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Interplay between familiarity and orientation in face processing: An ERP study

Tessa Marzi, Maria Pia Viggiano *

Department of Psychology, University of Florence, Italy

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Abstract

In order to tap the electrophysiological correlates of the perceptual and structural encoding stages of face processing, we investigated how inversion and familiarity affect the face-specific event-related potentials (ERPs) components. ERPs were recorded while participants performed a familiarity judgment task with upright and inverted photographs of famous and unknown faces. The early P100 component was found to be sensitive to facial configuration that is disrupted by face inversion. Noteworthy, in addition to the ongoing effect of orientation, an effect of familiarity, although limited to upright faces, emerged at the processing stage indexed by N170. Later on, as witnessed by the P250 component, the familiarity effect was generalized to both upright and inverted faces with a larger amplitude for inverted famous faces. All in all, the present results suggest that the face structural encoding stage is cognitively permeable by higher-order factors such as familiarity, especially when familiarity is crucial for mastering the task. From a more general viewpoint, these results indicate that face processing is subserved by multiple mechanisms in which structural (i.e. orientation) and semantic (i.e. familiarity) factors begin to interact at early processing stages with different time courses. The electrophysiological correlates of these mechanisms are documented by the differential involvement of the major ERP components in the "familiarity check". With upright faces familiarity affects the N170 component, while with inverted faces it affects later components, in keeping with a prolonged time course of the familiarity decision when orientation is not upright.

Keywords: Face processing; Structural encoding; Face recognition; ERPs; Configural processing; Inversion; Familiarity effect

1. Introduction

Understanding how the human brain recognizes faces is one of the most fascinating and challenging areas of research in cognitive neuroscience. Faces are particularly important stimuli and their recognition is crucial for social interaction. Whether or not specialized mechanisms exist for face processing is still under debate. In particular, there is disagreement about whether the neurocognitive operations involved in face processing are domain specific (Farah et al., 1998; Kanwisher, 2000; Carmel and Bentin, 2002) or common to those recruited in identifying members of a visually homogeneous object category for which one is expert, the so-called expertise hypothesis (Diamond and Carey, 1986; Gauthier and Tarr, 2002; Tanaka and Curran, 2001). Neuroimaging studies have localized a region, in the middle fusiform gyrus, that responds more strongly to faces than to objects, called the fusiform face area (FFA) (George et al., 1999; Kanwisher et al., 1997). The functional role of this region is now controversial. It could be an area specialized for face processing (Grill-Spector et al., 2004; Spiridon and Kanwisher, 2002; Kanwisher, 2000, 2006; Baker et al., 2007), part of a more distributed object-recognition system (Haxby et al., 2001; Haxby, 2006; Ishai et al., 2000, 2005) or an area subserving visual expertise processing that can be applied to any object category (Bukach et al., 2006).

The face inversion effect (FIE) is defined as the disproportionate drop in recognition of inverted as compared to upright faces. The FIE is considered a marker for the existence of neural networks specifically dedicated to faces because it has been repeatedly shown that the impairment in recognition of upside-down faces is stronger compared to that of inverted objects (Yin, 1969). The discovery of the FIE has led to the widespread belief that faces, unlike other objects, are perceived in a

* Corresponding author. Tel.: +39 55 2491628; fax: +39 55 2345326.
E-mail address: mpviggiano@psico.unifi.it (M.P. Viggiano).

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configural manner, that is as a “gestalt” or a whole. Unlike the processing of features, which is typical of object perception, configural processing is used for perceiving the distances and relations among physiognomic features such as the eyes, nose and mouth (for a review, see Maurer et al., 2003). The recognition of a known face does not appear to depend on the identification of a particular element (e.g. the nose or mouth), but on the recognition of the whole face that emerges as a perceptual gestalt. When faces are inverted the holistic configuration is no longer available and a featural or part-based processing is necessary leading to the typical drop in recognition speed and accuracy. The view that inverted faces are processed somewhat like objects, on the basis of their parts, is supported by the fact that individuals with acquired or congenital prosopagnosia do not show the classic FIE. Interestingly, they may even show better performance with inverted faces, probably because prosopagnostic patients commonly process faces with a feature-based strategy, since configural processing is impaired (Farah, 1996; Avidan et al., 2005; Behrmann et al., 2005). Although much research has used the FIE as a marker for specialized face recognition, the causes of this effect and its underlying neural correlates remain unclear. A possible neural localization for the behavioral FIE has recently been proposed by Yovel and Kanwisher (2005) who found that the FFA showed a greater neural sensitivity to differences between upright and inverted faces.

Electrophysiological studies have shed light on the temporal characteristics of the neuronal processing of faces. Face-specific event-related brain potential (ERP) modulations provide an important source of evidence for the existence of a specialized brain processing of physiognomic information. It has been repeatedly shown that faces elicit a specific negative potential, peaking at about 170 ms from stimulus onset (N170) at occipitotemporal sites, and a frontocentral positivity in the same latency range, the so-called vertex positive potential (VPP) (Eimer, 2000a; Bentin et al., 1996; Jeffreys, 1996; Botzel et al., 1995; Rossion et al., 1999). The N170 has become a marker for early human face processing because it was found to have larger amplitude for faces compared to butterflies or cars (Bentin et al., 1996). Sagiv and Bentin (2001) suggested that a face-specific mechanism reflected by the N170 is triggered whenever a stimulus contains sufficient information to generate the concept of a face. However, some studies have also shown an N170 effect when an object was categorized at the subordinate level (Tanaka, 2001) and when dog and bird experts were shown their objects of expertise (Tanaka and Curran, 2001). This might suggest that the level of categorization and degree of visual expertise are critical in explaining at least part of the difference in the N170 between faces and objects (Tarr and Gauthier, 2000). Recent studies challenge the N170 as being the earliest marker of selective face processing and draw attention to an earlier component, peaking between 100 and 120 ms post-stimulus (Taylor, 2002). The P100 ERP component is mainly generated in early extrastriate visual areas (Linkenkaer-Hansen et al., 1998) and is commonly thought to reflect low-level stimulus feature processing. This component has recently been found to be significantly larger for faces than for other object categories (Itier and Taylor, 2004a,b). A few recent studies have suggested that higher-order visual processing might already occur at this early stage. Successful categorization of stimuli as faces was found to correlate with the early P100 component (Itier and Taylor, 2002, 2004b; Linkenkaer-Hansen et al., 1998; Clark et al., 1996; Gomez et al., 1994) and also was reported to correlate with an early magnetoencephalography (MEG) component at 100–120 ms after onset, M100, while face recognition correlated with the later M170 (Liu et al., 2002), equivalent of the ERP N170 component.

An important result in favor of the specificity theory is that the N170 has been found to be particularly influenced by face rather than by object inversion. It is delayed for inverted as compared to upright faces (Bentin et al., 1996; Eimer, 2000b; Itier and Taylor, 2002, 2004a,b; Rossion et al., 2003b; de Haan et al., 2002) and its amplitude is larger for inverted than for upright faces (Rossion et al., 2000; Sagiv and Bentin, 2001; Eimer, 2000b; Rossion and Gauthier, 2002; Rossion et al., 1999). In relation to the behavioral literature, the effects of inversion on the N170 have been interpreted as a reflection of configural processing disruption (Maurer et al., 2003). The stimulus inversion interferes more with face processing than with object recognition. Face processing is probably due to a neural system that has evolved and specialized to process faces in a canonical orientation through everyday experience with upright faces. The N170 is thought to reflect structural encoding, that is, the extraction of a perceptual representation of the face (Eimer, 2000a,b; Rossion et al., 1999). One important question is whether there can be top-down influences arising from either task demands or familiarity effects at this early stage.

Psychological studies of face recognition have suggested a series of steps involving different cognitive processing stages. One of the most influential models (Bruce and Young, 1986) proposes that upright face processing is carried out in a hierarchical fashion by a number of relatively independent and sequential components, each of which performs specific computations such as structural encoding, familiarity decision, retrieval of semantic information and finally access to name generation. Each of these operations is potentially amenable to electrophysiological investigation. It has been argued that N170 reflects structural perceptual encoding rather than higher-order cognitive stages (Bentin et al., 1996). In keeping with this, it has been found that this component is not modulated by familiarity (Bentin and Deouell, 2000; Eimer, 2000b; Schweinberger et al., 2002). In contrast, there is evidence that the N170 can be influenced by higher-level processes such as task modulations (Goffaux et al., 2003), expertise (Tanaka and Curran, 2001), degree of face familiarity (Caharel et al., 2002, 2005), context (Galli et al., 2006; Righart and de Gelder, 2005), explicit facial decision (George et al., 2005) and priming (Jemel et al., 2003, 2005). Another study suggesting that early visual encoding can be cognitively penetrable is that by Bentin and Golland (2002). These authors found a modulation of the N170 for ambiguous schematic faces after exposure with normally configured versions of the faces. Thus, there is also evidence that the N170 can be influenced by top-down mechanisms, indicating that the neural mechanisms reflected by this component are not