



The face-sensitive N170 component in developmental prosopagnosia

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ABSTRACT

Individuals with developmental prosopagnosia (DP) show severe face recognition deficits in the absence of any history of neurological damage. To examine the time-course of face processing in DP, we measured the face-sensitive N170 component of the event-related brain potential (ERP) in a group of 16 participants with DP and 16 age-matched control participants. Reliable enhancements of N170 amplitudes in response to upright faces relative to houses were found for the DP group. This effect was equivalent in size to the effect observed for controls, demonstrating normal face-sensitivity of the N170 component in DP. Face inversion enhanced N170 amplitudes in the control group, but not for DPs, suggesting that many DPs do not differentiate between upright and inverted faces in the typical manner. These N170 face inversion effects were present for younger but not older controls, while they were absent for both younger and older DPs. Results suggest that the early face-sensitivity of visual processing is preserved in most individuals with DP, but that the face processing system in many DPs is not selectively tuned to the canonical upright orientation of faces.

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1. Introduction

People with prosopagnosia are unable to recognize and identify the faces of familiar individuals, despite normal low-level vision and intellect (Bodamer, 1947). Until recently, prosopagnosia was thought to result solely from acquired lesions to face-sensitive regions in occipito-temporal visual cortex, such as the middle and posterior fusiform gyri (e.g., Barton, 2008). However, the existence of a different form of prosopagnosia that occurs without history of neurological damage has now been established (e.g., Behrmann & Avidan, 2005; Duchaine & Nakayama, 2006b). In contrast to acquired prosopagnosia (AP), individuals with developmental prosopagnosia (DP) typically show severe impairments of face recognition that emerge in early childhood and are assumed to result from a failure to develop normally functioning face processing mechanisms (see Duchaine (2011), for a review).

The perception and recognition of faces is a complex achievement that is based on a number of functionally and anatomically distinct processing stages (Bruce & Young, 1986; Haxby & Gobbini, 2011). Problems at any of these stages could be responsible for the face recognition deficits in individuals with AP or DP. The question which face processing mechanisms are impaired in prosopagnosia has not yet been answered conclusively. In AP, two general sources of face recognition deficits have been distinguished—selective

impairments of early perceptual stages of face processing (apperceptive prosopagnosia; De Renzi, Faglioni, Grossi, & Nichelli, 1991), and face-selective deficits at later post-perceptual stages, which could include impairments of long-term face memory, or disconnections of face perception and face memory (associative prosopagnosia; De Renzi et al., 1991). An analogous distinction might also apply to individuals with DP.

To identify which stages in the face processing hierarchy are impaired in prosopagnosia, event-related brain potential (ERP) measures are particularly useful tools. ERPs provide online measures of neural activity and thus are able to track neural correlates of face perception and face recognition on a millisecond-by-millisecond basis. The earliest ERP markers of face recognition have been found at post-stimulus latencies of 200 ms and beyond (e.g., Schweinberger, Pfütze, and Sommer (1995), Begleiter, Porjesz, and Wang (1995), Bentin and Deouell (2000), Eimer (2000a), Schweinberger, Pickering, Jentzsch, Burton, and Kaufmann (2002)). For example, an occipito-temporal N250 component is triggered when famous faces are explicitly recognized, but not when these faces merely seem familiar (Gosling & Eimer, 2011). The N250 has been linked to an early stage of face recognition where incoming visual-perceptual information about a seen face is matched with stored representations of familiar faces in visual memory. We have recently employed this N250 component to trace the locus of face recognition deficits in DP (Eimer, Gosling, & Duchaine, 2012). Six of the twelve DPs tested showed an N250 component in response to famous faces on trials where they did not explicitly recognize these faces. This covert recognition effect

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indicates that visual memory for famous faces was intact in these DPs, and suggests that their face recognition deficits may be the result of disconnections between a visual store of familiar faces and semantic memory. Interestingly, the other six DPs tested in this study did not show such covert recognition effects for the N250 component, which indicates that the locus of face processing deficits differs across individuals with DP.

While the N250 component is linked to visual face memory and face recognition, the well-known face-sensitive N170 component reflects an earlier stage of face processing. The N170 is an enlarged negativity in response to faces as compared to non-face stimuli that is elicited between 150 and 200 ms after stimulus onset over lateral occipito-temporal areas, (e.g., Bentin, Allison, Puce, Perez, and McCarthy (1996), Eimer, Kiss, and Nicholas (2010), Eimer (2011), Rossion and Jacques (2011)). N170 components are typically accompanied by an enhanced positivity to faces at vertex electrode Cz (Bötzel & Grüsser, 1989; Jeffreys, 1989). Because the vertex positive potential (VPP) and the N170 component are usually closely associated, they are assumed to reflect the same underlying face-sensitive brain processes (e.g., Joyce and Rossion (2005)). Importantly, the N170 component is not affected by emotional facial expression (Eimer & Holmes, 2002, 2007) or by face familiarity (e.g., Bentin and Deouell (2000), Eimer (2000a)). This insensitivity to familiarity and emotional expression suggests that the N170 is linked to the perceptual structural encoding of facial features and configurations that occurs independently and in parallel with the analysis of emotional expression, and precedes the recognition and identification of individual faces (Bruce & Young, 1986).

Because the N170 component is a well-studied electrophysiological marker of face perception, finding out whether this component is preserved or abolished in AP or DP is important for our understanding of the nature of prosopagnosia. Given the firm links between the N170 and the perceptual structural encoding of faces, its absence in individuals with prosopagnosia would point to an early “apperceptive” locus of their face processing deficits. In contrast, if the N170 component was uniformly preserved in prosopagnosia, this would provide strong evidence of a post-perceptual “associative” locus of face recognition impairments.

The existing evidence with respect to the properties of the N170 component in prosopagnosia is inconclusive. Only very few studies have measured ERP markers of face processing in brain-damaged patients with AP. One study found no differential ERP modulations to faces versus houses in the N170 time range for patient PHD who has diffuse cortical damage including a focal left temporo-parietal lesion (Eimer & McCarthy, 1999), suggesting that AP can be due to a disruption of early face-selective perceptual processing stages. Longer-latency ERP markers of identity-sensitive face processing were also absent for the same patient (Eimer, 2000a). This was expected, as severe impairments in structural encoding should have knock-on effects on later face recognition processes. In contrast, another single-case study found a preserved face-selective N170 in prosopagnosic patient FD who had extensive lesions to ventral occipito-temporal cortex (Bobes et al., 2004). More recently, Dalrymple et al. (2011) recorded ERPs from five patients with AP, and found that the presence of a face-sensitive N170 depended upon the integrity of at least two of the three core face-sensitive regions (fusiform and occipital face areas, posterior superior temporal sulcus). Alonso-Prieto, Caharel, Henson, and Rossion (2011) reported a face-selective N170 component over the right but not left hemisphere for prosopagnosic patient PS, whose lesions include the left fusiform and right occipital face areas. In summary, these studies demonstrate that the face-sensitive N170 component is often absent in patients with AP, and that the presence of this component appears to be linked to

the structural and functional integrity of posterior face processing areas, in particular the middle fusiform and inferior occipital face areas.

The question whether the face-sensitive N170 component is present or absent in individuals with developmental prosopagnosia has been investigated in several studies, but no clear pattern has emerged so far. There is some evidence that the N170 can be strongly attenuated or entirely abolished in DP. Bentin, Deouell, and Soroker (1999) tested one participant with DP and found that N170 amplitude differences in response to faces versus non-face objects were reduced relative to 12 control participants. Along similar lines, Kress and Daum (2003) found no statistically reliable N170 amplitude differences between faces and houses for two participants with DP, whereas such differences were consistently present in eight control subjects. Bentin, De Gutis, D'Esposito, and Robertson (2007) reported the absence of a differential N170 response to faces as compared to non-face control objects (watches) in one DP, whereas this effect was reliably present in a group of 24 control subjects. However, results from other studies demonstrate that the N170 is not always abolished in DP. Harris, Duchaine, and Nakayama (2005) measured MEPs or ERPs in response to faces and houses in a group of DPs. Of the five DPs tested with MEG, three showed a face-sensitive M170 component, while two did not. Two DPs were tested with EEG, and one of them showed a face-sensitive N170. Righart and De Gelder (2007) observed enhanced N170 amplitudes for faces relative to non-face control objects (shoes) for two DPs, whereas no such effect was present for two other DPs. Minnebusch, Suchan, Ramon, and Daum (2007) tested four DPs and found reliable N170 amplitude differences between faces and houses for three of them. In a recent MEG study, Rivolta, Palermo, Schmalzl, and Williams (2012) reported enhanced M170 components to images of faces versus places for a group of six DPs, and this enhancement was similar in magnitude to the effect observed for a group of 11 control participants. Finally, in an experiment designed to study the impact of perceptual training on face recognition (De Gutis, Bentin, Robertson, & D'Esposito, 2007), an individual with DP who had no differential N170 response to faces versus watches prior to training showed an enhanced N170 to faces after training. Overall, the main conclusion to be drawn from existing studies of the N170 component in DP is that results are highly variable across individuals. One main aim of this study was to investigate the presence or absence of the N170 across a much larger sample of sixteen participants with DP.

In addition to its generic face-sensitivity, the N170 component is also highly sensitive to face inversion. Numerous behavioural studies have indicated that upright faces are processed in a more configural or holistic manner than inverted faces or objects (e.g., Tanaka and Sengco (1997), Young, Hallowell, and Hay (1987), Van Belle, de Graef, Verfaillie, Rossion, and Lefèvre (2010)), and that stimulus inversion has much stronger effects on the recognition of faces than on object recognition (Yin, 1969). These observations suggest that inversion-induced impairments of face recognition may be linked to disruptions of configural face processing, which may be tailored for specifically upright faces. In line with this view, a recent study that employed single-unit recording in the macaque middle face patch provided strong evidence that faces are represented by an upright template, regardless of the orientation of an observed face (Freiwald, Tsao, & Livingstone, 2009).

Many ERP experiments have demonstrated that the N170 in response to inverted faces is enhanced and delayed relative to the N170 that is triggered by upright faces (e.g., Bentin et al., 1996; Eimer, 2000b; Rossion et al., 2000; Itier, Alain, Sedore, & McIntosh, 2007). Two types of explanation have been proposed for the presence of inversion-induced enhancements of N170 amplitudes (Sadeh & Yovel, 2010). Quantitative accounts assume

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