# The Dorsomedial Prefrontal Cortex Plays a Causal Role in Integrating Social Impressions from Faces and Verbal Descriptions

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Several neuroimaging studies point to a key role of the dorsomedial prefrontal cortex (dmPFC) in the formation of socially relevant impressions. In 3 different experiments, participants were required to form socially relevant impressions about other individuals on the basis of text descriptions of their social behaviors, and to decide whether a face alone, a trait adjective (e.g., "selfish"), or a face presented with a trait adjective was consistent or inconsistent with the impression they had formed. Before deciding whether the target stimulus matched the impression they had previously formed, participants received transcranial magnetic stimulation (TMS) over the dmPFC, the inferior frontal gyrus (IFG, also implicated in social impression formation), or over a control site (vertex). Results from the 3 experiments converged in showing that interfering with dmPFC activity significantly delayed participants in responding whether a faceadjective pair was consistent with the impression they had formed. No effects of TMS were observed following stimulation of the IFG or when evaluations had to be made on faces or trait adjectives presented alone. Our findings critically extend previous neuroimaging evidence by indicating a causal role of the dmPFC in creating coherent impressions based on the integration of face and verbal description of social behaviors.

**Keywords:** dorsomedial prefrontal cortex, faces, impressions formation, inferior frontal gyrus, social inference, social traits, TMS

## Introduction

Human interactions are a source of extremely complex information that needs to be rapidly processed in order to meet the demands of the immediate social situation. Remarkably, individuals have developed the ability to draw inferences about other individuals' traits from minimal information (e.g., Ambady and Rosenthal 1993; Bar et al. 2006; Willis and Todorov 2006; Todorov et al. 2009). The process of forming impressions on others seems to occur automatically, as passive observation of another person's behavior is sufficient to trigger spontaneous inferences or coherent reactions about his/her traits (see Todorov and Uleman 2003; Van Duynslaeger et al. 2007; Uleman et al. 2008; Van der Cruyssen et al. 2009; de Gelder et al. 2011; Burra et al. 2013).

In the last decade, neuroimaging studies have deepened our understanding of the neural correlates of impression formation. These studies have identified a network of cortical and subcortical areas including the posterior cingulate cortex, the amygdala, the superior temporal sulcus, the inferior frontal gyrus, and the orbitofrontal cortex. In this network, the dorsomedial prefrontal cortex (dmPFC) seems to play a key role (e.g., Mitchell et al. 2004, 2005a, 2005b, 2005c, 2006; Schiller et al. 2009; Freeman et al. 2010; Baron et al. 2011; Cloutier, Kelley et al. 2011; Mende-Siedlecki et al. 2012). In fact, the medial PFC has been identified as a critical area in social cognition (for a review, see Amodio and Frith 2006) and, more specifically, in mentalizing about others' states (e.g., Fletcher et al. 1995; Stone et al. 1998; Gallagher et al. 2000).

With respect to social impressions formation, the dmPFC plays a role in the formation of impressions about both human and nonhuman agents (see Mitchell et al. 2005a, 2005b, 2005c; Mende-Siedlecki et al. 2012).

An interesting issue when considering the neural networks subtending impression formation has to do with the information one is confronted with when drawing a social inference. In particular, it has been suggested that the dmPFC would be preferentially activated when social inferences have to be drawn from verbal descriptions (adjective traits or descriptions of socially relevant behaviors) (see Kuzmanovic et al. 2012), but less so when inferences are drawn from nonverbal information like faces (but see Winston et al. 2002; Todorov and Engell 2008; Todorov et al. 2008; Mende-Siedlecki et al. 2012) or gestural behavior alone (Zaki et al. 2010; see also Kuzmanovic et al. 2012). Indeed, being simultaneously exposed to a face and a description of a socially relevant behavior elicits greater activation in the dmPFC than exposure to a face alone, suggesting that the role of the dmPFC in impression formation may be to integrate different sources of information (verbal descriptions and faces) (see Schiller et al. 2009; Baron et al. 2011; Mende-Siedlecki et al. 2012). This fits with the hypothesis that the dmPFC may represent an area of convergence between facial and behavioral information (Kim et al. 2004).

Despite wealth of neuroimaging evidence, no study has so far investigated whether the dmPFC plays a selective causal role in social impression formation. Patients' evidence suggests that bilateral damage to ventral sectors of the medial PFC may affect social/moral updating (e.g., Croft et al. 2010). However, patients' data are based on a limited number of cases, with high intersubjects variability in the size and etiology of the lesion. Brain stimulation may overcome these limitations by directly affecting—in a controlled and reversible way—neural activity in a targeted region, shedding light on the causal role of that region in mediating a particular function/behavior. In this study, we used transcranial magnetic stimulation (TMS) to directly investigate whether the dmPFC plays a causal role in the formation of social impressions. The main paradigm across the 3 experiments consisted in the presentation of 2 consecutive statements describing a person's positive (e.g., "He offered to help a neighbor fix a fence") or negative (e.g., "He criticized an old woman for being too slow") social behavior (in each trial, the 2 sentences were both of positive or negative valenced). Participants were instructed to generate a social impression about the person and to respond (depending on the experiment) whether a face, a trait adjective, or a face presented along with a trait adjective (adjective + face pair) was consistent with the social impression they had formed. TMS was delivered over either the dmPFC, the left IFG or over a control site (vertex). The IFG was chosen as a stimulation site in light of previous evidence showing that activity in this region is more responsive to social than to physical judgments of other individuals (see Mitchell et al. 2005a, 2005b). Two different sites of the dmPFC (one more posterior, Talairach y = 11, and one more anterior, y = 45) were targeted on the basis of neuroimaging results reported by Mitchell et al. (2005c) using a task similar to ours, and suggesting that both these sites were involved in social impression formation.

Results of the 3 experiments converge in pointing to a selective causal role of the dmPFC in deciding whether a face paired with a trait adjective matched the impression participants had previously formed about an agent. No effect of IFG stimulation was observed.

## **Experiment 1**

#### Materials and Methods

#### Participants

Twelve Italian students (3 males, mean age = 22.5 years, SD = 1.2) participated in the experiment. All participants were righthanded as assessed by a standard test (Oldfield 1971). Prior to the TMS experiment, each participant filled in a questionnaire (translated from Rossi et al. 2011) to evaluate compatibility with TMS. None of the participants reported neurological problems and history of seizures. None was taking medications that could interfere with neuronal excitability. Written informed consent was obtained from all participants before the experiment. The protocol was approved by the local ethical committee and participants were treated in accordance with the Declaration of Helsinki.

#### Stimuli

Experimental stimuli consisted of 60 young Caucasian male faces displayed in frontal pose and with a neutral expression, 120 written sentences, and 30 adjectives.

We created 60 experimental trials, each of them consisting of a face, 2 sentences and 1 adjective. Face stimuli were selected from a larger set of computer-generated faces (cf. http:// tlab.princeton.edu/databases/randomfaces/) for which rating scores (on a 9-point Likert scale) on different trait dimensions (including trustworthiness) are available (for details, see Oosterhof and Todorov 2008). From this set, we selected the 30 most-trustworthy (mean = 5.57, SD = 0.27) and the 30 leasttrustworthy (mean = 3.67, SD = 0.24) male faces.

Each face was associated with 2 declarative sentences referring to a social conduct. Sentences were taken and adapted to Italian from Mende-Siedlecki et al. (2012). Each sentence described how a person (of male gender only) behaved in a particular situation: Half of the sentences were positively valenced (e.g., "He helped an older man carry his luggage to his car") and half were negatively valenced (e.g., "He continually berated his wife in public"). More specifically, positively valenced sentences described a good/socially valuable behavior; negatively valenced sentences described a bad/socially questionable behavior. Negatively valenced sentences did not refer to extremely bad acts (such as murders, violence on children, etc.) but to moderately bad behaviors individuals could be confronted with in daily-life situations. Likewise, positively valenced sentences referred to "ordinary" positive behaviors (e.g., no heroic gestures).

Each untrustworthy face was paired with two negatively valenced sentences, and each trustworthy face with two positively valenced sentences. Positively and negatively valenced sentences were balanced with respect to sentence length (mean number of letters for positive sentences = 53.9, SD = 6.7; for negative sentences = 55.4, SD = 10.2,  $t_{(58)} < 1$ , P = 0.51). Thirty Italian adjectives were used, 15 positively and 15 negatively valenced. All the adjectives were selected from the Corpus CODIS of written Italian (http://corpora.dslo.unibo.it/coris\_ita. html): positive and negative adjectives were balanced for frequency (mean positive = 290.0, SD = 212.3; mean negative = 242.5, SD = 238.7; *t*-test on the log-transformed frequency:  $t_{(28)} < 1$ , P = 0.38) and word length (mean positive = 8.4, SD = 1.8; mean negative = 9.7, SD = 2.4;  $t_{(28)}$  = 1.31, P = 0.20). A pilot rating study (10 participants, 5 males, mean age = 25.5, SD = 2.2, none of which taking part in the TMS experiment) confirmed that negative and positive adjectives and sentences significantly differed for their social valence when evaluated on a 7-point Likert scale (1 = socially very negative; 7 = socially very positive): for adjective-traits,  $t_{(9)} = 21.56$ , P < 0.001 (mean for positive traits = 6.0, SD = 0.4, for negative traits = 1.7, SD = 0.3; Cronbach's  $\alpha = 0.99$ ); for sentences,  $t_{(9)} = 15.56$ , P < 0.001 (mean for socially negatively valenced sentences = 2.18, SD = 0.5; for positively valenced = 5.9, SD = 0.4; Cronbach's  $\alpha$  = 0.98).

Of the 60 trials presented in each experimental block, 30 consisted of pairs of positively valenced sentences and 30 of pairs of negatively valenced sentences. Half of the sentences (congruent trials) were followed by an adjective of the same valence (positive adjective following positive sentences; negative adjective following negative sentences) and half of the sentences (incongruent trials) were followed by an adjective of the opposite valence. Congruent and incongruent sentences were matched for length ( $t_{(58)} < 1.20$ , P = 0.24, mean number of characters for congruent sentences = 56.0; SD = 7.5; for incongruent sentences = 53.4; SD = 9.6). The same adjective was used twice in each experimental block: once in a congruent trial and once in an incongruent trial.

## Procedure

Participants were seated comfortably at a distance of 57 cm from a 17'' (1024 × 768 pixels resolution) TFT-LCD computer monitor and wore earplugs to minimize TMS click sound interference.

The timeline of an experiment trial is presented in Figure 1. As detailed below, sentences and trait- adjectives were always simultaneously presented with a face, in line with previous studies (e.g., Mitchell et al. 2005c, 2006; Schiller et al. 2009; Mende-Siedlecki et al. 2012; Gilron and Gutchess 2013). Each experimental block consisted of 60 trials. Each trial started



**Figure 1.** The timeline of an experimental trial in Experiment 1. A 10-Hz triple-pulse TMS was applied over the dmPFC (Talairach x = -7, y = 11, z = 59), the left IFG (Talairach x = -49, y = 17, z = 13) or over the vertex (control site).

with a fixation cross appearing in the middle of the screen for 1000 ms. This was followed by the presentation of a male face (measuring  $7 \times 7^{\circ}$  of visual angle) in the middle of the screen and a positively or negatively valenced sentence below it (black ink, 16- point Courier New) that fitted one line. Participants were instructed to form an impression of the person on the basis of the sentences (to be silently read). By pressing the space bar with their left hand, participants advanced to the second sentence, which was of the same valence as the previous one and with the same face centrally presented. Participants were instructed to form their impression about the person on the basis of this second sentence and then to press the space bar. In order to strengthen the formation of a consistent impression, high-trustworthy faces were always presented with positively valenced sentences and low-trustworthy faces with negatively valenced sentences. Reading of the 2 sentences was entirely self-paced, although participants were asked to be fast. TMS was given immediately after participants pressed the space bar following the reading of the second sentence (see details below). Next, (300 msec after disappearing of the second sentence) a positively or a negatively valenced adjective appeared below the face. Participants were instructed to indicate whether the adjective was consistent or inconsistent with the impression they formed about the person. Participants responded by pressing the left or right key using their right index and medium finger, respectively. They were instructed to be as accurate and fast as possible. Response key assignment was counterbalanced across participants.

The experiment consisted of one practice block and three experimental blocks, one for each TMS condition (dmPFC, IFG, vertex, see below). Within each experimental block, trial

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order was randomized for each participant. In the practice session, participants were first presented with all the sentences and adjectives in random order to familiarize with the stimuli used. Then, the experimental blocks were presented. The order of TMS sites was counterbalanced across participants.

#### Transcranial Magnetic Stimulation

Online neuronavigated TMS was performed with a Magstim Rapid<sup>2</sup> stimulator (Magstim Co., Ltd, Whitland, UK) connected to a 70-mm butterfly coil at a fixed intensity of 60% of the maximum stimulator output (e.g., Lewald et al. 2002; Campana et al. 2007). Triple-pulse TMS (10 Hz) was delivered after participants indicated that they had finished reading the second sentence. Accordingly, the first TMS pulse was given 200 ms before the onset of the adjective and the last pulse was immediately followed by the onset of the adjective. Targeted sites in different blocks were the dmPFC, the left IFG, and the vertex (control site). The vertex was localized as the point falling half the distance between the nasion and the inion on the same midline. The dmPFC and the left IFG were localized by means of stereotaxic navigation on individual estimated magnetic resonance images (MRI) obtained through a 3D warping procedure fitting a high-resolution MRI template with the participant's scalp model and craniometric points (Softaxic, EMS, Bologna, Italy). This procedure has been proven to ensure a global localization accuracy of about 5 mm, a level of precision closer to that obtained using individual MRI scans (Carducci and Brusco 2012). Anatomical Talairach coordinates (Talairach and Tournoux 1988) used for neuronavigation were obtained by converting MNI coordinates reported in a previous neuroimaging study on social impression formation (Mitchell et al.

2005c), and were x = -7, y = 11, z = 59 for the dmPFC (corresponding to the most dorsal peak of activation found by Mitchell et al. (2005c), when contrasting person-impression formation trials with other control experimental trials), and x = -49, y = 17, z = 13 for the left IFG. The coil was placed tangentially to the scalp with the handle pointing backward and held parallel to the midsagittal line in the vertex and dmPFC stimulation conditions, and pointing backward and rightward at a 45° angle from the midsagittal line in the left IFG condition.

## Results

A  $3 \times 2$  repeated-measures ANOVA with the within-subjects factors of TMS site (dmPFC, IFG, and vertex) and congruency (adjective congruent vs. incongruent with the previous sentences) was carried out on both accuracy scores and reaction time (RT) for correct responses.

## Accuracy

## Mean Accuracy for Experiment 1

Overall, participants consistently responded that the adjective matched/did not match the impression they had formed. In fact, accuracy was equal or over 94% in all the experimental conditions. The ANOVA revealed no significant main effect for either TMS (P = 0.09), congruency (P = 0.95), or the interaction TMS by congruency (P = 0.42) (mean accuracy for Experiment 1 is reported in Table 1).

#### RT (Correct Responses)

Figure 2 shows the mean response latencies for correct responses in the different TMS conditions. The ANOVA revealed a significant main effect of congruency,  $F_{1,11} = 14.63$ , P = 0.003,  $\eta_{\rm p}^2 = 0.57$ , indicating that participants took longer to respond to incongruent than congruent adjectives. The main effect of TMS was not significant (P=0.112). Most importantly, the interaction of TMS site by congruency was significant,  $F_{2,22} = 5.36$ , P=0.013,  $\eta_p^2=0.33$ . To clarify this interaction, we conducted an analysis of the simple effect of TMS for congruent and incongruent trials, separately. TMS did not affect RT in incongruent trials (P = 0.204). However, TMS had a significant impact on congruent trials, slowing down responses,  $F_{2,22} = 4.10$ , P = 0.031,  $\eta_p^2 = 0.27$ . Post hoc comparisons (Bonferroni–Holm correction applied) showed that dmPFC TMS delayed responses compared with vertex TMS,  $t_{(11)} = 3.56$ , P = 0.012, and to IFG TMS,  $t_{(11)} = 2.57$ , P = 0.052 (in this case, the difference approached significance, without correction: P = 0.026). The effects of IFG and vertex TMS were not significantly different from each other (P = 0.78).

## Experiment 2

In Experiment 1, TMS over the dmPFC significantly interfered with participants' decisions about the congruency of adjectives

## Table 1

Mean participants' accuracy ( $\pm \text{SEM})$  in congruent and incongruent conditions of Experiment 1, as a function of TMS

	Congruent	Incongruent
Vertex	94.4 (3.2)	95.3 (1.9)
dmPFC	97.8 (1.2)	96.2 (1.1)
IFG	93.9 (2.8)	94.3 (1.4)

with the social impressions they had previously formed. However, following previous studies (e.g., Mitchell et al. 2005c, 2006; Schiller et al. 2009; Mende-Siedlecki et al. 2012; Gilron and Gutchess 2013), in Experiment 1, both the sentences describing an individual's behavior and the final adjective were simultaneously presented with a face (i.e., in each trial, the same face appeared 3 times: with Sentence 1, with Sentence 2, and with the adjective). Thus, it is unclear whether the interference on social judgments we induced by stimulating the dmPFC was specific for the integration of a face with a verbal description of that person's social behavior, or it would have occurred also in case of a verbal description alone or a face alone. Experiment 2 was carried out to clarify this issue. In particular, as in Experiment 1, participants were required to read 2 statements describing a person's social behavior, but this time verbal descriptions were presented alone (i.e., with no face accompanying the description). According to the specific experimental condition, after reading the two sentences, participants had to decide whether: 1) an adjective presented with a face (as in Experiment 1), 2) an adjective alone, or 3) a face alone, matched the previously read descriptions.

## Materials and Methods

## Participants

Fourteen right-handed Italian students (2 males, mean age = 24.3 years, SD = 4.0) took part in the experiment. None of them had participated in Experiment 1. Inclusion criteria were the same as for Experiment 1.

## Stimuli, Procedure, and TMS

Stimuli (faces, adjectives, and statements describing a social behavior) were identical to those used in Experiment 1. The experiment consisted of 3 different blocks (1 per experimental condition) of 60 trials each. As in Experiment 1, each trial started with the self-paced reading of 2 text sentences describing a person's social behavior but, different from Experiment 1, no face was presented with the text descriptions (see Fig. 3 for the timeline of an experimental trial). After reading of the sentences, participants had to decide whether a target stimulus





**Figure 3.** The timeline of an experimental trial in Experiments 2 and 3. As in Experiment 1, participants were presented with 2 sentences describing positive or negative social behaviors but this time text descriptions were not accompanied by a face. Participants were asked to decide whether a face (only in Experiment 2), an adjective, or an adjective + face pair matches the impression they had formed. In Experiment 2, a 10 Hz triple-pulse TMS was delivered over the dmPFC (x = -7, y = 11, z = 59) and the vertex. In Experiment 3, TMS was delivered over a more anterior region of the dmPFC (x = -10, y = 45, z = 41), the left IFG (x = -49, y = 17, z = 13), and the vertex.

matched the social impression they had formed of that person. Depending on the experimental condition, the target stimulus consisted of: 1) a face paired with an adjective (adjective + face trials), in which the face was always consistent with the adjective (i.e., high-trustworthy faces were only presented with positively valenced adjectives, and low-trustworthy faces were only presented with negatively valenced adjectives); 2) an adjective alone (adjective-only trials); 3) a face alone (face-only trials). Within each block, in half of the trials the target stimulus was congruent with the text description, and in the other half incongruent. TMS was delivered as in Experiment 1; stimulation was given on the dmPFC and on the vertex as a control site. Participants performed the 3 experimental blocks consecutively for each of the 2 stimulation sites. The order of presentation of the 3 blocks and the order of the TMS sites stimulation was counterbalanced across participants.

## Results

Analyses were carried out as in Experiment 1. Data of one participant were excluded due to extremely long response latencies, exceeding the group mean of more than 2 SD. A repeated-measures ANOVA with experimental condition (adjective + face, adjective, face), TMS site (dmPFC vs. vertex) and congruency (congruent vs. incongruent) was performed on both accuracy scores and correct RT.

#### Accuracy

## Mean Response Accuracies for Experiment 2

The ANOVA revealed a significant main effect of congruency,  $F_{1,12} = 7.27$ , P = 0.019,  $\eta_p^2 = 0.38$ , as accuracy was overall higher

in congruent than incongruent trials (mean response accuracies for Experiment 2 are reported in Table 2). The main effect of condition,  $F_{2,24}=93.26$ , P < 0.001,  $\eta_p^2 = 0.89$ , and the main effect of TMS,  $F_{1,12}=6.71$ , P = 0.024,  $\eta_p^2 = 0.36$ , were both significant. None of the possible interactions reached significance (all Ps > 0.41). The main effect of experimental condition was due to accuracy being significantly lower in the face-only condition compared with the adjective-only condition,  $t_{(12)} = 11.51$ , P < 0.001, and the adjective + face condition,  $t_{(12)} = 10.49$ , P < 0.001. The adjective-only and the adjective + face condition did not significantly differ from each other (P =0.77). Accuracy was overall greater in congruent than incongruent trials. The significant effect of TMS was due to accuracy being overall slightly lower (1.8% less) for dmPFC compared with vertex stimulation.

## RT (Correct Responses)

Figure 4 shows mean participants' RT (for correct responses only). The ANOVA revealed a significant main effect of congruency,  $F_{1,12} = 28.24$ , P < 0.001,  $\eta_p^2 = 0.70$ , reflecting faster responses in congruent than incongruent trials. This rules out a possible interpretation of our results in terms of speed/accuracy trade-off, as responses to congruent trials were faster as well as more accurate than responses to incongruent trials. Neither the main effect of experimental condition (P = 0.12) nor the main effect of TMS (P = 0.96) reached significance. None of the two-ways interactions reached significance (all Ps> 0.28). The three-way interaction of experimental condition × congruency × TMS was significant,  $F_{2,24} = 3.47$ , P = 0.048,  $\eta_p^2$ = 0.22. The significant three-way interaction was further

Mean participants' accuracy (±SEM) in congruent and incongruent conditions of Experiment 2, as a function of TMS and experimental condition

	Adjective + face		Adjective		Face	
	Congruent	Incongruent	Congruent	Incongruent	Congruent	Incongruent
Vertex dmPFC	93.4 (2.1) 92.2 (1.9)	90.9 (3.0) 87.9 (3.5)	94.4 (1.7) 91.2 (3.1)	89.9 (3.5) 90.6 (2.9)	73.5 (5.4) 67.6 (4.0)	72.2 (4.4) 64.2 (3.7)

investigated by looking at the simple main effect of congruency and TMS (via repeated-measures ANOVA) within each experimental condition.

For the adjective + face condition, the ANOVA revealed a significant effect of congruency,  $F_{1,12} = 12.93$ , P = 0.004,  $\eta_p^2 =$ 0.52, no significant effect of TMS (P = 0.51) and a significant interaction congruency × TMS,  $F_{1,12} = 7.35$ , P = 0.019,  $\eta_p^2 =$ 0.38. Post hoc comparisons (Bonferroni-Holm correction applied) indicated that RT were comparable in incongruent trials for dmPFC and vertex TMS,  $t_{(12)} < 1$ , P = 0.75, whereas dmPFC TMS slowed down participants' responses in congruent trials compared with vertex TMS,  $t_{(12)} = 2.47$ , P = 0.058(without correction: P = 0.029). For the adjective-only condition, the ANOVA only revealed a significant effect of congruency,  $F_{1,12} = 8.45$ , P = 0.013,  $\eta_p^2 = 0.41$ , whereas neither the main effect of TMS (P = 0.67) nor the interaction TMS by congruency (P = 0.23), reached significance. A similar pattern was reported in the face-only condition: The ANOVA again revealed no significant main effect of TMS (P = 0.79) and no significant interaction congruency by TMS (P = 0.24), whereas the main effect of congruency this time only approached significance,  $F_{1,12} = 4.20, P = 0.063, \eta_p^2 = 0.23.$ 

## **Experiment 3**

In 2 meta-analyses clarifying the location and function of brain areas involved in social cognition, Van Overwalle (2009, 2011) suggested that the mPFC comprised between 30 and 60 mm (posterior-anterior axis) likely represents the "core" area for social cognition (mediating trait inferences on self and others), whereas the more posterior part of the medial frontal cortex, located between the 0 and 30 mm y-coordinate, would be mainly involved in conflict monitoring. Although, as acknowledged by Van Overwalle, these borders should not be taken too strictly, most of the neuroimaging studies reviewed by Van Overwalle (2009, 2011) are consistent with this subdivision. In Experiments 1 and 2, the targeted dmPFC site fell in the posterior dmPFC (y = 11). That site was chosen because it corresponded to the most dorsal peak of activation observed in the fMRI study by Mitchell et al. (2005c) when confronting activation associated to person-impression formation trials with other control conditions (requiring either to form impressions about objects or to memorize order of given statements about a person's behavior). The selective effect of dmPFC TMS on adjective + face trials in Experiment 2 rules out the possibility that stimulation was interfering with unspecific error monitoring mechanisms. However, to further control for this possibility, in Experiment 3, we applied TMS over a more anterior region of the dmPFC (y = 45) falling within the sector of the dmPFC assumed to be specifically involved in social reasoning (and less in conflict monitoring, see Van Overwalle 2009, 2011). The left IFG was also stimulated as in Experiment 1. We used the same paradigm of Experiment 2, but the face-only-condition



**Figure 4.** Mean participants' correct response latencies in milliseconds as a function of trial type (congruent vs. incongruent), TMS site (dmPFC and vertex), and experimental condition (adjective + face, adjective-only, face-only). The adjective + face condition (but not in the other conditions) dmPFC TMS significantly delayed responses compared with vertex stimulation in congruent trials. Error bars represent  $\pm 1$  SEM. (\*P < 0.05 uncorrected and <0.06 with Bonferroni–Holm).

was not included this time. In fact, results of Experiment 2 showed that participants were quite inconsistent in evaluating whether faces presented alone matched the social impression they had formed. Indeed, before deciding to definitely exclude this condition from Experiment 3, we asked a new group of 9 participants (not taking part in any of the TMS experiments) to evaluate the trustworthiness of all the faces used on a 1-7 Likert scale (1="not trustworthy at all"; 7="very trustworthy"). The resulting Cronbach's  $\alpha$  was equal to 0.53, indicating a suboptimal level of reliability. Additionally, we also carried out a further control experiment (see the Supplementary Material) in which participants had to decide about face trustworthiness (with no verbal description provided) while receiving stimulation over the dmPFC (x = -7, y = 11, z=59, as in Experiments 1 and 2) or over a control site (vertex). Interfering with dmPFC activity while evaluating trustworthiness of faces not preceded or accompanied by any verbal description did not affect participants' judgments.

#### Materials and Methods

#### Participants

Fifteen right-handed Italian students (5 males, mean age = 23.3 years, SD = 2.0) took part in the experiment (none of them had participated in either Experiment 1 or 2). Inclusion criteria were the same as those of Experiment 1.

#### Stimuli, Procedure, and TMS

The experimental paradigm was identical to Experiment 2, with the exception that the face-only condition was not included. TMS was delivered over the left IFG (x = -49, y = 17, z = 13, as in Experiment 1), the vertex (control), and over a site of the dmPFC (x = -10, y = 45, z = 41) corresponding to the center of activation in the region of interest reported by Mitchell et al. (2005c) when contrasting person-impression formation trials with all the other control conditions. Parameters and timing of TMS were the same as those of Experiment 2.

## Results

A repeated-measures ANOVA with experimental condition (adjective + face vs. adjective), TMS site (dmPFC, IFG, and vertex) and congruency (congruent vs. incongruent) was performed on both accuracy scores and correct RT.

#### Accuracy

*Mean Accuracies for Experiment 3.* The ANOVA revealed no significant main effects of either condition (P = 0.807), TMS site (P = 0.600) or congruency (P = 0.720). None of the possible interactions reached significance (all Ps > 0.29) (mean accuracies for Experiment 3 are reported in Table 3).

## RT (Correct Responses)

Mean correct RT are presented in Figure 5. The ANOVA showed a significant main effect of congruency,  $F_{1,14} = 39.05$ , P < 0.001,  $\eta_p^2 = 0.74$ , reflecting faster responses in congruent than incongruent trials. The effect of experimental condition was significant,  $F_{1,14} = 5.23$ , P = 0.038,  $\eta_p^2 = 0.27$ , indicating faster responses to adjectives than to face-adjective pairs. The main effect of TMS did not reach significance (P = 0.53). None of the two-ways interactions was significant (all Ps > 0.20). The threeway interaction of experimental condition × congruency × TMS was significant,  $F_{2,28} = 3.39$ , P = 0.048,  $\eta_p^2 = 0.19$ .

An analysis of the simple main effects of congruency and TMS within the adjective-only condition revealed a significant effect of congruency,  $F_{1,14} = 23.54$ , P = 0.001,  $\eta_p^2 = 0.63$ ; neither the main effect of TMS (P = 0.124) nor the interaction congruency × TMS (P = 0.475) were significant.

For the adjective + face condition, the analysis revealed a significant effect of congruency,  $F_{1,14} = 19.00$ , P = 0.001,  $\eta_p^2 = 0.58$ , no significant effect of TMS (P = 0.78) and a significant interaction congruency × TMS,  $F_{2,28} = 3.69$ , P = 0.038,  $\eta_p^2 = 0.21$ . Although none of the post hoc comparisons reached significance (all Ps > 0.05), the pattern behind the significant interaction (see Fig. 5) resembled that observed in Experiments 1 and 2: in particular, dmPFC TMS tended to selectively delay participants' responses in congruent trials compared with the other TMS conditions.

## Discussion

In 3 studies, we asked participants to form impressions about socially relevant traits of other individuals by reading descriptions of their behavior and then to decide whether a target stimulus (a face, an adjective, or a face-adjective pair) matched the impression they had formed. In line with previous behavioral evidence, participants took longer to respond when they had to match inconsistent than consistent adjectives with their impressions (e.g., see also Mitchell et al. 2002; Siebörger et al. 2007; Kim et al. 2012; Ma, Baetens, Vandekerckhove, Kestemont et al. 2014). Overall, TMS delivered over the dmPFC

Table 3

Mean participants' accuracy ( $\pm$ SEM) in congruent and incongruent trials of Experiment 3, as a function of TMS and experimental condition

	Adjective + fac	е	Adjective		
	Congruent	Incongruent	Congruent	Incongruent	
Vertex dmPFC IFG	94.5 (1.7) 95.7 (1.4) 94.5 (1.5)	94.3 (1.5) 94.3 (2.0) 96.5 (0.9)	95.9 (1.0) 95.4 (1.6) 95.4 (1.2)	93.5 (2.5) 94.3 (1.4) 96.6 (0.7)	

(both over a posterior, y = 11, and a more central site, y = 45) significantly delayed participants' trait inferences, but only when social inferences had to be drawn on trait adjectives presented together with a face (Experiments 1, 2, and 3) and only in congruent conditions. When faces alone or trait adjectives alone (Experiments 2 and 3) had to be evaluated in the light of previously read descriptions of positive or negative social conducts, no effect of dmPFC TMS was observed. Finally, interfering with the activity of the IFG had no effect on participants' socially relevant judgments (Experiments 1 and 3).

Our finding of a disruptive effect of TMS on the dmPFC during a task implying social judgments is in line with previous neuroimaging and patients' evidence showing that this region is selectively implicated in social impression formation (e.g., Mitchell et al. 2004, 2005a, 2005b, 2005c, 2006; Croft et al. 2010; Mende-Siedlecki et al. 2012; Ma, Baetens, Vandekerckhove, Van der Cruyssen et al. 2013). Our data significantly extend these previous findings showing that the dmPFC is not only implicated, but plays a causal role in such processes, at least when individuals have to decide whether a face paired with a trait description matches the impression they had formed about that agent. In fact, interfering with dmPFC activity did not affect responses to faces or trait adjectives when these were presented alone. Moreover, TMS over the dmPFC selectively delayed responses in congruent trials (i.e., trials in which the trait adjective was consistent with the impression formed about an individual). According to state-dependency accounts (Silvanto et al. 2008), the effects of TMS are dependent on the activation state of the stimulated neural populations. Activation states can be manipulated prior to TMS via adaptation or priming (see Silvanto et al. 2008). Our paradigm was not specifically conceived to induce adaptation or priming effects, yet our participants did respond to congruent information faster than to incongruent information, effectively showing a priming effect. Prior neuroimaging studies reported greater activation in the dmPFC in response to targets that were inconsistent with specific traits they had been previously associated with (e.g., Cloutier, Gabrieli et al. 2011; Ma et al. 2011; Mende-Siedlecki et al. 2012). In turn, using ERP, Van Duynslaeger et al. (2007) found that the mPFC was most strongly activated when the behavioral information was



**Figure 5.** Mean participants' correct response latencies in milliseconds as a function of trial type (congruent vs. incongruent), TMS site (dmPFC, vertex, and IFG), and experimental condition (adjective + face and adjective-only). Error bars represent  $\pm 1$  SEM.

consistent than inconsistent with previously read socially relevant trait descriptions. Combining fMRI adaptation with a task requiring to infer traits of others via reading behavioral statements preceded by sentences involving the same trait, an opposite trait or trait-irrelevant information, Ma, Baetens, Vandekerckhove, Kestemont et al. (2014) found similar adaptation effects in the mPFC for similar and opposite-trait conditions. Whether congruent information was accompanied by increased or decreased activation in the dmPFC cannot be determined on the basis of our results. Nonetheless, our results appear in line with prior priming-TMS studies reporting selective effects of TMS on congruent (cued) trials (see Campana et al. 2002; Silvanto et al. 2010; Mattavelli et al. 2011).

The lack of dmPFC stimulation effects (Experiments 2 and 3) in deciding whether an adjective trait presented alone (i.e., with no face) matched or not the impression one has created reading description of socially relevant conducts may be explained by the nature of the cognitive operation required. If reading the description of a social behavior induces the formation of an impression in quite an automatic way (Todorov and Uleman 2003), deciding whether an adjective matches or not such information may be based on a semantic inference that does not strictly involve social mentalizing regions but is likely mediated by a broader cortical network (e.g., Mason and Just 2004). Accordingly, there was a clear trend for faster responses in adjective-only trials compared with the other trials, indicating that different processes were at play. Indeed, it has been recently reported that bilateral ventromedial PFC damage does not impair cohesion and coherence in spoken discourse (Kurczek and Duff 2012). The presence of a face seems hence to be necessary for dmPFC TMS to significantly affect social traits inference. Nonetheless, when participants had to decide whether a face alone matched or did not match the impressions they had formed by reading descriptive statements, TMS did not significantly affect response latencies (Experiment 2). However, this null result needs to be interpreted with caution, given the high intersubjects variability in deciding about the trustworthiness of the faces used (as assessed by an additional behavioral control experiment).

In the adjective + face trials, the trait adjective was more predictive than the face in driving the inferential process (see also Schwarz et al. 2013), as suggested by the higher accuracy in adjective + face compared with face-only trials. Nonetheless, the presence of a face was not irrelevant for the final decision. Indeed, participants did pay attention to the face, as suggested by longer RT in adjective + face conditions than adjective-only conditions. Evaluating the face together with the trait adjective seems to have activated more the mentalizing network of which the dmPFC is part (see also Schwarz et al. 2013). This finding is in line with previous neuroimaging evidence indicating that responses in the dmPFC during impression formation are stronger for faces presented with verbal descriptions than for faces alone (Schiller et al. 2009; Mende-Siedlecki et al. 2012) and are in line with the hypothesis that the dmPFC may function as a convergence zone for face and behavioral information (Kim et al. 2004). Results of an additional experiment (reported in the Supplementary Material) corroborated this view by showing that dmPFC TMS did not affect participants' judgments about trustworthiness of faces when these were not preceded or accompanied by any verbal description.

Accuracies were overall very high across the 3 experiments (except for the face-only trials of Experiment 2, as already discussed above). In light of this, it is not surprising that we did not find reliable effects of TMS on accuracy scores. In fact, when accuracies are near ceiling, TMS may be unable to affect them, the effects of stimulation being more evident on RTs (see also Devlin and Watkins 2008). Accordingly, we only observed effects of TMS on accuracy scores in Experiment 2, where TMS over the dmPFC overall reduced accuracy compared with the baseline control (vertex) condition, supporting a role of this region in mediating social inferences.

Critically, we found no evidence for a role of the left inferior frontal gyrus in processing of either socially relevant or socially irrelevant information (Experiments 1 and 3). Using fMRI, Mitchell et al. (2005c) found BOLD increase not only in the dmPFC, but also in the left IFG (corresponding to the region we stimulated), when participants had to form social impressions about other individuals compared with forming an impression about an object or remembering the order of a series of socially relevant or irrelevant statements (note that no explicit response was required to participants in Mitchell et al. (2005c)). However, in a fMRI adaptation study (Ma, Baetens, Vandekerckhove, Kestemont et al. 2014) in which a task similar to ours was used and that required to make an explicit decision on whether a trait was consistent or inconsistent with a social trait to be inferred, adaptation effects were reported solely in the medial sector of the prefrontal cortex, with no evidence for specific involvement of dorsolateral sector (dlPFC). Accordingly, meta-analysis and review studies suggest that the type of social information that is mainly processed in the lateral sectors of the prefrontal cortex is typically linked to body movements (e.g., observed expressions or actions in others, see Avenanti, Candidi et al. 2013; de Gelder 2006; Van Overwalle and Baetens 2009; Urgesi et al. 2014). On the other hand, the experimental task we adopted required participants to make social decisions based on the coupling of relatively abstract verbal material with visual representations of static facial features. The fact that IFG does not appear to play a critical role in the task at hands is thus in line with this literature. Still, the left dlPFC has been found to be relevant in inhibiting inappropriate (social) responses as stereotyping (e.g., Richeson and Shelton 2003; Payne 2005; Knutson and Bossaerts 2007; Cattaneo et al. 2011; Cloutier, Gabrieli et al. 2011) and in detecting inconsistencies in the information flow regarding social aspects (Ma et al. 2011; Mende-Siedlecki et al. 2012). In these latter studies though, the role of the dlPFC seems not to be as specific for the social domain as that of the dmPFC, but rather to be related to a more general role of the dlPFC in exerting cognitive control over ongoing processes (e.g., Koechlin et al. 2003; Braver et al. 2009). Finally, it is possible that the region we stimulated was too inferior and too posterior, with previous studies finding a role of more rostral sectors of the dlPFC in updating social impressions (Mende-Siedlecki et al. 2012) or more superior sectors in inferring social traits (see Ma et al. 2011). In this regard, it is also important to stress that we stimulated before the onset of the adjective on which participants' response had to be based, likely interfering more with impression consolidation than with the detection of possible inconsistencies in the information flow.

Importantly, we found TMS to interfere with participants' responses both when TMS was delivered over a more posterior site of the dmPFC (Talairach y = 11, Experiments 1 and 2) and when it was delivered over a more central site (Talairach y=45, Experiment 3). This finding is in line with previous neuroimaging evidence pointing to an extensive region of dorsal mPFC in mediating social impression formation (see Mitchell et al. 2005c). The medial prefrontal cortex is a key node of the mentalizing system, which is preferentially activated when behavior that enables inferences to be made about goals, beliefs or moral issues is presented in abstract terms (Van Overwalle and Baetens 2009). Still, a further subdivision of functions may exist within the dmPFC. In particular, Van Overwalle (2009, 2011) suggested that the mPFC comprised between 30 and 60 mm (posterior-anterior axis) mainly mediates trait inferences on self and others, whereas more posterior sectors (0 > y < 30 mm, also including what is known as the)dorsal or caudal part of the cingulate cortex) would be mainly involved in error monitoring. According to Van Overwalle (2011) though, this subdivision should not be taken too strictly and may vary depending on the specific task used. Indeed, our task is likely to have involved different functions, ranging from mentalizing to detection of violation of expectation (error monitoring), thus interesting extensive sectors of the dmPFC. Accordingly, if stimulation of the more posterior site in the dmPFC only affected conflict monitoring, trials in which adjective alone had to be matched with previously read statements should have also been affected, whereas this was not the case.

In considering our results, it is worth noting that TMS can modulate activity not only in the neurons under the coil but also in interconnected regions (e.g., Siebner et al. 2009; Avenanti, Annella et al. 2013). Accordingly, although we specifically targeted the dmPFC, we cannot exclude that our effects also depended on stimulation indirectly affecting other cortical or subcortical sectors of the network mediating social inferences, such as the amygdala or the orbitofrontal cortex. Moreover, in our paradigm, the 2 sentences describing social conducts in each trial had always the same valence (i.e., positive-positive or negative-negative). In this respect, the task did not properly require updating of social impressions, but formation of a social impression (via reading of 2 same-valence sentences) to be matched with a target stimulus (i.e., a face, a trait adjective or a face-adjective trait). Future studies may assess whether TMS over the dmPFC affects updating of social impressions by presenting participants with both valence-congruent and valence-incongruent consecutive sentences.

Finally, our results on dmPFC fit with previous TMS studies reporting a role of the dmPFC in aspects of social cognition such as stereotyping (Cattaneo et al. 2011), affective theory of mind processing (e.g., Krause et al. 2012) or processing of others' emotions (e.g., Mattavelli et al. 2011; Balconi and Canavesio 2013). These findings converge in showing that the mPFC may work as a common substrate in creating (long-term memory) associations between behaviors, appearance, and personality traits to which we are likely to (automatically) refer when forming a social impression. In an evolutionary perspective, these associations help us generating predictions about others' behavior (e.g., Hassabis et al. 2013).

In sum, our study provides evidence for a causal role of the dmPFC in forming social-relevant impressions, contributing to a better understanding of the role of this region in social cognition.

## **Supplementary Material**

Supplementary material can be found at: http://www.cercor.oxford journals.org/.

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## Notes

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## References

- Ambady N, Rosenthal R. 1993. Half a minute: predicting teacher evaluations from thin slices of nonverbal behavior and physical attractiveness. J Pers Soc Psychol. 64:431.
- Amodio DM, Frith CD. 2006. Meeting of minds: the medial frontal cortex and social cognition. Nat Rev Neurosci. 7:268–277.
- Avenanti A, Annella L, Candidi M, Urgesi C, Aglioti SM. 2013. Compensatory plasticity in the action observation network: virtual lesions of STS enhance anticipatory simulation of seen actions. Cereb Cortex. 23:570–580.
- Avenanti A, Candidi M, Urgesi C. 2013. Vicarious motor activation during action perception: beyond correlational evidence. Front Hum Neurosci. 7:185.
- Balconi M, Canavesio Y. 2013. High-frequency rTMS improves facial mimicry and detection responses in an empathic emotional task. Neuroscience. 236:12–20.
- Bar M, Neta M, Linz H. 2006. Very first impressions. Emotion. 6:269–278.
- Baron SG, Gobbini MI, Engell AD, Todorov A. 2011. Amygdala and dorsomedial prefrontal cortex responses to appearance-based and behavior-based person impressions. Soc Cogn Affect Neurosci. 6:572–581.
- Braver TS, Paxton JL, Locke HS, Barch DM. 2009. Flexible neural mechanisms of cognitive control within human prefrontal cortex. Proc Natl Acad Sci USA. 106:7351–7356.
- Burra N, Hervais-Adelman A, Kerzel D, Tamietto M, de Gelder B, Pegna AJ. 2013. Amygdala activation for eye contact despite complete cortical blindness. J Neurosci. 33:10483–10489.
- Campana G, Cowey A, Casco C, Ousen I, Walsh V. 2007. Left frontal eye field remembers "where" but not "what". Neuropsychologia. 45:2340–2345.
- Campana G, Cowey A, Walsh V. 2002. Priming of motion direction and area V5/MT: a test of perceptual memory. Cereb Cortex. 1:663–669.
- Carducci F, Brusco R. 2012. Accuracy of an individualized MR-based head model for navigated brain stimulation. Psychiatry Res. 203:105–108.
- Cattaneo Z, Mattavelli G, Platani E, Papagno C. 2011. The role of the prefrontal cortex in controlling gender-stereotypical associations: a TMS investigation. Neuroimage. 56:1839–1846.
- Cloutier J, Gabrieli JDE, O'Young D, Ambady N. 2011. An fMRI study of violations of social expectations: when people are not who we expect them to be. Neuroimage. 57:583–588.
- Cloutier J, Kelley WM, Heatherton TF. 2011. The influence of perceptual and knowledge-based familiarity on the neural substrates of face perception. Soc Neurosci. 6:63–75.
- Croft KE, Duff MC, Kovach CK, Anderson SW, Adolphs R, Tranel D. 2010. Detestable or Marvelous? Neuroanatomical correlates of character judgments. Neuropsychologia. 48:1789–1801.
- de Gelder B. 2006. Towards the neurobiology of emotional body language. Nat Rev Neurosci. 7:242–249.
- de Gelder B, Van Honk J, Tamietto M. 2011. Emotion in the brain: of low roads, high roads and roads less travelled. Nat Rev Neurosci. 12:425.
- Devlin JT, Watkins KE. 2008. Investigating language organization with TMS. In: Wassermann E, Epstein C, Ziemann U, Walsh V, Paus T, Lisanby S, editors. The Oxford Handbook of Transcranial Stimulation. Oxford, NY: Oxford University Press. p. 479–499.
- Fletcher PC, Happé F, Frith U, Backer SC, Dolan RJ. 1995. Other minds in the brain: a functional imaging study of 'theory of mind' in story comprehension. Cognition. 57:109–128.

- Freeman JB, Schiller D, Rule NO, Ambady N. 2010. The neural origins of superficial and individuated judgments about ingroup and outgroup members. Hum Brain Mapp. 31:150–159.
- Gallagher HL, Happé F, Frunswick N, Fletcher PC, Frith U, Frith CD. 2000. Reading the mind in cartoons and stories: an fMRI study of 'theory of mind' in verbal and nonverbal tasks. Neuropsychologia. 38:11–21.
- Gilron R, Gutchess AH. 2013. Remembering first impression: effect of intentionality and diagnosticity on subsequent memory. Cogn Affect Behav Neurosci. 12:85–98.
- Hassabis D, Spreng RN, Rusu A, Robbins C, Mar R, Schacter DL. 2013. Imagine all the people: how the brain creates and uses personality models to predict behavior. Cereb Cortex. 24:1979–1987.
- Kim H, Somerville LH, Johnstone T, Andrew SP, Alexander L, Shin LM, Whalen PJ. 2004. Contextual modulation of amygdala responsivity to surprised faces. J Cogn Neurosci. 16:1730–1745.
- Kim S, Yoon M, Kim W, Lee S, Kang E. 2012. Neural correlates of bridging inferences and coherence processing. J Psycholinguist Res. 41:311–321.
- Knutson B, Bossaerts P. 2007. Neural antecedents of financial decisions. J Neurosci. 27:8174–8177.
- Koechlin E, Ody C, Kouneiher F. 2003. The architecture of cognitive control in the human prefrontal cortex. Science. 302:1181–1185.
- Krause L, Enticott PG, Zangen A, Fitzgerald PB. 2012. The role of medial prefrontal cortex in theory of mind: a deep rTMS study. Behav Brain Res. 228:87–90.
- Kurczek J, Duff MC. 2012. Intact discourse cohesion and coherence following bilateral ventromedial prefrontal cortex. Brain Lang. 123:222–227.
- Kuzmanovic B, Bente G, von Cramon DY, Schilbach L, Tittgemeyer M, Vogeley K. 2012. Imaging first impressions: distinct neural processing of verbal and nonverbal social information. Neuroimage. 60:179–188.
- Lewald J, Foltys H, Töpper R. 2002. Role of the posterior parietal cortex in spatial hearing. J Neurosci. 22:RC207.
- Ma N, Baetens K, Vandekerckhove M, Kestemont J, Fias W, Van Overwalle F. 2014. Traits are represented in the medial Prefrontal Cortex: an fMRI adaptation study. Soc Cogn Affect Neurosci. 9(8):1185–1192.
- Ma N, Baetens K, Vandekerckhove M, Van der Cruyssen L, Van Overwalle F. 2013. Dissociation of a trait and a valence representation in the mPFC. Soc Cogn Affect Neurosci. doi:10.1093/scan/nst143.
- Ma N, Vandekerckhove M, Van Overwalle F, Seurinck R, Fias W. 2011. Spontaneous and intentional trait inferences recruit a common mentalizing network to a different degree: spontaneous inferences activate only its core areas. Soc Neurosci. 6:123–138.
- Mason RA, Just MA. 2004. How the brain processes causal inferences in text: a theoretical account of generation and integration component processes utilizing both cerebral hemispheres. Psychol Sci. 15:1–7.
- Mattavelli G, Cattaneo Z, Papagno C. 2011. Transcranial magnetic stimulation of medial prefrontal cortex modulates face expressions processing in a priming task. Neuropsychologia. 49:992–998.
- Mende-Siedlecki P, Cai Y, Todorov A. 2012. The neural dynamics of updating person impressions. Soc Cogn Affect Neurosci. 8:623–631.
- Mitchell JP, Banaji MR, Macrae CN. 2005a. General and specific contributions of the medial prefrontal cortex to knowledge about mental states. Neuroimage. 28:757–762.
- Mitchell JP, Banaji MR, Macrae CN. 2005b. The link between social cognition and self-referential thought in the medial prefrontal cortex. J Cogn Neurosci. 17:1306–1315.
- Mitchell JP, Cloutier J, Banaji MR, Macrae CN. 2006. Medial prefrontal dissociations during processing of trait diagnostic and nondiagnostic person information. Soc Cogn Affect Neurosci. 1:49–55.
- Mitchell JP, Heatherton TF, Macrae CN. 2002. Distinct neural systems subserve person and object knowledge. Proc Natl Acad Sci USA. 99:15238–15243.
- Mitchell JP, Macrae CN, Banaji MR. 2004. Encoding-specific effects of social cognition on the neural correlates of subsequent memory. J Neurosci. 24:4912–49127.
- Mitchell JP, Macrae CN, Banaji MR. 2005c. Forming impressions of people versus inanimate objects: social-cognitive processing in the medial prefrontal cortex. Neuroimage. 26:251–257.

- Oldfield RC. 1971. The assessment and analysis of handedness: the Edinburgh inventory. Neuropsychologia. 9:97–113.
- Oosterhof NN, Todorov A. 2008. The functional basis of face evaluation. Proc Nati Acad Sci USA. 105(32):11087–11092.
- Payne BK. 2005. Conceptualizing control in social cognition: how executive functioning modulates the expression of automatic stereotyping. J Pers Soc Psychol. 89:488–503.
- Richeson JA, Shelton JN. 2003. When prejudice does not pay effects of interracial contact on executive function. Psychol Sci. 14:287–290.
- Rossi S, Hallett M, Rossini PM, Pascual-Leone A. 2011. Screening questionnaire before TMS: an update. Clin Neurophysiol. 122:1686.
- Schiller D, Freeman JB, Mitchell JP, Uleman JS, Phelps EA. 2009. A neural mechanism of first impressions. Nat Neurosci. 12:508–514.
- Schwarz KA, Wieser MJ, Gerdes AB, Mühlberger A, Pauli P. 2013. Why are you looking like that? How the context influences evaluation and processing of human faces. Soc Cogn Affect Neurosci. 8:438–445.
- Siebner HR, Hartwigsen G, Kassuba T, Rothwell JC. 2009. How does transcranial magnetic stimulation modify neuronal activity in the brain? Implications for studies of cognition. Cortex. 45:1035–1042.
- Siebörger FT, Ferstl EC, von Cramon DY. 2007. Making sense of nonsense: an fMRI study of task induced inference processes during discourse comprehension. Brain Res. 1166:77–91.
- Silvanto J, Muggleton N, Walsh V. 2008. State-dependency in brain stimulation studies of perception and cognition. Trends Cogn Sci. 12:447–454.
- Silvanto J, Schwarzkopf DS, Gilaie-Dotan S, Rees G. 2010. Differing causal roles for lateral occipital cortex and occipital face area in invariant shape recognition. Eur J Neurosci. 32:165–171.
- Stone VE, Baron-Cohen S, Knight RT. 1998. Frontal lobe contributions to theory of mind. J Cogn Neurosci. 10:640–656.
- Talairach J, Tournoux P. 1988. Co-planar Stereotaxic Atlas of the Human Brain. Thieme Medical, New York.
- Todorov A, Baron SG, Oosterhof NN. 2008. Evaluating face trustworthiness: a model based approach. Soc Cogn Affect Neurosci. 3:119–127.
- Todorov A, Engell AD. 2008. The role of the amygdala in implicit evaluation of emotionally neutral faces. Soc Cogn Affect Neurosci. 3:303–312.
- Todorov A, Pakrashi M, Oosterhof NN. 2009. Evaluating faces on trustworthiness after minimal time exposure. Soc Cognition. 27:813–833.
- Todorov A, Uleman JS. 2003. The efficiency of binding spontaneous trait inferences to actors' faces. J Exp Soc Psychol. 39:549–562.
- Uleman JS, Saribay AS, Gonzalez CM. 2008. Spontaneous inferences, implicit impressions, and implicit theories. Annu Rev Psychol. 59:329–360.
- Urgesi C, Candidi M, Avenanti A. 2014. Neuroanatomical substrates of action perception and understanding: an anatomic likelihood estimation meta-analysis of lesion-symptom mapping studies in brain injured patients. Front Hum Neurosci. 8:344.
- Van der Cruyssen L, Van Duynslaeger M, Cortoos A, Van Overwalle F. 2009. ERP time course and brain areas of spontaneous and intentional goal inferences. Soc Neurosci. 4:165–184.
- Van Duynslaeger M, Van Overwalle F, Verstraeten E. 2007. Electrophysiological time course and brain areas of spontaneous and intentional trait inferences. Soc Cogn Affect Neurosci. 2:174–188.
- Van Overwalle F. 2009. Social cognition and the brain: a meta-analysis. Hum Brain Mapp. 30:829–858.
- Van Overwalle F. 2011. A dissociation between social mentalizing and general reasoning. Neuroimage. 54:1589–1599.
- Van Overwalle F, Baetens K. 2009. Understanding others' actions and goals by mirror and mentalizing systems: a meta-analysis. Neuroimage. 48:564–584.
- Willis J, Todorov A. 2006. First impressions: making up your mind after a 100-ms exposure to a face. Psychol Sci. 17:592–598.
- Winston JS, Strange BA, O'Doherty J, Dolan RJ. 2002. Automatic and intentional brain responses during evaluation of trustworthiness of faces. Nat Neurosci. 5:277–283.
- Zaki J, Hennigan K, Weber J, Ochsner KN. 2010. Social cognitive conflict resolution: contributions of domain-general and domainspecific neural systems. J Neurosci. 30:8481–8488.