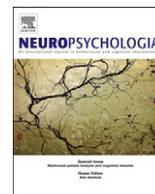




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## Spatial attention modulates early face processing

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### ABSTRACT

It is widely reported that inverting a face dramatically affects its recognition. Previous studies have shown that face inversion increases the amplitude and delays the latency of the face-specific N170 component of the event-related potential (ERP) and also enhances the amplitude of the occipital P1 component (latency 100–132 ms). The present study investigates whether these effects of face inversion can be modulated by visual spatial attention. Participants viewed two streams of visual stimuli, one to the left and one to the right of fixation. One stream consisted of a sequence of alphanumeric characters at 6.67 Hz, and the other stream consisted of a series of upright and inverted images of faces and houses presented in randomized order. The participants' task was to attend selectively to one or the other of the streams (during different blocks) in order to detect infrequent target stimuli. ERPs elicited by inverted faces showed larger P1 amplitudes compared to upright faces, but only when the faces were attended. In contrast, the N170 amplitude was larger to inverted than to upright faces only when the faces were not attended. The N170 peak latency was delayed to inverted faces regardless of attention condition. These inversion effects were face specific, as similar effects were absent for houses. These results suggest that early stages of face-specific processing can be enhanced by attention, but when faces are not attended the onset of face-specific processing is delayed until the latency range of the N170.

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### 1. Introduction

Facial recognition is one of the most important skills for human interaction and has been the focus of neuropsychological studies for decades. Three areas of the human brain have been identified as face-selective: the fusiform gyrus, known as the fusiform face area (FFA) (Kanwisher, McDermott, and Chun, 1997; McCarthy, Puce, Gore, and Allison, 1997; Sergent, Ohta, and MacDonald, 1992); the lateral inferior occipital gyri, known as the occipital face area (OFA) (Gauthier et al., 2000); and the superior temporal sulcus (Allison, Puce, and McCarthy, 2000; Hoffman & Haxby, 2000). Electroencephalographic (EEG) and magnetoencephalographic (MEG) studies aimed at measuring the timing of activation in these areas have consistently reported a prominent face-selective component (N170/M170), which typically peaks at around 170 ms after stimulus onset and is larger for faces than for non-face stimuli (houses, cars, scrambled faces, etc.) (e.g., Bentin, Allison, Puce, Perez, and McCarthy, 1996; Lu et al., 1991; Sams, Hietanen, Hari, Ilmoniemi, and Lounasmaa,

1997). Consistent with functional magnetic resonance imaging (fMRI) studies, event-related potential (ERP) and MEG studies have identified neuronal generators of the face-specific N170/M170 component in the fusiform gyrus and in the superior temporal sulcus (STS) (Liu, Harris, and Kanwisher, 2002; Itier & Taylor, 2004a).

There is evidence that an even earlier ERP/MEG component (P1/M100) may be increased in amplitude and latency for face stimuli, suggesting that face-specific neural processing is initiated earlier than the N170/M170. For example, Liu and colleagues (2002) found that the M100 component was enhanced by the successful detection of faces embedded in noise, and Debruille, Guillem, and Renault (1998) observed differential responses between known and unknown faces beginning at around 100 ms post stimuli onset.

Studies of inverted face processing have found that when faces were presented upside down their recognition was impaired to a greater extent than for other objects (Yin, 1969), a phenomenon known as the face inversion effect (FIE). Several MEG and ERP studies have found P1/M100 to be increased for inverted faces compared to upright faces (Itier & Taylor, 2002, 2004a, 2004b; Itier, Herdman, George, Cheyne, and Taylor, 2006; Linkenkaer-Hansen et al., 1998; Susac, Ilmoniemi, Pihko, and Supek, 2004; but

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see Rossion et al., 1999). These early face processing effects imply that at least some aspects of first-order face processing, such as defining a stimulus as a face via detection of its component features (Maurer, Le Grand, & Mondloch, 2002; Diamond & Carey, 1986), may take place prior to the N170/M170 response. Studies attempting to localize the neural sources of the P1/M100 elicited by faces have produced inconsistent results; some reports have suggested a source in the medial occipital cortex (Halgren, Raji, Marinkovic, Jousmaki, & Hari, 2000; Itier et al., 2006), while others have indicated sources in posterior extrastriate cortex (Linkenkaer-Hansen et al., 1998) or in higher level visual cortex of the mid-fusiform gyrus (Herrmann, Ehlis, Muehlberger, & Fallgatter, 2005). Previous studies have also found that face inversion delayed the latency of the N170 component (Bentin et al., 1996; Rossion et al., 1999, 2000; Rossion, Joyce, Cottrell, & Tarr, 2003; Itier & Taylor, 2002, 2004a, 2004b; Itier et al., 2006), and most but not all these studies also found enlarged N170 amplitudes to inverted faces compared to upright faces (Rossion et al., 1999, 2000; Itier & Taylor, 2002, 2004a, 2004b; Itier et al., 2006). These results suggest that inversion of a face may modify its processing over multiple time ranges.

Face processing has been considered to occur automatically or pre-attentively on the basis of ERP and MEG studies that reported little or no modulation of the N170/M170 by various manipulations of attention (Cauquil, Edmonds, & Taylor, 2000; Carmel & Bentin, 2002; Holmes, Vuilleumier, & Eimer, 2003; Downing, Liu, & Kanwisher, 2001; Furey et al., 2006). Recently, however, Crist, Wu, Karp, and Woldorff (2008) reported that the N170 component could indeed be modulated by the allocation of spatial attention; specifically, the authors found no significant N170 amplitude difference between faces and houses when they were unattended, but N170 amplitude was significantly larger for faces than houses when these stimuli were attended. These results suggest that the face processing as indexed by the N170 component is not invariably automatic but may be modulated by spatial attention.

Previous studies have reported that the early P1/M100 component can be modulated by factors such as facial configuration (Halit, de Haan, & Johnson, 2000), familiarity (Debruille et al., 1998), and emotional expression (Pourtois, Grandjean, Sander, & Vuilleumier, 2004; Pourtois, Thut, Grave de Peralta, Michel, & Vuilleumier, 2005). However, it remains unknown whether the early face processing revealed by the P1/M100 can be modulated by the allocation of spatial attention. The present experiment aimed to investigate the effects of spatial attention on face-specific processing in the latency range of the P1/M100 and N170 components and to localize the sources of neural activity modulated by attention. The ongoing EEG was recorded while two streams of visual stimuli were presented to the participants, a steady-state alphanumeric stimuli stream to one visual field and a face/house image stream to the opposite field. ERPs were recorded separately to upright and inverted faces and houses, while steady-state visual evoked potentials (SSVEPs) were concurrently recorded in response to the alphanumeric stream. On separate runs spatial attention was directed to either the face/house stream or the alphanumeric stream. Previous studies have shown that SSVEP amplitudes are enhanced by the allocation of spatial attention (e.g., Morgan, Hansen, & Hillyard, 1996; Müller & Hillyard, 2000; Mishra, Zinni, Bavelier, & Hillyard, 2011). Thus, modulations of SSVEP amplitudes here will demonstrate the effectiveness of the attention manipulation. The major question to be investigated in the present study is whether the effects of facial inversion on the P1 and N170 components can be modulated by spatial attention. Such modulations would indicate an influence of attention on the early processing of facial configurations.

## 2. Method

### 2.1. Participants

Thirteen right-handed subjects (five male, mean age 22 years) participated in this experiment after giving written informed consent. All subjects were recruited as volunteers and had normal or corrected-to-normal vision. The experimental procedures were approved by the Institutional Review Board of the University of California, San Diego, in compliance with the Declaration of Helsinki.

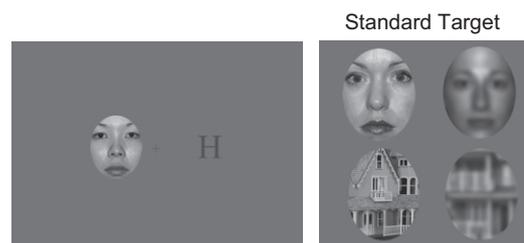
### 2.2. Experiment design

Two streams of stimuli were presented concurrently, one in the left and one in the right visual field. One stream consisted of a rapid serial visual presentation (RSVP) of alphanumeric characters ( $2^\circ \times 2^\circ$  visual angle) that appeared  $5^\circ$  laterally to a central fixation cross (see Fig. 1). This text stream consisted of non-target letters (96% of stimuli) and target numbers (4%). Each alphanumeric character appeared for 150 ms before being replaced by a subsequent character; thus the rate of stimulation was 6.67/s. The other stream of stimuli consisted of images of faces (from Nimstim Face Stimulus Set, Tottenham et al., 2009) and houses (both  $5^\circ \times 6^\circ$ ), which were presented in random order at an eccentricity of  $4^\circ$  from the center of fixation to the edge of the image. The face image set consisted of 35 faces (18 female), and the house image set consisted of 35 houses. The same face and house images were turned upside down to create matching inverted image sets. The stimuli onset asynchronies (SOAs) of successive face/house images were randomized between 600 and 900 ms in steps of 16.66 ms; specifically, each of the equiprobable SOAs was calculated as  $600 + N \times 16.66$  ms, where  $N$  was a randomly chosen integer between 0 and 18. All images were presented for 100 ms. The content of the image (face or house) was task-irrelevant, as the subject's task was to detect infrequent (20%) blurry-image targets (either faces or houses). While the face/house and alphanumeric streams differed in their SOAs, the overall target probabilities per unit time were approximately equal for the two tasks (attend blurry images or attend numbers).

During each block, subjects were asked to maintain fixation on the central cross while covertly directing attention to the instructed side (left or right) in order to detect targets in the stream presented on that side (numbers if attending to the RSVP sequence or blurry images if attending to the face/house sequence). For half of the blocks, face/house images were presented on the right side, and the alphanumeric stream on the left, and for the other half, the left/right locations were reversed. The locations of stimuli were counter balanced with respect to whether they were attended or unattended. Each subject performed 28 blocks consisting of 80 face/house images each; overall, each image was presented 16 times to each subject, eight times on the left (four attended, four unattended) and eight times on the right (four attended, four unattended).

### 2.3. EEG recording and analyses

Subjects sat in a dimly lit recording chamber while the EEG was recorded from 62 electrode sites (Electro-Cap International, Eaton, OH) using a modified 10–20 system montage (Di Russo, Martinez, & Hillyard, 2003). Standard 10–20 sites were FP1, FP2, F7, F3, Fz, F4, F8, T7, C3, Cz, C4, T8, P7, P3, Pz, P4, P8, O1, Oz, O2 and M1. Additional intermediate sites were AF3, AFz, AF4, FC5, FC3, FC1, FCz, FC2, FC4, FC6, C5, C1, C2, C6, TP7, CP5, CP3, CP1, CPz, CP2, CP4, CP5, TP8, P5, P1, P2, P6, PO7, PO3, POz, PO4, PO8, I5, I3, Iz, I4, I6, SI3, SIz and SI4 (10–10 system, Nuwer et al., 1998). The electrode impedances were kept below 5 k $\Omega$ . All signals were amplified (SA Instruments, San Diego, CA) with a gain of 10,000 and digitized at 250 Hz with an amplifier band pass of 0.01–80 Hz. The right mastoid electrode served as the online reference during data acquisition. Horizontal eye movements were



**Fig. 1.** Left: examples of stimuli in the condition where the face/house images were presented on the left and letters were presented on the right. The task was to detect blurry images in the face/house sequence or numbers in the alphanumeric sequence according to an instruction presented at the start of each block. The location of the face/house images was balanced on the left and right across blocks. Right: examples of standard stimuli (clear) and target stimuli (blurry) for faces and houses.

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