^2 = .27; F_2(3, 33) = 3.67, p < .05, \eta_p^2 = .25$]. Overall, RTs were significantly longer for trustworthiness judgments than for sex judgments, and for untrustworthy than for trustworthy faces. The main effect of TMS condition reflected significantly longer RTs for rTMS over the left STS compared to sham stimulation for the data based on the predetermined classification of trustworthiness ($p_1 < .05$), but not for the data based on the

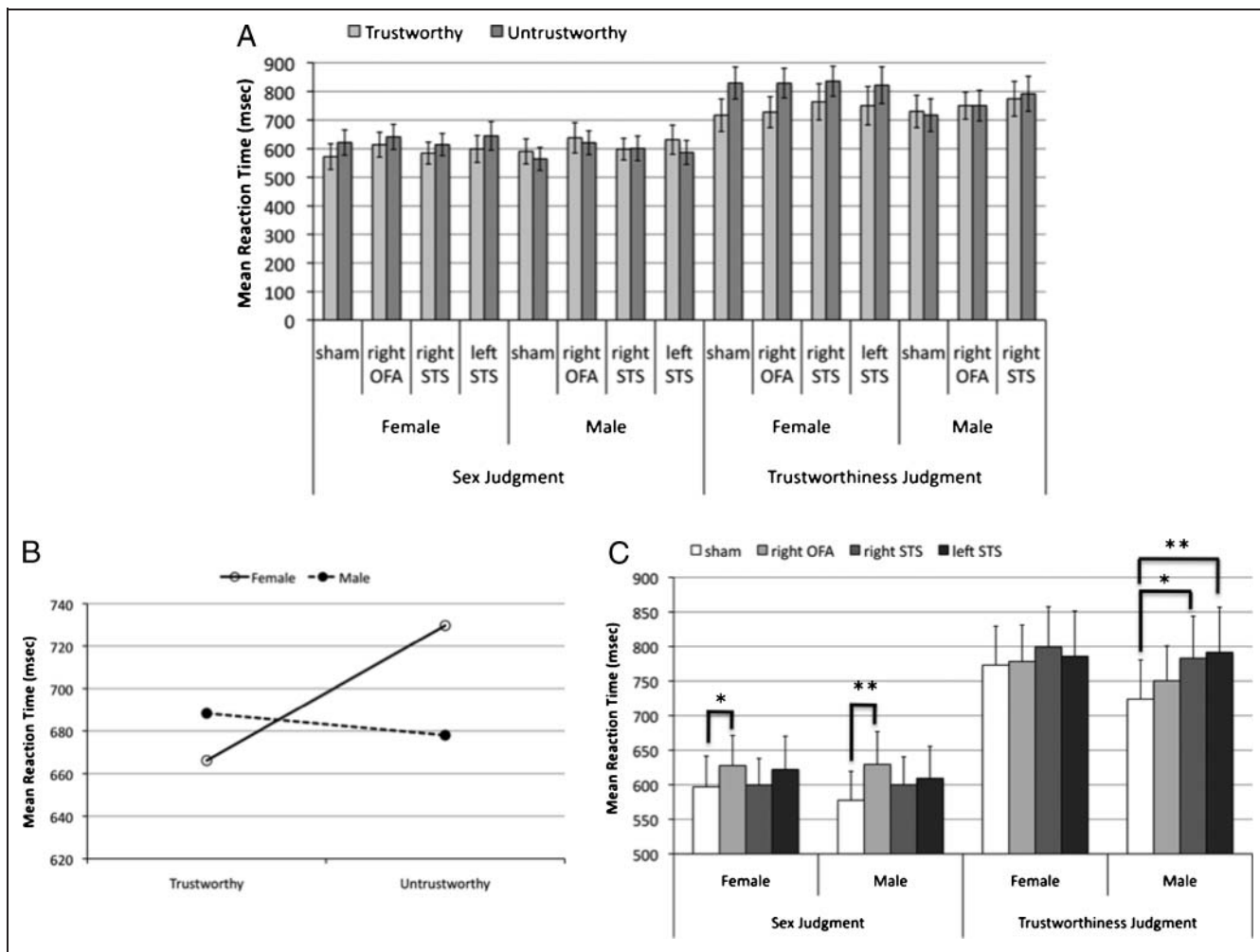


Figure 3. (A) Mean RTs for each task, as a function of TMS condition and the sex and trustworthiness of the faces. (B) Mean RTs collapsed across task and TMS condition, to illustrate the significant Sex \times Trustworthiness interaction. (C) Mean RTs collapsed across trustworthiness of the faces, to illustrate the significant Task \times TMS condition \times Sex interaction. The data plotted here for the trustworthiness task are based on the predetermined classification of trustworthiness from the Oosterhof and Todorov (2008) stimuli used as a criterion for accuracy. Error bars represent ± 1 SEM across participants ($n = 12$). Prior to statistical analyses, RTs were inverse-transformed. *Significantly different at $p < .05$; **significantly different at $p < .01$.

participant's own post-TMS judgments ($p_2 = .11$). (For all other pairwise comparisons, $ps > .75$.)

More importantly, there were significant interactions between sex and trustworthiness [$F_1(1, 11) = 30.19, p < .0005, \eta_p^2 = .73$; $F_2(1, 11) = 26.13, p < .0005, \eta_p^2 = .7$], and between task and TMS condition [$F_1(3, 33) = 4.19, p < .05, \eta_p^2 = .28$; $F_2(3, 33) = 4.32, p < .05, \eta_p^2 = .28$]. The latter interaction was itself qualified by a significant three-way interaction with sex for the data on the basis of the predetermined classification of trustworthiness [$F_1(3, 33) = 3.59, p < .05, \eta_p^2 = .25$], which showed a nonsignificant trend for the data based on the participant's own post-TMS judgments [$F_2(3, 33) = 2.64, p = .066, \eta_p^2 = .19$]. No other interactions or main effects were significant (all $ps > .095$).

The significant Sex \times Trustworthiness interaction (illustrated in Figure 3B) indicated that participants were reliably faster in making judgments about trustworthy than untrust-

worthy female faces [$F_1(1, 11) = 29.0, p < .0005, \eta_p^2 = .73$; $F_2(1, 11) = 27.43, p < .0005, \eta_p^2 = .71$] and, conversely, marginally faster in making judgments about untrustworthy than trustworthy male faces [$F_1(1, 11) = 4.68, p = .053, \eta_p^2 = .3$; $F_2(1, 11) = 5.21, p < .05, \eta_p^2 = .32$].

An examination of the significant three-way interaction (illustrated in Figure 3C) revealed significant Task \times TMS condition interactions for female faces [$F_1(3, 33) = 4.8, p < .01, \eta_p^2 = .3$; $F_2(3, 33) = 6.5, p < .005, \eta_p^2 = .37$] and for male faces [$F_1(3, 33) = 3.53, p < .05, \eta_p^2 = .24$; $F_2(3, 33) = 2.56, p = .071, \eta_p^2 = .19$]. Nonetheless, whereas the effect of TMS condition was significant for sex judgments on female faces [$F(3, 33) = 4.87, p < .01, \eta_p^2 = .31$] and on male faces [$F(3, 33) = 5.0, p < .01, \eta_p^2 = .31$], it was significant only for male faces when participants were judging trustworthiness [male faces: $F_1(3, 33) = 4.78, p < .01, \eta_p^2 = .3$; $F_2(3, 33) = 3.07, p < .05, \eta_p^2 = .22$; female faces: both $ps > .2$]. For sex judgments, RTs were

reliably longer when rTMS was applied over the right OFA compared to sham stimulation for female faces ($p < .05$) and for male faces ($p < .01$). For trustworthiness judgments on male faces, RTs were reliably longer for rTMS over the right STS ($p_1 = .02, p_2 = .066$) and over the left STS ($p_1 = .003, p_2 = .067$) compared to sham stimulation.

So far, these analyses of RTs implicate a critical role for the right OFA in sex but not in trustworthiness judgments regardless of the sex of the face, and critical roles for the right and left posterior STS in trustworthiness but not in sex judgments for male but not female faces. Next, in order to compare directly the effect of rTMS across sites of interest relative to a baseline condition, a normalized TMS-effect measure was calculated as follows (e.g., D'Ausilio et al., 2009; Ellison, Lane, & Schenk, 2007). The RTs for correct responses resulting from rTMS at each site for each condition and participant were normalized with respect to the baseline (sham) RTs for that participant according to the following formula: $(\text{TMS}_x - \text{sham TMS})/\text{sham TMS} * 100$, where x denotes the TMS site. Given that the effects of interest on the trustworthiness task were very similar across the RT datasets based on the two criteria for accuracy, we chose to enter into these TMS-effect calculations those RTs for which trustworthiness judgment accuracy was determined on the basis of the Oosterhof and Todorov (2008) stimulus classification.

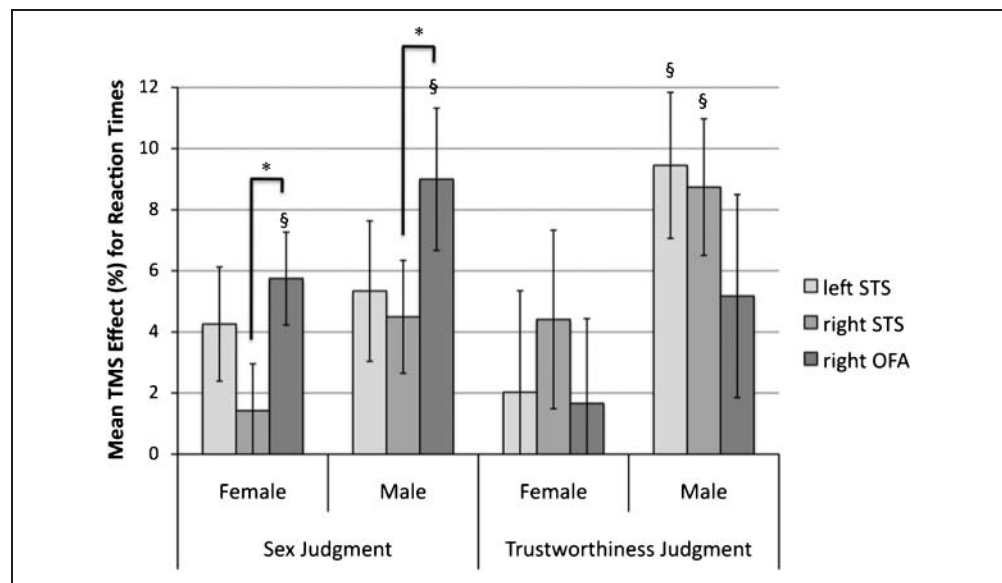
Analyses of Transcranial Magnetic Stimulation Effects for Reaction Times

The TMS-effect measures (summarized in Figure 4) were examined using separate repeated measures ANOVAs, with task, TMS site, trustworthiness, and sex of the faces as factors. There was a significant main effect of sex [$F(1, 11) = 5.45, p < .05, \eta_p^2 = .33$], reflecting a larger TMS effect for male than for female faces. The critical interaction between

task and TMS site was significant [$F(2, 22) = 4.46, p < .05, \eta_p^2 = .29$]; however, this was qualified by a marginally significant Sex \times Task \times TMS site interaction [$F(2, 22) = 3.23, p = .059, \eta_p^2 = .23$]. All other main effects and interactions were not significant (all $ps > .09$). The Task \times TMS site interactions were significant both for female faces [$F(2, 22) = 3.77, p < .05, \eta_p^2 = .26$] and for male faces [$F(2, 22) = 4.55, p < .05, \eta_p^2 = .29$]. For sex judgments, planned contrasts revealed significantly greater TMS effects for stimulation over the right OFA than over the right but not left STS for female and male faces (both $ps < .05$). Confirming the RT analyses reported above, one-tailed, one-sample t tests revealed that only the TMS effect for the right OFA was significantly greater than 0, both for female faces [$t(11) = 3.78, p < .01, r = .48$] and for male faces [$t(11) = 3.87, p < .01, r = .49$]. For trustworthiness judgments, planned contrasts revealed that the TMS effects for the right and left STS did not differ significantly from the TMS effect for the right OFA for either female or male faces (all $ps > .3$). Nonetheless, confirming the RT analyses, the TMS effects for both the right and left STS were significantly greater than 0, but only for male faces [right STS: $t(11) = 3.91, p < .01, r = .49$; left STS: $t(11) = 3.96, p < .01, r = .5$], not female faces ($ps > .4$).

In summary, the analyses of the TMS effects for RTs confirmed that only the right OFA is implicated in sex judgments from faces (regardless of the sex of those faces). By contrast, both the right and left STS are implicated in trustworthiness judgments from male (but not female) faces. In addition, however, the lack of a difference in the TMS effects across stimulation sites for the trustworthiness task raises the possibility that the right OFA has a role in evaluating trustworthiness, in addition to the right and left STS. We explored this issue further by analyzing the RT distributions across experimental conditions (e.g., Balota, Yap, Cortese, & Watson, 2008; Ratcliff, 1979).

Figure 4. Mean TMS effect for RTs (% change relative to the sham stimulation baseline), as a function of task, sex of the face, and TMS site. For the trustworthiness task, the data plotted are based on the predetermined classification of trustworthiness from the Oosterhof and Todorov (2008) stimuli. Error bars represent ± 1 SEM across participants ($n = 12$). *Significantly different at $p < .05$; §significantly greater than 0 at $p < .01$.



Analyses of Reaction Time Distributions

The ex-Gaussian function is commonly used to model RT distributions because it is well described by three easily interpretable parameters, does not require the large number of observations per cell required by some other ways of characterizing RT distributions, and has good theoretical justification (Heathcote, Popiel, & Mewhort, 1991; Ratcliff, 1979). The shape of the ex-Gaussian is described by μ , which is a measure of central tendency (the mean); σ , which is a measure of dispersion (the standard deviation); and τ , which is a measure of positive skew. Following several other investigators (e.g., Balota et al., 2008; Heathcote et al., 1991), we fitted the ex-Gaussian distribution to each individual participant's RT data for correct responses in each of the eight experimental conditions constituted by the factorial combination of task and TMS condition (i.e., collapsed across trustworthiness). This was achieved using a set of Matlab functions created by Lacouture and Cousineau (2008), which uses maximum likelihood estimation to determine the parameters of the ex-Gaussian that best fit the given RT distribution. Three repeated measures ANOVAs with task (trustworthiness, sex) and TMS condition (right OFA, right STS, left STS, sham) as factors were conducted, one for each of the ex-Gaussian parameters (μ , σ , and τ). For μ there was a significant main effect of task [$F(1, 11) = 26.92, p < .0005, \eta_p^2 = .71$], corresponding to the analyses of mean correct RTs reported above. Importantly, for τ there were significant main effects of task [$F(1, 11) = 17.34, p < .005, \eta_p^2 = .61$] and TMS condition [$F(3, 33) = 4.08, p < .05, \eta_p^2 = .27$]. Values of τ were significantly larger for trustworthiness judgments than for sex judgments and for rTMS over the right OFA and the right (but not left) STS compared to sham (all $ps < .05$). All other main effects and interactions were not significant (all $ps > .25$).

Given that τ is a measure of positive skew, these results indicate that the relatively longer RTs were, on average, longer for trustworthiness judgments than for sex judgments and for rTMS over the right STS and right OFA compared to sham stimulation. To illustrate and examine further these effects, we constructed quantile plots (Jiang, Rouder, & Speckman, 2004) as follows. For each participant in each condition, the RTs for correct responses were ordered from shortest to longest and then the 1/50 quantiles were calculated. We chose to divide the distribution of correct RTs into 50 quantile bins because larger numbers of quantiles tend to produce better fits (Heathcote, Brown, & Mewhort, 2002), and we had a maximum of 80 and a minimum of 57 correct RTs in each of the eight conditions. Next, the quantile RTs for the sham condition were subtracted from the corresponding quantile RTs for each of the other rTMS conditions (right OFA, right STS, left STS), separately for each task, in order to provide a measure of the rTMS effect at each site across the distribution of RTs for each task and participant. Finally, group distributions for each condition were created by averaging the rTMS effect quantile RTs across participants at each of the 50 levels.

These group distributions are plotted in Figure 5. (Given that there was no significant difference in the τ value between the left STS and sham conditions, and for the sake of clarity, we have not plotted on these graphs the rTMS effect quantile RTs for the left STS.)

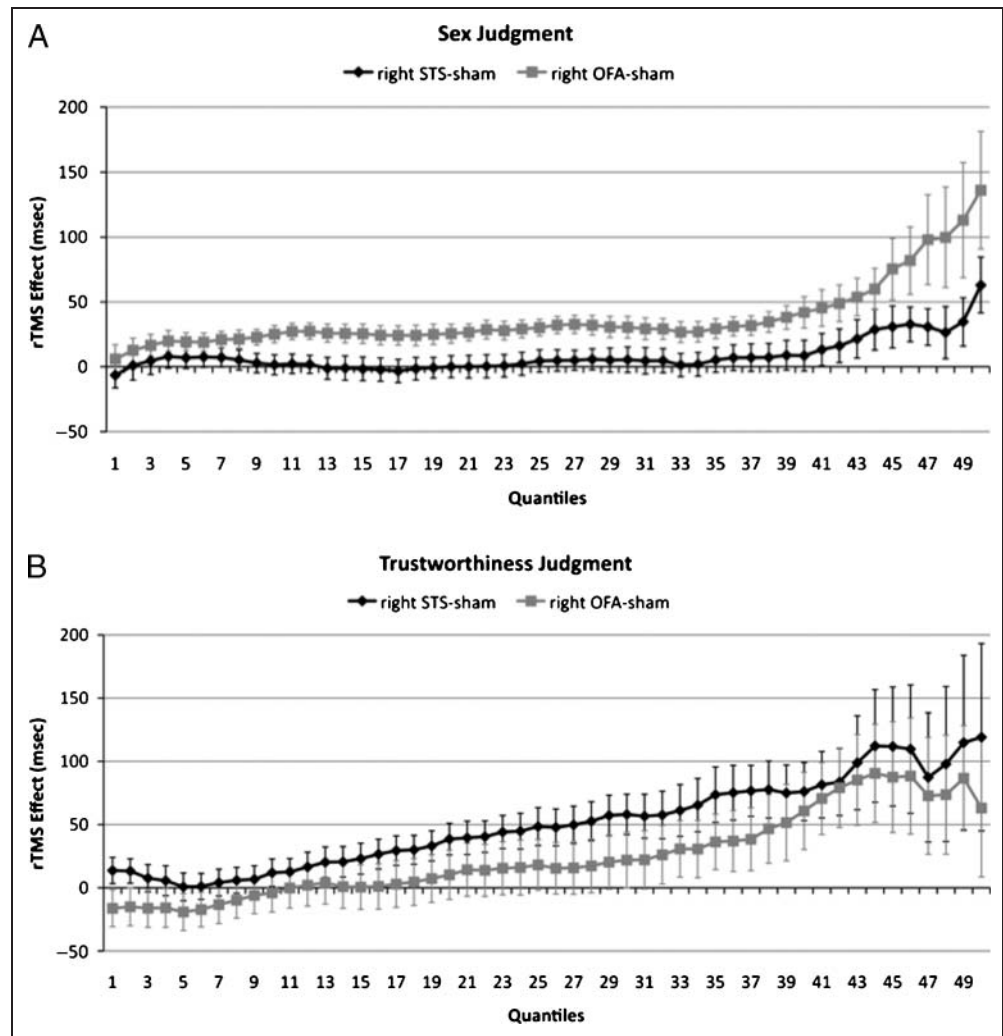
As is clear from Figure 5, rTMS over the right OFA prolonged RTs for sex judgments across the whole range of RTs, and this effect for the right OFA is always higher than that for the right STS (indeed, the effect for the right STS never gets much above 0). For trustworthiness judgments, however, there is little difference between the effects for the right STS and the right OFA, although it is clear that the effect for the right STS is consistently higher than that for the right OFA over much of the RT distribution. Nonetheless, notice the relatively steep increase in the rTMS effect for the right OFA toward the right of the distribution, which begins around the 38th quantile bin. It is only between the 40th and 46th quantile bins (inclusive) that the rTMS effect for the right OFA is significantly above 0, whereas for the right STS the rTMS effect is significantly above 0 between the 15th and 46th quantile bins ($p < .05$, one-tailed, one-sample t tests, uncorrected for multiple comparisons). Thus, whereas the right STS plays a critical role in judgments of trustworthiness across a large range of the RT distribution, the right OFA plays a critical role in judgments of trustworthiness only for those faces to which participants take longer to respond and, therefore, presumably find more difficult.

Earlier we established that participants were significantly slower in making sex and trustworthiness judgments about untrustworthy than trustworthy female faces and, conversely, were significantly slower for trustworthy than untrustworthy male faces. We thus expected to find that the right tail of the RT distribution for the trustworthiness task would contain more female untrustworthy faces and more male trustworthy faces than the left tail. ANOVAs were conducted to compare the frequencies of correct responses for male and female trustworthy and untrustworthy faces in each of the lowest and highest 13 quantile bins (1–13 and 38–50). In the long RT range, there were significantly more untrustworthy than trustworthy female faces [$F(1, 11) = 12.92, p < .005, \eta_p^2 = .54$], whereas in the short RT range, there were significantly more trustworthy than untrustworthy female faces [$F(1, 11) = 14.74, p < .005, \eta_p^2 = .57$]. There was no significant difference in the number of male trustworthy and untrustworthy faces in the long RT range ($p > .65$), whereas there was a nonsignificant trend for more untrustworthy than trustworthy male faces in the short RT range [$F(1, 11) = 3.47, p = .089, \eta_p^2 = .24$].

Analyses of Accuracy

The mean proportion correct performance is summarized in Figure 6. An ANOVA with task, TMS condition, trustworthiness of the face, and sex of the face as repeated measures variables was conducted on the arcsine-transformed proportion correct data. There were significant main effects

Figure 5. Quantile plots for the (A) sex judgment and (B) trustworthiness judgment tasks, showing the rTMS effects (in milliseconds) for the right OFA (gray line and squares) and the right STS (black line and diamonds) relative to sham stimulation. The rTMS effects were calculated by subtracting each sham stimulation quantile RT from the corresponding quantile RT for the right OFA or right STS conditions, then averaging these differences across participants. Error bars represent ± 1 SEM across participants ($n = 12$).



of task [$F_1(1, 11) = 29.71, p < .0005, \eta_p^2 = .73; F_2(1, 11) = 48.34, p < .00005, \eta_p^2 = .82$] and trustworthiness [$F_1(1, 11) = 6.16, p < .05, \eta_p^2 = .36; F_2(1, 11) = 4.28, p = .063, \eta_p^2 = .28$]. Participants were more accurate in judging the sex of the faces than their trustworthiness and in making judgments about trustworthy than untrustworthy faces. There were no significant main effects of TMS condition or sex (all $ps > .15$). There was a significant Trustworthiness \times Sex interaction [$F_1(1, 11) = 11.91, p < .01, \eta_p^2 = .52; F_2(1, 11) = 7.29, p < .05, \eta_p^2 = .4$], which was qualified by a marginally significant interaction with task for the data based on the predetermined classification of trustworthiness [$F_1(1, 11) = 4.44, p = .059, \eta_p^2 = .29$], but not for the data based on the participant's own post-TMS judgments [$F_2(1, 11) = 1.14, p = .31, \eta_p^2 = .09$]. None of the other interactions was significant. The significant three-way interaction reflected the fact that participants were reliably more accurate with trustworthy than untrustworthy female faces, both for sex judgments [$F(1, 11) = 7.9, p < .05, \eta_p^2 = .42$], and for trustworthiness judgments [$F_1(1, 11) = 10.32, p < .01, \eta_p^2 = .48; F_2(1, 11) = 10.0, p < .01, \eta_p^2 = .48$]. However, accuracy did not differ significantly

between trustworthy and untrustworthy male faces for either task (all $ps > .45$).

DISCUSSION

This study examined whether two cortical regions specifically responsive to faces—the right OFA and a posterior region of the STS in each hemisphere—have distinct, critical roles in two face-processing abilities: judging sex and trustworthiness. Effects of event-related rTMS applied over these areas were assessed using measures of RT and accuracy on speeded-response tasks. Four novel results were reported.

First, the ability of participants to judge whether faces were female or male was impaired when rTMS was delivered over the right OFA, relative to a sham stimulation baseline condition, but not when it was delivered over the right or left STS. Furthermore, the rTMS effect for sex judgments was significantly greater for the right OFA than it was for the right but not the left STS. (The rTMS effects for the right and left STS did not differ significantly from each other.)

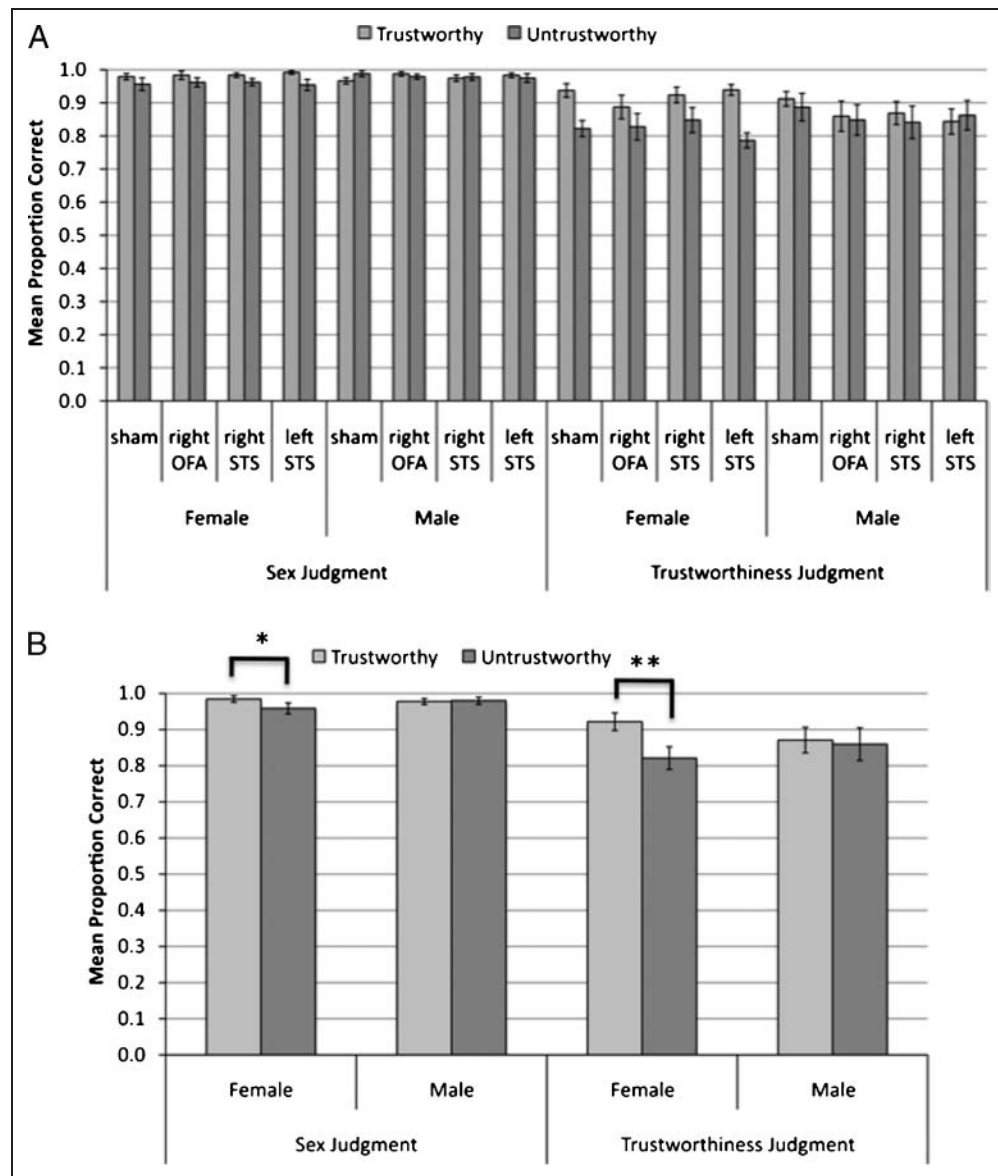
Thus, the right OFA plays a critical role in the judgment of a face's sex, but the right and left STS do not.

The second novel finding was that the ability of participants to judge whether the same faces were trustworthy or untrustworthy was disrupted when rTMS was delivered over the right or left STS, compared to sham stimulation, but only for male faces and not when rTMS was delivered over the right OFA. Thus, the right and left STS play critical roles in the judgment of a face's trustworthiness. Nonetheless, for trustworthiness judgments, the rTMS effects over the right and left STS and the right OFA did not differ significantly from each other. Thus, our results hint at a possible role also for the right OFA in trustworthiness evaluations, or even that some trustworthiness judgments rely on structural cues related to the face's sex.

The third novel finding related to task performance irrespective of TMS condition. Overall, participants were faster and more accurate in judging the sex and trustworthiness

of female faces when those faces were trustworthy than when they were untrustworthy. Conversely, participants were faster (although not more accurate) in judging the sex (but not trustworthiness) of untrustworthy than trustworthy male faces. These results are consistent with previous work showing that ratings of trustworthiness are influenced by the perceived masculinity/femininity of faces and that ratings of masculinity/femininity are influenced by the degree of trustworthiness (e.g., Oosterhof & Todorov, 2008; Perrett et al., 1998). Together, these findings indicate that the processes underpinning sex and trustworthiness judgments about faces are not entirely independent. These two capacities might draw upon a partially overlapping set of visual cues or rely on at least partially overlapping neural mechanisms, or both. As noted, we found no evidence that the right or left STS is critically involved in sex judgments. Yet, there was a small indication that the right OFA has a role in trustworthiness judgments, which fits

Figure 6. (A) Mean proportion correct scores for each task, as a function of TMS condition and the sex and trustworthiness of the faces. (B) Mean proportion correct scores collapsed across TMS condition, to illustrate the significant Task \times Sex \times Trustworthiness interaction. For the trustworthiness task, the accuracy data plotted here are those based on the predetermined classification of trustworthiness from the Oosterhof and Todorov (2008) stimuli. Error bars represent ± 1 SEM across participants ($n = 12$). Prior to statistical analyses, mean proportion correct values were arcsine transformed. *Significantly different at $p < .05$; **significantly different at $p < .01$.



with an influential model according to which the STS receives inputs from the OFA (e.g., Haxby et al., 2000). We further tested for a possible critical role for the right OFA in trustworthiness judgments by analyzing the distribution of RTs, which revealed our fourth novel finding: rTMS over the right OFA prolonged trustworthiness judgment RTs only for faces with relatively longer RTs. These faces included significantly more untrustworthy than trustworthy females (whereas the converse was true for the left tail of the RT distribution). Given that participants tended to make more errors in judging the trustworthiness of untrustworthy than trustworthy female faces, as well being slower, the right OFA's contribution appears to be critical only for those faces that participants find particularly difficult.

Right Occipital Face Area Involvement in Sex and Trustworthiness Judgments

We reasoned that the right OFA would play a critical role in allowing observers to discriminate the sex of faces because this ability relies principally on a set of invariant (structural) facial cues, particularly certain spatial relations between features, the size of the face and aspects of its 2-D and 3-D shape, and the processing of at least some of which involves the OFA (e.g., Fox et al., 2009; Rhodes et al., 2009; Rotshtein et al., 2007). Two previous TMS studies demonstrated a critical role for the right OFA in discriminating faces on the basis of differences in the shape of internal face parts, alone (Pitcher et al., 2007) or in combination with cues related more to the shape of the face (Pitcher et al., 2009), but not on the basis of differences in the spatial relations between face parts (Pitcher et al., 2007). In the light of these findings, our results thus suggest that right OFA's involvement in sex judgments may be related more to the processing of face shape and individual facial features than to the processing of spatial relations between features. Future experiments could test this hypothesis directly.

Our findings also suggest a critical but more circumscribed role for the right OFA in trustworthiness judgments. Application of rTMS over the right OFA prolonged only those RTs toward the right tail of the distribution for trustworthiness judgments. A plausible explanation of this finding is that right OFA's critical role is in a processing stage subsequent to an initial structural encoding, but only for faces for which the first feed-forward volley of processing to the STS (whether it originates from the OFA or not) does not provide sufficient information for the observer to reach a decision about their trustworthiness. That the OFA's role in certain face perception tasks might be particularly important at a later processing stage is consistent with the findings of another TMS study showing a critical role for the OFA in integrating information relevant to expression and identity at around 170 msec poststimulus onset (Cohen Kadosh, Walsh, & Cohen Kadosh, 2011). Our results further

revealed a predominance of female untrustworthy faces at the right tail of the RT distribution, suggesting that there is something about these faces that makes judgments of their trustworthiness more difficult and more susceptible to disruption by rTMS over the right OFA. Perhaps decreasing the trustworthiness of female faces does not make them appear as negatively valenced as does decreasing the trustworthiness of male faces by the same amount. This possibility was not addressed in the work reported by Oosterhof and Todorov (2008, 2009) and Said et al. (2009) that examined the relationship between trustworthiness and expressive valence. Nonetheless, if true, it does suggest why the right OFA was more critical for judging the trustworthiness of untrustworthy than trustworthy female faces: Untrustworthy female faces, on this account, are less likely to provide sufficient expressive cues to trustworthiness for a decision to be made on the basis of STS outputs alone and are therefore more likely to rely on additional structural cues, and thus, to recruit the OFA. Alternatively, perhaps a higher-level cognitive bias was influencing our participants' judgments, such as the expectations that men will tend to express anger more readily than women and that women will tend to smile more frequently than men (e.g., Barrett & Bliss-Moreau, 2009; Kring & Gordon, 1998). If this were the case, however, it is not at all clear why the right OFA would have a critical role in processing untrustworthy (and thus more angry or less happy) female faces. Future research should address these issues.

Findings from another TMS study also point to a possible role for the right OFA in trustworthiness judgments, albeit less directly and in apparent conflict with our own findings. Pitcher, Garrido, Walsh, and Duchaine (2008) reported that TMS delivered over the right OFA impaired discrimination of facial expressions of emotion, but not discrimination of identity, within 60–100 msec from stimulus onset but not later (100–170 msec from stimulus onset), implicating a critical early role for the right OFA in distinguishing among emotional expressions based on an analysis of individual facial features. Thus, it is possible that the right OFA plays a similar role in allowing observers to discriminate faces on the basis of their trustworthiness, given that judging the trustworthiness of faces amounts to evaluating their valence, and thus, (in part) their expressiveness (Oosterhof & Todorov, 2009; Todorov, 2008). Yet such an early role for the right OFA in trustworthiness judgments conflicts with the later role for the right OFA in such judgments suggested by the findings reported here. An important goal for future research will be to examine the timing of the involvement of the OFA and the STS in sex and trustworthiness judgments, by applying TMS at different time windows and by varying the timings of stimulation onset and offset to pinpoint the onset and duration of OFA and STS involvement. MEG or EEG would also be useful in this regard, either on their own or in conjunction with TMS. It will also be interesting to test for the critical involvement of the left as well as right OFA in trustworthiness and sex judgments.

Right and Left Superior Temporal Sulcus Involvement in Trustworthiness Judgments

Why might have rTMS over the right and left STS impaired trustworthiness judgments for male faces only? At least part of the reason is probably a corollary of the reason we suggested above for the right OFA's involvement in trustworthiness judgments for trustworthy female faces: The probability that a summary measure such as mean RT will reveal a significant effect of rTMS over the STS for a set of faces (in this case, females) will be small if a contribution of the STS alone is insufficient to enable a decision about a large proportion of those (female) faces. Nonetheless, it is notable that the rTMS effect on trustworthiness judgments for the right STS was not significant for the 14 leftmost bins of the RT distribution (i.e., for the relatively short RTs) and that there was a trend for more untrustworthy than trustworthy male faces around this part of the distribution. One implication of this result that deserves further investigation is that there were certain faces (particularly untrustworthy males) whose trustworthiness could be accurately discriminated even without a critical contribution from one or the other of the right and left STS.

We hypothesized a critical role for face-selective STS in allowing observers to discriminate trustworthy from untrustworthy faces because evaluation of trustworthiness relies at least partly on changeable facial cues related to movements of the facial muscles, particularly changes in expressive valence (e.g., Oosterhof & Todorov, 2008, 2009; Said et al., 2009), the processing of which is thought to involve the STS more than the OFA (Haxby et al., 2000). Yet regions of superior temporal cortex, particularly in the STS, are also involved in processing others' eye gaze (e.g., Kingstone, Tipper, Ristic, & Ngan, 2004; Puce, Allison, Bentin, Gore, & McCarthy, 1998). Indeed, one study has shown that TMS delivered over right posterior superior temporal cortex interfered with the ability to distinguish changes in gaze but not expression across two successively presented static faces (Pourtois et al., 2004). Current evidence suggests separable coding of different aspects of eye gaze in distinct regions of the STS, with posterior STS activation to eyes reflecting a contribution to the decoding of the intentions of the observed individual toward objects or other people (Pelphrey, Viola, & McCarthy, 2004; Calder et al., 2002) and anterior STS activation to eyes reflecting dissociable coding of different gaze directions (Calder et al., 2007). Thus, it is notable that the region of the STS that was stimulated had a posterior rather than anterior location and that eye gaze direction varied little in the face stimuli that we used. An interesting avenue for future research will be to examine whether the processing of information about the eyes or eye gaze is central to posterior STS's involvement in evaluating trustworthiness from faces.

Numerous functional imaging studies have shown posterior STS involvement in mentalizing, that is, in the ability to attribute mental states to others (for a recent review, see Carrington & Bailey, 2009). Indeed, Winston et al. (2002)

suggest that the posterior STS activation that they recorded when participants judged the trustworthiness of faces may reflect this region's involvement in a component of mentalizing, namely, determining other people's intentions. The posterior STS region implicated in mentalizing, which is part of a wider network that includes regions of medial prefrontal and parietal cortices, tends to be a little more posterior than the face-selective region of the posterior STS, and indeed, is often labeled as part of the temporo-parietal junction (TPJ; e.g., Saxe & Kanwisher, 2003). Nonetheless, it is possible that, in targeting the face-selective posterior STS with rTMS in the present study, we also stimulated the TPJ because of the proximity or intersection of these two functional regions. If so, then the impairment in judging trustworthiness that we report would probably not be a disruption to face processing per se but rather, a disruption to the capacity to mentalize. Although this possibility has yet to be tested, we believe it is unlikely. First, we localized the posterior STS for each participant individually, on the basis of fMRI BOLD-response selectivity for faces, and the spatial resolution of TMS is quite high (approximately 1 cm for the coils used in the present study). Second, it is not obvious that evaluating the trustworthiness of someone from his or her face alone consists in attributing a mental state to that person, or even in assessing his or her intentions. In these circumstances, we believe it is more appropriate to describe the posterior STS's involvement in trustworthiness judgments as underpinning an assessment of the face's valence (Todorov, 2008), which does not involve the attribution of a mental state but provides information about the person behind the face (good/bad, approachable/unapproachable) that might feed in to an assessment of his or her intentions.

Conclusion

Our results suggest a degree of functional independence between the right OFA and the bilateral STS. The right OFA is critically involved in classifying the sex of faces and the posterior STS is involved in evaluating their trustworthiness. Our findings also suggest a possible but more circumscribed critical role for the right OFA in the evaluation of trustworthiness, perhaps at a processing stage subsequent to its initial role in feeding forward information to other face-processing regions such as the STS. Further work must be done to discover how these regions interact, fusing structural and expressive cues in order to enable us to extract and evaluate social information from faces. As well as the additional TMS and neuroimaging studies suggested above, this further work could involve testing people with lesions to the OFA or STS. For example, might Patient D. F., who has substantial lesions to bilateral inferior occipital cortex, and thus lacks the OFA (Steeves et al., 2006), be unable to discriminate the trustworthiness of faces? Or, given that the sex and trustworthiness of faces are not entirely independent dimensions, might D. F.'s judgments of trustworthiness be influenced by how masculine or feminine

the faces are? And might even her sex judgments be influenced by the trustworthiness of the faces?

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Reprint requests should be sent to Anthony P. Atkinson, Department of Psychology, Durham University, Science Laboratories, South Road, Durham, DH1 3LE, UK, or via e-mail: a.p.atkinson@durham.ac.uk.

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