Contrasting hemispheric asymmetries for emotional processing from event-related potentials and behavioural responses

Giulia Prete[1*], Paolo Capotosto[2,3], Filippo Zappasodi[2,3] and Luca Tommasi[1]

[1] Department of Psychological Science, Health and Territory, 'G. d'Annunzio' University of Chieti-Pescara, Italy

[2] Department of Neuroscience, Imaging and Clinical Science, 'G. d'Annunzio' University of Chieti-Pescara, Italy

[3] Institute for Advanced Biomedical Technologies, 'G. d'Annunzio' University of Chieti-Pescara, Italy

* Corresponding author:

Giulia Prete

BLOCCO A, Via dei Vestini 31

I-66013 Chieti, Italy

e-mail: giulia.prete@unich.it

Tel.: +39 871 3554216

Fax: +39 871 35542163

Abstract

Objective: Four main theories concerning hemispheric asymmetries for emotional processing have been proposed: the Right Hemisphere Hypothesis (RHH: the right hemisphere is specialized in processing all emotions), the Valence Hypothesis (VH: the left/right hemisphere is superior in positive/negative emotion processing, respectively), the Modified Valence Hypothesis (MVH: the right-hemispheric superiority at posterior sites is followed by a valence specific activity at frontal sites), and the Motivational Model (MM: the left/right hemisphere is superior in approaching-related/avoidance-related emotions, respectively).

Method: In a divided visual field paradigm, we presented happy and angry faces to 16 healthy participants, either unilaterally or bilaterally, in order to test the aforementioned theories.

Results: Behavioural results provided support for the VH and correlational analysis revealed that handedness influences the rightward bias for positive emotions. The amplitude of P1, N170 and P2 ERP components at parietal sites (selected by means of topographic maps) was larger in the right than in the left hemisphere, independently of the emotional expression of the stimuli, supporting the RHH. At frontal sites, no asymmetry was found in bilateral conditions, whereas in unilateral conditions a mixed pattern of hemispheric asymmetries emerged.

Conclusions: We conclude that there is no correspondence between behavioural and electrophysiological results concerning asymmetries for emotion processing, and that the VH and the RHH are not mutually exclusive.

Keywords: Event-related brain potentials; Emotions; Hemispheric asymmetries; Divided visual field; Faces.

Running title: Hemispheric asymmetries for emotional faces

Public Significance Statements:

We investigated cerebral asymmetry for positive and negative emotions (happiness and anger), due to the central role of emotions in everyday life. The results revealed that negative emotions are mainly processed in the right hemisphere. Concerning positive emotions, electrophysiological results confirmed a right-hemispheric superiority, whereas our behavioral findings showed a left-hemispheric superiority, which was stronger in participants with a stronger right hand preference. We conclude that hand preference can influence the hemispheric asymmetries for positive emotions.

Introduction

Different neural structures are involved in the processing of facial emotions, to be the fusiform gyrus and the superior temporal sulcus for face perception (Haxby, Hoffman & Gobbini, 2000), and the amygdala and the orbitofrontal cortex for emotional content (Pessoa & Adolphs, 2010). Event Related Potentials (ERPs) have shown that emotional faces, compared to neutral faces, trigger a sustained positivity with a broad frontoparietal scalp distribution and an enhanced negativity over lateral posterior areas (Eimer & Holmes, 2002, 2007; Batty & Taylor, 2003; Eimer, Holmes & McGlone, 2003; Prete et al., 2015a). These different ERP components have been interpreted as reflecting distinct stages in the processing of emotional expressions: the early positive component (P1) has been associated to the mechanisms involved in the very rapid detection of emotions (Eimer & Holmes, 2002), and a later positivity (P2) has been suggested to reflect the subsequent processing of emotional faces at a higher-order stage. Between these two positive peaks, a negative component triggered around 130-200 ms post-stimulus (often called N170) has been shown to be related to facial processing, independently of the specific emotional content (Eimer & Holmes, 2002).

A critical point in the literature concerning the cerebral correlates of emotion processing is that of hemispheric asymmetries: two main hypotheses have been proposed, among others, and both have received support from several studies (see Fusar-Poli et al., 2009, for a meta-analysis). The Right Hemisphere Hypothesis (RHH) suggests that the right hemisphere is superior than the left hemisphere in emotional processing (Gainotti, 2012). The Valence Hypothesis (VH) proposes that the right hemisphere is more involved in processing negative emotions, and that the left hemisphere is superior in processing positive emotions (Baijal & Srinivasan, 2011). The Modified Valence Hypothesis (MVH) reconciles the two positions by proposing posterior right-hemispheric superiority for all emotions, followed by a frontal valence-specific involvement (Davidson, 1984; Killgore & Yurgelun-Todd, 2007). An additional point of view is the Motivational Model (MM, Poole & Gable, 2014), according to which the frontal asymmetry is not attributable to the emotional valence of the stimuli, but is dependent upon a motivational account, with a left-hemispheric involvement in approach-related stimuli (e.g., happiness: positive valence, but also anger: negative valence), and a right-hemispheric involvement in withdrawal-related stimuli (e.g., fear; Angus & Harmon-Jones, 2016; Harmon-Jones, Gable, & Peterson, 2010). A new viewpoint has been proposed by Shobe (2014) who reviewed a number of studies showing that both hemispheres process all emotions but at different levels. According to this model the right hemisphere is specialized in perception and detection of all (positive and negative) emotions at a basic level. The left hemisphere shows a bias for positive stimuli, and it is specialized in higher level interpretation of all emotional stimuli, once processed by the right hemisphere. In this perspective, the left hemisphere may direct the response to the emotional stimuli, but this process requires the right-hemispheric basic emotional interpretation.

These different models have been alternatively supported, by both behavioural and electrophysiological/neuroimaging studies, so much so that differential hemispheric contributions have been highlighted. Starting from the knowledge of the contralateral projections in the human visual system, hemispheric superiority for emotional detection has been investigated at a behavioural level by means of the divided visual field paradigm. In this paradigm, an image is presented in one visual hemifield for a period shorter than that needed to act a saccade (about 150 ms: tachistoscopic presentation) and the observer is asked to gaze ahead, so that the stimulus directly reaches the contralateral hemisphere (left visual field/right hemisphere and *vice versa*). Based on this assumption, emotional stimuli can be presented tachistoscopically either in one hemifield, or in the two hemifields simultaneously, in order to investigate how each hemisphere processes emotions, by asking participants to detect their emotional content. Each of these paradigms has been used with emotional stimuli (e.g., images of angry and happy faces). It has been found that when only one emotional face is tachistoscopically presented in one visual field, the emotional judgments of participants provide support for the VH, positive emotions being better recognized when presented in the right visual field (RVF), and negative emotions being better recognized when presented in the left visual field (LVF; Prete et al., 2014, 2015c). However, when two emotional faces with positive/negative emotions are simultaneously presented in the LVF/RVF, the emotional judgments of participants are mainly driven by the emotional expression presented in the LVF, thus supporting the RHH (Prete et al., 2015b,c). By using a similar lateralized presentation, different results have been collected. For instance, Torro-Alves and colleagues (2011) asked participants to recognize a target emotion in a paradigm in which the target and a distracting expression were simultaneously presented. The authors found that emotional targets were better and faster recognized when presented in the LVF, supporting the RHH. In contrast with this result, by using a similar paradigm Jansari et al. (2011) found that positive emotions were better recognized when presented in the RVF and negative emotions were better recognized when presented in the LVF, supporting the VH. Tamietto and colleagues (2007) exploited both unilateral and bilateral presentations of emotional faces and asked participants to detect a target complex emotion. They failed to find hemispheric asymmetries in either paradigm, and they found a better performance in both accuracy and reaction times in bilateral displays with two emotionally congruent faces, proposing that inter-hemispheric cooperation occurs during the processing of complex emotions. Compton and colleagues (2005) presented two different emotional expressions in the upper portion of the left and right visual field, and participants were asked to respond whether the emotional expression of a third face presented in the lower portion of one visual hemifield matched either of the top two faces. Both accuracy and reaction times showed an across-field advantage for angry and happy faces, but not for neutral faces. The authors concluded that subcortical pathways may be responsible for the enhanced inter-hemispheric emotional processing. Finally, Reuter-Lorenz and colleagues (1983) presented emotional and neutral faces in the two hemifields and asked participants to identify the side containing the emotional stimulus. They found that right-handed participants were faster when happy faces were presented in the RVF and when sad faces were presented in the LVF, whereas the opposite pattern was found in left-handers, showing that hemispheric asymmetries for emotional faces are dependent upon handedness (see Casasanto, 2009).

Electrophysiological evidence appears mixed: in an ERP study, Laurian and colleagues (1991) found a stronger right centroparietal activity when participants were required to classify emotional faces (with positive or negative expression) and neutral faces presented centrally, showing a right-hemispheric involvement across all emotions and thus supporting the RHH. However, Angus and Harmon-Jones (2016) have recently reviewed a number of studies supporting the MM, starting from evidence concerning alpha asymmetry. Specifically, the authors highlighted a right-hemispheric involvement in withdrawal-related emotions (e.g., fear: negative valence, withdrawal-related), and a left-hemispheric involvement in approach-related emotions (e.g., anger: negative valence, but approach-related). Nevertheless, Baijal and Srinivasan (2011), examining the N1 component, found that when emotional stimuli are presented either in the LVF or in the RVF, the right hemisphere is more involved in processing negative valence (sad expression), thus supporting the VH. In a fMRI study, Killgore and Yurgelun-Todd (2007) exploited the paradigm of chimeric faces (stimuli constituted of a happy or a sad hemiface juxtaposed to a neutral hemiface) in order to present an emotional expression only in one hemifield, and they found support for the MVH. The authors found a right-hemispheric activity in posterior areas for both positive and negative emotional stimuli, together with a valence-specific frontal activity - the anterior regions of the left hemisphere being more involved in positive emotional processing, and the anterior regions of the right hemisphere being more involved in negative emotional processing. Finally, in a recent ERP study (Prete et al., 2015a), a posterior right-hemispheric superiority was found at parieto-occipital sites, but no asymmetrical activation at frontal sites, during the central presentation of faces containing subliminal emotional expressions.

The behavioural results described insofar seem to suggest that the unilateral or bilateral presentation of expressions is a possible key to explain the different patterns of cerebral asymmetries for emotions. To our knowledge, however, no previous electrophysiological study has taken into consideration the issue of the number of emotional stimuli presented at once in the two visual fields, considering that in the majority of studies emotional stimuli are presented in the center of the visual field. The aim of the present study is to compare the theories of hemispheric superiority in emotion processing, using unilateral and bilateral presentation of positive and negative emotional faces. To disentangle the possible effect of the valence/motivational account on cerebral asymmetries, we chose to use anger as the negative expression and happiness as the positive expression. We did not insert in the stimuli set the neutral expression or other emotional expressions because we aimed at directly disentangle the hypotheses concerning hemispheric asymmetries (RHH, VH, MVH, MM). For this reason we decided to use a positive, approach-related emotion (happiness) and a negative, approach-related emotion (anger), which should lead to a specific pattern of hemispheric asymmetries, depending on the specific hypothesis considered. We analyzed both parietal and frontal P1, N170 and P2 components, in order to control for possible differences in hemispheric asymmetries between posterior/anterior brain regions, and thus to test the MVH. The specific expectations based on the different models proposed were the following:

i) RHH: stronger right-hemispheric activity for all emotions, with no difference between happy and angry faces;

ii) VH: stronger left/right-hemispheric activity for happy/angry faces, respectively;

iii) MVH: stronger right-hemispheric activity for all stimuli at parietal sites, but stronger left/right activity for happy/angry faces at frontal sites, respectively;

iv) MM: stronger left-hemispheric activity for both angry and happy faces.

Based on the findings by Reuter-Lorenz et al. (1983), who found contrasting patterns of hemispheric asymmetries in left- and right-handers, we also calculated the correlation between handedness and hemispheric asymmetries for positive/negative emotions. Because the frontal activity was one of the main aspects of interest of the study, we administered a passive viewing paradigm. However, in order to obtain behavioral evidence, we inserted a number of behavioural trials in which ERPs were not recorded, and participants were required to rate the emotional expression of the stimuli.

Materials and methods

Participants

Sixteen right-handed volunteers (mean age: 27.25 ± 0.93; 9 females) with normal or corrected-to-normal vision and without previous psychiatric or neurological history took part in the study. Sample size was calculated using the G*POWER software version 3.1.9.2 for F test (repeated measures ANOVA, within factors) using 0.33 as the effect size of F (see Prete et al., 2015a), error probability of 0.05, correlation among repeated measures of 0.5 and nonsphericity correction of 1. The sample size calculated by the software was 14, but considering a potential 10% drop out, the final sample size was increased to 16 participants. All participants were right-handers, with a mean handedness score of 78.85 (± 8.64), as measured by the Italian version of the Edinburgh Handedness Inventory (Salmaso & Longoni, 1985), in which a score of -100 corresponds to a total left preference, and +100 corresponds to a total right preference. Informed consent was obtained from all participants prior to testing. The whole procedure was carried out in accordance with the principles of the Declaration of Helsinki and it was approved by the Ethics Committee for Biomedical Research of the University 'G. d'Annunzio' of Chieti and Pescara.

Stimuli

Stimuli were selected from the Karolinska Directed Emotional Faces (Lundqvist et al., 1998), a database of female and male faces with neutral and emotional expressions: photographs in frontal view of 15 female and 15 male faces in angry (AN) and in happy (HA) poses were extracted. Female faces with strong makeup and male faces with beard were discarded. Facial stimuli were handled by means of the software Photoshop (Adobe Systems Inc., San Jose, CA, USA): they were converted into gray-scale images measuring 8.41° x 9.69° of visual angle (248 x 270 pixels), seen at a distance of about 57 cm (screen resolution: 1024 x 768 pixels). Additionally, a black and white checkerboard (10 cycles per image) with the same size of the facial stimuli was created, and all stimuli (faces and checkerboard) were equated for mean luminance.

Procedure

Participants were tested individually in a dark room. They were seated about 57 cm from the computer screen. Before the start of the task, written instructions were presented: participants were asked to fixate the cross presented in the center of the screen throughout the task, and to pay attention at the emotional expression of faces, which would be presented either in the left visual field (LVF), in the right visual field (RVF), or in both visual fields simultaneously (two faces presented together, one in the LVF and one in the RVF). It was specified that when one face was presented in one visual field (VF), a black and white checkerboard would be presented in the other VF, so that in any trial two stimuli were presented together, one in each VF. It was also specified that during the bilateral presentations, the two emotional faces could express the same emotion or two different emotions. Participants were instructed that only when the black central cross became red (Behavioural trials), they had to express a judgment about the emotion just seen, using a 5-point Likert scale (1 = very angry; 2 = angry; 3 = neutral; 4 = happy; 5 = very happy). In the bilateral presentations (in which the emotional faces could express the same emotion or two different emotions) participants were required to express only one judgment, corresponding to their first overall impression. They were invited to reduce as much as possible any movements, to gaze the central cross for all of the duration of the task and to press the response keys using the right hand (only in the Behavioural trials). Prior to the beginning of the experimental sessions, 16 training trials were carried out, in order to allow participants to become familiar with the task and with the response scale.

Each trial started with a black fixation cross presented in the center of the white screen for 500 ms. In the following 125 ms the fixation cross remained visible and stimuli were presented: they could be constituted either by an emotional face presented in one hemifield and the checkerboard presented in the other hemifield (unilateral presentation conditions), or by two emotional faces presented in the two hemifields (bilateral presentation conditions). The center of each stimulus was placed at 9.19º of visual angle to the left/right of the center of the screen. After the stimulus had disappeared, an interstimulus interval (ISI) preceded the following trial. During the ISI the fixation cross was always visible: in 88.24% of the trials the ISI was randomized between 1200 ms and 1800 ms (step: 150 ms), during which the black cross indicated that no response was required (EEG trials). In the remaining 11.76% of the trials the ISI lasted 2000 ms, during which the fixation cross became red, meaning that an emotional judgment was required (Behavioural trials), otherwise the next trial started. Behavioural trials were used to force participants to focus their attention on the emotional content of the stimuli (the cross became red after the stimuli disappeared, during the ISI, so that participants had to pay attention to the emotional content of the faces in all of the trials), and in order to obtain emotional judgments, with no risk of compromising frontal ERPs in the EEG trials.

The task was composed of 960 EEG trials and 128 Behavioural trials, divided into 4 sessions (272 trials each). Thus, 120 EEG trials and 16 Behavioural trials were presented for each of the 8 conditions: 4 unilateral conditions (emotional expression-VF of presentation: AN[GRY]-LVF, AN-RVF, HA[PPY]-LVF, HA-RVF), and 4 bilateral conditions (emotional expression in the LVF-RVF: AN-AN, HA-HA, AN-HA, HA-AN). Participants were allowed to take a break among sessions. Presentation order of the stimuli was randomized within and across participants and sessions. The paradigm was administrated by means of E-Prime 2.0 software (Psychology Software Tools, Inc., Pittsburgh, PA, U.S.A.), and it lasted about 45 minutes. EEG signals were recorded during EEG trials, whereas emotional judgments and reaction times (RTs) were collected during Behavioural trials.

Data Acquisition and analysis

EEG data were recorded by means of a 128 electrode net (Electrical Geodesic, version 1.1), placed according to an augmented 10-20 system. Skin/electrode impedance was below 50 KΩ. EEG data were sampled at 150 Hz and processed off-line. Two electro-oculographic channels were used to monitor eye movements and blinking. For the analysis we filtered between 0.1 and 40 Hz, and the acquisition time was set from -0.5 to +1 s after the stimulus. For each participant, 120 EEG trials were collected in each of the 8 experimental conditions (i.e., 4 unilateral conditions, and 4 bilateral conditions). The EEG single trials contaminated by eye movements, blinking, or involuntary motor acts (e.g. mouth, head, trunk or arm movements) were rejected off-line. The EEG epochs with ocular and other types of artifacts were preliminarily identified by means of a computerized automatic procedure and then corrected by an autoregressive method validated in previous studies (Moretti et al., 2003; Babiloni et al., 2003, 2005; Capotosto et al., 2009, 2012, 2014, 2015). In order to remove the effects of the electric reference, EEG single trials were re-referenced by the common average reference, which includes the averaging of amplitude values at all electrodes and the subtraction of the mean value from the amplitude values at each single electrode. Following artifact removal, an average number of 111 (± 5) trials for each experimental condition was available for the EEG analysis.

The global field power of EEG showed 3 main peaks for all participants in the following time windows: 100-150 ms, 150-200 ms, 200-280 ms. Topography of the EEG activity in these time intervals showed parietal maxima and frontal maxima. Therefore P1, N170 and P2 amplitudes and latencies, separately, were considered at parietal (P7 and P8 electrodes) and frontal (F3 and F4) sites. In particular, for each condition, the latencies of the ERP components were extracted for the electrode that showed the highest amplitude across the electrodes of interest (i.e., P7, P8, F3, F4; time windows = P1: 100-150 ms; N170: 150-200 ms; P2: 200-280 ms).

Amplitude values for each peak were subjected to a repeated-measure analysis of variance (ANOVA) for unilateral and bilateral conditions, separately. Concerning the unilateral conditions, Emotion (Anger, Happiness), Visual field of presentation (LVF, RVF) and Hemisphere (Left, Right) were used as within-subject factors. In the bilateral conditions, Emotion (AN-AN, HA-HA, AN-HA, HA-AN) and Hemisphere (Left, Right) were used as within-subject factors.

Similar analyses were carried out for the latencies. Specifically, they were subjected to two ANOVAs carried out for the unilateral and the bilateral conditions, separately. In the unilateral conditions, Emotion (Anger, Happiness) and Visual field of presentation (LVF, RVF) were used as within-subject factors, and the latencies were considered only for the hemisphere contralateral to the side of presentation of the facial stimulus. In the bilateral conditions, Emotion (AN-AN, HA-HA, AN-HA, HA-AN) and Hemisphere (Left, Right) were used as within-subject factors.

All statistical analyses were computed by means of the Statistica 8.0 software (StatSoft. Inc., Tulsa, USA), and post-hoc comparisons were carried out by using Duncan tests ($p < 0.05$).

Results

Behavioural results

Emotional judgments (from 1=very angry to 5=very happy) and reaction times (RTs) were used as the dependent variable in two series of repeated-measure ANOVAs, similar to those carried out for the ERP latencies.

The ANOVA carried out on the emotional judgments in the unilateral conditions showed a main effect of Emotion ($F_{(1, 15)} = 51.86$, $MSE = 43.34$, $p < 0.001$, $\eta_p^2 = 0.77$): Happy faces were judged as more happy than Angry faces, confirming that the emotional expressions were correctly categorized by the participants (angry: 2.12 ± 0.09; happy: 3.76 ± 0.12). The main effect of Visual field ($F_{(1, 15)} = 8.67$, $MSE = 2.3$, $p = 0.01$, $\eta_p^2 = 0.37$) showed that the emotional judgments were higher (more positive valence) when stimuli were presented in the RVF (3.13 ± 0.18) than in the LVF (2.75 ± 0.17), whereas the Emotion X Visual field interaction was not significant ($F_{(1, 15)} =$

1.44, $p = 0.249$). In the bilateral conditions, the effect of Emotion was significant ($F_{(3, 45)} = 28.24$, $MSE = 6.87$, $p < 0.001$, $\eta_p^2 = 0.65$), and post-hoc comparisons confirmed that AN-AN condition received the lowest emotional judgment, and that HA-HA condition received the highest emotional judgment, than all of the other conditions ($p < 0.003$ for all comparisons: AN-AN = 2.78 ± 0.12; HA-HA = 3.85 ± 0.15; AN-HA = 3.30 ± 0.14; HA-AN = 2.99 ± 0.10). The difference between AN-HA and HA-AN condition did not reach statistical significance ($p = 0.08$).

In the unilateral conditions, the ANOVA carried out on the RTs revealed that only the interaction between Emotion and Visual field was significant ($F_{(1, 15)} = 4.77$, $MSE = 9734$, $p = 0.045$, $\eta_p^2 = 0.24$), and post-hoc comparisons revealed shortest RTs for happy faces presented in the RVF than for all of the other conditions ($p < 0.004$ for all comparisons; Figure 1a). In the bilateral conditions, the effect of Emotion was significant ($F_{(3, 45)} = 5.32$, $MSE = 30890$, $p = 0.003$, $\eta_p^2 = 0.26$): RTs were longer for AN-AN than for HA-HA condition ($p = 0.008$), and they were longer for HA-AN than for AN-HA ($p = 0.021$) and HA-HA conditions ($p = 0.002$; Figure 1b).

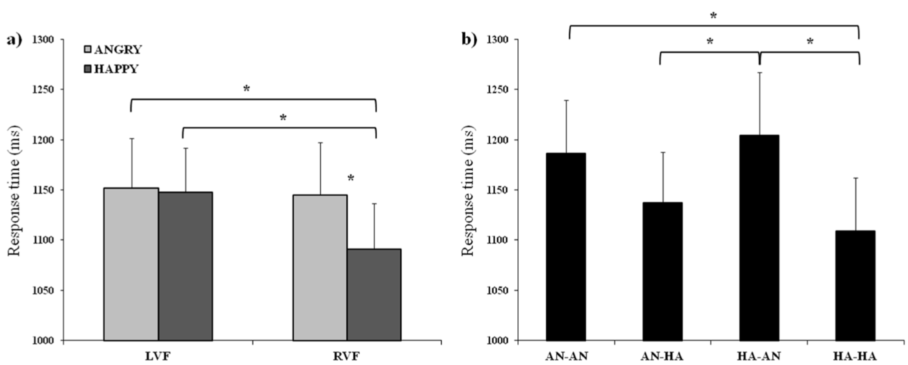

Figure 1: Reaction times in Behavioural trials for a) unilateral conditions (AN-LVF, AN-RVF, HA-LVF, HA-RVF, with AN: angry; HA: happy; LVF: left visual field; RVF: right visual field), and b) bilateral conditions (LVF-RVF: AN-AN, AN-HA, HA-AN, HA-HA). Error bars represent standard errors and asterisks show the significant differences.

Moreover, a series of Pearson's tests were carried out in order to investigate the possible correlation between the handedness scores and both emotional judments and RTs. In particular, in unilateral conditions, emotional judgments and RTs for angry and for happy faces presented in the RVF were subtracted to those obtained when the same stimuli were presented in the LVF (AN = RVF – LVF; HA = RVF – LVF). Similarly, emotional judgments and RTs for the angry-happy condition were subtracted to those obtained in the happy-angry condition (AN-HA – HA-AN). The difference between LVF and RVF for unilateral conditions and that between AN-HA and HA-AN conditions allows us to obtain a score corresponding to a lateralized bias. Specifically, in unilateral conditions, higher scores correspond to a RVF bias for each emotional expression; in the bilateral conditions higher scores represent a RVF-bias for happy faces. Concerning the emotional judgments, the resulting distributions were compared to the handedness scores (Figure 2a). In the unilateral conditions, there was a positive correlation between happy faces and handedness (r = 0.51, p = 0.045; Figure 2a, central panel), but not between angry faces and handedness (r = 0.22, p = 0.40; Figure 2a, left panel), showing a left-hemispheric superiority for recognizing positive emotions in the stronger right hand preference. In the bilateral conditions, the result showed a positive correlation (r = 0.50, p = 0.048; Figure 2a, right panel), confirming that participants with a stronger right hand preference better recognized positive emotions when presented in the RVF.

Concerning the RTs for unilateral conditions, the resulting distributions – in which lower scores represented a RVF-advantage – were compared to the handedness scores (Figure 2b). There was a negative correlation between happy faces and handedness (r = -0.52, p = 0.039; Figure 2b, central panel), but not between angry faces and handedness (r = -0.33, p = 0.21; Figure 2b, left panel), showing that participants with a stronger right hand preference processed faster positive emotions presented in the RVF. Finally, in bilateral conditions, no significant correlation was found between the RTs and handedness (r = -0.39, p = 0.14; Figure 2b, right panel).

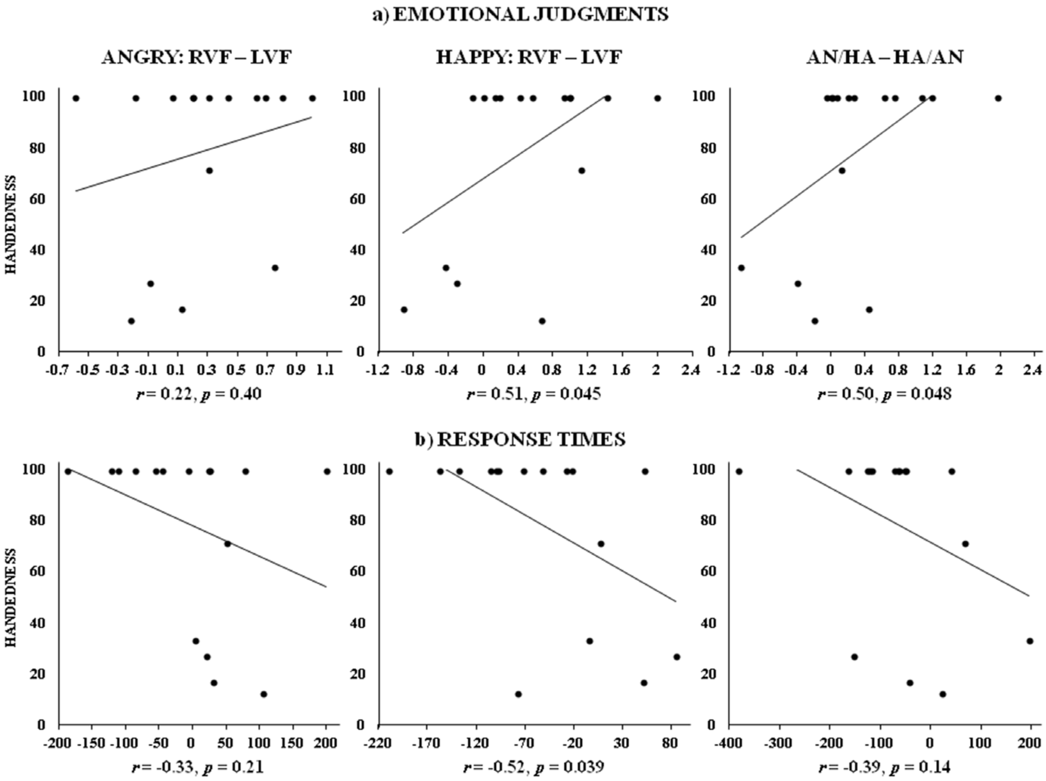

Figure 2: Correlations between handedness scores and a) emotional judgments (upper panel), and b) Response Times (RTs: lower panel) for faces presented in the LVF subtracted to the RVF considering angry expression (AN: leftmost column), happy expression (HA: central column), and for happy/angry condition subtracted to angry/happy condition (AN/HA – HA/AN: rightmost column).

ERP results

Figure 3 shows the temporal evolution of the topographic maps over the whole scalp of the grand-average ERPs for each condition separately, in the time interval from 100 to 280 ms.

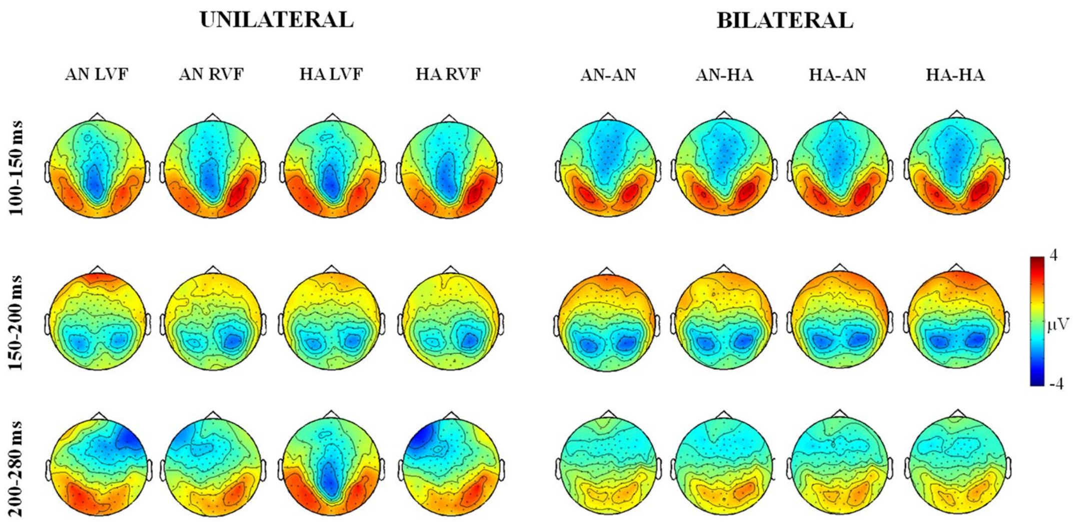

Figure 3: Temporal evolution of the topographic maps over the whole scalp of the grand-average ERPs in the three time windows selected (100-150 ms, 150-200 ms, 200-280 ms), for unilateral conditions (AN-LVF, AN-RVF, HA-LVF, HA-RVF; with AN: angry; HA: happy; LVF: left visual field; RVF: right visual field) and bilateral conditions (AN-AN, AN-HA, HA-AN, HA-HA).

Topographic maps confirmed activations in posterior and frontal sites, corresponding to the latencies of the ERP peaks P1, N170, P2.

Parietal sites (P7/P8)

Figure 4 shows the grand averages for unilateral and bilateral conditions, at P7/P8 sites, separately for each condition, and the waveform elicited by emotional expressions.

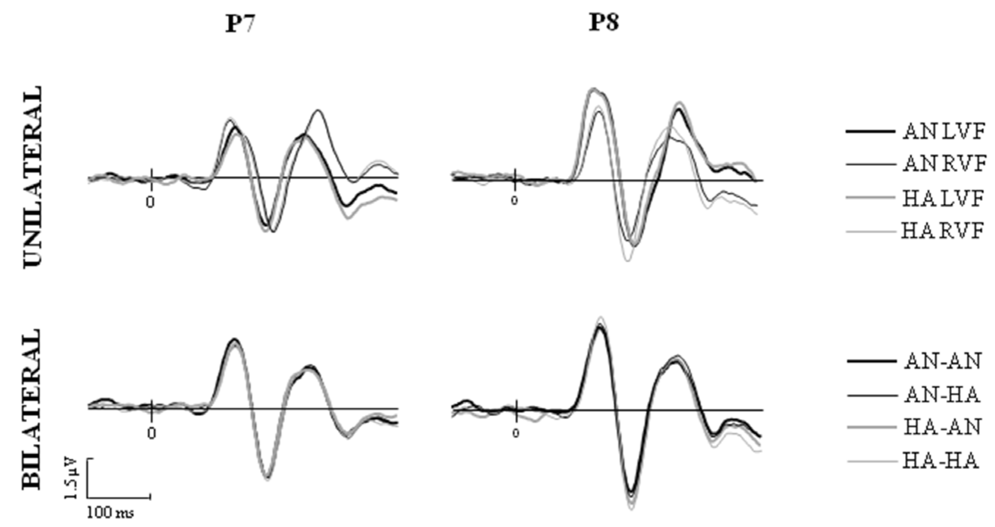

Figure 4: Grand average of ERP waveforms for the left and right parietal EEG derivations (P7, P8) in a time window from 100 ms before face presentation (vertical line) to 400 ms after face presentation for unilateral conditions (upper panel: AN-LVF, AN-RVF, HA-LVF, HA-RVF; with AN: angry; HA: happy; LVF: left visual field; RVF: right visual field) and bilateral conditions (lower panel: AN-AN, AN-HA, HA-AN, HA-HA).

P1 amplitude and latency

In the unilateral conditions the ANOVA carried out on the P1 amplitude revealed a significant main effect of Hemisphere ($F_{(1, 15)} = 8.44$, $MSE = 84.37$, $p = 0.011$, $\eta_p^2 = 0.36$), showing an enhanced P1 in the right hemisphere (3.91 ± 0.31 μV) with respect to the left hemisphere (2.28 ± 0.30 μV). The interaction between Hemisphere and Visual field was significant ($F_{(1, 15)} = 17.19$, $MSE = 59.1$, $p < 0.001$, $\eta_p^2 = 0.53$), and post-hoc comparisons showed that the P1 amplitude in the left hemisphere was higher when stimuli were presented in the RVF than in the LVF ($p = 0.003$), whereas in the right hemisphere, the P1 amplitude was higher when stimuli were presented in the LVF than in the RVF ($p = 0.04$). Moreover, when stimuli were presented in the LVF, the P1 was higher in the right hemisphere than in the left hemisphere ($p < 0.001$), whereas this difference was not significant considering stimuli presented in the RVF ($p = 0.58$; Figure 5).

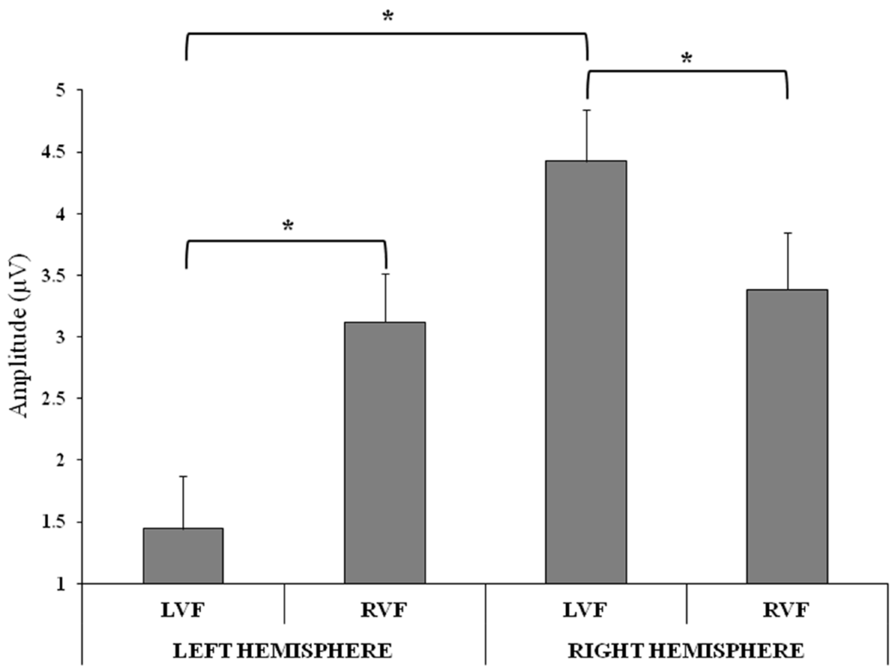

Figure 5: Interaction between Hemisphere and Visual field in the unilateral conditions for the P1 amplitude at parietal sites (P7, P8). Error bars represent standard errors, asterisks show the significant differences.

In the bilateral conditions the ANOVA carried out on the P1 amplitude revealed a main effect of Hemisphere ($F_{(1, 15)} = 8.63$, $MSE = 111.2$, $p = 0.01$, $\eta_p^2 = 0.36$), confirming a stronger P1 in the right (4.92 ± 0.35 μV) than in the left hemisphere (3.05 ± 0.25 μV). Also the interaction between Hemisphere and Condition was significant ($F_{(3, 45)} = 3.25$, $MSE = 2.86$, $p = 0.03$, $\eta_p^2 = 0.18$), and post-hoc comparisons confirmed an enhanced amplitude of the P1 in the right hemisphere compared to the left hemisphere in all of the bilateral conditions ($p < 0.001$ for all comparisons). Moreover, in the right hemisphere the P1 was higher in the HA-HA compared to the AN-HA ($p = 0.008$) and the AN-AN conditions ($p = 0.053$; Figure 6).

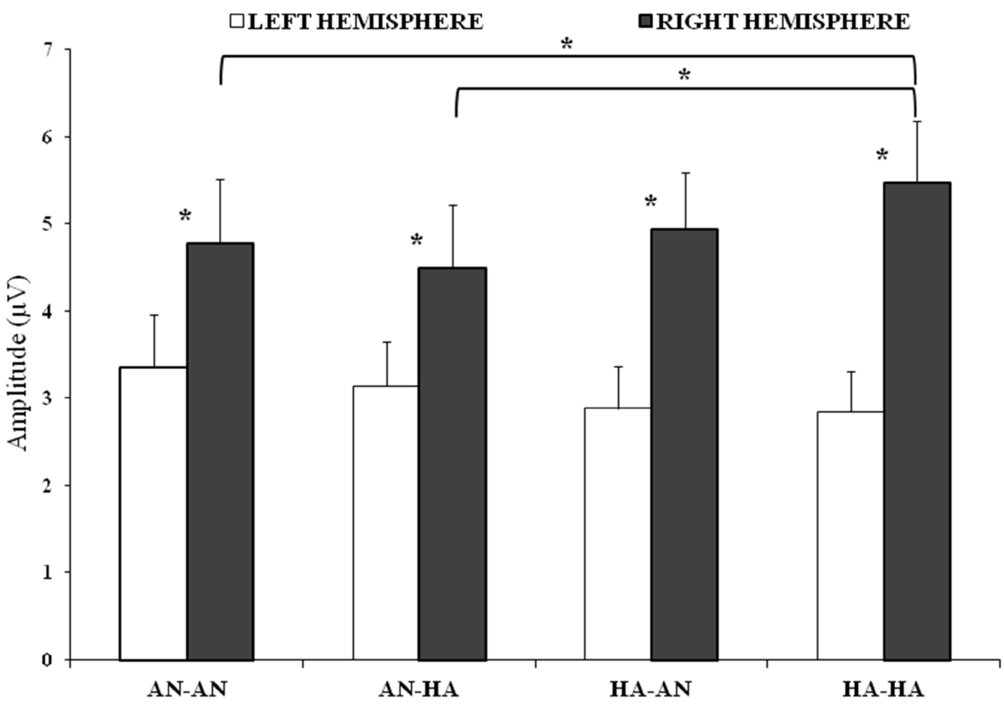

Figure 6: Interaction between Hemisphere and Condition in the bilateral presentations for the P1 amplitude at parietal sites (P7, P8). Error bars represent standard errors, asterisks show the significant differences.

Statistical analyses carried out on the P1 latencies did not reveal significant main effects or interactions, for either bilateral or unilateral conditions.

N170 amplitude and latency

The ANOVA carried out on the N170 amplitude for the unilateral conditions showed a main effect of Visual field ($F_{(1, 15)} = 12.7$, $MSE = 24.99$, $p = 0.003$, $\eta_p{}^2 = 0.46$): the N170 was enhanced for faces presented in the LVF (-2.34 ± 0.23 µV) than in the RVF (-1.45 ± 0.27 µV).

In the bilateral conditions the ANOVA carried out on the N170 amplitude did not show significant main effects nor interactions. Similarly, the ANOVAs carried out on the N170 latencies did not reveal significant results concerning unilateral or bilateral conditions.

P2 amplitude and latency

Considering the amplitude of the P2 component in the unilateral conditions, the ANOVA showed a main effect of Visual field ($F_{(1, 15)} = 6.24$, $MSE = 19.83$, $p = 0.024$, $\eta_p^2 = 0.29$): the P2 was enhanced for faces presented in the LVF (2.50 ± 0.27 μV) than in the RVF (1.71 ± 0.31 μV). The interaction between Visual field and Hemsiphere was significant ($F_{(1, 15)} = 37.61$, $MSE = 150.33$, $p < 0.001$, $\eta_p^2 = 0.71$), as well as all of the post-hoc comparisons. Specifically, the P2 was enhanced in the hemisphere contralateral to the visual field of face presentation: it was higher in the left hemisphere for stimuli presented in the RVF than in the LVF ($p = 0.015$), and it was higher in the right hemisphere for stimuli presented in the LVF than in the RVF ($p < 0.001$). Similarly, for stimuli presented in the LVF the amplitude of the P2 component was stronger in the right than in the left hemisphere ($p = 0.008$), whereas for stimuli presented in the RVF it was stronger in the left than in the right hemisphere ($p < 0.001$; Figure 7).

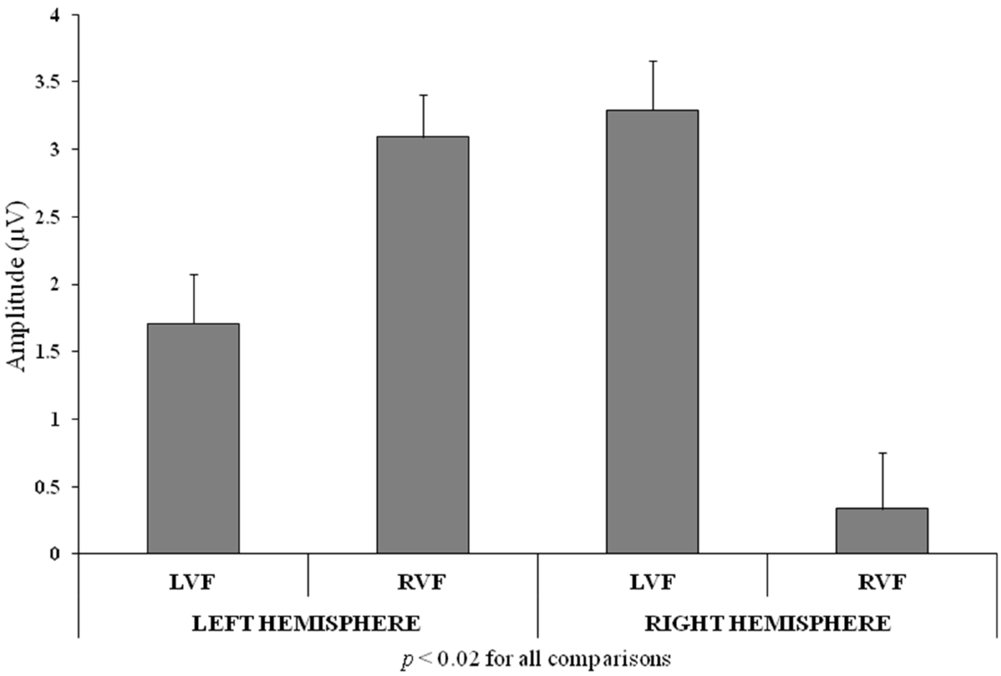

Figure 7: Interaction between Visual field and Hemisphere in the unilateral conditions for the P2 amplitude at parietal sites (P7, P8). Error bars represent standard errors. All comparisons are significant.

In the bilateral conditions the ANOVA on the P2 amplitude showed a main effect of Hemisphere ($F_{(1,\ 15)} = 11.38$, $MSE = 66.84$, $p = 0.004$, $\eta_p^2 = 0.43$), the P2 component being enhanced in the right hemisphere (3.44 ± 0.23 μV) with respect to the left hemisphere (1.99 ± 0.24 μV).

The ANOVAs carried out on the P2 latencies did not reveal significant results neither concerning the unilateral nor the bilateral conditions.

Frontal sites (F3/F4)

P1 amplitude

The ANOVA carried out on the unilateral conditions showed a main effect of Emotion ($F_{(1,\ 15)} = 5.23$, $MSE = 2.88$, $p = 0.037$, $\eta_p^2 = 0.26$), the amplitude of the P1 component being enhanced for happy faces (1.12 ± 0.16 μV) than for angry faces (-0.82 ± 0.17 μV). The interaction between Hemisphere and Visual field was also significant ($F_{(1,\ 15)} = 17.23$, $MSE = 7.78$, $p < 0.001$, $\eta_p^2 = 0.53$), and post-hoc comparisons showed that when stimuli were presented in the LVF, the amplitude of the P1 was higher in the left than in the right hemisphere ($p = 0.005$), whereas when the stimuli were presented in the RVF, the P1 was higher in the right than in the left hemisphere ($p = 0.032$). This ipsilateral activity was mainly lateralized in the right hemisphere, in fact the P1 amplitude in the right hemisphere was enhanced for stimuli presented in the RVF than in the LVF ($p = 0.002$), even if a trend for a stronger activity in the left hemisphere when faces were presented in the LVF than in the RVF was also present ($p = 0.091$).

Neither main effects nor interactions reached statistical significance in the ANOVA carried out on the P1 amplitude in the bilateral conditions.

N170 amplitude

The ANOVA carried out in the unilateral conditions revealed a significant interaction between Hemisphere and Visual field ($F_{(1, 15)} = 13.42$, $MSE = 5.27$, $p = 0.002$, $\eta_p^2 = 0.47$). Post-hoc comparisons showed an enhanced amplitude of the N170 in the right hemisphere for faces presented in the LVF than in the RVF ($p = 0.001$), and they also showed a stronger N170 in the right hemisphere than in the left hemisphere for stimuli presented in the LVF ($p < 0.001$).

The ANOVA carried out on the N170 amplitude in the bilateral conditions did not show significant results.

P2 amplitude

In the unilateral conditions the ANOVA carried out on the P2 amplitude showed a main effect of Hemisphere ($F_{(1, 15)} = 8.55$, $MSE = 8.27$, $p = 0.01$, $\eta_p^2 = 0.36$), the P2 component being enhanced in the right hemisphere (-1.84 ± 0.19 μV) with respect to the left hemisphere (-1.33 ± 1.19 μV).

Statistical analyses carried out on the P2 amplitude in the bilateral conditions did not show significant main effects nor interaction.

Discussion

The aims of the present study were to assess hemispheric asymmetries for emotional processing, and to investigate the possible effects of the presentation of one or two emotional faces presented at once on these expected asymmetries. Different patterns of results have been hypothesized (see the Introduction), according to the different theories proposed in the literature. Moreover, previous behavioural evidence revealed that the presentation of one emotional face in a VF lends support to the VH (Prete et al., 2014, 2015c), whereas the simultaneous presentation of two emotional faces in the two VFs lends support to the RHH (Prete et al., 2015b,c). No previous studies have specifically explored the issue of the number of faces presented as a possible tool to further investigate hemispheric asymmetries in emotional detection by means of electrophysiological measures. One of the most interesting evidence in the present study is that behavioural and EEG results revealed different patterns of results: in fact, emotional judgments and RTs provide support for a left-hemispheric superiority in the processing of positive emotions (RVF presentation), together with a right-hemispheric superiority in the processing of negative emotions (LVF presentation), thus supporting the VH (e.g., Baijal & Srinivasan, 2011). Moreover, emotional judgments were slower when a happy face was presented in the LVF and an angry face was presented in the RVF with respect to the opposite condition and also with respect to the condition in which two happy faces were presented in the two VFs. The conclusion about the behavioural results is that, independently of the number of stimuli presented, the left/right hemispheres are superior in processing positive/negative emotions respectively, thus supporting the VH. Moreover, the faster recognition of happy than angry faces in the bilateral presentations confirmed the already known faster processing of positive emotions (Leppänen & Hietanen, 2004).

Correlation analyses revealed that this left-hemispheric superiority in the recognition of positive emotions is more robust in participants with a stronger right preference, revealing that handedness can influence hemispheric asymmetries for emotional processing, at least at a behavioural level (Reuter-Lorenz, Givis & Moscovitch, 1983; Casasanto, 2009). This result could be viewed as a possible key to understand the different patterns of results alternatively supported in the literature in this field, showing inconsistent evidences of hemispheric dominance for positive and negative valence stimuli in different studies. Specifically, we found that a higher right hand preference, as measured by the handedness questionnaire, is positively correlated with faster and increased positive judgments for happy faces presented in the RVF (left hemisphere), both in unilateral and bilateral presentations, even if no difference emerged for angry faces. This observation suggests that the right-hemispheric superiority for negative emotions is independent of handedness, but that the left-hemispheric superiority for positive emotions is correlated to handedness. Right-hemispheric superiority for negative emotions is proposed by the RHH, VH, and MVH theories, but the cerebral asymmetries for positive emotions as proposed to occur at different time frames. We can speculate that the different pattern of results found in this context could be due to the different degree of handedness preference in the samples tested. Nevertheless, the sample of right-handed participants prevents us to further explore this issue, but future studies could shed light on this point. In this frame, the results by Reuter-Lorenz and colleagues (1983) confirmed this speculation: the authors found that right-handers were faster at recognizing happy/sad faces presented in the RVF/LVF, respectively, and they also found the opposite pattern in left-handers (see Casasanto, 2009; Marzoli, Prete & Tommasi, 2014).

Despite the support for the VH found in the behavioural performance, the electrophysiological evidence does not support this pattern of hemispheric asymmetries for positive/negative emotions. No significant result was found concerning the latencies in any of the components analyzed, showing that in the present study ERPs latencies are not affected by the emotional content of the stimuli. Concerning ERPs amplitude at posterior sites, the results show an enhancement of the amplitude in the right than in the left hemisphere for the P1 component both in unilateral and bilateral presentations, independently of the emotional valence of the stimuli, thus not supporting the VH (according to which we expected to find a left-hemispheric superiority for positive emotions). This hemispheric asymmetry was also found for the P2 component, but only in bilateral conditions, whereas in unilateral conditions an enhanced P2 amplitude was found when stimuli were presented in the LVF than in the RVF. These findings show a right-hemispheric superiority for both angry and happy faces and support the RHH (Gainotti, 2012), according to which the right hemisphere is superior in the processing of all emotions, and the MVH (Davidson, 1984), according to which this right-hemispheric superiority for all emotions is restricted to the posterior cortical sites. The MM (Poole & Gable, 2014), suggesting that the left hemisphere is more involved in approach-related emotions (thus both angry and happy faces) is not supported by the present data. At frontal sites, the P2 amplitude was enhanced in the right hemisphere than in the left hemisphere in the unilateral conditions, and this is the only evidence of hemispheric asymmetry at frontal sites. This result seems to suggest that between the RHH and the MVH, the latter theory (according to which a left-hemispheric superiority for positive emotions would be expected) does not find support in the present results. The absence of a clear lateralization in the frontal areas is in line with the conclusion suggested by Davidson (2002). The author suggested that the main task of the prefrontal cortex during emotional processing is not to mediate emotional responses, but it is to moderate the activity in other structures of the emotional circuit, namely the amygdala. Nevertheless, contrasting results have been obtained in a number of ERP studies in which emotional stimuli were presented centrally. For instance, Graham and Cabeza (2000) found no asymmetries at parietal sites during the presentation of happy and neutral faces, but they found a stronger frontal activity in the left/right hemisphere for happy/neutral faces, respectively. However, by presenting film clips eliciting happiness and anger, Waldstein et al. (2000) confirmed the left-hemispheric superiority for positive emotions, but they did not find asymmetries for negative emotions in the frontal areas. Finally, a similar pattern of results as that found in the present study was instead described by Sobótka and colleagues (1992), who showed that positive or negative emotional experiences induced a stronger P2 in the right hemisphere at posterior sites, but no asymmetries at frontal sites.

Together with the rightmost cortical activity for both positive and negative emotions, ERPs in the unilateral presentation also confirmed that in the posterior sites P1 and P2 components were enhanced in the hemisphere contralateral to the hemifield in which the face had been presented, as expected by the contralateral projections of the human visual system. At frontal sites, however, the amplitude of P1 was enhanced ipsilaterally and the P2 did not show hemispheric asymmetries. Moreover, the stronger amplitude of the P1 for happy than for angry faces in both unilateral and bilateral presentation in the frontal cortex confirms the more efficient processing of positive than negative emotions already found in the behavioural results.

Finally, as regard the face-related N170 component, which is known to be independent of the emotional content of the stimuli (Eimer & Holmes, 2002), this component was found not to be lateralized during the bilateral presentations, either at parietal or frontal sites, and was found to be enhanced in the parietal cortex when a face was presented in the LVF, and in the frontal areas in the hemisphere contralateral to the side of presentation of the face.

To conclude, the present study shows that i) there is no strict correspondence between behavioural evidence and ERP components regarding hemispheric asymmetries for positive and negative emotions; ii) at parietal sites both P1 and P2 are stronger in the right than in the left hemisphere independently of the positive or negative valence of the stimuli and independently of the number of emotional faces presented; iii) at frontal sites the amplitude of P2 is enhanced in the right hemisphere, independently of the emotional content of the stimuli, but only in the unilateral condition; iv) RTs show a LVF-right hemisphere/RVF-left hemisphere advantage for negative/positive emotions, respectively; v) the rightward bias for happiness found in the behavioural results is positively correlated with the degree of handedness.

Concerning this last point, caution is needed because only right-handed participants took part in the present study. The evidence that participants with a higher degree of hand-preference showed the stronger left-hemispheric superiority for positive emotions seems to suggest that the handedness can be a possible explanation for the behavioural pattern of results found here. In order to further explore this possibility, in a future study a sample of both right- and left-handed participants (strong and mixed degree of hand-preference) should be tested with a paradigm similar to that used here. In accordance with the abovementioned speculation, at the behavioural level a LVF/RVF superiority is expected for negative/positive emotions, respectively, in participants with strong hand-preference, and an opposite pattern is expected in participants with mixed hand-preference. At the electrophysiological level one would expect that the right-hemispheric superiority found here is true across the whole sample, independently of the handedness of the participants. Following this idea, the bias in the behavioural performance could be intended as linked to the stronger readiness to positively evaluate stimuli occurring in the hemispace in which the dominant hand usually acts (i.e., the right hemispace for right-handers and the left hemispace for left-handers). Moreover, it would be interesting to include all of the basic emotions, as well as emotional stimuli other than faces (e.g., emotional words, clips, body images), in order to explore the pattern of hemispheric asymmetries beyond the happy and the angry facial expressions, and thus to evaluate the possibility to generalize these results to all positive and negative emotional stimuli.

Conclusions

In regards to theories of hemispheric asymmetries in emotional processing, the results of the present study seem to support both the VH and the RHH: a valence-specific asymmetry is supported by the behavioural evidence, but a stronger right-hemispheric activity independent of the emotional expression is revealed by the electrophysiological results. The MM is not supported, since in no component and condition a stronger left-hemispheric activity was found. Moreover, the lack of evidence of a valence-specific activity at frontal sites does not support the MVH. We also found that the presentation of two emotional faces in the two visual fields does not elicit remarkable differences in ERPs with respect to the presentation of just one emotional face in a hemifield, thus the idea according to which the number of emotional stimuli presented at once could be the key variable underlying hemispheric asymmetries for emotional detection does not find support here. We can conclude that the VH and the RHH, the most acknowledged hypotheses in this field, are not mutually exclusive, and further studies are needed to explore the possibility that the degree of handedness could be a possible key to shed more light on which of the two theories better explains the complex frame of cerebral imbalance for processing emotional stimuli with positive and negative valence.

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