Source analysis of the N170 to faces and objects

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To clarify the neural sources for the face-sensitive N170, ERPs were recorded in 16 subjects viewing upright and inverted faces, and compared to seven object categories. Source analyses were performed for each category and each subject at the latency of the N170. Larger source intensities were found in the posterior superior temporal sulcus region (STS) for faces compared to objects. STS intensities were highly correlated to the N170 amplitude over both hemispheres only for faces. The results suggest that one of the major sources of the N170 is the STS region and that the larger N170 amplitude to inverted faces is due to increased activation of that source for inverted faces rather than a recruitment of additional areas. *NeuroReport* 15:1261–1265 © 2004 Lippincott Williams & Wilkins.

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INTRODUCTION

The negative electrophysiological component N170 responds maximally to face stimuli over temporo-parietal regions of the human scalp between 140 and 190 ms, and is larger and often earlier to upright faces than to other visual object categories [1–3]. Only a few studies to date have investigated its neural sources and the results are controversial. Some have found its source in ventral temporal cortical areas that could correspond to the fusiform gyrus (FG) [4,5], a region found more active to faces than objects in fMRI studies [6]. A common bilateral source of N170 to faces, words and cars has been reported in the posterior FG [7], with the differences among categories only in the extent of lateralization, intensity and orientation of the dipoles. However, other studies have found face N170 sources in more lateral parts of the temporal cortex [8,9]. The possible origin of the N170 in the FG is at odds with the finding that fMRI activity in that region is reduced [10,11] or unchanged [12] for inverted compared to upright faces, while face inversion increases the latency and amplitude of N170 [1–4,13]. A recent study found the same N170 sources for inverted and upright faces [9]. Similarly, contrast reversal delays and enhances the N170 [4] while it decreases the FG activation [14]. Similar inconsistencies are found between intracranial and surface ERPs. The face-specific N200 component is recorded directly from the cortical surface on the occipital-temporal cortex, primarily the FG [15], but unlike N170, N200 was not larger to inverted than upright faces although it was delayed by inversion [16]. The origin of N170 thus remains unclear and its precise relationship to the N200 and to the fMRI activation in the FG is still undetermined.

The above-cited studies that attempted to find the source of N170 used dipole localization and only one or no other object category as a comparison. The aim of the present study was to compare the brain areas involved in the source of the N170 recorded in response to upright and inverted faces and seven object categories. We used a distributed inverse solution [17,18] that estimates 3D current density distributions rather than classic dipole analyses.

MATERIALS AND METHODS

Subjects: The 16 healthy young adults tested (seven females, mean age 24.9 years) had normal or corrected-to-normal vision and gave informed written consent. The procedure was approved by the French CNRS ethics committee (COPE).

Stimuli and procedure: The subjects pressed a button to a target checkerboard stimulus. Nine non-target categories were used (50 different pictures each): textures, mushrooms, flowers, houses, lions, tools, road signs, upright and inverted faces. Subjects viewed five blocks of 99 trials (10 pictures of each category plus nine targets). Pictures subtended a visual angle of $9 \times 11^{\circ}$ and were presented for 500 ms with a 1700–2100 ms SOA. A central fixation cross was presented between stimuli. Stimuli and block orders were randomized across subjects.

EEG recordings and source analyses: ERPs were recorded via a 35 electrode EasyCap (10/10 system) including three ocular sites to monitor eye movements. During recording (500 Hz sampling rate), electrodes were referenced to Cz; an average reference was calculated off-line. Impedances were

kept $<5\,K\Omega$. Artifacts $>100\,\mu V$ were rejected and averages were digitally filtered (0.1–30 Hz). Only non-target trials were analyzed. For each subject and condition, N170 was measured at TP9, TP10, P7, P8, PO9, PO10, O1 and O2 sites, within a ± 30 ms window centered on the maximum of the grand-average means. The N170 mean latency was earlier for upright than inverted faces and all other categories [3]. Source analyses were performed on the grand-averages and on individual ERP data at the latency of the maximum N170 for each subject and each category using the distributed and linear inverse solution LAURA. This Local AUto-Regressive Average solution based on interpolation formulas [17,18] uses a realistic head-model and 4024 solution points in the gray matter. LAURA makes no *a priori* assumption on the number of the sources and their locations and can deal with multiple simultaneously active sources [18]. It estimates 3D current density distributions rather than dipolar sources and has been successfully used for ERP data (see [19] for a review).

RESULTS

N170 was larger to upright and inverted faces than to objects, and was delayed and enhanced by face inversion (Fig. 1). A full analysis of the ERP data is published elsewhere [3]. Here we only report the source localization. Different sources were found for the various categories (Fig. 2), with more temporal activation for faces and more occipital activation for most objects. Several regions were found for all categories in both hemispheres: the inferior occipital gyrus, the middle occipital gyrus, the cuneus, the lingual gyrus (occipital lobe) as well as the posterior part of the superior temporal gyrus and the middle temporal gyrus (temporal lobes). The last two regions are situated around the superior temporal sulcus (STS) and we will thus refer to the STS region in the rest of the paper [20]. For each subject within each category, we found these same regions active and we calculated the mean number of solution points and the mean source intensity (mA/m^3) per brain region. As we used an average brain to perform these source analyses, it was more accurate to regroup the sub-regions into two main regions, an occipital and a temporal region. MANOVA analyses using two factors (category (9) and hemisphere (2)) were performed on these main regions for the number of solution points and for source intensity values. We also performed analyses contrasting the seven object categories and the two face categories (face–object factor).

Number of significant solution points: A larger number of significant solution points was found in the STS region for faces compared with objects (effect of category, $F(8,270)=2.11$, $p<0.035$, face–object effect: $F(1,284)=13.93$, $p<0.0001$; Table 1) but no category effect was found in the occipital region ($p<0.325$).

Mean source strength over the significant solution points (intensity): In the STS region larger intensities were found for upright and inverted faces compared with objects (effect of category, $F(8,270)=10.09$, $p<0.0001$, effect of face–object: $F(1,284)=78.18$, $p<0.0001$). In the occipital region, greater intensities were found for inverted faces only (effect of category, $F(8,270)=6.37$, $p<0.0001$, effect of face–object: $F(1,284)=47$, $p<0.0001$). A trend towards a hemisphere effect was found for the temporal region ($p<0.053$) that reached significance with the face–object factor ($F(1,284)=6.08$, $p<0.014$), reflecting greater intensities in the right temporal region than in the left. No hemisphere difference was found for the occipital region. No interactions were found in any analysis.

Correlations: For each category, Spearman correlations (non-parametric) were performed between the mean intensities found for each subject in the occipital and temporal regions for each hemisphere and N170 amplitude at homologous electrode sites. No correlations were found for texture, flowers or tools. For the other objects, correlations were weak, lateralized and found only at some electrodes (Table 2). In contrast, for upright and inverted faces intensities in the STS region were highly correlated with N170 amplitudes over both hemispheres, with the highest correlations found for posterior parietal sites (Table 2), especially for the right hemisphere (Fig. 3). The correlations were negative because of the sign (polarity) of the N170. For occipital regions, only sporadic significant correlations were seen between the source intensities and occipital sites, but only for lions, upright and inverted faces.

DISCUSSION

This paper investigated the main neural sources generating the N170 ERP component recorded for seven object categories and upright and inverted faces. Using LAURA inverse solution that calculates 3D current density distributions, we found that sources for faces and objects at the latency of the N170 peak were very different (Fig. 2). However, at the latency of objects' N170, the global field power, representing the energy in the system, was close to noise level [3] and thus the inverse solution performed at the various object N170 latencies gave sources of very low strengths (note the different scales for objects and faces on Fig. 2). Several regions were found active at the N170 latencies for all categories. Our aim was to isolate the regions contributing most to the generation of the scalp ERP components. It was thus important to link the source strengths (intensities) with the recorded N170 amplitudes. Unlike most studies that only analyzed sources on grand averages [4,5,7], we performed the analyses for all subjects and all categories and could assess the results statistically.

Two main regions were found across categories and subjects: an occipital region and the STS region. No differences among categories were found in the occipital region. However, in the STS, a larger number of points and greater source intensities were found for upright and inverted faces compared to the object categories, with intensities being largest over the right hemisphere. These STS intensities were negatively correlated with the N170 amplitudes (i.e., the higher the intensity, the larger (more negative) the N170) over both hemispheres only for faces. These results suggest that a major source of the face N170 is the posterior STS region. We have shown that the N170 to faces is the result of a supplementary cluster of activity revealed as an extra map in segmentation analyses not found for other objects that suggested the face N170 was qualitatively different from the objects N1 [3]. The present results argue that this supplementary activity arises mainly from the STS (Fig. 2).

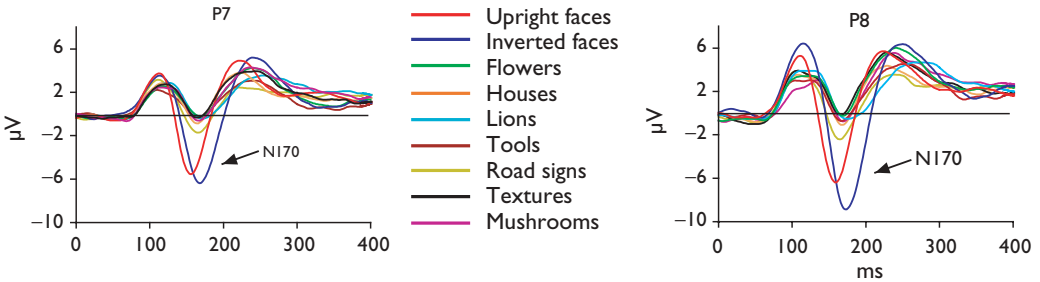

Fig. 1. ERPs to upright and inverted faces and seven object categories recorded at temporal parietal sites P7/P8, where the N170 was usually largest. Note the much larger N170 for faces than objects and the delayed and larger N170 to inverted than upright faces.

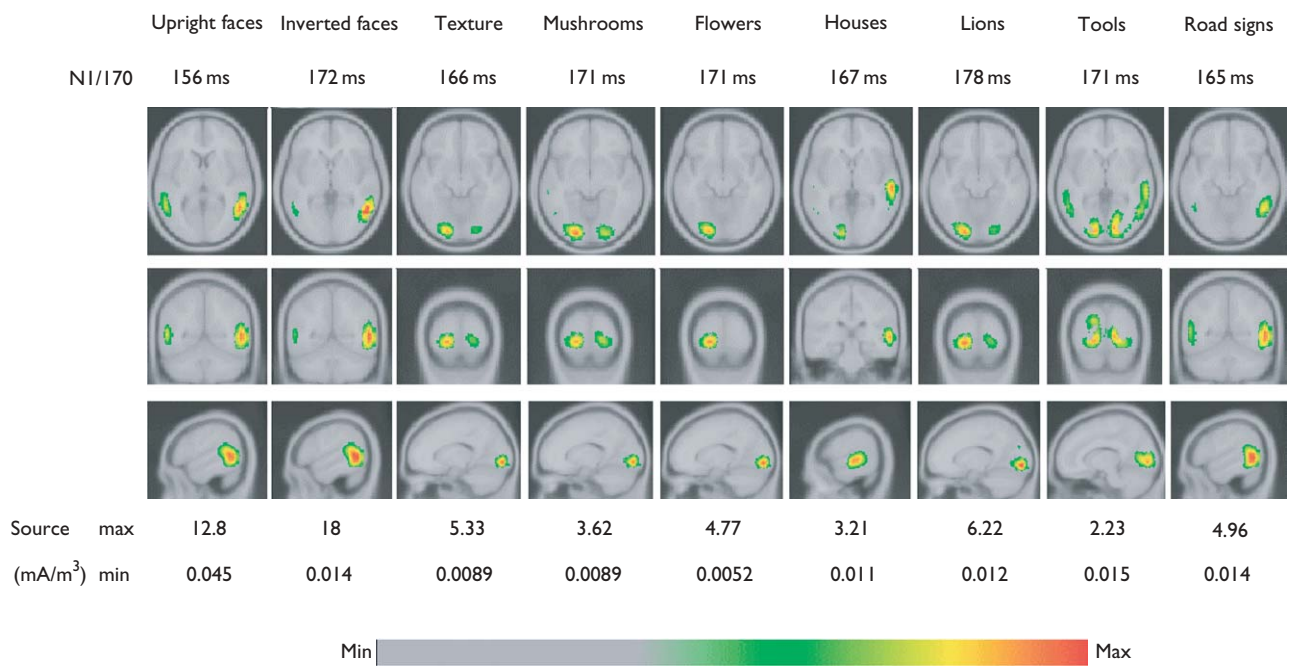

Fig. 2. Results of the source analyses performed on the grand averages of the nine categories at the latency of their maximum N1/N170 component. Ventral, coronal and sagittal plans are displayed per category at the coordinates where activation was maximum. Note the differences in localization between faces and objects and the different scales used because of the large intensity difference among categories. If the same scale had been used for all categories, activations would have been seen only for faces. On the figure, right side is on the right, left side is on the left.

Table 1. Results of the source analysis of N1-N170 component. Mean number of solution points and mean intensities (in mA/m^3) obtained for occipital and temporal (STS) regions are displayed for hemispheres (LH – RH) and categories (faces – objects). Standard deviations are in parenthesis. Note the larger number of points and greater intensities for faces than objects in the temporal (STS) region.

		Number of solution points		Source intensities (mA/m^3)	
		Temporal (STS)	Occipital	Temporal (STS)	Occipital
Faces	LH	29.09 (23.77)	11.84 (15.44)	11.7 (9.9)	11 (8.9)
	RH	40.16 (16.68)	9.41 (14.24)	15.2 (9.2)	11.3 (8.9)
Objects	LH	23.72 (21.53)	17.54 (16.76)	5.15 (4.9)	5.84 (5.3)
	RH	23.43 (20.41)	7.88 (12.85)	6 (4.9)	4.7 (4.7)

No correlations were found for textures, tools and flowers. Although some correlations were found between the STS region and other objects' N170 amplitudes, they were restricted to either the right (mushrooms, houses) or the left hemisphere (lions, road signs) and were mainly found at occipital sites. The correlations between the STS source intensity and N170 amplitude at both P7 and P8 sites was unique to the face category. These results for objects

Table 2. Spearman correlations (r) between source intensities found in the STS region and the N1/N170 amplitudes at all sites where they were measured, for all categories.

		LH				RH			
		P7	PO9	O1	TP9	P8	PO10	O2	TP10
STS region	Texture	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
	Mushrooms	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	-0.51^{*}	n.s.
	Flowers	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
	Houses	n.s.	n.s.	n.s.	n.s.	n.s.	-0.56^{*}	-0.62^{*}	n.s.
	Lions	-0.53^{*}	-0.55^{*}	n.s.	-0.63^{**}	n.s.	n.s.	n.s.	n.s.
	Tools	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
	Road signs	n.s.	n.s.	-0.52^{*}	n.s.	n.s.	n.s.	n.s.	n.s.
	Upright faces	-0.7^{***}	-0.55^{*}	-0.62^{**}	-0.57^{*}	-0.93^{***}	-0.72^{***}	-0.86^{***}	n.s.
	Inverted faces	-0.81^{***}	-0.63^{**}	n.s	-0.52^{*}	-0.86^{***}	-0.72^{***}	-0.77^{***}	n.s.

Only significant correlations are reported.
$^{*}p < 0.05–0.02$;
$^{**}p < 0.01–0.005$;
$^{***}p < 0.004–0.0001$.
n.s., non-significant.

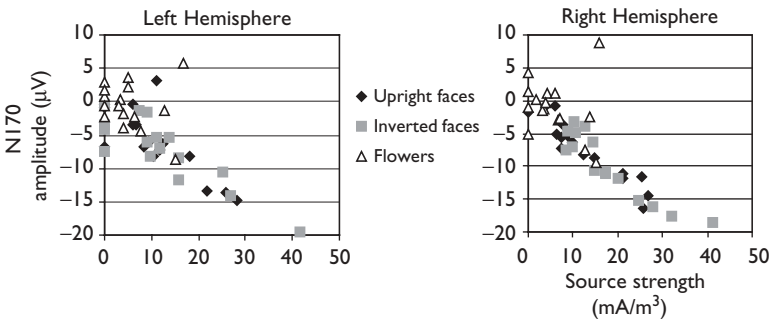

Fig. 3. Correlations between N1/170 amplitudes and source intensity in the STS region for upright and inverted faces and one object category (flowers) in the left and right hemispheres. The face N170 amplitude at P7/8 sites had a high negative correlation with source intensity in the STS region especially in RH, while no significant correlation was found for objects.

parallel the more medial and occipital distribution of N1 compared with the more lateral and temporal distribution of the face N170 [3].

We found no solution points in the fusiform gyrus (FG), which is found in all fMRI studies on face processing. This region could be too deep and ventral for its activity to be recorded on the scalp. Alternatively, given that sources in the STS would be close to the parietal temporal electrodes where N170 is maximal, activity in the FG could have been obscured, despite the presence of electrodes low over posterior and lateral scalp sites. In an analogous manner MEG that records primarily tangential fields, has localized the source of the M170 to the FG, and does not find sources over the STS [21,22]. These complementary findings strongly suggest parallel activations of both FG and STS regions, but depending on the neuroimaging technique, only one or the other is 'seen'.

This last explanation is supported by recent findings [9] showing that between 140 and 200 ms both FG and a lateral temporal region were activated simultaneously, but independently, for face processing. The authors used both ERP and MEG techniques and recorded the FG source from the MEG but not from the ERP system, while the opposite was true for the recording of the lateral source [9]. The cause is likely the orientation of the generators, the FG source being tangential while the lateral source would be radial. Another ERP study found that N170 to faces seemed to originate from lateral occipito-temporal region as well as from the FG [8].

The reason why the FG but not the STS was found in other dipole analyses [4,5,7] is not clear. It could be that the sources, presumably simultaneously active at the latency of the N170, are more or less active depending on the task. In fMRI studies, it has been shown that attention to gaze elicited a stronger response in the STS than attention to identity, which elicited larger responses in the FG [23]. The ERP studies that found ventral sources were explicit face recognition studies [4,5] or included attention directed towards the faces (e.g. orientation judgment [7]) while studies that reported lateral activation focused attention on a non-face target category (e.g. checkerboard in the present study and in [9], butterflies [24]) or were passive tasks [8].

An alternative explanation is that dipole and 3D current density source analyses give different results due to the different computational algorithms. The discrepancies found in the literature could thus be more methodological than task-based. However, two ERP studies that found the lateral source active used dipole solutions [8,9], suggesting that this is more than simply a dipole/3D current density modeling issue. Furthermore, the STS source is compatible with inversion and contrast-reversal effects on N170, while the FG source is not.

Finally, we found no difference in the source localization between inverted and upright faces apart from larger intensities for inverted faces as also reported in other studies [9]. The main difference between these face types is the delayed and larger activation for inverted faces, rather than the recruitment of additional cortical regions for inverted faces, as seen in some fMRI studies [11]. However, these studies focused on ventral regions of interest such as the FG. A recent fMRI study focusing on the STS region found larger activation for inverted than upright faces [25], in agreement with inversion effects on N170 and thus with its source in that lateral region.

CONCLUSION

Using a 3D current density source technique we found that one of the major sources of the N170 component is the STS region, the strength of which was correlated with the N170 amplitude at P7/8 sites for faces only. In contrast, the other object categories showed lateralized activation, with low intensity sources that sometimes correlated with the N1 at more occipital sites. The use of a different source technique (dipole *vs* 3D current density) and/or the effect of attention directed to face or to non-face categories might explain the N170 source found preferentially in the STS or the FG, in earlier studies.

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