



The anatomic basis of the right face-selective N170 IN acquired prosopagnosia: A combined ERP/fMRI study

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ABSTRACT

The N170 waveform is larger over posterior temporal cortex when healthy subjects view faces than when they view other objects. Source analyses have produced mixed results regarding whether this effect originates in the fusiform face area (FFA), lateral occipital cortex, or superior temporal sulcus (STS), components of the core face network. In a complementary approach, we assessed the face-selectivity of the right N170 in five patients with acquired prosopagnosia, who also underwent structural and functional magnetic resonance imaging. We used a non-parametric bootstrap procedure to perform single-subject analyses, which reliably confirmed N170 face-selectivity in each of 10 control subjects. Anterior temporal lesions that spared the core face network did not affect the face-selectivity of the N170. A face-selective N170 was also present in another subject who had lost only the right FFA. However, face-selectivity was absent in two patients with lesions that eliminated the occipital face area (OFA) and FFA, sparing only the STS. Thus while the right FFA is not necessary for the face-selectivity of the N170, neither is the STS sufficient. We conclude that the face-selective N170 in prosopagnosia requires residual function of at least two components of the core face-processing network.

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1. Introduction

Face perception is a computationally demanding high-level object recognition task that may involve highly specialized and possibly even face-dedicated cognitive processes. The temporal profile of the neural processing involved in face perception has been measured using event-related potentials (ERP). These show that between 140 and 200 ms after the appearance of a face there is a negative deflection that is larger in amplitude for faces than for non-face objects (Bentin, Allison, Puce, Perez, & McCarthy, 1996; Botzel, Schulze, & Stodieck, 1995; Jeffreys, 1989). Based on the timing of its emergence and the stimuli that elicit it, it has been proposed that this “face-selective N170” may be associated with encoding of face structure (Eimer,

2000; Taylor, McCarthy, Saliba, & Degiovanni, 1999) and/or the detection of faces (Bentin et al., 1996; Zion-Golumbic & Bentin, 2007).

A consistent finding across all studies is that the face-selective N170 is largest in the posterior temporal regions, and larger on the right compared to the left hemispheres (Bentin et al., 1996; Eimer, 1998; Jacques, d'Arripe, & Rossion, 2007; Rossion, Joyce, Cottrell, & Tarr, 2003; Webb et al., 2010). In parallel, studies using functional magnetic resonance imaging (fMRI) have revealed a face-processing network in the human ventral occipitotemporal stream, which is also more prominent in the right hemisphere (Fox, Iaria, & Barton, 2009; Kanwisher, McDermott, & Chun, 1997; Sergent, Ohta, & MacDonald, 1992). It consists of a core system in the occipitotemporal visual extrastriate cortex, as well as an extended system in more distant cortical regions (Haxby, Hoffman, & Gobbini, 2000). The core system is made up of three areas: the occipital face area (OFA) in the inferior occipital gyrus (Gauthier et al., 2000; Haxby et al., 2000), the fusiform face area (FFA) in the middle lateral fusiform gyrus (Grill-Spector, Knouf, & Kanwisher, 2004), and the superior temporal sulcus (STS) in the lateral temporal cortex (Hasselmo, Rolls, & Baylis, 1989; Haxby et al., 2000). The extended system includes regions connected to

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the core system that perform face-related, though not necessarily face-specific, functions. These areas, which include the anterior temporal lobe, amygdala, auditory cortex, intraparietal sulcus, and insula, are involved in tasks such as accessing semantic information related to identity, evoking an emotional response to a face, and pre-lexical speech perception, like lip reading (Haxby et al., 2000).

Which components of this face-processing network play critical roles in the generation of the face-selective N170 continues to be a subject of debate. Based on the fact that the N170 is strongest at electrode sites T5 and T6 – P7 and P8 in new ERP terminology (Rossion & Jacques, 2008) – some propose that the N170 is generated in occipitotemporal regions (Bentin et al., 1996). Alternatively, it has been suggested that the N170 is generated in the STS, given that the N170 amplitude is greater to eyes than to faces and that the STS is activated by moving eyes (Puce, Allison, Bentin, Gore, & McCarthy, 1998). Source analyses have produced mixed results, with some suggesting localization of the face-selective N170 in fusiform gyri (Itier & Taylor, 2002; Rossion et al., 2003; Schweinberger, Pickering, Jentsch, Burton, & Kaufmann, 2002) as well as the equivalent M170 on magnetoencephalography (Deffke et al., 2007), but others locating it in lateral temporal cortex (Shibata et al., 2002; Watanabe, Kakigi, & Puce, 2003), more specifically in the STS region (Itier & Taylor, 2004). More recently, inter-subject correlations of fMRI and ERP measures of face-selectivity showed high correlations between the face-selective N170 and face activation in both the FFA and the STS, but not in the OFA (Sadeh, Podlipsky, Zhdanov, & Yovel, 2010). Dual contributions from FFA and STS are also consistent with another observation that added incremental noise to face images and found that intra-subject changes in the N170 correlated with changes in the bilateral fusiform and superior temporal gyri (Horovitz, Rossion, Skudlarski, & Gore, 2004).

Part of the difficulty with N170 localization is that though ERP is a particularly precise measure of the temporal properties of brain function, it provides only a coarse measure of spatial location. An alternate, more direct, approach to the localization of ERP phenomena is to examine their status in human subjects with lesions to various components of the face-processing network. Recent refinements to face-localizer paradigms have made it possible to identify the components of the core system reliably in single subjects (Fox et al., 2009), and therefore to make definitive conclusions about the absence or presence of these components in patients with focal brain damage. Particularly informative may be studies of patients with acquired prosopagnosia, who have lost the ability to recognize the identity of faces following a cerebral insult (Bodamer, 1947). The anatomic locus of their brain damage is quite variable in both its lateralization and anterior-posterior extent (Barton, 2008a, 2008b). Most common are bilateral or right-sided lesions, with left hemispheric damage alone being quite rare (Barton, 2008a, 2008b). Lesions commonly affect the medial occipitotemporal lobe, with a possibility of affecting parts of the core network, but can also affect mainly anterior temporal structures (Barton, 2008a, 2008b; Evans, Higgs, Antoun, & Hodges, 1995).

Our goal was to investigate the anatomic basis of the face-selective N170 by recording ERPs in five patients with acquired prosopagnosia. We first used fMRI to determine the status of the components of the core face-processing network in each individual. We then recorded ERPs while patients viewed pictures of novel faces and objects and used a single-subject analytic method to determine which patients had a preserved face-selective N170 component. By relating the post-lesional status of the core network to the status of the face-selective N170 we sought to determine which areas are necessary and/or sufficient for this face-processing ERP component.

2. Materials and methods

2.1. Participants

Patients with acquired prosopagnosia were recruited as part of an ongoing international collaborative prosopagnosia study from subjects who had responded to a website, www.faceblind.org, where they also completed a screening evaluation. On-site they also performed an extensive neuropsychological battery (Table 1). Healthy control participants ($n = 10$, 3 male, mean age 28, range 18–59 years) were recruited from the community at the University of British Columbia. All participants were right-handed except for one control subject (EW). All had normal or corrected-to-normal vision. The protocol was approved by the institutional review boards of Vancouver General Hospital and the University of British Columbia, and all subjects gave informed consent in accordance with the declaration of Helsinki.

2.1.1. Case reports

B-AT1 (B = bilateral; AT = anterior temporal) is a 24-year-old right-handed man. Three years prior to testing, he contracted herpes simplex viral encephalitis and was initially comatose. Since recovery, he has noted difficulty recognizing faces and learning new faces, though he can recognize some family members. General memory and mental functioning is unaffected, allowing him to attend college and hold full-time employment. Visual fields were normal and acuity was 20/20 in both eyes. He has mild topographagnosia and mild anomia for low-frequency items, although he retained semantic knowledge about these items. He performed normally on most neuropsychological tests (Table 1) but was borderline on the Cambridge Face Memory Test (Duchaine & Nakayama, 2006) and impaired on the Cambridge Face Perception Test (Duchaine, Yovel, & Nakayama, 2007), Faces portion of the Warrington Recognition Memory Test (Warrington, 1984) and on a modified familiar face recognition test, which used pictures of his relatives rather than celebrities, due to a limited knowledge of the latter. Impaired performance on the Word List immediate recall was also observed (27/48), while performance was normal on all other memory tests, including the Word portion of the Warrington Recognition Memory Test. Structural MRI scans showed bilateral anterior temporal lobe damage extending medially to the fusiform gyri, slightly more prominent in the right hemisphere (Fig. 1).

R-AT2 (R = right; AT = anterior temporal) is a 30-year-old left-handed woman. Five years prior to testing she was diagnosed with herpes simplex viral encephalitis. One of the earliest residual symptoms she noted was that places looked unfamiliar. She would know where she was but the locations seemed strange. She was able to recognize voices on the phone and people by their body type and walk, but could not recognize their faces. Visual fields were normal, and acuity without correction at far was 20/15 in both eyes. She performed normally on most neuropsychological tests (Table 1) but was impaired on the Cambridge Face Memory Test, the Faces portion of the Warrington Recognition Memory Test and on the Famous Faces recognition test. On a measure of general intelligence (WAIS-R), she achieved a Full Scale IQ within the average classification of intelligence, with no significant difference between Verbal and Performance IQ. Structural MRI scans showed a right anterior temporal lobe lesion extending posteriorly to the medial aspect of the fusiform gyrus (Fig. 1).

R-IOT4 (R = right; IOT = inferior occipital-temporal) is a 57-year-old right-handed man. He had a right carotid artery dissection that led to a right posterior cerebral arterial infarct because of a fetal circulation pattern. When his wife visited a few hours after admission to hospital, he did not recognize her face, but did recognize her voice and gait. When he was discharged three days later, he did not recognize the route taking him home and only recognized his own house by the columns at its entrance. Since then he has found that he gets lost inside the houses of his friends. When meeting neighbors he cannot recognize their faces and relies on other cues, such as the dog that they are walking. He had some difficulties with short-term memory and concentration initially. All symptoms improved partially over the following months. Visual acuity was 20/30 and he had a left homonymous hemianopia. During reading he had difficulty finding the left side of long words but showed normal comprehension. He performed well on most neuropsychological tests (Table 1) and even on the Faces portion of the Warrington Recognition Memory Test, but he was severely impaired at the Cambridge Face Memory Test, Cambridge Face Perception Test, and the Famous Faces recognition test. Structural MRI scans showed a right inferomedial occipital lesion extending from the inferior calcarine fissure to the middle and lateral aspects of the mid-fusiform gyrus (Fig. 1).

R-IOT1 (R = right; IOT = inferior occipitotemporal) is a 49-year-old left-handed man who, 12 years prior to testing, had an occipital hemorrhage from rupture of an arteriovenous malformation. Immediately following this event he complained of trouble recognizing hospital workers and needed to rely on hairstyle, facial hair, or voice for person recognition, a problem that persists. Acuity was 20/20 in both eyes but he had a partial left superior quadrantanopia and mild topographagnosia. His history suggested letter-by-letter reading immediately following the hemorrhage, although this had resolved long before the time of testing. He performed well on all neuropsychological tests, including the Benton Facial Recognition Test; the famous face test and the test of facial imagery; however he was impaired on the Cambridge Face Memory Test, Cambridge Face Perception Test, and the Faces portion of the Warrington Recognition Memory Test (Table 1). Of note, for the famous faces test, he said he recognized the images rather than the people, as some of these were well-known photographs: on a second test of famous faces his performance was

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