



Temporo-parietal contribution to the mental representations of self/other face

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ABSTRACT

Face recognition requires comparing the current visual input with stored mental representations of faces. Based on its role in visual recognition of faces and mental representation of the body, we hypothesized that the right temporo-parietal junction (rTPJ) could be implicated also in processing mental representation of faces. To test this hypothesis, we asked 30 neurotypical participants to perform mental rotation (laterality judgment of rotated pictures) of self- and other-face images, before and after the inhibition of rTPJ through repetitive transcranial magnetic stimulation. After inhibition of rTPJ the mental rotation of self-face was slower than other-face. In the control condition the mental rotation of self/other faces was not significantly different. This supports that the role of rTPJ extends to mental representation of faces, specifically for the self. Since the experimental task did not require to explicitly recognize identity, we propose that unconscious identity attribution affects also the mental representation of faces. The present study offers insights on the involvement rTPJ in mental representation of faces and proposes that the neural substrate dedicated to mental representation of faces goes beyond the traditional visual and memory areas.

1. Introduction

Face recognition is a fundamental human ability, with dedicated cortical resources (Hoffman & Haxby, 2000) and especially important for identity attribution (Tsakiris, 2008). Far from being limited to the mere visual perception, identity attribution relies on higher-level cognitive mechanisms, such as the creation and manipulation of mental representations of faces. Despite its importance in daily life activities, the nature of the relationship between such mental representations and identity attribution remains unclear. In particular, it is still unknown whether identity attribution happens consciously after the comparison between the current visual input and the mental representations of faces, or whether it might start unconsciously in a previous step and then could influence the creation and processing of mental representations of faces themselves.

How to experimentally investigate mental representation of faces? This is possible via “mental rotation”, an active cognitive task in which participants are asked to identify the laterality of images of body parts (Cona, Panozzo, & Semenza, 2017; Ionta, Fourkas, & Aglioti, 2010). Concerning images of faces, usually a colored dot is positioned on one

side of a face image, which is then rotated in different orientations. Participants are asked to establish the side on which the dot appears, which requires mental rotation of the image into the upright position. With this approach, recent and seminal work showed the difference between mental rotation of faces versus inanimate objects (Tanaka, 2018; Yin, 1969) and between mental rotation of self-face and other-face images (Tong & Nakayama, 1999; Zeugin, Arfa, Notter, Murray, & Ionta, 2017).

At the brain level, the temporo-parietal junction in the right hemisphere (rTPJ) is the ideal candidate to neurally encode the relationship between identity attribution and mental representation of faces (Devue & Brédart, 2011). rTPJ has been implied in visual perception of faces (Gobbini & Haxby, 2007; Kesner et al., 2018), observation of self-face images (Heinisch, Dinse, Tegenthoff, Juckel, & Brüne, 2011), visual discrimination of self versus other faces (Decety & Lamm, 2007), and progressive identity attribution (Payne & Tsakiris, 2017). Indeed the disruption of neural activity in rTPJ through repetitive transcranial magnetic stimulation impairs the ability to distinguish self from other faces (Uddin, Molnar-Szakacs, Zaidel, & Iacoboni, 2006). In addition, rTPJ plays a important role also in mental processing of other bodily

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images (van Elk, Duizer, Sligte, & van Schie, 2017) and the mental representation of human bodies (Blanke, Ionta, Fornari, Mohr, & Maeder, 2010), including the mental differentiation of self versus other full bodies (Ganesh, van Schie, Cross, de Lange, & Wigboldus, 2015). Thus, since identity attribution is related to mental representation of faces and rTPJ is involved in both identity attribution and mental representations of the body, we hypothesized that rTPJ might play a role also in mental processing of faces, with a further distinction between the mental representation of self and other faces. To test this hypothesis we asked 30 neurotypical participants to perform mental rotation of self- and other-face images (without addressing faces' identity), in presence of non-invasive inhibition of rTPJ through repetitive transcranial magnetic stimulation and in a control condition (same inhibition protocol but performed over the vertex).

2. Materials and methods

2.1. Participants

30 right-handed neurotypical participants were enrolled in the study (15 women, age: 24.9 ± 4.8 years). All participants had normal or corrected to normal vision and no history of epilepsy, no neurological diseases, and no contraindications to transcranial magnetic stimulation. Prior to the experiment, each participant signed the informed consent and safety forms. The experimental procedures were in accordance with the local Ethics Committee and the Declaration of Helsinki 2013.

2.2. Setup

The experiment comprised two sessions. In the experimental session, rTPJ was inhibited. In the control session, the TMS coil was positioned over the vertex (control site), because its stimulation is not supposed to directly influence cortical areas (Ortiz-Tudela, Martin-Arevalo, Chica, & Lupianez, 2018). The positioning of the coil for rTPJ inhibition was based on the standard 10–20 system for electroencephalography, using the *Cp6* position to inhibit rTPJ and the *Cz* position to inhibit the vertex (Heinisch et al., 2011). During the inhibition protocol, the electroencephalography cap was removed, and participants remained still on a chinrest.

2.3. Procedure

Each participant took part to both sessions in counterbalanced order. During the sessions, participants sat in front of a computer screen, with their head fixed at 60 cm from the screen. An eye tracker (EyeLink 1000; SR Research Ltd., Mississauga, Ontario, Canada) was positioned just under the screen to monitor the participant's gaze and to use its direction as a response key (to avoid musculoskeletal movements; Fig. 1). Participants provided responses by fixating a designated area on the screen ("virtual buttons") (Zeugin et al., 2017). We used the software *Experiment builder* (SR Research Ltd., Mississauga, Ontario, Canada) provided with the eye tracker to program and present the experimental stimuli (images) and record behavioral data (response times, RTs).

2.4. Stimuli

In each session, participants were presented with images of self- or other-face with a black dot on one cheek (left or right; Fig. 1) and rotated in 12 orientations (0° to 330° , in steps of 30°). Self- and other-face images were presented separately in two different blocks. Each block contained only one identity. The order of the blocks was counterbalanced. In each block, each image was repeated three times, resulting in a total of 36 images per block.

Experimental Setup

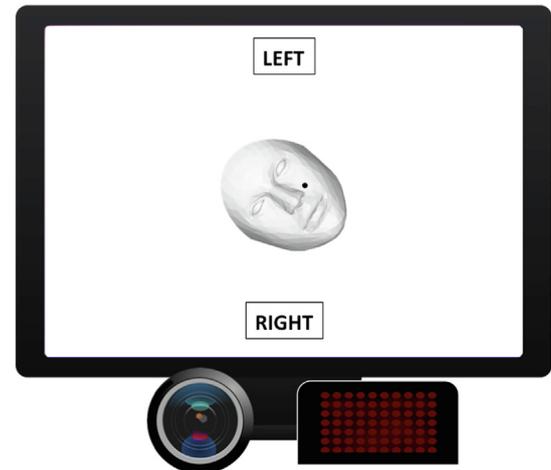


Fig. 1. Experimental setup. Self-face and other-face images were presented in the middle of the computer screen (replaced here by an avatar face for representational purposes). Two virtual buttons "LEFT" and "RIGHT" (the response buttons) were positioned above and below the face, in counterbalanced order. An eye-tracker located under the computer screen monitored the gaze of the participants, which was used also to record the response times.

2.5. Task

To perform mental rotation, participants were asked to determine the side of the face where the dot was positioned. A fixation cross appeared at the beginning of the trial. After 500 ms, a self-face or other-face appeared. To provide responses, participants fixated the "virtual buttons" situated on the top and bottom of the image in counterbalanced order and indicating, each separately, the two possible answers ("Left" or "Right"; Fig. 1). RT and accuracy were automatically recorded. RT was defined as the time between the image onset and the time when participants started to fixate one virtual response button for more than 300 ms. At the beginning of each session, participants were enrolled in a short training session, similar to the real task so that they could familiarize with the setup, but with images presented at different orientations to avoid visual habituation.

2.6. Brain inhibition

Before the experimental sessions, the resting motor threshold of each participant was determined (Fig. 2). To this aim, three electrodes (The Electrode Store, Model 1025, www.electrodestore.com) were placed on the left hand of the participant and were directly connected to the transcranial magnetic stimulation device (Rapid2 Magstim, The Magstim Company Limited, Spring Gardens, Whitland, Carmarthenshire, Wales, UK). The first electrode recorded muscular activity from the first dorsal interosseus muscle. The second electrode recorded tendon activity from the knuckle between the proximal and the middle phalanx of the index. The third electrode was placed on the head of the ulna bone and was used as a baseline. To determine the resting motor threshold, single pulses of transcranial magnetic stimulation (separated by a minimum of 7 s for preventing interference) were administered to the participant's right motor cortex in the region corresponding to the left index finger (approximately 4 cm below the vertex in the right hemisphere, in a coronal plane). This approach was used to regulate the TMS intensity until we obtained at least five motor evoked potentials in the first electrode out of ten single pulses, with a minimum of $50 \mu\text{V}$ (Huang, Chen, Rothwell, & Wen, 2007).

Once the resting motor threshold was determined, the inhibition protocol was performed for 20 min and consisted in 1200 transcranial

Timeline

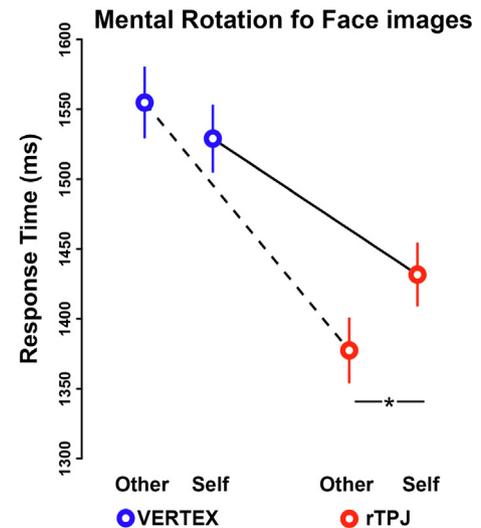
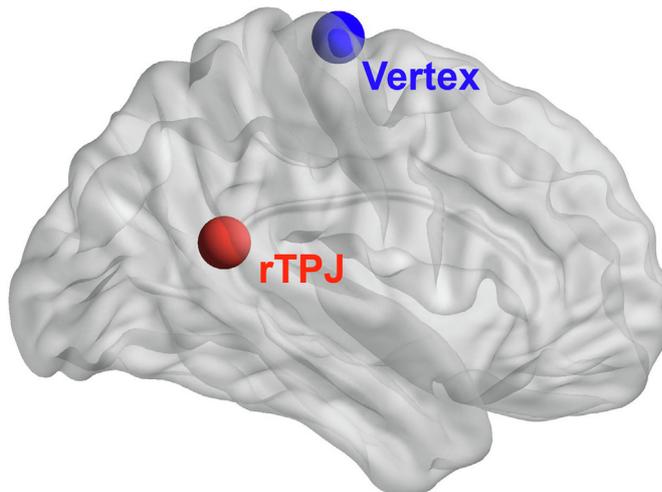
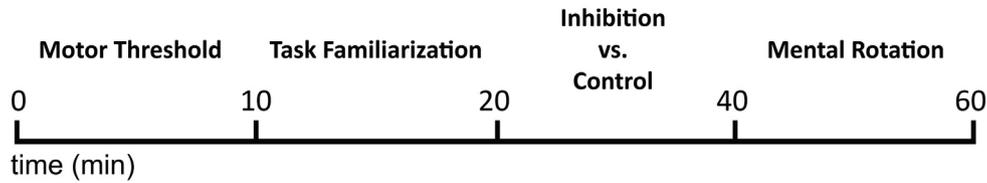


Fig. 3. A) Mental Rotation of Faces was performed after the inhibition of rTPJ (red) and vertex (control; blue). **B)** The significant interaction between Area and Identity indicated that, after the inhibition of rTPJ, mental rotation of self-face images was slower with respect to other-face images vertex. Such difference was not significant after the control condition. Asterisks indicate significant differences. Error bars represent standard error. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

magnetic pulses, at 90% voltage of the specific participant's resting motor threshold, and with a frequency of 1 Hz. To prevent interference between rTPJ versus vertex inhibition, these two sessions were performed at least seven hours apart from each other (see Fig. 3).

2.7. Data analysis

The goal of the experiment was to investigate the possible role of rTPJ in mental representation of self- and other-faces. Therefore, RTs were analyzed by a mixed linear model with the following within-subject factors: *Area* of inhibition (rTPJ, control), *Identity* of face images (self, other), and *Orientation* of images [four levels: *UP* (average of RTs for images presented at 330°, 0°, and 30°); *RIGHT* (average of 60°, 90°, and 120°); *DOWN* (average of 150°, 180°, 210°); *LEFT* (average of 240°, 270°, 300°)]. The identity of the subject was set as a random effect. To exclude any artifacts due to, for example, unexpected noise before or after the participant's response (coughing, mumbling, external noise), RTs shorter than 300 ms and longer than 5000 ms were removed from the analysis (Cooper & Shepard, 1975; de Lange, Helmich, & Toni, 2006; Sekiyama, 1982; Steggemann, Engbert, & Weigelt, 2011). In addition, two tails 95% confidence interval was used to exclude outlier trials within each participant from log-transformed RTs. RTs for incorrect trials were also removed from the analysis. This procedure led to perform statistical analyses on 94.3% of the original dataset. Post-hoc tests were Bonferroni-corrected for multiple comparisons. Partial eta square (η_p^2) were used as effect sizes. Statistical analysis was performed with the R software [R Core Team, Vienna, Austria].

3. Results

The significant interaction between Identity and Area [$F(1,29) = 4.3$; $p < 0.05$; $\eta_p^2 = 0.002$] showed that the inhibition of rTPJ was associated with significantly slower mental rotation of self- (1431.6 ms) than other-face images (1377.3 ms; $p < 0.05$).

Conversely, after the control condition the difference between the mental rotation of self- (1529 ms) and other-face images (1554.8 ms) was not significant (Fig. 3). In addition, the significant main effect of Area [$F(1,29) = 34.6$; $p < 0.001$; $\eta_p^2 = 0.01$] showed that mental rotation was generally faster after the inhibition of rTPJ (1404.4 ms) with respect to control (1541.9 ms). Finally, the significant main effect of Orientation [$F(3,116) = 23.38$; $p < 0.001$; $\eta_p^2 = 0.03$] showed that participants' RTs were non-monotonic at 180° [0° (1366.4 ms), 90° (1437.0 ms), 180° (1618.4 ms), and 270° (1476.6 ms)]. Post-hoc comparisons of the Orientation main effect showed that participants' performance was significantly different for images presented at each orientation (all $p < 0.05$), except 90° with respect to 270° ($p > 0.05$). As the main effect of Orientation has been repeatedly confirmed in previous studies, it will not be further discussed here.

4. Discussion

The present study shows that the neural activity in rTPJ (i) plays a key role on the mental manipulation of face representations, and (ii) differentially influences the mental representations of self- versus other-faces.

4.1. Faster mental rotation of faces after rTPJ inhibition

With respect to the control condition, the inhibition of rTPJ determined faster mental rotation of faces, suggesting that rTPJ is causally involved in mental representation of faces. Previous work showed the importance of rTPJ in visual perception of faces (Genetti, Khateb,

Heinzer, Michel, & Pegna, 2009; Lombardo et al., 2010). The present findings extend this theoretical background by introducing the idea that rTPJ plays an important role also at the representational level of face processing. Typically, mental rotation of faces relies on the integration between vision and somatosensation, as shown by the increase of RTs for the mental rotation of inverted face images with respect to inanimate objects (H. Tanaka, 2018). Such a stronger influence of image orientation on the latency of mental rotation indicates a greater reliance on somatosensory (instead of visual) strategies for the mental manipulation of bodily representations (Conson, Mazzarella, & Trojano, 2013; Devlin & Wilson, 2010; Ionta, Perruchoud, Draganski, & Blanke, 2012; Perruchoud, Michels, Piccirelli, Gassert, & Ionta, 2016; Wraga, Creem, & Proffitt, 2000; Wraga, Shephard, Church, Inati, & Kosslyn, 2005; Zacks, Mires, Tversky, & Hazeltine, 2002; Zacks, Ollinger, Sheridan, & Tversky, 2002). Considering the established role of rTPJ in multisensory and, in particular, visuo-somatosensory integration (Blanke, 2012; Graziano & Gross, 1993; Ionta et al., 2011; Ionta, Martuzzi, Salomon, & Blanke, 2014; Quinn et al., 2014), we interpret the present speeding up of mental rotation of faces as a sign that the inhibition of rTPJ shortcuts (at least partially) the time-consuming process of visuo-somatosensory comparison and results in faster mental rotation. More in details, we suggest that in normal conditions rTPJ compares the face-related visual input (from the primary visual cortex) with the somatosensory input (from the primary somatosensory cortex). This process takes time and, in the present study, was free to happen during the control condition, which indeed resulted in a longer mental rotation. In this vein, we propose that the inhibition of rTPJ blocked this visuo-somatosensory comparison and the visual input was immediately transformed into "purely" visual mental representations. In other words, we interpret the facilitation of mental rotation after inhibition of rTPJ as a sign of the rupture of time-consuming multisensory comparisons, which are still present in the control condition. This interpretation is in line with the idea that face representations are treated by the brain as holistic elements (DeGutis, Wilmer, Mercado, & Cohan, 2013) and that rTPJ has a role in the integrated representation of faces (J. W. Tanaka & Farah, 1993) and bodily representation in general (Wang, Callaghan, Gooding-Williams, McAllister, & Kessler, 2016). Thus, despite the hierarchy of the involvement of rTPJ in the different phases of face processing is yet to be fully understood, the present study puts forward that the neural substrate dedicated to mental representation of faces goes beyond the traditional visual or memory areas.

4.2. Implicit self-other discrimination in face representation

After the inhibition of rTPJ, but not the control site, mental rotation of self-face images was slower than other-face images. It is worth noting that participants were not asked to explicitly indicate identity. On this basis, we interpret this result as a sign that implicit self-other discrimination mechanisms can influence the creation and manipulation of mental representations of faces.

The specific effect of rTPJ inhibition on self-face representation extends previous work on (i) the behavioral influence of identity on the mental rotation of faces and (ii) the neural substrate of mental representations of self/other faces. At the behavioral level, showing that the inhibition of rTPJ produced a specific impairment in the mental manipulation of self-face images, the present study is in line and extends previous evidence that in normal conditions, when rTPJ is functioning properly, self-face images are processed faster than other-face ones (Keyes & Brady, 2010; Sugiura et al., 2006; Sugiura et al., 2005). It might be argued that a previous study showed that identity affects the mental rotation of faces in an orientation-specific manner, with a larger influence of image orientation on mental rotation of self- than other-face images (Zeugin et al., 2017). The absence of the interaction between Identity and Orientation in both the rTPJ and control conditions of the present study either could be related to a general effect of brain

inhibition, or can be explained by methodological differences, e.g. in the experimental stimuli (mental rotation images). In contrast to the study by Zeugin et al., 2017, in which the experimental stimuli comprised images of faces with a black patch covering one eye and ocular orbit, in the present study the experimental stimuli presented a black dot positioned about 2 cm away from one nostril. While the region of the eye is crucial for face-based identity recognition (Joyal, Jacob, Cigna, Guay, & Renaud, 2014), the regions around the nose are usually neglected during conscious visual recognition of faces (Van Belle, Ramon, Lefèvre, & Rossion, 2010). This could explain why in the present study the interaction between Identity and Orientation was not significant: because the black dot was placed in a region irrelevant for conscious attribution of face identity.

At the neural level, the slower mental rotation for self-face images following rTPJ inhibition found in the present study fits and extends previous evidence that rTPJ is involved in body representation (Berlucchi & Aglioti, 2010; Blanke et al., 2005; Tsakiris, Costantini, & Haggard, 2008), is more active during visual recognition of self- than other-face (meta-analysis in van Veluw & Chance, 2014), is involved in voluntary mental transformations of perspective taking (Santesteban, Banissy, Catmur, & Bird, 2012), and responds more strongly during the mental rotation of full-body egocentric reference frames with respect to allocentric ones (Ganesh et al., 2015). Accordingly, with respect to sham, the inhibition of rTPJ through cathodal transcranial direct current stimulation results in longer response times for self-related full-body mental rotation (van Elk et al., 2017). Similarly, the inhibition of rTPJ via transcranial magnetic stimulation disrupts the typical advantage for mental rotations of self which are congruent with physical rotations, with respect to incongruent rotations (Wang et al., 2016). In this framework, we propose that the present findings sustain that not only rTPJ is involved in visual recognition of self-face and global mental representations of the full body, but also it plays a key role in the intersection between these two constructs, being causatively associated with the mental representation of self-face and the discrimination between self and other face. Since our experimental task did not require participants to explicitly indicate the identity of the face images, the implication of rTPJ in determining identity-related behavioral differences can be considered part of an implicit identity attribution mechanism associated with mental representation of faces. Along this line, the present study's results sit at the intersection and constitute the bridge between the role of rTPJ in processing implicit body representations (Coslett, Buxbaum, & Schwobel, 2008; Medina, Jax, & Coslett, 2009) and its implication in mentally transforming these representations to assume different points of view (Wang et al., 2016).

It might be argued that the present finding that rTPJ inhibition determined slower mental rotation of self- than other-face images is in contrast with previous brain stimulation studies reporting that visual recognition of self-face is facilitated by the inhibition of rTPJ (Heinisch, Kruger, & Brune, 2012; Uddin et al., 2006) and impaired by the hyper-activation of rTPJ (Payne & Tsakiris, 2017). As both these studies required participants to perform a conscious visual identity recognition task, they could be considered evidence that rTPJ is causatively involved in visual recognition of self. However, their approach was different from the present study, in which (i) participants were not asked to attribute identity and (ii) the experimental task involved active mental manipulation of face images, not visual recognition. In addition, although both studies support an identity-dependent directionality of the neural activity in rTPJ during face recognition, it is worth noting that in the former study the difference between rTPJ inhibition and sham was at a trend level ($p = 0.075$). In a similar vein, the latter study might suffer from an intrinsically low spatial resolution of the brain stimulation device used to target rTPJ, it could be biased by the administration of the hyper-activation, inhibition, and sham conditions to three different groups of participants, and its results are in contrast with more recent evidence based on a device with higher spatial resolution and showing that self-inhibition does not necessarily occur in response

to hyper-activation of rTPJ (Martin, Huang, Hunold, & Meinzer, 2019).

5. Conclusions

The present study shows a facilitation effect of rTPJ inhibition on mental representation faces further modulated by face identity. These results support that rTPJ is a multimodal region involved in implicit self-other discrimination of mental representations of faces. This conclusion can have profound clinical relevance. In line with current trends in biomedical solutions for restoring damaged sensorimotor loops (Pisotta, Perruchoud, & Ionta, 2015), the direct causality between activity in rTPJ and cognitive processing of face could help understand and treat the sensorimotor base of face perceptual disorders, including prosopagnosia (Kagan, 2007).

Declaration of Competing Interest

All authors declare no conflicts of interest.

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