N250r: a face-selective brain response to stimulus repetitions

Stefan R. Schweinberger,CA Vyv Huddy and A. Mike Burton

Department of Psychology, University of Glasgow, 58 Hillhead Street, Glasgow G12 8QB, UK

CACorresponding Author: stefan@psy.gla.ac.uk

Received 24 March 2004; accepted 22 April 2004

DOI: 10.1097/01.wnr.0000131675.00319.42

We investigated event-related brain potentials elicited by repetitions of cars, ape faces, and upright and inverted human faces. A face-selective N250r response to repetitions emerged over right temporal regions, consistent with a source in the fusiform gyrus. N250r was largest for human faces, clear for ape faces, non-significant for inverted faces, and completely absent for cars. Our results suggest that face-selective neural activity starting at ~200 ms and peaking at ~250–300 ms is sensitive to repetition and relates to individual recognition. *NeuroReport* 15:1501–1505 © 2004 Lippincott Williams & Wilkins.

Key words: Event-related brain potentials; Face perception; N250r; Priming; Repetition

INTRODUCTION

The ability to recognize thousands of faces is an amazing achievement of the human perceptual system, and may be mediated by specialized cortical modules [1]: neuroimaging identified the fusiform face area as a region responding particularly strongly to faces [2]. However, faces provide a range of social information about identity, but also about emotion, gender, or attentional focus (e.g. via eye gaze). These aspects of face processing involve different brain regions which normally act in concert [3]. Three prominent face-responsive areas have been identified by neuroimaging: The early visual analysis of faces, perception of identity, and perception of changeable aspects (e.g. eye gaze, expression) have been related to the lateral occipitotemporal cortex, fusiform gyrus, and superior temporal sulcus areas, respectively [3].

While neuroimaging provides information about brain regions active in a particular task, we used event-related brain potentials (ERPs), which provide more precise information about the timing of neural events, and focused on two ERPs observed in face perception. The N170, a negative ERP at ~170 ms, is larger to faces than to most other stimuli, and has often been regarded as a face-selective response [4]. The N170 is reduced if the configuration of facial features is distorted [4], and is enhanced and delayed for inverted faces [5]. N170 appears to be insensitive to face familiarity [6,7] or repetitions [8]. Moreover, non-human primate faces elicit an N170 which is similar to [9] or larger than [10] that elicited by human faces. Thus, while the N170 may reflect an early visual process tuned to detect faces, perhaps in the occipitotemporal face area [3,4], it is probably not related to individual recognition [4,11].

The N250r is an ERP modulation that was recently reported to occur for immediate repetitions of faces. This negativity for repeated relative to non-repeated faces peaks at ~230–300 ms over inferior temporal regions [8,11,12]. It is typically lateralised to the right hemisphere, and larger for familiar than unfamiliar faces, suggesting a relationship to individual recognition [8,12]. Inverse source localisation suggests that N250r is generated in fusiform gyrus, whereas N170 is generated in posterior–lateral occipitotemporal cortex [11].

Although N250r may reflect recognition of individual faces in the fusiform, it has been unclear as yet whether this response is selective for faces. Using an immediate repetition paradigm, we investigated the selectivity of N170 and N250r responses to faces by contrasting them with those elicited by control stimuli. We sequentially presented pairs of inverted faces, ape faces, and cars as controls (Fig. 1). The second stimulus of each pair was either a repetition or a non-repetition of the first. In ~11% trials, the second stimulus was an oddball target (a butterfly), to which participants made a speeded key press. This ensured that the other stimulus categories did not differ in task relevance, and also that ERPs to these categories were uncontaminated by motor activity.

While object recognition typically involves the recognition of the basic category (e.g. chair, car, etc.), face recognition requires the recognition of individual exemplars. Faces are a homogeneous category where individuals share number and basic arrangement of features (mouth, eyes, etc.), and recognition is thought to require configural rather than feature-based processing. Because some seemingly face-selective processes might be more properly described as mediating the recognition of individual within-class exemplars [13], a strong test for face selectivity is to use individual objects with a similarly homogeneous configuration. We therefore created front views of all stimuli, so that cars, like faces, had invariant spatial configuration of features.

Importantly here, we studied effects of face inversion on N250r and N170. The N170 inversion effect (larger and later responses for inverted faces) has been taken to reflect increased difficulty in encoding a face. We argue that N250r reflects perceptual memory for faces [12], and hence we predicted that inverted faces should not elicit a sizeable N250r as they are unlikely to have strong representations in memory.

MATERIALS AND METHODS

Participants: Sixteen right-handed participants (six women) aged between 18 and 39 years (mean 25.0) contributed data. Informed consent was obtained from all participants. The study was approved by the Faculty Ethics Committee, University of Glasgow. All participants reported normal or corrected-to-normal vision.

Stimuli and apparatus: Forty exemplars of each of five categories of stimuli were obtained: faces, inverted images of the same faces, ape faces, front views of cars, and butterflies. Stimuli from the first four categories were arranged into 320 pairs: 160 repetition trials (two identical stimuli), and 160 non-repetition trials (two different stimuli of the same category). In 40 further pairs (oddball trials), a butterfly was preceded by a stimulus randomly taken from one of the other four categories.

Stimuli were software-edited using Adobe Photoshop, converted to greyscale with black background, and framed within an area of 170 × 216 pixels (6.0 × 7.6 cm).

Procedure: For each trial, a white fixation cross was first presented for 1000 ms, was then replaced by S1 (1000 ms), followed by the fixation cross (1000 ms), and finally S2 (1000 ms). There was no inter-trial interval, such that participants saw a continuous series of stimuli with equal stimulus onset asynchronies (SOAs; Fig. 1). The 360 repetition, non-repetition, and oddball trials were presented in a random fashion in blocks of 64, with intervening rest periods.

Participants were asked to press a key with the right index finger whenever they saw a butterfly, but to make no response for other stimuli. Responses to butterflies were scored correct if the correct key was pressed within 200–1000 ms after S2 onset.

Event-related potentials: EEG was recorded with sintered Ag/AgCl electrodes in an Easy-Cap^{TM}, at the 64 sites AF$_z$, F$_z$, FC$_z$, C$_z$, CP$_z$, P$_z$, PO$_z$, I$_z$, F$_1$, F$_2$, FC$_1$, FC$_2$, C$_1$, C$_2$, CP$_1$, CP$_2$, P$_1$, P$_2$, F$_3$, F$_4$, FC$_3$, FC$_4$, C$_3$, C$_4$, CP$_3$, CP$_4$, P$_3$, P$_4$, F$_5$, F$_6$, FC$_5$, FC$_6$, C$_5$, C$_6$, CP$_5$, CP$_6$, P$_5$, P$_6$, Fp$_1$, Fp$_2$, AF$_7$, AF$_8$, F$_7$, F$_8$, FT$_7$, FT$_8$, T$_7$, T$_8$, TP$_7$, TP$_8$, P$_7$, P$_8$, PO$_7$, PO$_8$, O$_1$, O$_2$, FT$_9$, FT$_{10}$, PO$_9$, PO$_{10}$, F'_9, F'_{10}, TP$_9$ and TP$_{10}$. TP$_{10}$ served as initial common reference, and AF$_z$ served as ground. Impedances were $<10\,k\Omega$ (typically $<5\,k\Omega$). Horizontal electrooculogram (EOG) was monitored from F'_9 and F'_{10}. Vertical EOG was monitored bipolarly from above and below the right eye. Signals were recorded with DC (40 Hz low-pass, −6 dB attenuation, 12 dB/octave), and sampled at 250 Hz.

Offline, 1500 ms epochs were generated, starting 208 ms before S2 onset. Automatic artifact detection software provided an initial sorting of trials, and all trials were then visually inspected for artifacts. We discarded trials with non-ocular artifacts, saccades, and incorrect key presses. For all other trials, we corrected ocular blink contributions.

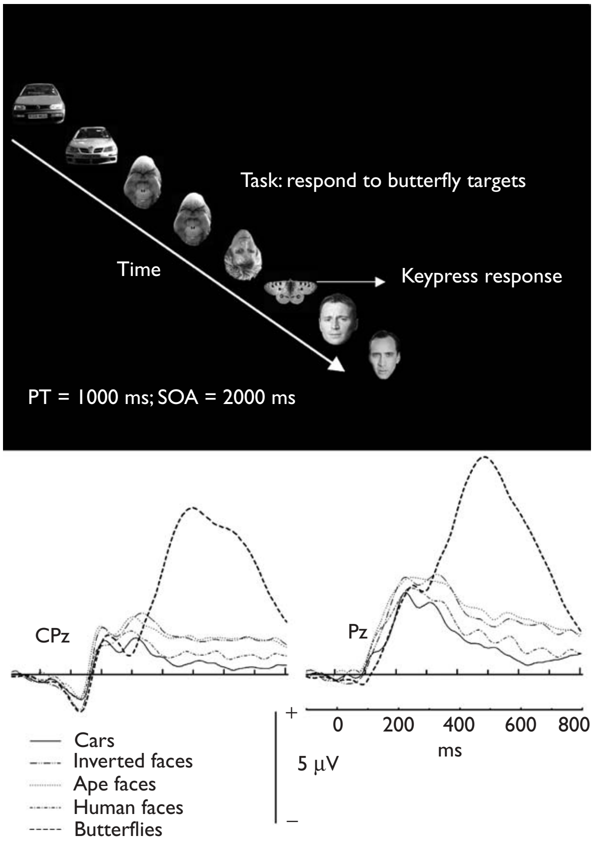

Fig. 1. Top: Task structure. Pairs of either human faces, inverted faces, ape faces, or front views of cars were presented sequentially (SOA=2000 ms) such that the second stimulus of each pair could be a repetition or a non-repetition of the first. In ∼11% of the pairs the second stimulus was a butterfly. Participants performed speeded keypress responses to butterfly stimuli only. Bottom: The late positivity (P300) at two central–parietal electrodes to butterfly targets, relative to all other stimuli.

ERPs were averaged separately for each experimental condition, digitally low-pass filtered (10 Hz, zero phase shift) and recalculated to average reference, excluding the vertical EOG. ERPs to S2 were quantified by taking mean amplitudes in the segments 170–200 ms (N170) and 265–315 ms (N250r), at 10 temporal and occipitotemporal sites at which these ERPs were most prominent both in previous research and in this study (P$_5$, P$_6$, P$_7$, P$_8$, TP$_7$, TP$_8$, PO$_7$, PO$_8$, TP$_9$ and TP$_{10}$). Analyses reported for N170 include these electrodes. Considering its focal right temporal topography (Fig. 2), analyses reported for N250r are for the site of maximal activity (P$_8$). We obtained the same pattern of results, though at slightly lower levels of significance, when analysis of N250r was done on all 10 electrodes above. Statistical analysis for N400 was done for the segment 350–500 ms at P$_z$.

RESULTS

The mean response time to butterflies was 505 ms, and participants failed to respond on only 1.4% of these stimuli.

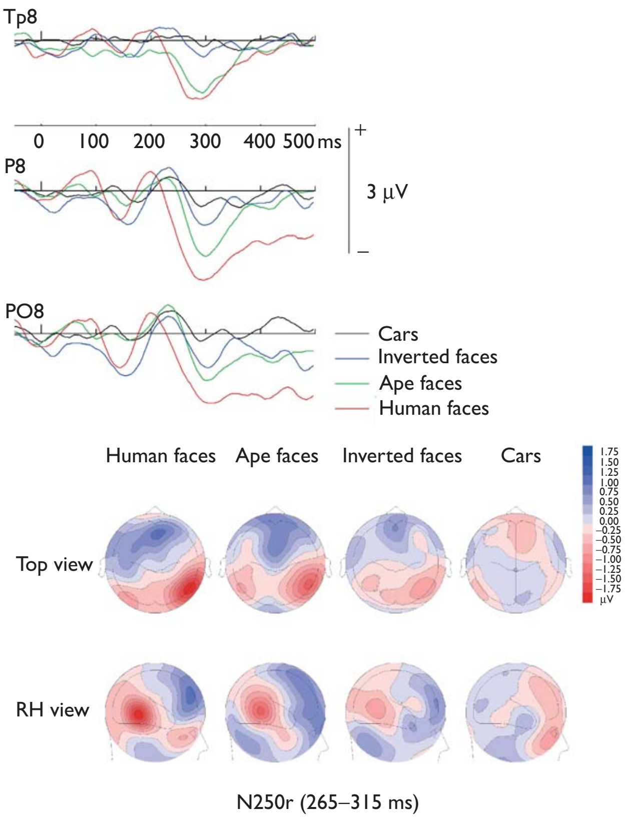

Fig. 2. Top: ERP difference between repeated and unrepeated stimuli for each category and three right temporal sites. The N250r onsets at ~220 ms and peaks at ~280 ms, with largest amplitudes for human faces, followed by ape faces, and small or absent responses for inverted faces and cars. Bottom: N250r voltage maps (spherical spline interpolation, 110° equidistant projection). Note the right inferior temporal negativity for human faces, a similar but smaller effect for ape faces, and the absence of any such effect for cars.

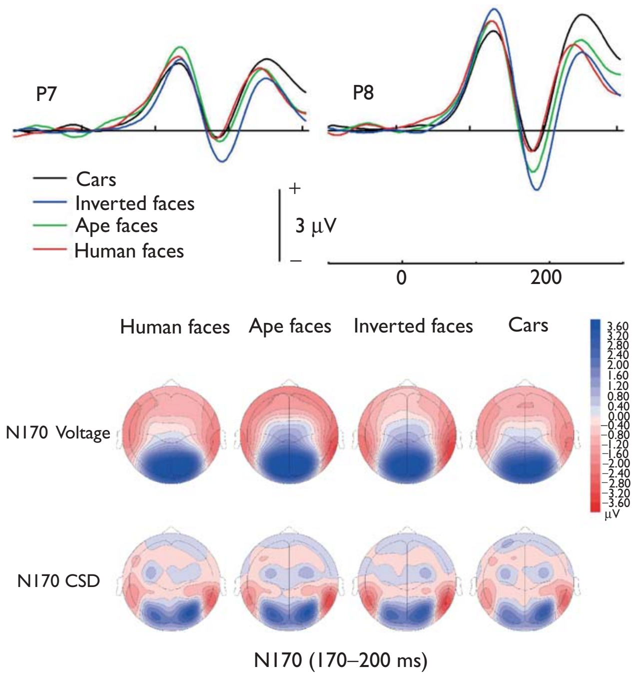

Fig. 3. Top: The N170 response from left (P7) and right (P8) posterior temporal sites. N170 (latency ~180 ms) is larger over the right hemisphere. This response is virtually identical for faces and cars, is increased for ape faces, and largest (and slightly delayed) for inverted faces. Bottom: N170 voltage maps for each stimulus category (top row), and CSD maps for the same data (bottom row).

At central–parietal electrodes we observed a large P300, a typical response to infrequent task-relevant events [4], to the butterfly targets relative to all other stimuli (Fig. 1).

Repetition had a strong effect on N250r amplitude (F(1,15)=18.4, $p<0.001$) which interacted with category, (F(3,45)=5.4, $p<0.01$). N250r was largest for human faces (F(1,15)=33.0, $p<0.0001$), still clear for ape faces (F(1,15)=10.2, $p<0.01$), but reduced to insignificance for inverted faces (F(1,15)=2.5, $p=0.13$) and absent for cars (F<1) (Fig. 2). The N250r for human faces had a strong right inferior temporal maximum. This topography was very similar for ape faces. For inverted faces, the (non-significant) repetition-related difference also exhibited a small right temporal negativity. By contrast, such a repetition effect was completely absent for cars (Fig. 2).

We observed no effect of repetition on N170 amplitude, neither in a main effect nor in any interaction with other factors (all F<1). However, there was an overall effect of category (F(3,45)=8.7, $p<0.001$). Relative to upright faces, N170 was larger for inverted faces (F(1,15)=31.6, $p<0.0001$) and ape faces (F(1,15)=13.2, $p<0.01$). Importantly, N170 was virtually identical for upright faces and cars (F(1,15)<1; Fig. 3). N170 topography was also remarkably similar for all four categories, and consistent with a source in the lateral occipitotemporal cortex of both hemispheres, with some preponderance of the right hemisphere [11]. Such a source is in line with the current source density (CSD) maps which are particularly sensitive to superficial cortical generators (Fig. 3).

We performed regional source localisation using BESA (Version 5.0), for both the face-elicited N170 and the N250r, closely following the procedure described in an earlier paper which also gives further discussion of this method [11]. Spatial principal component analysis (PCA) was used to determine, for each time interval, the number of sources necessary to describe the data. For N170 we used the 170–200 ms interval for unrepeated faces. One PC explained 98.1% variance, and we therefore fitted one pair of sources (one per hemisphere; no constraints for localization except for a symmetry constraint of the two sources [11]). For N250r, we used the 265–315 ms segment for the difference between repeated and unrepeated faces. Since noise levels are higher in difference waves, we averaged responses for upright human and ape faces to improve signal-to-noise ratio. One PC explained 96.0% variance, and we fitted one pair of sources as described above. The Talairach coordinates for the centres of activity were $x=\pm 44$, $y=-75$, $z=-4$ for the face-elicited N170, and $x=\pm 48$, $y=-49$, $z=-1$ for the N250r. Although localisation from scalp-recorded ERPs has limitations, we note that these coordinates correspond remarkably well to both previous localisations of these components [11], and to the lateral occipital face area (N170) and the fusiform gyrus (N250r) as described by functional imaging [3].

As we argued earlier, N250r reflects perceptual identification of faces. It is therefore important to ascertain that the N250r does not reflect semantic processing. In previous studies in which repetitions were task-relevant (e.g. when requiring an overt response), N250r was accompanied by a subsequent central–parietal N400 ($\sim$300–500 ms) [11,12,14]. However, N250r occurs well before the N400 which is associated with semantic activation [15]. In the present study in which repetitions were task-irrelevant, we did not see an N400 at all ($F(1,15) < 1$). The present task therefore allows us to better separate the N250r from common subsequent repetition-related ERP modulations, and demonstrates an independence of N250r from N400.

DISCUSSION

We observed a brain response to stimulus repetitions at $\sim$220–350 ms over right inferior temporal regions (N250r) that exhibits strong selectivity for faces: N250r was completely absent for repetitions of cars, showing that it clearly is no response to the repetition of visual stimuli in general. Relative to that for human faces, the response was smaller but still clear for ape faces. Inversion effects on N250r were in striking opposition to those seen for N170, which exhibits increased amplitudes. By contrast, and supporting our prediction, N250r was diminished for inverted faces. This is consistent with the hypothesis that the N250r reflects perceptual identification of faces, as identification is also strongly reduced by inversion. Facial representations used for recognition might be quite flexible, and are subject to transient adaptations depending on immediately prior visual experience [16]. Similarly, our research on N250r suggests that this response relates to a transient [17] activation of facial representations in the right or bilateral fusiform gyrus that is quite specific to the precise visual experience [11]. The N250r is therefore a potential candidate for a neural mechanism in fusiform cortex mediating transient aftereffects of facial representations induced by adaptation. This intriguing hypothesis awaits further research.

Our results also provide strong evidence against the view that the N170 is a face-selective response. This view has already been weakened by evidence that a sizeable N170 can be elicited by non-face stimuli such as artificial objects (greebles), chairs, or shoes [18]. However, the N170 elicited by these objects was somewhat smaller than that elicited by faces. In our study, front views of cars elicited an N170 that was indistinguishable from that elicited by upright faces. Thus, individual exemplars of objects that are as visually similar as faces, and have homogenous configuration, can elicit a comparable N170 response. Although we do not make strong claims here regarding the precise function reflected in N170 (see [6]), the inversion effects are in line with suggestions that the N170 reflects the difficulty in perceptually encoding a homogeneous visual pattern [19].

As a result of our use of similar exemplars within each category, we can exclude the possibility that the face selectivity of the N250r was caused by the perceptual homogeneity of stimuli. While our findings are in line with a domain-specific mechanism [1] for face recognition, they do not necessarily rule out a role for expertise [20]. The expertise hypothesis states that repeated exposure to exemplars of unfamiliar objects will result in the recruitment of similar neural mechanisms as those used for face processing. While the role of expertise was not the subject of the present study, our participants were presumably more familiar with front views of cars than images of apes. Nevertheless, one might argue that human expertise in face processing might easily generalize to ape faces (but not cars). However, this idea may be weakened by findings that adults can discriminate human but not monkey faces [21]. Thus, the finding that apes, but not cars, elicit an N250r is difficult to reconcile with a purely expertise-based account. In ERP research, much of the controversy around selectivity *vs* expertise has centred on whether N170 is a face-selective or an expertise-based brain response [9,22]. This is unfortunate because, while selectivity is often discussed for processes that mediate individual recognition of faces, the N170 does not seem to be strongly related to individual recognition. That said, an important future question is whether a role of visual expertise can be demonstrated for N250r.

Our source localisation suggests that both N170 and N250r are generated in ventral temporal cortex. Source reconstruction from scalp-recorded EEG clearly needs to be complemented by converging evidence. We propose a link between N250r and activity of the right or bilateral fusiform gyri which are believed to mediate the recognition of facial identity [3,6]. In line with the latter suggestion, haemodynamic activation of the fusiform face-sensitive area is strongly modulated by face repetitions [23–25]. Thus, the present findings can help to guide future research that aims to delineate not only the localisation but also the timing properties of different components within the human neural system for face processing [3,6].

REFERENCES

1. Kanwisher N. Domain specificity in face perception. *Nature Neurosci* 2000; **3**:759–763.
2. Kanwisher N, McDermott J and Chun MM. The fusiform face area: a module in human extrastriate cortex specialized for face perception. *J Neurosci* 1997; **17**:4302–4311.
3. Haxby JV, Hoffman EA and Gobbini MI. The distributed neural system for face perception. *Trends Cogn Sci* 2000; **4**:223–233.
4. Bentin S, Allison T, Puce A, Perez E and McCarthy G. Electrophysiological studies of face perception in humans. *J Cogn Neurosci* 1996; **8**:551–565.
5. Rossion B, Delvenne J-F, Debatisse D, Goffaux V, Bruyer R, Crommelinck M *et al*. Spatio-temporal localization of the face inversion effect: an event-related potentials study. *Biol Psychol* 1999; **50**:173–189.
6. Schweinberger SR and Burton AM. Covert recognition and the neural substrate for face processing. *Cortex* 2003; **39**:9–30.
7. Bentin S and Deouell LY. Structural encoding and identification in face processing: ERP evidence for separate mechanisms. *Cogn Neuropsychol* 2000; **17**:35–54.
8. Schweinberger SR, Pfütze E-M and Sommer W. Repetition priming and associative priming of face recognition: evidence from event-related potentials. *J Exp Psychol Learn Mem Cogn* 1995; **21**:722–736.
9. Bentin S and Carmel D. Accounts for the N170 face-effect: a reply to Rossion, Curran, & Gauthier. *Cognition* 2002; **85**:197–202.
10. de Haan M, Pascalis O and Johnson MH. Specialization of neural mechanisms underlying face recognition in human infants. *J Cogn Neurosci* 2002; **14**:199–209.
11. Schweinberger SR, Pickering EC, Jentzsch I, Burton AM and Kaufmann JM. Event-related brain potential evidence for a response of inferior temporal cortex to familiar face repetitions. *Cogn Brain Res* 2002; **14**: 398–409.
12. Pfütze E-M, Sommer W and Schweinberger SR. Age-related slowing in face and name recognition: evidence from event-related brain potentials. *Psychol Aging* 2002; **17**:140–160.

13. Damasio AR, Damasio H and Van Hoesen GW. Prosopagnosia: anatomic basis and behavioral mechanisms. *Neurology* 1982; **32**:331–341.
14. Pickering EC and Schweinberger SR. N200, N250r and N400 Event-related brain potentials reveal three loci of repetition priming for familiar names. *J Exp Psychol Learn Mem Cogn* 2003; **29**:1298–1311.
15. Barrett SE and Rugg MD. Event-related potentials and the semantic matching of faces. *Neuropsychologia* 1989; **27**:913–922.
16. Leopold DA, O'Toole AJ, Vetter T and Blanz V. Prototype-referenced shape encoding revealed by high-level aftereffects. *Nature Neurosci* 2001; **4**:89–94.
17. Schweinberger SR, Pickering EC, Burton AM and Kaufmann JM. Human brain potential correlates of repetition priming in face and name recognition. *Neuropsychologia* 2002; **40**:2057–2073.
18. Rossion B, Gauthier I, Tarr MJ, Despland P, Bruyer R and Linotte S. The N170 occipito-temporal component is delayed and enhanced to inverted faces but not to inverted objects: an electrophysiological account of face-specific processes in the human brain. *Neuroreport* 2000; **11**:69–74.
19. Eimer M. Effects of face inversion on the structural encoding and recognition of faces: evidence from event-related brain potentials. *Cogn Brain Res* 2000; **10**:145–158.
20. Gauthier I, Skudlarski P, Gore JC and Anderson AW. Expertise for cars and birds recruits brain areas involved in face recognition. *Nature Neurosci* 2000; **3**:191–197.
21. Pascalis O, de Haan M and Nelson CA. Is face processing species-specific during the first year of life? *Science* 2002; **296**:1321–1323.
22. Rossion B, Curran T and Gauthier I. A defense of the subordinate-level expertise account for the N170 component. *Cognition* 2002; **85**:189–196.
23. Henson RN, Goshen-Gottstein Y, Ganel T, Otten LJ, Quayle A and Rugg MD. Electrophysiological and haemodynamic correlates of face perception, recognition and priming. *Cerebr Cortex* 2003; **13**:793–805.
24. Henson RNA, Shallice T, Gorno-Tempini ML and Dolan RJ. Face repetition effects in implicit and explicit memory tests as measured by fMRI. *Cerebr Cortex* 2002; **12**:178–186.
25. Henson R, Shallice T and Dolan R. Neuroimaging evidence for dissociable forms of repetition priming. *Science* 2000; **287**:1269–1272.

Acknowledgements: Supported by BBSRC grant 17/S14233 to S.R.S. and A.M.B.