



ERP evidence for the speed of face categorization in the human brain: Disentangling the contribution of low-level visual cues from face perception

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ABSTRACT

How fast are visual stimuli categorized as faces by the human brain? Because of their high temporal resolution and the possibility to record simultaneously from the whole brain, electromagnetic scalp measurements should be the ideal method to clarify this issue. However, this question remains debated, with studies reporting face-sensitive responses varying from 50 ms to 200 ms following stimulus onset. Here we disentangle the contribution of the information associated with the phenomenological experience of a face (phase) from low-level visual cues (amplitude spectrum, color) in accounting for early face-sensitivity in the human brain. Pictures of faces and of a category of familiar objects (cars), as well as their phase-scrambled versions, were presented to fifteen human participants tested with high-density (128 channels) EEG. We replicated an early face-sensitivity – larger response to pictures of faces than cars – at the level of the occipital event-related potential (ERP) P1 (80–100 ms). However, a similar larger P1 to phase-scrambled faces than phase-scrambled cars was also found. In contrast, the occipito-temporal N170 was much larger in amplitude for pictures of intact faces than cars, especially in the right hemisphere, while the small N170 elicited by phase-scrambled stimuli did not differ for faces and cars. These findings show that sensitivity to faces on the visual evoked potentials P1 and N1 (N170) is functionally dissociated: the P1 face-sensitivity is driven by low-level visual cues while the N1 (or N170) face-sensitivity reflects the perception of a face. Altogether, these observations indicate that the earliest access to a high-level face representation, that is, a face percept, does not precede the N170 onset in the human brain. Furthermore, they allow resolving apparent discrepancies between the timing of rapid human saccades towards faces and the early activation of high-level facial representations as shown by electrophysiological studies in the primate brain. More generally, they put strong constraints on the interpretation of early (before 100 ms) face-sensitive effects in the human brain.

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1. Introduction

How fast can a visual stimulus be categorized as a face by the human brain? This question is of interest because measurements of processing speed in the visual system can constrain models of its functional organization. For instance, human observers can release a button when a face is present in a centrally presented natural scene as fast as about 250–300 ms following stimulus onset (Rousselet, Mace, & Fabre-Thorpe, 2003). When two scenes are presented simultaneously in the left and right visual fields, observers are even capable of initiating a saccade towards the scene containing a face as fast as 100–110 ms after stimulus onset (Crouzet, Kirchner, & Thorpe, 2010; for original studies with animal categorization tasks, see Kirchner and Thorpe (2006) and Thorpe, Fize,

and Marlot (1996)). Such short latencies between stimulus onset and correct behavioral responses suggest that these tasks are performed on the basis of a single feedforward sweep through the visual system (Thorpe & Fabre-Thorpe, 2002). Moreover, information might not even be able to reach high-level visual areas in such a short time scale, suggesting that extremely fast perceptual decision about the presence of a face in a visual scene may rely on evidence from low-level visual cues. For instance, it has been shown that saccades towards faces can be based merely on Fourier amplitude spectrum (AS) of the images rather than on information that is associated with the phenomenological experience of seeing a face in the stimulus (a high level visual representation), that is, phase information (Honey, Kirchner, & VanRullen, 2008; although see Cerf, Harel, Einhäuser, & Koch, 2008).

To date, these observations of extremely fast behavioral face detection have been difficult to reconcile with data obtained with the classical method used to infer the time-course of processing in the human brain at a global scale, namely event-related potentials (ERPs). As other visual stimuli, flashed faces elicit a sequence of ERPs – obtained by averaging segments of EEG time-locked to

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stimulus onset (Cobb & Dawson, 1960) – on the scalp, with the most prominent visual EPs taking place before 200 ms. These visual EPs have been described as (1) the C1, a component peaking at about 70 ms that is observed only for large stimuli at occipitoparietal sites of the midline and reverses polarity for stimuli presented in the upper/lower visual field, suggesting a major source in the primary visual cortex (Clark, Fan, & Hillyard, 1995; Di Russo, Martinez, Sereno, Pitzalis, & Hillyard, 2002; Jeffreys & Axford, 1972; but see Ales, Yates, & Norcia, 2010 for recent evidence that the C1 may arise from a combination of activation in striate and early extrastriate areas); (2) the P1 (called C2 by Jeffreys & Axford, 1972 and also referred to as P100 in some studies), a 100 ms peak component over central and lateral posterior electrode sites and thought to originate from dorsal and ventral extrastriate visual areas (Di Russo et al., 2002) and (3) a N1 component, or a complex of posterior negative components, peaking between 130 and 200 ms and whose distribution and response properties may vary substantially with the kind of visual material presented. Precisely, the visual N1 is particularly large in response to faces and most prominent on lateral occipito-temporal electrode sites.¹ When elicited by faces, this lateral N1 has been termed the N170 (Bentin, McCarthy, Perez, Puce, & Allison, 1996). Although magnetoencephalography (MEG) is sensitive to only a subset of the sources generating the EEG scalp components (i.e., tangential sources), MEG studies have also reported a sequence of similar visual responses or ERMf components, and in particular a M1/M100 and M170 in response to faces (e.g., Halgren, Raji, Marinkovic, Jousmaki, & Hari, 2000; Linkenkaer-Hansen et al., 1998; Liu, Harris, & Kanwisher, 2002; Okazaki, Abrahamyan, Stevens, & Ioannides, 2008; Sams, Hietanen, Hari, Ilmoniemi, & Lounasmaa, 1997; Watanabe, Kakigi, & Puce, 2003).

Considering this sequence of electrophysiological events reflecting visual processes, a question of interest is the following: along that sequence, what is the latency at which there is evidence that faces are processed differently from other visual stimuli, and can this time frame be related to behavioral markers of face detection?

While no modulation of the C1 elicited by faces as opposed to other visual stimuli has been reported to our knowledge, there have been reports of face repetition effects at extremely short latencies, sometimes as early as 45–80 ms (George, Jemel, Fiori, & Renault, 1997; Morel, Ponz, Mercier, Vuilleumier, & George, 2009; Mouchetant-Rostaing, Giard, Bentin, Aguera, & Pernier, 2000a; see also Seeck et al., 1997 for intracranial reports) or even at 30–60 ms (Braeutigam, Bailey, & Swithenby, 2001). However, such face repetition effects have been found at extremely early latencies, sometimes before or within the time-range of early primary visual cortex activation. Moreover, they differ between studies in terms of their scalp topography and timing, and several studies have found that these effects are not specific to faces or even to high-level visual stimuli (e.g., George et al., 1997; Mouchetant-Rostaing, Giard, Delpuech, Echallier, & Pernier, 2000b). Consequently, their significance with respect to the speed of face processing is doubtful.

In contrast, it is precisely because of its consistent larger response to faces than other visual stimuli that most studies have focused on the N170, a component whose positive counterpart on the central electrode sites – the vertex positive potential (VPP) – was the focus of early studies (Bötzel & Grusser, 1989; Jeffreys, 1989; see Joyce & Rossion, 2005). Like the VPP, the N170 (Bentin et al., 1996; Bötzel, Schulze, & Stodieck, 1995; George, Evans, Fiori, Davidoff, & Renault, 1996) has an average peak latency of about

160 ms over lateral occipital electrode sites in most studies, but its latency varies between 140–200 ms in individual brains. Its larger amplitude to faces than other visual stimuli may start as early as 120–130 ms (Bentin et al., 1996; Bötzel et al., 1995; Itier & Taylor, 2004a, 2004b; Rossion et al., 2000; Rousselet, Husk, Bennett, & Sekuler, 2008; for a review see Rossion & Jacques, 2008). Considering the faster visual responses recorded in the monkey than the human brain (e.g., Schroeder, Molholm, Lakatos, Ritter, & Foxe, 2004), this time-frame could well be compatible with the mean onset latency of neurons responding selectively to faces found in the monkey infero-temporal cortex (IT), i.e., about 90–100 ms (e.g., Kiani, Esteky, & Tanaka, 2005). That is, the mean onset latency of the N170 face effect – i.e., the larger response to faces than other visual categories – appears to correspond roughly to the time at which face-selective cells activity could be initiated in the human brain (Rossion & Jacques, 2008). Supporting this view, a large and typical N170 response is elicited by very different kinds of stimuli as long as they are readily perceived (i.e., interpreted) as faces by the visual system (i.e., photographs, schematic faces, line drawings, faces made by object parts, inverted faces, half-faces, isolated eyes, ... see Rossion and Jacques (2011) for a review).

However, if one considers that roughly 20 ms are necessary to activate the brain stem structures involved in oculomotor control, this 120–130 ms onset time-frame for the N170 is still incompatible with the speed of the 100–110 ms fastest saccades towards faces recently recorded (Crouzet et al., 2010). This reasoning suggests that the earliest saccadic responses towards faces are based on low-level visual information characterizing faces rather than face perception *per se*. In this context, it is particularly interesting that the P1 component, peaking at about 90–100 ms, has also been reported as being larger to pictures of faces than objects in a number of studies (e.g., Eimer, 1998; Goffaux, Gauthier, & Rossion, 2003; Herrmann, Ehlis, Muehlberger, & Fallgatter, 2005; Itier & Taylor, 2004a, 2004b; M1 in MEG studies, e.g., Halgren et al., 2000; Liu et al., 2002; Okazaki et al., 2008). These P1 face effects, starting shortly before 100 ms, are much less consistent than the N170 face effects, and so far, to our knowledge, they have been observed only with face photographs. Nevertheless, P1 sensitivity to faces is found in a sufficiently large number of studies, and thus should not be ignored when addressing the question of the speed of face categorization in the human brain (Rossion & Jacques, 2008). Moreover, there is recent evidence that P1 amplitude is correlated with neural activation in a right hemisphere face-sensitive area of the lateral inferior occipital cortex as identified in fMRI (Sadeh, Podlipsky, Zhdanov, & Yovel, 2010), and that early (60–100 ms) TMS-induced disruption of activation in this area may impair face processing (Pitcher, Walsh, Yovel, & Duchaine, 2007). Finally, intracerebral recordings from epileptic patients undergoing investigation prior to surgery show that category-related information, in particular about faces vs. object categories can be present in the response of areas in the ventral visual pathways as early as 100 ms after stimulus onset (Liu, Agam, Madsen, & Kreiman, 2009).

Considering these observations altogether, it can be hypothesized that these early face-related activities, in particular the face-sensitivity observed on the human scalp, i.e., the P1 face-effect, would reflect low-level visual cues that differentiate faces from other objects, most notably amplitude spectrum and perhaps category-related color cues. In contrast, the typical larger N170 response to faces than to objects would be largely driven by the shape of the stimulus, that is, the information that is associated with perceptual awareness of a face (Rossion & Jacques, 2008, 2011).

Previous EEG or MEG studies support this view, but only indirectly. For instance, early M1 differences between full color photographs of faces and objects may disappear when schematic

¹ T5/T6, or P7/P8 in 64-channel systems in the 10–20 electrode convention, or lower channels when available (see Rossion & Jacques, 2008).

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