Research Report

Inversion and contrast-reversal effects on face processing assessed by MEG

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\textbf{ABSTRACT}

The processing of upright, inverted and contrast-reversed faces was investigated using MEG. Peak and global field power analyses revealed that the M100, M170 and M220 components were delayed for inverted and contrast-reversed compared to normal upright faces but no amplitude modulations were found. Source analyses using an event-related SAM beamformer technique revealed bilateral occipital sources for the M100 and M220 components. For the M170, two distinct sources simultaneously active were found, a bilateral and posterior source (M170A) and a right lateralized ventral and more anterior source (M170B) around the fusiform gyrus. None of the sources varied in location or intensity between face types. However, although different from the M100, the location of the M170A was not significantly different from that of the M220, suggesting the latter could be a reactivation of the former. Confirming previous ERP results on the processing of inverted faces, the present study extends the findings to contrast-reversed face stimuli and suggests that deviations from the standard upright face format do not activate extra areas but simply result in the delayed activation of the sources generating the M100, M170 and M220 components. The data confirm the sensitivity of the M100 to face manipulations and further suggest that the M170 is generated by two distinct sources, one of which situated in occipital extrastriate areas (M170A) could be reactivated around 220 ms to generate the M220 component.

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\textbf{1. Introduction}

Face processing has been studied intensively using various neuroimaging techniques and the localization of its neural substrates has been extensively described (Haxby et al., 2000; Ishai et al., 2005) but the dynamics of the brain networks involved are not fully understood.

Electro- and magneto-encephalography studies of face processing have focused mainly on the first 200 ms following stimulus onset. In event-related potential (ERP) studies, the emphasis has been on an early negative component recorded maximally over occipito-temporal sites, the N170, occurring between 140 and 200 ms post-stimulus onset. The N170 is larger for faces than all object categories tested, and thought
to reflect encoding processes where a perceptual representation of the face is extracted (Bentin et al., 1996; Bötzelt and Grüsser, 1989; Bötzelt et al., 1995; Carmel and Bentin, 2002; Eimer, 2000b; George et al., 1996; George et al., 2005; Itier and Taylor, 2004b; Itier et al., 2006; Jemel et al., 2003b, Rossion et al., 1999b, 2000; Taylor et al., 1999). There are fewer magnetoecephalography (MEG) than ERP studies on face processing but a similar component has been seen around 170 ms on posterior-lateral sensors that appears to be as sensitive to face stimuli as the ERP N170 (Halgren et al., 2000; Linkenkaer-Hansen et al., 1998; Liu et al., 2000, 1999; Lu et al., 1991; Sams et al., 1997; Sato et al., 1999; Streit et al., 1999; Swithenby et al., 1998; Watanabe et al., 1999a; Xu et al., 2005). However, this component, termed 2M, OT165 or M170 depending on the study, does not always behave like the N170 and whether it is the magnetic equivalent of the N170 or reflects at least partially different brain activities is still debated (Itier and Taylor, 2004c; Jemel et al., 2001). Recent studies have shown that the M170 amplitude was correlated with the successful identification of faces (Liu et al., 2002; Tanskanen et al., 2005; Xu et al., 2005) while its preceding component, the M100 (1M or MO110), occurring between 90 and 140 ms post-stimulus onset and maximal over occipital sites, also showed some face sensitivity (Halgren et al., 2000; Linkenkaer-Hansen et al., 1998; Liu et al., 2002) but no correlation with identification rates (Liu et al., 2002; Tanskanen et al., 2005; Xu et al., 2005). In ERPs, the P1 component preceding the N170 is also sensitive to face stimuli (Itier and Taylor, 2002, 2004a,b; Linkenkaer-Hansen et al., 1998; Taylor et al., 2001a) and some studies have reported repetition effects linked to identity processing for the N170 (Campanella et al., 2000; Itier and Taylor, 2002, 2004a; Jemel et al., 2003a). Taken together, these studies suggest that a crude face detection starts as early as the M100/P1 while the M170/N170 reflects refined stages where identity encoding could begin (Itier and Taylor, 2002, 2004a,b; Jemel et al., 2003a; Linkenkaer-Hansen et al., 1998; Liu et al., 2002).

Many face studies focused on the inversion effect as a means for investigating face particularity (for a review, see Rossion and Gauthier, 2002), and some also included the contrast-reversal (photo-negative) effect. Upside-down and negative faces are less accurately recognized and are processed more slowly than normal upright faces. Such effects are disproportionate for faces compared to objects (Galper, 1970; Kemp et al., 1996; Yin, 1969). ERP studies have consistently shown that the N170 is delayed and larger for inverted than upright faces (Bentin et al., 1996; de Haan et al., 2002; Eimer, 2000a; Itier et al., 2006; Itier and Taylor, 2002, 2004a,b; Rossion et al., 1999b, 2000; Sagiv and Bentin, 2001; Taylor et al., 2001a) and a few studies reported similar effects for the P1 (Itier and Taylor, 2002, 2004a,b; Taylor et al., 2001a). Although much less studied, contrast-reversal of face stimuli affects N170 similarly to inversion (Itier et al., 2006; Itier and Taylor, 2002, 2004a) and decreases P1 amplitude (Itier and Taylor, 2002; 2004a,b). In contrast, MEG studies found that the M170 was delayed but not larger in amplitude for inverted faces (Linkenkaer-Hansen et al., 1998; Liu et al., 2000; Taylor et al., 2001b; Watanabe et al., 2003) except in one report that found similar inversion effects on the M100 (Linkenkaer-Hansen et al., 1998). Like the P2 in ERP studies, the peak following the M170, the M220 (OT256 in Halgren et al., 2000), is even less studied than the P1/M100 and its role in face processing is unknown. To our knowledge, no MEG study investigated the effects of contrast-reversal on any MEG components and the inversion effects on M100 and M220 are still not determined.

The first goal of the present study was thus to investigate the effects of inversion and contrast-reversal of face stimuli on M100, M170 and M220 MEG components and to compare them to those reported on their ERP homologues. We thus adapted the paradigm from a previous ERP study (Itier and Taylor, 2002) to MEG. Blocks of upright, inverted and contrast-reversed faces (Fig. 1) were presented to the subjects, using a 2-back repetition task to maintain attention (only new faces were analyzed here). Showing different effects than what has been reported in ERP studies would argue in favor of the ERP and MEG components reflecting different processes and could help us better understand the various steps of normal face processing.

Most of the source analyses reported in the literature focused on the M170/N170 components and found a source in inferior temporal areas for both the N170 (Itier and Taylor, 2002; Rossion et al., 2003b; Schweinberger et al., 2000; Watanabe et al., 2003) and the M170 (Halgren et al., 2000; Linkenkaer-Hansen et al., 1998, 2000; Liu et al., 2000; Lu et al., 1991; Sams et al., 1997; Sato et al., 1999; Streit et al., 1999; Swithenby et al., 1998; Taylor et al., 2001b, 2003). This source is consistent with the fusiform gyrus (FG) face-sensitive area found in fMRI and PET studies (Halgren et al., 1999; Haxby et al., 1999; Kanwisher et al., 1997; McCarthy et al., 1997; Puce et al., 1995; Sergent and Signerot, 1992). However, recent studies (Itier and Taylor, 2004c; Watanabe et al., 2003) found that the N170 originated mainly from superior lateral temporal areas, consistent with the involvement of a lateral source also found in some fMRI studies surrounding the superior temporal sulcus (STS) region (Ishai et al., 2005; Puce et al., 1995) and with intracranial recordings of the face-specific component N200 (Allison et al., 1999; McCarthy et al., 1999; Puce et al., 1999). Activity from such a lateral source is likely diminished or nonexistent in the MEG because of a radial orientation (Watanabe et al., 2003), suggesting the M170 and M170 components could reflect simultaneously active but distinct sources. Beside this unresolved issue, few studies attempted to find the sources of P1/M100 and the less studied M220/P2 components.

Fig. 1 – Example of upright, inverted and contrast-reversed (negative) faces as used in the experiment.
Thus, the second goal of our study was to investigate the sources of the M100, M170, and M220 components, and to compare their locations and intensities among upright, inverted, and contrast-reversed face stimuli. We used the Synthetic Aperture Magnetometry (SAM) technique (Robinson and Vrba, 1999), a spatial filtering algorithm that has been recently applied to source analyses of MEG data in auditory (Herdman et al., 2004), visual (Fawcett et al., 2004) and somatosensory modalities (Gaetz and Cheyne, 2003; Taniguchi et al., 2000). In these studies the SAM beamformer was used as a frequency filter that calculated the source power changes across a given time period for certain frequency bands, relative to baseline. Recently, an event-related SAM version has been developed that allows time-locked source activity to be calculated instantaneously, at a single given latency (Cheyne et al., 2006) that is more amenable to studying evoked brain responses. We applied the erSAM method to investigate sources contributing to the generation of the M100, M170 and M220 components.

2. Results

2.1. Behavioral analyses

Inverted and negative faces elicited higher false alarms, lower hit rates and longer reaction times than upright faces (Table 1) as shown by face type effects found for the percent of false alarms for new faces (F(2,40)=20.89, p<0.0001, ε=0.99), the percent of hits for repeated faces (F(2,40)=10.23, p<0.001, ε=0.85), and the reaction times to repetitions (F(2,40)=5.1, p<0.005, ε=0.99).

2.2. Event-related field (ERF) and global field power (GFP) peak analyses

The event-related magnetic field recorded to all three face types was composed of three successive components (Fig. 2a). The M100, recorded maximally between 95 and 154 ms at occipito-temporal sites, was usually negative in polarity over the left hemisphere and positive over the right (Figs. 2a, b). The following component was recorded maximally between 140 and 213 ms over similar temporal-occipital sensors and corresponded to the well studied M170. In all 20 subjects, it was of positive polarity on the left and negative polarity on the right hemisphere (Figs. 2a, b). In all but 2 subjects, a second field, more occipital and of inverted polarity compared to the lateral temporal M170, was recorded simultaneously (clearly seen on the example in Fig. 2a). The third magnetic component following the M170, the M220 component, was maximal between 205 and 260 ms over similar occipito-temporal sensors as for the previous two components. However, for 7 subjects, it was found at central and parietal sites. The M220 was generally of opposite polarity to the lateral-temporal M170.

An effect of face type was found for the M100 latency (F(2,38)=4.29, p=0.021, ε=0.99) due to a small but consistent delay (4 ms mean delay ±1 ms standard error) for inverted compared to upright faces (p=0.035). Negative faces were not significantly different from upright faces (p=1) (Fig. 2b). M170 latency was delayed for inverted (p<0.005) (8 ms±2) and negative (p<0.005) (5 ms±1) faces compared to upright faces (Fig. 2b) (effect of face type, F(2,38)=12.17, p<0.0001, ε=0.81). M220 showed the same main effect of face type (F(2,38)=5.79, p<0.01, ε=0.83), with inverted faces yielding later M220 (8 ms±3) than upright faces (p<0.05). Although negative faces tended to yield delayed M220 latencies as well (4 ms±2), this did not reach significance (p=0.1). No effects of hemisphere were found for latencies. No effects of face type were found for any amplitude measures. An effect of hemisphere was found for the amplitudes of M170 (F(1,19)=8.65, p<0.0001) and M220 (F(1,19)=25.59, p<0.0001), due to negative amplitudes on the right hemisphere and positive amplitudes on the left hemisphere for the M170 while the opposite was found for the M220. When absolute values were used to check for power differences across hemispheres, no effects of hemisphere were found in any analyses. No face type by hemisphere interactions were found.

No effect of face type was found on latency (p=0.42) nor amplitude (p=0.66) for the global field power (GFP) peak of the M100 component (Fig. 3). However, similar results as the ones seen with the ERF measures were found for the GFP of the M170, its latency being delayed (F(2,38)=6.16, p<0.006, ε=0.92) for inverted (p=0.02) and negative (p=0.04) compared to upright faces (by 10 ms±3 and 9 ms±3 respectively), while no effect was found for its amplitude (p=0.54). Again, as seen with ERF measures, the GFP peak of the M220 component showed a main effect of face type (F(2,38)=3.7, p<0.05, ε=0.83), with later latencies for negative than upright faces (15 ms±5) (p=0.015). However, the difference between inverted and upright faces (9 ms±5) was not significant (p=0.3).

2.3. Source analysis using event-related Synthetic Aperture Magnetometry (erSAM)

Although we expected group averages of the erSAM images to contain significant spatial smearing due to the lack of individual structural MR images to align each individual’s image to the template brain, clear and separable peaks could be identified in the group images in appropriate regions of the occipital and temporal areas according to the Talairach coordinates. In addition, any such smearing will be equivalent across experimental conditions making relative comparisons between the conditions meaningful. For this reason we report peak locations in Talairach coordinates in the following section (Table 3), although these brain locations are based on a single best fit MRI to the MNI template brain and must be interpreted as approximate locations only. For each source,
Fig. 2 – (a) Individual data of one typical subject showing the M100, M170 and M220 components for upright, inverted and negative faces across all sensors with their associated topographies. The maximum and minimum field amplitudes are ±300 fT for the M170 and M220 components (all face types), ±200 fT for the M100 inverted and negative faces and ±250 fT for M100 for upright faces. (b) Time course of the magnetic field recorded for that same subject at two lateral sensors MLT14 (left hemisphere) and MRT14 (right hemisphere) showing the delay in latency of the M100 and M170 components for inverted and negative faces compared to upright faces.
only subjects for whom the source was found (see Table 2) were taken into account in the group averages.

2.3.1. Source of the M100 component
The source of the M100 was found in the occipital lobe, medially and bilaterally for all face types and all subjects (Fig. 4). No significant difference in the intensity of the sources (as represented by the voxel of maximum intensity) was found across face types ($p = 0.91$) or hemisphere ($p = 0.59$). None of the MANOVA tests on the source coordinate differences across face types were significant, suggesting that the location of these bilateral M100 sources did not differ among face types. The mean coordinates obtained by averaging the coordinates of the voxels of maximum intensity for each subject and each condition were found around the cuneus, lingual gyrus and BA17 (Table 3). Note that the voxels of maximum intensity vary from subject to subject and thus the average across subjects should only be taken as an approximation of the centroid of the activation.

2.3.2. Source of the M170 component
For the M170, two distinct sources were found in most subjects, one bilateral occipital, the M170A, and one anterior and ventral to the M170A in the right hemisphere only, the M170B (Fig. 4). For both sources, the MANOVA tests on the source coordinate differences between face types yielded no significant effect. In the right hemisphere, the M170B was significantly different in location from the M170A for upright ($F(3,13) = 31.12, p < 0.0001, n = 16$), inverted ($F(3,16) = 24.95, p < 0.0001, n = 19$) and negative faces ($F(3,14) = 41.14, p < 0.0001, n = 17$), confirming the existence of two distinct source clusters (Fig. 5). The means and distributions of the peak voxels revealed that the M170B was more lateral (Fig. 5A), ventral and anterior (Fig. 5B) than the M170A source, for all three face types. For the right hemisphere, the group mean coordinates obtained for the M170A were found in the region of the occipital lobe (around the middle and inferior occipital gyri) while for the left hemisphere, coordinates were found around the occipitotemporal junction (Table 3). The M170B, in contrast, was found in the superior aspect of the cerebellum in the vicinity of the inferior surface of the fusiform gyrus (FG) for upright and negative faces, and around the fusiform gyrus for inverted faces. Taking into account (i) the approximation of the coordinates due to the absence of the individuals’ structural MRIs, (ii) the fact that this represents the centroid of the group distribution, and (iii) that no significant difference was found among face types, we believe that this M170B source was situated in or near the FG for all face types. For the intensity measures, no face type differences were found for either M170A or M170B sources.

2.3.3. Source of the M220 component
As seen for the M100, the M220 was bilateral for all three face types (Fig. 4), situated in the occipital lobe around the middle occipital gyrus region (Table 3) except for negative faces for which the sources were more temporal. No significant differences in the intensity of the sources were found across face types ($p = 0.29$) or hemispheres ($p = 0.3$). Similarly, none of the MANOVA tests performed on the coordinate differences across face types were significant, suggesting that the location of the M220 source did not vary significantly among face types.

2.3.4. Comparison of the source locations
The sources of the M100 and M170A differed significantly for upright ($F(3,17) = 8.97, p < 0.001, n = 20$) and inverted ($F(3,17) = 8.66, p < 0.001, n = 20$) faces in the left hemisphere, and for negative faces in both right ($F(3,16) = 5.14, p = 0.011, n = 19$) and left hemispheres ($F(3,16) = 4.58, p = 0.017, n = 19$). The source of the M100 was also significantly different from that of the M220 for both hemispheres for upright faces ($F(15,3) = 6.04, p = 0.007, n = 18$) for the right hemisphere, $F(17,3) = 8.94, p < 0.001, n = 20$, for the left hemisphere) and negative faces ($F(16,3) = 4.88, p = 0.013, n = 19$ for RH, $F(16,3) = 4.58, p = 0.017$).

| Table 2 – Number of subjects for whom the sources of the M100, M170A, M170B and M220 components were found as a function of face type and hemisphere |
|----------------|---------|---------|---------|---------|
|               | M100    | M170A   | M170B   | M220    |
| Upright       | RH      | LH      | RH      | LH      |
|               | 19      | 20      | 0       | 20      |
| Inverted      | RH      | LH      | RH      | LH      |
|               | 18      | 20      | 16      | 19      |
| Negative      | RH      | LH      | RH      | LH      |
|               | 19      | 20      | 18      | 18      |

Note that the M170A was found for all subjects, all conditions and both hemispheres.

1 Although 18 subjects presented an M170B in the negative condition (Table 2), only 17 presented both the M170A and M170B, resulting in $n = 17$ subjects for the direct comparison M170A-M170B location.
n=19, for LH), and for inverted faces on the left hemisphere ($F(17,3)=8.66, p<0.001, n=20$). In all cases, the M100 was more medial, posterior and superior than the M170A and M220. In contrast, the sources of the M220 were very similar to those found for M170A. A direct comparison showed no significant differences for upright and inverted faces for both hemispheres. The only significant difference was found for negative faces in the right hemisphere ($F(3,15)=4.39, p<0.05, n=18$).

## 3. Discussion

This paper investigated the effects of inversion and contrast-reversal on the early steps of face processing, using a 2-back repetition paradigm in MEG. We used peak measures of the event-related fields and global field power to assess the effects of these two kinds of face manipulation on the M100, M170 and M220 components. We also used the new beamformer erSAM source analysis technique to investigate the brain sources of these components and their possible spatial variations across upright, upside-down and contrast-reversed faces.

Behavioral measures showed a decrease in accuracy and increase in reaction times for inverted and negative faces compared to upright faces, replicating the effects found in previous behavioral and ERP studies (Galper, 1970; Itier and Taylor, 2002; 2004a; Yin, 1969). The analyses of the ERF and GFP peaks yielded different results for the M100 and M220 but converging results for the M170. While no face type effects were found for the M100 on the GFP, a significantly delayed M100 was found for inverted compared to upright faces with the ERF measures. M220 showed a face type effect in both analyses but the significant pair-wise comparisons were different, showing later latencies for inverted faces with ERF measures and later latencies for negative faces with GFP measures. These discrepancies are likely due to the measures, the ERF being assessed at one sensor while the GFP represents the total power across all sensors. If the activation is broader sources of these components and their possible spatial variations across upright, upside-down and contrast-reversed faces.

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<table>
<thead>
<tr>
<th>Component</th>
<th>Upright</th>
<th>Inverted</th>
<th>Negative</th>
</tr>
</thead>
<tbody>
<tr>
<td>M100</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>M170</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>M220</td>
<td></td>
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</tbody>
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**Fig. 4** – Group averaged event-related SAM images obtained for the M100, M170 and M220 components for each face type. The sources are shown as maximum intensity projections in the Talairach coordinate system (maximum and threshold values expressed in pseudo-z scores). For all sub-plots, the voxels shown passed the group statistical threshold of $p<0.01$. Two distinct sources were found for the M170, called the M170A (A) and M170B (B). Because of the different intensities of the various sources, the color scale, which was adapted to each face type and component to reveal all peaks, uses a specific threshold (equivalent to a minimum value) and maximum value. This figure is used to illustrate the sources and their position relative to each other but a direct comparison of the source intensity across components or face types is not possible from the figure due to the different scales.
and less focal, as it was for the M100 and M220 components, the GFP measure may be less sensitive to small variations such as those recorded here, compared to the ERF which focuses on the sensor of maximal activity. Both were convergent however on the M170 peak, showing delayed latencies for both inverted and negative compared to upright faces. This is likely due to less inter-subject variability for that peak along with much larger intensities.

The M100 and M170 latency effects are consistent with previous studies on the face inversion effect measured in MEG (Linkenkaer-Hansen et al., 1998; Liu et al., 2000; Taylor et al., 2001b; Watanabe et al., 2003) as well as in ERPs (Bentin et al., 1996; Bötzel and Grüsser, 1989; Bötzel et al., 1995; Carmel and Bentin, 2002; Eimer, 2000a; Eimer et al., 2000b; George et al., 1996; George et al., 2005; Itier and Taylor, 2004b; Itier et al., 2006; Jemel et al., 2003b; Rossion et al., 1999b, 2000; Taylor et al., 1999). Although the role of the P2 in face processing is unknown, it has been suggested to index stages of familiarity and recognition (Bentin et al., 1996; Grüsser et al., 1989; Grill-Spector et al., 2004) or deeper processing as a function of stimulus ambiguity (Latinus and Taylor, 2005). At later latencies than the P2, other ERP components such as the N250 at occipito-temporal sites and long-lasting amplitudes are clearly related to familiarity and recognition stages (Itier and Taylor, 2004a; Schweinberger et al., 1995, 2002, 2004) and the P2 has been shown to be correlated with these later long-lasting amplitudes (George et al., 2005). A similar interpretation

Table 3 – Mean coordinates x, y and z (mm) and localization in the Talairach system of the voxels of maximal intensity obtained after erSAM analyses for all peaks, all three face types and both hemispheres

<table>
<thead>
<tr>
<th></th>
<th>Upright</th>
<th></th>
<th>Inverted</th>
<th></th>
<th>Negative</th>
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</tr>
</thead>
<tbody>
<tr>
<td>M100</td>
<td>LH</td>
<td>−22−81</td>
<td>Occipital lobe, cuneus</td>
<td>−23−78</td>
<td>Occipital lobe, cuneus</td>
<td>−21−79</td>
</tr>
<tr>
<td></td>
<td>RH</td>
<td>−23−81</td>
<td>Occipital lobe, cuneus</td>
<td>−23−83</td>
<td>Occipital lobe, lingual gyrus</td>
<td>−19−84</td>
</tr>
<tr>
<td>M170A</td>
<td>LH</td>
<td>−36−70</td>
<td>Temporal lobe</td>
<td>−36−69</td>
<td>Temporal lobe</td>
<td>−30−97</td>
</tr>
<tr>
<td></td>
<td>RH</td>
<td>−32−80</td>
<td>Occipital lobe, MOG</td>
<td>−28−80</td>
<td>Occipital lobe</td>
<td>−34−78</td>
</tr>
<tr>
<td>M170B</td>
<td>RH</td>
<td>−38−54−25</td>
<td>Cerebellum (fusiform gyrus)</td>
<td>−46−58</td>
<td>Fusiform gyrus</td>
<td>−35−60</td>
</tr>
<tr>
<td>M220</td>
<td>LH</td>
<td>−29−73</td>
<td>Occipital lobe, MOG</td>
<td>−28−76</td>
<td>Occipital lobe, MOG</td>
<td>−29−69</td>
</tr>
<tr>
<td></td>
<td>RH</td>
<td>−35−74</td>
<td>Occipital lobe</td>
<td>−33−73</td>
<td>Occipital lobe, MOG</td>
<td>−34−72</td>
</tr>
</tbody>
</table>

Because of the absence of individual structural MRIs and the transformation of the MNI to Talairach system, these coordinates should be used carefully and only as an approximation of the centroid of the clusters. MOG=middle occipital gyrus; IOG=inferior occipital gyrus.

Fig. 5 – Three-dimensional representation of the x, y and z coordinates (mm) of the voxels of maximum intensity obtained for M170A and M170B sources for the three face types and all individual subjects in whom they were found. M170B, which was found only on the right hemisphere, was more lateral (A), inferior and anterior (B) than M170A. Neither source differed significantly across the three face types (see Table 3).
could be invoked for the M220 although more studies on that component are required. The latency delays found on almost all components suggest that face processing, from encoding to recognition, is sensitive to orientation and contrast manipulations. These effects have been suggested to be due to the disruption of the face configuration rather than to the alteration of physical low-level properties of the stimuli (Eimer, 2000b; Itier and Taylor, 2002, 2004a; Rossion et al., 1999b; Rossion et al., 2000), leading to impaired recognition as shown by decreased accuracy rates and increased reaction times. The ERP/MEG component comparisons considered here are indirect given that different populations, experimental set-up, stimuli and tasks were used across studies, and caution in interpretation is thus required.

In contrast to the latency effects, we found no amplitude differences between face types for any of the measured components. In the case of the M170, this agrees with previous MEG studies on inversion (Linkenaer-Hansen et al., 1998; Liu et al., 2000; Taylor et al., 2001b; Watanabe et al., 2003) but not with ERP studies where, compared to upright faces, a larger N170 amplitude is almost always seen for inverted (de Haan et al., 2002; Eimer, 2000a; Itier et al., 2006; Itier and Taylor, 2002, 2004a; Rossion et al., 1999b, 2001; Taylor et al., 2001a) and negative faces (Itier and Taylor, 2002, 2004a; Itier et al., 2006). Other similar differences between the M170 and N170 can be found in the literature. The M170 does not show a larger amplitude to isolated eyes than to full faces (Taylor et al., 2001b; Watanabe et al., 1999b), unlike what is found for the N170 (Bentin et al., 1996; Jemel et al., 1999; Taylor et al., 2001a). Similarly, the N170 is not sensitive to the direction of seen gaze in static face or eye stimuli (Taylor et al., 2001c) while the M170 is (Taylor et al., 2001b). There is thus accumulating evidence that the M170 is not merely the magnetic equivalent of the N170 but rather reflects at least partially distinct processes.

This amplitude difference between N170 and M170 can be understood in light of recent source analyses. In a simultaneous recording of EEG and MEG, two dipole sources were found to be active simultaneously but independently at the latency of the N170/M170 for upright faces (Watanabe et al., 2003). One source was in the inferior temporal cortex around the FG while the other was in lateral temporal areas, possibly the STS region. The authors suggested that N170 was mainly generated by a radially oriented lateral source, whereas the M170 was mainly generated by a tangentially oriented inferior temporal source. Because MEG is less sensitive to radially oriented sources, it is partially blind to the lateral source. In contrast, ERPs record both sources but the strength of the temporal source showing more activation for inverted faces than the fusiform source. Similarly, the absence of amplitude modulation of the M170 and of the intensity of its source for negative faces, in comparison to the increased ERP N170 amplitude with contrast-reversal, could be due to a difference of sensitivity of the STS and FG sources to contrast-reversal. We recently suggested that the increase in N170 amplitude with inversion and contrast-reversal could in fact be driven by the eye region processed in the lateral temporal source (Itier et al., 2006).

The hypothesis that the M170 and N170 components do not reflect exactly the same processes can also be applied to the M100/P1 and M220/P2 components, based on the amplitude differences observed. While no amplitude differences between face types were found for M100 and M220, a larger P2 amplitude for inverted than upright faces (Itier and Taylor, 2002, 2004a,b; Linkenaer-Hansen et al., 1998; Taylor et al., 2001a) and a smaller P2 for contrast-reversed faces (Itier and Taylor, 2002, 2004a) have been reported in ERP studies. The lack of data on these components however, prevents any firm conclusion regarding their functional equivalence. Again, the amplitude difference could be explained simply by the lack of sensitivity of MEG to the radially oriented sources or by a real functional difference between the components.

One approach to the comparison between these ERP and MEG components is to study their respective sources. We used a new beamformer technique, the erSAM (Cheyne et al., 2006) that allowed us to analyze the sources of all three components at the latency of their maximal activity. Unlike other techniques, erSAM is well suited to deal with simultaneously active sources with overlapping temporal patterns of activity, which was most appropriate for the M170 given the model of activation of the N170/M170 reported by previous studies (Watanabe et al., 2003), as described above.

A bilateral occipital source was found for the M100 component, which did not differ between the three face types. This occipital localization centered around the lingual gyrus and cuneus is consistent with previous studies (Halgren et al., 2000; Tanskanen et al., 2005) although they modeled the M100 by a single dipole situated in posterior occipital midline. In ERPs, the P1 is usually modeled by two symmetrical dipoles also situated occipitally (Di Russo et al., 2001; Foxe and Simpson, 2002; Itier and Taylor, 2002; Rossion et al., 1999a; Taylor et al., 2004). Thus our M100 sources are in agreement with the literature and further highlight potential advantages of using erSAM over dipole fitting techniques to separate multiple sources in close proximity to each other within the inferior temporal and occipital regions.

Our source analyses of the M170 component revealed two different sources, the M170A situated occipitally and bilaterally, and the M170B, right lateralized, situated more ventrally, laterally and anteriorly around the fusiform gyrus region. These two sources were significantly different in location for all face types across subjects. The M170B is consistent with all MEG studies who systematically found the fusiform gyrus as the main source of the M170 (Halgren et al., 2000; Linkenaer-Hansen et al., 1998; Liu et al., 2000; Lu et al., 1991; Sams et al., 1997; Sato et al., 1999; Swinnen et al., 1998; Taylor et al., 2001b; Watanabe et al., 1999b, 2003). It could also
correspond to the face-sensitive fusiform gyrus area reported in fMRI and PET studies (Haxby et al., 1999, 2000; Kanwisher et al., 1997; Puce et al., 1995; Sergent et al., 1992, but see Furey et al., 2006). The fact that the M170B source did not vary between upright and inverted faces, neither in intensity nor in location, agrees with the literature (Linkenkaer-Hansen et al., 1998; Liu et al., 2000; Taylor et al., 2001b; Watanabe et al., 2003). The present data extend these findings to contrast-reversed faces, for which the same M170B was also found, with no significant variation in location or intensity compared to upright faces.

In contrast to the M170B, our finding of the M170A source is a new result that has, to our knowledge, never been reported before in the MEG literature. However, in the ERP field, we recently reviewed the development of the N170 from 4 years of age until adulthood and found a double peak for the N170 across four developmental studies (Taylor et al., 2004). The first peak, that we termed the N170a, was found mostly in young children but did not mature much until 10–11 years of age, after which it disappeared. It was modeled by two symmetrical dipoles situated occipitally and medially. The second peak called the N170b, was found across all age groups, matured linearly until late adolescence and was modeled by a symmetrical pair of dipoles situated ventrally, laterally and more anteriorly than the sources of the N170a (see Fig. 7 of Taylor et al., 2004). These two N170 peaks and their modeled sources very much resemble the present M170A and M170B sources. We had hypothesized that the orientation of these two N170 generators changed across age. In light of the present MEG sources, we postulate that both sources are present in adults and that the orientation of the N170a source is very likely tangential and thus better seen with MEG (M170A source). Interestingly, this M170A source, centered around the middle and inferior occipital gyri (MOG, IOG), is consistent with an occipital face-sensitive area reported in fMRI and PET studies in the inferior and middle occipital cortices (Gauthier et al., 2000; Halgren et al., 1999; Haxby et al., 1999, 2000; Ishai et al., 2005; Sergent et al., 1992). Given the absence of structural MRIs, our source localization is not precise, yet the M170A source was occipital and significantly different from the right M170B and also from the M100 in early visual areas. It could thus well correspond to the “occipital face area” (Gauthier et al., 2000). From these MEG data and the ERP results reported in the literature, there would thus be three different sources simultaneously active generating the N170/M170 complex: a lateral temporal source in the posterior STS region recorded by ERPs (N170), a fusiform gyrus source recorded by MEG (M170B), and a more medial inferior occipital source (M170A) also recorded by MEG. These three sources agree with the model of face processing derived from the fMRI and PET literature (Haxby et al., 2000). The reason why classic dipole analyses of the M170 never reported this M170A source may be due to its relatively close location to the fusiform source, preventing the two sources to be dissociated by dipoles but successively separated by eSAM.

In contrast to the M100, the localization of the M220 source did not differ significantly from that of the M170A for all face types (except for negative faces on the left hemisphere) while it was significantly different from that of the M100. It was centered around the MOG and situated more laterally and anteriorly than the M100. The M220 component presented a relatively similar topography to the M170, although sometimes more central and parietal. Like M170, it was delayed by inversion and contrast-reversal. Because the source coordinates and intensity did not vary among face types, the M220 could be a reactivation, 50 ms later, of part of the M170A source. A recent case of a prosopagnosic patient who had an intact and functional right FG area but a damaged right OFA suggested that the OFA was necessary for normal face processing and was likely activated by the FG through a feedback mechanism (Rossion et al., 2003a). It is tempting to draw the parallel with the present findings and to suggest that the M220 could reflect the (re)activation of this OFA after activation of the fusiform source around 170 ms, or at least part of that source. Two MEG studies have found that the FG was active twice, at the latency of the M170 and again later around 230–250 ms (Streit et al., 1999; Switenby et al., 1998). A recent paper also found that the BOLD response obtained in the face-sensitive fusiform gyrus area implicated in face identity processes, was primarily due to the late MEG components (>250 ms) and not to the M170 itself (Furey et al., 2006). This latency is later than that of the M220 and could correspond instead to the ERP N250, a negative component occurring around 250–300 ms, sensitive to face identity repetition and recognition (Itier and Taylor, 2004a; Schweinberger et al., 1995, 2002, 2004) and modeled by dipoles in the fusiform gyrus (Schweinberger et al., 2002). The growing evidence that the fusiform gyrus is activated at different times during the processing of faces supports the possibility of a reactivation of the OFA (M170A). If this hypothesis is correct, this would further suggest that the face processing network involves the simultaneous activation of the fusiform gyrus and the OFA around 170 ms followed by a reactivation of the OFA (maybe through feedback from the fusiform) around 220 ms and then by the reactivation of the fusiform gyrus around 250 ms and later. The fact that the late (>250 ms) amplitudes have been related to the identity recognition processes (Itier and Taylor, 2004a; Schweinberger et al., 1995, 2002, 2004) and correlated with the P2 amplitude (George et al., 2005), suggests the implication of the whole P2-N250 complex, and by analogy that of the M220 and later components, in face identification. Similar (or overlapping) occipito-temporal regions would thus be activated during encoding (M170) and face identification (M220 and later components). The precise dynamics of this face processing system should be addressed by future studies of network connectivity.

In conclusion, the present study showed that inversion and contrast-reversal of faces impaired face processing by delaying the activation of the early face-sensitive network, thus not supporting the hypothesis of a recruitment of additional object areas. The source analyses revealed various occipito-temporal areas that were simultaneously active and possibly reactivated later on during face processing, among which the fusiform gyrus and the inferior-middle occipital areas seem to play a central role in both encoding and identification steps. The results suggest a dynamic face network in which the M220 component plays an important and previously underestimated role that future work will need to address.
4. Experimental procedures

4.1. Subjects

Twenty-one young healthy volunteers (10 female, 19–30 years, 3 left-handed) participated in the study. The peaks of one subject could not be identified so this subject was rejected, leaving 20 subjects for all analyses. All subjects had normal or corrected-to-normal vision and signed informed written consent. A medical visit was done prior to the experiment, required by the French Comité Chargé de la Protection des Personnes en Recherche Biomédicale (CCPPRB) who approved the protocol.

4.2. Stimuli

Grayscale photographs of 360 different faces (half female faces) were used. Faces were without earrings, glasses, mustache, beard or any paraphernalia that could help recognition. Eighteen blocks of 30 faces were presented, of which 10 repeated randomly after one intervening face (2-back repetition). Faces were blocked by face type, with 1/3 of the blocks presented upright in normal contrast (Upright), 1/3 upside-down in normal contrast (Inverted) and 1/3 upright in contrast-reversed format (Negative). Inverted and negative faces were obtained from normal pictures using Photoshop 5.0 (Fig. 1). Mean pixel luminance and root-mean-square (RMS) contrast for the upright and inverted faces were 91.44 and 0.473, respectively. For negative stimuli, mean luminance was 100.89 and mean RMS contrast was 0.467. To avoid recognition to be based on gender, half of the blocks contained only female faces, the other half only male faces. Across blocks, subjects saw 180 faces (120 “new”—i.e., seen for the first time +60 repetitions) of each face type. Two blocks of one face type were always presented in succession (one female block, one male block) and always followed by 2 blocks of another face type. Block order was counterbalanced and face format shuffled across subjects so that faces seen in one format by one subject always presented in succession (one female block, one male block) and always followed by 2 blocks of another face type. Block order was counterbalanced and face format shuffled across subjects so that faces seen in one format by one subject were seen in a different format by another subject (e.g., subject 1 saw block 1 inverted while subject 2 saw that same block in negative format as block 11).

4.3. Procedure and MEG recording

Neuromagnetic activity was recorded in the MEG center at the Pitié-Salpêtrière Hospital in Paris (France). Subjects were comfortably seated in the MEG machine, inside the dimly lit magnetically shielded room. Prior to data acquisition, three localization coils were placed at the nasion and pre-auricular points on each subject to localize the subjects’ head relative to the MEG sensors. Head localization was completed three times, once every 3 blocks of stimuli (one block consisted of 6 series of pictures). Head positions were compared off-line to ensure that the averages across all series were possible.

Stimuli (approximately 3.6”x4.2” visual angle) were projected on a screen 1.25 m in front of subjects, by a video-projector situated outside the room. Faces were presented on a black background for 500 ms with a random ISI (1200–1600 ms) during which a white fixation cross appeared. Subjects pressed a button as quickly and accurately as possible as soon as they recognized that a face had repeated. They were told some faces would repeat after 0 to 4 faces maximum, to prevent them from attempting to memorize all faces in a block while staying naïve about the 2-back rule. Debriefing at the end of the study suggested that subjects did not perceive that all faces repeated after 1 intervening face only. Accuracy and reaction times were recorded. Short pauses were given between blocks.

The study was run on a whole-head MEG system (CTF/VSM MedTech, Ltd., Canada) containing 151 radial gradiometers around the scalp and 29 reference gradiometers and magnetometers for ambient field correction. MEG fields were recorded with a sampling rate of 625 Hz for 1400 ms including a 200 ms pre-stimulus baseline (bandpass 0–100 Hz).

4.4. Data analysis

Data were analyzed in the MEG laboratory of the Rotman Research Institute of Baycrest Centre and the Hospital for Sick Children in Toronto (Canada). For all ANOVA analyses, the Greenhouse–Geisser adjusted degrees of freedom were used along with t-tests using the Bonferroni correction for multiple comparisons.

4.5. Behavioral analyses

Mean percent hit rate and mean reaction times for repeated faces as well as mean percent false alarms for new faces were computed. Due to an insufficient number of trials for the repeated faces, all the subsequent analyses reported in this paper were performed for “new” faces only.

4.6. MEG peak analyses

For event-related field (ERF) and global field power (GFP) peak analyses, ~200 to 600-ms epochs were used and trials baseline corrected. Trials contaminated with ocular movements or other artifacts (>500 fT) in that time window were rejected. The remaining trials were averaged according to face type. Only good trials without a behavioral response (i.e., no false alarms) were included in the averages and epochs were filtered between 1 and 20 Hz for ERFs peak picking and 0–30 Hz for GFP. An average of 105 trials (90–115) was obtained for all conditions and subjects.

For the ERF peak, the M100 and M170 components (n=20) were measured at the lateral temporal and occipital sensors where they were maximal and at the latency where the maximum amplitude was found on each hemisphere and for each face type, as routinely done in ERP studies. The M100 [95–154 ms across subjects and conditions] and the M170 [140–213 ms] were measured at similar sensors (e.g., MLO/MRO21, MLO/MRO12, MLO/MRO32, MLT/MRT26, MLT/MRT14). For the M220 peak [205–260 ms, n=20], which was very broad,

\[2\] We used 0–30 Hz for the GFP because we were initially interested in late components that could have disappeared in the 1-Hz filtering used for peaks. The 20–vs. 30-Hz low-pass filtering did not change anything between ERF and GFP peak measures.
a 20-ms time window was used to define the maximum amplitude over each hemisphere and the latency picked was the middle of that window. The M220 was more variable in location, often found at similar occipital and temporal sensors as the two other components but also sometimes at parietal and central sites (e.g., MLC15, MRP31).

The global field power, calculated as the standard deviation of the voltage recorded across the scalp\(^3\), reflects the power across the whole head at a particular latency. We calculated the GFP for each subject and each condition, across the entire epoch. Latencies and amplitudes of the first, second and third GFP peaks corresponding respectively to the M100, M170 and M220 components, were measured and analyzed separately (Fig. 3).

Behavioral measures, ERF for the M220 latency component, and GFP latencies and amplitudes were analyzed separately using repeated measures ANOVAs with one within-subject factor (face type: upright/inverted/contrast-reversed). For M100 and M170 ERF, and M220 amplitude, a 3 (face type) × 2 (hemisphere) ANOVA was used.

4.7. Source analysis using the event-related Synthetic Aperture Magnetometry (erSAM) technique

We used a new event-related SAM beamformer technique (Cheyne et al., 2006) to analyze the sources of the peaks. The erSAM analysis was performed for each subject and each peak, at the same latency as that measured from the sensors. Similar to the SAM method described by Robinson and Vrba (1999), erSAM uses the individual trials of each condition and the forward solution for optimal current direction to calculate a spatial filter for each voxel using a minimum-variance beamforming algorithm. Each filter is then noise-normalized and used to calculate the virtual sensor for that voxel, which represents the voxel’s activation time course. A SAM volume, i.e., the 3D power distribution of the virtual sensors, is thus obtained for each condition and each subject at the time point of interest (Cheyne et al., 2006), i.e., the peaks of the three early MEG components in the present study. In previous applications of this method, the individuals’ structural MRIs were used to constrain the SAM images to each subject’s individual anatomy and to allow for spatial normalization and group averaging of the source images in stereotaxic space. However, because we did not have our subjects’ structural MRIs, we used a default bounding volume to compute the SAM images. For group averaging we selected a best fit MRI from a group of 20 individual brains obtained from the database of the Hospital for Sick Children based on the head dimensions (calculated using the head localization coils). This was used to put individual SAM volumes into the Talairach stereotaxic space using the MNI template normalization provided in SPM2 (www.fil.ion.ucl.ac.uk/spm/software/spm2/). A group average of these normalized SAM volumes was then computed for each condition and each peak (Fig. 4). Images were thresholded using a nonparametric permutation test for group SAM images based on baseline data (Chau et al., 2004; Cheyne et al., 2006). In other words, the individuals’ data were used to threshold the group-averaged images.

The analysis of the M100 and M220 revealed one peak per hemisphere. In contrast, for the M170, two distinct sources were found in most subjects, termed A and B (see results section). The M170A was found bilaterally. On the left hemisphere, two sources showed a second sub-peak for the M170A in the inverted condition, and 9 subjects in the upright condition. These two sub-peaks were distinct but spatially close and did not survive the statistical threshold in the group images. The M170B, in contrast, was found exclusively in the right hemisphere except for one subject who also showed an M170B peak on the left hemisphere for negative faces.

For each subject and condition, the x, y and z coordinates of the voxel of maximum power and its intensity value were obtained on each hemisphere for each peak (except for M170B found only in the right hemisphere). To test whether the localization of the sources changed across face types, we performed a MANOVA on the x, y, z coordinate differences (i.e., three dependent variables). Thus, for each peak on each hemisphere, a separate analysis was run on the three coordinate differences obtained for upright minus inverted faces and for upright minus negative faces. These analyses tested the null hypothesis that the sources obtained for a given peak for inverted and negative faces were co-located with those obtained for upright faces. We used the Wilk’s Lambda multivariate test. A significant value meant that the source location did change between the two face types compared. Using the same rationale, we performed a MANOVA test on the coordinate differences obtained for (M170A–M170B), for each face type (right hemisphere only), to test whether they were significantly different. From inspection of the group averages (Fig. 4), the M170A looked similar in location to the M220 but different from the M100. We thus performed MANOVAs on the coordinate differences obtained for (M170A–M100), (M170A–M220) and (M220–M100), for each face type and each hemisphere separately.

Finally, the maximum intensity values of the sources were compared across face types using a 3 (face type) by 2 (hemisphere) ANOVA, for each component (M100, M170, M220). For the M170, we also compared the intensity of sources A and B within the right hemisphere using a 3 (face type) by 2 (source) ANOVA. As peaks were not always found on both hemispheres in all conditions for all subjects, the MANOVA and ANOVA analyses did not always include the same number of subjects. The precise number of subjects included in each analysis is given in the result section.

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\(^3\) The GFP is calculated by the following formula:

\[
\text{GFP}_n = \sqrt{n \sum_{i=1}^{n} U_i^2}
\]

Where \(n\) = number of electrodes, \(U_i\) = measured voltage of electrode \(i\).

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