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Processing of featural and configural aspects of faces is lateralized in dorsolateral prefrontal cortex: A TMS study

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ABSTRACT

Facial recognition relies on distinct and parallel types of processing: featural processing focuses on the individual components of a face (e.g., the shape or the size of the eyes), whereas configural (or "relational") processing considers the spatial interrelationships among the single facial components (e.g., distance of the mouth from the nose). Previous neuroimaging evidence has suggested that featural and configural processes may rely on different brain circuits. By using rTMS, here we show for the first time a double dissociation in dorsolateral prefrontal cortex for different aspects of face processing: in particular, TMS over the left middle frontal gyrus (BA8) selectively disrupted featural processing, whereas TMS over the right inferior frontal gyrus (BA44) selectively interfered with configural processing of faces. By establishing a causal link between activation in left and right prefrontal areas and different modes of face processing, our data extend previous neuroimaging evidence and may have important implications in the study of face-processing deficits, such as those manifested in prosopagnosia and autistic spectrum disorders.

Introduction

We are exposed to thousands of faces and yet we are able to recognize those which are familiar from those which are not. Further, we can detect subtle changes in another's face, and we are able to recognize similarities in two people's faces, such as those occurring between brothers or sisters, parents and children. Facial processing is thus a quite sophisticated ability. Converging evidence suggests that face processing involves a complex network of cortical and subcortical areas (Gobbini and Haxby, 2007; Haxby et al., 2002; Ishai, 2008; Ishai et al., 2005; Natu and O'Toole, 2011). In particular, facial recognition seems to be based on distinct and parallel types of processing (Bombari et al., 2009; Mondloch et al., 2002; see Carbon, 2011): on the one hand, featural processing takes into account the identity of single components of a face (e.g., the shape or the size of the eyes), whereas configural processing considers the relations among those features (Carbon and Leder, 2005; Leder and Carbon, 2006; see Maurer et al., 2002 for a review). This latter type of processing can further be distinguished in: (i) sensitivity to first order relations, i.e., the relative position of the different features with respect to each other (in a face, typically the two eyes are above the nose and above the mouth); (ii) holistic processing, i.e., binding all the features into a single percept (gestalt), and (iii) sensitivity to second order relations (or relational processing; Rhodes, 1988) which consists in perceiving the distance among features (e.g., the distance between the eyes or between the mouth and the nose). Paradigms investigating featural-based and relational-based (i.e., sensitive to second-order relations) processes, such as the "Jane faces task" (Maurer et al., 2007; Mondloch et al., 2002) employ stimuli differing in single features (e.g., varying the shape of the eyes) while keeping their distance constant, or varying the spacing between the features without changing the single elements of the face.[1] Humans are usually better in detecting differences between faces due to featural than relational changes (Carbon and

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[1] It is worth noting that changes in spacing between facial elements may also slightly affect the way facial parts are perceived and that featural changes may also slightly affect how the whole configuration appears. Nonetheless, the validity of the featural and relational sets of the Jane faces task in selectively tapping on the corresponding processes has been extensively proven (Maurer et al., 2002, 2007; Mondloch et al., 2002, 2003, 2010). In particular, a critical validity test for the Jane faces task was the demonstration in Mondloch et al. (2002) (in which the test was first used) of higher inversion costs for the relational set than for the featural set, in line with long-standing evidence on inversion effects (e.g., Collishaw and Hole, 2000; Freire et al., 2000; Murray et al., 2000).

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Leder, 2005; Freire et al., 2000; Mercure et al., 2008; Mondloch et al., 2002, 2010); moreover, featural processing seems to emerge earlier in development compared to the ability to detect relational changes (Cashon and Cohen, 2004; Mondloch et al., 2002, 2003).

At the neural level, partially different neural circuits have been found to be involved in featural-based and relational-based facial recognition mechanisms. Examining brain activation during the execution of the Jane faces task, Maurer et al. (2007) reported a higher activation during same–different face judgments in areas of the right hemisphere, including the fusiform gyrus (adjacent to – but not overlapping with – the fusiform face area), the frontal and the inferior parietal cortex, when faces differed in terms of relational rather than featural aspects (see also Rotshtein et al., 2007). Left middle prefrontal activity instead was prominent for featural processing (Maurer et al., 2007; see also Lobmaier et al., 2008, for a left hemisphere predominant activation during featural processing of faces). This lateralization pattern is consistent with what is usually found for local/global processing of hierarchical stimuli (e.g., Martinez et al., 1997). Consistent with this, studies using ERPs have shown that the amplitude and the hemispheric lateralization of the N170 component – a negatively peaked component occurring approximately 170 ms after stimulus onset that differentiates faces and objects (see Bentin et al., 1996) – are modulated by presentation of featural or configural changes in face stimuli (Scott and Nelson, 2006; but see Mercure et al., 2008). Scott and Nelson (2006) found that the right hemisphere N170 was significantly greater for relational compared to featural processing, whereas the left hemisphere N170 exhibited the opposite pattern (Scott and Nelson, 2006). Using the Jane faces task, Mercure et al. (2008) observed that the P2 component was reduced in amplitude when elicited by a featural manipulation compared to a relational manipulation. Since the P2 component is likely to reflect the effects of visual cortical feedback (Kotsoni et al., 2006, 2007), the authors hypothesized that the larger P2 associated to configural processing may depend on faces with spacing manipulations relying to a higher degree on visual cortical feedback and thus requiring longer processing times compared to stimuli differing for single features only (Mercure et al., 2008).

However, ERPs and fMRI data are only correlational in nature, that is, they provide information on how manipulation of behavior may affect neural activity. Conversely, brain stimulation techniques such as TMS allow one to establish a causal link between a cortical site and a specific task, by directly modulating brain activity as the source of behavior. Here we used TMS to investigate the causal role of specific brain regions in featural and relational processing of faces. Specifically, we investigated the causal role of two regions in the dorsolateral prefrontal cortex, the right inferior frontal gyrus (rIFG, BA44) and the left middle frontal gyrus (lMFG, BA8), in featural and configural processing of faces using the Jane faces task (Mondloch et al., 2002). Participants were presented with two faces in sequence and had to decide whether they were identical or not (in case of a difference, the change could be featural or configural). rTMS was applied at 100, 150 and 200 ms after the appearance of the second face, in line with previous evidence showing differences in the ERPs pattern within this time window depending on the type of process – configural vs. featural – required (Mercure et al., 2008; Scott and Nelson, 2006). In a previous fMRI study (Maurer et al., 2007) during the execution of the Jane faces task (Mondloch et al., 2002) the rIFG has been implicated in the processing of second-order relations in faces, while lMFG has been associated to featural processing. If these regions in the DLPFC play a causal role in processing of faces, their stimulation should modulate participants' performance in same–different judgments for faces. More specifically, the rIFG should interfere with relational processing of faces (i.e., detecting changes in spacing between facial elements), but not with featural processing (i.e., detecting changes in the single features), whereas for the lMFG the opposite pattern is expected.

Method

Participants

Sixteen students of the University of Pavia (mean age: 22.06 years, SD: 1.53, range: 20–25, 4 males) took part in the experiment. Prior to the experiment, each participant filled in a questionnaire (translated from Rossi et al., 2011) to evaluate compatibility with TMS. None of the volunteers reported neurological problems, familiarity for seizures nor was taking any medication that could interfere with neuronal excitability. Written informed consent was obtained from all participants before the experiment. The protocol was approved by the local ethical committee and participants were treated in accordance with the Declaration of Helsinki.

Material and procedure

Participants were seated comfortably at a distance of 57 cm from a 17″ TFT-LCD computer monitor (screen resolution: 1440 × 900 pixels; refresh rate: 60 Hz) and wore earplugs to minimize TMS click sound interference. Stimuli were part of the Jane faces task set (Mondloch et al., 2002) and consisted of nine gray-scale images (image resolution: 72 × 72 dpi) of Caucasian female faces, eight of which were derived from the photograph of a single face (called "Jane") (see Fig. 1A). "Jane's sisters" were obtained by either replacing Jane's eyes and mouth with matching features from different females (featural set, four pictures) or by varying the spatial position of the eyes or the mouth (relational set, four pictures; see Mondloch et al., 2002 for further details). Participants were asked to judge whether two shortly consecutive presented faces were identical or differed in some aspects, by pressing the corresponding key with the index or the middle finger of the right hand. Response speed was stressed in addition to accuracy. Each volunteer took part in four blocks of stimulation (one for each TMS condition, see below) for each set (featural or relational). The two sets were run separately to allow time for each style of processing to emerge but participants were not explicitly informed about the distinctions (see Maurer et al., 2007). The order of presentation of the blocks belonging to the two sets was counterbalanced across participants. Each block consisted of 40 face-pairs presented in random order. All the 20 "different" face-pair possible combinations were presented once (with the order of the two faces being inverted), while all the 5 "same" face-pair combinations were presented four times. The timeline of an experimental trial is shown in Fig. 1B. Face stimuli were presented in the middle of the screen (subtending a visual angle of approximately 12° in height and 8° in width). Each trial started with a 1000 ms long central fixation cross followed by a blank screen for 500 ms and by the presentation of the first face that remained visible for 200 ms. The presentation of the first face was followed by a blank screen lasting 300 ms (as in Maurer et al., 2007). Then, the second face was presented: duration of the second face presentation was not pre-determined but the face remained visible until participants responded ("same or different face?").

Before the experiment, a short slide presentation was displayed to explain the task. The difference in the identity between stimuli was emphasized, but no cues were given about the type of changes that could occur. Further, prior to each set presentation, short practice blocks were performed in order to familiarize participants with the task and with TMS. Practice blocks included 20 trials each (ten "different" face trials and ten "same" face trials); the face stimuli used in the practice bocks did not belong to the sets employed in the experimental blocks and consisted of four faces and their modified version, obtained by changing either featural or configural details. The software E-prime 2.0 (Psychology Software Tools, Pittsburgh, PA) was used for stimuli presentation, data collection and TMS triggering. The whole experiment took approximately 90 min.