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Research report

Virtual lesion of right posterior superior temporal sulcus modulates conscious visual perception of fearful expressions in faces and bodies

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ABSTRACT

The posterior Superior Temporal Suclus (pSTS) represents a central hub in the complex cerebral network for person perception and emotion recognition as also suggested by its heavy connections with face- and body-specific cortical (e.g., the fusiform face area, FFA and the extrastriate body area, EBA) and subcortical structures (e.g., amygdala). Information on whether pSTS is causatively involved in sustaining conscious visual perception of emotions expressed by faces and bodies is lacking. We explored this issue by combining a binocular rivalry procedure (where emotional and neutral face and body postures rivaled with house images) with off-line, 1-Hz repetitive transcranial magnetic stimulation (rTMS). We found that temporary inhibition of the right pSTS reduced perceptual dominance of fearful faces and increased perceptual dominance of fearful bodies, while leaving unaffected the perception of neutral face and body images. Inhibition of the vertex had no effect on conscious visual perception of neutral or emotional face or body stimuli. Thus, the right pSTS plays a causal role in shortening conscious vision of fearful faces and in prolonging conscious vision of fearful bodies. These results suggest that pSTS selectively modulates the activity of segregated networks involved in the conscious visual perception of emotional faces or bodies. We speculate that the opposite role of the right pSTS for conscious perception of fearful face and body may be explained by the different connections that this region entertains with face- and body-selective visual areas as well as with amygdalae and premotor regions.

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1. Introduction

Information conveyed by emotional expressions is of crucial importance for social interactions. Studies of category-specific visual perception indicate that the selective processing of neutral bodies and faces occurs in dedicated regions of the occipito-temporal cortex (Occipital Face Area, [Peelen & Downing, 2005]; Extrastriate Body Area, [Downing, Jiang, Shuman, & Kanwisher, 2001; Urgesi, Berlucchi, & Aglioti, 2004; Urgesi, Candidi, Ionta, & Aglioti, 2007]; Fusiform Face Area, [Haxby, Hoffman, & Gobbini, 2000; Kanwisher, McDermott, & Chun, 1997]; Fusiform Body Area, [Moro et al., 2012; Schwarzlose, Baker, & Kanwisher, 2005]). A recent MEG study indicates that these regions process facial and body images at different timings as early as 100 msec after image presentation (Meeren, de Gelder, Ahlfors, Hämäläinen, & Hadjikhani, 2013). The specificity of body and face processing extends to the posterior Superior Temporal Sulcus (pSTS [de Gelder & Partan, 2009; Pinsk et al., 2009; Tsao, Moeller, & Freiwald, 2008]), which is a crucial node of the visual system that functions as a hub for the processing of socially relevant stimuli (Lahnakoski et al., 2012). There is substantial neuroimaging evidence in support of the role of the pSTS in socially relevant processes. This region is also activated during the processing of others' intentions and mental state attributions, even irrespective of the affective content of the observed actions (David et al., 2006; Lahnakoski et al., 2012; Saxe & Kanwisher, 2003). Many studies have demonstrated that pSTS is involved in the processing of facial and bodily postures, movements and emotions (Allison, Puce, & McCarthy, 2000; Baseler, Harris, Young, & Andrews, 2013; Candidi, Stienen, Aglioti, & de Gelder, 2011; Grèzes, Pichon, & de Gelder, 2007; Kret, Pichon, Grèzes, & de Gelder, 2011; Pichon, de Gelder, & Grezes, 2009; Puce, Allison, Bentin, Gore, & McCarthy, 1998; Vuilleumier & Pourtois, 2007; Zhu et al., 2012). This fundamental role of STS is possibly dependent on its functional connections with medio-temporal structures (amygdala) (Amaral, Behniea, & Kelly, 2003; Catani, Jones, Donato, & Ffytche, 2003; Furl, Henson, Friston, & Calder, 2013) and with parieto-frontal areas (Rizzolatti & Matelli, 2003; Seltzer & Pandya, 1994) which are also causally involved in the perception of neutral postures (Avenanti, Candidi, & Urgesi, 2013; Urgesi, Candidi, & Avenanti, 2014). Despite its activation during conscious perception of emotional face and body images, it is presently unknown whether the pSTS plays a specific causal role in sustaining conscious perception of neutral and emotional faces and bodies.

Important information on the neural correlates of conscious visual perception has been obtained by using binocular rivalry paradigms where two different images, each steadily displayed to one eye, compete over time for perceptual dominance (Tong, Meng, & Blake, 2006). Direct recordings from cortical cells of monkeys and neuroimaging studies in humans have described activity of both monocular and binocular cells correlating with subjective perception during rivalry (Leopold & Logothetis, 1996; Logothetis, Leopold, & Sheinberg, 1996; Polonsky, Blake, Braun, & Heeger, 2000; Tong, Nakayama, Vaughan, & Kanwisher, 1998; Wunderlich, Schneider, & Kastner, 2005). Other studies found that conscious perception of the rivaling stimulus correlated with the activity of high-order, category-specific regions involved in the processing of visual stimuli (i.e., faces and places) (Tong et al., 1998; Wilson, 2003; Williams, Morris, McGlonem, Abbott, & Mattingley, 2004).

Previous brain stimulation studies explored the neural correlates of interocular competition of low-level visual stimuli (Carmel, Walsh, Lavie, & Rees, 2010; Kanai, Bahrami, & Rees, 2010; Kanai, Carmel, Bahrami, & Rees, 2011; Zaretskaya & Bartels, 2013). However, no information on the causal role of the pSTS in conscious perception of higher-order, category- and emotion-specific stimuli is currently available. We explored whether conscious visual dominance of socially relevant stimuli such as emotional expressions displayed by faces and bodies is supported by activity in high-order visual areas (right pSTS) possibly through its connections with lower-level, category specific visual areas, as well as with the amygdalae and fronto-parietal regions. To address this issue we applied off-line, inhibitory repetitive Transcranial Magnetic Stimulation (rTMS) to the right pSTS in healthy participants and measured the time of conscious dominance of emotional and neutral faces and bodies that rivaled a neutral, non-body, control stimulus (house) (Figs. 1 and 2). The vertex was used as control site. If inhibition of the right pSTS induces similar effects on emotional or neutral face and body processing this would suggest that this region has the same role in supporting the perceptual dominance of these stimuli. By contrast, finding category- and emotion-specific different effects would suggest that the right pSTS plays a different role in the networks underpinning emotional face and body expression processing respectively.

2. Method

2.1. Participants

Sixteen right-handed healthy volunteers (Mean age = 23.8 years, SD = 1.9) (Briggs & Nebes, 1975) with normal or

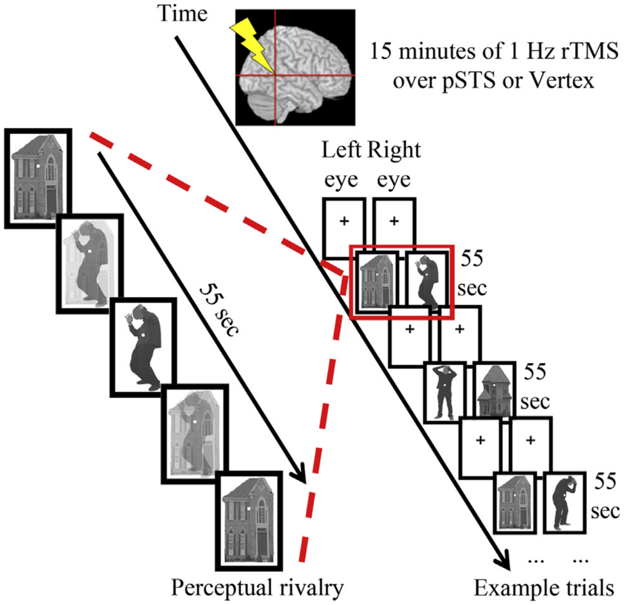

Fig. 1 – Timeline of the experimental trial and experimental set-up.

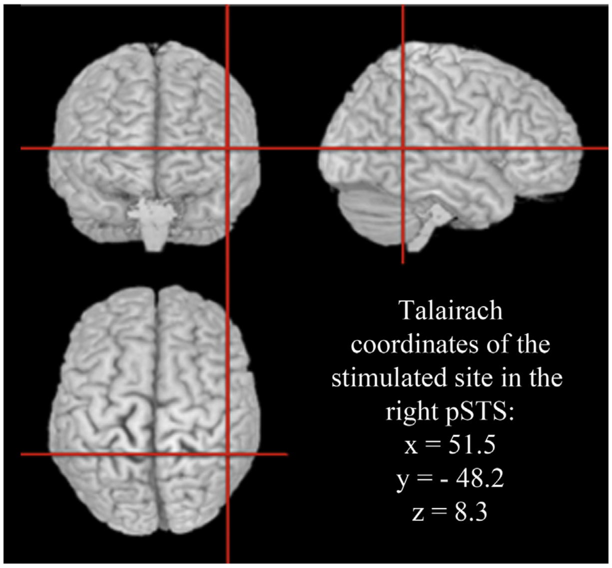

Fig. 2 – Reproduction of the TMS stimulation sites on a brain template. The average Talairach coordinates used in our study were the following: $x = 51.5$, $y = -48.2$, $z = 8.3$. The average coordinates used in our study were closer to a face-area (face pSTS Talairach coordinates: $x = 47$, $y = -63$, $z = 13$) than a body-selective area (body pSTS: $x = 45$, $y = -67$, $z = 14$) (Pinsk et al., 2009). A recent ALE meta-analysis on the loci activated during perception of static face and body images reported the following clusters in the temporal region: static face perception right pSTS, MNI $x = 52$, $y = -44$, $z = 8$; static body perception right MTG, MNI $x = 50$, $y = -66$, $z = 4$ (Grosbras, Beaton, & Eickhoff, 2012, Table VII). Peuskens, Vanrie, Verfaillie, and Orban (2005) reported that the form of the perceived human figure and the motion implied in its posture interacted in modulating the activity of the right STS (MNI $x = 57$, $y = -48$, $z = 12$).

corrected-to-normal vision received 30 euros for participating in the study. The experimental procedures were approved by the ethics committee of the Fondazione Santa Lucia (Rome, Italy) and were in accordance with the ethical standards of the 1964 Declaration of Helsinki. None of the participants had neurological, psychiatric or other medical problems or contraindications to rTMS (Wassermann, 1998).

2.2. *Stimuli*

The experimental visual stimuli consisted of bodies, faces and houses. The body stimuli portrayed images of actors expressing fear or showing emotionally neutral expressions (e.g., combing their hair) with their face covered by an opaque oval patch (Stienen & de Gelder, 2011). The face stimuli portrayed two different actors. Each one assumed either a neutral or an emotional expression (NimStim Face Stimulus Set, http://www.macbrain.org/resources.htm). A total of four pictures of bodily expressions (2 fearful and 2 neutral) and four pictures of facial expressions were used. Two pictures of houses (as control stimuli) were taken from a set that has been extensively used in other studies and is known to activate brain areas (Aguirre, Zarahn, & D'Esposito, 1998; Epstein & Kanwisher, 1998; Levy, Hasson, Avidan, Hendler, & Malach, 2001; Van den Stock, van de Riet, Righart, & de Gelder, 2008) that are different from those typically activated by bodies and faces (Fig. 3).

To control for contrast and brightness the mean grey-value and standard deviation were calculated for each image and the grey values of each image were adjusted to fall within the grey value range of ±1 SD from the overall mean of the pictures.

All stimuli were fitted into an area with a white background of 3°*4.83° enclosed by a black frame with a border thickness of .29° and with a central white fixation dot to enhance stable fusion and eye convergence. The center of the rivaling stimuli was positioned 11.89° left and right of the center of the screen, similar to the mirror stereoscope method (Blake & Logothetis, 2002). This procedure resulted in 8 body-house and 8 face-house displays (4 bodily/facial expressions × 2 houses). The displays were left-right mirrored to control for eye dominance and totaled 16 body-house and face-house displays.

The stimuli were presented on a 19″ PC screen with the refresh rate set to 60 Hz; responses were collected with Presentation 11.0.

2.3. *Experimental procedures*

2.3.1. *rTMS and neuronavigation*

The optimal scalp position (OSP) for inducing Motor Evoked Potentials (MEPs) in the right first dorsal interosseus (FDI) muscle was found by moving the coil in steps of 1 cm over the left primary motor cortex until the largest MEPs were observed. The resting Motor Threshold (rMT) was defined as the lowest intensity able to evoke five out of ten MEPs with an amplitude of at least 50 µV in the relaxed FDI. The average rMT intensity was 53% ± 10% of the maximum stimulator output.

Subsequently, the cortical target site (right pSTS) and a control condition (vertex) were localized. The pSTS area was identified on each participant's scalp with the SofTaxic Navigator system (EMS). Skull landmarks (nasion, inion and two preauricular points) and about 60 points providing a uniform representation of the scalp were digitized by means of a Polaris Vicra Optical Tracking System (NDI, Canada). Coordinates in Talairach space were automatically estimated by the SofTaxic Navigator from an MRI-constructed stereotaxic template. The scalp locations that corresponded best to those same regions of the right pSTS we studied previously (Candidi et al., 2011) were identified and marked with a pen. Group mean (±SD) coordinates ($x = 51.5 \pm 1.0$, $y = -48.2 \pm .9$, $z = 8.3 \pm .7$) corresponded to Brodmann area 22. The vertex was identified by finding a point midway between the inion and the nasion and equidistant from the left and right intertragal notches (Pitcher, Walsh, Yovel, & Duchaine, 2007).

Repetitive TMS (rTMS) was performed via a figure-of-eight coil (Magstim polyurethane-coated coil) connected to a Magstim Super Rapid Transcranial Magnetic Stimulator (Magstim, Whitland, Dyfed, U.K.). Previous studies have shown that rTMS at 1 Hz temporarily reduces the excitability of the stimulated cortex for a time window that outlasts the period of stimulation. During the stimulation of pSTS the coil was

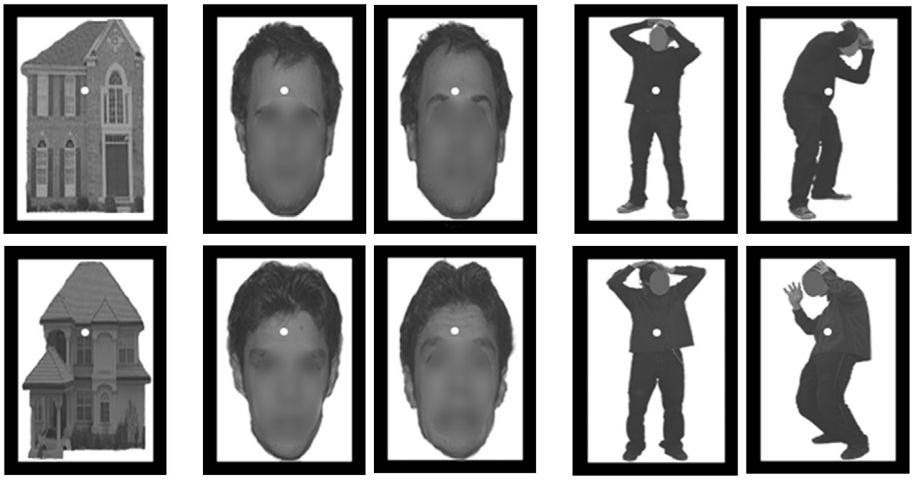

Fig. 3 – The image shows the entire stimulus set. Emotional and neutral face and body stimuli were pitted against a house image. The top and bottom rows show the stimuli used with different participants. Due to publication restrictions the face stimuli are blurred in the figure. Please contact the first author for the face stimuli used in the experiment.

held tangentially to the scalp, with the handle pointing backward and medially at a 45° angle from the nasion-inion line. The vertex was stimulated with the handle pointing backward horizontally in line with the transverse plane. During 1 Hz stimulation intensity was set at 90% of the individual rMT and the average stimulation intensity was 48% ± 9% of the maximum stimulator output. During stimulation, participants wore earplugs and sat comfortably in a chair in a dimly lit room with their hand relaxed on a pillow. None of the participants reported phosphenes, hand muscular twitches during rTMS of pSTS and vertex, or showed any discomfort.

2.3.2. *Binocular rivalry task*

Two different pairings of the house with bodies/faces were used in two subgroups of participants (Fig. 3) with the only aim of making sure that the duration of the rivalry sessions was within the ≈15-min inhibition window induced by rTMS stimulation. Participants performed two experimental sessions (each associated with the rTMS of different cortical sites). Each session consisted of 16 rivalry stimuli trials (i.e., periods of continuous rivalry image presentation). The rivalry stimuli trials were as follows: 4 fearful body-house (i.e., two fearful body-house trials with the house presented to one eye and two to the other eye), 4 neutral body-house, 4 fearful face-house, and 4 neutral-face house. Each trial lasted 55 sec. Thus, the total viewing time for each stimulus pair (e.g., fearful face-house independent of the eye of presentation) was 220 sec. This resulted in a total viewing time of 14.7 min for each experimental session. The bodies and faces were presented in a blocked design, meaning that the body-house and face-house pairs were not randomly mixed within the same session. Trials displaying neutral and fearful expressions were randomized (Fig. 1). We had face and body images rival a house image so that differences between the neutral and the emotional version of bodies and faces associated with either the implied motion or the relation to objects could not affect the dominance time. Furthermore, any differential impact of these features was controlled for by including a control stimulation site (i.e., the vertex) in the experimental design.

Prior to the rTMS experiment sessions the participants performed one practice session consisting of two rivalry trials with stimulus exemplars that were different from the experimental ones. When the participants indicated that they fully understood the procedures, the main experiment was started. Subsequently, the right pSTS or vertex was stimulated for 15 min. The starting site was counterbalanced across participants and the starting block was alternated between body-house and face-house pairings. After the first experiment session the participants rested for 45 min before the next site was stimulated.

Before each trial two empty frames were shown with a black fixation dot in the center. The participants were instructed to push and hold a button labeled “Y” with the middle finger to initiate a trial only if they saw one dot and one frame. This ensured that the participants fused the two black frames throughout the experiment. Subsequently, a body-house or face-house rivalry pairing trial was presented for 55 sec. Whenever participants saw a body (face) or a house in isolation they were instructed to release the “Y” button and push and hold the “X” and “Z” buttons, respectively, with their index or ring finger. The participants responded with their right hand and the fingers associated with the “X” (Face/Body) and “Z” (Houses) buttons were counterbalanced across participants. When they saw both stimuli they were told to push and hold the button labeled “Y”. The software program recorded the length of time each button was pressed. The participants were naïve to the presentation techniques and no reference was made to emotions.

During the rivalry stimuli pairings, the participant's head was kept still using a headrest. A black 70 cm wooden divider was placed between the screen and the middle of the eyes. The total distance between the screen and the eyes was 77 cm. Participants wore glasses on which two wedge-shaped prism lenses of 6 DVA were fitted. The prisms adjusted the viewing angle from which light from the screen entered each eye, ensuring that the laterally presented stimuli would fall close to the participants' fovea. The wooden divider was placed between the eyes to keep the visual signals separated.

At the end of the experimental procedures a short validation session was performed in which all stimuli were presented twice for two seconds to both eyes simultaneously. Participants were instructed to categorize the bodies and faces as fearful or neutral using two buttons. The averaged proportion of correct responses was .97 (SD = .09) for recognizing fearful faces, .97 (SD = .09) neutral faces, .90 (SD = .26) fearful bodies and .85 (SD = .32) for recognizing neutral bodies. A two-way repeated measurement ANOVA with stimulus type (face/body) and emotion (neutral/fear) as within-subject factors did not reveal a significant main effect or an interaction.

Finally, participants were asked to rate the perceived intensity of motion implied in each stimulus using a 10 cm Visual Analogue Scale (VAS, upper limit of the scale = strongest sensation of motion; lower limit = no sensation of motion).

2.4. *Data handling*

For each participant the cumulative viewing time (CVT) was computed separately for face and body blocks. Thus, CVT refers to the time a face (body), a house or a house-face or house-body composite was reported (Table 1).

The main analysis focused on the amount of time spent perceiving a body or a face, i.e., either neutral or emotional. (Analyses of house and mixed percepts were also performed to exclude the possibility that rTMS on one site induced changes in their dominance time). In addition to the general analysis, and based on the fact that *a priori* direct comparisons between the processing of faces and bodies are undesirable because of large, low-level visual differences between these stimuli, we performed two separate, hierarchically lower ANOVAs, one for the face and one for the body, with CVT (emotion (fearful/neutral) and stimulation site (vertex/right pSTS) as within-subject factors, see Results). Post-hoc comparisons were carried out using Duncan's test.

One participant reported having difficulty performing the task (i.e., no perception of fearful faces) and was excluded from the analysis which was run on 15 participants.

To test whether the changes observed in the dominance time of different stimuli after stimulation of the pSTS might be due to the activity of one or two different networks we correlated the dominance times in the conditions affected by the TMS at the individual level.

3. Results

An exploratory, three-way repeated measures ANOVA with stimulation site (vertex/right pSTS), stimulus type (face/body) and emotion (fearful/neutral) as within subject factors was performed on the cumulative viewing times for each stimulus. Overall this analysis showed that the inhibition of the right pSTS (and not the vertex) selectively reduces the dominance time of fearful (but not of the neutral) faces while increasing the dominance time of fearful (and not neutral) body postures.

In more detail no main effect was significant (all Ps > .166) while the two-way interaction between the stimulus type (face/body) and emotion (fearful/neutral) factors was found to be significant ($F_{(1,14)} = 9.78$, $p = .007$, partial $\eta^2 = .41$). Post-hoc comparisons showed that the viewing time for bodily neutral expressions was significantly lower than that for bodily fearful expressions (M = 47.40 sec, SD = 19.85; M = 54.77 sec, SD = 20.47; $p = .020$). In addition, the higher-level three-way interaction between stimulus type (face/body), stimulation site (pSTS/vertex) and emotion (fearful/neutral) was significant ($F_{(1,14)} = 10.21$, $p = .006$, partial $\eta^2 = .42$) and further explained the two-way interaction. Two repeated-measures ANOVA were performed on the cumulative viewing times of reporting faces and bodies in order to further reduce the data; they were based on two notions: 1) the higher-order significant triple interaction showing opposite effects of site and emotion on faces and bodies respectively; 2) as *a priori*, direct comparisons between the processing of faces and bodies are undesirable because of large, low-level visual differences between these stimuli.

3.1. *Faces*

The repeated measures ANOVA with stimulation site (vertex/right pSTS) and emotion (fearful/neutral) as within-subject factor revealed a significant interaction between emotion and site ($F_{(1,14)} = 5.38$, $p = .036$, partial $\eta^2 = .28$) highlighting the selective reduction of conscious visual perception of fearful faces compared to neutral ones when the pSTS was inhibited and to vertex stimulation (Fig. 4 left part). Specifically, post-hoc tests showed that the cumulative viewing time of fearful faces was shorter when the pSTS was inhibited compared to neutral faces ($p = .030$) and shorter than the viewing times of both neutral and fearful faces when the vertex was stimulated ($p = .041$, $p = .014$, respectively). There was no difference

Table 1 – Total dominance times (mean ± SD in seconds, n = 15) for each perceived image after stimulation of the pSTS and the vertex.

	Neutral face			Fearful face		
	Face	House	Mixed	Face	House	Mixed
pSTS	60.67 ± 22.90	52.10 ± 20.32	87.57 ± 36.19	50.94 ± 23.01	51.82 ± 25.28	90.06 ± 35.00
vertex	59.61 ± 21.78	53.92 ± 21.54	89.47 ± 33.63	62.55 ± 26.35	50.85 ± 24.14	89.80 ± 39.09
	Neutral body			Fearful body		
	Body	House	Mixed	Body	House	Mixed
pSTS	45.01 ± 23.14	49.83 ± 25.95	100.49 ± 46.85	58.77 ± 25.26	50.87 ± 23.24	91.18 ± 38.42
vertex	49.80 ± 20.44	53.55 ± 18.13	100.57 ± 36.34	50.76 ± 20.42	53.23 ± 18.40	97.85 ± 30.43

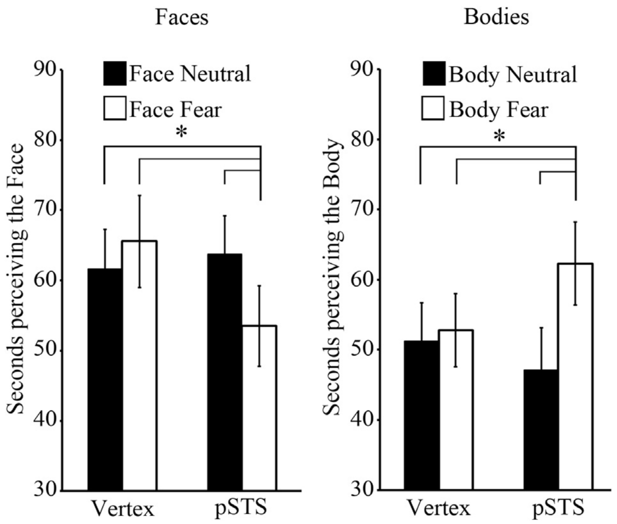

Fig. 4 – Group average conscious perception time (in sec ± SD) for neutral and fearful faces (left part) and bodies (right part) after stimulation of the right pSTS and the vertex.

between the viewing times of fearful and neutral faces when the vertex was stimulated ($p = .483$).

3.2. *Bodies*

The repeated measures ANOVA revealed a significant interaction between emotion and site ($F_{(1,14)} = 6.57$, $p = .023$, partial $\eta^2 = .32$), highlighting that the transient inhibition of the right pSTS increases the conscious visual dominance of fearful body postures with respect to neutral ones or to vertex stimulation (Fig. 4 right part). More specifically, post-hoc tests showed that when the pSTS was stimulated, the cumulative viewing times of fearful bodies was longer than that of neutral bodies ($p = .003$) and longer than the viewing times of both neutral and fearful bodies when the vertex was stimulated ($p = .029$, $p = .040$, respectively). Crucially, instead, there was no difference between the viewing times of fearful and neutral bodies when the vertex was inhibited ($p = .790$). In addition, a significant main effect of emotion was revealed ($F_{(1,14)} = 6.86$, $p = .020$, partial $\eta^2 = .33$) showing that the viewing times for fearful bodies were longer than for neutral bodies; interestingly, this effect was entirely accounted for by the double interaction, which showed that fearful bodies induced longer viewing times only after stimulation of the pSTS.

3.3. *No effect of stimulus pairing*

To study possible effects resulting from the fact that 8 participants received different stimulus pairings than the remaining 7 participants, two additional ANOVAs including stimulus pairing as a covariate were performed for face and body stimuli, respectively. The ANOVAs revealed that the interaction effect found for viewing time of faces and bodies was still significant confirming the presence of the selective reduction and facilitation of conscious visual dominance of fearful face and body stimuli after the inhibition of pSTS, (respectively $F_{(1,13)} = 5.908$, $p = .030$, partial $\eta^2 = .31$ (emotional face pSTS lower than emotional face vertex $p = .008$ and emotional face pSTS lower than neutral face pSTS $p = .019$) and $F_{(1,13)} = 6.375$, $p = .025$, partial $\eta^2 = .33$ (emotional body pSTS higher than emotional body vertex $p = .038$ and emotional body pSTS higher than neutral body pSTS $p = .003$)) and that stimulus pairing itself did not interact with this or any other term ($p > .060$ for face and $p > .182$ for body) or reached statistical significance as a factor (both $Ps > .206$).

3.4. *No effect of inhibitory repetitive transcranial magnetic stimulation of the vertex and the right posterior temporal sulcus on the conscious perception of houses and mixed images*

To test the hypothesis that the inhibitory stimulation of one of the two cortical sites (vertex/right pSTS) induced a systematic effect on the perceptual dominance of either the control stimulus (house) or the fusion between the experimental and the control stimulus (face/house and body/house mixture), we ran the same ANOVA that was performed on data concerning the time of dominance of the experimental stimuli (fearful face, fearful body, neutral face, neutral body) on the data concerning the dominance time of the house, face-house or body-house mixtures.

No significant results were revealed by the repeated measures ANOVAs with emotion (fearful/neutral) × site (vertex/right pSTS) × stimulus (face/body) as within-subject factors on the viewing time of houses, face-house or body-house mixtures (all $Ps > .333$ for mixtures, and all $Ps > .379$ for houses). This excludes the possibility that the results on faces and bodies were due to inhibitory or facilitatory effects on the perception of houses or mixtures.

3.5. *No correlation between emotional face and emotional body effects*

To test whether the reduction and the facilitation of emotional face and body dominance found after stimulation of the pSTS could be explained by a possible push–pull effect with neurons selective for one stimulus (e.g., face) exerting an opposite effect on neighboring cells selective for the other stimulus (e.g., bodies), we calculated two indexes of the pSTS effects for emotional faces and bodies at the individual level using the formulas:

$$x = (pSTS\ Fearful\ face) - (Vertex\ Fearful\ face)$$

$$y = (pSTS\ Fearful\ body) - (Vertex\ Fearful\ body)$$

and tested their correlation. No significant correlation between reduction of emotional faces and increase of emotional body dominance was found ($r = .387$, $p = .154$).

3.6. *Implied movement*

The results of within-subject ANOVA with stimulus type (face/body) and emotion (fearful/neutral) on the VAS ratings of the perceived implied motion in the stimuli showed a main effect of stimulus type ($F_{(1,14)} = 43.419$, $p = .00001$), explained by higher VAS ratings for bodies with respect to faces ($p = .0002$), and a main effect of emotion ($F_{(1,14)} = 30.088$, $p = .00008$), where fearful stimuli induced higher sensations of motion than neutral stimuli ($p = .0002$). The interaction between stimulus and emotion was significant ($F_{(1,14)} = 7.1586$, $p = .018$). This pattern of results is important because it excludes that the opposite effects found for fearful body postures and facial expressions dominance were due to the motion implied in the stimuli. Indeed, although at a subjective level the motion implied in the fearful stimuli was stronger than that in the neutral ones in both face ($p = .0002$) and body ($p = .0007$) images, rTMS to pSTS had opposite effects on emotional faces and bodies.

4. Discussion

The present study shows that a transient inhibition of the right pSTS reduced the visual dominance of a fearful face and facilitated the conscious perception of a fearful body compared with a rivaling house (control) stimulus. This double dissociation was entirely specific for emotional stimuli because no changes were observed in the conscious dominance time of neutral postures. Thus, inhibition of the pSTS brought about an imbalance of activity in body- and face-related neural networks where the emotional value of the stimuli is coded. The category specific modulation of emotional faces and bodies dominance suggests that the pSTS plays a different role in the conscious visual perception of these stimuli, possibly via its connections to two independent networks for face and body expression processing.

We discuss two different explanations for this result. First we describe evidence on the relative difference in category selectivity for (emotional) body and face representation in pSTS. Secondly we discuss the possibility that the effect found after pSTS inhibition reflects an inhibition of the “emotional face network” (mostly interfering with activity in amygdala-FFA connections) and a facilitation of the “emotional body network” (facilitating activity in amygdala-fronto-parietal regions). We conclude by presenting possible models to interpret the present findings.

4.1. *Categorical segregation: processing of static emotional faces and bodies in STS*

Although several single cell recording studies in monkeys and fMRI studies in monkeys and humans (de Gelder & Partan, 2009; Pinsk et al., 2009; Popivanov, Jastorff, Vanduffel, & Vogels, 2012; Puce & Perrett, 2003; Zhu et al., 2012) hint at segregated representations for face and body in the superior temporal cortex, the body seems to be mapped in a more posterior part of STS with respect to faces. However, obtaining clear evidence for a complete segregation of face and body responsive regions in the temporal cortex of humans has proven difficult (Pinsk et al., 2009, Pinsk, De Simone, Moore, Gross, & Kastner, 2005; Tsao, Freiwald, Knutsen, Mandeville, & Tootell, 2003). Importantly, studies of category selectivity that have provided evidence for segregated face and body areas used neutral face and body images rather than facial and bodily expressions (but see van de Riet, Grezes, & de Gelder, 2009). Ventral and lateral occipito-temporal regions are activated by the emotional content of face (Vuilleumier & Pourtois, 2007; Vuillemier, Richardson, Armony, Driver, & Dolan, 2004) and body expressions (Atkinson, Vuong, & Smithson, 2012; de Gelder, 2006; de Gelder, Snyder, Greve, Gerard, & Hadjikhani, 2004; Peelen, Atkinson, Andersson, & Vuilleumier, 2007; Pichon et al., 2009; Sinke, Sorger, Goebel, & de Gelder, 2010). The best candidate structure for mediating the coding of consciously seen emotional expressions may be the amygdala, which has direct anatomical connections with the temporal cortex (Amaral et al., 2003; Catani et al., 2003) as well as with premotor and motor cortex (Grèzes, Valabrègue, Gholipour, & Chevallier, 2014; Pessoa, 2014) and is specifically activated by the perception of emotional face and body stimuli (Hadjikhani and de Gelder, 2003; de Gelder et al., 2004; Sinke et al., 2010).

Thus far, no study has tested the causal contribution of the pSTS to the conscious perception of emotional face and body postures in a rivalry paradigm. By showing a selective effect of rTMS for fearful face- and body-stimuli, the present results are in line with a neural representation of emotional face and body postures in the right pSTS that is implemented in intermingled cells. More importantly, our finding that the effects are specific for fearful stimuli, provides evidence that face- and body-selective patches in the right pSTS show a selective but opposite causal role in supporting visual dominance of monocularly presented, category-specific, emotional stimuli. This opposite effect of pSTS inhibition on the conscious perception of fear expressed by faces and by bodies may be related to the fact that differences in the neural processing of two stimuli and the corresponding implications for social behavior. For example, the networks engaged in processing the emotions of body postures may strongly depend on action perception and action preparation mechanisms supposedly implemented in temporo-parieto-frontal networks while perception of facial expression may rely more heavily on processing in occipito-temporal visual networks.

4.2. *Network modulations: sensorimotor and visual contributions to the conscious visual perception of fearful stimuli*

The pSTS is connected to parietal and (pre)motor regions via direct and indirect anatomical pathways (Catani et al., 2003; Rizzolatti & Matelli, 2003; Seltzer & Pandya, 1994). Studies indicate that inhibition of pSTS activity is associated with an increase of premotor activity during the observation of dynamic (Arfeller et al., 2013) and implied body movements (Avenanti, Annella, Candidi, Urgesi, & Aglioti, 2013). Arfeller et al. (Arfeller et al., 2013) showed that inhibitory 1 Hz rTMS over left and right pSTS induced an increase in BOLD activity in premotor regions in individuals observing hand actions. Avenanti, Annella, et al. (2013) reported increased somatotopic cortico-spinal facilitation during implied action observation after pSTS 1 Hz rTMS inhibition. Backward connections also exist from premotor to pSTS regions as shown by monkey studies (Hietanen & Perrett, 1993; 1996). These connections are thought to inhibit the pSTS response to motion displays in the case where the movement is generated by the monkey himself. The functional connections between premotor and superior temporal sulcus may be the basis for Hebbian learning during the predictive perception of body postures sequences (Keysers & Gazzola, 2014; Perrett, Xiao, Barraclough, Keysers, Oram, 2009). The present findings complement the above evidence by suggesting that an increase in premotor activity after pSTS inhibition may compensate for the reduced visual information and thus facilitate the conscious visual perception of emotional body postures. The fact that this effect is selective for emotional body postures may be related to stronger premotor activation for emotional than for neutral body postures (de Gelder et al., 2004; Grèzes et al., 2007). This is in line with the idea that premotor activity has a perceptual function during observation of implied body action (Avevanti, Candidi, et al., 2013; Urgesi et al., 2014). No study has yet provided evidence as to whether the activation of frontal regions plays a role in emotional facial expression perception. Facial expressions induce mimicry in the observer and activate occipital, temporal, subcortical and frontal regions (Fusar-Poli et al., 2009; de Gelder et al., 2004; Jabbi & Keysers, 2008; Johnston, Mayes, Hughes, & Young, 2013; van de Riet et al., 2009; Seitz et al., 2008). Studies indicate that frontal regions are activated during the observation of static fearful facial expressions, possibly via the neuro-modulatory role of the amygdala (Morris et al., 1996, 1998). The results of the present study suggest that observation of implied movement in emotional body postures may boost premotor activity after pSTS inhibition with the effect of enhancing conscious visual dominance of fearful body postures. Such a compensatory activity may not occur in the face-network (Haxby et al., 2000) after pSTS inhibition with the consequence that no increase of fearful face dominance was observed.

Evidence consistent with this comes from Fairhall and Ishai (2007) who used static fearful face expressions and analyzed the functional connectivity between the OFA and other regions of the core (FFA, STS) and extended face system (Amygdala, Inferior Frontal Gyrus). These authors found that attending to static fearful expressions increases the functional connectivity between the FFA and the amygdala while leaving unaffected the connections between FFA, the amygdalae and premotor regions. We speculate that our pSTS inhibition may have reduced amygdala activity which in turn inhibited FFA, ultimately reducing the dominance of fearful but not of neutral faces.

4.3. *Models of pSTS role in emotional face- and body-dominance*

Four possible mechanisms of action of the rTMS may account for the category- and valence-specific dissociation we report in this study.

1) Our inhibitory stimulation may have targeted a predominantly face-selective portion of the pSTS (Pinsk et al., 2009; Weiner & Grill-Spector, 2011), inducing a facilitation of neighboring pSTS body-selective regions either by specific face-body connections or by "push–pull" passive effects for non-preferred stimuli (Allison, Puce, & McCarthy, 2002; Mullin & Steeves, 2011; 2013).
2) Another possibility is that pSTS inhibition had a specific effect on face-selective (or body-selective) regions of the amygdala and induced a "push–pull" facilitatory/inhibitory mix of effects (via lateral inhibition) on neighboring body-selective (or face-selective) cortical regions (Atkinson et al., 2012; Peelen et al., 2007; Vuilleumier, Richardson, Armony, Driver, & Dolan, 2004).

However, the absence of a significant correlation between the fearful face and the fearful body effect following pSTS inhibition suggests that a "push–pull" effect may not be at play. Rather our stimulation might have targeted both face and body neurons connected to different networks with opposite effects on the visual dominance of emotional faces and bodies (Fig. 5).

3) Thus it seems more reasonable that rTMS may have inhibited both face- and body-selective pSTS regions which, however, might have opposite facilitatory/inhibitory connections with the amygdala, the fusiform gyrus in the case of fearful facial stimuli and other fronto-parietal networks in the case of fearful body stimuli.
4) It is also possible that the stimulated pSTS region projected to segregated parts of the amygdala showing dissociated responses to fearful bodies and faces (Harris, Young,

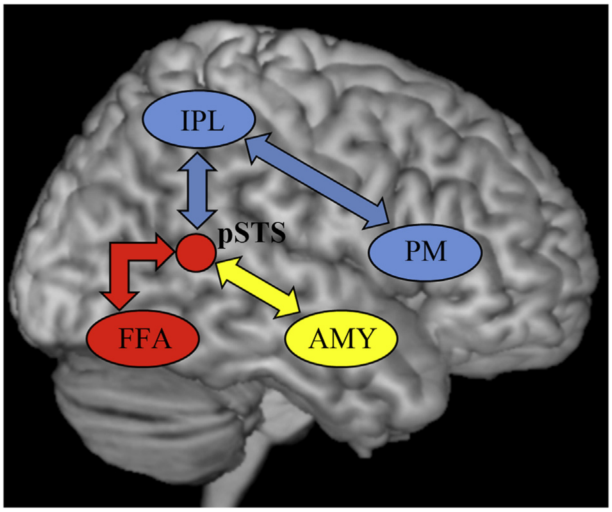

Fig. 5 – Schematic representation of the purported patterns of connectivity within the occipito-temporal, amygdala, parietal and frontal regions, possibly explaining the reduction and facilitation effect on fearful face and body processing, respectively, after inhibition of the pSTS. The present results support the notion that the right pSTS is functionally connected to face and body networks but that these connections may have an opposite function in the maintenance of conscious perception of emotional examples of these stimuli. Red connections with the fusiform face area indicate a possible inhibitory pathway to the conscious dominance of fearful face images after the transient inhibition of the righr pSTS; blue connections indicate a possible pathway to premotor regions facilitating conscious dominance of fearful body postures after the inhibition of the temporal region.

Andrews, 2014; Mormann et al., 2012), which could have facilitated and inhibited conscious perception of the two stimuli respectively.

5. Conclusion

Our study provides evidence for a causal role of the right pSTS in modulating category- and valence-specific perceptual dominance of face and body expression stimuli. In particular, transient inhibition of this region increases the dominance of fearful body postures and decreases the dominance of fearful face expressions but leaves the perception of neutral body and face postures unaffected. These results expand current knowledge about the role of the pSTS in mediating social signal processing by showing the crucial role of this region in modulating conscious visual perception of emotional body and face images.

Author contributions

B.M.C.S., M.C., S.M.A. and B.d.G. designed the research; B.M.C.S., M.C. performed the research; B.M.C.S. and M.C. analyzed the data; B.M.C.S., M.C., S.M.A. and B.d.G. wrote the paper.

Conflict of interest

The authors declare no competing financial interests.

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