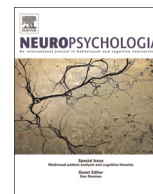




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The activation of visual face memory and explicit face recognition are delayed in developmental prosopagnosia



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ABSTRACT

Individuals with developmental prosopagnosia (DP) are strongly impaired in recognizing faces, but the causes of this deficit are not well understood. We employed event-related brain potentials (ERPs) to study the time-course of neural processes involved in the recognition of previously unfamiliar faces in DPs and in age-matched control participants with normal face recognition abilities. Faces of different individuals were presented sequentially in one of three possible views, and participants had to detect a specific Target Face ("Joe"). EEG was recorded during task performance to Target Faces, Nontarget Faces, or the participants' Own Face (which had to be ignored).

The N250 component was measured as a marker of the match between a seen face and a stored representation in visual face memory. The subsequent P600f was measured as an index of attentional processes associated with the conscious awareness and recognition of a particular face. Target Faces elicited reliable N250 and P600f in the DP group, but both of these components emerged later in DPs than in control participants. This shows that the activation of visual face memory for previously unknown learned faces and the subsequent attentional processing and conscious recognition of these faces are delayed in DP. N250 and P600f components to Own Faces did not differ between the two groups, indicating that the processing of long-term familiar faces is less affected in DP. However, P600f components to Own Faces were absent in two participants with DP who failed to recognize their Own Face during the experiment. These results provide new evidence that face recognition deficits in DP may be linked to a delayed activation of visual face memory and explicit identity recognition mechanisms.

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1. Introduction

Individuals with prosopagnosia are unable to recognize and identify the faces of familiar individuals, despite normal low-level vision and intellect (Bodamer, 1947). This problem can be caused by impairments at early perceptual stages of face processing (aperceptive prosopagnosia) or by selective deficits of long-term face memory (associative prosopagnosia; De Renzi et al., 1991). Acquired prosopagnosia (AP) usually results from lesions to face-sensitive regions in occipito-temporal visual cortex, including the fusiform gyri (e.g., Barton, 2008). In contrast, individuals with developmental prosopagnosia (DP) have no history of neurological damage (Behrmann and Avidan, 2005; Duchaine and Nakayama, 2006a; see Towler and Eimer, 2012; Susilo and Duchaine, 2013; for recent reviews). In DP, face recognition deficits are typically present from an early age, and are believed to be linked to a failure to develop normally functioning face recognition mechanisms. All

individuals with DP have a core deficit in recognising familiar individuals, whereas other aspects of face processing may or may not be affected. For example, some DPs perform poorly on perceptual face matching tasks while others perform within the normal range (Duchaine et al., 2007; Duchaine, 2011).

The functional and neural causes of the face recognition impairments in DP are still largely unknown. Functional neuroimaging studies have often observed relatively normal brain activation patterns to faces versus non-face objects within the core posterior face processing network (Hasson et al., 2003; Avidan et al., 2005; Avidan and Behrmann, 2009; Furl et al., 2011; Avidan et al., 2014). However, temporal face areas were found to be reduced in size and showed less face-selectivity in DPs (Furl et al., 2011), and face-selective activation in the inferior anterior temporal lobe was absent in a group of DPs (Avidan et al., 2014). Other subtle structural differences between DP and control participants have been observed in multiple occipito-temporal regions (Behrmann et al., 2007; Garrido et al., 2009).

Due to the limited temporal resolution of fMRI-based measures, these studies cannot reveal possible differences in the time-course of face perception and recognition processes between DPs and

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participants with unimpaired face recognition. Such differences can be revealed by ERP measures. Most ERP studies of DP have focused on the face-sensitive N170 component that emerges as an enhanced negativity to faces versus non-face objects between 150 and 200 ms after stimulus onset over lateral occipito-temporal areas (e.g., Bentin et al., 1996; Eimer et al., 2010; Eimer, 2011; Rossion and Jacques, 2011; see also Thierry et al., 2007, and Rossion and Jacques, 2008, for debates about the functional interpretation of the N170). A recent study from our lab (Towler et al., 2012) demonstrated that the generic face-sensitivity of the N170 does not differ between DPs and control participants (see also Towler et al., 2014), but found atypical effects of face inversion on N170 amplitudes for individuals with DP. The N170 component is usually not affected by the familiarity of a face (Bentin and Deouell, 2000; Eimer, 2000; but see Caharel et al., 2011), and is believed to reflect processes involved in the perceptual structural encoding of faces that occur prior to the recognition and identification of individual faces. For this reason, studies focused on the N170 component alone cannot provide direct electrophysiological markers of impaired face recognition that is at the core of the face processing deficits in DP.

ERP markers of identity-related face processing emerge at post-stimulus latencies beyond 200 ms. A repeated encounter with the face of a particular individual elicits an enhanced negativity at inferior occipito-temporal electrodes at around 250 ms after stimulus onset (e.g., Schweinberger et al., 1995; Begleiter et al., 1995; Schweinberger et al., 2002; Zimmermann and Eimer, 2013). This repetition-induced N250r component has been linked to the activation of a representation of a specific face in visual memory that is triggered by its match with a currently presented face (Schweinberger and Burton, 2003). The N250r is larger for repetitions of famous faces as compared to unfamiliar faces (Herzmann et al., 2004), suggesting that pre-existing long-term representations of individual faces are activated particularly strongly when a matching face is perceived. A similar N250 component is also triggered by famous faces versus novel faces (e.g., Gosling and Eimer, 2011), and is assumed to reflect the match between a perceptual representation of a particular familiar face and a representation of the same face that is stored in long-term visual face memory. If the N250 component is generated during the activation of visual memory traces for a particular individual face, studying whether and when this component is elicited in participants with DP may yield new insights into possible impairments of early visual face recognition processes in DP.

In a recent ERP study (Eimer et al., 2012), we employed the N250 component to investigate the recognition of pre-experimentally known famous faces in DP. Participants with DP and control participants had to discriminate faces of famous versus unfamiliar individuals. As would be expected, DPs detected less than 30% of all famous faces, even though subsequent tests revealed that they knew 95% of these individuals. However, those relatively few famous faces that were successfully recognized triggered N250 components that were similar to those observed for participants with unimpaired face recognition (Gosling and Eimer, 2011). For six of the twelve DPs tested, N250 components were triggered by famous faces on trials when these faces were judged to be unfamiliar, suggesting that stored visual face representations can be activated even when faces are not explicitly recognized (covert recognition). The explicit recognition of a particular individual face is associated with a sustained broadly distributed positivity that emerges around 400 ms after stimulus onset. This late positive component (P600f; Gosling and Eimer, 2011) is similar in its time-course and scalp distribution to the P3b component that is observed in many target-nontarget discrimination tasks, and is assumed to be linked to the allocation of attentional resources during the explicit categorization or

identification of task-relevant stimuli (e.g., Folstein and Van Petten, 2011). In our earlier study (Eimer et al., 2012), P600f components were only elicited on trials where DPs correctly reported a famous face, in line with the view that the P600f reflects the conscious recognition of an individual face.

Our previous ERP results (Eimer et al., 2012) suggest that when DPs successfully identify a pre-experimentally known famous face, the processes involved in the matching of perceptual and long-term visual memory representations (as reflected by the N250 component) and explicit face recognition (marked by the P600f component) are not qualitatively different from participants with unimpaired face processing abilities (see Towler and Eimer, 2012, for more detailed discussion). The goal of the present study was to investigate the recognition of pre-experimentally unfamiliar target faces in participants with DP. When the face of a particular unfamiliar individual is designated as task-relevant, a visual representation of this face is stored in short-term face memory. The activation of this representation by a match with a currently seen face should therefore elicit an N250 component, and the subsequent attentional processing and explicit recognition of this face should give rise to a P600f component. Comparing these two components and their time-course between DPs and control participants could therefore reveal differences in the processes involved in the recognition of learned unfamiliar faces that may be linked to the face recognition impairments in DP.

A second issue addressed in the present study was whether participants' own faces would show a normal pattern of visual face memory activation and explicit recognition in DPs. Because one's own face is highly familiar and salient, and is strongly represented in long-term face memory, it should be rapidly recognized even when it is not explicitly task-relevant, and this should be reflected by N250 and P600f components to own versus unfamiliar faces. The question whether and to what degree the recognition of one's own face is impaired in prosopagnosia has not yet been studied systematically. Some patients with severe AP fail to recognize themselves in the mirror (Sergent and Poncet, 1990) and some individuals with DP also report difficulties in recognizing their own face (e.g., Duchaine et al., 2007). Our earlier study (Eimer et al., 2012) has shown that long-term visual memory representations of famous faces are activated when DPs successfully recognize one of these faces. In the present experiment, we investigated whether this is also the case for participants' own faces under conditions where these faces are formally task-irrelevant.

To address these questions, we adopted an experimental paradigm that was developed by Tanaka et al. (2006). Single face images were presented sequentially, and participants had to respond to a previously studied but otherwise unknown Target Face ("Joe"), while ignoring other task-irrelevant distractor faces. One of these distractors was the participants' Own Face. Tanaka et al. (2006) found that both Target Faces and Own Faces triggered occipito-temporal N250 components, even though the latter were task-irrelevant. This shows that the N250 reflects the activation of long-term face memory as well as the activation of a recently learned representation of a previously unfamiliar face in short-term memory. The N250 to participants' own face was already present in the first half of the experiment, while the N250 to target faces only emerged during the second half, suggesting that an episodic representation of a previously unfamiliar target face builds up gradually (see also Kaufmann et al., 2009). Target Faces and Own faces also elicited a sustained positivity that peaked around 500 ms post-stimulus in the study by Tanaka et al. (2006), analogous to the P600f component observed in our previous studies of famous face recognition (Gosling and Eimer, 2011; Eimer et al., 2012).

Ten participants with DP and a group of ten age-matched control participants had to memorize a particular Target Face

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