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Research report

Early stages of perceptual face processing are confined to the contralateral hemisphere: Evidence from the N170 component

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ABSTRACT

High-level visual object processing is often assumed to be largely position-independent. Here we demonstrate that when faces and non-face objects simultaneously appear in opposite visual hemifields, the face-sensitive N170 component of the event-related brain potential (ERP) is exclusively generated in the contralateral hemisphere. The effects of face inversion on N170 amplitudes and latencies also show strong contralateral biases. These results reveal that retinotopic biases in low-level visual cortex extend well into category-selective high-level vision. We suggest that the contralateral organisation of face-sensitive visual processing results from generic competitive interactions between hemispheres during the simultaneous perception of visual objects.

1. Introduction

High-level object vision is often believed to depend upon representations which are independent of the retinal position of an object. This popular view is explicit in hierarchical models of the primate ventral visual stream (e.g., Ungerleider & Mishkin, 1982). Such models assume that early stages of visual processing in striate and extrastriate occipital cortex represent simple features in a small spatially restricted region of the visual field, whereas complex object representations in inferior temporal cortex (IT) are largely position-invariant. While it is certainly true that receptive field size and the complexity of stimulus selectivity increases along the occipitotemporal visual pathway (e.g., Desimone & Gross, 1979; Gross, Rocha-Miranda, & Bender, 1972; Rousselet, Thorpe, & Fabre-Thorpe, 2004; Tsao, Freiwald, Tootell, & Livingstone, 2006), the question whether these changes are accompanied by a corresponding decrease in retinotopic biases of visual neurons has remained controversial (see Kravitz, Saleem, Baker, Ungerleider, & Mishkin, 2013, for a review). For example, single-unit data have demonstrated a strong bias towards the

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contralateral visual field in macaque anterior IT (Desimone & Gross, 1979; Op De Beeck & Vogels, 2000). While some human functional neuroimaging studies have suggested that high-level visual object representations are not strongly affected by changes in retinotopic position (e.g., Grill-Spector et al., 1999), others found evidence for strong position-dependence (e.g., Kravitz, Kriegeskorte, & Baker, 2010; Niemeier, Goltz, Kuchinad, Tweed, & Vilis, 2005; see also Afraz & Cavanagh, 2008, for the retinotopic nature of behavioural face adaptation effects). Hemond, Kanwisher, and Op De Beeck (2007) demonstrated a preference for contralateral stimuli in face- and object-selective regions. This preference was largest in primary visual cortex, and smaller but still reliably present in more anterior regions, such as the fusiform face area (FFA). The observation that this contralateral bias was present both for preferred and non-preferred visual categories (e.g., for non-face objects in face-selective areas; Hemond et al., 2007) suggests that it primarily reflects retinotopic input from lower-level visual areas that are not category-selective.

The limited temporal resolution of fMRI precludes direct insights into the emergence of contralateral biases in category-selective visual processing within the first 200 msec after stimulus onset. The aim of the present study was to use event-related brain potentials (ERPs) to investigate whether early stages of category-selective processing in the human brain are position-dependent or position-invariant. We measured the face-sensitive N170 component, which is an enhanced negativity for faces as compared to non-face objects that is typically observed around 140–200 msec after stimulus onset over posterior occipito-temporal electrode sites (e.g., Bentin, Allison, Puce, Perez, & McCarthy, 1996). The N170 is assumed to reflect early visual-perceptual structural encoding stages that precede face recognition and identification (Eimer, 2000a). Source localisation studies have pointed to middle fusiform gyrus (FFA), inferior occipital gyrus (OFA), and the superior temporal sulcus (STS) as possible generators of the N170 (Bötzel, Schulze, & Stodieck, 1995; Itier & Taylor, 2004; Rossion, Joyce, Cottrell, & Tarr, 2003; Watanabe, Kakigi, & Puce, 2003). Intracranial recordings from pre-surgical patients have recently observed face-selective responses in the right OFA and FFA in the same time-window as the N170 component (Jonas et al., 2012; Parvizi et al., 2012; see also Horovitz, Rossion, Skudlarski, & Gore, 2004; Sadeh, Podlipsky, Zhdanov, & Yovel, 2010, for correlations between haemodynamic and ERP markers of face processing).

In addition to its generic face-sensitivity, the N170 is also affected by manipulations known to impair face recognition, such as contrast reversal (Itier & Taylor, 2002), scrambling the locations of facial features (George, Evans, Fiori, Davidoff, & Renault, 1996; Zion-Golumbic & Bentin, 2007), and stimulus inversion (e.g., Bentin et al., 1996; Eimer, 2000b; Rossion et al., 1999; 2000). Relative to upright faces, the N170 to inverted faces is delayed and enhanced. The delay of the N170 in response to inverted faces suggests that the onset of face-specific processing is delayed when inversion alters the prototypical spatial relationships between face parts (Rossion et al., 2000). The inversion-induced increase of N170 amplitudes has been attributed to the increased difficulty of processing inverted faces (e.g., Rossion et al., 1999), or to the additional recruitment of populations of eye-selective neurons (Itier, Alain, Sedore, & McIntosh, 2007) or populations of object-selective neurons (Rossion et al., 1999, 2000; Rosburg et al., 2010) by upside-down faces.

The aim of the current study was to find out if the N170 component shows a contralateral bias. Is the differential N170 response to faces versus non-face objects exclusively triggered over the contralateral hemisphere or is it also elicited on the ipsilateral side? Are the effects of face inversion on N170 amplitudes and latencies restricted to the contralateral side or are they unaffected by the retinal location of upright and inverted faces? These questions have not been systematically addressed, because face and non-face stimuli were presented at fixation in nearly all previous N170 studies. With foveal stimulus presentation, the N170 is elicited bilaterally, and is often more pronounced over the right hemisphere (see Eimer, 2011; Rossion & Jacques, 2011, for reviews). In one earlier study from our lab (Eimer, 2000c), faces or non-faces (chairs) were presented unilaterally on the left or right of fixation. The N170 component was larger over the contralateral hemisphere, but was also present ipsilaterally (see also Rousselet, Husk, Bennett, & Sekuler, 2005, for the presence of bilateral face-sensitive N170 components to single laterally presented faces and houses). While larger contralateral N170 amplitudes to faces presented in the left or right visual field (e.g., Eimer, 2000c; Jacques & Rossion, 2004; Kovács, Zimmer, Volberg, Lavric, & Rossion, 2013; see also Smith, Gosselin, & Schyns, 2004, for evidence of larger N170 amplitudes triggered by the contralateral eye for centrally presented faces) may suggest that face-specific perceptual processing has a retinotopic bias, such findings need to be interpreted with caution. Because the N170 is a visual evoked ERP component, it is affected by basic physical stimulus features such as luminance, spatial frequency, and, importantly, retinal location (for a discussion of low-level stimulus properties and the face-sensitive N170 component, see Rossion & Jacques, 2008). Visual evoked components to single visual stimuli on the left or right side tend to be generally larger over the contralateral hemisphere, regardless of the category of these stimuli (e.g., Clarke et al., 1994; Jeffreys & Axford, 1972), and enhanced contralateral N170 amplitudes to unilateral faces may reflect this basic fact. For this methodological reason, it is preferable to use bilateral stimulus displays when investigating contralateral biases in category-selective perceptual face processing, as reflected by the N170 component.

There are also empirical reasons to assume that contralateral biases in category-specific object processing may differ for unilateral and bilateral visual displays. Single-unit studies of neurons in monkey temporal cortex (Chelazzi, Duncan, Miller, & Desimone, 1998) have revealed that these neurons respond to the identity of single visual objects regardless of whether they are presented in the contralateral or ipsilateral hemifield. In contrast, when two or more objects appear simultaneously in opposite visual hemifields, these neurons respond selectively to the contralateral object, but remain largely unaffected by the identity of the object in the ipsilateral hemifield. The presence of a competing object in the other hemifield appears to be sufficient to eliminate stimulus-specific neural responses in the ipsilateral hemisphere, presumably by inhibiting category-specific input signals from contralateral to ipsilateral temporal cortex (see also Hornak, Duncan, & Gaffan, 2002). If this is the case, contralateral