

Dissociable roles of the human somatosensory and superior temporal cortices for processing social face signals

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Abstract

Faces are multi-dimensional stimuli bearing important social signals, such as gaze direction and emotion expression. To test whether perception of these two facial attributes recruits distinct cortical areas within the right hemisphere, we used single-pulse transcranial magnetic stimulation (TMS) in healthy volunteers while they performed two different tasks on the same face stimuli. In each task, two successive faces were presented with varying eye-gaze directions and emotional expressions, separated by a short interval of random duration. TMS was applied over either the right somatosensory cortex or the right superior lateral temporal cortex, 100 or 200 ms after presentation of the second face stimulus. Participants performed a speeded matching task on the second face during one of two possible conditions, requiring judgements about either gaze direction or emotion expression (same/different as the first face). Our results reveal a significant task–stimulation site interaction, indicating a selective TMS-related interference following stimulations of somatosensory cortex during the emotional expression task. Conversely, TMS of the superior lateral temporal cortex selectively interfered with the gaze direction task. We also found that the interference effect was specific to the stimulus content in each condition, affecting judgements of gaze shifts (not static eye positions) with TMS over the right superior temporal cortex, and judgements of fearful expressions (not happy expressions) with TMS over the right somatosensory cortex. These results provide for the first time a double dissociation in normal subjects during social face recognition, due to transient disruption of non-overlapping brain regions. The present study supports a critical role of the somatosensory and superior lateral temporal regions in the perception of fear expression and gaze shift in seen faces, respectively.

Introduction

Faces convey many social and communicative signals used to interpret intentions and affective states of others (Blakemore *et al.*, 2004). Among these, gaze direction and emotion expression constitute two distinct changeable facial attributes simultaneously present within a unique visual stimulus. Several findings suggest that these elaborate aspects of face perception involve different cognitive processes (Bruce & Young, 1986) and different neural substrates (Haxby *et al.*, 2000).

An influential model of emotion processing in the human brain (Damasio, 1994) has proposed that, beyond the visual analysis of facial traits by the occipito-temporal pathway, explicit recognition of emotional expression in faces may depend on the activation of somatosensory representations within the viscerosomatic system. Such activation might reflect the access of visual information to an internally constructed somatic record, allowing the viewer to match the emotional expression of seen faces with bodily dependent traces associated with personal experiences of the same emotion.

Accordingly, primary somatosensory areas (especially in the right hemisphere) may actively participate in the recognition of visually presented emotions. However, this prediction has not been directly verified in normal individuals, although a recent brain-imaging study (Winston *et al.*, 2003) reported an activation within right somatosensory cortex when normal subjects made expression judgements, as opposed to gender judgements from the same face stimuli. In support of Damasio's model, data from brain-damaged patients (Adolphs *et al.*, 2000) have shown that lesions of the right somatosensory cortex may be associated with impaired recognition of facial expressions, particularly for negative emotions such as fear or anger. However, these brain lesions usually extended beyond SI and SII, often involving the insula, also critically implicated in emotional processing (Calder *et al.*, 2001; Critchley *et al.*, 2004).

By contrast, single-cell recordings in monkeys (Perrett *et al.*, 1985) and brain imaging in humans (Puce *et al.*, 1998) indicate that the processing of gaze direction recruits specific brain structures in the posterior part of the superior temporal sulcus (STS), also with a right hemispheric dominance (Puce & Perrett, 2003). STS appears critical for perception of changeable features in faces, whereas other regions in the inferior temporal cortex extract invariant facial traits for

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identity recognition (Haxby *et al.*, 2000). Moreover, neuronal populations in STS may respond to other dynamic aspects of faces beyond gaze shifts, including lip movements and emotion expression (Hasselmo *et al.*, 1989; Ojemann *et al.*, 1992; Haxby *et al.*, 2000) as well as complex social cues such as trustworthiness (Winston *et al.*, 2002).

Therefore, although these data suggest that non-overlapping brain systems may contribute to expression and gaze processing (see also Hietanen & Leppanen, 2003), it is still unclear whether there is a true functional dissociation between these distant cortical regions within the right hemisphere during face perception. In addition, neuropsychological and imaging data do not inform about the exact time-course of somatosensory and STS activity. Thus, it is unclear whether the right somatosensory contribution to emotion recognition is part of an 'early' perceptual process (Adolphs *et al.*, 2000) or a later appraisal stage subsequent to visual analysis and emotion recognition in other brain regions. In addition, there is no report of patients with focal brain damage showing a double dissociation between recognition of gaze and expression (Blakemore *et al.*, 2004).

One way to address this issue directly is provided by single-pulse transcranial magnetic stimulation (TMS) because both STS and somatosensory regions are accessible to interference by brief magnetic stimulation (Walsh & Cowey, 1998). Here we used single-pulse TMS to test in normal viewers for a distinct role of right somatosensory cortex and right superior temporal cortex in social face recognition. By comparing the effects of TMS applied over these two regions in the same volunteers, while they performed two different tasks on the same face stimuli, we were able to determine any preferential involvement of right somatosensory cortex in the perception of negative facial expressions and of right superior lateral temporal cortex in the perception of gaze shifts. We predicted that TMS delivered over right somatosensory cortex should interfere selectively with emotion recognition (not with gaze recognition). Conversely, we predicted that TMS over the right posterior STS should predominantly disrupt the perception of eye gaze direction (more than the perception of emotional expression). In addition, we also hypothesized that emotion recognition might be more affected for fearful than for happy expressions (see Adolphs *et al.*, 2003), and that gaze perception might be differentially affected for dynamic eye gaze shifts relative to static gaze (see Puce *et al.*, 1998). Alternatively, TMS over STS regions might interfere with the detection of any dynamic changes affecting either gaze direction or expression (see Haxby *et al.*, 2000). Across all conditions, single-pulse TMS was delivered either 100 or 200 ms post-face onset, in keeping with human EEG data suggesting an activation of right STS at these early latencies (Puce & Perrett, 2003). Our results provide the first demonstration that in the normal human brain, TMS applied at the same time-delays and at the same intensity over different cortical regions can produce dissociable effects during face processing, as hypothesized based on previous neuropsychological studies (Damasio, 1994; Adolphs *et al.*, 2000).

Methods

Subjects

Participants were 12 right-handed paid subjects (five males and seven females) from the Université catholique de Louvain, aged between 21 and 28 years (SD 2 years), who took part in the present TMS study following approval of the local ethics committee. Participants had normal or corrected to normal vision, and had no neurological history (all were screened for epilepsy and for the presence of metallic

implants). They were given extensive information and gave written consent before participation.

Stimuli

The face stimuli were grey-scale standardized photographs of 20 different individuals with either a fearful or a happy emotion expression (ten males and ten females selected from two distinct face sets, namely the Ekman series, Ekman & Friesen, 1976; and the Karolinska Directed Emotional Faces set, Lundqvist *et al.*, 1998). Each face stimulus was enclosed within a rectangular frame measuring 6.1×8.9 cm, subtending $5.0 \times 7.3^\circ$ of visual angle at a 70-cm viewing distance (173×251 pixels on a 256 grey-level scale). All stimuli were presented on a black background, on a 17-inch computer screen.

To manipulate carefully the gaze direction of each of the 40 original standardized face stimuli (Fig. 1A), we used a semi-automatic method whereby we reconstructed each face picture with the projection of a simplified three-dimensional (3D) model of the eye bulbs as two spheres, in order to control accurately the direction of perceived gaze. First, a texture mapping of the eyes was created, which consists in wrapping a 2D image onto a 3D surface to provide a colour appearance to this surface without having to model complex geometrical details. In a second step, the spheres of the eyes model were rotated in 3D space using trigonometric rules such that the two eyes were converging in a realistic manner at a virtual target point located in front of the subject. This computer-based approach allowed us to create two variants of the same standardized emotional faces, differing only in their gaze direction (either straight or parametrically deviated leftward or rightward). Thus, from the 40 original face pictures, we created two new face sets: one with gaze deviated 30° leftward and another set with gaze deviated rightward, resulting in 120 different face pictures in total. Thirty degrees was chosen after pilot experiments with our stimuli because they showed that such an averted gaze direction ensured unambiguous perception of deviated gaze as compared with the original face pictures. Moreover, when a face with averted gaze was combined in a close temporal succession with the same face showing a straight gaze, these stimuli produced a compelling impression of gaze shift.

TMS

The equipment consisted of a Magstim model 200 Magnetic stimulator (Magstim, UK). We used a figure of eight coil, each winding measuring 7 cm (maximum output 2 T) producing the maximum electric field below its centre, with a focal zone of maximum stimulation (Cohen *et al.*, 1990). The centre of the coil was positioned over the cortical site to be stimulated (right somatosensory vs. right superior lateral temporal cortex) in a parasagittal line with the handle pointing posteriorly. Rate of stimulation did not exceed 0.3 Hz. A PC running e-prime (Psychology Software Tools, Inc., Pittsburgh, PA, USA) and the stimulator were interconnected, allowing us to trigger TMS time-locked to the second face either 100 or 200 ms after the stimulus presentation. To determine the intensity of TMS stimulation, we adopted a similar strategy as previous studies (e.g. Harris *et al.*, 2002), and used the resting motor threshold as a reference intensity value to calculate in each individual subject the stimulation intensity for somatosensory and superior lateral temporal sites. The resting motor threshold was determined as follows. The point over which low-intensity TMS evoked a visible twitch in the contralateral hand muscles was considered as the location of the primary motor area (M1). Resting motor thresholds were defined as the TMS intensity

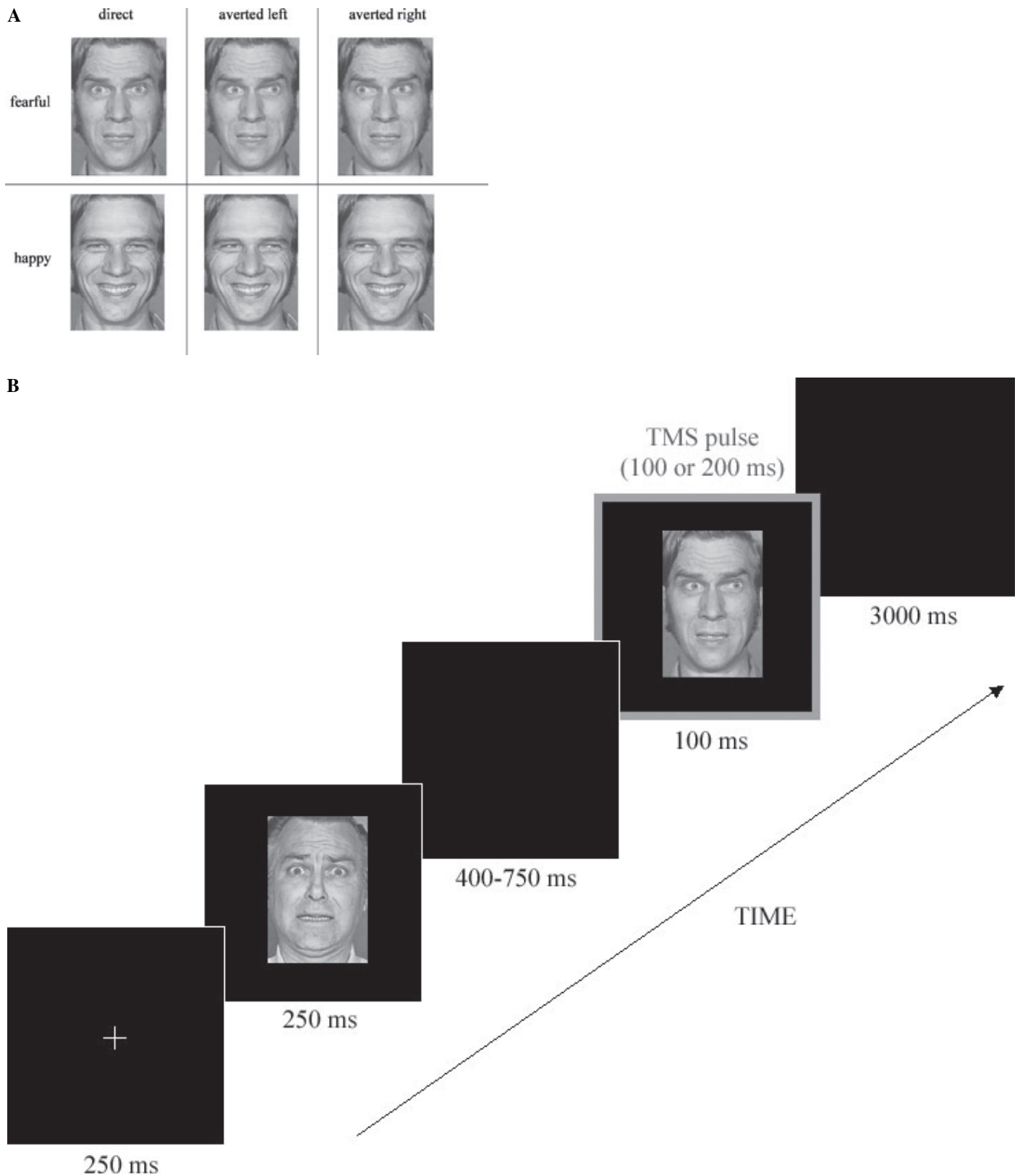


FIG. 1. (A) The six face categories used in our TMS experiment. (B) The procedure used showing the sequence of events within a trial.

evoking a visible twitch in the contralateral hand muscles in 50% of the stimulations applied over M1. Magnetic single pulses were delivered at an intensity of 10% above the motor threshold measured

in the ipsilateral M1 before the experimental session. Following this procedure, mean intensity used was low (43.8% of the maximum stimulator output), ranging from 32 to 55% across subjects.

Selection and confirmation of TMS sites

Participants wore a closely fitting EEG cap. Using the 5% electrode system (Oostenveld & Praamstra, 2001), the right somatosensory and right superior lateral temporal cortices were located and marked over the EEG cap on the right side (C4 and CP6, respectively) of the head (for a similar approach to localize primary somatosensory cortex, see Harris *et al.*, 2002). The mean distance between these two regions was ~5 cm. Right somatosensory position was situated ~1 cm posterior and lateral to the position at which the motor excitability threshold was usually obtained. Right primary motor cortex (M1) was also marked for each participant after detection by TMS.

The accurate localization of stimulation sites was confirmed for three out of 12 subjects (Fig. 2) using off-line co-registration between TMS sites and structural MRI (Noirhomme *et al.*, 2004). The precise position of the coil was tracked with a 3D coordinates system (Polhemus Isotrak II system, Kaiser Aerospace Inc.) that gives the *x*, *y* and *z* coordinates of each point relative to a fixed radio-frequency magnetic field transmitter. Stimulation sites were recorded with a digitizing receiver pen, relative to a second receiver fixed to the subject's forehead. Then, more than 60 points were digitized over the scalp surface. This contour of the scalp was plotted in 3D space and matched semi-automatically with the 3D reconstruction of the head surface obtained from MR images, using software developed in the laboratory and based on the Visual Tool Kit (VTK) library. A transformation matrix was calculated, which computed any point of the 3D coordinate system into the MR system. As the position of the coil over right somatosensory, right superior lateral temporal and right M1 was digitized during the last trials, the transformation matrix allowed us to determine the location of the coil relative to the head. A line normal to the plane of the coil was drawn from the centre of the coil through the scalp and skull until it crossed the brain surface. This cortical impact point was considered as the site where TMS was maximal. Depending on the cortical region of interest, co-registration accuracy of a few millimetres is attainable. This co-registration

technique allowed us to ascertain that C4 and CP6 in the 10–20 EEG system reliably overlapped with somatosensory and superior lateral temporal cortex, respectively (Fig. 2).

Procedure

Each trial consisted of a pair of two successive faces (Fig. 1B). To maximize the processing of emotion expression or gaze direction (and also to avoid uncontrolled repetition effects of face identity within a pair), the two faces within a pair were always two different person identities but with the same gender. Before each trial an alerting symbol appeared at the centre of the screen for 250 ms and was followed after 250 ms by the presentation of the first face for 250 ms. At the offset of the first face, a random time interval between 400 and 750 ms (mean = 575 ms) was introduced to avoid any anticipation for the second critical face (probe stimulus). This second face was displayed for 100 ms in order to discourage eye movements. On all trials, a single TMS pulse was delivered either 100 or 200 ms following the presentation of the second face in the pair. The interval between trials was kept constant at 3 s, respecting standard recommendations for the practice of single-pulse TMS (Wassermann, 1998). Reaction times (RT) were calculated from the second face onset. Subjects were seated comfortably on a chair at 70 cm viewing distance in front of the screen and were positioned so that the display centre was at their eye level, aligned with their sagittal midplane.

Subjects were required to make a rapid two-alternative forced-choice concerning either emotional expression or gaze direction of the faces, and responded by pressing one of two buttons on a serial response box. In half of the blocks, subjects were instructed to judge whether the second face had the same 'emotion expression' as the first face or not. Participants were told that only two emotion categories were used (fear and happiness), resulting in four possible stimulus combinations. In the other half of the blocks, subjects were asked to judge whether the second face had the same 'gaze direction' as the

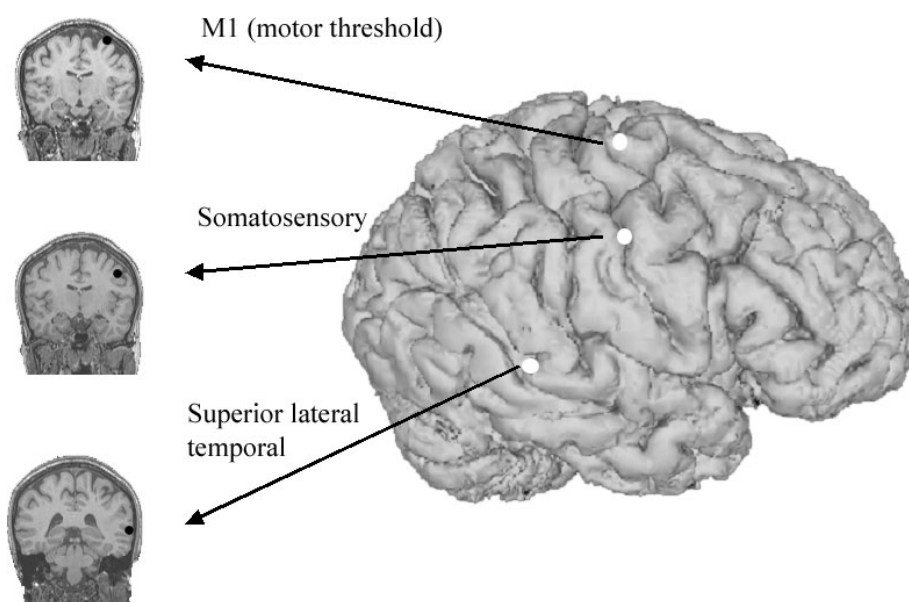


FIG. 2. Co-registration between TMS and individual brain MRI scan. Coronal sections and 3D reconstruction of the brain surface in one participant, showing the estimated cortical sites of magnetic stimulation (right frontal-M1, right somatosensory and right superior lateral temporal cortices). A beam perpendicular to the surface of the figure-of-eight coil was computed from the centre of the coil (under which the induced current is the strongest) and the impact point on the 3D-reconstructed cortical surface was considered as the point of stimulation. Each black mark (sections) is the computed mean impact point (> 60 digital measures, see Methods) for each of the three TMS sites.

first face or not. Participants were also told that only two gaze directions were possible (straight or averted), again resulting in four possible combinations. Thus, there were two possible sequences (same/different) for each emotion and each gaze direction in the second face probe (i.e. static vs. dynamic sequence). The side of same–different response keys was alternated across subjects. This sequential matching task ensured that response factors were kept identical across the two different task conditions. Before starting the experiment, a block of 24 training trials was presented.

The experiment consisted of eight experimental sessions (2 TMS sites \times 2 Tasks \times 2 different blocks), each containing 32 pairs of faces (total 256 pairs). Within a session, the experimenter constantly applied the TMS coil over the same spot. These eight sessions corresponded to four different blocks of 32 pairs, each presented only once at each stimulation site. The four blocks consisted of two different lists (lists 1 and 2 containing the total set of facial stimuli), each being elaborated in two different versions (versions A and B). Lists 1 and 2 shared the same stimulus structure but included partly different face identities. Versions A and B were identical, except that the two delays between stimulus onset and TMS (100 and 200 ms) were counterbalanced across these two versions. Each list contained an equal number of male and female faces. In each list, 32 pairs of faces expressing the same emotion (16 happy–happy and 16 fearful–fearful pairs) were pseudo-randomly presented with 32 pairs of faces expressing different emotions (16 happy–fearful and 16 symmetric pairs). Orthogonally to the four emotion conditions, the 32 pairs of faces in each list were also divided into four conditions of gaze direction, each with an equal number of trials. As a result, in each list, 32 pairs of faces with the same gaze orientation (16 averted–averted and 16 direct–direct pairs) were randomly presented with 32 pairs of faces with different gaze orientations (16 averted–direct pairs and 16 reverse pairs). The two faces constituting an ‘averted–averted’ pair always gazed towards the same direction (left–left or right–right), but never towards different directions (left–right or right–left).

The stimulus lists were counterbalanced across participants for the stimulation site (somatosensory vs. superior lateral temporal) and the task (emotion expression vs. gaze direction). This procedure ensured that participants equally saw each face stimulus across all conditions and stimulation sites. Task order was also counterbalanced across participants. Note that this design was chosen to use the same face stimuli equally across the two different tasks (emotion vs. gaze recognition), as well as to keep the response requirement identical in all conditions (same/different matching judgements), but this was not intended to enable a fully factorial design (i.e. with a gaze factor in the emotion judgement task, or an emotion factor in the gaze judgement task). Therefore, the relevant stimulus dimensions concerned expression only (fearful vs. happy faces, regardless of gaze) during the emotion task, and gaze only (shifting vs. static eyes, regardless of expressions) during the gaze direction task, with 32 trials for each condition in each task. A subsidiary analysis carried out in a fully factorial manner with respect to eye gaze and expression (i.e. with fewer trials in each condition) did not point to any significant interaction between these two factors across all conditions (see below).

Results

Accuracy

No reliable TMS-related interference effect on accuracy was produced using our single-pulse protocol. Performance was high for all stimulus conditions in both tasks ($> 91\%$ correct) and did not vary with Site

($F_{1,11} = 0.01$, $P = 0.92$) or TMS delay ($F_{1,11} = 0.51$, $P = 0.49$). Overall, subjects tended to make more errors during the emotion task (90.3% correct) than during the gaze direction task (92.7% correct), but this difference was not significant ($F_{1,11} = 4.08$, $P = 0.07$) and did not interact with the site of stimulation ($F_{1,11} = 0.31$, $P = 0.59$).

RTs

As illustrated in Fig. 3, single-pulse TMS significantly modulated the speed of correct perceptual decisions across the different tasks and different stimulus conditions, with a distinct pattern of effects during TMS over the right somatosensory cortex relative to the right lateral temporal cortex.

These effects were first examined by a repeated-measure ANOVA with Task (gaze vs. emotion judgements), Site (somatosensory vs. superior temporal), Delay (100 vs. 200 ms), Sequence (same vs. change), Expression of stimulus probe (fearful vs. happy) and Eye direction in stimulus probe (averted vs. straight) as separate factors. Results showed main effects of Expression ($F_{1,11} = 8.43$, $P = 0.014$), Eye direction ($F_{1,11} = 14.66$, $P = 0.003$) and Sequence ($F_{1,11} = 4.74$, $P = 0.052$), with significant two-way interactions of Sequence with Expression ($F_{1,11} = 61.46$, $P < 0.001$) and with Eye direction ($F_{1,11} = 4.65$, $P = 0.054$), as well as three-way interactions of Task \times Sequence \times Expression ($F_{1,11} = 45.20$, $P < 0.001$) and of Task \times Sequence \times Eye direction ($F_{1,11} = 9.74$, $P = 0.010$). Expression and Eye direction showed no significant two-way interactions ($F_{1,11} = 0.13$, $P = 0.73$). This complex pattern of RTs mainly reflected the fact that trials with a dynamic change in expression or gaze direction (from the first to the second face in the sequence) differed as a function of the task and of the stimulus probe. RTs were generally slower on trials with different rather than same expressions (mean 740 vs. 703 ms), except for two successive fearful faces in the emotion task (leading to much slower responses than for two successive happy faces: 777 vs. 631 ms, $t_{11} = 7.83$, $P < 0.001$, with no such difference between expressions in the gaze task: 682 vs. 668 ms, $t_{11} = 1.38$, $P = 0.19$). Conversely, RTs were only slightly slower for trials with dynamic rather than static gaze direction (mean 691 vs. 675 ms), except for significantly faster responses on two successive faces with straight eyes relative to other gaze conditions (630 vs. 720 ms for straight–straight vs. averted–averted sequence, $t_{11} = 4.31$, $P < 0.001$, with no such effect of gaze direction in the emotion task: 702 vs. 705 ms, $t_{11} = 0.22$, $P = 0.83$). However, there was no main effect of Site ($F_{1,11} = 0.45$, $P = 0.52$) and no Task–Site interaction ($F_{1,11} = 0.45$, $P = 0.52$) in this first analysis. Other main effects and interactions also failed to reach significance, except for a trend for a five-way interaction of Site \times Sequence \times Expression \times Eye direction \times Delay ($F_{1,11} = 4.11$, $P = 0.07$).

To simplify this analysis according to our conditions of primary interest, we performed a second analysis on the speed of correct perceptual judgements made for different aspects of the same face stimuli (i.e. different facial expression and different gaze conditions) during the two tasks and during stimulation of the two sites. Our *a priori* hypothesis was that TMS over somatosensory and STS regions might differentially affect the recognition of fearful vs. happy expressions during the emotion judgement task, and the recognition of dynamic gaze shifts vs. static gaze in the gaze judgement task. For the emotion perception conditions, we therefore compared judgements of fearful and happy expressions, regardless of gaze direction, by pooling together trials with fearful–fearful and happy–fearful face pairs (i.e. all trials requiring recognition of fear in the second face, which was presented at the time of perceptual decision prior to the TMS pulse), as opposed to trials with happy–happy and fearful–happy face pairs (i.e.

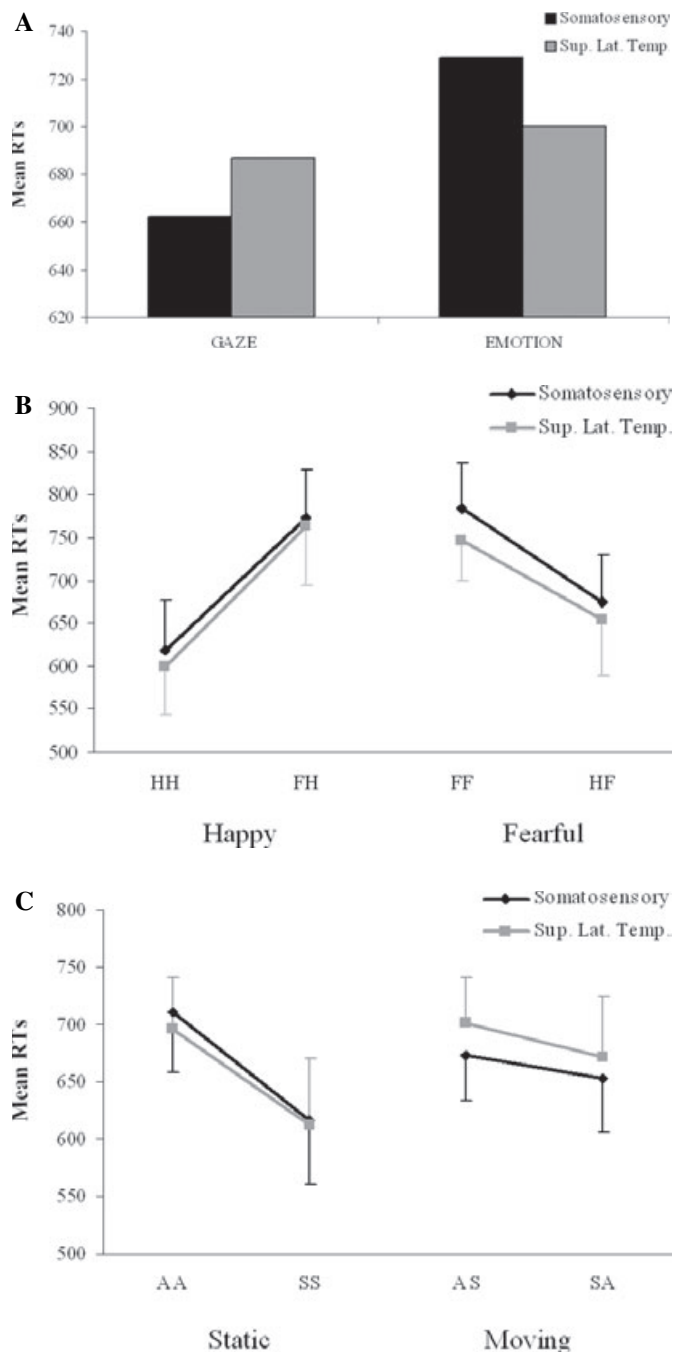


FIG. 3. (A) Task-Site interaction ($P = 0.007$) showing a selective TMS-related interference produced by somatosensory stimulations during emotion judgements for fearful faces (fearful-fearful + happy-fearful sequence), and conversely a selective interference produced by superior lateral temporal stimulations during gaze judgements for faces with shifted eyes (averted-straight + straight-averted sequence). (B) Results (mean RT \pm SEM) for the emotion expression task, according to the two critical stimulus conditions with either happy faces [happy-happy (HH) and fearful-happy (FH) sequence] or fearful faces at the time of perceptual decisions [fearful-fearful (FF) and happy-fearful (HF) sequence]. (C) Results (mean RT \pm SEM) for the gaze direction task, according to the two critical conditions with either unchanged gaze direction [straight-straight (SS) and averted-averted (AA) sequence] or shifted gaze at the time of perceptual decisions [averted-straight (AS) and straight-averted (SA) face sequence].

all trials requiring recognition of happy expressions in the second face). For the gaze perception conditions, we compared trials with gaze shifts and those with static eye gaze, regardless of emotional expressions, by pooling together all face pairs with averted-straight and straight-averted eyes (i.e. requiring detection of a gaze shift), as opposed to those with straight-straight and averted-averted eyes (i.e. not requiring any detection of gaze shifts).

We then performed a direct statistical comparison using a 2 (Task) \times 2 (Site) \times 2 (Delay) repeated-measures ANOVA on median RTs across these predefined stimulus conditions of interest (faces with fearful expressions vs. shifted eyes). This analysis confirmed a significant critical interaction of Task \times Site ($F_{1,11} = 11.04$, $P = 0.007$), with no modulation by the factor delay ($F_{1,11} = 1.00$, $P = 0.34$). This interaction (Fig. 3A) reflected significantly slower judgements for emotional fearful expressions when single-pulse TMS was applied over somatosensory cortex relative to STS (paired t -test, $t_{11} = 1.80$, $P = 0.05$), and conversely slower judgements for gaze shifts when TMS was applied over STS compared with somatosensory cortex (paired t -test, $t_{11} = 2.79$, $P = 0.009$). Therefore, performance in both tasks was influenced by the stimulation site, but in opposite directions, while the stimuli and the task remained the same across each stimulation condition. There was no other main effect or interaction.

In addition, we also examined whether TMS over somatosensory or STS regions might differentially affect face expression recognition on trials with a dynamic expression change vs. the same expression across the two successive faces. A 2 (Site) \times 2 (Sequence) \times 2 (Delay) ANOVA was performed on correct RTs from the emotion task only, pooling over happy and fearful faces, but showed no significant main effect or no Site-Sequence interaction ($F_{1,11} = 1.58$, $P = 0.23$). Similarly, considering each type of expression in the face probes separately (fearful or happy) disclosed no significant Site-Sequence interaction during expression judgements (all $P > 0.20$), but there was a significant main effect of Site on fearful face probes ($F_{1,11} = 6.25$, $P = 0.03$).

Finally, the specificity of TMS interference over the two brain sites was further investigated by taking into account the stimulus content in both tasks separately. In the emotion task (Fig. 3B), as expected from previous behavioural studies (Baumeister *et al.*, 2001), our participants showed a negative emotion bias effect (i.e. they were overall slower to judge fearful relative to happy faces regardless of the site of stimulation; $F_{1,11} = 10.02$, $P = 0.009$). Moreover, *post-hoc* analyses indicated that the interference caused by TMS was selective for these negative emotional expressions: participants showed the slowest RTs when they had to match two consecutive fearful faces when TMS was delivered over the right somatosensory cortex (mean RT 790.4 ms), with such judgements being delayed by more than 50 ms as compared with the same condition when TMS was applied over the right superior lateral temporal cortex (mean RT 738.0; $t_{11} = 2.48$, $P = 0.02$), despite the fact that both the task and the face stimuli were identical in each of these two TMS conditions. There was no significant RT difference between somatosensory and superior lateral temporal stimulations for judgements of happy expressions ($t_{11} = 0.65$, $P = 0.26$).

In contrast, in the gaze task (Fig. 3C), the participants showed the largest TMS-related interference on trials during which they had to match eye direction in a face with a leftward or rightward gaze following a face with straight gaze when TMS pulses were delivered over the superior lateral temporal cortex (mean RTs 679.3 ms). These judgements were 30 ms slower in this condition as compared with stimulation over somatosensory cortex during the same task on the same probe stimuli (651.3 ms; $t_{11} = 2.15$, $P = 0.03$). Moreover, a

similar difference was also observed in the reverse condition, i.e. when judging gaze shifts from averted to straight eye direction (702.5 vs. 672.3 ms for superior lateral temporal and somatosensory, respectively, $t_{11} = 1.74$, $P = 0.05$). There was no significant RT difference between the two sites for judgements of static gaze directions ($t_{11} = 0.21$, $P = 0.42$). Thus, in the gaze task, the interference effect of TMS on STS was confined to trials with shifted eyes.

Discussion

In this study, we directly tested the hypothesis that right somatosensory cortex and right superior lateral temporal cortex in the human brain might make a distinct contribution to explicit perception of social signals in faces. Based on behavioural (Hietanen & Leppanen, 2003), neuropsychological (Adolphs *et al.*, 2000), functional neuroimaging (Puce *et al.*, 1998; Winston *et al.*, 2003) and neurophysiological data (Perrett *et al.*, 1985), we predicted that the right somatosensory cortex should be selectively involved in the recognition of emotional facial expressions, whereas the right lateral superior temporal cortex should be more concerned with processing of gaze shifts. By using TMS to deliver single pulses over these two different regions in healthy volunteers, we were able to interfere selectively with emotional and gaze judgements depending on stimulus content and stimulation sites, in agreement with the hypothesized anatomic–functional dissociation. These results show that TMS provides a powerful tool to validate or invalidate hypotheses about the anatomical and temporal organization of cognitive processes (Walsh & Cowey, 1998).

Our subjects performed two different tasks (emotion or gaze judgements) on the same standardized face stimuli, while emotional expression (fearful/happy) and gaze direction (straight/averted) were orthogonally manipulated, using a new computer-based approach to modify the gaze direction of each face carefully without distorting pictorial details of the eyes (such as contrast or pupillary diameter). A similar sequential matching task was used for the two task conditions. Thus, during the emotion task, participants had to judge facial expressions regardless of gaze direction, whereas during the gaze task, they judged eye gaze direction regardless of expression, although the face stimuli and response requirements (same/different) were identical across tasks. Our results revealed a clear task-dependent functional dissociation between the right somatosensory cortex and right superior temporal cortex. TMS over somatosensory areas interfered with the recognition of fearful expressions in the emotion task, whereas TMS over superior temporal cortex interfered with perception of eye position shifts in the gaze task. Moreover, our co-registration between TMS and MRI data indicated that anterior stimulations were accurately delivered to cortical regions corresponding to SI–SII areas, close to the Rolandic sulcus but above the frontal operculum (consistent with previous work using the same landmarks, Harris *et al.*, 2002), whereas the posterior stimulation site accurately corresponded to the posterior STS (see Fig. 2).

Because we did not implement a sham condition in our design (where the magnetic field does not enter the brain although the touch on the scalp and the sound of the coil are nearly identical to the active TMS conditions, see Robertson *et al.*, 2003), we cannot entirely rule out the possibility that TMS to either site affected performance on both tasks to some degree, although more on one than the other. However, our most critical findings clearly indicate a differential effect of TMS depending on the site of stimulation (right somatosensory vs. right superior lateral temporal cortex), the task at hand (emotion vs. gaze recognition), and also the stimulus content (fearful expression vs. shifted eye gaze), providing new support for a differential role of these

two brain regions in social face processing at these early latencies post-stimulus onset. More generally, our results have important implications for models of face recognition (Bruce & Young, 1986), suggesting a crucial anatomic–functional segregation between neural systems processing these two different changeable aspects of faces (expression vs. gaze). Such a distinction is not implemented in current neural models of face recognition (Haxby *et al.*, 2000), in which both aspects have been related to a common substrate in STS.

An important new result from our study concerns a specific role of somatosensory cortex in the perception of fearful expressions in faces. These data significantly extend recent brain-imaging results (Winston *et al.*, 2003) by showing for the first time in normal subjects that the right somatosensory cortex is directly implicated in the recognition of a visually presented emotion, at an early latency following stimulus onset (< 200 ms). The present findings agree with previous neuropsychological data (Adolphs *et al.*, 2000) reporting a correlation between lesions in somatosensory regions and impairments in visual recognition of facial expressions, although such impairments were not restricted to fear but extended to other emotions. Our study goes beyond this traditional approach in brain-damaged patients by demonstrating not only a crucial contribution of the right somatosensory cortex in emotion recognition in healthy viewers, but also by suggesting an early time-course of this somatosensory activation, as well as a remarkable task-dependent and stimulus-content selectivity. However, the relative ‘early’ involvement of somatosensory cortex in the recognition of fearful expressions needs to be further investigated, by contrasting more directly early vs. long latencies between stimulus onset and TMS pulse or by manipulating this factor parametrically, because it is possible that using longer latencies might have shown equal or even greater interference.

We found that single-pulse TMS over the right somatosensory cortex did not produce a general RT interference in recognizing facial emotions, but selectively affected the perception of fearful expressions (not happy expressions). Participants made slower responses when they had to match two consecutive fearful faces while TMS was applied over the right somatosensory region, relative to the other expressions and to STS stimulations. It is not entirely clear why only the perception of fearful faces is disrupted by somatosensory stimulations, but several possibilities may account for this differential effect. First, this may be consistent with neuropsychological findings in a large population of brain-damaged patients (Adolphs *et al.*, 1996) that happiness can still be recognized normally despite the presence of focal lesions at various locations, including somatosensory-related areas. Happy faces are also more easily recognized through a single visual feature (smile), making them possibly less dependent on the somatosensory system than fearful faces. Alternatively, it is possible that the excitability threshold of somatosensory regions to show a TMS-related interference may vary according to the emotion category, unlike brain lesions typically destroying a whole region in patients who showed more general deficits across all expressions (Adolphs *et al.*, 2000). Finally, recognizing fearful faces might require a stronger activation of internal somatic representations than the recognition of happy faces (Adolphs *et al.*, 2000). Fearful faces constitute biologically relevant and salient events that indirectly inform about a potential threat, presumably leading to a more massive somatic behavioural preparation as compared with happy faces. Additional single-pulse TMS studies are needed to test these hypotheses and to explore if some interference can also be obtained for the recognition of happy expressions (or other emotion categories) with TMS applied over the same right somatosensory region at higher intensities.

More importantly, our TMS results provide new evidence for theories of emotion suggesting that recognition of affective states or

signals in other people may recruit internal representations of one's own somatic expression associated with such emotion, perhaps partly simulated via an 'as-if loop' process (Damasio, 1994; Adolphs *et al.*, 2000). There is a growing consensus in considering emotion as a process that consists of co-ordinated changes in a set of several core components, including appraisal processes, peripheral arousal, motor expression, action tendencies and subjective feeling (see Scherer, 2000). Our new data support a critical interaction between some of these components during the visual recognition of fearful faces in normal subjects, by showing that the right somatosensory cortex participates in an early perceptual process necessary for explicit judgements about the emotional expression of seen faces (Adolphs *et al.*, 2000).

Our results also reveal a task-specific interference induced by single-pulse TMS over the right superior lateral temporal cortex, close to the posterior STS (see Fig. 2), affecting the perception of distinct facial signals conveyed by eye gaze. We found that TMS selectively disrupted responses during trials in which a gaze shift occurred between the first and second presentation of faces in a pair (i.e. from straight to averted gaze or vice versa), whereas responses on trials with static gaze positions (straight-straight and averted-averted pairs) were not influenced by TMS. These results indicate that TMS effects during gaze processing were remarkably content-specific, concerning the perception of gaze shifts only, rather than static eye positions. These findings agree with a wide range of neurophysiological and brain-imaging experiments showing an important role of the posterior STS in processing biological motion, including gaze shifts (Hoffman & Haxby, 2000; Puce & Perrett, 2003). Here we show that STS activity may directly contribute to explicit perception of gaze shifts in seen faces. The selective effect of TMS on gaze shifts is unlikely to reflect a more general impairment in the perception of apparent motion (e.g. due to interference with general motion processing in more posterior V5/MT complex) because there was a substantial interval (400–750 ms) between the first and second face in the sequential pairs.

By contrast, we did not observe any interference in the emotion task for magnetic stimulations applied over the same right STS region, suggesting a greater susceptibility of this particular region to TMS interference during gaze monitoring than during emotion judgements in the current task setting. This negative result contrasts with several brain-imaging studies (e.g. Phillips *et al.*, 1998; Iidaka *et al.*, 2001; Narumoto *et al.*, 2001) indicating an activation of STS (or middle temporal gyrus) during processing of facial expressions (Haxby *et al.*, 2000). This discrepancy might tentatively be related to the different experimental conditions, or to differences between haemodynamic measures of brain activity as compared with the present TMS study. STS activation to facial expressions is often observed when emotional faces are contrasted with neutral faces, whereas our study did not use neutral face expressions. STS is also activated in tasks associated with 'theory of mind' or social evaluations such as trustworthiness (Winston *et al.*, 2004). Therefore, responses to facial expressions observed by imaging studies in STS might potentially reflect more complex processing related to the appraisal of intention or social relevance of faces, extracting crucial gaze cues in order to interpret the significance of facial expressions. Moreover, it is also possible that the human STS may contain distinct subregions, which might be differentially sensitive to gaze, expression or other facial signals (Blakemore *et al.*, 2004; Winston *et al.*, 2004). Such anatomical segregation within the STS could potentially account for the apparent difference between our findings and previous imaging reports. Further single-pulse TMS studies combined with fine-grained co-registration methods are needed to investigate this possible specialization within right STS during social face perception.

Finally, we found that the factor delay (i.e. TMS pulses delivered either 100 or 200 ms post-stimulus onset) did not modulate emotional effects in somatosensory cortex nor gaze effects in superior lateral temporal cortex. We selected these two delays based on previous neurophysiological data in humans indicating an activation of STS at these early latencies (Puce & Perrett, 2003), but also with the aim to test specifically for an early recruitment of both temporal and somatosensory areas during the initial perceptual processing stages of social face recognition (as suggested by Adolphs *et al.*, 2000, but never formally tested). Here, we found early effects of TMS over both somatosensory and STS regions for emotion and gaze judgements, respectively, but no timing difference between areas and tasks with our two different delays. This suggests that these regions may participate at similar early perceptual latencies, in a selective way, to different aspects of social face recognition. Thus, social face recognition may involve parallel processing routes within non-overlapping brain regions. However, some caution is required to interpret this lack of timing difference because TMS effects are not always transient but may last several tens of milliseconds after a single pulse (e.g. Thut *et al.*, 2003). Clearly, the precise time-course and neuro-anatomical circuits subserving social face processing need to be further elucidated, as well as their connections with other cortical and subcortical areas involved in the appraisal of emotional events and in the emotional response.

In summary, our results reveal a striking task-dependent double-dissociation in the perception of social face attributes in the healthy human brain, with a crucial and early role of non-overlapping areas in somatosensory and superior lateral temporal cortex of the right hemisphere, respectively implicated in the recognition of fearful expressions and in the detection of gaze shift in seen faces.

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Abbreviations

RT, reaction time; STS, superior temporal sulcus; TMS, transcranial magnetic stimulation.

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