NeuroImage

www.elsevier.com/locate/ynimg
NeuroImage 32 (2006) 352 – 367

Comparing neural correlates of configural processing in faces and objects: An ERP study of the Thatcher illusion

Luc Boutsen,[a,b,*] Glyn W. Humphreys,[b] Peter Praamstra,[b] and Tracy Warbrick[b]

[a]*School of Life and Health Sciences, Aston University, Birmingham B4 7ET, UK*
[b]*School of Psychology, University of Birmingham, Birmingham, UK*

Received 29 July 2005; revised 7 February 2006; accepted 13 March 2006
Available online 24 April 2006

In the Thatcher illusion, a face with inverted eyes and mouth looks abnormal when upright but not when inverted. Behavioral studies have shown that thatcherization of an upright face disrupts perceptual processing of the local configuration. We recorded high-density EEG from normal observers to study ERP correlates of the illusion during the perception of faces and nonface objects, to determine whether inversion and thatcherization affect similar neural mechanisms. Observers viewed faces and houses in four conditions (upright vs. inverted, and normal vs. thatcherized) while detecting an oddball category (chairs). Thatcherization delayed the N170 component over occipito-temporal cortex to faces, but not to houses. This modulation matched the illusion as it was larger for upright than inverted faces. The P1 over medial occipital regions was delayed by face inversion but unaffected by thatcherization. Finally, face thatcherization delayed P2 over occipito-temporal but not over parietal regions, while inversion affected P2 across categories. All effects involving thatcherization were face-specific. These results indicate that effects of face inversion and feature inversion (in thatcherized faces) can be distinguished on a functional as well as neural level, and that they affect configural processing of faces in different time windows.

Introduction

Human faces form a crucial source of information for the control of behavior. The importance of faces has led to the suggestion that face perception is functionally specific, and that its underlying cognitive mechanisms can be distinguished from those concerning nonface objects (Farah et al., 1998). One source of evidence comes from the face inversion effect, where recognition of faces is disproportionately more affected by inversion than recognition of nonface objects (e.g., Bartlett and Searcy, 1993; Farah et al., 1995; Leder and Bruce, 2000; Rakover and Teucher, 1997; Rhodes et al., 1993; Searcy and Bartlett, 1996; Valentine, 1988; Yin, 1969). Inversion reduces the availability of configural information in faces (i.e., the spatial relations between critical face parts; Diamond and Carey, 1986). As a result, the extracted information from inverted faces is more feature-based, involving individual face parts independent of their spatial relations or context.

The Thatcher illusion

Another compelling demonstration of the importance of configural information for faces comes from the Thatcher illusion (Thompson, 1980). Here, a face in which the eyes and mouth are inverted relative to the rest of the face ('thatcherized') looks grotesque when the face is viewed upright but looks relatively normal when it is viewed upside down. Indeed, an inverted thatcherized face is difficult to distinguish from a normal (undistorted) inverted face. Feature inversion distorts the spatial relations between face parts and hence the configural information contained in a face; this configural distortion is more salient for upright than for inverted faces. In various behavioral tasks (ratings, recognition), the effect of configural distortions (including thatcherization) to faces was more dependent on orientation than that of featural distortions (changing the colour or shape of features; Bartlett and Searcy, 1993; Rhodes et al., 1993). For example, the rated bizarreness of thatcherized, but not of feature-distorted faces, decreased dramatically as faces were rotated away from upright (Murray et al., 2000). Thatcherization also affects tasks that involve perceptual encoding of faces (without memory requirements). Boutsen and Humphreys (2003) found that same–different matching of simultaneously presented face pairs was affected by inversion for normal but not for thatcherized faces. These effects occurred even when feature-based matching was prevented by comparing faces of different identities, strengthening the suggestion that inversion of face parts disrupts the coding of configural information.

Electrophysiological studies of configural face processing

In the past decade, behavioral evidence for distinct modes of face processing has been complemented by evidence from neuroimaging and electrophysiological studies. Of particular relevance

* Corresponding author. School of Life and Health Sciences, Aston University, Birmingham B4 7ET, UK. Fax: +44 121 204 4090.
E-mail address: L.Boutsen@aston.ac.uk (L. Boutsen).
Available online on ScienceDirect (www.sciencedirect.com).

1053-8119/$ - see front matter © 2006 Elsevier Inc. All rights reserved.
doi:10.1016/j.neuroimage.2006.03.023

are event-related potential (ERP) studies of the P100 (P1), N170, P200 (P2) components measured over posterior cortex. These components can be modulated in latency and/or amplitude, by face inversion, whole-part changes, configural changes (scrambling), and contrast reversal (Bentin et al., 1996; Bötzel et al., 1995; Eimer, 1998, 2000a,b; George et al., 1996; Itier and Taylor, 2002, 2004b; Rossion et al., 1999; Sagiv and Bentin, 2001). In particular, the N170 component (a negative deflection reaching maximum amplitude ~150–200 ms post-stimulus at occipito-temporal electrode sites) has been interpreted as a face-sensitive neural correlate. The N170 is larger in amplitude to faces than to objects and is increased in latency and/or amplitude by face inversion (e.g., Bentin et al., 1996; Rossion et al., 1999), image scrambling (George et al., 1996), face or face-like parts (Bentin et al., 2002), and changes in face context (Eimer, 1998). At the same time, the N170 is unaffected by nonperceptual factors (e.g., familiarity; Bentin and Deouell, 2000; Eimer, 2000a). These findings suggest that the N170 reflects the perceptual encoding of faces, and that its sensitivity to inversion reflects a change in processing as a result of the disruption of configural information (e.g., Itier and Taylor, 2002; Rossion et al., 1999). In addition, face inversion can also modulate earlier (P1) and later (P2) positive components (Linkenkaer-Hansen et al., 1998; Itier and Taylor, 2002); these positive components are not thought to be face-specific, as their peak amplitude is similar to face and nonface stimuli (Rossion et al., 2003; Sagiv and Bentin, 2001). These observations from ERPs have also been supplemented by functional magnetic resonance imaging (fMRI) studies that demonstrated effects of face inversion on the hemodynamic response in occipito-temporal regions (Aguirre et al., 1999; Haxby et al., 1999; Kanwisher et al., 1998).

Many studies have investigated ERP effects of face configurations by manipulating inversion (e.g., Eimer, 2000a,b; Itier and Taylor, 2004a; Rossion et al., 1999; Rossion et al., 2003). Other manipulations used include contrast reversal (Itier and Taylor, 2002), schematic drawings or paintings (Sagiv and Bentin, 2001; Linkenkaer-Hansen et al., 1998), face parts in isolation (Bentin et al., 1996), and deletion of face parts (Eimer, 1998). Surprisingly, few studies have manipulated the spatial relations between the features in a face while maintaining the identity of the individual face features. For instance, in studies that used image 'scrambling', the identity of individual face features was not preserved (Bentin et al., 1996; Sagiv and Bentin, 2001; Taylor et al., 2001). Few ERP studies have presented whole face configurations in ways other than inversion while preserving face part information (although see George et al., 1996).

Due to its dramatic orientation-dependent perceptual effects, the Thatcher face illusion is a suitable manipulation for the study of neural correlates of configural face processing. If the N170 component reflects perceptual processing of configural information in faces, then one would expect the N170 to be influenced by thatcherization more for upright than for inverted faces, as in the latter case, configural information is less available. Recently, two ERP studies investigated the effect of the Thatcher face illusion on different ERPs components (Milivojevic et al., 2003; Carbon et al., 2005). Milivojevic et al. (2003) measured ERPs over occipito-temporal electrodes in response to normal and thatcherized faces presented at various orientations during a gender discrimination task. The P100, N170, and P250 were increased in amplitude when observers viewed thatcherized upright faces, but this effect disappeared or was attenuated when faces were rotated. This finding parallels the perceptual illusion. Interestingly, the change in perception of a thatcherized face after inversion was accompanied by a change not only in the face-sensitive N170 component, but also in the P100 and P250, that do not display face sensitivity. This suggests that local feature inversion might affect perceptual processes invoked by faces and nonface objects alike.

More recently, Carbon et al. (2005) measured ERPs to normal and thatcherized faces presented in three orientations (0° [upright], 90°, and 180°) in a recognition task. In contrast to Milivojevic et al. (2003), Carbon et al. (2005) found that only the N170 component was increased by thatcherization for upright faces; this effect was reduced for inverted faces. Thatcherization did not influence the P1 and had only a small effect on the P250 component. Although this result demonstrates a neural correlate of the Thatcher illusion for the N170 component, it also is at variance with Milivojevic et al.'s (2003) findings that (i) the N170 for inverted faces is unaffected by thatcherization, and (ii) that earlier and later components are also influenced by thatcherization. Moreover, Carbon et al.'s (2005) results are in line with an imaging (fMRI) study by Rotshtein et al. (2001) who found that thatcherization affected neural activity in specific cortical regions (the lateral occipital complex) for both upright and inverted faces; this contrasts with the behavioral effects of the Thatcher illusion. Together, these discrepancies are somewhat problematic for a coherent functional interpretation of neural modulations by configural changes in faces.

The present study

The above studies are important for an understanding of face processing because inversion and other configural manipulations may have distinct neural effects. While inversion preserves the spatial relations between internal face parts and their context, it distorts the global face configuration. Thatcherization in an upright face, on the other hand, distorts the configuration by changing the local relations between features, while preserving the orientation of the context. We report a comparison of the effects of inversion and thatcherization to assess whether the underlying neural processes that are modulated by these manipulations are the same. We investigated the effect of thatcherization on ERP components (P1, N170, and P2) that were previously influenced by face thatcherization and/or inversion. Our study differs in several respects from previous ones. First, as the effects of thatcherization and inversion are thought to affect perceptual stages in face processing (rather than memory-based identification or recognition), we used an oddball paradigm (cf., Bentin et al., 1996) requiring the simple discrimination between faces and objects (houses or chairs) and involving passive viewing of faces, without responses or additional face-specific task demands. This enabled equal treatment of the factors of interest (orientation, thatcherization) in the EEG analysis, as well as avoiding contamination of the EEG response to faces by potentials related to response preparation processes.

Second, we investigated whether effects of thatcherization and inversion are confined to faces or extend to objects (houses and chairs). Previous ERP studies of the Thatcher illusion only used face stimuli (Milivojevic et al., 2003; Carbon et al., 2005). With houses, we investigated effects of thatcherization as well as inversion, while with chairs, we investigated the effect of inversion only. The use of an additional nonface category (chairs) also allowed us to evaluate the domain specificity of ERP components and inversion effects to faces. If perceptual encoding of faces solely is sensitive to thatcherization, then we would expect effects