The face-specific N170 component reflects late stages in the structural encoding of faces

Martin Eimer

Department of Psychology, Birkbeck College, University of London, Malet Street, London WC1E 7HX, UK

Received 18 April 2000; accepted 5 May 2000

INTRODUCTION

Evidence from behavioural [1–3], neuropsychological [4–6] and single cell recording studies [7,8] suggests that face recognition is based on specific processes implemented by specialized brain systems. Recent results from ERP and functional imaging studies also support the hypothesis of face-specific processing modules. fMRI studies have identified a region in the fusiform gyrus (fusiform face area, FFA) which is strongly activated when faces are presented, but not in response to houses, scrambled faces or hands [9,10]. A large negative ERP component with a latency of 170 ms (N170) is elicited at lateral posterior electrodes by faces, but not by cars, hands, houses, furniture or scrambled faces [11–17]. While such face-specific responses are likely to be generated by brain mechanisms involved in the processing of faces, it is unclear which stages in the analysis of faces they reflect. The fact that the N170 is entirely unaffected by face familiarity [16,17] suggests that this component is linked to the pre-categorical structural encoding of faces rather than to later processes responsible for face recognition and identification. However, structural encoding is in itself a multi-stage process. Its early stages involve the detection of heads in the visual field and the processing of individual face components, whereas later stages are responsible for the configurational analysis of faces. The N170 might be generated by processes sensitive to the presence of a head in the visual field or to single salient internal facial features like the eyes [11,13]. Alternatively, it might reflect processes involved in the analysis of the global configuration of whole faces.

To obtain further insight into which aspects of structural encoding from simple head detection up to the holistic analysis of prototypical configurations of faces [18] are reflected by the N170, ERPs were recorded in response to systematically varied face and non-face stimuli. In part I, four different views of heads (front, profile, cheek, and back view: see Fig. 1) and two types of non-face stimuli (hands and houses) were presented. If the N170 was related to head detection it should not be systematically affected by head rotation. If it reflected the processing of salient internal face components or the configurational analysis of whole faces, this component should be large for front and side views where internal features are visible, and attenuated or entirely absent for back views where internal features are hidden from view. The face stimuli used in part I were identical to the stimuli used in a recent fMRI study ([19], Experiment 4) which measured FFA responses to different face views. FFA activations were equally strong to front and profile views, reduced to cheek views, and even weaker for back views. By using the identical stimulus set in the present experiment, it is possible to directly compare the response profiles of the FFA and the N170 component of the ERP.

To further investigate the relative contributions of internal and external facial features to the N170, part II of the present study compared ERP responses to intact upright and inverted faces to ERPs elicited by upright faces without internal or external features (Fig. 1) and ERPs to non-face stimuli. If the N170 was triggered by salient internal features, it should be reduced or absent when these features are eliminated, but not when external features are removed. If this component was generated by later stages of
of structural encoding involved in the configurational analysis of whole faces, the elimination of internal as well as external features should result in an attenuated N170.

MATERIALS AND METHODS

Subjects: Twelve paid volunteers (six female), aged 21–34 years (mean 24.8 years) participated in the experiment. All subjects were right-handed and had normal or corrected-to-normal vision.

Stimuli and procedure: Subjects were seated in a dimly lit sound attenuated cabin, with response buttons under their left and right hands. Stimuli were photographs of faces, houses, and hands that were presented centrally on a computer monitor in front of a white background. In part I, faces were images of 13 males taken from four different viewpoints (see Fig. 1 for examples): front (0° rotation), profile (90°), cheek (135°) and back (180°). In addition, 13 images of houses and 13 images of hands were presented. In part II, 16 house and 16 hand images were presented together with 16 images of faces (eight male, eight female). All faces were front-view, and were either intact and upright (standard faces), intact and inverted, without internal features, or without external features (Fig. 1 for examples). Stimuli were presented for 100 ms, separated by intertrial intervals of 1200 ms, and occupied a visual angle of about 3 \times 4.5°. The experiment consisted of two parts of six successive blocks. Each block consisted of 105 trials. The participants’ task was to respond with a left or right manual button press (response side varied between blocks).

Fig. 1. Examples of the different face categories shown. In part I, faces were front, profile, cheek, and back views of human heads. In part II, a subset of faces was presented without internal features (No Internal) or without external features (No External).
whenever a stimulus was immediately repeated on successive trials. This happened in 15 trials per block. In the remaining 90 trials, exemplars of the six stimulus categories (front, side, cheek, and back views of faces plus hands and houses in part I; standard and inverted intact faces, upright faces without internal or external features, plus hands and houses in part II) were presented in random order and equiprobably (15 presentations per category and block). Participants were instructed to respond as quickly as possible to stimulus repetitions only and to maintain central eye fixation. Practice blocks of 40 trials were delivered prior to both experimental parts.

**ERP recording and data analysis:** Recordings were made from Ag-AgCl electrodes at Fz, Cz, Pz, T5, O1, T6 and O2, referenced to an electrode positioned on the tip of the nose. Horizontal EOG was recorded bipolarly from electrodes at the outer canthi of both eyes; vertical EOG was recorded from electrodes above and below the right eye. Electrode impedance was kept below 5 Ω. Amplifier bandpass was 0.10–40 Hz. EEG and EOG were sampled with a digitization rate of 200 Hz. ERP analyses were restricted to non-repetition trials. Trials with eyeblinks, lateral eye movements or overt responses were excluded. Repeated measures analyses of variance (ANOVAs) and paired t-tests were performed on N170 mean amplitude and peak latency values measured at T5 and T6 in the 140–190 ms post-stimulus interval relative to a 100 ms pre-stimulus baseline. Greenhouse–Geisser corrections to the degrees of freedom were performed when appropriate.

**RESULTS**

There was no significant difference between response times to immediate stimulus repetitions in parts I and II (535 ms vs 544 ms). Participants missed 6.4% of all repetitions and responded incorrectly to non-repetitions on 1.2% of all trials.

Figure 2 (top) shows ERPs elicited at lateral temporal electrodes T5 and T6 by standard (intact upright front-view) faces and ERPs elicited by hands and houses in parts I (left) and II (right). Relative to both non-face categories, standard faces elicited an enlarged N170, and this was reflected in highly significant effects of stimulus category (face vs non-face) obtained in both experimental parts when ERPs to standard faces were analysed together with ERPs to hands and houses. A highly significant effect of stimulus category (face vs non-face) was obtained (F(1,11) = 12.64; p < 0.005), demonstrating that albeit reduced relative to front and profile views, the face-specific N170 was not completely eliminated for cheek and back views.

In part II, a highly significant effect of face category was obtained when standard faces and faces with removed internal or external features were analysed together (F(2,22) = 22.25; p < 0.001; ε = 0.910), primarily reflecting the fact that standard faces elicited larger N170 components than faces without internal and external features (Fig. 2, right). Subsequent t-tests confirmed that relative to standard faces, N170 was reduced for faces without internal and external features (all t(11) > 3.06; all p < 0.011). N170 amplitudes to faces without internal features tended to be larger than to faces without external features (Fig. 3, bottom), and this difference was significant at T6 (t(11) = 3.03; p < 0.011). To test whether N170 amplitudes elicited by faces lacking either internal or external features were larger than N170 amplitudes elicited by non-face stimuli, ERPs elicited by these face stimuli were analysed together with ERPs to hands and houses. A highly significant effect of stimulus category (face vs non-face) was obtained (F(1,11) = 10.07; p < 0.009), demonstrating that the absence of either internal or external features attenuates, but does not eliminate the face-specific N170.

Figure 2 (right) also suggests that N170 latencies were affected by face inversion and by the absence of internal or external features in part II. N170 peak latencies (averaged across T5 and T6) were 161 ms (standard faces), 166 ms (faces lacking internal features) and 170 ms (both for inverted intact faces and for faces lacking external features). Subsequent t-tests revealed that these latency differences were all statistically reliable (all t(11) > 2.24; all p < 0.047).

**DISCUSSION**

Several ERP studies [11–17] have found that faces elicit an enlarged N170 at lateral posterior electrodes. This negative ERP component is likely to be generated by face-specific brain processes involved in the pre-categorical structural encoding of faces [16,17]. The present study investigated which aspects of structural encoding are reflected by the N170 by studying its sensitivity to a series of systematically varied face stimuli. In part I, ERPs were recorded in response to standard (intact, upright, front-view) faces, to different head views (profile, cheek, back) and to non-face stimuli (hands and houses). A face-specific N170 component was elicited at lateral posterior electrodes by standard faces, and this component was equally large for profile views, but considerably reduced for cheek and back views. This response profile of the N170 to head rotation is strikingly similar to the response pattern observed for the FFA in an fMRI study which employed identical face stimuli [19]. Although this correspondence does not necessarily imply that FFA activations and the N170 are generated by identical brain processes, it does suggest that face-specific fMRI and ERP responses reflect at least partially overlapping stages in face processing. The fact that N170 amplitudes were strongly influenced by variations in head
Fig. 2. Grand averaged ERPs elicited at lateral temporal electrodes T5 and T6 between stimulus onset and 300 ms after stimulus onset in response to the different face and non-face stimuli in part I (left) and part II (right). Top: ERPs to standard faces (upright intact front-view; thick solid lines) and non-faces (hands and houses; thin lines). Middle and bottom: ERPs to standard faces (solid lines) and non-standard faces (dashed lines).
views demonstrates that the N170 does not simply reflect head detection. The attenuation of the N170 for cheek and back views, where internal features were increasingly hidden from view, suggests that the N170 is highly sensitive to these features. However, since both cheek and back views elicited reliably larger N170 amplitudes than non-face stimuli, the occlusion of internal features does not seem to completely eliminate this component.

The relative contributions of internal and external features to the N170 was investigated in part II, where ERPs elicited by standard faces and inverted intact faces were compared to ERPs to faces lacking either internal or external features, as well as to ERPs to non-faces. As expected, eliminating internal features resulted in a decrease of N170 amplitudes. However, this decrease was by no means less pronounced when only external face components were absent, which does not support the view that the N170 is exclusively tuned to internal features. In fact, the decrease of N170 amplitude relative to standard faces even tended to be larger for faces without external features than for faces without internal features (Fig. 3, bottom). Relative to hands and houses, larger N170 components were elicited by incomplete faces, demonstrating that the absence of either internal or external features does not completely eliminate the N170. N170 latencies were also systematically affected in part II. Relative to standard faces, the N170 elicited by inverted faces was delayed. This latency shift caused by face inversion replicates previous findings [11,20] and is most likely due to inadequate configural information provided by upside-down faces [20]. In line with this idea, the removal of internal and external features also resulted in N170 latency shifts. While a small but reliable N170 delay was measured in response to faces without internal features, the delay produced by the absence of external features was equivalent to the delay resulting from face inversion.

CONCLUSION
The face-specific N170 is generated by brain processes involved in the structural encoding of faces. These processes are not merely responsible for head detection, or for the processing of salient internal face features. Instead, they seem to be devoted to the configurational analysis of whole faces. The N170 is elicited maximally by face stimuli that are optimal for face recognition and identification (front and profile views, both internal and external features present). Other types of faces trigger an attenuated N170, and this attenuation is a function of the degree to which these stimuli differ from 'optimal' faces. This response profile suggests that the N170 is linked to late stages of structural encoding, where representations of global face configurations are generated in order to be utilized by subsequent face recognition and identification processes [21].

REFERENCES
Acknowledgements: This research has been supported by a grant from the Human Frontier Science Program (HFSP). The author thanks Nancy Kanwisher and Frank Tong for allowing the use of images from the Harvard Vision Science Laboratory.