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The role of the left inferior frontal gyrus in episodic encoding of faces: An interference study by repetitive transcranial magnetic stimulation

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The role of the left inferior frontal gyrus in episodic encoding of faces: An interference study by repetitive transcranial magnetic stimulation

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Despite extensive research on face recognition, only a few studies have examined the integration of perceptual features with semantic, biographical, and episodic information. In order to address this issue, we used repetitive transcranial magnetic stimulation (rTMS) to target the left inferior frontal gyrus (IFG) and the left occipital face area (OFA) during a face recognition task. rTMS was delivered during the encoding of "context" faces (i.e., linked to an occupation, e.g., "lawyer") and "no-context" faces (i.e., linked to a nonword pattern, e.g., "xxxx"). Subjects were then asked to perform a recognition memory task. Accuracy at retrieval showed a mild decrease after left OFA stimulation, whereas rTMS over the left IFG drastically compromised memory performance selectively for no-context faces. On the other hand, absence of rTMS interference on context faces might be due either to the fact that pairing an occupation to a face makes the memory trace stronger, therefore less susceptible to rTMS interference, or to a different functional specificity of the left IFG subregions.

Keywords: Episodic encoding; Transcranial magnetic stimulation; Left IFG; Left OFA; Context; Memory; Prefrontal cortex; Recognition; rTMS.

INTRODUCTION

In order to understand how a face is encoded and stored in our brain, it is necessary to investigate how perceptual and semantic attributes are processed, such that a detailed episodic memory trace is laid down in long-term memory (Galli, Feurra, & Viggiano, 2006; Yovel & Paller, 2004).

Imaging studies showed signal covariations in the left prefrontal areas during the encoding of visual stimuli such as faces or scenes (Kirchhoff, Wagner, Maril, & Stern, 2000; McDermott, Buckner, Petersen, Kelley, & Sanders, 1999). Specifically, the left inferior frontal gyrus (left IFG) seems to be involved in face encoding (Haxby et al., 1996), and there's still a debate on whether face perception elicits activation

within a distributed cortical network involving this region (Ishai, 2008; Wiggett & Downing, 2008). Moreover, some interferential studies with repetitive transcranial magnetic stimulation (rTMS) definitely showed the causal role of the left prefrontal cortex in episodic encoding and memory formation (Kohler, Paus, Buckner, & Milner, 2004; Rossi et al., 2001; Turriziani et al., 2008).

In contrast, a different brain area named occipital face area (OFA), in the inferior occipital gyrus, seems to be more sensitive to physical aspects of the face stimulus rather than to face identity (Rotshtein, Henson, Treves, Driver, & Dolan, 2005). The OFA is involved in features discrimination of faces (Pitcher, Walsh, Yovel, & Duchaine, 2007) and it is among the three most important face-selective regions, in addition to the fusiform face area (FFA) (Kanwisher, McDermott, & Chun, 1997) and the superior temporal sulcus (STS) (Hoffman & Haxby, 2000; Puce, Allison, Bentin, Gore, & McCarthy, 1998). Despite its right hemispheric dominance, several imaging studies demonstrated its bilateral activation in face perception (Ishai, Schmidt, & Boesiger, 2005) and a main activation of the left occipito-temporal areas in face repetition (Pourtois, Schwartz, Seghier, Lazeyras, & Vuilleumier, 2005a).

In addition, classical studies revealed that the left hemisphere has an additional advantage for discriminating episodic and semantic tracks compared with the right hemisphere (Tulving, Kapur, Craik, Moscovitch, & Houle, 1994): Incoming items can be analyzed at different levels, ranging from shallow sensory analyses (form, pitch, etc.) to deeper semantic analyses involving meaning (Kapur et al., 1994). According to the previously reported neuroimaging and TMS studies, we first decided to test the involvement of the left IFG and OFA in episodic encoding of faces and then to gain insight on the possible dissociation related to the presence/absence of a deeper semantic context. Thus, we used rTMS to causally address the functional relevance of these areas in an old–new memory task. RTMS delivered online during the task transiently interferes with the neural activity of a given cortical target (Harris, Clifford, & Miniussi, 2008), thereby directly verifying whether such effects are associated with different behavioral consequences (Pascual-Leone, Walsh, & Rothwell, 2000; Rossini & Rossi, 2007; Walsh & Cowey, 2000).

In order to clarify whether the left IFG and the left OFA actively work during memory formation processes, a face recognition paradigm was used. In the study phase, faces were presented either in association with a semantic information (context faces, e.g. "teacher", "lawyer") or with a nonsense information (no-context faces, e.g., "xxxx"). In the test phase, context, no-context and new faces were presented in isolation, thus without any contextual cue. Then subjects were asked to perform an old/new judgment. By rTMS applied at encoding, we targeted the left IFG and the left OFA, and subsequently tested subjects' performance at retrieval. In order to control for site-specificity, Vertex stimulation was included at encoding, while no-TMS conditions tested basal subjects' performance.

Such a protocol allowed us to causally address whether there might be an involvement of the left IFG in episodic memory processes for faces and to gain insight into a differential engagement of the left IFG at encoding between a semantic condition (context face) and a neutral one (no-context).

MATERIALS AND METHODS

Participants

Twelve healthy participants (5 males and 7 females) ranging in age from 20 to 35 years took part in the experiment. All reported themselves to be right-handed, native English speaking, and with no history of neurological or psychiatric problems, or substance abuse. The experiment was approved by the UCL Committee on the Ethics of Human Research. Subjects were fully informed of the nature of the research and signed an informed consent to participate.

Apparatus and materials

Stimuli were presented centrally on an SVGA 17-inch monitor set at 1024×768 resolution and refresh rate of 100 Hz. Three hundred and forty-four grayscale pictures of faces were selected from the "Extended Multimodal Face Database – XM2VTSdb" (Messer, Matas, Kittler, Luettin, & Maitre, 1999). All stimuli were pre-processed by Adobe Photoshop graphics software. They were of approximately equivalent luminance and contrast and had no distinct emotional facial expressions.

Participants viewed the display at a distance of about 60 cm from the center of the monitor, with their right and left index fingers resting on the key buttons and spaced 5 cm apart in order to avoid any middle and index finger biases due to a different sensitivity and strength for the button pressure.

Task

In the study (encoding) phase, half of the faces (context faces) were preceded by a slide reporting the occupation of the person depicted; the other half (no-context faces) were preceded by a slide reporting a nonword pattern (e.g., "xxxx") (for the occupations list, see Table 1).

For each presented face, subjects were additionally required to perform a gender discrimination task (Figure 1a), in order to verify that attention was actually directed to the stimuli. Participants were instructed that later they would be involved in a memory task.

In the test (retrieval) phase, previously presented faces and new ones were shown on a blank background and subjects made an old/new discrimination judgment (Figure 1b). The experiment was divided in four blocks (encoding/retrieval) labeled according to the rTMS site (Left IFG, Left OFA, Vertex, and No-TMS). Each block was split into two sub-blocks per session. In each block, 13 context and 13 no-context faces were presented. The same 26 faces plus 17 new ones were presented during the test phase. The inter-trial interval was randomized between 2 and 4 s after subjects' response either for the encoding block or for the retrieval one. The time interval between encoding and retrieval was about 10 min (Kohler et al., 2004) for each block. Stimuli presentation and blocks order were randomized across subjects.

TABLE 1
Occupations list

Researcher	Telephone operator	Interior decorator
Risk analyst	Data processor	Sales agent
Eye specialist	Anthropologist	Civil engineer
Product developer	Notary	Baker
Commercial director	Marketing executive	Professor
Media manager	Chemist	Student
Painter	Teacher	Broker
Recruiter	Modeler	Assessor
Hygienist	Project leader	Biologist
Travel consultant	Writer	Translator
Singer	Ambassador	Politician
Sales coordinator	Journalist	Architect
Portfolio manager	Photographer	Adviser
Librarian	Safety coordinator	Restaurant manager
Customer executive	Estimator	Cleaner
Supervisor	Dancer	Hairdresser
Musician	Art director	Geologist
Barrister	Interpreter	Psychotherapist
General manager	Lawyer	Counselor
Planner	Procurement officer	Dentist
Copywriter	Statistician	Business adviser
Astrologist	Physiotherapist	Tailor
Ecologist	Pensioner	Chef
Stylist	Tutor	Physicist
Wine maker	Editor	Designer
Reporter	Doctor	Shop assistant

At the beginning of the experimental session, a practice block of 6 study and 9 test faces was delivered and repeated twice.

A PC running E.Prime software allowed the presentation of stimuli and recording of the responses. Accuracy and reaction times (RTs) from image presentation to the button press were measured on each trial for the memory task.

TMS protocol

Stimulation sites for TMS were identified on each participant's scalp using the Brainsight TMS-magnetic resonance imaging co-registration system (Rogue Research, Montreal, Canada), through conversion of the Montreal Neurological Institute (MNI) stereotaxic coordinates to the participant's normalized brain using the software SPM2. The Talairach coordinates for the left OFA (–42, –74, –8) corresponded to those of a previous functional magnetic resonance imaging (fMRI) study on face processing (Hasson et al., 2003). The left IFG coordinates (–49, 23, 13) corresponded to those of a previous fMRI study on episodic memory encoding and semantic memory retrieval (Prince, Tsukiura, & Cabeza, 2007) (Figure 2). The Vertex stimulation site was defined as a point midway between the inion and the nasion and equidistant from the left and right intertragal notches. Since this is mechanistically excluded by face and memory processes, it was considered as a control site for possible unspecific or arousal effects of TMS induced by somatosensory and acoustic effects. Stimulation was delivered through a MagStim Super Rapid stimulator with four external boosters with a maximum output of approximately 2 T (MagStim, Whitland, UK). A figure-of-eight 70-mm coil was used for the stimulation held by hand tangential to the scalp, with the handle pointing backwards and laterally, angled at 45° from the midline sagittal axis of the participant's head. The position of the coil with respect to the marked sites was checked continuously.

The rTMS was delivered during the encoding phase and it consisted of six pulses for 500 ms (10 Hz) starting at the face onset. Stimulation intensity was kept at 110% of the participant's motor threshold (MT). MT was determined at rest, defined as the minimal intensity of stimulation capable of inducing a visible twitch of the contralateral right abductor pollicis brevis (APB) muscle by a single pulse delivered at the best scalp position over the motor cortex (Rossi, Hallett, Rossini, & Pascual-Leone, 2009).

In order to minimize discomfort or pain at the stimulation site, irritation, and mood changes, we delivered some 10 Hz trains of stimulation (TMS
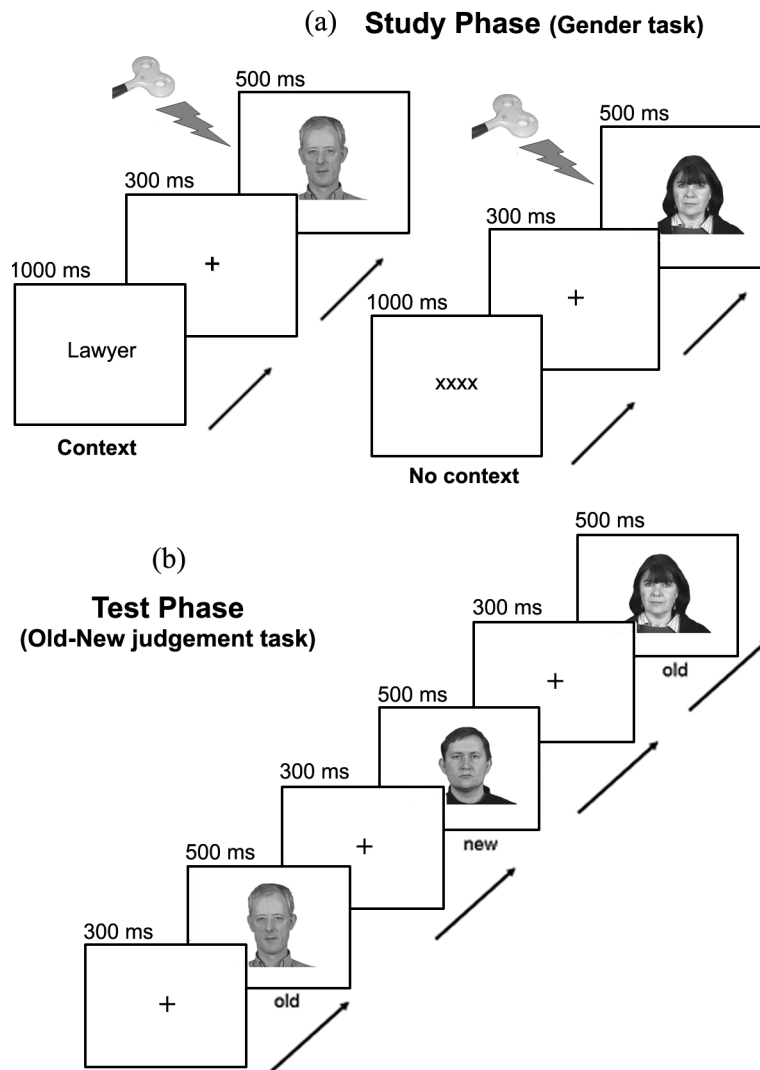
(a)   **Study Phase (Gender task)**

(b)

Test Phase
(Old-New judgement task)

Figure 1. Experimental task: (a) In the study phase, context and no-context faces were presented to subjects, who performed a gender discrimination task. rTMS (10 Hz–500 ms) was delivered at face onset. (b) In the test phase, previously presented faces were presented along with new ones, and participants had to perform old/new discriminations task.

training) on our subjects before the start of the experiment, asking them about any discomfort and eventually slightly adjusting the orientation of the coil. The order of the four experimental conditions (No TMS, left IFG, left OFA, and Vertex) was counterbalanced across subjects.

Data analysis

A two-way repeated measures analysis of variance (ANOVA) on accuracy scores and RTs, with four-level TMS site of stimulation factor (Left IFG, Left OFA, Vertex, and No-TMS) and three-level condition (context, no-context, new faces) was carried out,

taking account of any possible old–new effect as typically reported in recognition memory studies (Fraser, Bridson, & Wilding, 2007; Galli, Feurra, & Viggiano, 2006; Kazmerski & Friedman, 1997). Huynh-Feldt correction was applied when necessary to compensate for the violation of the assumption of sphericity. In the presence of significant interactions, corrected pairwise comparisons (Tukey's test) were performed. The level of significance was $p = .05$.

RESULTS

The ANOVA analysis on accuracy scores showed a significant interaction between the two main factors,
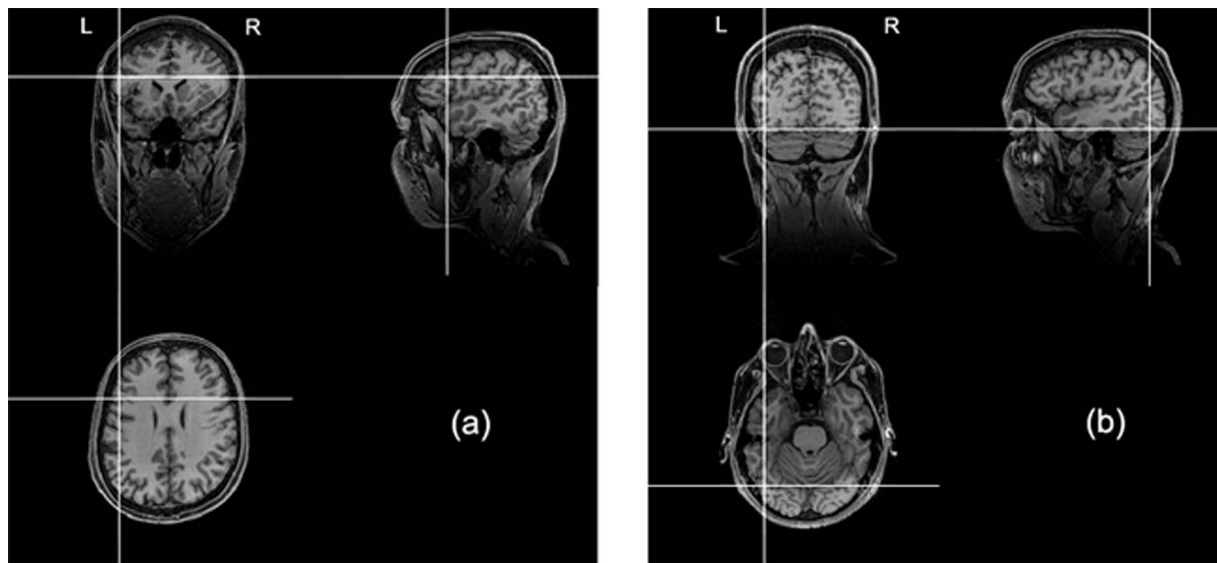
Figure 2. Areas of interest localized in one subject by normalization of his structural scan: (a) Left IFG based on Talairach coordinates: −49, 23, 13. (b) Left OFA based on Talairach coordinates: −42, −74, −8.
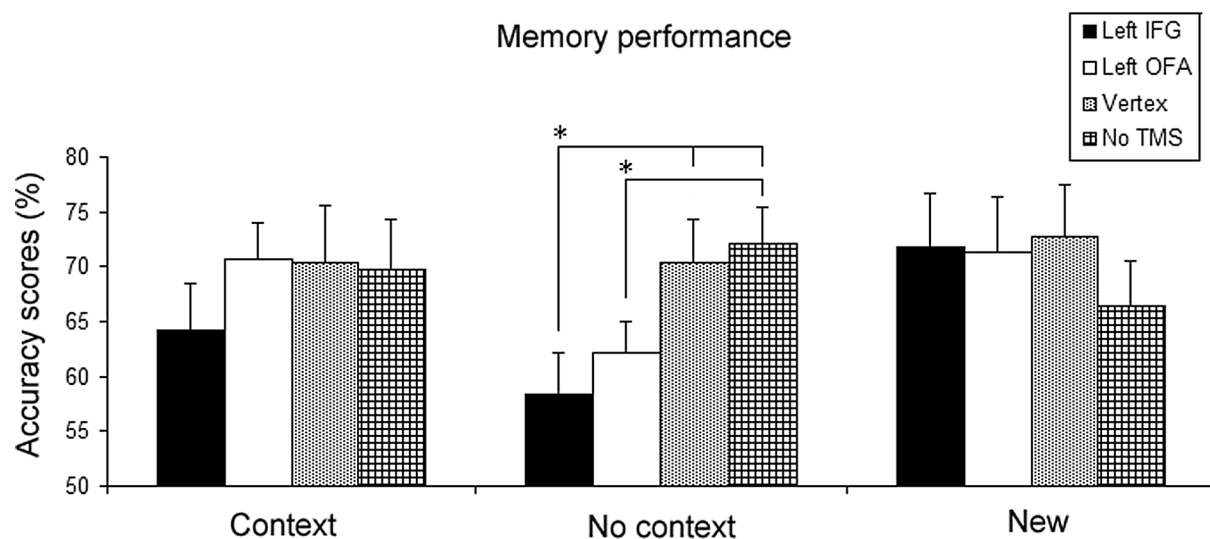

Figure 3. Percentage of memory accuracy for context, no-context, and new faces after rTMS in encoding (study phase). The error bars correspond to one standard error of the mean (*SEM*); * indicates a significant difference for no-context faces between Left IFG and Vertex, Left IFG and No-TMS, Left OFA and No-TMS.

$F(3.3, 37) = 2.975$, $MSE = 139.162$, $p = .039$. Post-hoc comparisons showed that rTMS delivered in encoding over the left IFG and left OFA significantly impaired the performance during the retrieval phase for stimuli belonging to the no-context condition: for the left IFG with respect to no-TMS ($p < .001$) and Vertex ($p = .006$) and for the left OFA compared to the no-TMS ($p = .034$) (Figure 3). An old–new near-significant effect emerged for no-context with respect to new faces ($p = .061$) (Figure 3) when stimulation was delivered over the left IFG.

No significant interaction was found for context stimuli.

In addition, a significant main effect emerged for site of stimulation factor, $F(3, 33) = 3.358$, $MSE = 77,987$, $p = .030$, but not for condition, $F(2, 22) = 0.508$, $MSE = 558.867$, $p = .608$. Post-hoc comparisons revealed that Left IFG stimulation compared to Vertex stimulation during the encoding phase significantly decreased the accuracy level in the test phase ($p = .022$). There were no significant results for the response time (RT) data.

DISCUSSION

The present study examined whether differential activity in the left prefrontal and occipito-temporal areas during encoding might reflect changes in the behavioral response of subjects performing a face recognition memory task. The new findings reported here support our initial hypothesis that OFA might have a major role for low-level mechanisms related to structural processes of faces. Indeed, we found that when the encoding of faces with no identity (no-context faces) is associated with disruptive rTMS over the left OFA, subjects' performance during the memory task significantly decreased compared to the no-TMS condition. This result is consistent with the idea that the OFA, besides participating to the memory trace formation, is highly sensitive to physical aspects of the face rather than to face identity (Rotshtein et al., 2005). This finding is supported by the neuropsychological evidence that a lesion to the left occipito-temporal area leads to an impairment in remembering unfamiliar faces, while the ability to recognize familiar faces is unaltered (Vuilleumier, Mohr, Valenza, Wetzel, & Landis, 2003). However, the detrimental effect of rTMS emerged exclusively vs. the no-TMS condition. Thus, we cannot exclude any unspecific rTMS effect, as the tactile and/or auditory stimulation. Further investigations might allow one to test the possibility that the left OFA may be involved in processing unfamiliar faces, whereas the right one is a part of a network specialized in identity recognition (Steeves et al., 2009).

The most striking result is provided by the direct evidence of a role of the left IFG in episodic encoding of faces. rTMS on the left IFG resulted in a strong decline of subsequent memory performance. Indeed, accuracy scores revealed that rTMS targeted at left IFG during the encoding process of no-context faces significantly reduced the probability of their retrieval, compared to our control conditions (Vertex and No-rTMS), suggesting that once encoded, retention in memory of featural and relational information could be partly compromised.

The absence of any effect on context faces may be related to different, not mutually exclusive, mechanisms: Different mechanisms consider that context face memory trace is probably stronger, and therefore less susceptible to rTMS interference, than that of no-context faces. Mutually exclusive mechanisms consider a neocortical dissociation within the left IFG between its anterior and posterior sections (Badre & Wagner, 2007; Prince et al., 2007). Whereas the anterior region showed greater activation for famous than for unknown faces during their first presentation, the posterior region seems more involved in encoding new stimuli, such as unfamiliar faces (Pourtois, Schwartz, Seghier, Lazeyras, & Vuilleumier, 2005b). In this study, contextual information makes the faces more familiar to the subjects, therefore more susceptible to slight changes in the encoding processes involving the left IFG. Along this line of reasoning, further imaging studies showed an increase of activation in the left IFG for episodic encoding and recognition of unfamiliar faces (Hofer et al., 2007). Taken together, these findings may suggest an involvement of the left IFG in the encoding of unfamiliar stimuli, whereas the right IFG may be involved in the retrieval of familiar, meaningful stimuli (Katanoda, Yoshikawa, & Sugishita, 2000). Indeed, a recent study by Manenti and coworkers showed that contextual manipulation (faces associated to names) during encoding processes produces a different engagement of dorsolateral prefrontal cortex (DLPFC) to operate a successful retrieval, depending on the individual subjects' strategy (Manenti, Cotelli, Calabria, Maioli, Miniussi, 2009).

Face recognition is a complex process that relies on a network of multiple brain regions associated with different processes, from structural analysis to retrieval of person-specific information. These processes are not activated in a strictly serial manner, as postulated by influential models (Bruce & Young, 1986). Rather, early visual analysis of faces can be modulated by the information flow from higher-order areas, which may mediate the retrieval of biographical, episodic, and semantic information referred to one's previous experience. Our study is in line with recent findings that left prefrontal areas, including left DLPFC and left IFG, participate in the encoding and recognition processes of visual stimuli (Kohler et al., 2004; Rossi et al., 2001, 2004; Viggiano et al., 2008; Zhang et al., 2008). In the current experiment, we test an interpretation about the role of left IFG and left OFA for faces in episodic encoding, showing an accurate specialization within the prefrontal areas. Such a functional specialization might account for the complex network related to memory processes that predicts left prefrontal activation during episodic encoding.

Despite the lack of a "non-face condition" (the experiment would have lasted too long for a TMS protocol), the experiment has been accurately controlled both for the two face conditions and for the stimulation blocks (Left IFG, Left OFA, Vertex, No-TMS). Thus, it is intriguing to consider the possibility of using this experimental paradigm for investigating memory decline in mild cognitive impairment (MCI) and mild Alzheimer's disease (AD) patients, since in both cases they may show deficits of episodic

and semantic memory related to person knowledge (Clague, Dudas, Thompson, Graham, & Hodges, 2005).

TMS has been successfully used to causally investigate episodic memory processes in the verbal (Rami et al., 2003; Sandrini, Cappa, Rossi, Rossini, & Miniussi, 2003) and visuospatial (Floel et al. 2004; Rossi et al. 2001, 2004, 2006; Turriziani et al., 2008) domains. On the other hand, we have to consider some limitations. It is only possible to use TMS and rTMS over dorsal and lateral areas of the neocortex. Stimulation over the most anterior frontal regions (orbital frontal) is generally painful for subjects (Rossi et al., 2009) and the temporal neocortex (i.e., hippocampus) is not directly accessible since it is too deep for the TMS-induced field (Rossi et al., 2009). Thus, we couldn't stimulate other face regions such as FFA and STS. However, future TMS applications may allow researchers to clarify the role of different subregions of the prefrontal cortex, which is the main area of integration of visual information between the ventral and the dorsal visual pathways (Ungerleider, Courtney, & Haxby, 1998), and to fully understand the neural mechanisms of episodic and semantic memory in their different subdomains.

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