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Highlights

- Upright Arcimboldo paintings elicit face-like N170 amplitude in the right hemisphere.
- This hemisphere processes global face configurations irrespective of their features.
- Inverted Arcimboldo paintings elicit object-like N170 amplitude in both hemispheres.
- Inversion disrupts holistic processing of Arcimboldo paintings.
- They are perceived as objects when inverted due to the lack of local facial features.

Early holistic face-like processing of Arcimboldo paintings in the right occipito-temporal cortex: Evidence from the N170 ERP component

Short title: Early holistic processing of Arcimboldo paintings in the right hemisphere

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Abstract

The properties of the face-sensitive N170 component of the event-related brain potential (ERP) were explored through an orientation discrimination task using natural faces, objects, and Arcimboldo paintings presented upright or inverted. Because Arcimboldo paintings are composed of non-face objects but have a global face configuration, they provide great control to disentangle high-level face-like or object-like visual processes at the level of the N170, and may help to examine the implication of each hemisphere in the global/holistic processing of face formats. For upright position, N170 amplitudes in the right occipito-temporal region did not differ between natural faces and Arcimboldo paintings but was larger for both of these categories than for objects, supporting the view that as early as the N170 time-window, the right hemisphere is involved in holistic perceptual processing of face-like configurations irrespective of their features. Conversely, in the left hemisphere, N170 amplitudes differed between Arcimboldo portraits and natural faces, suggesting that this hemisphere processes local facial features. For upside-down orientation in both hemispheres, N170 amplitudes did not differ between Arcimboldo paintings and objects, but were reduced for both categories compared to natural faces, indicating that the disruption of holistic processing with inversion leads to an object-like processing of Arcimboldo paintings due to the lack of local facial features. Overall, these results provide evidence that global/holistic perceptual processing of faces and face-like formats involves the right hemisphere as early as the N170 time-window, and that the local processing of face features is rather implemented in the left hemisphere.

Keywords: Face-sensitive N170 ERP component, Arcimboldo paintings, Holistic face-like processing, Right occipito-temporal cortex, Inversion effect, Visual categorization.

1. Introduction

The visual system is particularly fast and efficient in categorizing stimuli, especially for faces, which constitute one of the most salient stimuli for social interactions. Event-related potentials (ERPs) have reported an early positive component (P1) peaking at around 100 ms, sometimes larger in response to faces than objects (Eimer, 1998; Herrmann, Ehlis, Muehlberger, & Fallgatter, 2005; Itier & Taylor, 2004; for equivalent findings in the same time-range with magnetoencephalography (MEG), see Halgren, Rajj, Marinkovic, Jousmäki, & Hari, 2000; Liu, Harris, & Kanwisher, 2002), an effect due to low-level visual properties (Halgren et al., 2000; Rossion & Caharel, 2011; Rossion & Jacques, 2008; Tanskanen, Nasanen, Montez, Paallysaho, & Hari, 2005). A more robust and consistent difference between face and object categories was found at the level of the N170 (or the M170 in MEG) peaking at around 160 ms over occipito-temporal sites (Bentin, Allison, Puce, Perez, & McCarthy, 1996; Eimer, 2000a,b; Halgren et al., 2000; Itier, Latinus, & Taylor, 2006; Itier & Taylor, 2004; Liu et al., 2002; Rebaï, Poiroux, Bernard, & Lalonde, 2001; Rossion, Joyce, Cottrell, & Tarr, 2003; Rousselet, Macé, & Fabre-Thorpe, 2004; for a recent review see Rossion & Jacques, 2011), a component whose positive frontocentral counterpart—the vertex positive potential (VPP) – was the focus of early studies (Bötzel & Grusser, 1989; Jeffreys, 1989; see Joyce & Rossion, 2005). The N170 component is larger for faces relative to all other objects, especially in the right hemisphere (e.g., Bentin et al., 1996; Rossion, Joyce, Cottrell, & Tarr, 2003), and is considered a marker of face-sensitive processing (Bentin et al., 1996; Eimer, 2000a).

Unlike the P1, this N170 *face-effect* does not appear to be driven by low-level properties but by high-level face representations (Rossion & Caharel, 2011; Rossion & Jacques, 2008). Moreover, the N170 is as large for schematic faces, painted portraits (Sagiv & Bentin, 2001), or monkey faces as for natural faces (Carmel & Bentin, 2002; de Haan, Pascalis, & Johnson, 2002;

Itier et al., 2006), showing that the N170 is not only sensitive to natural face photographs but also to any stimulus containing enough information to be perceived as a face by the visual system. Furthermore, Bentin and collaborators, using schematic stimuli for which the face-likeness is ambiguous, showed that the N170 amplitude increases only when participants are aware of the face-likeness of the stimuli (Bentin & Golland, 2002; Bentin, Sagiv, Mecklinger, Friederici, & von Cramon, 2002), supporting the view that this N170 *face-effect* reflects subjective perception of faces based on the activation of their neural representations in the visual system.

The inversion of natural faces enhances N170 amplitude and delays its latency (Bentin et al., 1996; Caharel, Bernard, Lalonde, Fiori, & Rebaï, 2006; Eimer, 2000a; de Haan et al., 2002; Itier et al., 2006; Rebaï et al., 2001; Rossion, Delvenne, Debatisse, Goffaux, Bruyer, Crommelinck, & Guérit, 1999; Rossion, Gauthier, Tarr, Despland, Bruyer, Linotte & Crommelinck, 2000; Rousselet et al., 2004), whereas the inversion of objects induces a smaller N170 latency delay while its amplitude is unchanged (Eimer, 2000c, Itier et al., 2006; Rossion et al., 2000, 2003; Rousselet et al., 2004). This N170 face inversion effect is generally explained by the fact that the disruption of configural/holistic information by inversion would slow down and increase the difficulty of face processing (Rossion et al., 1999, 2000, 2003; Rossion & Gauthier, 2002). In support of this interpretation, the global configuration of two-tone Mooney pictures (Mooney, 1956) leads to a face percept when presented upright, but because inversion disrupts the perception of this configuration they are no longer perceived as face-like when presented upside-down, as their local parts are too ambiguous to be perceived as face parts. As a consequence and contrary to natural faces, Mooney faces elicit a larger N170 when presented upright rather than upside-down (George, Jemel, Fiori, Chaby, & Renault, 2005; Latinus & Taylor, 2005). In summary, previous observations account for global/holistic processing of the configuration of upright faces or face-like stimuli indexed by a large N170 compared to non-face

object categories, while inverted stimuli induce a N170 face inversion effect (i.e. larger N170 amplitude with inversion) only when local features are also interpretable as face-like.

There is strong evidence supporting the view that the right hemisphere is dominant in holistic face perception (Hillger & Koenig, 1991; Sergent, 1988; Sergent, Ohta & MacDonald, 1992). For example, a recent fMRI study (Rossion, Dricot, Goebel & Busigny, 2011) using face-like stimuli such as Mooney faces and Arcimboldo paintings found reliable increased responses in the right “fusiform face area” (FFA; e.g., Kanwisher, McDermott & Chun, 1997) but not in the left FFA when the stimuli were presented upright and perceived as faces compared to the same stimuli presented upside-down and not perceived as faces. Moreover, the adaptation paradigm in ERPs has proven to be a particularly well-suited and powerful tool to investigate the nature of face representations during early stages of face processing. This consists of the presentation of an initial (adapting) face for several seconds followed shortly by a second (target) face leading to the reduction of the N170 amplitude after consecutive presentation of the same compared to a different facial identity (Caharel, d’Arripe, Ramon, Jacques, & Rossion, 2009; Caharel, Jiang, Blanz, & Rossion, 2009; Jacques d’Arripe, & Rossion, 2007). In this way, the observations of an ERP study indicate that holistic perception of individual faces involves the right hemisphere as early as 160 ms after stimulus-onset by using the so-called composite *face-effect*¹ (Jacques & Rossion, 2009). Thus, the right hemisphere appears to be specialized in holistic face perception at several levels of processing.

¹ The composite *face-effect* is a particularly persuasive illustration of holistic processing of individual faces in which the same top parts of faces are perceived as being slightly different when they are aligned with different bottom parts (Young, Hellawell, & Hay, 1987).

The main objective of the present study was to investigate the early visual processing of natural faces relative to other objects and face-like stimuli by means of the inversion paradigm. In particular, face-like stimuli were paintings by Giuseppe Arcimboldo (1527-1593) in which organizations of non-facial features, such as fruits, vegetables, and other objects, are perceived as a face. Contrary to Mooney stimuli which are two-tone (black and white) face images lacking interpretable local facial features and which can only be processed as a face at the global level, local features in Arcimboldo paintings are real objects and can be perceived as such. Hence, they can be processed globally as a face when presented upright, locally as objects when presented upside-down, providing a suitable control to disentangle high-level face-like or object-like visual processes during the N170 time-range. Furthermore, the comparison between natural faces and Arcimboldo portraits also provides a useful way to assess the respective contributions of global/holistic face processing and local face features processing on the functional properties of the N170, as face parts are absent in Arcimboldo portraits and local face processing would be recruited only with natural faces. We used in the present experiment an orientation discrimination task in order to focus participant's attention in the same way on each category of stimuli and avoid attentional bias to one specific category, in particular on natural human faces.

Our main hypothesis was that perceiving faces in Arcimboldo paintings should increase the N170 amplitude compared to objects, becoming more similar to the amplitude generated by natural faces. We also hypothesized that when faces are no longer perceived in inverted Arcimboldo paintings, as inversion disrupts holistic processing, the N170 amplitude should decrease to become more similar to the amplitude elicited by objects. In other words, inversion should increase the N170 amplitude for natural faces but decrease the one for Arcimboldo portraits. These expected effects depending on holistic/global processing (or not) of Arcimboldo paintings should appear mainly in the right rather than in the left hemisphere. In addition, because

the precise configuration of a natural human face is not respected in upright Arcimboldo paintings, they should be processed slower (measured by later N170 latencies and response times) than natural faces due to an increased difficulty in holistic processing. Because inversion increases the processing difficulty for natural faces, inverted natural faces should be processed more slowly (indexed by later N170 latencies and response times) than upright ones, and the difference between Arcimboldo paintings and natural faces should disappear when presented upside-down.

2. Material and Methods

2.1. Participants

Fifteen right-handed volunteers from 18 to 28 years of age (8 females; mean 22.5 ± 2.3) participated in the experiment. All participants had normal or corrected-to-normal visual acuity.

2.2. Stimuli

Three categories of stimuli, including natural human faces (without glasses or make-up, and with a neutral expression), Arcimboldo paintings, and familiar objects (car, house, chair, lamp, cup, etc.) were used (ten stimuli in each category, see Fig.1.A. for examples). All photographs were calibrated in levels of grey and equated for mean luminance (luminance values $\approx 12 \text{ cd/m}^2$) and size with Adobe® Photoshop® 7.0 software. All stimuli subtended approximately 2.8° to 3.7° of visual angle. Each stimulus was presented from two different orientations, either upright or inverted at 180° .

(Figure 1 about here)

2.3. Procedure

After electrode-cap placement, participants were seated in a light- and sound-attenuated room, at a viewing distance of 90 cm from a computer monitor. Stimuli were displayed at the center of the screen on a light grey background. At the start of each trial, a fixation point appeared in the center of the screen for 200 ms, followed by the presentation of the test stimulus for 1000 ms. The offset of the stimulus was followed by an inter-trial interval of about 1200 ms (randomized between 1000-1400 ms) (Fig. 1B). Participants performed a two forced-choice orientation discrimination task and gave their response by pressing one of two keys with their right hand (keys counterbalanced across participants). They were instructed to maintain eye gaze fixation to the center of the screen during the whole trial and to respond as accurately and as fast as possible. Participants performed 50 trials per condition (10 stimuli in each category repeated 5 times each in both orientations). Thus, a total of 300 trials was presented in a pseudo-random order (to avoid the immediate repetition of the same stimulus) in 5 experimental blocks (60 trials per block) with self-timed breaks taken in-between.

2.4. EEG recordings

Electroencephalographic activity was recorded from 32 surface electrodes according to the 10-20 classification system with a reference electrode placed in the fronto-central position (AFz). A common average reference was recalculated off-line. The EEG was amplified, digitized at a rate of 256 Hz, filtered (band-pass 0.1 Hz to 100 Hz), and stored with DeltamedTM software. Electrode impedance was kept below 5 K Ω . The EEG was continuously recorded along with codes synchronized to stimulus delivery for averaging sample epochs offline. The EEG was then segmented into 1250 ms epochs, including a 250 ms baseline before stimulus onset and a 1000

ms interval after stimulus onset for ERP averaging. ERPs were corrected relative to the 250 ms baseline. ERPs were then extracted by creating individual averages for each electrode and each condition. Only trials with correct responses were included in the averages and trials contaminated with ocular movements or artifacts ($> 100 \mu\text{V}$) were rejected. In the final phase, the data were digitally low-pass filtered with a cut-off of 48 Hz.

2.5. Data analyses

2.5.1. Behavior

Accuracy (percent correct) and mean correct response times (RTs) ranging between 200 and 1500 ms were computed for each condition and submitted to a repeated-measure analysis of variances (ANOVA) with *Category* (Natural faces, Arcimboldo portrait, Objects), and *Orientation* (upright vs. inverted) as within-subject factors.

2.5.2. Electrophysiology

Two visual ERP components were analyzed: the P1 (maximal at approximately 110 ms) and the N170 (maximal at approximately 164 ms). Peak amplitude and latency of both components were extracted automatically at the maximum amplitude value between 80 and 140 ms for the P1 and at the minimum amplitude value between 130 and 190 ms for the N170 at different pairs of occipito-temporal electrodes in the left and right hemisphere where they were the most prominent (for the P1: O1/2, and for the N170: P7/8, PO7/8). Amplitude and latency of the P1 and N170 were submitted to separate repeated-measure ANOVAs with *Category*, *Orientation*, *Hemisphere* (left vs. right), and *Electrode* (2 levels for the N170 only) as within-subject factors. Greenhouse-Geisser corrections were applied with adjusted degrees of freedom,

corresponding to the epsilon (ϵ) value and post-hoc comparisons were performed with the Tukey HSD test.

3. Results

3.1. Behavioral data

Participants performed the orientation discrimination task successfully, with an average accuracy level of 95.8%, but no significant effects of *Category* ($F(2,28)=.97$, $\epsilon=.76$, $p=.188$), *Orientation* ($F(1,14)=1.13$, $p=.31$) or the interaction between these two factors ($F(2,28)=.47$, $\epsilon=.77$, $p=.58$). In contrast, analyses performed on RTs revealed significant effects of *Category* ($F(2,28)=5.31$, $\epsilon=.76$, $p<.0197$), *Orientation* ($F(1,14)=10.51$, $p=.006$) and most importantly, a significant interaction between these two factors ($F(2,28)=6.41$, $\epsilon=.93$, $p<.006$). This interaction showed a significant effect of *Category* for upright ($F(2,28)=10.61$, $\epsilon=.57$, $p<.0039$) but not for inverted ($F(2,28)=0.40$, $\epsilon=.96$, $p<.664$) orientations. For upright orientations, RTs were faster for natural faces than Arcimboldo paintings and objects (respectively, $p=.001$, $p=.002$) and there was no difference between the latter two ($p=.98$). This interaction also revealed faster RTs for upright than inverted orientations for natural faces ($p<.001$) but not for Arcimboldo paintings ($p=.52$) or objects ($p=.79$). RTs for each category depending on orientation are presented in Table 1.

(Table 1 about here)

3.2. Electrophysiological data

3.2.1. P1 component

In terms of latency, no effect was found for *Category* ($F(2,28)=2.12$, $\epsilon=.83$, $p=.15$), *Orientation* ($F(1,14)=1.55$, $p=.23$), or the *Category* x *Orientation* interaction ($F(2,28)=.74$, $\epsilon=.81$,

$p=.46$). Null results were also obtained on P1 amplitude for *Category* ($F(2,28)=1.49$, $\epsilon=.98$, $p=.24$), *Orientation* ($F(1,14)=.04$, $p=.84$), or the *Category* x *Orientation* interaction ($F(2,28)=1.65$, $\epsilon=.98$, $p=.251$). The absence of any effects on the earlier visual P1 component is consistent with the assumption that the P1 reflects the processing of low-level physical properties (contrast, luminance, spatial frequency, color) (Halgren et al., 2000; Rossion & Caharel, 2011; Rossion & Jacques, 2008; Tanskanen et al., 2005). Thus, these results suggest that the effects observed on the subsequent N170 component cannot be driven by low-level differences between conditions.

3.2.2. N170 component

Main effects of *Category* ($F(2,28)=12.16$, $\epsilon=.88$, $p=.0003$) and *Orientation* ($F(1,14)=7.59$, $p=.015$) were found for the N170 latency. In addition, there was a significant *Category* x *Orientation* interaction ($F(2,28)=4.09$, $\epsilon=.74$, $p=.042$) (Fig. 2). For upright orientations, N170 latency to natural faces was shorter relative to Arcimboldo paintings ($p<.027$) and objects ($p<.039$), but did not differ between the latter two ($p=.77$) ($F(2,28)=12.97$, $\epsilon=.85$, $p=.0003$). For inverted orientations, the *Category* factor showed only a trend ($F(2,28)=3.51$, $\epsilon=.73$, $p=0.07$). This *Category* x *Orientation* interaction revealed also that the N170 was delayed with the inversion of natural faces ($p<.0001$), but not with Arcimboldo pictures ($p=.417$) or objects ($p=.481$) (Fig. 4). There was no other significant effect on the N170 latency (all $p > .05$).

(Figure 2 about here)

With respect to the N170 amplitude, the *Category* factor was significant ($F(2,28)=85.53$, $\epsilon=.95$, $p<.0001$) and interacted with *Orientation* factor ($F(2,28)=19.81$, $\epsilon=.69$, $p<.0001$).

However, and most interestingly, these effects on N170 amplitude were qualified by a significant interaction between *Category*, *Orientation* and *Hemisphere* ($F(2,28)=3.80$, $\varepsilon=.98$, $p<.035$).

In the right hemisphere, the *Category* x *Orientation* interaction was significant ($F(2,28)=20.32$, $\varepsilon=.70$, $p<.0001$), as the N170 amplitude for upright orientations was larger for natural faces and Arcimboldo paintings than for objects (respectively, $p=.0002$ and $p=.0008$) with no difference found between natural faces and Arcimboldo paintings ($p=.805$) (*Category* effect: $F(2,28)=27.29$, $\varepsilon=.94$, $p<.0001$). However, for inverted orientations, the N170 was larger for natural faces than Arcimboldo portraits ($p=.00013$) and objects ($p=.00012$) with no significant difference between the latter two ($p=.195$) (*Category* effect: $F(2,28)=60.58$, $\varepsilon=.72$, $p<.0001$) (Figs. 2 and 3). This interaction between *Category* and *Orientation* in the right hemisphere also revealed an increase in amplitude with inversion of natural faces ($p=.0011$) but a decrease in amplitude with inversion of Arcimboldo paintings ($p=.0048$) and no change in amplitude with inversion of objects ($p=.114$) (Fig. 4).

(Figure 3 about here)

In the left hemisphere (*Category* x *Orientation* interaction: ($F(2,28)=7.95$, $\varepsilon=.91$, $p=.003$), the N170 amplitude for upright orientations was larger for natural faces than for Arcimboldo portraits ($p=.047$) and larger for these categories than for objects (respectively, $p<.001$; $p=.007$) (*Category* effect: $F(2,28)=23.57$, $\varepsilon=.91$, $p<.0001$). For inverted orientations, the N170 amplitude was larger for natural faces than Arcimboldo portraits ($p=.0003$) or objects ($p<.0001$) with no difference detected between the latter two ($p=.142$) (*Category* effect: $F(2,28)=34.13$, $\varepsilon=.78$, $p<.0001$) (Figs. 2 and 3). A significant *Orientation* effect was observed only for natural faces ($p=.0013$), not for Arcimboldo portraits ($p=.373$) or objects ($p=.797$) (Fig. 4).

(Figure 4 about here)

4. Discussion

The main objective of the present study was to explore early visual processing of natural faces relative to objects and face-like stimuli represented by Arcimboldo paintings in which the global organizations of non-facial objects (fruits, vegetables, books, etc.) are perceived as a face. The use of these stimuli allowed dissociating high-level face-like or object-like visual processes, specifically to dissociate the respective contributions of the global/holistic processing of face configurations and the local processing of face features. It also permitted the assessment of the involvement of each hemisphere in both types of processing during the N170 temporal window.

At the behavioral level, our results showed that the orientation discrimination task was performed successfully for each category. However, orientation discrimination was faster for natural faces than for objects and Arcimboldo portraits in upright orientations. Moreover, this effect disappeared in upside-down orientations, given an inversion effect (longer RTs with inversion) observed only for natural faces. These data corroborate those of numerous studies showing that face processing was more drastically disturbed by inversion than various object categories through a wide variety of tasks, such as an orientation detection task (Itier et al., 2006), a categorization task (Rousselet et al., 2003) or a recognition task (Diamond & Carey, 1986; Yin, 1969). This finding has been considered to be the hallmark of face configural processing, more disrupted by inversion than other object processing (Yin, 1969). However, in a face/non-face detection task, Latinus and Taylor (2006) reported behavioral inversion effects for natural human faces as well as schematic, and Mooney faces. The type of task used in this study might have increased attentional bias to faces and might explain these disparities in the results.

Interestingly, our RT results mirrored those observed for the N170 latency, as natural faces were processed earlier than objects or Arcimboldo paintings in the upright orientation, but

not in the inverted one, since the N170 latency was delayed only with inverted natural faces. The latency delay of the N170 is generally found when the stimulus does not fully fit with an upright natural face template for which humans have an extensive expertise, such as inverted faces (e.g., Bentin et al., 1996; Caharel et al., 2006; Eimer, 2000a; de Haan et al., 2002; Itier et al., 2006; Rebaï et al., 2001; Rossion et al., 1999; Rousselet et al., 2004), misaligned face halves (Jacques & Rossion, 2010; Letourneau & Mitchell, 2008), scrambled facial features (Caharel et al., 2006; George, Evans, Fiori, Davidoff, & Renault, 1996; Zion-Golumbic and Bentin, 2007), presentation of eyes alone or faces without eyes (e.g., Bentin et al., 1996; Eimer, 1998; Itier et al., 2006; Itier, Alain, Sedore, & McIntosh, 2007), but also when the precise configuration of a human face is not respected (see Carmel & Bentin, 2002; Latinus & Taylor, 2006; Sagiv & Bentin, 2001 for similar results with other face-like stimuli). According to Perrett and collaborators, the most convincing interpretation of this effect is that neurons in the ventral visual stream accumulate evidence that a face is presented more slowly if the stimulus is transformed, as they observed delayed response of face-selective neurons to inverted faces in the monkey infero-temporal cortex (Perrett, Mistlin, Chitty, Smith, Potter, Broennimann, & Harries, 1988). Likewise, intracranial EEG recordings in the brain of epileptic patients showed a significant delay of the intracranial N170 over the middle fusiform gyrus in response to inverted faces (Rosburg, Ludwig, Dimpelmann, Alba-Ferrara, Urbach, & Elger, 2010). Hence, whereas Arcimboldo paintings are perceived as faces in the upright orientation, the visual system categorizes them more slowly than natural faces (as indexed by the N170 latency delay) since they do not entirely fit with a natural face template.

Concerning the right hemisphere and concordant with our main assumptions, the N170 amplitude did not differ between natural faces and Arcimboldo portraits, but both were larger than the one generated by objects in upright orientations. These results extend those where no differences were found in N170 amplitudes for faces under different formats (natural, painted,

schematic, and animal) (e.g., Carmel & Bentin, 2002; Itier et al., 2006; Latinus & Taylor, 2006; Rousselet et al., 2004; Sagiv & Bentin, 2001), confirming that the N170 component reflects the involvement of a mechanism triggered by every stimulus sharing the same configuration as a face (Carmel & Bentin, 2002; Sagiv & Bentin, 2001). In particular, because Arcimboldo portraits consist of non-face objects, our results indicate that they are initially processed holistically on the basis of their global face configuration rather than as objects.

The inversion effects for each category in the right hemisphere support and refine this interpretation. As generally observed, the N170 amplitude was larger only with inversion of natural faces (Bentin et al., 1996; Caharel, Bernard, Lalonde, Fiori, & Rebaï, 2006; Eimer, 2000a; de Haan et al., 2002; Itier et al., 2006; Rebaï et al., 2001; Rossion et al., 2000; Rousselet et al., 2004). Two main interpretations have been proposed to explain this paradoxical effect. Inverted faces may be less efficiently processed in face-selective infero-temporal areas with large receptive fields, leading to an increased activation in more posterior lateral occipital areas with smaller receptive fields (e.g., Rossion et al., 2000). One may also hypothesize that when faces are presented upright, only face-selective neurons involved in global face configuration respond, but when faces are presented upside-down, eye-selective neurons are necessary and respond as well (Itier et al., 2007). Thus, larger N170 amplitudes following inversion are observed only when local features contain facial cues and lead to face perception. Both interpretations consider that activation of neural representations of global face configurations is sufficient for processing upright faces, whereas the processing of inverted faces requires the activation of finer local representations of the features.

In support of this view, and similarly to the reduced N170 amplitude found with inverted Mooney faces (George et al., 2005; Latinus & Taylor, 2005), our results showed that the inversion of Arcimboldo paintings decreased the N170 amplitude. This effect indicates impaired

detection of these portraits as faces following inversion, because holistic processing cannot extract a global face format, allowing analysis of their local parts (the so-called analytic processing) in a manner similar to that of objects. Indeed, for inverted orientations, the N170 amplitude in the right hemisphere did not significantly differ between Arcimboldo paintings and objects, both reduced relative to natural faces. Moreover, no inversion effect on the N170 amplitude was found for objects (Bentin et al., 1996; Eimer, 2000a,b; Rebaï et al., 2001; Rossion et al., 2000), suggesting that these stimuli involve the processing of local parts in both orientations.

In sum, our results in the right hemisphere showed that due to a face holistic processing, Arcimboldo portraits involve face-like processing in the upright orientation, but object-like processing in the inverted one. They also indicate that the processing of upright faces only allows the extraction of the global face configuration irrespective of local features (face parts or object parts), and they tend to support the view (Itier et al., 2007; Rossion et al., 2000) that face-like processing of inverted stimuli is attributed to the recruitment of additional local features, made possible only with the presence of local face parts.

In the left hemisphere, the N170 amplitude was larger in response to natural faces than Arcimboldo paintings for upright orientations, suggesting that the left hemisphere is less implicated in the holistic processing of faces than the right. This result supports the view that the left hemisphere is specialized in analytic processing of local features of the face (Hillger & Koenig, 1991; Sergent, 1982). In other words, because local face parts are absent in Arcimboldo portraits, local cues must be interpreted as face-like to generate a N170 *face-effect* in the left hemisphere. Hence, the decreased N170 for Arcimboldo portraits might be explained by the involvement of object processing constituting these stimuli, such as for the reduced N170 amplitudes observed with objects compared to faces (Bentin et al., 1996; Eimer, 2000a, 2000b;

Rebaï et al., 2001; Rossion et al., 2000). However, we found larger amplitudes for upright Arcimboldo faces than upright objects, suggesting a residual holistic face-like process. As a consequence, during upright presentation, the left hemisphere might not be exclusively involved in the processing of face parts (absent in Arcimboldo portraits) but also in the processing of global face formats, perhaps through communication with the right hemisphere as previously indicated for face identity and/or expression processing on the basis of behavioral experiments (Compton, 2002), and recently confirmed for face identity with functional neuroimaging (Verosky & Turk-Browne, 2012) and ERPs (Godard, Leleu, Rebaï & Fiori, in press).

For inverted orientations, the difference between Arcimboldo paintings and objects disappeared in the left hemisphere, explained by a small (but not significant) decrease of the N170 amplitude with inversion of Arcimboldo paintings but not for objects. This time, Arcimboldo paintings might be processed in the same fashion as objects with no residual holistic face-like processing because the global face configuration cannot be processed in the case of inverted stimuli. Moreover, the inversion effect was significant for natural faces (larger N170 amplitude with inversion), corroborating the necessity of implementing an additional processing to observe this effect in both hemispheres, as more local and finer representations must be extracted to process faces presented upside-down (Itier et al., 2007; Rossion et al., 2000). In summary, these observations reinforce the view that the left hemisphere is involved relatively more in the processing of local rather than global face cues (Hillger & Koenig, 1991; Sergent, 1982).

5. Conclusions

In conclusion, the present study indicates modulations of the face-sensitive N170 component in response to Arcimboldo paintings attributable to different processes depending on

orientation and hemisphere: holistic processing for upright Arcimboldo paintings resulting in a face-like N170 effect especially in the right hemisphere, and local parts (analytic) processing for inverted ones accounted by an object-like N170 effect in both hemispheres. Because Arcimboldo paintings are perceived as faces in the upright orientation due to the global face configuration, but perceived from various objects that constitute these stimuli in the inverted orientation, this study provides a useful control for the understanding of high-level visual processes at the level of the N170. In particular, our observations support the view that the N170 ERP component is the first electrophysiological index of the activation of a global/holistic face representation in the human brain (Rossion & Jacques, 2011) as well as the first component showing dominance of the right hemisphere in holistic face perception (Hillger & Koenig, 1991; Rossion et al., 2011; Sergent, 1988; Sergent et al., 1992).

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Figure Captions

Figure 1. (A) Examples of the three categories of stimuli used in the experiment, and (B) timeline of the stimulus presentation during one trial.

Figure 2. Grand average ERP waveforms elicited by the three categories of stimuli in upright (top) and inverted (bottom) orientations at left and right pooled occipito-temporal electrode sites (waveforms averaged for electrodes P7/8, PO7/8) where the N170 components peaked maximally.

Figure 3. Peak amplitude of the N170 component measured at left and right pooled occipito-temporal electrode sites (averaged for electrodes P7/8, PO7/8) displayed for all three categories in upright (top) and inverted (bottom) orientations (* $p < .05$; n.s = non-significant result).

Figure 4. Grand average ERP waveforms recorded at right and left pooled occipito-temporal electrode sites (waveforms averaged for electrodes P7/8 and PO7/8) showing the inversion effect for all three categories.

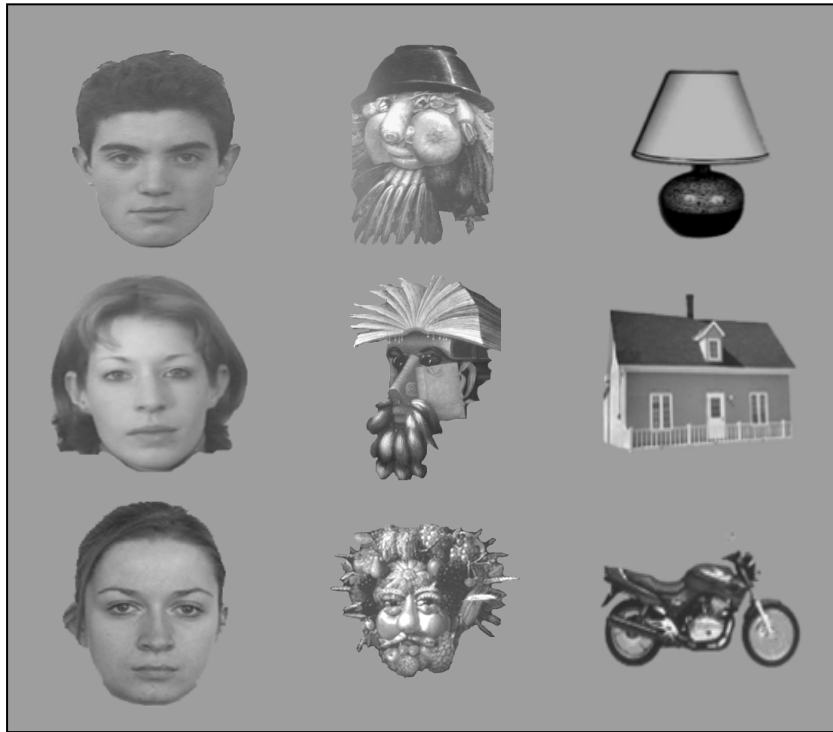
Table 1

Mean reaction times in ms (\pm SE) for each category and orientation.

	Natural faces	Arcimboldo paintings	Objects
Upright	619.49 \pm 20.16	711.87 \pm 19.56	707.35 \pm 18.01
Inverted	701.20 \pm 32.20	720.89 \pm 24.47	712.59 \pm 16.37

Figure 1

A



B

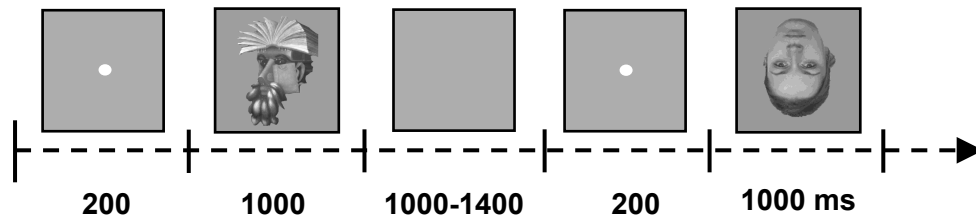
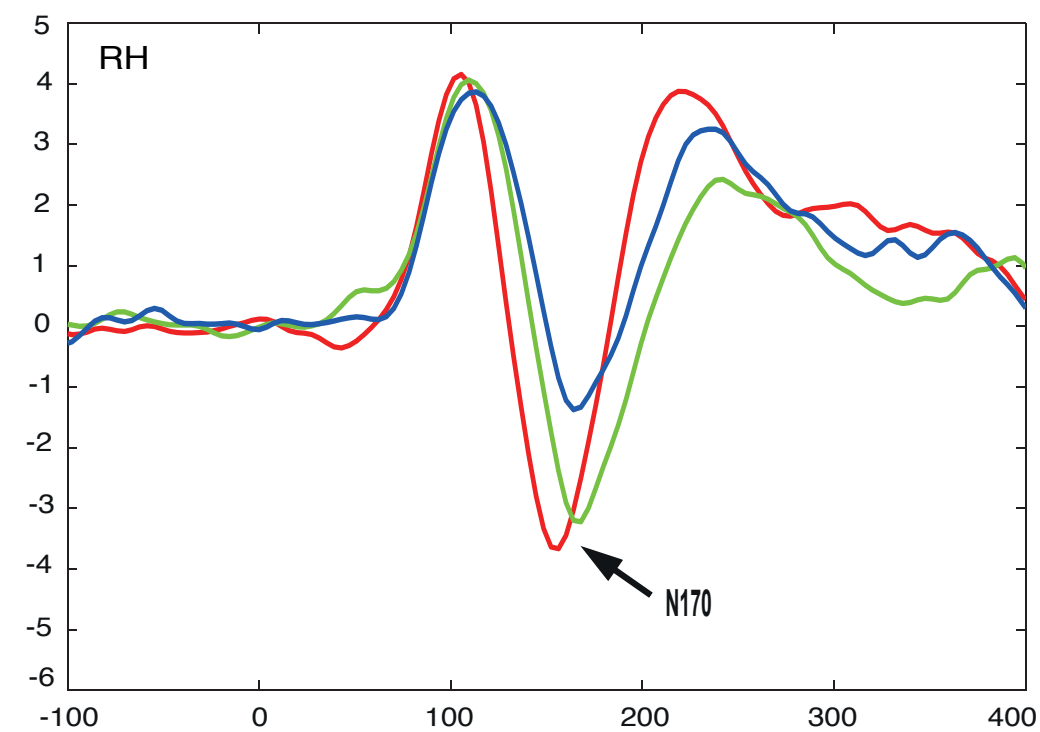
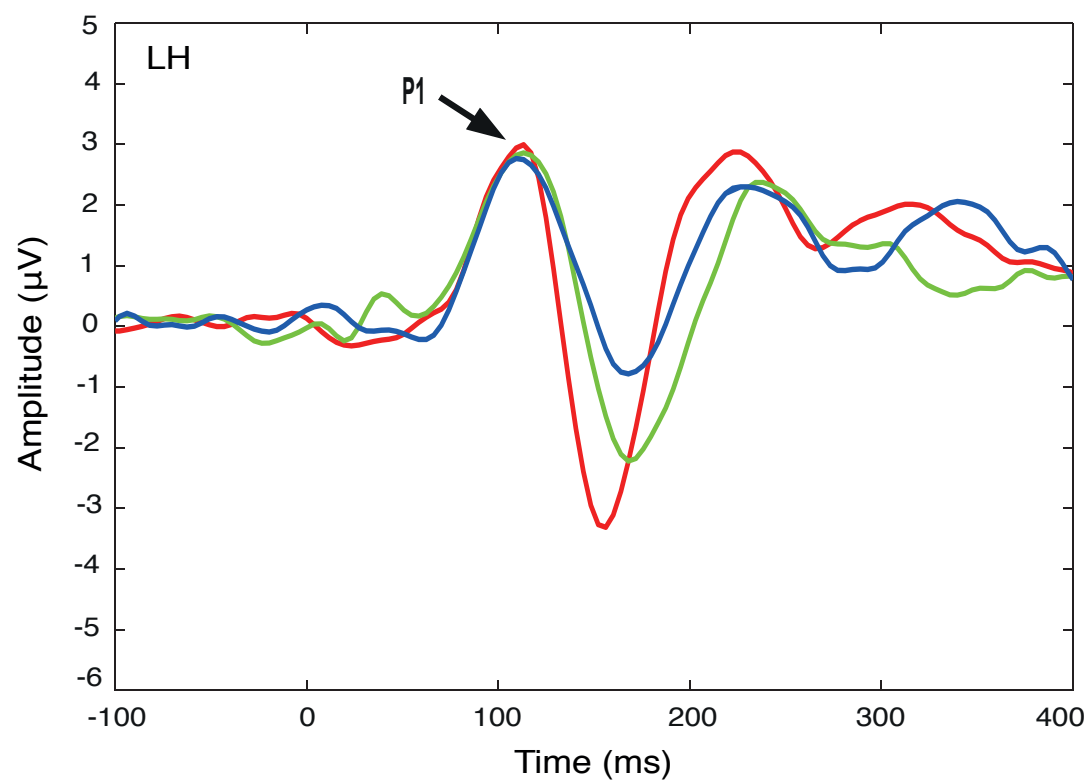


Figure 2

Upright orientations



Inverted orientations

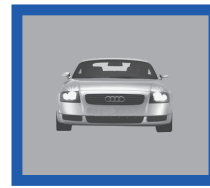
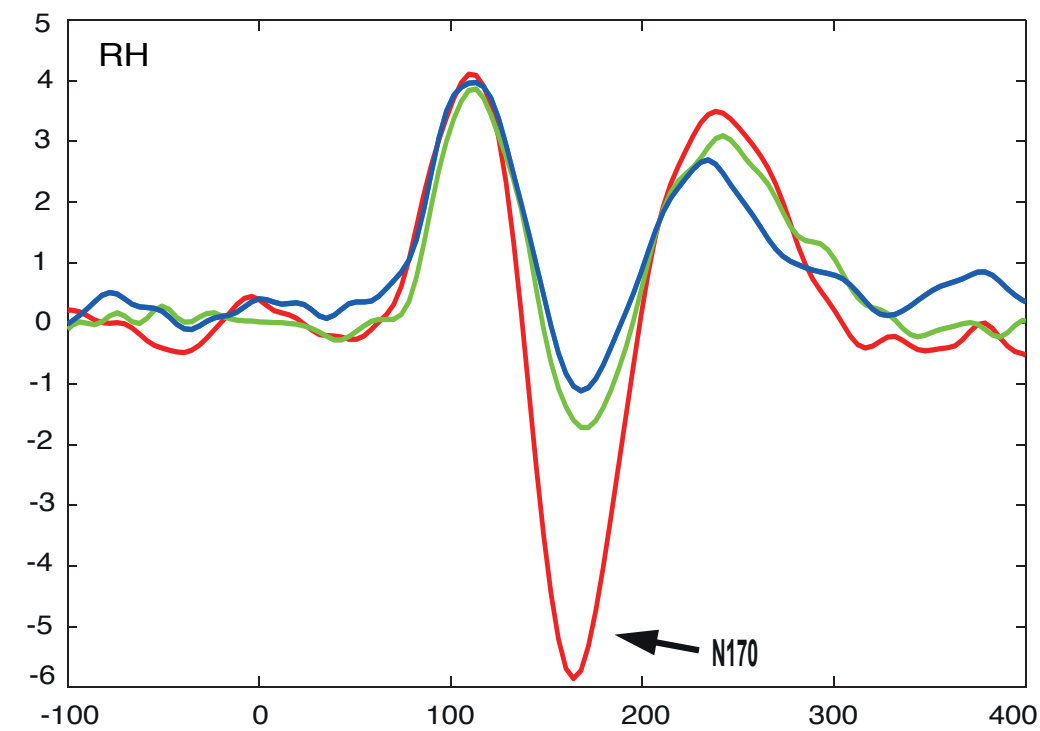
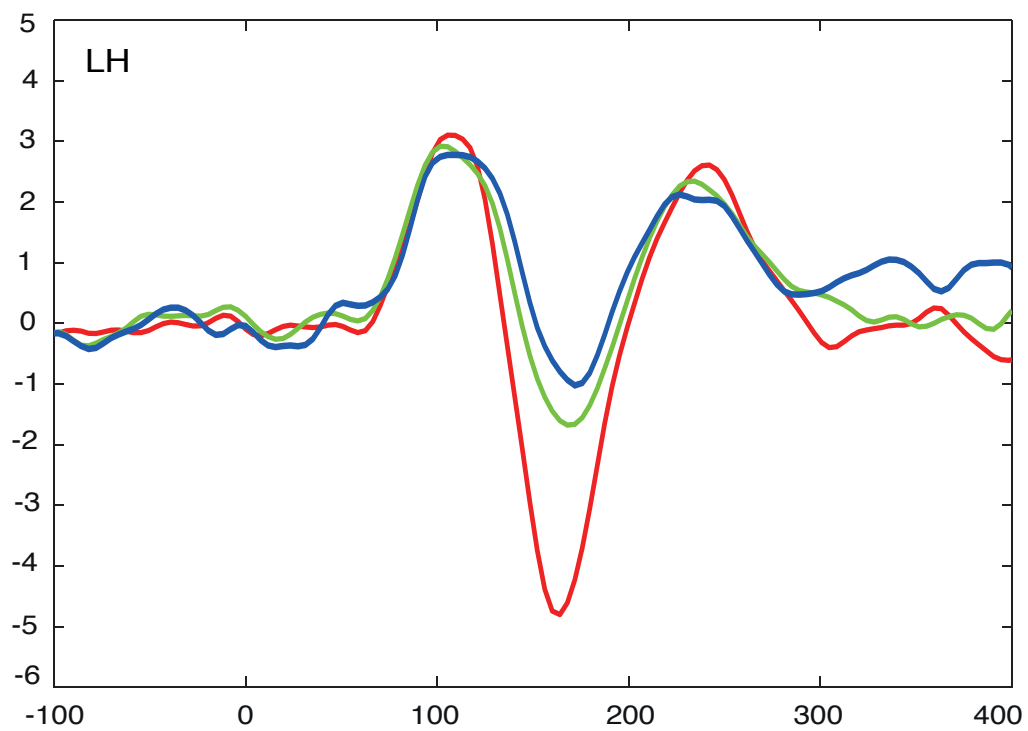
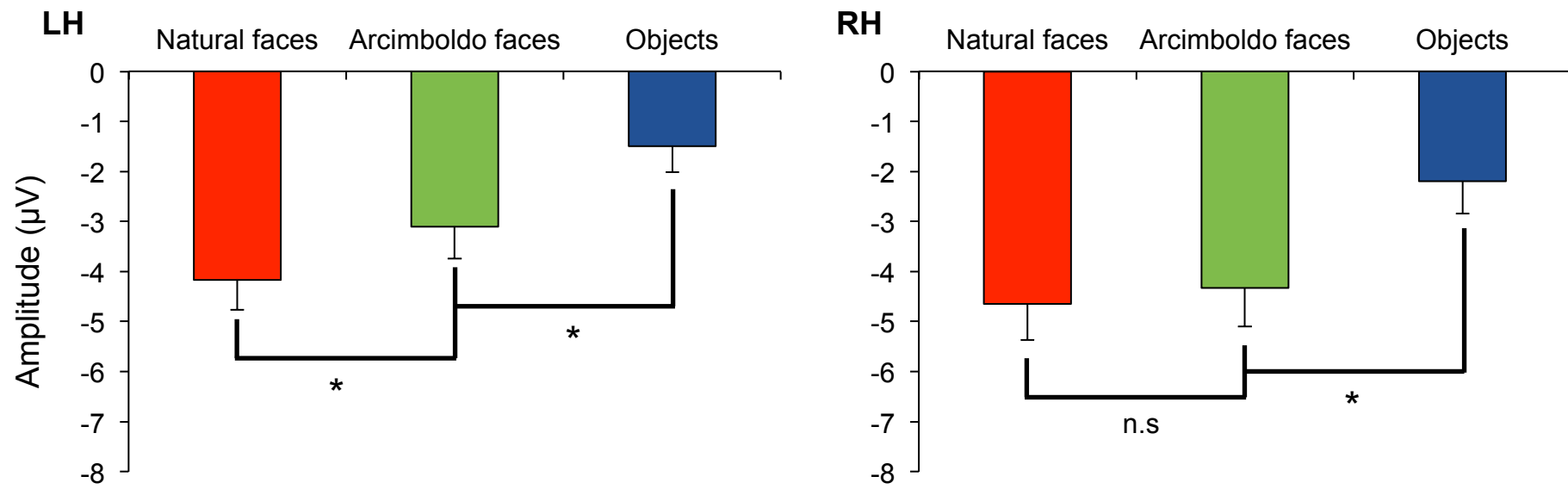


Figure 3

Upright orientation



Inverted orientation

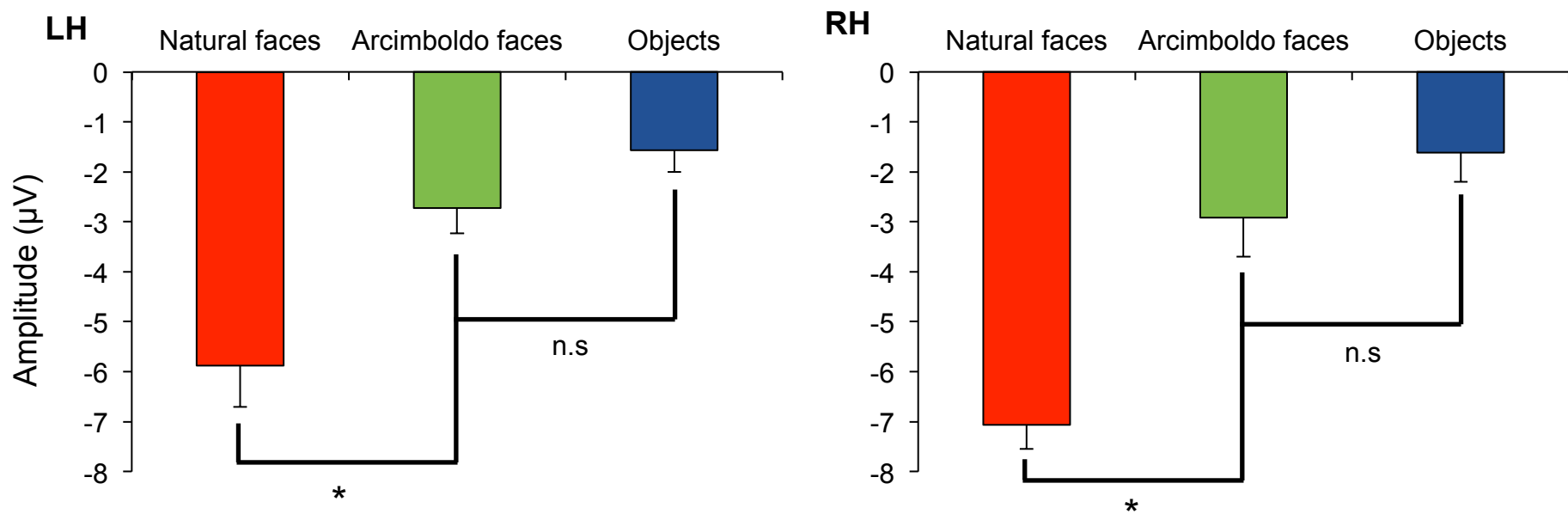


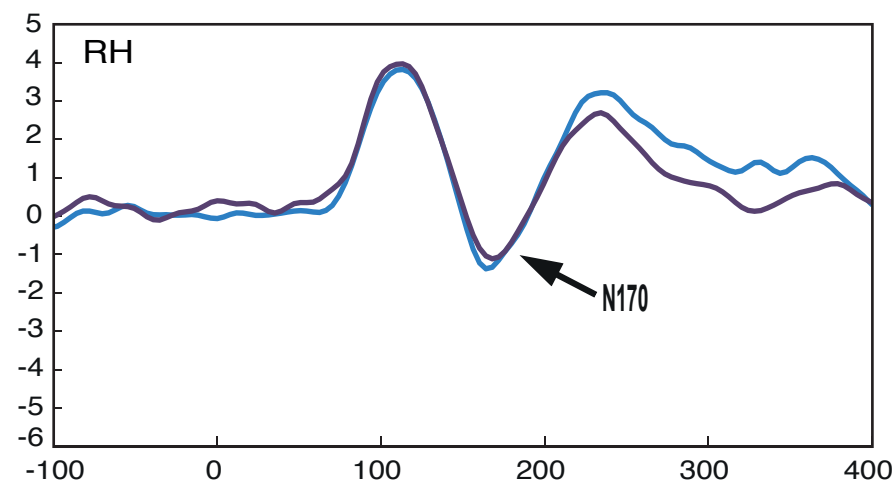
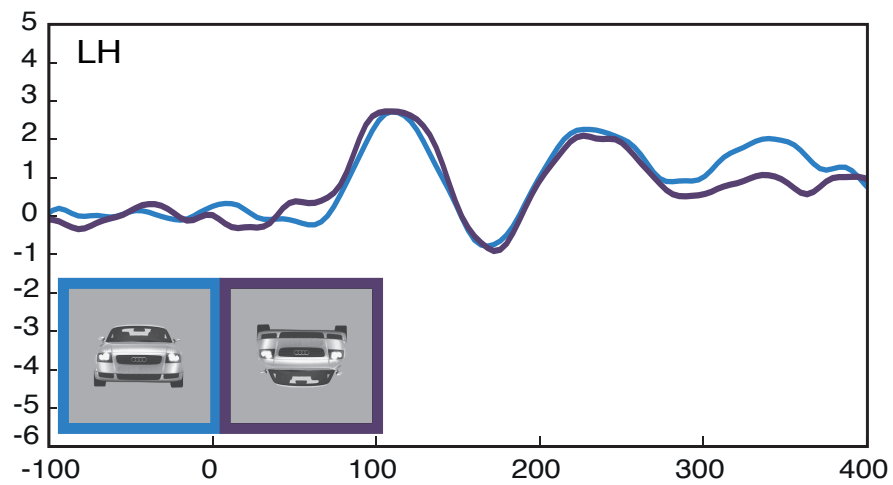
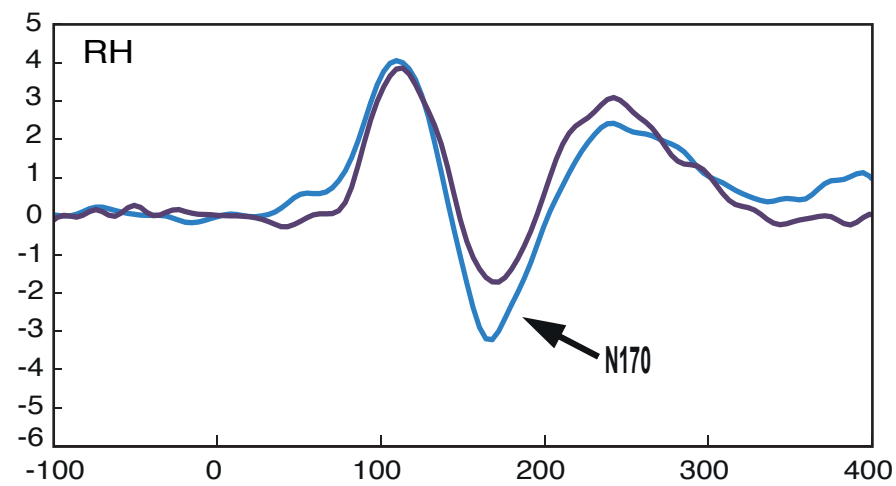
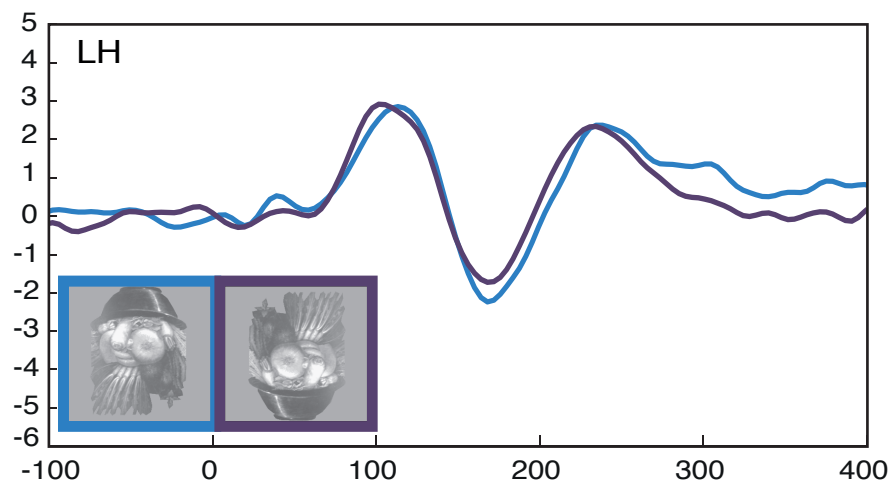
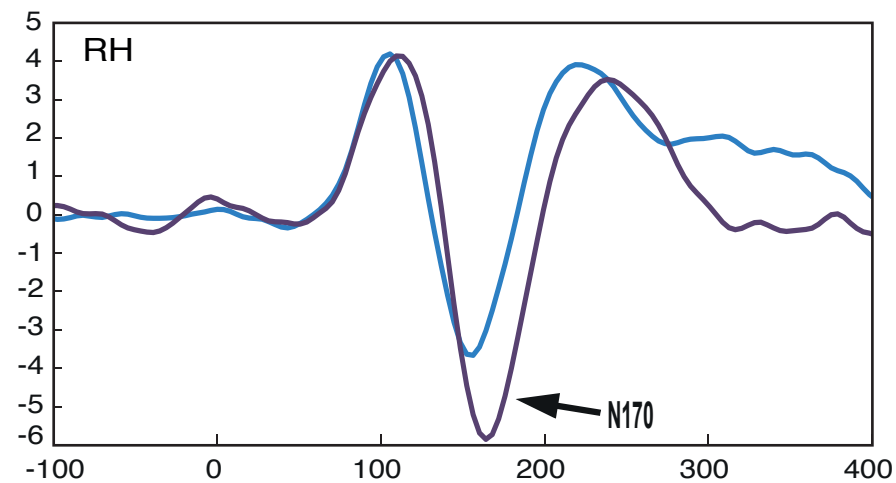
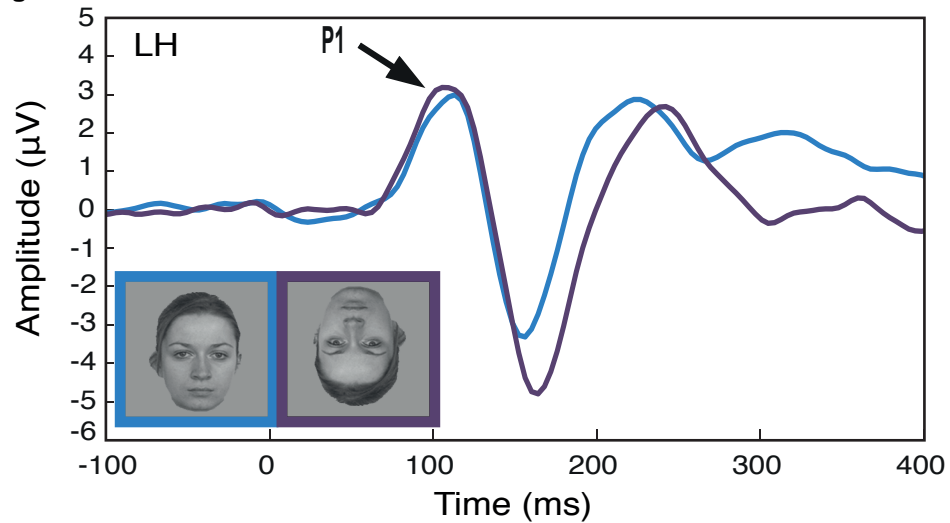
Figure 4

Figure 2 black & white

[Click here to download Supplementary Material: Fig2_NB.pdf](#)

Figure 3 black & white

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Figure 4 black & white

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