



An event-related potential component sensitive to images of the human body

Guillaume Thierry,^{a,*} Alan J. Pegna,^{a,d} Chris Dodds,^{a,b} Mark Roberts,^a Sébastien Basan,^c and Paul Downing^a

^a*School of Psychology, University of Wales, Bangor, Gwynedd LL57 2AS, UK*

^b*MRC Cognition and Brain Sciences Unit, Cambridge, UK*

^c*INSERM U455, Fédération de Neurologie, Hôpital de Purpan, Toulouse, France*

^d*Laboratory of Experimental Neuropsychology, Neuropsychology Unit, Geneva University Hospital, Geneva, Switzerland*

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One of the critical functions of vision is to provide information about other individuals. Neuroimaging experiments examining the cortical regions that analyze the appearance of other people have found partially overlapping networks that respond selectively to human faces and bodies. In event-related potential (ERP) studies, faces systematically elicit a negative component peaking 170 ms after presentation—the N170. To characterize the electrophysiological response to human bodies, we compared the ERPs elicited by faces, bodies and various control stimuli. In Experiment 1, a comparison of ERPs elicited by faces, bodies, objects and places showed that pictures of the human body (without the head) elicit a negative component peaking at 190 ms (an N190). While broadly similar to the N170, the N190 differs in both spatial distribution and amplitude from the N1 components elicited by faces, objects and scenes and peaks significantly later than the N170. The difference between N190 and N170 was further supported using topographic analyses of ERPs and source localization techniques. A unique, stable map topography was found to characterize human bodies between 130 and 230 ms. In Experiment 2, we tested the four conditions from Experiment 1, as well as intact and scrambled silhouettes and stick figures of the human body. We found that intact silhouettes and stick figures elicited significantly greater N190 amplitudes than their scrambled counterparts. Thus, the N190 generalizes to some degree to schematic depictions of the human form. Overall, our findings are consistent with intertwined, but functionally distinct, neural representations of the human face and body.

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Introduction

One of the critical functions of vision is to provide information about the identities, emotional states and actions of other individuals. This information enables the human brain to deal effectively with complex social situations. To understand how this complex process is implemented at the neural level, neuropsychological testing of patients, brain imaging and electrophysiology has been used to investigate the functional neuroanatomy and neural time-course of the perception of other people and their movements. Here, we report an event-related potential (ERP) investigation of the neural correlates of the perceptual analysis of human faces and bodies.

Many lines of evidence point to the existence of face-selective neural mechanisms. In prosopagnosic patients, face perception is selectively impaired, with relative sparing of object perception (Farah, 2004). The discovery of a patient with the reverse pattern of performance, i.e., selective impairment in object recognition while face recognition is relatively preserved (Moscovitch et al., 1997), points to a double dissociation suggesting relative functional segregation of face and object processing in the human brain (for a review, see also Kanwisher, 2000). Face-selective neural responses have been observed using functional magnetic resonance imaging (fMRI) in several regions of the human occipitotemporal cortex, including the posterior inferior occipital lobe (Puce et al., 1996), posterior superior temporal sulcus (Allison et al., 2000) and posterior fusiform gyrus (Kanwisher et al., 1997; Puce et al., 1996). Finally, intracranial electrodes (Allison et al., 1994; Allison et al., 1999; Halgren et al., 1994) and scalp ERPs (Bentin et al., 1996; Jeffreys, 1989) have revealed an early face-selective visual ERP response. This response, which in surface ERPs manifests as a negative peak over occipitotemporal regions at about 170 ms post-stimulus, has been labeled the N170. It has been proposed that the N170 is face-selective (Itier and Taylor, 2004), is increased in amplitude by inversion of faces but not other objects (Rossion et

* Corresponding author.

E-mail address: g.thierry@bangor.ac.uk (G. Thierry).

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al., 2000) and is relatively invariant to face repetition (Campanella et al., 2002; Guillaume and Tiberghien, 2001; Henson et al., 2003; but see Itier and Taylor, 2004; Schweinberger et al., 2002a; Schweinberger et al., 2002b), emotional expression (Batty and Taylor, 2003; Eimer, 2000; Eimer and Holmes, 2002; Stekelenburg and de Gelder, 2004) and to the status of faces as task-relevant targets (Carmel and Bentin, 2002; Cauquil et al., 2000). This and other evidence have been taken to argue that the N170 reflects early and obligatory activation of a domain-specific mechanism for visual analysis of faces (Carmel and Bentin, 2002), although this interpretation remains debated (see Rossion et al., 2002).

With regard to the neural representations of bodies, much of the emphasis has been on biological movement. A number of fMRI studies have demonstrated selective responses to biological motion of whole bodies and body parts. Such selective activations have been shown in the posterior superior temporal sulcus (reviewed in Allison et al., 2000), the ventral prefrontal cortex (Rizzolatti et al., 2001) and the inferior parietal lobule (Buccino et al., 2004; Fogassi et al., 2005). Additionally, two focal brain regions have been identified that respond selectively to static images of the human body. One of these, the extrastriate body area (EBA), lies at the posterior end of the inferior temporal sulcus. This region responds robustly to human bodies and body parts relative to faces, objects and object parts (Downing et al., 2001). Another body-selective focus, dubbed the fusiform body area (FBA), is found in the posterior fusiform gyrus (Peelen and Downing, 2005). This region overlaps closely with the fusiform face area; indeed at the group-average level, the two areas are nearly identical. However, three recent studies (Peelen et al., 2006; Peelen and Downing, 2005; Schwarzlose et al., 2005) provide evidence for distinct, dissociable face- and body-selective representations within this region.

One finding that emerges from the fMRI studies reviewed above is that faces and bodies evoke activity in distinct but adjacent neural regions. Faces, bodies and particularly face and body movements activate the posterior superior temporal sulcus, and bodies activate the nearby posterior inferior temporal sulcus. Similarly, both bodies and faces selectively activate the posterior

fusiform gyrus. Thus, the posterior cortical networks that process these highly significant (and clearly related) stimuli are substantially intertwined.

Given both the similarities and differences between face- and body-selective brain activations, it is tempting to ask whether there is a body-sensitive ERP waveform analogous to the N170 elicited by faces. If so, such a component might prove a valuable tool to investigate early stages of visual categorization (in particular, its neural time-course). Given the evidence reviewed above, we might expect to find that a body-sensitive ERP signature, should one exist, will be similar in scalp distribution to that of the N170. To compare ERPs elicited by bodies and faces, we used an approach similar to that used in previous fMRI studies (e.g., Downing et al., 2001): first, we used widely different stimulus types to identify a potential body-selective ERP component. Then, we used more tightly controlled comparisons to further test the properties of that component. In Experiment 1, photographs of faces, human bodies (without heads), scenes and objects were presented (Fig. 1, left). These conditions allowed us to identify a candidate body-selective response and to compare it to that elicited by faces. In Experiment 2, in order to test the generality of that response, the four categories from Experiment 1 were presented, along with human silhouettes, scrambled silhouettes, stick figures of human bodies and scrambled stick figures (Fig. 1, right). An ERP component genuinely reflecting the neural processing of the human body should respond more to images of bodies – whether realistic or abstract – than to other kinds of images.

Materials and methods

Participants

Twelve individuals (7 males, 5 females, mean age 26 ± 7.1) took part in Experiment 1, and 12 other individuals (8 males, 4 females, mean age 24 ± 4.3) took part in Experiment 2. All participants were right-handed with normal or corrected-to-normal

Experiment 2

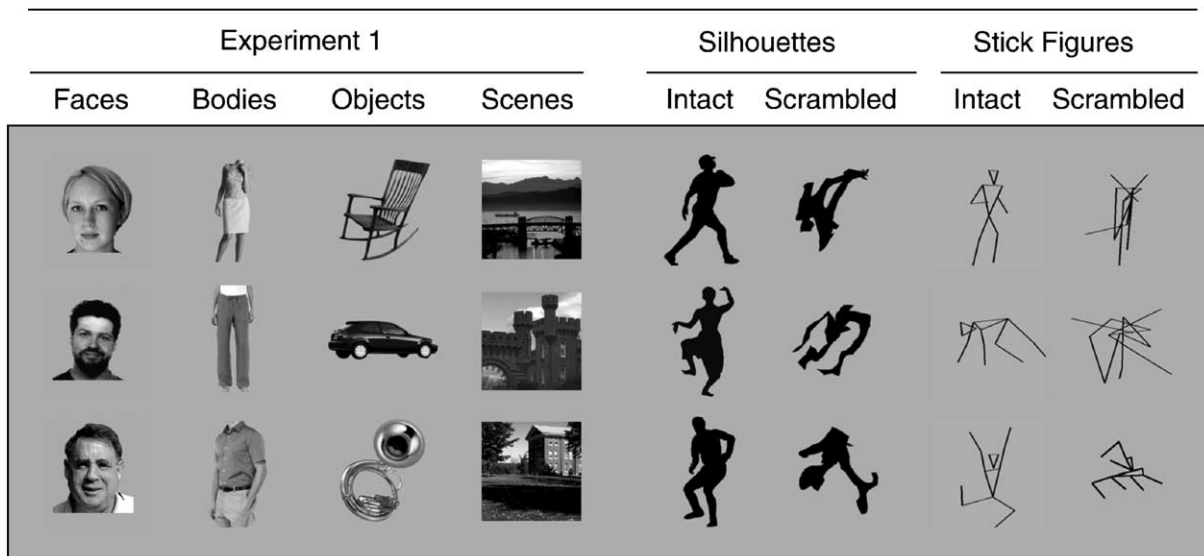


Fig. 1. Stimulus conditions and examples. Experiment 1 tested the ERPs elicited by faces, bodies, objects and scenes. Experiment 2 tested these conditions as well, in addition to silhouettes and stick figures of human bodies, and scrambled versions of the same images.

vision and were paid with cash or compensated with course credits. Data from one participant in Experiment 1 were discarded due to excessive artifacts. All procedures were approved by the ethics committee of the School of Psychology, University of Wales, Bangor.

Stimuli

The stimuli in Experiment 1 were 100 male and female faces, 100 male and female clothed bodies (with heads absent), 100 objects (including cars, chairs, flowers, foods, musical instruments and tools) and 100 scenes (such as street views). In addition to these four categories, Experiment 2 also tested 100 human silhouettes, 100 scrambled silhouettes, 100 stick figures (schematic representations of the human body) and 100 scrambled stick figures. Sample stimuli are shown in Fig. 1.

Design and procedure

Images were displayed for 200 ms on a uniform gray background and subtended a maximum of $4^\circ \times 4^\circ$ of visual angle. Each image was followed by a 1300 ms blank gray screen. In each recording session, two identical images were shown in immediate succession on 20 occasions. Participants were instructed to perform a “1-back” task by pressing the spacebar of a keyboard with the right hand whenever a repetition occurred. In Experiment 1, the initial design was constructed by pseudo-randomly arranging one presentation of each image from each condition. This was modified by inserting 20 image repetitions at random locations. Thus, there were a total of 420 trials in Experiment 1.

Experiment 2 was constructed similarly, except that the images from each of the eight conditions were first divided into two sets of 50 images per condition. These sets were arranged into two separate series, each with 420 total trials (including repetition trials). For each series in Experiments 1 and 2, two different random stimulus orders were constructed. In both experiments, trials in which a stimulus repetition occurred were removed from the analyses.

ERP recording and processing

EEG signals were sampled at 1 kHz from 64 Ag/AgCl electrodes referenced to Cz and placed according to the extended 10–20 convention (American Electroencephalographic Society, 1991). Impedances were kept below 9 k Ω . Signals were filtered on-line between 0.01 and 40 Hz. Ocular artifacts were mathematically corrected using Scan 4.2 (Neuroscan, Inc.). Remaining artifacts were manually rejected upon visual inspection. EEG epochs ranging from –100 to 1000 ms relative to stimulus onset were baseline corrected in reference to pre-stimulus activity before ERP averaging. Finally, ERPs were re-referenced to the global average reference. Peak detection was carried out automatically, time-locked to the latency of the peak at the electrode of maximal amplitude on the grand average ERP (Picton et al., 2000). Peak amplitudes were collected from electrodes PO7, P7, PO9, O1, O2, P8, PO10 and PO8 and were subjected to a repeated measures analysis of variance with category (4 levels in Experiments 1 and 8 levels in Experiment 2), hemisphere (2 levels) and electrode (4 levels) as factors using a Greenhouse–Geisser correction where applicable. Post hoc paired *t* tests were systematically adjusted using the Bonferroni correction for multiple comparisons in

Experiment 1. In Experiment 2, post hoc comparisons were tested with the least significant differences measure; no correction was applied since predictions for each contrast were made on the basis of results from Experiment 1. ERP component topographies were compared based on mean amplitudes measured over 36 electrodes distributed over the scalp (AF3, AF4, C1, C2, C5, C6, CP1, CP2, CP5, CP6, F3, F4, F7, F8, FC1, FC2, FC5, FC6, FP1, FP2, FT7, FT8, O1, O2, P1, P2, P5, P6, P7, P8, PO10, PO7, PO8, PO9, TP10, TP9). Interactions involving the electrode factor were controlled using the vector normalization as recommended by McCarthy and Wood (1985).

Evoked potential microstates

ERPs elicited by each of the 4 categories in Experiment 1 were analyzed using a topographical mapping approach. This approach considers the succession of electrical scalp potential maps that follow the onset of an event and determines the segments of time during which these maps remain stable. As changes in scalp topographies necessarily reflect changes in activation of the underlying cerebral generators, it has been hypothesized that the periods of stable map topographies, or segments, must correspond to particular steps in information processing during which a given neural network configuration is active. These segments have consequently been termed functional microstates (Lehmann, 1987; Michel et al., 1999; Michel et al., 2001). The relevance of topographical analyses has been demonstrated by the fact that variations in brain activity between experimental conditions produce differences in microstates (Blanke et al., 2005; Itier and Taylor, 2004; Khateb et al., 2002; Pegna et al., 2004).

Functional microstates within ERP map series are determined using a spatial k-means cluster analysis. First, the dominant maps appearing over time in each of the experimental conditions are identified. This step is based on the analysis of normalized data and is independent of the reference used or global amplitude modulations. The smallest set of maps that accounts for the greatest amount of variance is then selected using a cross validation criterion (Pascual-Marqui et al., 1995). Once the segments involved in each grand average ERP have been determined, differences between conditions are evaluated statistically. This is achieved by searching for the functional microstates in each individual's ERP map series using strength-independent spatial correlations (Pegna et al., 1997). The subject's scalp topography at each time point is compared with the microstates obtained from segmentation of the grand mean ERPs of each condition over subjects. The map at each time point of the participants' dataset is then compared with the most highly correlated microstate, and, for every subject, the amount of variance (as a percentage), explained by the microstate, is established (see Khateb et al., 2002; Pegna et al., 1997). The measure of explained variance thus reflects the “goodness-of-fit”, indicating how well the individual's data are explained by a given microstate. Statistical comparison of these values can then be carried out to compare the significance of the microstate across experimental conditions.

Source localization

The final step of analysis consisted in determining the brain regions responsible for each of the microstates identified during the segmentation procedure. This was carried out using a distributed linear inverse solution, based on a Local Auto-Regressive Average

(LAURA) model of the unknown current density in the brain (Grave de Peralta Menendez et al., 2001). This algorithm uses a realistic head model with 4024 lead field nodes equally distributed within the gray matter of an average brain (derived from scans from the Montreal Neurological Institute, Montreal, Canada). Like other inverse solutions of this family, LAURA is capable of dealing with multiple simultaneously active sources of a priori unknown location. This source localization algorithm has been used in a number of previous paradigms involving cognitive tasks (Blanke et al., 2005; Khateb et al., 2002; Michel et al., 2001; Pegna et al., 2004).

Results

Behavioral results

Mean performance on the 1-back task was 91.88% (SE = 2.95). Accuracy did not differ significantly between conditions in either experiment (all P s > 0.67).

ERP results

In both experiments, all stimulus categories elicited a typical visually evoked P1–N1–P2 complex that was maximal at parieto-occipital sites (Fig. 2). Our main component of interest was the N1; we also report results of the initial P1 response for comparison.

P1 component

In Experiment 1, the P1 peaked at 134 ms on average and was maximal at parieto-occipital sites. P1 latency was significantly modulated by category ($F[3,30] = 4.6$, $P < 0.01$). Post hoc tests corrected for multiple comparisons showed that the P1 elicited by objects (mean = 137 ms) was significantly delayed relative to faces (mean = 131 ms, $P < 0.01$) and bodies (mean = 134 ms, $P < 0.05$). No other latency effect was found. P1 amplitudes did not differ significantly across categories ($F[3,30] = 1.794$, $P > 0.1$).

In Experiment 2, the P1 peaked at 132 ms on average and was maximal at parieto-occipital sites. P1 latency was significantly modulated by category ($F[7,77] = 5.82$, $P < 0.0001$). Post hoc tests showed that the P1 elicited by objects was significantly delayed relative to faces ($P < 0.01$) but not relative to bodies ($P > 0.1$). In addition, scrambled stick figures elicited a P1 peaking significantly earlier than bodies ($P < 0.05$). P1 amplitudes differed significantly across categories ($F[7,77] = 3.39$, $P < 0.01$). Post hoc comparisons showed that this main effect was driven by significant amplitude differences between the P1 elicited by stick figures and the P1s elicited by faces, objects and scenes (all P s < 0.05).

N1 component

In Experiment 1, the grand average N1 elicited by faces peaked at 174 ms and was maximal at electrode PO10. In contrast, the N1 elicited by bodies peaked at 194 ms and was maximal at electrode P8 (Fig. 2). Stimulus category affected N1 peaking latencies significantly as shown by a condition main effect on N1 latency ($F[3,30] = 9.11$, $P < 0.0001$). Post hoc paired t tests showed that the 20 ms lag between the peak of body and face N1s was significant ($P < 0.05$, corrected for multiple comparisons). In addition, N1 amplitudes over the 8 parieto-occipital electrodes

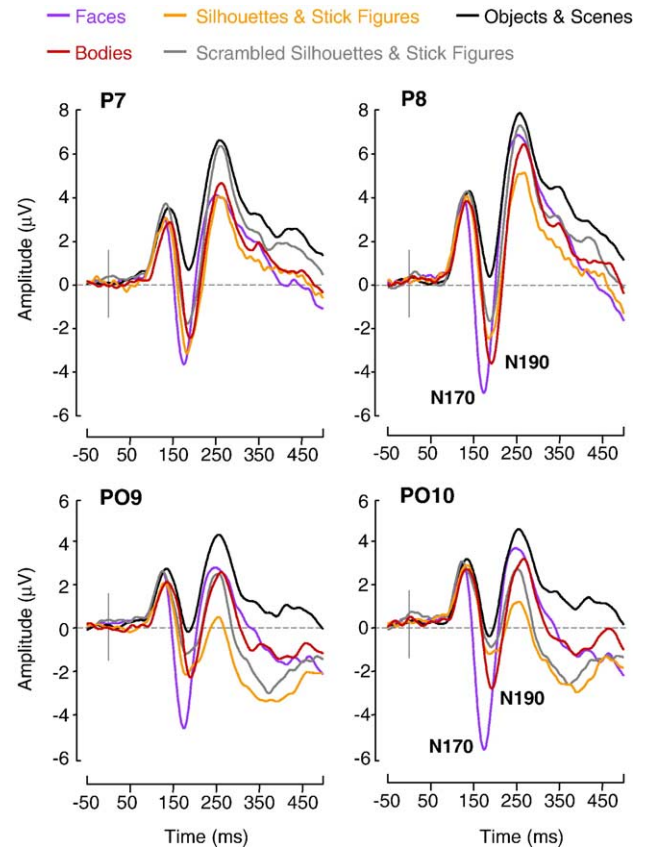


Fig. 2. ERP results. Event-related potentials measured at electrode P7, P8, PO9 and PO10 by faces, bodies and other conditions over the two experiments grouped by category (silhouettes and stick figures, scrambled silhouettes and stick figures, and object and scenes). The N1 elicited by faces peaked around 170 ms (N170) and was maximal at PO10, whereas the N1 elicited by all other stimuli peaked between 185 and 190 ms. Bodies elicited an N1 peaking at approximately 190 ms (N190) that was maximal at P8. Differences in peak latencies were significant for faces versus bodies in both experiments. In Experiment 1, all N1s were of significantly different amplitudes except object and scene N1s.

differed significantly in all pair-wise comparisons between stimulus types except for objects versus scenes (all $P < 0.05$; main effect $F[3,30] = 17.19$, $P < 0.0001$). Therefore, the N1 elicited by faces was significantly larger in amplitude than that elicited by bodies, and both the face and body N1s were significantly more negative than N1s elicited by objects and scenes. The topographical analysis revealed differences in N1 topography across categories as shown by a significant category \times electrode interaction ($F[4.8,42.81] = 4.93$, $P < 0.01$).

In Experiment 2, the N1 elicited by faces peaked at 170 ms and was maximal at electrode PO10. The N1 elicited by bodies peaked at 190 ms and was maximal at P8. The N1s elicited by intact body silhouettes and stick figures peaked at 185 and 193 ms, respectively, and their amplitude at P7 and P8 (electrodes of maximum amplitude) was significantly greater than that elicited by scrambled versions of these stimuli (main effect $F[1,11] = 29.1$; $P < 0.0001$). The ratio of the amplitudes (intact: scrambled) was approximately 4:3 for silhouettes and 2:1 for stick figures (Fig. 3). The N1 to intact silhouettes and stick figures differed significantly from the response to faces in latency (silhouettes: $P < 0.005$ and stick figures: $P < 0.0001$) and from the response

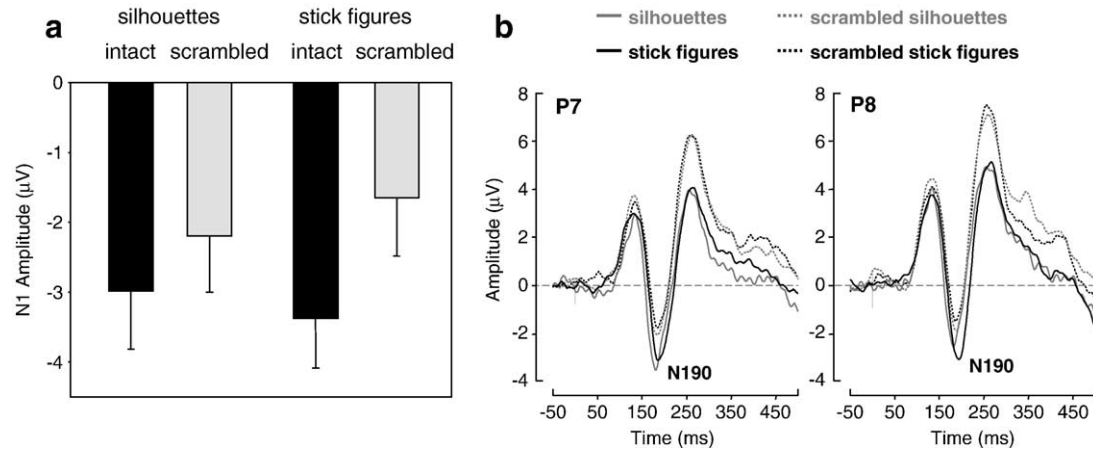


Fig. 3. Selectivity of the N190 for schematic representation of the human body. (a) The N1s elicited by silhouette and stick figures were significantly greater in amplitude than N1s elicited by scrambled control images. Differences between intact and scrambled versions of the stimuli were also significant within each category as shown by sample paired t tests (silhouettes: $P < 0.05$ and stick figures $P < 0.0001$). Error bars display standard errors of the mean. (b) ERPs elicited by silhouette, stick figures and their scrambled counterparts at electrodes of maximum amplitude (P7 and P8).

to photographs of objects and scenes in amplitude (all comparisons $P < 0.0001$) but did not differ on either measure from the response to photographs of bodies (both $P > 0.1$).

The topographical analysis over 36 electrodes compared faces, bodies, silhouettes and stick figures. A repeated measures ANOVA involving all four stimulus types revealed a significant category \times electrode interaction ($F[3.95,43.46] = 3.73$, $P < 0.05$). A repeated measures ANOVA comparing bodies, silhouettes and stick figures, however, failed to show any difference in N1 topography between representations of the human body ($F[4.47,49.24] = 1.70$, $P > 0.1$).

In summary, the N1 elicited by bodies (a) was close in amplitude to that elicited by faces but peaked significantly later, (b) had a different topography from the N170 elicited by faces and (c) generalized across photographs, silhouettes and line drawings. Moreover, this pattern was fundamentally different from that found in the P1 range.

Segmentation analyses

The map series for the 4 ERP conditions (faces, bodies, objects and scenes), between 0 ms (stimulus onset) and 400 ms, was entered into the topographical segmentation procedure described in

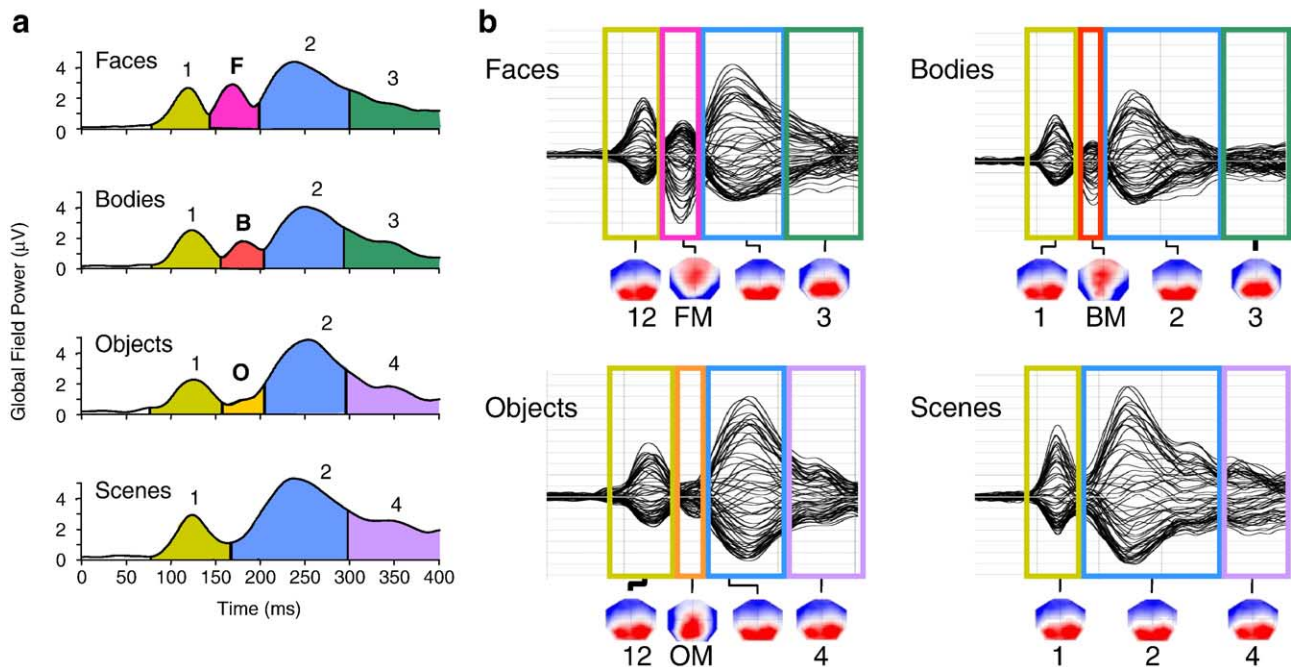


Fig. 4. EEG microstate analysis. (a) Segmented global field power plots obtained in Experiment 1. Boundaries of each microstate identified by the segmentation procedure are indicated by vertical bars. The second segment was selective for faces (F), bodies (B) and objects (O). (b) Map segmentations superimposed on traces of the 64 channel recordings are shown for faces, bodies, scenes and objects. Stable ERP topographies for each microstate are shown below ERP traces. FM = face map, BM = body map, OM = object map. Numbered maps correspond to segment numbers in panel a. Blue areas depict negative potentials and red areas depict positive potentials.

the Materials and methods section. The modified cluster analysis identified 7 maps that best explained the grand average ERPs (Fig. 4). A first meaningful functional microstate, corresponding to the P1 (map 1), was visible in all four conditions and appeared at 89 ms for faces, 64 ms for bodies, 49 ms for objects and 63 ms for scenes. Following map 1, a condition-sensitive microstate emerged for the three conditions, faces, bodies and objects, that were consequently termed maps F, B and O, respectively. Their window of occurrence was: map F, 151–206 ms; map B, 165–214 ms; and map O, 163–212 ms. The following microstate was common to all four conditions and was found after maps F, B and O, except in the case of scenes where it appeared directly after map 1. Finally, the last microstate appeared after map 2 and was different for faces and bodies on the one hand (map 3) and objects and scenes on the other (map 4).

In order to assess the selectivity of maps F, B and O in statistical terms, each of these maps was compared to individual map series. More specifically, the amount of variance explained by microstates F, B and O was computed in each of the three experimental conditions (face, body and object) for each participant between 130 and 230 ms after stimulus onset. Due to the lower signal-to-noise ratio in the individual map series, a large amount of residual variance must be expected in the comparison with grand average microstates. Nevertheless, if indeed the 3 microstates are selective for their corresponding condition, each should explain on average significantly more of the variance in the individual ERPs in that condition, relative to the others.

Between 130 and 230 ms, the mean (\pm SD) amount of variance explained by map F in individual ERPs was 0.49 (0.21) for faces, 0.40 (0.21) for bodies and 0.39 (0.21) for objects. The differences were compared using parametric statistics. In order to ensure that the distribution of measures of explained variance was Gaussian, the Shapiro–Wilks W test for normality was applied, yielding probabilities of $P > 0.1$ for these and the subsequent distributions, such that normality could not be rejected. A repeated measures ANOVA was therefore carried out showing that the difference between conditions was significant ($F[2,20] = 7.00$; $P < 0.05$). A

linear contrast analysis showed that map F explained significantly more variance in the individual ERPs for faces than in the other two conditions ($F[1,10] = 11.03$; $P < 0.01$).

Between 130 and 230 ms, the mean (\pm SD) amount of variance explained by map B in each of the participants was 0.3 (0.17) for faces, 0.35 (0.18) for bodies and 0.28 (0.18) for objects. The difference between conditions was significant ($F[2,20] = 4.39$; $P < 0.05$), and a post hoc contrast analysis showed that map B explained significantly more variance in the individual ERP for bodies than in the other two conditions ($F[1,10] = 6.02$; $P < 0.05$).

Finally, between 130 and 230 ms, the mean (\pm SD) amount of variance explained by map O in each of the participants was 0.18 (0.12) for faces, 0.21 (0.18) for bodies and 0.27 (0.18) for objects. The difference between conditions was again significant ($F[2,20] = 4.36$; $P < 0.05$), and post hoc test showed that map O explained significantly more variance in the individual ERP for objects than in the other two conditions ($F[1,10] = 7.89$; $P < 0.05$).

Source localization

The brain electrical sources responsible for microstates F, B and O were estimated using the LAURA source localization algorithm (Grave de Peralta Menendez et al., 2001, Fig. 5). All three maps were associated with sources in the right posterior extrastriate cortex. Maps F and B involved slightly more anterior portions of the right temporo-occipital region relative to map O. When comparing the source localizations for maps F and B, the region activated for map B in the right temporo-occipital area was larger and more extensive dorsally. Relative to map B, Map F was related to more ventral generators.

Discussion

Taken together, the significant differences in peak latency and topography between the face and body N1s, and the existence of distinct ERP microstates for faces, bodies and objects, point to a

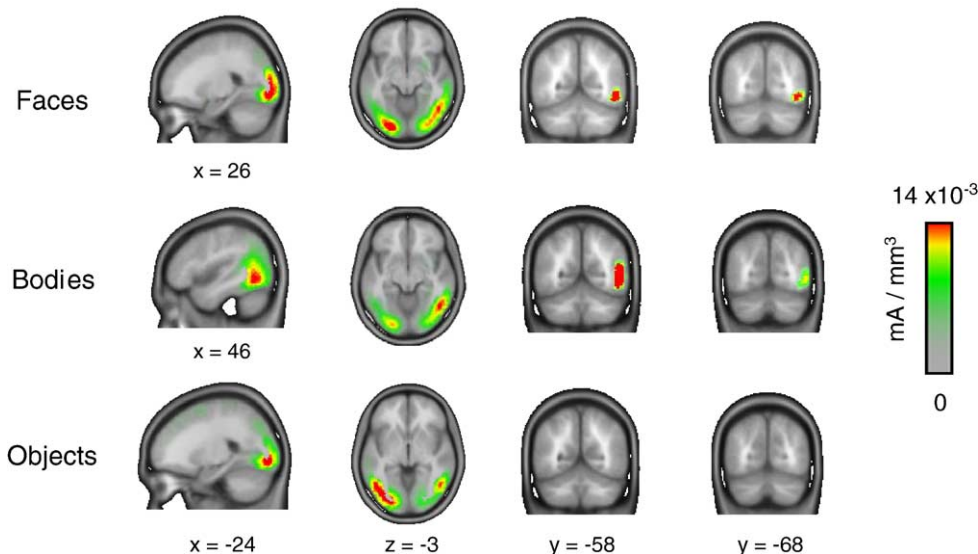


Fig. 5. LAURA source analysis. Source analyses (Grave de Peralta Menendez et al., 2001) for the maps F, B and O revealed sources concentrated in the bilateral posterior inferior occipital and temporal cortex for faces. Relative to faces, sources for bodies were localized more anteriorly and dorsally, with a predominance in the right hemisphere. Plane coordinates are given in Talairach space.

potential electrophysiological dissociation between the responses to faces and human bodies. Furthermore, the relative generalization of the N190 to schematic depictions of the body suggests that the neural processes characterized are not merely responding to low-level perceptual features. In other words, the N190 may index the extraction of abstract properties of the human form (i.e., information relevant for categorization) rather than the processing of low-level visual features that are only present in fully detailed photographs of bodies. This view is, moreover, compatible with recent results showing that body parts rotated at impossible orientations elicit differences between 190 and 230 ms (Overney et al., 2005).

A small number of previous studies have identified an N170-like potential to bodies or body parts, but these have rarely contrasted body and face responses directly. In a recent study, Stekelenburg and de Gelder (2004) found similar N170 and vertex-positive ERP components as well as similar effects of inversion (i.e., delayed and enhanced responses) for faces and bodies. However, the body stimuli used in their study included blurred faces. A recent fMRI study showed that even highly blurred face stimuli, when presented in the correct relationship to a body, can engage face-selective cortical areas (Cox et al., 2004). Thus, it is not clear whether the study of Stekelenburg and de Gelder (2004) measured the independent neural signatures of body processing per se or rather involved contextual face processing in the body conditions.

In another recent study, ERPs elicited by faces and bodies (without heads) were compared in adults and 3-month-old infants (Gliga and Dehaene-Lambertz, 2005). Although the authors found significant latency and topography differences between the N1s elicited by faces and bodies, the authors did not expand on the differences between the two N1s because the focus was on the comparison of processing capacity in infants and adults. However, the average peak delay of 24 ms between the face and body N1s reported by the authors is remarkably close to that observed in the present study (~20 ms).

The electrophysiological responses to human hands and faces have been measured with scalp ERPs (Kovacs et al., 2005; Mouchetant-Rostaing et al., 2000) and with intracranial electrode recordings (Allison et al., 1999; McCarthy et al., 1999; Puce et al., 1999). Kovacs et al. (2005) presented faces, hands or scrambled control stimuli as adapting stimuli followed by a brief test stimulus (hand or face) and measured the effects of the adaptor on gender judgments of the test stimulus. Both hands and faces elicited similar N170s at occipitotemporal recording sites (e.g., P7 and P8). The authors noted a somewhat different topography for the face- and hand-related N170s but attributed this to a difference in the brightness of the hand and face stimuli, which also influenced the P1 responses over occipital sites. Note that in the present study such category effects were not seen in the P1 range.

Intracranial recordings comparing the response to images of hands and faces (Allison et al., 1999; McCarthy et al., 1999; Puce et al., 1999) have provided three findings that bear on the present results: (1) face-selective recordings were made from the lateral and ventral occipitotemporal surface; (2) hand-selective recordings were also made from the lateral and ventral occipitotemporal surface but from different sites that were not face-selective, with a more anterior center of mass on the lateral surface; and (3) face-selective intracranial ERPs were characterized by a negativity peaking 200 ms post-stimulus (N200) whereas hand-selective responses peaked 30 ms later. Our findings are not inconsistent

with these results since the early negativity to bodies peaked later than that to faces and had more anterior generators. However, comparisons between surface ERPs and cortical recordings can only be tentative as latency/topography differences between healthy participant ERPs and intracranial recordings in pharmaco-resistant epileptic patients could derive from cognitive impairment following repeated seizures, intake of anticonvulsant medication or functional reorganization subsequent to the presence of epileptic foci (see for example Allison et al., 1999; Krolak-Salmon et al., 2004; Liu et al., 2002, or Bennett, 1992 for an overview).

What are the cortical sources of the early negative potentials evoked by bodies and faces? As noted above, intracranial recordings in humans indicate localized patches of early (~200 ms) face- and hand-selective activity at both ventral and lateral occipitotemporal sites, in the general region of face- and body-selective fMRI responses (Allison et al., 2000; Downing et al., 2001; Kanwisher et al., 1997; Peelen and Downing, 2005). With respect to scalp ERP, while a strong consensus has yet to emerge, the current evidence suggests that the N170 largely originates from lateral occipitotemporal sites (Henson et al., 2003; Itier and Taylor, 2004) with a contribution from the superior temporal gyrus (Horovitz et al., 2004), while the MEG homologue – the “M170” – is considered to originate from the posterior fusiform gyrus (Halgren et al., 2000). Given the similarity of the source analyses for faces and bodies in the present ERP investigation, it is likely that the N190 reported here is primarily driven by lateral sites. As the EBA is particularly selective for static body images relative to the pSTS (see for instance Grossman and Blake, 2002; Saxe et al., 2004), it might contribute substantially to the N190, although this conclusion can only be tentative. A contribution from ventral fusiform regions to the N190 cannot be ruled out, although the sensitivity of ERP to this area of cortex is likely to be relatively weak due to its location. Further characterization of ventral/lateral generators contributing to the N170 and N190 will require combined MEG/EEG and fMRI/EEG recording (e.g., Horovitz et al., 2004) as well as ERP recording in neuropsychological patients with focal cortical lesions (e.g., Eimer and McCarthy, 1999).

It must be noted at this point that a difference in N1 peak latency does not necessarily imply a difference in the time-course of activation of underlying neural substrata. Depending on the synchrony of activity in underlying generators and the conformation of the cortex, the summation of currents can theoretically result in surface peaks of different latencies. One could speculate that latency differences between the N170 and the N190 originate in a differential involvement of primary visual areas for instance since faces and bodies are perceptually quite different. Such differences, however, would most likely have induced measurable variations in the P1 range, which we did not see (there were no latency or amplitude differences between body and face P1s).

Finally, our results provide further support for the face selectivity of the N170. One of the most thorough tests of that selectivity was reported by Itier and Taylor (2004), who compared the ERPs elicited by upright faces, inverted faces, houses, textures and five other object categories (but not bodies or body parts). Remarkably, all object categories other than faces (and animals) used in their study elicited an N1 of very small amplitude, which stands in contrast to the N1 amplitudes we found for bodies. Using similar segmentation analyses to those reported here, they found a selective early map for faces in the 140–180 ms range that was not shared by the other stimuli (see also Rousselet et al., 2004). The

present finding of different maps for faces and bodies provides new support for the view that faces –and indeed bodies– are “special”.

Conclusion

Our results introduce the N190, an electrophysiological marker of activity in the cortical systems that analyze the form of the human body. In future, the N190 might prove a valuable tool for understanding how neural networks involved in high-level object recognition contribute more generally to solving the “social vision” problem by extracting information about the appearance, identity, actions and intentions of other humans.

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