Research Report

Face processing stages: Impact of difficulty and the separation of effects

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ABSTRACT

Cognitive models of face perception suggest parallel levels of processing yet there is little evidence of these levels in studies of brain function. Series of faces that engage different processes (photographs, schematic and Mooney faces (incomplete two-tone faces)) were presented upright, inverted and scrambled; subjects performed a face/non-face discrimination while event-related potentials (ERPs) were recorded. Different patterns in N170 latency and amplitude provided evidence of multiple steps in face processing, which can be seen at the ERP level. We showed that first-order configural and holistic processing were evident at the N170. N170 latency indexed task difficulty for the upright faces, yet the face inversion effect was independent of difficulty. N170 amplitude inversion effect was unique to photographic faces. Separable ERP effects were found for the processing engaged by the three face types, although the P1 and N170 sources did not differ. Thus, it appears that common brain sources underlie the early processing stages for faces (reflected in the P1 and N170), whereas the P2 showed activation of primary visual areas for the non-photographic faces and reactivation of the same regions as the N170 for the photographic faces.

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1. Introduction

As proposed in the model of Bruce and Young, faces engage multiple levels of processing, related to the type of information extracted from faces (Bruce and Young, 1986). Empirically testing these levels or stages of processing has utilized various types of face modifications in recognition protocols (e.g., scrambled, morphed, composite or inverted faces). The most widely used is face inversion, as presenting faces upside down affects the configural processing leading to decreases in recognition accuracy, increases in reaction times and subjective reports of greater difficulty. This is referred to as the face inversion effect (Yin, 1969). Maurer et al. (2002) proposed that faces involve three separable levels of processing: first, faces are processed as first-order relational configuration (eyes above nose, above mouth), which leads to the holistic perception of faces (i.e., a face versus a non-face), which is the second level of processing. The third level is the second-order relational configuration (spatial relations among facial features) that gives faces their individual distinctiveness and allows identity recognition (Maurer et al., 2002). To determine if these levels have distinct neural patterns, faces that differentially invoke these levels of processing need to be compared (Fig. 1).

Photographs of faces evoke event-related potentials (ERPs), P1 and N170, sensitive to face inversion: these ERP peaks are
delayed and larger for inverted faces (Bentin et al., 1996; Itier and Taylor, 2002, 2004; Rossion et al., 2000; Taylor et al., 2001). Inverted schematic (smiley) faces, however, evoke a delayed but not enhanced N170 (Henderson et al., 2003; Sagiv and Bentin, 2001), while for inverted Mooney faces (incomplete two-tone representation of faces (Mooney, 1957)) P1 and N170 are neither delayed nor enhanced (Latinus and Taylor, 2005). The ERP inversion effect for photographic faces has been argued to be due to difficulty (George et al., 1996; Rossion et al., 1999), yet difficulty is greater for Mooney than photographic faces (George et al., 1997, 2005; Kanwisher et al., 1998; Latinus and Taylor, 2005), faces which do not show this ERP inversion effect. How does inversion affect neural processing such that this varies as a function of the type of face? These differences in the neural signature, dependent on the type of face, provide an opportunity to elucidate the underlying neural processing for faces.

The three types of faces used in the present study involve different levels of processing proposed in the above theoretical model (Maurer et al., 2002). Mooney faces rely primarily on holistic processing (Latinus and Taylor, 2005; Moscovitch et al., 1997). As features are often not distinguishable in Mooney faces, the first order configural stage cannot be completed; moreover without clear features, the third stage also would not be completed (George et al., 2005). Mooney faces of well-known people can be recognized individually, particularly if primed (Jemel et al., 2003) suggesting that holistic processing may be sufficient for recognition of very well known faces. In contrast, schematic faces engage only the first and second levels of processing, as they contain no identity information (Sagiv and Bentin, 2001), while photographic faces invoke all three levels of processing. Differences among stimulus categories can be amplified by increasing task difficulty; this is effected for faces by presenting them upside down.

In order to elucidate neural activity underlying face processing, the three face types were presented with upright, inverted and scrambled (non-face/control) formats, while ERPs were recorded. Subjects performed a face detection task; ERP peak latencies and amplitudes were analyzed. Data were further analyzed with Cartool analysis software, which solves for the brain sources of ERP patterns (Michel et al., 2001). As the three face types should engage different stages of face processing, particularly when inverted, we could determine if these levels of processing activated different brain regions by comparing across face types.

2. Results

Photographic and schematic faces, whether upright, inverted or scrambled, were better detected as faces than Mooney faces (\(F_{2,26}=96.11, p<0.001\); accuracy for inverted faces was lower than for upright faces or scrambled faces (\(F_{2,26}=11.55, p=0.001\)) driven by inverted Mooney faces (type×subtype: \(F_{4,52}=18.72, p<0.001\)) (see Table 1). Reaction times (RTs) were the fastest to photographic faces and the slowest to Mooney faces (\(F_{2,26}=108.44, p<0.001\). A general effect of subtype was observed (\(F_{2,26}=37.72, p<0.001\)) as non-faces (i.e. scrambled faces) were the slowest categorized regardless of face type; and as reaction times to inverted faces were slower than to upright faces across face types (see Table 1), with the largest difference seen for Mooney faces (type×subtype: \(F_{4,52}=4.87, p=0.006\)).

As accuracy reached ceiling, \(d'\), that saturates less than accuracy, was calculated for upright faces and inverted faces as a better index of task difficulty. No differences were seen between \(d'\) for photographic \((d'=3.88)\) and schematic faces \((d'=3.61)\), but \(d'\) for Mooney faces \((d'=2.15)\) was significantly lower than for photographic and schematic faces.

![Fig. 1 – Examples of the upright, inverted and scrambled faces used in the experiment. Top: Mooney faces, middle: photographs, and bottom: schematic faces.](image)

Table 1 – Mean accuracy (correctly identifying the stimulus as a face or not) and RTs to each face type

<table>
<thead>
<tr>
<th>Face Type</th>
<th>% Hits (±SEM)</th>
<th>RTs ms (±SEM)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Photographic</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Upright</td>
<td>98.52 (±0.51)</td>
<td>522.07 (±18.03)</td>
</tr>
<tr>
<td>Inverted</td>
<td>98.88 (±0.37)</td>
<td>534.73 (±17.86)</td>
</tr>
<tr>
<td>Scrambled</td>
<td>95.56 (±0.92)</td>
<td>596.26 (±13.58)</td>
</tr>
<tr>
<td><strong>Mooney</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Upright</td>
<td>87.59 (±1.47)</td>
<td>600.45 (±17.35)</td>
</tr>
<tr>
<td>Inverted</td>
<td>67.53 (±3.54)</td>
<td>664.64 (±21.58)</td>
</tr>
<tr>
<td>Scrambled</td>
<td>81.33 (±2.14)</td>
<td>708.04 (±15.10)</td>
</tr>
<tr>
<td><strong>Schematic</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Upright</td>
<td>98.33 (±1.52)</td>
<td>543.20 (±19.23)</td>
</tr>
<tr>
<td>Inverted</td>
<td>96.54 (±1.05)</td>
<td>565.20 (±21.06)</td>
</tr>
<tr>
<td>Scrambled</td>
<td>92.65 (±0.50)</td>
<td>626.38 (±14.14)</td>
</tr>
</tbody>
</table>

Note that inversion disrupted face detection as measured by RTs for all three face types, and accuracy particularly for Mooney faces. RTs to scrambled faces (i.e., saying that the stimulus was not a face) were the longest.
lower \( F_{2,28}=92.062, p<0.001 \) reflecting greater difficulty in the detection of Mooney faces. \( d' \) was smaller to inverted than upright faces \( F_{1,14}=19.349, p=0.001 \), driven by the Mooney faces \( \text{type} \times \text{orientation}: F_{2,28}=23.173, p<0.001 \), which were particularly difficult to perceive as faces when inverted (Table 1).

The ERP components were measured for the nine different face types over posterior-temporal scalp, where they were the largest. Significant effects of face type or orientation were not seen on the P1, except for schematic faces evoking the largest. Significant effects of face type or orientation were not face types over posterior-temporal scalp, where they were the inverted (Table 1).

As the N170 delay observed for inverted faces has been explained to be due to increased difficulty (George et al., 1996; Rossion et al., 1999), we determined whether this could account for the delayed N170 to Mooney faces by correlating \( d' \) and N170. The correlation between \( d' \) (index of task difficulty) and N170 latency across face types (upright and inverted) showed a linear relation (Fig. 2b)—greater difficulty (lower \( d' \)) was correlated with longer N170 latencies \( (R^2=0.37, p<0.0001) \). We then calculated new N170 latencies for the three face types adding in, as an estimate of task difficulty, the slope of the regression curves from these correlations. N170 latency no longer varied with face type \( (F_{2,28}=0.280, \text{n.s.}) \), but remained delayed for inverted photographic and schematic faces (orientation, \( F_{1,14}=40.67, p<0.001 \); \text{type} \times \text{orientation}: \( F_{2,28}=12.85, p<0.001 \) (Fig. 2c). Difficulty accounted for N170 differences among face types, but not the inversion effect. The remaining inversion delay could reflect a ceiling effect. \( d' \) saturation depends on the number of trials (45 in the present case) leading to a maximum \( d' \) in our experiment of 4.57. Only 7 points were at this level (Fig. 2b). To avoid the ceiling effect in \( d' \), analyses were also done without those 7 points. N170 latencies calculated, taking into account the slope of this regression curve, were again delayed for inverted photographic and schematic faces but not for Mooney faces. We also ran regressions on each face type separately and found that only with schematic faces was there a significant correlation \( (R^2=0.3044, p<0.001) \) between \( d' \) and N170 latency. Thus, it is particularly across face types that difficulty impacts N170 latency (Table 2).

N170 was larger to photographic and schematic than Mooney faces \( (F_{2,28}=5.32, p=0.014) \). A general effect of subtype \( (F_{2,28}=53.0, p<0.001) \) was seen on N170 amplitude due to scrambled faces evoking the smallest N170 (Table 2). A face type by subtype interaction \( (F_{4,52}=13.98, p<0.001) \) and post-hoc tests revealed that (i) inversion of photographs led to an enhanced N170 \( (p<0.004) \), while there was no difference with

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**Fig. 2** – N170 latency correlations with \( d' \). (a) Mean N170 latency (±SEM) for each face type and for upright (●) and inverted (○) versions. Note that N170 latency is delayed for Mooney faces compared to schematic and photographic faces \( (*p<0.001) \), but the delayed N170 latency observed for inverted faces \( (p<0.01) \) is only seen for schematic and photographic faces. (b) Negative correlation between N170 latency (y axis) and \( d' \) (x-axis) \( (R^2=0.37, p<0.0001) \). Each subject’s data point is shown for each face type: photographic \( □ \), schematic \( ▴ \) and Mooney faces \(▵\). The average for each face type and format are shown with the same symbols but in gray. (c) N170 latency (±SEM) after including the slope of the regression curves (i.e. – 6.1313; legend is the same as for panel a. Note that N170 latency is no longer delayed for Mooney faces compared to photographic and schematic faces, unlike N170 for their inverted formats which remain delayed. NB: taking account of the task difficulty (i.e. including the slope of the regression curves) increased N170 latency as it is an inverse correlation.
Schematic faces yielded a different map (map 3) (Fig. 4a), that graphic faces (map 2), but the P2 for both Mooney faces and the underlying P2 was the same to upright and inverted photosphere dominance for the ventral source. Brain topography both occipital and lateral temporal sources, with right hemi-occipital and temporal regions; N170 showed activation of illustrated (Fig. 4b). P1 showed bilateral medial distribution in solutions were applied to these maps and brain sources are to help categorize ambiguous stimuli (Latinus and Taylor, 2005) corresponding to the three peaks of interest. Segmentation analyses revealed that 4 maps were sufficient to explain differences among the six conditions. The topographic maps for P1 and N170 to photographic faces along the ventral pathway, implying involvement of fewer brain regions in early processing of photographic faces.

3. Discussion

The manipulations of inversion and scrambling faces produced the classic effects of longer RTs and decreased accuracy consistent with increased difficulty, across the three face types. The effect of inversion was particularly marked for Mooney faces, as reported in studies with these two-tone stimuli (George et al., 2005; Jeffreys, 1993; Latinus and Taylor, 2005). The present study also found a distinct pattern of amplitude and latency effects on N170 for the three types of faces. N170 was larger for photographic than non-face stimuli; the N170 enhancement to inversion was seen for photographic and Mooney faces concordant with a host of studies showing that N170 reflects face processing. This was not seen for schematic faces, which can be accounted for by a context effect. It has been shown by Bentin and Golland (2002) that scrambled schematic faces evoke a large N170 during a face detection paradigm, but only when they have been primed by non-scrambled versions (Bentin and Golland, 2002).

Interestingly, the largest N170 amplitude differences between face and non-face stimuli appear in paradigms where attention is not directed towards the faces. When the subject’s task is face recognition or detection, the N170 to all stimuli is larger whether they are faces or not (e.g. George et al., 2005) as is the case in the present study. N170 latency was the same for upright photographic and schematic faces, but delayed for Mooney faces. Face inversion increased N170 latency only for photographic and schematic faces. N170 amplitude was smaller for Mooney faces compared to photographic faces. The latter appeared to be a reactivation of the ventral pathway active for the P1 and N170, implying involvement of fewer brain regions in early processing of photographic faces.

### Table 2 - Mean latencies and amplitudes for the three ERP components by condition

<table>
<thead>
<tr>
<th>Component</th>
<th>Photographic</th>
<th>Mooney</th>
<th>Schematic</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Upright</td>
<td>Inverted</td>
<td>Scrambled</td>
</tr>
<tr>
<td></td>
<td>Scrambled</td>
<td>Inverted</td>
<td>Scrambled</td>
</tr>
<tr>
<td>P1 Latency (ms) ±SEM</td>
<td>108.02±2.58  &amp;  110.03±3.54 &amp; 105.71±3.38 &amp; 108.31±3.86 &amp; 109.10±3.79</td>
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<td></td>
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<tr>
<td>P1 Amplitude (µV) ±SEM</td>
<td>5.85±0.74 &amp; 5.50±0.63 &amp; 3.56±0.58 &amp; 6.03±0.88 &amp; 5.70±0.71</td>
<td></td>
<td></td>
</tr>
<tr>
<td>N170 Latency (ms) ±SEM</td>
<td>161.03±1.67 &amp; 177.66±2.76 &amp; 163.92±1.62 &amp; 180.40±3.23 &amp; 179.49±4.09</td>
<td></td>
<td></td>
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<tr>
<td>N170 Amplitude (µV) ±SEM</td>
<td>7.21±0.94 &amp; 6.09±0.90 &amp; 7.07±0.83 &amp; 5.52±0.76 &amp; 4.34±0.79</td>
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<tr>
<td>P2 Latency (ms) ±SEM</td>
<td>227.56±4.23 &amp; 234.89±1.99 &amp; 226.50±2.91 &amp; 236.25±4.34 &amp; 234.02±2.57</td>
<td></td>
<td></td>
</tr>
<tr>
<td>P2 Amplitude (µV) ±SEM</td>
<td>4.60±1.38 &amp; 2.84±1.07 &amp; 3.67±1.11 &amp; 3.00±1.35 &amp; 3.81±1.07</td>
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</table>

Inversion for the other two face types (p>0.25) and (ii) scrambled faces had smaller N170s for photographic (p<0.001) and Mooney (p<0.007) faces, but not schematic faces (p>0.89) (Fig. 3). In summary, N170 was larger for face stimuli than non-face stimuli except for schematic faces and the N170 amplitude inversion effect was unique to photographic faces. P2, which is proposed to reflect deeper processing engaged to help categorize ambiguous stimuli (Latinus and Taylor, 2005), was delayed for inverted faces compared to upright faces and non face stimuli (F(2,26)=4.36, p=0.024). P2 was also delayed for Mooney faces compared to both other face types (F(2,26)=5.96, p=0.013). These effects were driven by the N170 latency delay, as peak to peak analyses (N170 to P2 latency) were not significant. A general effect of face type was seen on P2 amplitude (F(2,26)=8.96, p=0.002) due to P2 being larger for photographic than for Mooney faces; P2 amplitude for schematic faces was between that to photographic and Mooney faces. P2 was sensitive to subtype as it was larger to scrambled stimuli compared to faces (F(2,26)=8.15, p=0.007).

Segmentation and source analyses were performed on the relevant segments (Michel et al., 2004). By directly comparing across different face types with configurational modifications, the present data argue that...
N170 is sensitive to these levels of face processing, plus a further analytical process when faces are inverted.

Photographic and schematic upright faces initially engage first-order relations processing, followed by holistic processing. In contrast, the first processing that would be reliably invoked by Mooney faces is holistic (Latinus and Taylor, 2005); Mooney faces often do not have identifiable features (two eyes, over nose, over mouth) and are seen as a whole or gestalt image. The delayed N170 observed for Mooney faces, compared to both other face types, was accounted for by increased task difficulty, as when N170 latency was corrected for difficulty – indexed by $d'$ – no differences were seen among Mooney, schematic and photographic faces. Thus, the first effect seen on N170 is the almost simultaneous recruitment of first-order relations and holistic processing; recruitment of the latter is modulated by difficulty. Mooney faces evoke a smaller N170 as they recruit only holistic processing whereas, holistic and first-order relations appeared additive for schematic and photographic faces leading to a larger N170 (see model, Fig. 5a).

The face inversion effect on N170 differed across face types as when inverted, schematic and photographic faces produced delayed N170s, an effect not seen for Mooney faces. This inversion effect on N170 latency remained even after correction for task difficulty. Hence, the N170 delay for inverted faces does not appear to be due to difficulty as has been suggested in the literature (George et al., 1996; Rossion et al., 1999). Instead we suggest that the latency shift with inversion is due to a further process being recruited or engaged by photographic and schematic faces when these faces were upside down (Sagiv and Bentin, 2001). We submit that analytic processing, i.e. extraction of detailed information, which is invoked for feature by feature analysis of stimuli within the context of facial configuration, is the further process recruited by photographic and schematic faces. Analytical processing is used for objects (Haxby et al., 1999), which also show a delayed N170 compared to faces (Itier and Taylor, 2004; Itier et al., 2006). Thus, the involvement of additional analytic processing for inverted photographic and schematic faces, which entails slower, serial analysis of faces, would produce the delayed N170s (Fig. 5b).

In contrast, Mooney faces would not typically engage analytic processing as features are not readily distinguishable in this face type. Whether upright or inverted Mooney faces engage holistic processing; this could explain the latency being the same for these faces despite orientation.

Photographic and schematic faces evoked a similar N170 when upright; however, the face inversion effect differed between these two face types, as only photographic faces showed an amplitude enhancement when inverted. The same N170 for upright photographic and schematic faces could suggest that second-order relations are not processed at the N170 stage, as this processing is argued to be recruited only for photographs (Sagiv and Bentin, 2001). This would be consistent with studies showing that N170 is not sensitive to familiarity (Eimer, 2000a,b; Rossion et al., 1999) which requires second-order configuration processing.

Differences in N170 amplitude when schematic and photographic faces were inverted could be due to the way they use analytic processing. Inverted photographic faces would engage additional analytical processing to aid in face identification, producing the larger N170. In contrast, inverted schematic faces would recruit analytic processing to improve face detection not face identification, leading to a delayed but not enhanced N170 (Sagiv and Bentin, 2001). This is also supported by behavioural results as inversion reduced accuracy somewhat and increased RTs for photographic and schematic faces, whereas for Mooney faces dramatic effects were seen on accuracy and RTs, as only holistic processing is not sufficient for face detection of these inverted faces.

An alternative explanation for the face inversion effect on the N170 is that second-order configural processing is evoked...
for upright faces automatically, whether photographic, schematic or Mooney. When inversion disrupts this processing, no further configural processing continues for the schematic faces, as they do not contain identity information (Sagiv and Bentin, 2001), nor for the Mooney faces, as recognizing identity in inverted Mooney faces was not possible in the present task. With this model, N170 would index the spatial/relational configural processing of faces (Bentin et al., 1996; Eimer, 1998; Itier and Taylor, 2004). For inverted photographic faces only, analytical processing would be superimposed on the three standard stages of face processing, the addition of which would yield the larger, later N170 peak.

Source analyses showed that regardless of the face type or orientation, the same brain areas seemed activated for N170. In other words, although one can differentiate the stages of face processing with N170 latency and amplitude patterns, these stages nevertheless appear to engage the same neural generators. In contrast, neural mechanisms underlying P2, proposed to reflect deeper processing of stimuli, showed face type differences in localisation. P2 was larger to scrambled faces than upright and inverted faces, in accordance with previous results with Mooney faces (Latinus and Taylor, 2005). The P2 showed a bilateral reactivation of the ventral visual pathway for photographic faces but activation in the left occipito-temporal brain regions for Mooney and schematic faces. These data suggest that P2 reflects a left-lateralised, thus perhaps more analytical re-processing of the primary visual features for these simplified or impoverished face stimuli, whereas continued configural processing was seen for photographic faces, likely to facilitate identification (Caharel et al., 2002). It may be this activation associated with P2, which differs for the atypical faces, that has led to the suggestion in the fMRI literature of differing sources for configurally different faces (Haxby et al., 1999). As fMRI is

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Fig. 4 – Segmentation and source analyses on grand averages for upright and inverted version of each face type. (a) Segmentation analysis: GFP function over time (0–300 ms). Note that the 4 maps that are sufficient to explain all of the data in this time window, correspond to time intervals around each peak measured. (b) Source analysis on the different segments underlying P1 (z = −4 mm), N170 (z = −2 mm) and P2 (for Mooney and schematic faces: z = −10 mm and for photographic faces (z = −4 mm), showing the brain areas activated for these processing stages; only P2 shows a face-type effect.
averaged across time, then for the photographic faces the activation at the N170 and reactivation of the same areas at the P2 latency would be seen as a single area of activation on fMRI. With the schematic and Mooney faces, wider brain regions would appear active on fMRI.

4. Conclusions

The present study demonstrates that the ERP component sensitive to faces (N170) reflects different levels of processing, effectively representing the sum of up to four processing stages, with their temporal incongruities yielding the distinct amplitude and latency patterns of the N170 as a function of the type of face and its orientation. This temporal–spatial separation would be obscured by fMRI. We also show that different face-related processes engage the same brain sources for the P1 and N170 activation, but varied with face type for the later P2. Finally, we suggest that difficulty does not account for the neurophysiological face inversion effect.

5. Experimental procedures

Fifteen young adults (6 men, mean age = 25.8 years) participated in the study. All had normal or corrected-to-normal vision;
three were left-handed. They reported taking no medication and had no history of neurological, ophthalmological or systemic disease. They gave informed written consent. The experiment was approved by the French Comité Opérationnel pour l’Ethique dans les Sciences de la Vie du CNRS.

Stimuli used in the experiment were grayscale photographic faces, schematic faces and Mooney faces as well as scrambled, non-face stimuli made from the three types of faces. Non-faces were scrambled versions of the upright faces: for Mooney faces, black-and-white patches of the images were moved to create nonsense stimuli; for schematic faces, patches that contained parts of the features were moved and the outlined broken; for photographic faces, square patches were randomly moved in the pictures using a Photoshop option. These different face types were presented in upright, inverted or scrambled format. There were 45 different pictures of these nine categories and, to prevent a repetition effect, no pictures were presented both upright and inverted (see Fig. 1, upright, inverted and scrambled faces).

Subjects sat in a darkened room in a comfortable chair. Stimuli were presented centrally on a grey screen 60 cm in front of the subjects. The stimuli subtended 10°×11° of visual angle: they were presented for 300 ms in random order using Presentation 6.0, with an ISI between 1200 and 1600 ms. Subjects fixated a small white cross that appeared centrally on the screen between the pictures. They performed a face versus non-face detection task; they pressed a keyboard key for faces with one hand and another key for non-face stimuli with the other hand. The hand used for faces was counter-balanced across subjects. Five blocks of 81 randomly ordered stimuli (9 of each category) were presented in random order. Short breaks were given to subjects between blocks.

Accuracy and reaction times were recorded using Presentation 6.0. Electrophysiological data were recorded using 32 electrodes inserted in a cap (Easy Cap) plus three ocular electrodes to record eye movements. The electrodes were placed according to the 10/10 system. FCz was the reference during acquisition, and an average reference montage was calculated off-line. The ground was located at Fpz. Impedances were kept under 5kΩ. EEG was recorded using Neuroscan 4.2, the signal was amplified using Synamps system with a 500 gain. Data were recorded with a frequency of 1000 Hz through a band pass of 0.1–100 Hz with a notch at 50 Hz. Continuous data files were epoched into 800 ms (100 ms pre-stimulus, 700 ms post) epochs. After baseline correction, trials with artifacts between −100 and 500 ms, ±100 μV were rejected. Epochs were then averaged as a function of stimulus subtype and response, i.e. only the trials with correct behavioural responses were included, and filtered at 0.1–30 Hz.

We measured latencies (from stimuli onset) and amplitude (from baseline) of three ERP components (P1, N170 and P2) over parieto-occipito-temporal sites where they were maximal. Peak analyses were performed on individual data for each condition, within a 30 ms time-window centered at the peak in the appropriate grand average. P1 was measured at electrodes P7/P8 and O1/O2 in a 80–130 ms time-window, N170 was measured at electrodes PO9/PO10 and P7/P8, in a 140–200 ms time-window and P2 was measured between 200 and 260 ms at P7/P8, O1/O2 and P3/P4 electrodes. The peak latencies and amplitudes were submitted to repeated measures analysis of variance, within subjects factors were face format (3 levels (upright, inverted, scrambled) and face type (3 levels, photographic, Mooney, schematic), as well as hemisphere and electrode (2 levels for P1 and N170, 3 levels for P2) for peak amplitudes (Picton et al., 2000).

To investigate brain sources involved in the different stages of face processing we performed a segmentation analysis of the scalp activity into microstates preliminary to source analysis using Cartool software (Denis Brunet, Functional Brain Mapping Laboratory, Geneva, Switzerland). Functional microstates reflect stable configurations or maps of scalp electromagnetic activity over time intervals; variations in signal stability are seen as changes in map configuration. Segmentation is a spatio-temporal cluster-analysis that determines the predominant configuration over time. The cluster analysis defines the optimal numbers of maps that describe the data (Michel et al., 2001). Segmentation maps are represented in the global field power (GFP, equivalent to the instantaneous standard deviation of the scalp potential measurement) over the time period of interest, here between 0 and 300 ms (Fig. 4a). Source analyses were completed on the appropriate segments using a distributed inverse solution (LAURA) (Michel et al., 2001).

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