

# The face-sensitive N170 and VPP components manifest the same brain processes: The effect of reference electrode site

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## Abstract

**Objective:** (1) To investigate the hypothesis that the vertex positive potential (VPP) and the N170 ERP components reported in the face processing literature are two manifestations of the same brain processes whose relative amplitude in a given experiment is dependent on reference electrode; (2) to investigate whether differences in face/object results reported in studies looking at the VPP and N170 are attributable to the location of reference.

**Methods:** EEG was recorded from 53 scalp electrodes referenced online to the left mastoid while subjects viewed face, car and word stimuli. Off-line, the data were systematically re-referenced to the common average, averaged mastoids, averaged earlobes, non-cephalic, and nose. The correlation of timing, amplitude, and effects was investigated across reference electrodes.

**Results:** (1) The amplitude of the N170 and VPP components varies in a precisely inverse manner across reference; (2) the peaks of the N170 and VPP are temporally coincident for all reference electrodes, (3) both components can be accounted for by the same dipolar configuration, and (4) the components show identical functional properties.

**Conclusions:** The VPP and N170 are two ‘faces’ of the same brain generators.

**Significance:** The differential N170/VPP effects observed in ERP studies can be accounted for by differences in reference methodology.

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**Keywords:** N170; VPP; Reference; Face processing; ERP; Methodology

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## 1. Introduction

There have long been debates over what constitutes a reliably neutral reference electrode for electrophysiological studies of human brain activity. Numerous studies over the years have not been able to provide a general solution to this problem that crosses all types of evoked potential recordings (e.g. visual, auditory, somatosensory, etc.). As a result, laboratories will tend to defer to a particular reference either because lab personnel have historically used it, or because it is found in the majority of the literature for the field of research in question. There are circumstances, however, when researchers investigating similar phenomena under

similar experimental paradigms use different reference electrodes. In such cases, it is beneficial to know how changing the reference point can affect the results for useful cross-study comparisons to be made.

A good illustration of this issue can be taken from event-related potential (ERP) studies investigating the time course of face processing in humans. Earlier studies, using few channels and mastoids or ear references, described a large positive potential, the so-called vertex positive potential (VPP), peaking at fronto-central sites between 140 and 180 ms following the onset of a face stimulus (Bötzel and Grusser, 1989; Jeffreys, 1989; for a review see Jeffreys, 1996). For the past 10 years, however, with the advent of higher density channel systems covering a large portion of the head (Gevins et al., 1994; Tucker, 1993), most face processing studies focus on a large negative component

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peaking at about the same latency over occipito-temporal regions, termed the N170 (Bentin et al., 1996; Bötzel et al., 1995; George et al., 1996).<sup>1</sup> The main feature of these two scalp components is their enhanced response to faces compared to other multiple object categories (e.g. Bentin et al., 1996; Bötzel et al., 1995; Itier and Taylor, 2004a; Jeffreys, 1996; Rossion et al., 2000, 2003).

In general, this literature has treated these components (VPP and N170) as two separate phenomena, with little cross-referencing of results. However, the functional similarity and temporal coincidence of these peaks suggest that they are largely flip sides of the same neural generators. Methodological differences between studies indicate that the choice reference electrode location may determine which component is more prevalent in a given study. Thus, it is critical to determine how reference affects electrophysiological components so that results can be compared across studies. In this study, this issue is examined by presenting subjects with face and object stimuli and re-referencing the data to several commonly used reference sites.

## 2. The neurophysiology underlying ERPs

Measurements of phasic changes in brain activity related to an event (external or internal) have been used for more than 40 years to measure subsecond components of sensory, motor and cognitive processes (Regan, 1989; Rugg and Coles, 1995). Event-related potentials (ERPs) are distant manifestations of the synchronous activity of populations of neurons within the brain. This coordinated activity is approximated by a dipole with a negative and positive end whose signal can be recorded by electrodes placed on the surface of the scalp.

The location and orientation of those dipoles plays a critical part in the potentials (i.e. difference between the active and reference electrodes) observed at the scalp. The size of the potential difference depends on many factors, including: (1) the location of the electrodes, (2) the distance between the electrodes, and, (3) both the orientation and location of the active dipoles relative to the electrodes. The distance between the two electrodes affects how sensitive they are to the orientation and location of the dipole sources, and the location of the electrodes relative to the orientation of the dipoles can affect the polarity of the recorded signal and how strongly the dipole signal is observed. In the simplest case, the reference and recording leads are equidistant to a dipole source, and thus the signal from that generator will be represented in the data recorded at

both sites. If the electrodes are at opposite ends of the dipole, referencing one to the other (i.e. subtracting one from the other) will result in a potential difference, the size of which will vary depending on how close the leads are to the source (i.e. closer leads will yield larger potentials). If, however, the electrodes are at the same end of the dipole, referencing will effectively subtract out the signal, regardless of the distance between the dipole and the leads, and no potential will be observed at the recording lead. This scenario changes if one lead is closer to the source, whether on the same or different end of the dipole as the other lead. In this case, the dipole activity will be more strongly represented at the closer lead and even when both leads are on the same end of the dipole, subtraction will leave some signal intact. Again, if the leads are at opposite ends of the dipole, subtraction/referencing will magnify the dipole signal.

Given these examples, the difficulty of choosing an appropriate reference is clear: a reference must be found that picks up little of the signals recorded at other electrodes so that those signals will be preserved. There are several additional factors to consider. First, the electroencephalogram is generated by large dipole layers, making it difficult to find a cephalic location that is far enough from neural generators and recording leads to qualify as truly 'inactive'. Second, skull openings (e.g. eye sockets, sinus cavities, areas where the skull is thinner) provide a low resistance path through which current from various generators will tend to flow. Thus references near such openings (e.g. nose) may yield a very different scalp distribution than references that are more distant from them. All these factors illustrate that in order to observe a reasonably pure representation of the underlying neural activity, finding a reference that is as neutral as possible, or at least neutral relative to the potentials of interest, is critical.

## 3. The debate over the location of the reference electrode

As early as 1950, debates were already arising as to what reference provides an adequate baseline signal (i.e. a signal approximating zero). Differing opinions have resulted in the use of many different references, including the common average (average of all scalp sites), linked or averaged mastoids, linked or averaged earlobes, centro-frontal channel, nose tip, sterno-vertebral non-cephalic sites, ankle, chin, and knee. While this debate may seem purely methodological, the location of a reference channel can have important theoretical consequences. Studies investigating the same processes using different reference leads may emphasize different results, since each reference will introduce its own unique fluctuations into a recording, which can reduce/cancel or increase/reveal activity at other electrodes. Katznelson (1981) provides a detailed discussion of the logic behind the reference electrode and some factors to take into consideration when choosing one.

<sup>1</sup> Note that the N170 in response to faces can be assimilated to the posterior visual N1 component observed in response to any visual stimulus (e.g. Curran et al., 2002; Vogel and Luck, 2000). It is particularly large in response to faces and peaks around 160–170 ms (see Rossion et al., 2002 for a brief discussion about the N1/N170 labeling in this literature).

A brief summary of the points relevant to the current study is presented here.

The complexity of the relationship between reference sites, orientation and location of dipole generators, and the characteristics of the electrical propagation of signals across the skull and through the brain led [Katznelson \(1981\)](#) to propose that the best solution is to report each data set using two or more reference schemes in order to ascertain the overlap in findings. A different approach has been to conduct specific studies to determine the appropriate reference for particular types of experimental designs. These methodological studies search for sites that are inactive with respect to the potentials of interest (i.e. visual potentials during a visual task). Some of these studies are discussed below in conjunction with various strengths and weaknesses of several different reference leads.

### 3.1. Cephalic references

The most common cephalic references are the linked- or averaged-earlobes or mastoids and the common average. Other less widely used cephalic references include the nose and chin.

Linked and averaged earlobe or mastoid references, in which two electrodes are linked or averaged together to create a reference signal, have been used extensively in EEG/ERP studies, in particular for visual and auditory evoked potentials ([Regan, 1989](#)). The placement of the earlobe or mastoid electrodes for these references is the same, namely one electrode on each earlobe or on the mastoid bone behind each ear. However, linking and averaging are quite different.

Linking two electrodes together, prior to amplification, theoretically will effectively short two leads, forcing the signals to be the same ([Katznelson, 1981](#)). This short can create a low resistance path that modifies the potential distribution over the whole scalp ([Katznelson, 1981](#); [Nunez, 1990](#)). If impedances of two electrodes are not the same, current will flow more readily through one electrode than the other, shifting the effective reference away from the middle of the head and towards the lower resistance site ([Garneski and Steelman, 1958](#)), thus affecting the observed distribution and distorting asymmetries. In practice, however, this does not appear to be so problematic as the skin-electrode impedance is higher than the brain impedance and will exert more influence over the recorded signal ([Gonzalez Andino et al., 1990](#)).

Averaging, by comparison, simply takes the mean of the two electrode signals and has been supported as a better option than linking to avoid distributional distortion ([Davidson et al., 2000](#); [Nunez, 1990](#)). However, the averaged ear/mastoid reference is not without its own problems; [Goldman \(1950\)](#) and [Katznelson \(1981\)](#) found that it showed too much volume-conducted activity from adjacent areas of the brain to serve as a baseline. The proximity of this reference to occipito-temporal generators

would certainly make it suspect for certain types of experiments, e.g. studies of high-level visual processing, where a number of generators are thought to be located in the occipito-temporal cortex.

In fact, the mastoid and earlobe references are active in a number of different experimental designs. Earlobe references show significant visual-evoked potential (VEP) activity during visual tasks ([Lehtonen and Koivikko, 1971](#)), auditory-evoked potential (AEP) activity during auditory tasks ([Lehtonen and Koivikko, 1971](#); [Streletz et al., 1977](#); [Wolpaw and Wood, 1982](#)), and somatosensory-evoked potential (SEP) activity during somatosensory tasks ([Dowman and Goshko, 1992](#)). Similarly, mastoid references have also shown activity during both auditory ([Streletz et al., 1977](#); [Wolpaw and Wood, 1982](#)) and somatosensory tasks ([Dowman and Goshko, 1992](#)). Further, averaged mastoids/earlobes are not optimal for evaluating hemispheric differences because such a reference may reduce them.

The common average reference, recommended by recent guidelines for scalp electrophysiological research ([Picton et al., 2000](#)), is created by averaging together signals from all recorded scalp electrodes on the theory that a constant zero average is maintained across the scalp ([Bertrand et al., 1985](#); [Offner, 1950](#)). However, how close a particular average reference is to that theoretical zero depends on the number and location of the sensors going into that average ([Dien, 1998](#); [Katznelson, 1981](#)). It is difficult to get a good sampling of frontal and ventral signals (i.e. electrodes cannot reasonably be placed to sample a full sphere around the brain) so any average will necessarily be more heavily weighted towards central and posterior, lateral and dorsal locations. Further, fewer the electrode signals used to create the average, the larger influence each of them will have on the resulting average signal. This can affect the phase and amplitude relationship between the reference and the other scalp electrodes creating complications in the interpretation of the spatial characteristics of recorded data. This latter problem can be minimized with a large enough sample of electrodes—e.g. at least 20 ([Katznelson, 1981](#)). Other researchers have criticized the common average reference for possibly introducing ‘ghost potentials’ ([Desmedt et al., 1990](#)) because of the undersampling of the bottom half of the brain, or for producing distortions of focal activities ([Tomberg et al., 1990](#)). In fact, the problem of the absence of a true neutral point also applies to other references and will particularly affect the average reference when one uses sparse arrays of channels and focuses on isolated sites (for a critical analysis of these latter statements and of the use of the average reference, see [Dien, 1998](#)).

Other less widely used cephalic references have been tested only under limited circumstances, e.g. the nose does show AEP activity ([Streletz et al., 1977](#)), while the chin appears to be inactive during visual tasks ([Lehtonen and Koivikko, 1971](#)). However, as stated above, these types of references, which are close in proximity to skull openings

(mouth, throat, eye sockets, sinus cavities), must be used with caution as the openings provide low resistance paths for electrical signals potentially distorting their distributional characteristics.

### 3.2. Non-cephalic references

Several non-cephalic sites have also been used, including the sterno-vertebral non-cephalic reference, the knee and the ankle.

The sterno-vertebral non-cephalic reference is created by averaging together signals from the sterno-clavicular junction and vertebrae C7. Katznelson (1981) states that this non-cephalic reference may be effective as a neutral site because brain-related electrical current lines are confined mainly to the head with little current flowing through the neck, e.g. no potential difference between neck and hand was found indicating that the neck contains minimal EEG. Under many experimental circumstances, this reference does indeed appear to be inactive, including those in which VEP (Lehtonen and Koivikko, 1971) and AEP (Lehtonen and Koivikko, 1971; Streletz et al., 1977; Wolpaw and Wood, 1982) activity were recorded. However, the results from somatosensory studies are less clear, with some showing SEP activity with the non-cephalic reference (Lehtonen and Koivikko, 1971), and some not (Dowman and Goshko, 1992). This pattern of results is very similar to that observed above for the cephalic mastoid reference, suggesting that some cortical generators may be strong enough, and oriented in such a way so as to make the non-cephalic reference active under certain circumstances. In addition, even when using the sterno-clavicular junction on the right collar-bone, which is further away from the heart, EKG activity at these sites can be problematic, albeit not for all studies (e.g. Dowman and Goshko, 1992).

A number of studies have looked at other non-cephalic reference sites but results are less complete. For example, during auditory tasks, it appears that knee and ankle sites are

inactive (Wolpaw and Wood, 1982). Theoretically, any non-cephalic reference should be similar to the effective reference at the sterno-vertebral site, with some series resistance added, as the reference gets further away from the head. However, there is also added electrical noise with distance such as that from the EKG and also from the electrical activity of the muscles (electromyogram, EMG).

Thus, it appears there is no ‘ideal’ reference electrode for all experimental circumstances. Because different laboratories favor different reference sites, and the locus of relevant neural generators are many times unknown, it is important to understand how choice of reference electrode can affect data, rather than to simply take a recommendation at face value. Knowing how to interpret results obtained using different reference sites is essential.

### 4. The VPP and N170: two ‘faces’ of the same dipoles?

As mentioned above, an area of research where the location of the reference electrode may have a large theoretical impact is human face processing, where two temporally coincident potentials showing a larger amplitude response to faces than to other categories of stimuli, the VPP and the N170, have been reported. There are reasons to believe that the VPP and the N170 may actually be manifestations of the same underlying neural generators (see Jeffreys, 1989 for a first proposal of this ideal): they show a high degree of similarity in function (see Table 1), timing, and localized sources (e.g. Itier and Taylor, 2004a; Jemel et al., 2003; Rossion et al., 1999a,b, 2003).

Most striking, both components exhibit their largest amplitude responses for faces as compared to objects; no other scalp component has been described with this response property. In addition, the N170 and VPP amplitude in response to faces is highly correlated (Jemel et al., 2003), and both components show a latency delay when faces are inverted (see Rossion et al., 1999b). In fact,

Table 1  
Functional properties observed for both the VPP and N170

| Response properties   | VPP   | N170  |
|---|---|---|
| Evoked by faces and non-face categories, but larger for faces   | Bötzel et al. (1995),<br>Jeffreys (1996)                    | Bentin et al. (1996), Itier and Taylor (2004a),<br>Rossion et al. (2000)                          |
| Delayed for faces presented upside-down   | Eimer (2000a), Itier and Taylor (2004a),<br>Jeffreys (1993) | Bentin et al. (1996), Eimer (2000a), Itier and Taylor (2002, 2004a), Rossion et al. (1999a, 2000) |
| Evoked by a wide variety of 2D facial representations: schematic and realistic images, heads of humans but also of monkey faces | Jeffreys (1996)   | Sagiv and Bentin (2001), Carmel and Bentin (2002)   |
| Invariant to familiarity of the face  | Grusser et al. (1991), Rossion et al. (1999a)               | Eimer (2000a,b), Rossion et al. (1999a), Bentin and Deouell (2000), Schweinberger et al. (2002)   |
| Delayed by contrast inversion   | Itier and Taylor (2002)                                     | Itier and Taylor (2002), Jeffreys (1989)  |
| Usually larger with upside-down inversion   | Rossion et al. (1999a)                                      | Eimer (2000a), Rossion et al. (1999a), Sagiv and Bentin (2001)                                    |
| Peak latency: between 140 and 180 ms following the presentation of a face   | All studies   | All studies   |

the functional similarity between these components is so remarkable that they have both been associated with the same stage of face processing, namely the ‘structural encoding stage’ of Bruce and Young’s (1986) face processing model by authors who have studied these components independently (e.g. Bentin et al., 1996, 1999; Eimer, 1998, 2000; Jeffreys, 1989, 1996).

In addition to functional similarities, latencies of these peaks are quite similar (e.g. Eimer, 2000a,b; Itier and Taylor, 2002, 2004a; Jemel et al., 2003; Rossion et al., 1999a,b). However, there is a large degree of inter-subject and inter-study variability in the peak latency of the VPP and the N170 (i.e. reported latencies between 140 and 200), making comparisons of two components across studies or conditions difficult.

Further indirect support for the assumption that the VPP and the N170 form part of the same component has been found in studies that have attempted to localize equivalent sources of these peaks, using dipole modeling (e.g. BESA; Scherg, 1990). N170 and VPP can *both* be reasonably accounted for by a *single* dipolar source model involving a pair of symmetrical dipoles located in the occipito-temporal cortex, pointing towards the centro-frontal surface (Bötzel et al., 1995; Itier and Taylor, 2002; Rossion et al., 1999a; Schweinberger et al., 2002).

Despite the striking similarities, some investigators have argued that the N170 and VPP may reflect the activity of two different sources (e.g. Bentin et al., 1996; Bötzel et al., 1995; Eimer, 2000a; George et al., 1996), e.g. Bentin et al. (1996) reported a ‘P190’ that peaked 20 ms later than their reported N170, suggesting that these two components were different. However, since no analyses of the P190 with respect to the N170 were reported, it is difficult to evaluate this conclusion. Other authors have also emphasized small latency or functional differences between two peaks, and suggested that their sources were different (e.g. Bötzel et al., 1995; George et al., 1996).

In summary, while there seems to be many similarities between the N170 and VPP that are suggestive of a common neural source, there may also be some differences that need to be resolved empirically. Since the visual processing of faces takes place in occipito-temporal regions rather than below the vertex, it is understandable that the attention of researchers is now focused on the N170 component. Nevertheless, a number of findings made at the level of the VPP are relevant for subsequent studies and our understanding of the time course of face processing (see Jeffreys, 1996).

In order to equate results of the N170 and VPP, the issue of whether or not they are largely manifestations of the same neural generator must be resolved. The current paper addresses this issue by reanalyzing ERP data from a previous study (Rossion et al., 2003), where a strong N170 component was elicited in response to faces, objects and words. Simultaneous recordings were taken from several different references leads and off-line the data

were independently re-referenced to the common average, averaged earlobes, averaged mastoids, sterno-vertebral non-cephalic, and nose references. A systematic analysis was performed on all resulting data looking at both morphological changes that occurred as a function of changes in reference electrode, as well as changes in the amplitude and distribution of standard N170/VPP effects as a function of reference. Since our main goal is to clarify the relationship between these two components, which are elicited largely by faces, most of the analyses and discussion will concentrate on the face ERPs. However, the relationship of these components to non-face objects and words will also be addressed. For detailed analyses of the effects of orientation on the two peaks, the reader is referred to Rossion et al. (2003).

## 5. Materials and methods

### 5.1. Subjects

Participants were 10 male and 6 female students (all right-handed, mean age 27.5, age range 21–39) from the University of California, San Diego who were paid for their participation. The data of one subject were excluded due to poor signal-to-noise ratio.

### 5.2. Stimuli

The stimulus set consisted of 16 grayscale images of cars (3/4 right-facing view), 16 grayscale images of faces (full-frontal, Caucasian, 8 males, 8 females), and 16 words (4–7 letters, black Helvetica font),<sup>2</sup> each presented on a gray background. Face and car images have been used in several previous ERP experiments and found to elicit clear N170 responses (e.g. Rossion et al., 2000). At 100 cm from the monitor, face images subtended  $\sim 4.19 \times 5.08^\circ$  of visual angle, and cars and words subtended  $\sim 6.96 \times 3.01^\circ$  of visual angle. Inverted versions of 48 stimuli were created by flipping images horizontally, resulting in 96 different stimulus items used in this experiment.

### 5.3. Procedure

Participants were seated in a shielded chamber  $\sim 100$  cm from a computer monitor. They were presented with 4 consecutive blocks of 96 trials with a rest period of  $\sim 1$  min in between blocks. They were asked to fixate the center of the screen and on each trial were shown an image of a car, a face, or a word for 250 ms in either its upright or inverted orientation. The inter-stimulus interval varied randomly

<sup>2</sup> The 16 words were: dog, hat, job, baby, farm, game, idea, king, mine, note, rock, chair, labor, plant, table, voice.

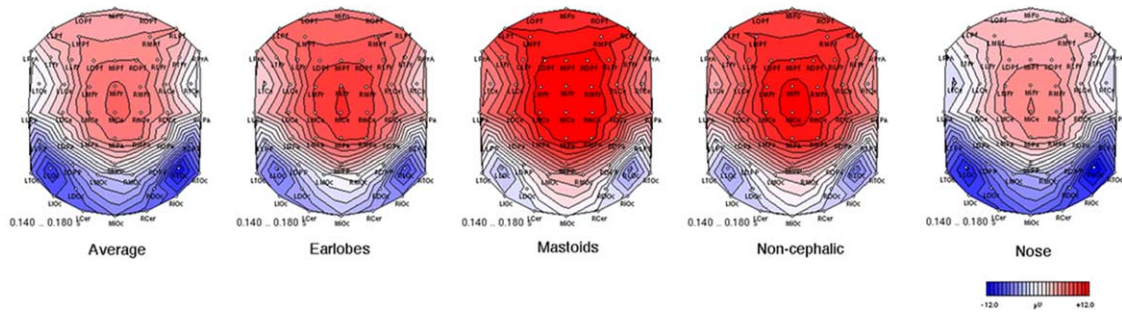


Fig. 1. 2D maps. N170/VPP topographical distribution across 5 reference electrodes.

from 1250 to 1750 ms. Subjects judged whether each stimulus was upright or inverted, pressing a button with the index or middle finger of their dominant and, respectively, to register their decision. Each stimulus was presented 8 times (4 times upright, 4 times inverted). The stimulus order was randomized for each block and all stimuli were presented in the center of the computer monitor.

#### 5.4. EEG recording

The electroencephalogram (EEG) was recorded using 53 tin electrodes (10–20 system + additional sites) embedded in an elastic cap. Twelve electrodes were below the T7–Oz–T8–Fpz equator axis. Four additional electrodes (outer cantus and beneath each eye) were used to monitor eye movement and blinks. The data were referenced online to an electrode placed on the left mastoid. Additional reference recordings were taken from electrodes placed at

the right mastoid, left and right earlobes, nose tip, right sternoclavicular junction, and vertebrae C7. Electrical activity was digitized at 500 Hz and was bandpass filtered online from 0.01 to 100 Hz. Subjects were instructed to refrain from blinking and moving their eyes and bodies, as the corresponding artifacts interfere with EEG signals.

#### 5.5. EEG/ERP analyses

EEG data were analyzed using EEprobe 2.0 (ANT, Inc.) running on Red Hat Linux 7.0. The EEG was filtered with a 201-point digital 30 Hz low-pass filter, with cut-off frequencies of 29 dB (−3 dB point), and a stop-band attenuation of −63.3 dB (50 Hz and above). Then EEG and EOG artifacts were removed using a (−40; +40 µV) deviation over 200 ms intervals on frontal electrodes and using a (−35; +35 µV) deviation over 200 ms intervals on all other electrodes. Excessive blink artifacts (in 7 subjects)

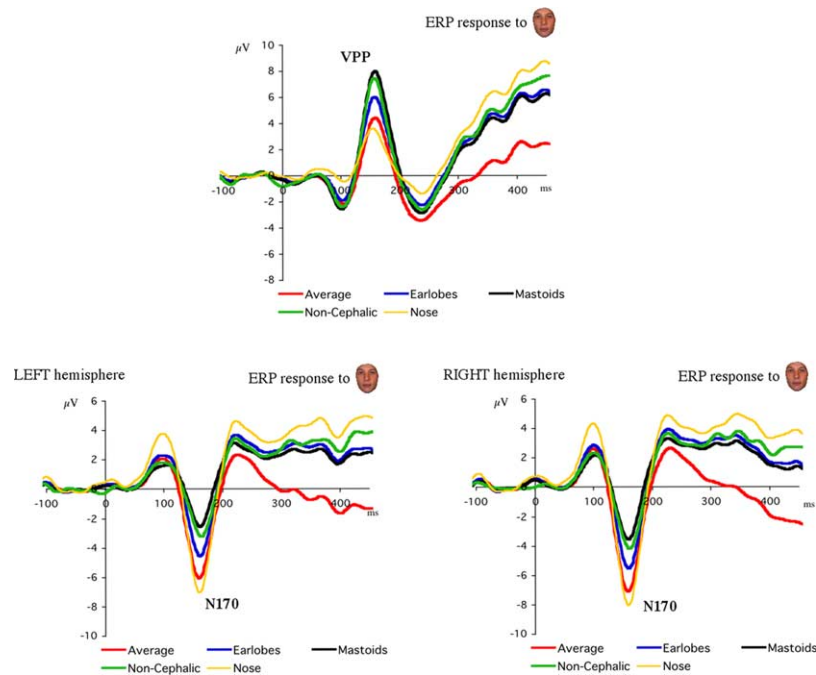


Fig. 2. The N170 in response to faces at left and right occipito-temporal sites (LLOC and RLOC), and the VPP at CZ, for 5 reference electrodes. Note the larger N170 in the right hemisphere for all reference electrodes.

were corrected by a subtraction of VEOG propagation factors, based on PCA-transformed EOG components (Nowagk and Pfeifer, 1996). Since EEG data can be freely re-referenced after collection algorithmically (Dien, 1998; Osselton, 1965), averaged ERPs were re-referenced off-line to multiple reference sites: averaged mastoids, averaged earlobes, non-cephalic (averaged sternoclavicular junction and vertebrae 7), nose, and common average (an average of 53 electrodes) signals.

### 5.6. Statistical analysis

Peak amplitude and latency values of the N170 and VPP were extracted automatically on 20 ms windows centered around the maximum amplitude of the grand average waveforms at several electrode sites: 5 left hemisphere occipito-temporal sites (LLOC, LIOC, LTOC, LDEC, LCER, see Fig. 1, and Rossion et al., 2003), 5 right hemisphere occipito-temporal sites (RLOC, RIOC, RTOC, RDEC, RCER), and 3 medial vertex sites (MIFR, MICE, MIPF). Electrodes displayed on the figures were right and left lateral occipital channels (RLOC and LLOC, Fig. 1) where the most prominent N170 component was observed in all conditions (see Fig. 1). Repeated-measures ANOVAs were computed on peak amplitudes of the N170 and VPP as measured at these sites across all 5 reference points. Because the exact peaks were often extremely difficult to determine accurately in the data of individual subjects for each reference electrode (e.g. N170 with mastoid reference), no analysis of peak latency differences was performed with the factor reference. However, as reported previously (Rossion et al., 2003), an analysis on the peak latency of the N170 and the VPP with the average reference electrode was included in the present manuscript, to illustrate the functional similarity between the two peaks.

The ANOVA for the N170 amplitude was performed on the data from left and right occipito-temporal sites (with the data from the 5 electrodes within each hemisphere pooled). The ANOVA consisted of 4 factors: *Reference* (5 levels: average, nose, non-cephalic, mastoids, earlobes), *Category* (3 levels: faces, cars, words), *Orientation* (2 levels: upright, inverted), and *Hemisphere* (2 levels: left, right). The ANOVA for the VPP was performed on 3 medial vertex sites (with the data from 3 electrodes pooled) and consisted of 3 factors: *Reference* (levels: average, nose, non-cephalic, mastoids, earlobes), *Category* (3 levels: faces, cars, words), and *Orientation* (2 levels: upright, inverted). Additional analyses were performed on non-pooled data with *Electrode* as a factor. As there were no main effects of *Electrode* or any interactions of *Electrode* with any other factor, only the pooled statistics are reported here. Post-hoc *t* tests ( $P < 0.05$ ) with Greenhouse–Geisser corrections were used to localize simple effects. Topographical displays were based on the whole scalp region.

## 6. Results

The results for analyses dealing with reference site comparisons are reported below. For detailed analyses and discussion of the effects of condition (e.g. differences between categories across orientation), the reader is referred to Rossion et al. (2003).

### 6.1. Qualitative comparison of the N170 and VPP in response to faces

Event-related potentials in response to faces at occipito-temporal sites were marked by well-defined P1 and N170 peaks followed by a slow positive shift (Figs. 2 and 3). The amplitude of the P1 was fairly consistent across reference electrode, differing only for the nose reference, whereas the amplitude and distribution of the N170 differed systematically with reference electrode (see Fig. 2). The nose elicited the largest N170 followed in order by an average, earlobes, non-cephalic, and mastoid references, respectively (see Fig. 2). The amplitude of the N170 to faces was larger over right than left hemisphere sites for all references (see Fig. 2).

Event-related potentials (ERPs) at vertex sites were marked by small N1 peaks ( $\sim 100$  ms) and well-defined VPP peaks. The amplitude of the N1, like the P1 at occipito-temporal sites, was fairly consistent across reference electrode, differing only for the nose reference (Figs. 2 and 3). Like the N170, the amplitude of the VPP differed systematically with reference electrode (see Figs. 1–3), showing the opposite pattern to the N170: here the nose elicited the smallest VPP followed in increasing order by an average, earlobes, non-cephalic, and mastoid references, respectively (see Figs. 2 and 3). In general, the amplitude of

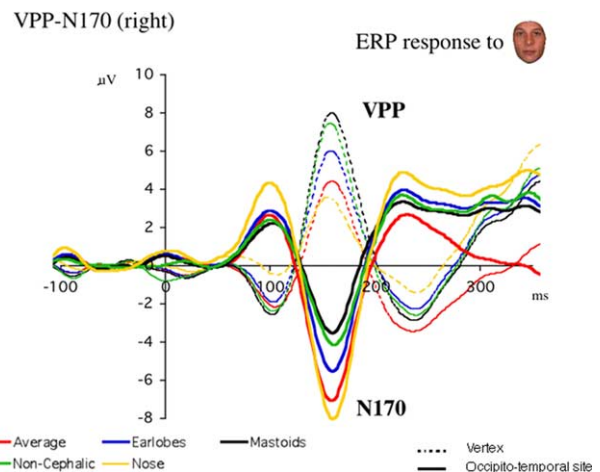


Fig. 3. The N170–VPP complex. The waves recorded at the maximal right occipito-temporal site (RLOC) are superimposed to the same waves measured at CZ. Note the perfect synchronization in time of the two sides of the complex, and the reversed order of amplitude according to the reference electrode selected (i.e. the larger the N170, the smaller the VPP).

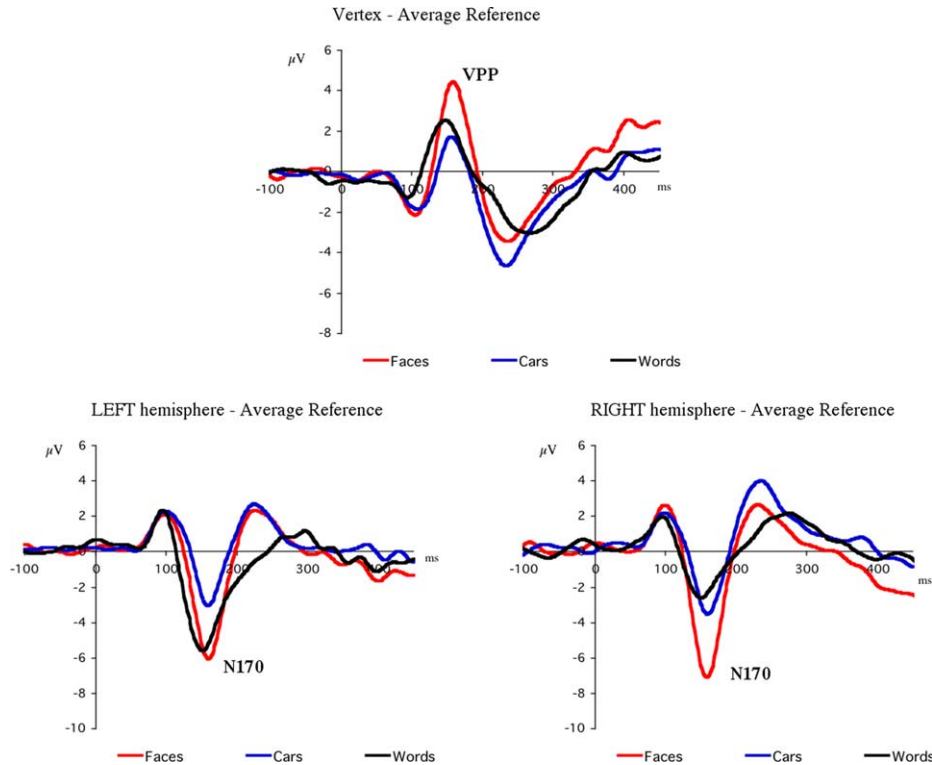


Fig. 4. The VPP–N170 complex in response to faces, cars and words, using the average reference (LLOC and RLOC sites). Note the large N170 recorded in response to word stimuli in the left hemisphere, as large as for faces.

the VPP was the largest for faces, followed by words and then cars (see Figs. 4 and 5) although the size of these differences varied with reference electrode.

When the N170 and VPP are compared directly (see Fig. 3), a complete reversal of amplitude with reference electrode is observed. Those references showing the largest N170 at occipito-temporal sites show the smallest VPP at vertex sites, and vice versa. Further, the peak latencies of the N170 and VPP correspond precisely, strongly suggesting that they are opposite sides of the same neural

generators. In fact, when source localization is performed in the time window that subsumes the N170 and VPP peaks, the vast majority of the variability can be explained by two symmetrical sources located in occipito-temporal cortex (see Fig. 6, and figures in Rossion et al., 2003). It should be noted that this source localization was performed using the average reference; however, source localization is theoretically reference-independent since it is represented by the same constant in both the source model and the estimate of the sources from the data (Scherg, 1990).

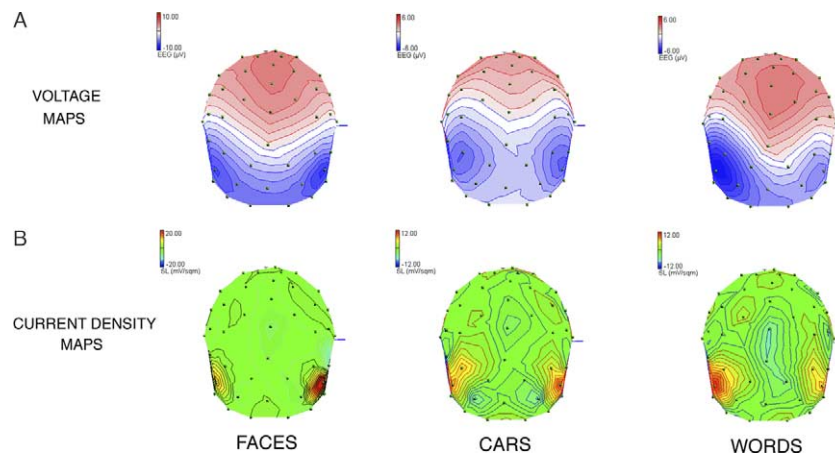


Fig. 5. (A) Topographical maps (peak maximum, average reference, 162 ms for faces; 164 ms for cars; 156 ms for words) of the N170–VPP complex for 3 categories of stimuli used (upright presentations). (B) Scalp current density maps for 3 conditions at same latencies.



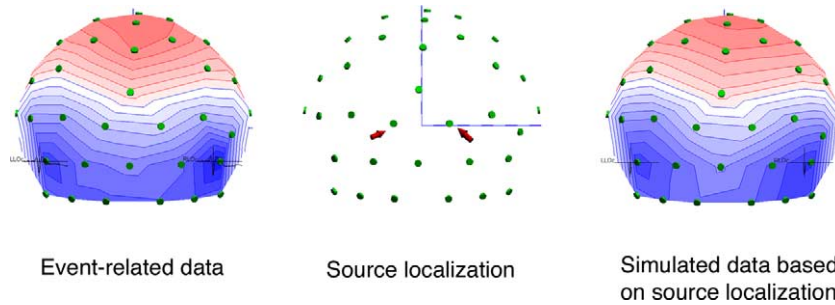


Fig. 6. Source localization of the N170–VPP in response to faces. One pair of stationary dipoles was fitted in the time window around the peak latency of the N170 and VPP component (140–180 ms) using *Advanced Source Analysis* (ASA 2.2, ANT, Inc.; for details about source localization procedures in this study, see methods section of Rossion et al., 2003). As illustrated, both peaks can be accounted for by the same unique dipolar configuration, which accounted for 98.64% of the variance of the signal on the whole scalp (i.e. 98.64% correlation between actual and simulated EEG data during this time window). The EEG recomputed from the dipole pair is almost indistinguishable from the original EEG data.

While the VPP consistently peaked a few milliseconds earlier than the N170 in the averaged data, latencies were quite similar (see Table 2). However, because the peaks are often extremely difficult to determine accurately in the data of individual subjects for each reference electrode, no analysis of peak latency differences was performed.

6.2. The N170/VPP complex in response to non-face categories

The VPP/N170 response to words and cars was similar to that observed for faces (see Figs. 4 and 5). In general, at left hemisphere electrodes, faces showed the largest N170, followed by words and then cars, while at right hemisphere electrodes, faces showed the largest N170 followed by cars and then words.

6.3. Peak latencies analyses using the average reference

There was a main effect of *Category* on the N170 latency ( $F(2,28)=4.98, P<.05$ ), mainly due to a faster response to pictures of words vs. cars:  $P=.023$  and a non-significant trend compared to faces ( $P=.068$ ). The N170 latency did not differ between faces and cars ( $P=.29$ ). There was also

a main effect of *Orientation* ( $F(2,28)=64.29, P<.001$ ), reflected by a longer N170 latency for upside-down presentations for all categories, marginally significant for words (see Fig. 4; Faces,  $P<.001$ ; Cars,  $P<.001$ ; Words,  $P=.054$ ).

VPP latency effects were strikingly identical to those observed at the N170 (see Fig. 4). There were main effects of *Category* ( $F(2,28)=9.22, P<.001$ ) due to earlier peak latency for words, and of *Orientation* ( $F(2,28)=22.62, P<.001$ ) due to the delay resulting from inversion. These effects were qualified by a significant interaction between the two factors ( $F(2,28)=4.89, P<0.05$ ). The delay with inversion was significant for faces ( $P<.001$ ) and cars ( $P<.01$ ), but not for words ( $P=.31$ ).

6.4. N170 amplitude analyses

The N170 analysis on amplitudes revealed significant main effects of *Reference* ( $F(4,14)=93.11, P<0.0001$ ), *Category* ( $F(2,14)=87.47, P<0.0001$ ), and *Hemisphere* ( $F(1,14)=13.19, P<0.001$ ), and significant *Reference* × *Category* ( $F(8,15)=11.64, P<0.0001$ ) and *Category* × *Hemisphere* ( $F(2,14)=28.03, P<0.0001$ ) interactions.

The main effect of *Reference* was due to larger N170 amplitudes using the nose reference than using all other

Table 2  
Amplitude of the N170–VPP for all conditions across reference

|              | Nose    | Average | Earlobes | Mastoid | Non-cephalic |                   | Nose    | Average | Earlobes | Mastoid | Non-cephalic |
|--------------|---------|---------|----------|---------|--------------|-------------------|---------|---------|----------|---------|--------------|
| <i>Faces</i> |         |         |          |         |              | <i>Inv. Faces</i> |         |         |          |         |              |
| LLOC         | -7.0594 | -6.0657 | -4.5419  | -2.5432 | -3.2341      | LLOC              | -7.6034 | -6.1375 | -4.9208  | -2.9750 | -4.0211      |
| RLOC         | -8.0659 | -7.1130 | -5.5458  | -3.5506 | -4.1734      | RLOC              | -8.3151 | -6.8688 | -5.6340  | -3.6665 | -4.7728      |
| MiFr         | 3.6007  | 4.4404  | 6.0303   | 8.0094  | 7.4687       | MiFr              | 2.5530  | 4.0127  | 5.2338   | 7.2012  | 6.1292       |
| <i>Cars</i>  |         |         |          |         |              | <i>Inv. Cars</i>  |         |         |          |         |              |
| LLOC         | -4.5261 | -3.0531 | -3.3119  | -2.1889 | -3.2267      | LLOC              | -4.8018 | -3.0740 | -3.7006  | -2.6103 | -3.4809      |
| RLOC         | -4.9464 | -3.5338 | -3.7706  | -2.6670 | -3.6993      | RLOC              | -4.9172 | -3.1746 | -3.8012  | -2.7110 | -3.6000      |
| MiFr         | 0.5357  | 1.7191  | 1.4985   | 2.5742  | 1.5377       | MiFr              | -0.1161 | 1.4371  | 0.8330   | 1.9083  | 1.1566       |
| <i>Words</i> |         |         |          |         |              | <i>Inv. Words</i> |         |         |          |         |              |
| LLOC         | -6.2703 | -5.5998 | -5.3640  | -4.1541 | -4.8369      | LLOC              | -6.7321 | -5.5248 | -5.4055  | -4.0637 | -5.1466      |
| RLOC         | -3.2699 | -2.6074 | -2.3654  | -1.1637 | -1.8977      | RLOC              | -4.6336 | -3.4942 | -3.3352  | -2.0021 | -3.0137      |
| MiFr         | 2.0116  | 2.5358  | 2.7828   | 3.9755  | 3.6201       | MiFr              | 2.3708  | 2.9052  | 3.1363   | 4.4633  | 3.7697       |

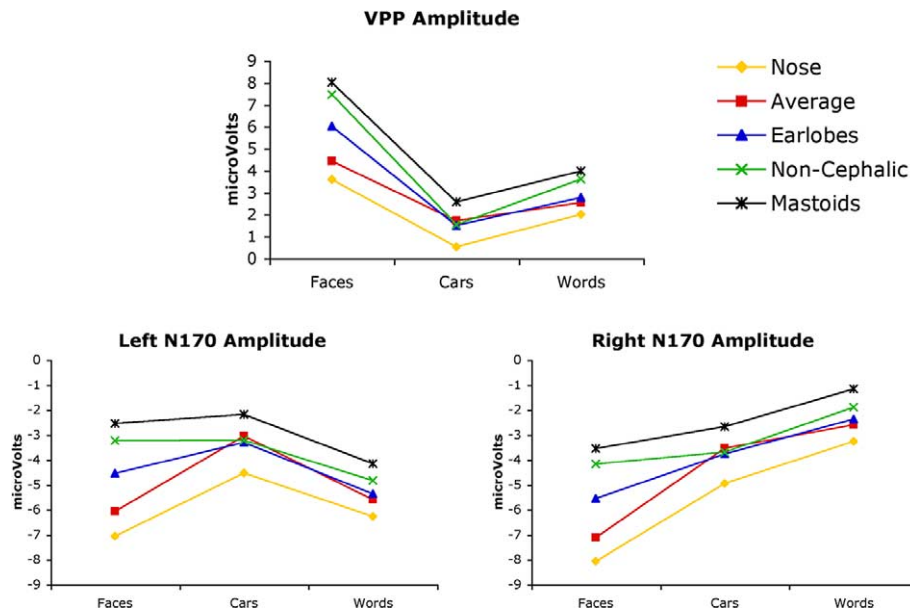


Fig. 7. Amplitude values across 5 reference electrodes for 3 categories of stimuli used (LLOC and RLOC electrodes are illustrated). Note the absence of difference between faces and cars at the level of the N170 when using the mastoids or the non-cephalic reference.

references ( $P < 0.05$ ), and larger N170 amplitudes using the average and earlobe references than using non-cephalic and mastoid references ( $P < 0.05$ ; see Figs. 2, 3 and 6).

The main effect of *Category* was due to larger N170 amplitudes for faces than for words and cars (both  $P < 0.05$ ), and larger N170 amplitudes for words than cars ( $P < 0.05$ , see Figs. 4 and 7).

The *Category* × *Reference* interaction was due to different effects of category with each reference. There were no differences between faces, cars, and words using mastoid and non-cephalic references. With an average reference, faces, words, and cars were all significantly different from one another (all  $P < 0.05$ ). With the earlobe reference, faces elicited a larger N170 than cars ( $P < 0.05$ ), and with the nose reference faces elicited a larger N170 than cars and words ( $P < 0.05$ , see Fig. 7).

The *Category* × *Hemisphere* difference was due to the strong left hemisphere bias for words (Fig. 4). In the left hemisphere, both faces and words elicited larger N170's than cars ( $P < 0.05$ ), while in the right hemisphere faces elicited a larger N170 than both words and cars ( $P < 0.05$ ).

### 6.5. VPP amplitude analyses

The VPP analysis on amplitudes revealed significant main effects of *Reference* ( $F(4,14) = 19.10$ ,  $P < 0.0001$ ) and *Category* ( $F(2,14) = 118.31$ ,  $P < 0.0001$ ), and a significant *Reference* × *Category* interaction ( $F(8,14) = 2.82$ ,  $P < 0.005$ ).

The main effect of *Reference* was due to a significantly larger VPP amplitude using the mastoid reference than using the nose, average and earlobe references, a significantly larger VPP amplitude using the non-cephalic

reference than using average and nose references, and a significantly larger VPP amplitude using the earlobe and average references than using the nose reference (all comparisons  $P < 0.05$ , see Fig. 2).

The main effect of *Category* was due to a larger VPP for faces than for words and cars, and a larger VPP for words than cars ( $P < 0.05$ , see Figs. 4 and 7).

The interaction of *Reference* with *Category* was due to differential effects of category across reference sites (see Fig. 7). Using the average reference, faces showed a larger VPP than cars ( $P < 0.05$ ). Using the earlobe, faces showed a larger VPP than both cars and words (both  $P < 0.05$ ). Using both mastoid and non-cephalic references, faces showed a larger VPP than words and cars, and words showed a larger VPP than cars (all comparisons  $P < 0.05$ ). Finally, using the nose reference, faces and words showed a larger VPP than cars ( $P < 0.05$ ).

### 6.6. Correlation measures

Pearson ( $r$ ) correlation coefficients were computed between amplitude values for the N170 and VPP recorded at the electrode sites where the components were maximal on an average (MIPf and RLOC/LLOC), using average reference values (showing clearly both sides of the dipole), and are reported in Table 3. For all conditions, these correlation values were highly significant ( $P < 0.001$ ).

## 7. Discussion

The main goal of the present study was to test the hypothesis that the temporally coincident vertex positive

Table 3  
Latency of the peak of the N170–VPP for all conditions across reference

|              | Nose | Average | Earlobes | Mastoid | Non-cephalic |                   | Nose | Average | Earlobes | Mastoid | Non-cephalic |
|--------------|------|---------|----------|---------|--------------|-------------------|------|---------|----------|---------|--------------|
| <i>Faces</i> |      |         |          |         |              | <i>Inv. faces</i> |      |         |          |         |              |
| LLOC         | 162  | 160     | 162      | 162     | 164          | LLOC              | 164  | 164     | 164      | 162     | 164          |
| RLOC         | 160  | 158     | 160      | 160     | 162          | RLOC              | 164  | 166     | 166      | 166     | 166          |
| MiFr         | 154  | 158     | 158      | 158     | 156          | MiFr              | 166  | 164     | 166      | 166     | 164          |
| <i>Cars</i>  |      |         |          |         |              | <i>Inv. cars</i>  |      |         |          |         |              |
| LLOC         | 162  | 160     | 160      | 160     | 160          | LLOC              | 166  | 164     | 164      | 164     | 166          |
| RLOC         | 160  | 158     | 158      | 158     | 158          | RLOC              | 166  | 164     | 164      | 164     | 168          |
| MiFr         | 152  | 156     | 156      | 156     | 156          | MiFr              | 156  | 162     | 162      | 162     | 160          |
| <i>Words</i> |      |         |          |         |              | <i>Inv. words</i> |      |         |          |         |              |
| LLOC         | 152  | 152     | 152      | 152     | 156          | LLOC              | 166  | 158     | 164      | 164     | 172          |
| RLOC         | 152  | 150     | 150      | 150     | 152          | RLOC              | 164  | 158     | 160      | 160     | 162          |
| MiFr         | 142  | 148     | 148      | 148     | 144          | MiFr              | 134  | 152     | 150      | 152     | 140          |

VPP and occipito-temporal N170 potentials in response to faces are flip sides of the same generators. Early ERP research in face processing was dominated by an interest in the VPP (e.g. Bötzel and Grusser, 1989; Jeffreys, 1989), but most studies carried out in the past 10 years have concentrated on the N170. We believe that this shift of interest is due to two factors: the advent of high-density EEG recording systems (Gevins et al., 1994; Tucker, 1993), and perhaps even more importantly, the increasing use of the common average and other anterior locations on the head (nose, chin) as reference sites. Yet, number of critical observations were previously made using the VPP as a marker of face processing at this latency (see Jeffreys, 1996 for a review), such that establishing the relationship between the two potentials should help researchers to make progress in tracking the time course of face and object processing. Moreover, the emphasis on one or the other side of the component may depend on the goals of the experimenter and the conditions used, as discussed below. In addition, our observations suggest that ERP results regarding this VPP/N170 component should always be considered in relation to the location of the reference electrode, since this can have a dramatic influence on the functional effects observed. We will first discuss the evidence taken both from our study and the current literature supporting the direct association between the VPP and the N170, before discussing the implications for future work in this area.

As described previously (Rossion et al., 2003), between 130 and 170 ms, clear components were observed at most electrode sites (Fig. 1). Over anterior and midline sites, the deflection was positive-going, showing the morphology and distribution typical of the VPP. Over lateral posterior sites, this peak was negative-going, with the morphology and distribution characteristic of the N170 (Figs. 1–5). Regarding the relationship between the two peaks and the goal of the present study, several observations are worth noting. First, the amplitude of both the anterior VPP and the posterior N170 in response to faces varied systematically with reference electrode. Most strikingly, the variation showed a precisely inverse relationship between the VPP

and N170: the largest N170 peak was observed with the nose reference followed by average, earlobe, non-cephalic and mastoid references, respectively, whereas the largest VPP was observed with the mastoid reference, followed by the non-cephalic, earlobe, average and nose, respectively (Figs. 2 and 3). Second, peaks of these components were within 2–8 ms of each other for each reference, in line with previous studies (see Table 2). For example, using the average reference, the peak of the VPP at midline electrodes occurred at ~158 ms while the peak of the N170 at posterior sites occurred at ~160 ms (Table 2). Third, the latency delay for faces presented upside-down observed only on the VPP and N170, across all reference electrodes (Fig. 8), is indicative of a remarkable functional similarity between the two peaks.

### 7.1. The VPP and the N170: two ‘faces’ of the same phenomenon

When addressing the question of the relationship between the VPP and N170, one has to consider both physiological (topography, amplitude, latency, frequency), and functional properties (modulations by stimulus and task factors) of the two peaks.

#### 7.1.1. Physiological parameters

One striking feature observed in the current data is the exact phase reversal between the N170 and VPP, as illustrated in Figs. 1 and 3 (see also Figs. 2, 4, 7 and 8). The respective amplitudes of the N170 and VPP appear to vary inversely according to the location of the reference: the closer/further the reference from the peak on the scalp, the smaller/larger the peak amplitude (e.g. mastoids for N170/VPP). As illustrated in Fig. 3, the whole component appears shifted upward (negative towards positive) between the nose (minimal VPP, maximal N170) and mastoid (maximal VPP, minimal N170) references and vice-versa. Clearly, this phase reversal between the VPP and N170 is found for all the locations of the reference electrode (Fig. 3).

The latency of the two peaks is virtually identical (Fig. 3; Table 2), as in previous studies reporting latency values for

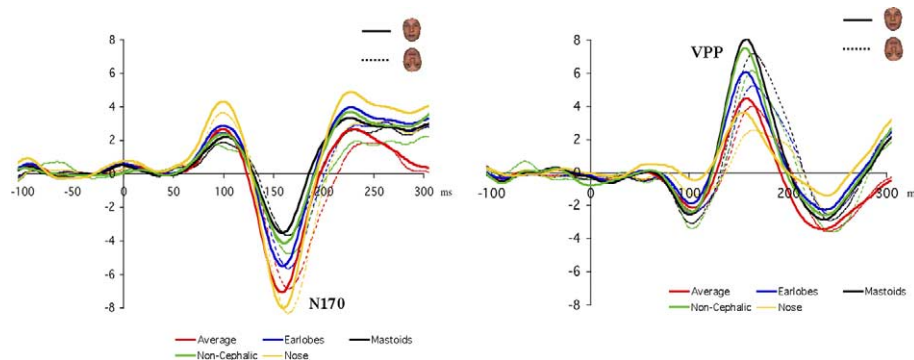


Fig. 8. ERPs in response to faces presented upright and upside-down, in the right hemisphere and at the vertex. The N170–VPP complex was delayed in response to inverted stimuli (dotted lines) for all the reference electrodes used. Note the absence of effect of inversion at the level of the preceding P1/N1 component.

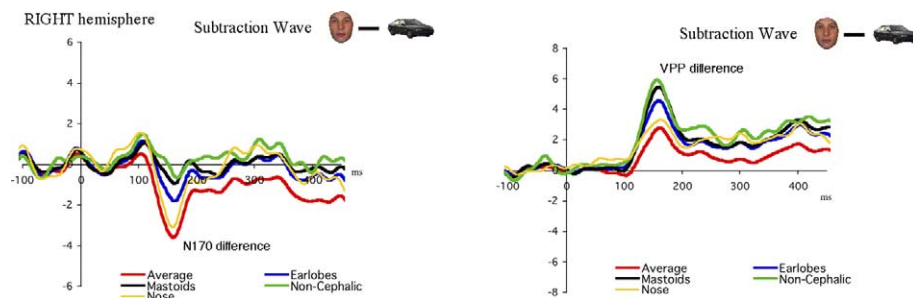


Fig. 9. Difference waves between faces and cars at the (right) occipito-temporal level (RLOC) and at CZ. Note the absence of difference between faces and cars at the level of the N170 when using the mastoids or the non-cephalic reference and the inversion of amplitude difference between the two sites.

both the VPP and N170 (see Table 1). A few studies have suggested latency differences between the two peaks, but without substantial empirical support. In their study, Bötzel et al. (1995) described the N170 as ‘peak C’ (maximum at T5 and T6) and the VPP as a ‘peak D’ (maximum at CZ), both larger for faces than for objects. They consider these peaks as different components because ‘*the different peak latencies of peaks C and D, which are obvious from our data provide strong evidence that they are generated by different intracranial sources*’ (Bötzel et al., 1995, p. 141). However, this ‘obvious’ peak latency difference was 4 ms (176 ms for the N170, and 180 ms for the VPP) in their report. Bentin et al. (1996) have also suggested a larger difference between the N170 and a ‘P190’ thus supposedly peaking around 20 ms later, but no systematic analysis of this P190 parameter was reported.<sup>3</sup> In general, the peak latency of the N170 and VPP is highly similar in all studies (see Table 1) but there can be large inter-subject and inter-study variability, with peaks between 140 and 200 ms, as noted by Jeffreys (1996). Hence, the VPP has been termed the P150 in some studies (e.g. Schendan et al., 1998—who referred to the negative component as the N150) and the P190 in others

(e.g. Bentin et al., 1996). Besides the large inter-subject variability in terms of latency of this component, it is well known that non-independent low-level visual parameters such as the luminance, contrast, and spatial frequency of the stimuli strongly modulate the latency of visual components (e.g. Musselwhite and Jeffreys, 1982; Russel et al., 1987). Accordingly, an adequate comparison of latency and amplitude parameters of the VPP and N170 should not be made across experiments, but only within the same experiment. Correlation values between peak amplitudes—reported in Table 3—are also particularly high in the present study, as previously demonstrated (Jemel et al., 2003).

In the frequency domain, both peaks lie in the lower alpha range (7–9 Hz) and present the same width (Fig. 3), showing that it is not only the peak latency but the onset and offset of the wave that are temporally coincident. Thus, whether the posterior N170 arises because of time- and phase-locked evoked potentials superimposed to independent non-phase locked oscillations, or because of a phase resetting of such oscillations in the lower alpha range (Klimesch et al., 2004; Makeig et al., 2002), the same mechanisms seem to account for both the positive (fronto-central VPP) and negative waves observed on the scalp at that latency.

<sup>3</sup> In fact, preliminary report of these findings gave a peak latency of 180 ms for the central positive component (Allison et al., 1994).

Finally, it was shown previously on these data that the VPP/N170 could be modeled adequately by a single equivalent dipolar bilateral source rooted in the occipito-temporal junction (see Fig. 6). These physiological similarities between these face-related components were observed previously. Jeffreys (1989, 1996) noted that the source of the VPP ‘suggested bilateral sites of origin in areas of the temporal cortex oriented perpendicularly with respect to the overlying scalp’ and ‘... that an equivalent dipole source generating a negative potential at the inferior cortical surfaces will produce a corresponding positive potential over the upper regions of the cortex and scalp’ (Jeffreys, 1996, p. 23). This author used a mastoid reference in his recordings and had little sampling over occipital and occipito-temporal sites. In particular, no electrodes were placed at or below the scalp region over the middle temporal gyrus (T5/T6 in the 10–20 system, Homan et al., 1987). Thus, the scalp recorded N170 was not observed in these data. However, Jeffreys (1989) did report the presence of the temporal negativities when using the nose reference in one of his subjects, describing it as ‘the temporal counterpart of the VPP’ (p. 200). The distribution of the N170 and VPP and their differential sensitivity to reference site are suggestive of common neural generators located in the temporal lobes and oriented on an axis between occipito-temporal and fronto-central midline electrode locations, in agreement with the outcome of dipole localization studies (Bötzel et al., 1995; Halgren et al., 2000; Itier and Taylor, 2002; Rossion et al., 1999a, 2003; Schweinberger et al., 2002; Watanabe et al., 2003). This N170/VPP equivalent dipole source can be related to the regions of the ventral processing stream where larger responses to faces compared to objects have been found in humans using neuroimaging, with a clear right hemisphere advantage (see Haxby et al., 2000): the middle fusiform gyrus, the inferior occipital cortex, and the superior temporal sulcus (STS). Rather than originating from a single one of these sources, the scalp N170/VPP component most likely reflects a weighted vector sum of multiple generators activated in interlocked time courses in these regions. An important contribution of the regions of the superior temporal sulcus (STS), where the largest proportion of face-selective cells is found in the monkey (e.g. Baylis et al., 1987; Perrett et al., 1992), is also suggested by recent MEG studies (Henson et al., 2003) and source localization using 3D current density distributions (Itier and Taylor, 2004b).

Finally, it is worth relating our observations to the recordings of intracranial field potentials in response to faces from the surface of the occipito-temporal extrastriate cortex of patients with medically refractory epilepsy (Allison et al., 1994, 1999). The most prominent potentials found in these studies were N200 s in response to faces recorded from the ventral and lateral parts of the occipito-temporal cortex (Allison et al., 1999). The relationship between the N200 and the scalp N170 is unclear. Besides

their identical polarity and similar latencies,<sup>4</sup> they also present functional similarities (e.g. the face-N200 being reduced for non-face object categories and delayed to faces presented upside-down, McCarthy et al., 1999) suggesting that the scalp N170 reflects the vector summation of cortical surface N200 s. N200 s recorded on the lateral part of the occipito-temporal cortex (e.g. middle temporal gyrus) may contribute directly to the N170, whereas the most prominent N200 s generated at the inferior surface of the occipito-temporal cortex (e.g. fusiform gyrus) will also contribute to the scalp N170 directly if they are oriented *obliquely* to the lateral temporal surface (see Rossion et al., 2003). Moreover, these latter sources will generate a large positive counterpart maximal at central sites (VPP) and covering most of the superior pole of the head. Referencing the scalp ERPs to the average reference, a nose electrode or a centro-frontal channel (CZ, FZ) will thus substantially increase the amplitude of the N170 at occipito-temporal sites indirectly (i.e. through the positive counterpart of the N170).

#### 7.1.2. Functional properties of the VPP and N170

A critical factor to consider when discussing whether the VPP and N170 are different manifestations of the same activity or not is their functional properties: can the N170 and VPP be dissociated based on their differential responses to various stimulus and/or task manipulations? One problem is that, to our knowledge, only one study has systematically compared the two peaks under various conditions (Jemel et al., 2003). Interestingly, these authors showed a remarkable correlation of the amplitude of the VPP and N170 across various levels of contrast in the face stimuli. Importantly, the posterior PI recorded in that study was not modified by contrast level, and thus was uncorrelated with the VPP/N170 component. Other than this source of evidence, one has to rely on the functional characteristics of the VPP and the N170 as they have been extracted from similar manipulations in different studies. In Table 1, the main common functional properties of the components are summarized: their response properties appear to be identical, at least for the characteristics that have been described for both components.

The most striking functional similarity between the VPP and the N170 is their large amplitude for faces as compared to objects—no other scalp component presents this response property. In addition, the amplitude *difference* between faces and objects at the level of the N170 and VPP is highly correlated (see Fig. 9). For instance, in studies using several object stimuli (e.g. Itier and Taylor, 2004a; Rossion et al., 2000), the N170 and VPP amplitude was found to covary

<sup>4</sup> As acknowledged by the authors (e.g. Bentin et al., 1996), the approximate 20 ms longer latency of N200 s relative to scalp N170 could be attributed to differences between patients under medication and normal subjects. Most importantly, the 2 components have not been compared in the same subjects with the same stimuli.

remarkably across these multiple object categories (Itier and Taylor, 2004a, Fig. 3).

Another notable feature is the peak latency delay observed when faces are presented upside-down, at both N170 and VPP sites (see Rossion et al., 1999b). This effect, which was first reported for the VPP by Jeffreys (1993), appears to be independent of the location of the reference, as illustrated in Fig. 8. In contrast, while the N170 is generally increased in response to inverted faces (e.g. Carmel and Bentin, 2002; Itier and Taylor, 2002; Rossion et al., 1999b), Jeffreys (1993) found no increase of the VPP amplitude with inversion. However, when both components have been reported in the same study, they are again correlated: either both peaks are significantly increased in response to upside-down faces (e.g. Itier and Taylor, 2002; Rossion et al., 1999b), or both are not (e.g. the present study; Goffaux et al., 2003). This illustrates once again that a comparison between the response properties of the VPP and N170 should be made within the same study.

At this stage, to our knowledge, there are only two clear functional differences between the N170 and VPP, although the interpretation of these effects does not necessarily lead to the conclusion that different dipoles are involved in generating the components. First, ERP recordings in infants indicate that the N170 appears relatively early in the developmental course (e.g. in 6- and 12-month-old infants) although with a much longer latency than in adults (De Haan et al., 2002). This latency delay decreases with age until by 14 years old it resembles that of the adult (Taylor et al., 1999). However, the positive counterpart (VPP) is not observed in children until age 12 (Taylor et al., 1999). While this observation may support the N170/VPP dissociation hypothesis, it was suggested that the absence of the VPP in young children is due to modifications of the cortex folding, and accordingly dipole orientation, with age and brain development (Taylor et al., 1999) rather than the sudden appearance of a new dipolar source with identical functional properties to the N170.

Second, it appears that peripheral presentations of faces elicit an N170, but no VPP. Eimer (2000a) found that both faces and chairs elicited the N170 when presented peripherally that was larger to faces than chairs, and smaller for peripherally than centrally presented stimuli. However, he found no reliable VPP nor any face–chair differences at central electrodes to peripherally presented stimuli. A similar result was reported by Jeffreys et al. (1992). Although Eimer (2000a) interpreted these findings as an evidence against the idea that these two effects reflect a unitary generator, this is not the only possible interpretation. It is also possible that the orientation of the equivalent occipito-temporal dipole is sensitive to the eccentricity of the visual field stimulation, as indicated by the modulation of the N170 itself to the eccentricity of the stimulus, and the observation that the N170 is larger for contralateral stimulations (Eimer, 2000a). Complicating the picture further, these modulations can be reference-dependent.

It has been observed, for instance, that changing the location of the reference electrode (mid-frontal vs. earlobes) may affect the amplitude of VEPs in response to upper visual field stimulations, whereas VEPs to lower visual field stimulations are unaffected (Michael and Halliday, 1971).

To conclude, the functional similarity between the N170 and VPP in response to faces is so remarkable that they have been both associated with the same stage(s) of face processing, by authors who have studied these components independently (e.g. Bentin et al., 1996, 1999; Eimer, 1998, 2000; Jeffreys, 1989, 1996). However, it should be noted that the remarkable neurophysiological and functional similarities between the N170 and the VPP could be modulated by changes in both stimuli and task. Certain experimental conditions may recruit additional processes that are active at about the same time as the VPP/N170 but whose contributions differ by scalp position. Hence, they may modulate the properties of one and/or the other component to a greater degree. In addition, there are actually at least two distinct processes reflected by the N170 and VPP already, one in each hemisphere, which can yield asymmetric effects (e.g. words vs. faces in Fig. 4). Source analysis procedures could help tease apart such differential contributions. In sum, our claim is that in normal conditions of visual stimulation, the VPP and N170 in response to faces largely represent two flip sides of the same underlying generators, but one cannot rule out the possibility that additional generators—unrelated to face processing per se—will modulate the surface properties of one of the two peaks.

## 7.2. *Categorical differences may be reference electrode-dependent*

We stated earlier that comparisons of the N170 and VPP should be made within the same study. Even so, one should take into account the location of the reference electrode, since it can differently affect the functional (task and stimulus modulation) features of the VPP and the N170. For instance, the category-related differences observed for the N170 and VPP described here varied with reference electrode (Figs. 7 and 9). In general, at a reference for which a particular component was large, categorical differences tended to be magnified. Conversely, at references where a particular component was small, categorical differences were compressed such that they were insignificant. In other words, the pattern of categorical differences varied, for the most part, systematically with the size of the observed peak.

### 7.2.1. *Averaged mastoid and sterno-vertebral non-cephalic*

The averaged mastoid and sterno-vertebral non-cephalic references gave identical results. Both these references yielded the smallest amplitude N170, with no significant category differences (faces vs. other stimuli), and the largest amplitude VPP, with significant differences between all categories. Both these effective references are in a good

position to pick up a strong negative signal from equivalent dipoles in the occipito-temporal junction, oriented largely perpendicular to the equatorial plane of the head. They are on the same side of the dipole as N170 electrodes over temporal cortex, and at the opposite side of the dipole from VPP electrodes over midline central sites. Thus, these references will tend to cancel out this dipole signal at N170 electrodes and magnify it at VPP electrodes.

### 7.2.2. Averaged earlobe

The averaged earlobe reference yielded mid-amplitude peaks at both N170 and VPP sites. At N170 sites, this reference was only sensitive to the largest categorical difference (i.e. between faces and cars), whereas at VPP sites it was sensitive to all but the smallest categorical difference (i.e. was sensitive to the difference between faces and words/cars, not to words/cars). While it is more neutral than the mastoid reference with respect to the posterior negativity, as evidenced by its comparatively elevated sensitivity to large categorical differences at N170 sites, it is not completely inactive with respect to this dipole. It picks up enough signal from the negative end of the dipole to eliminate smaller category differences at N170 sites. As with the mastoid and non-cephalic sites, it shows differences at the VPP electrodes. However, because it does not pick up as strong a negative signal from the negative end of the dipole, it does not magnify the smallest category difference at the VPP, as do the mastoid and non-cephalic references. Rather it picks up only on the two largest of the 3 differences.

### 7.2.3. Common average reference

The common average reference yielded a large peak at N170 sites and a small peak at VPP sites. At N170 sites, this reference was sensitive to all categorical differences, whereas at VPP sites it was sensitive only to the largest categorical difference (i.e. between faces and cars). While it appears to effectively lie vertically between the positive and negative ends of the dipole (i.e. it picks up both N170 and VPP peaks), it appears closer to the positive vertex; differences observed at N170 sites are amplified as compared to differences at VPP sites.

### 7.2.4. Nose reference

The nose reference yielded the largest peak at N170 sites and the smallest peak at VPP sites. At N170 sites, this reference differentiated faces from words and cars, whereas at VPP sites it significantly differentiated faces and words from cars. The amplitude of the peaks with respect to this reference is easily explained: it is the furthest reference from the negative pole of the neural generator and closest to the positive pole. Thus, much of the positive signal at VPP electrodes gets attenuated and the negative signal at the opposite end, near N170 electrodes, gets amplified. The categorical differences are not as straightforward, as they do not correspond as closely to the general finding that

the larger the peak, the more amplified the categorical differences, and vice versa. However, because this reference is close to many skull openings (i.e. eye sockets, sinus cavities) there can be distortion in the distribution of the signals, making it difficult to predict what differences will be observed. In addition, there are different dipole orientations associated with the categories and this can also affect the observed signals (Trujillo et al., 2005).

### 7.3. Which reference electrode for measuring face and object ERPs?

Clearly, it is the case that the location of the reference electrode can have a profound impact on what effects are observed in a particular experiment. The current results can help to explain some of the apparently contradictory patterns observed in other studies. For example, George et al. (1996) found that the N170 was increased and delayed to scrambled faces but the VPP was not significantly modulated. Itier and Taylor (2004a) also found a larger N170 response to inverted faces, but the effect was not significant at the level of the VPP. Interestingly, despite this, these authors considered both peaks as forming part of the same component (see Itier and Taylor, 2004a, p. 137). In these cases, a nose reference (George et al., 1996) or a common average reference with a small number of channels (e.g. Itier and Taylor, 2004a) was used enhancing amplitude differences at the level of N170 and compressing differences at the VPP, as shown in the present study. Accordingly, one must be careful in interpreting minor functional differences between the peaks as an evidence for their dissociation (e.g. George et al., 1996), given that the reference electrode is not neutral. A stronger criterion for dissociating the two peaks would be to show a *double* functional dissociation between the VPP and the N170 within the same study (e.g. larger amplitude for condition A than B at the N170 peak, and B larger than A at the VPP peak). To our knowledge, no such results have been found.

Finally, an important question to resolve is which reference electrode should be used in face processing studies using ERPs, and which peak—the N170 or the VPP or both—should be the focus of interest?

Since visual processing of faces takes place in occipito-temporal regions rather than in regions situated below the vertex, it is perfectly understandable that the attention of researchers is now focused on the N170 rather than on the VPP. The sources of the component are also closer to the N170, as indicated by dipole localization and current density mapping (e.g. Henson et al., 2003; Itier and Taylor, 2004b). One clear advantage of measuring face-related activity at this latency on posterior leads rather than the vertex is that it allows one to measure lateralization. Most studies find a (small) right hemisphere advantage in the amplitude of the N170 in response to faces (e.g. Bentin et al., 1996; Rossion et al., 2003), whereas the response to objects is more bilateral, and is strongly left-lateralized for

letter strings (Figs. 4 and 5). Using the mastoid reference and concentrating on the vertex will mask these lateralization effects and may fail to disclose amplitude differences at right or left posterior electrode sites (e.g. Schendan et al., 1998).

In general, our study suggests that the average reference most optimally captures categorical and hemispheric differences at the N170, at least if the number of channels is large enough. Furthermore, the average creates the most optimal balance between the positive and negative peaks (i.e. neither one is too small to show significant differences) allowing for comparisons across the N170 and VPP literature. Likewise, performing visual analysis of recordings that use an average reference is much easier than visual analyses using other references as the patterns of the dipole fields and field slopes are more clearly visible.

The earlobes also provide a good compromise between the two peaks because, even though they sample some visual activity, they are relatively free of artifacts. However, because of their proximity to sites where the N170 is maximal, and given the current emphasis in the literature on the N170, they do not create as optimal a balance as the average reference. While the nose reference gives rise to the largest N170 peaks, it is close to many skull openings (i.e. eye sockets, sinus cavities) and is contaminated by eye movement artifacts (Trujillo et al., 2005). Thus, the distribution of the signals may be suspect. The mastoid and the sterno-vertebral non-cephalic references will reveal differences at the vertex but may mask important categorical differences and hemispheric effects that can only be observed at temporal electrodes (see also Kiefer et al., 1998). Finally, adding a non-cephalic channel in some studies may be interesting since re-referencing to that ‘neutral’ channel will provide some clues as to the orientation of the equivalent dipolar sources of the component of interest.

Although there are many factors supporting concentration on the N170, there are also a number of findings made at the level of the VPP that are still relevant for our understanding of the temporal course of face processing (see Jeffreys, 1996). In fact, a number of ‘findings’ at the level of the N170 such as the delay observed for upside-down faces (Bentin et al., 1996; Rossion et al., 1999b), contrast negative faces (Itier and Taylor, 2002), isolated eyes (Bentin et al., 1996; Taylor et al., 1999) or faces without one or several features (e.g. Eimer, 1998), were described previously at the level of the VPP (Jeffreys, 1989, 1996). More recently, a number of researchers have attempted to modulate the N170 amplitude using adaptation or competition paradigms in which the response to a second stimulus is modulated (or not) by the presentation of a first stimulus when the delay between the presentation the two stimuli is short (e.g. Kovacs et al., 2004) or when they are presented concurrently (Jacques and Rossion, 2004; Rossion et al., 2004). This line of research can be directly related to preliminary work on the VPP (Jeffreys, 1996), showing adaptation effects of the component in ‘dual pulse’

paradigms (e.g. two face pictures presented sequentially with a short stimulus onset asynchrony).

Rather than focusing on one of the two components, other researchers who use high-density EEG systems advocate a more general approach, the global field power (GFP; Lehmann and Skrandies, 1984), which reduces the data from multiple channels into a single-time series. This approach considers all channels from the scalp rather than a few channels selected subjectively either a priori, or after visual inspection of data, and was used previously in studies of face processing (e.g. Caldara et al., 2003; Milivojevic et al., 2003). An obvious limitation of the approach is the complete loss of spatial information. Despite the widespread distribution of activity on the scalp during the VPP/N170 time window (e.g. Fig. 1), the components of interest are largely limited to a few channels, and the use of the GFP would necessarily include channels which not only pick up little of the activity of interest, but are also prone to artifacts (e.g. F7/F8 or T7/T8), adding noise to the analyses. Another possibility is to use a reference-free estimate of the current flows such as the Laplacian or current source density (CSD) mapping (Nunez, 1981, 1990; Perrin et al., 1989). Such mappings suggest that sources of the VPP/N170 component are indeed very close to occipito-temporal recording sites (e.g. see Henson et al., 2003; or Fig. 5 of the present study), and that there are most likely no sources close to the vertex contributing to the component (Fig. 5). However, one should be careful in interpreting such CSD maps since it is well-known that the CSD will emphasize shallow sources only, and thus is not suitable for imaging potentials from deep or distributed sources (Dien, 1998; Perrin et al., 1989).

## 8. Conclusion

The current study takes a large step toward resolving the question of whether the N170 and VPP in response to faces and non-face categories are flip sides of the same neural generator or are two distinct and dissociable components. Several results support the conclusion that they are in fact signals coming from the same equivalent dipoles. First, the amplitude of both the N170 and VPP vary in a systematic, inverse manner with respect to each other across reference site. This variation is so tightly coupled between these components that it seems unlikely that it could have been produced by independent generators. Second, the peaks of these two components always occur within 8 ms of each other for the given reference and category. Third, the distribution of these components is indicative of symmetric dipole generators in the temporal lobes with the poles oriented. Fourth, the size and pattern of category-related effects observed at temporal N170 and vertex VPP sites also varied quite systematically and were well explained by the location of the references with respect to the VPP and N170 recording electrodes and with respect to the proposed orientation and location of the dipoles. Fifth, data from this



study and the literature illustrate the functional equivalence between the two peaks, such as the delay observed with inverted faces, which is independent of the reference used. Finally, reviewing previous results in light of the current data explained some of the apparently contradictory results that were being presented as evidence that these two components involve separate generators. In addition, the current work shed light on the importance of choice of reference when measuring the N170/VPP component, some factors that influence the effectiveness of a particular reference, and how reference electrode can affect the observed signals and functional differences.

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