Right hemisphere or valence hypothesis, or both? The processing of hybrid faces in the intact and callosotomized brain.

note finali coverpage

(Article begins on next page)

22 June 2024
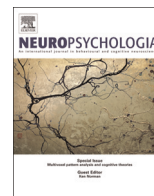
Right hemisphere or valence hypothesis, or both? The processing of hybrid faces in the intact and callosotomized brain

Q1 Giulia Prete [a],*, Bruno Laeng [b], Mara Fabri [c], Nicoletta Foschi [d], Luca Tommasi [e]

[a] Department of Neuroscience, Imaging and Clinical Science, 'G. d'Annunzio' University of Chieti-Pescara, Italy
[b] Department of Psychology, University of Oslo, Norway
[c] Department of Clinical and Experimental Medicine, Neuroscience and Cell Biology Section, Polytechnic University of Marche, Ancona, Italy
[d] Regional Epilepsy Centre, Neurological Clinic, "Ospedali Riuniti", Ancona, Italy
[e] Department of Psychological Science, Humanities and Territory, 'G. d'Annunzio' University of Chieti-Pescara, Italy

ARTICLE INFO

ABSTRACT

The valence hypothesis and the right hemisphere hypothesis in emotion processing have been alternatively supported. To better disentangle the two accounts, we carried out two studies, presenting healthy participants and an anterior callosotomized patient with 'hybrid faces', stimuli created by superimposing the low spatial frequencies of an emotional face to the high spatial frequencies of the same face in a neutral expression. In both studies we asked participants to judge the friendliness level of stimuli, which is an indirect measure of the processing of emotional information, despite this remaining "invisible". In Experiment 1 we presented hybrid faces in a divided visual field paradigm using different tachistoscopic presentation times; in Experiment 2 we presented hybrid chimeric faces in canonical view and upside-down. In Experiments 3 and 4 we tested a callosotomized patient, with spared splenium, in similar paradigms as those used in Experiments 1 and 2. Results from Experiments 1 and 3 were consistent with the valence hypothesis, whereas results of Experiments 2 and 4 were consistent with the right hemisphere hypothesis. This study confirms that the low spatial frequencies of emotional faces influence the social judgments of observers, even when seen for 28 ms (Experiment 1), possibly by means of configural analysis (Experiment 2). The possible roles of the cortical and subcortical emotional routes in these tasks are discussed in the light of the results obtained in the callosotomized patient. We propose that the right hemisphere and the valence accounts are not mutually exclusive, at least in the case of subliminal emotion processing.

© 2015 Published by Elsevier Ltd.

1. Introduction

Hemispheric lateralization in facial emotion processing remains a controversial issue in the field of cognitive neuroscience despite the number of studies that have delved into the issue for decades. Remarkably, opposite patterns of hemispheric superiority have been suggested, although a number of studies have failed in finding cerebral asymmetries (see Demaree et al., 2005; Torro-Alves et al., 2008 for a review; Fusar-Poli et al., 2009 for a meta-analysis of about more than 100 studies). The two currently leading hypotheses are the 'right hemisphere hypothesis' (RHH; Gainotti, 1972; Levy et al., 1983a,b) and the 'valence hypothesis' (VH, Davidson et al., 1987; Baijal and Srinivasan, 2011). According to the RHH, the right hemisphere is superior to the left hemisphere in the analysis of all emotions, whereas, according to the VH, the right hemisphere is specialized in negative emotion processing and the left hemisphere is specialized in positive emotion processing.

An attempt to reconcile the VH and the RHH was proposed by , who supported the view according to which the VH and the RHH could coexist (the "modified valence hypothesis", MVH). In this model, the emotional processing involves both hemispheres: the classical hemispheric superiority in a valence-specific emotional analysis would depend on pre-frontal specialization (in which left prefrontal cortex would be specialized in positive emotion processing and right prefrontal cortex would be specialized in negative emotion processing), with posterior areas showing right-hemispheric superiority in all emotional processing (Davidson, 1984; Borod, 1993). Despite this theory remained mostly ignored for decades, it has been recently confirmed by Killgore and Yurgelun-Todd (2007), by means of an fMRI paradigm in which a posterior right-hemispheric activation was shown during nonconscious emotional face processing, but also an anterior bilateral

* Correspondence to: Department of Neuroscience, Imaging and Clinical Science, University of Chieti, BLOCCO A, Via dei Vestini 29, I-66013 Chieti, Italy. Fax: +39 871 35542163.
E-mail address: giulia.prete@unich.it (G. Prete).

valence-specific activation (see also Thomas et al., 2014). Another perspective has been recently proposed by Najt et al. (2013), that of a "negative only valence hypothesis", suggesting right-hemispheric superiority for only some negative emotions (i.e., anger, sadness and fear) but not all (e.g., disgust).

As mentioned above, however, the results of the majority of studies have tended to interpret their laterality results as exclusively in favor of either the VH or the RHH. For example, asked participants to recognize a target emotion in a divided visual field paradigm in which the target and a distracting expression were simultaneously presented, finding that emotional targets were better and faster recognized when presented in the left visual field, supporting the RHH (Torro-Alves et al., 2011). In contrast, Jansari et al. (2011), using a similar paradigm, found support for the VH, since positive emotions were better recognized when presented in the right visual field (RVF) and negative emotions were better recognized when presented in the left visual field (LVF). Moreover, Tamietto et al. (2007), exploiting both unilateral and bilateral presentations of emotional faces and asking participants to detect a target complex emotion, failed to find hemispheric asymmetry in either paradigm. Moreover they found that responses were faster and more accurate in bilateral displays with two emotionally congruent – and physically different – faces, proposing a 'redundant target effect' according to which interhemispheric cooperation, rather than lateralized asymmetry, occurs during the processing of complex emotions (Tamietto et al., 2007).

Importantly, it is generally accepted that the right hemisphere is specialized in low spatial frequency analysis (possibly supporting global or configural processing), whereas the left hemisphere is specialized in high spatial frequency analysis (supporting local or coordinate processing; Sergent, 1982; Hellige, 1996; Proverbio et al., 1997; Peyrin et al., 2003; Han et al., 2002). Interestingly, it seems that the emotional content of faces may be mainly conveyed by a specific range of spatial frequencies, since a number of studies support a dominant role of low spatial frequencies in emotion processing and that of high spatial frequencies in identity recognition of faces (e.g., Vuilleumier et al., 2003); however, also in this domain, there are contrasting results, with some studies supporting the opposite perspective, i.e. identity recognition based on low spatial frequencies and emotional content based on high spatial frequencies (Gao and Maurer, 2011).

In the present study, we attempt to address the above inconsistencies in laterality effects of emotional processing by using a recent paradigm, based on the presentation of images filtered at different spatial frequencies and overlapped to each other in order to constitute a single target stimulus (Schyns and Oliva, 1999). Specifically, 'emotional hybrid faces' are stimuli created by amalgamating the low spatial frequencies of an emotional face with the high spatial frequencies of the same face with a neutral pose. In a study using emotional hybrid faces, Laeng et al. (2010) found that observers could not identify above chance the emotional content of such stimuli, judging them all as neutral, although the emotional expressions (happy, angry, sad or afraid) was present within the range of the lower spatial frequencies (1–6 cpi). Despite being hidden from awareness, the hidden emotional content of stimuli did stimulate the "emotional brain", influencing the participants' friendliness evaluations: hybrid happy faces were judged as more friendly and hybrid angry faces as less friendly than neutral faces (Laeng et al., 2010, 2013a,b; Leknes et al., 2013). This pattern of results suggests that low spatial frequencies can feed a core emotional processing of social stimuli.

However, the use of these stimuli in follow-up studies in which the stimulus presentation was tachistoscopically lateralized, has led to conflicting results, alternatively supporting either the RHH or the VH. That is, one study showed that the presentation of hybrid faces in the left visual field led to lower friendliness scores than the presentation of the same stimuli in the right visual field, generally supporting the VH (Prete et al., 2014a,b). In the same study, it was also shown that this asymmetry could manifest itself more robustly when the presentation time of stimuli became shorter. To further investigate the role of cerebral hemispheres using hybrid faces, tested two patients with callosal resection (D.D. C., with total callosotomy, and A.P, with a large anterior callosotomy) and a control group, exploiting the fact that bilateral tachistoscopic presentation of two identical or different emotional hybrid faces or emotional unfiltered faces would be processed by each contralateral hemisphere. Contrary to the previous study by, Prete et al. (2014a,b) the evidence from the split-brain patients supported the RHH when two hybrid faces were simultaneously presented. Moreover, the RHH was supported when unfiltered faces were presented, but only in the anterior callosotomized patient and in the control group. However, a left-hemispheric superiority was found in the completely callosotomized patient, which could be attributed to extinction in a paradigm with double field presentations (Prete et al., 2013).

In the present study we re-assessed the processing of hybrid faces with the main aim of clarifying the relative strengths of the RHH and the VH. Considering the contrasting results obtained in previous studies, we were interested in better understanding potential hemispheric competences in subliminal emotion processing, exploiting both unilateral and bilateral presentation paradigms. Thus, based upon the paradigms already used, we manipulated two specific conditions (i.e., presentation time and eccentricity of lateralized presentation of the stimuli). Specifically, we investigated (i) which is the shortest exposure time for a hidden emotion to exert an influence on the observers' social judgments, and which are the effects of different exposure times on the hemispheric roles (Experiment 1), given the evidence according to which a shorter presentation time corresponds to a stronger support for the VH (Prete et al., 2014a,b); and (ii) how eccentricity of lateralized presentations (e.g., parafoveal versus extrafoveal) can modulate hemispheric asymmetries (Experiment 2), given the evidence according to which the extrafoveal presentation of hybrid faces supports the RHH (Prete et al., 2013). In addition, we assessed the interaction between parafoveal presentation of two hemifaces (by means of the classical paradigm of chimeric faces) with holistic processing, manipulated by means of face inversion (Experiment 2), assuming that the inversion of faces disrupts the holistic processing based on the low spatial frequency (Tanaka and Farah, 1993; Collishaw and Hole, 2000; Maurer et al., 2002). We hypothesized that in the case in which the RHH and the VH are mutually exclusive, we should find that either the very rapid presentation of lateralized hybrid faces (Experiment 1), other than the chimeric faces paradigm, reveal a RHH pattern (as previously found by means of bilateral presentations), or that the chimeric faces paradigm (Experiment 2), other than the unilateral tachistoscopic presentation, confirm the VH account (as previously found by means of unilateral presentation). To sum up, we tried to disentangle what kind of experimental manipulation could clarify the dispute between the RHH and the VH in the field of subliminal emotions.

Finally, to strengthen the possible evidence of hemispheric asymmetries in subliminal emotion analysis, we tested A.P., a callosotomized patient who lacks the corpus callosum, with the exception of the splenium that was spared by the surgeon. The callosal resection is an invasive and obsolete treatment that was carried out until a few years ago in order to prevent the spread of epileptic foci in drug-refractory epileptic conditions, but it is substantially out of use nowadays. An anterior callosal resection does not lead to the "classical disconnection syndrome" resulting, for example, in alexia for stimuli presented in the left visual field

(Sperry et al., 1969), but represents a unique opportunity that could allow us to draw conclusions based on selective interhemispheric disconnection. Previous studies carried out with split-brain patients showed that both hemispheres are capable of face processing, with some differences in hemispheric competences: for example, the right hemisphere seems better able in perceptual matching tasks and the left hemisphere in verbal description tasks (Levy et al., 1972); moreover, the right hemisphere appears superior in others' faces recognition, whereas the left hemisphere appears superior in own face recognition (Turk et al., 2002; Uddin et al., 2005). Coming to emotional processing, Stone et al. (1996) showed the ability of both hemispheres of a split-brain patient in matching facial expressions with emotional words, but they found higher accuracy of the right hemisphere in a discrimination task. Moreover, Làdavas et al. (1993) presented a split-brain patient with subliminal emotional scenes in the LVF or in the RVF, asking him to discriminate between emotional and neutral content: the authors found that the patient was able to carry out the task, but showed no cerebral asymmetry, except for the right hemisphere producing a stronger autonomic response to emotional than neutral stimuli, corresponding to an increase in heart rate. Due to the rarity of callosotomized patients, there have been few studies on emotional processing that assessed the effects of the resection of the anterior corpus callosum. However, in a recent study, the patient A.P. was tested in a paradigm based on emotional chimeric faces, showing a right-hemispheric dominance (Prete et al., 2014a, b). Moreover, the ability of a complete split-brain patient (D.D.C.) and A.P. in subliminal emotion processing was demonstrated by using hybrid faces (Prete et al., 2013).

On the basis of the above results we expected that the performance of A.P. in hybrid faces processing could contribute relevant information about the complex field of cerebral asymmetries in emotional analysis (Experiments 3 and 4). In fact, we assumed that the intact splenium would prevent the possible spatial neglect found in total split-brain patients (Prete et al., 2013), but the callosal disconnection would help in elucidate hemispheric competences which remain unclear in the literature on emotional processing. It should be noted that, if on one hand the subcortical nature of subliminal emotion analysis is well-known (Adolphs et al., 1994), on the other hand the role of frontal areas in emotional evaluations has also been shown, with particular involvement of the orbito-frontal and the cingulate cortices (see Pessoa and Adolphs, 2010; Tamietto and De Gelder, 2010 for reviews). In this view, and according to the previous results obtained with the same patient (Prete et al., 2013), A.P.'s performance during both unilateral and bilateral presentation paradigms should be seen as a further test of hemispheric competences in the subliminal emotion domain.

2. Experiment 1

In Experiment 1 we exploited a divided visual filed paradigm as in, Prete et al. (2014a,b) but we reduced the presentation time of hybrid faces in order to establish the shortest presentation time needed by these stimuli to modulate the social judgments of participants. Moreover, we tried to stress the condition under which the implicit processing of the emotional information carried by low spatial frequencies can effectively occur, with the main aim to better assess the hemispheric competences in emotion processing.

2.1. Material and methods

2.1.1. Participants

The task was administrated to 64 volunteering participants (40 females; age: 24.83 ± 0.61). The mean handedness score of the sample was 82.59 (± 5.51), as assessed by a short version of the Edinburgh Handedness Inventory (Oldfield, 1971), including 3 left-handed males and 1 left-handed female. All participants had normal or corrected-to-normal vision, and they were unaware of the purpose of the study. They were tested as volunteers at the Psychobiology Laboratory of the University of Chieti (Italy). The experimental procedure was approved by the local ethical committee.

2.1.2. Stimuli

Stimuli consisted of photographs of female and male faces selected from the Karolinska Directed Emotional Faces (Lundqvist et al., 1998), a face database in which professional actors pose different facial expressions corresponding to basic emotional expressions. They were presented in gray-level, at a resolution of 260×270 pixels, measuring $4.8° \times 6.3°$ of visual angle seen at a distance of 72 cm. The faces of 6 females and 6 males were presented in neutral pose (NE) and in hybrid happy (HA) and hybrid angry (AN) poses. The hybrid faces were created by manipulating the images by means of MatLab software (Mathworks Inc., Natick, MA), obtaining one image (happy or angry pose) filtered at low spatial frequency and another image (neutral pose) filtered at high spatial frequency. In order to obtain the hybrid happy and the hybrid angry faces, the emotional face filtered at low spatial frequencies (1–6 cycle/image) was superimposed to the neutral image of the same person filtered at high spatial frequencies (7–128 cycle/image; see Fig. 1). Faces presented as neutral in the experiment were unfiltered or broadband.

2.1.3. Procedure

Participants comfortably sat in a dark room, at a distance of about 72 cm from the computer screen (YASHI, resolution: 1280×1024 pixels, refresh rate: 70 Hz), and they were tested individually. The whole sample 64 participants was divided into two subgroups: 32 participants were tested in a condition in which a mask immediately followed each stimulus ('Mask group': $N=32$; females: 20; age: 25.5; handedness: 85.89), and 32 participants were tested in a similar task but without the mask
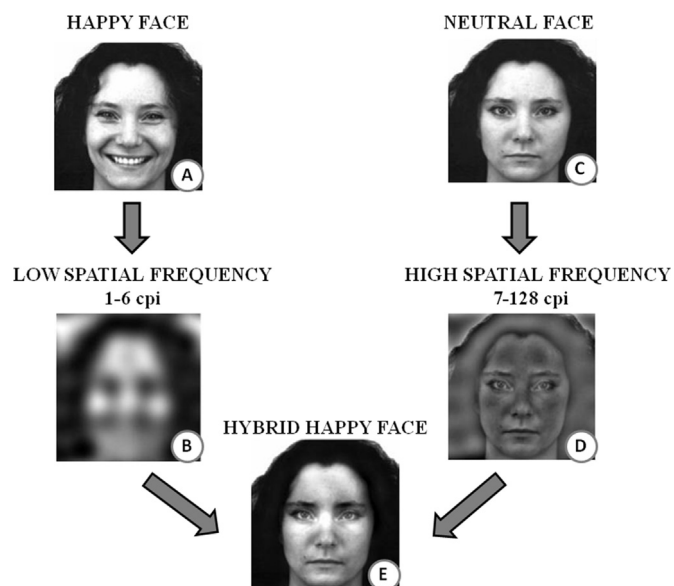

Fig. 1. An example of stimulus preparation: (A) Happy face from the Karolinska Directed Emotional Faces database; (B) same happy face filtered in low spatial frequency (from 1 to 6 cpi); (C) neutral pose of the same individual; (D) same neutral face filtered in high spatial frequency (from 7 to 128 cpi) and (E) "Hybrid happy" face: image obtained by superimposing image B to image D.

following each stimulus ('Non-Mask group': $N=32$; females: 20; age: 24.29; handedness: 79.77).

In each trial, after a blank screen lasting 1 s, a fixation cross ($0.02° \times 0.02°$ of visual angle) positioned in the center of the white screen was presented for 2 s and then the stimulus appeared for either 128 ms, 85 ms, or 28 ms. Stimuli could be presented either in the center of the screen, or laterally, at $2.4°$ of visual angle from the inner edge of the stimulus to the left or to the right of the fixation cross. For the Mask group each stimulus was followed by the presentation of a mask, lasting 100 ms, consisting of a black and white checkerboard (subtending $4.8° \times 6.3°$ of visual angle) located in the same position as the face that immediately preceded it. Then, the screen remained blank until the participant gave her/his rating, after which the next trial started. For the Non-Mask group, the structure of the trial was the same, except for the checkerboard mask, which was absent. The mask ensured that each stimulus was viewed just for its presentation time, removing the possibility of a persistent trace of the image onto the retina. However, since in previous studies with hybrid faces, masking was not used, we chose to test its effect comparing the two conditions (with/without the presence of the mask).

All stimuli were shown three times and their presentation order was randomized across and within participants.

Participants were asked to keep their gaze at fixation in the center of the screen until the face disappeared. Then they were required to evaluate how much the face had appeared friendly, using a 5-point Likert scale in which 1 corresponded to "very unfriendly" and 5 corresponded to "very friendly" (1: "very unfriendly"; 2: "unfriendly"; 3: "neutrality point"; 4: "friendly"; 5: "very friendly"). Half participants in each subgroup pressed the numeric keys using the right hand, the other half using the left hand.

Before starting the experimental session, participants were presented with 10 stimuli to familiarize with the task and with the friendliness scale. The whole paradigm was subdivided into three parts, to allow participants to make two breaks, in order to remain vigilant for the whole duration of the experiment.

The task was administered by means of E-Prime software (Psychology Software Tools, Inc., Pittsburgh, PA) and it lasted about 40 min.

2.2. Results

Statistical analyzes were conducted by means of the software Statistica 8.0.550 (StatSoft. Inc., Tulsa, USA). Due to the small number of left-handers and considering the possible confounding results related to participants' handedness, the 4 left-handed participants were excluded from the analysis. Furthermore, three right-handed females were excluded from the analysis because their mean scores were above 2 standard deviations from the sample mean. A repeated-measures analysis of variance (ANOVA) was carried out, using Emotion (happy, neutral, angry), Sex of face (female, male), Position (center, left, right) and Time (28 ms, 85 ms, 128 ms) as within-subject factors, and the friendliness ratings of faces as dependent variable. Post-hoc comparisons were carried out by Duncan tests.

In a preliminary split-plot ANOVA, Sex of participants (female, male), Hand used to respond (left, right) and Mask (present, absent) were considered as between-subject factors. However, none of these factors were significant as main effects (Sex of participants: $F_{(1, 49)}=0.07$, $p=0.794$; Hand: $F_{(1, 49)}=0.44$, $p=0.509$; Mask: $F_{(1, 49)}=0.85$, $p=0.361$), nor in interaction with other between- and within-subject factors, thus they were excluded from further analyzes.

The interaction Emotion X Sex of face X Position was significant ($F_{(4, 224)}=4.5$, $MSE=0.1$, $p=0.002$, $\eta^2=0.07$; Fig. 2). Of note, female
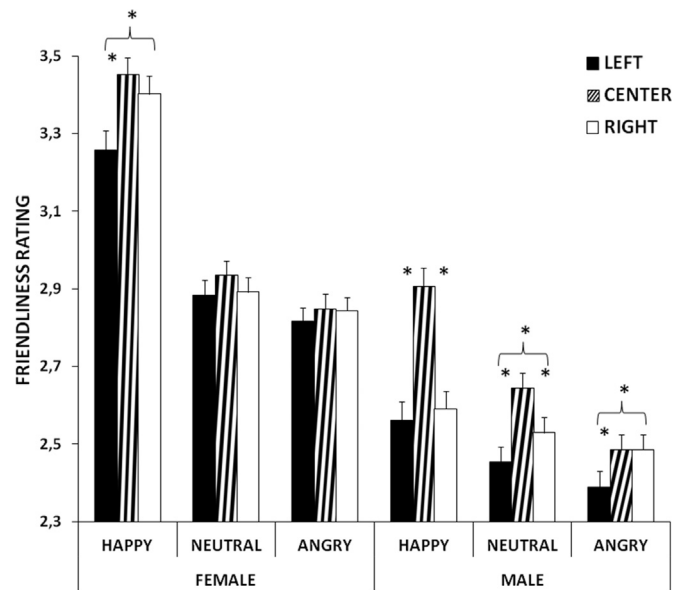
Fig. 2. Interaction Emotion X Position X Sex of face: mean ratings of hybrid faces (happy, neutral and angry) in left-side (black bars), central (textured bars) and right-side (white bars) presentation, for female (left panel) and male (right panel) faces, on the friendliness scale (range: 1–5). Error bars represent standard errors. Asterisks show the significant comparisons ($p<0.05$) within female and male faces.

faces shown at each position and in each emotional pose were judged as more friendly than male faces ($p<0.001$, for all comparisons). Importantly, female happy faces were judged as less friendly when presented in the left than in the right visual field and centrally ($p<0.001$, for both comparisons), whereas there were no differences among positions for neutral and angry female faces. Male happy faces were judged as more friendly when presented centrally than laterally ($p<0.001$, for both comparisons), but there was no significant difference between left and right visual field presentations ($p=0.386$); on the other hand, male neutral and angry faces were judged as less friendly when presented in the left than in the right visual field (neutral: $p=0.045$, angry: $p=0.008$), and centrally (neutral: $p<0.001$; angry: $p=0.009$); finally, only neutral male faces were judged as more friendly when presented centrally than in the right visual field ($p<0.001$).

The interaction Emotion X Position was significant ($F_{(4, 224)}=7.5$, $MSE=0.15$, $p<0.001$, $\eta^2=0.12$). Post-hoc comparisons indicated that in all positions happy faces were judged as more friendly than neutral and angry faces ($p<0.001$, for all comparisons), and in central and left visual field presentations angry faces were judged as less friendly than neutral faces (central: $p<0.001$; left visual field: $p=0.042$), whereas this comparison failed to be significant in the right visual field presentations ($p=0.164$). Moreover, happy faces were judged as more friendly when presented in right than in left visual field ($p=0.003$), and they were judged as more friendly when presented centrally than laterally ($p<0.001$, for both comparisons). Neutral faces were judged as more friendly when presented centrally than in the left visual field ($p<0.001$) and in the right visual field ($p=0.007$). Finally, angry faces were judged as less friendly when presented in the left visual field than in the right visual field ($p=0.039$) and centrally ($p=0.042$).

The interaction Emotion X Sex of face was significant ($F_{(2, 112)}=35.36$, $MSE=0.24$, $p<0.001$, $\eta^2=0.39$), and all post-hoc comparisons were significant. In the interaction Sex of face X Position ($F_{(2, 112)}=8.54$, $MSE=0.13$, $p<0.001$, $\eta^2=0.13$) all post-hoc comparisons were significant except that between female faces presented centrally and in the right visual field. The interaction

Table 1

Results of Duncan's post-hoc comparisons for the interaction Emotion X Time (the 'Mean' column contains the mean friendliness ratings for each condition).

EMOTION X TIME		Mean	HAPPY			NEUTRAL			ANGRY		
			28 ms	85 ms	128 ms	28 ms	85 ms	128 ms	28 ms	85 ms	128 ms
HAPPY	28 ms	2.99	–								
	85 ms	3.04	*0.083*	–							
	12 8ms	3.06	**0.011**	*0.366*	–						
NEUTRAL	28 ms	2.77	**< 0.001**	**< 0.001**	**< 0.001**	–					
	85 ms	2.74	**< 0.001**	**< 0.001**	**< 0.001**	*0.286*	–				
	128 ms	2.66	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	**0.009**	–			
ANGRY	28 ms	2.70	**< 0.001**	**< 0.001**	**< 0.001**	**0.011**	*0.119*	*0.256*	–		
	85 ms	2.63	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	*0.153*	**0.014**	–	
	128 ms	2.61	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	*0.057*	**< 0.001**	*0.563*	–

Emotion X Time was significant ($F_{(4, 224)}=6.81$, $MSE=0.12$, $p < 0.001$, $\eta^2=0.11$, see Table 1 for all post-hoc values).

The main effect of Emotion was significant ($F_{(2, 112)}=50.6$, $MSE=0.83$, $p < 0.001$, $\eta^2=0.47$; hybrid happy: 3.03 ± 0.022; neutral: 2.72 ± 0.016; hybrid angry: 2.64 ± 0.016). Post-hoc comparisons showed that happy faces were judged as more friendly than both neutral and angry faces ($p < 0.001$, for both comparisons), and that angry faces were judged as slightly less friendly than neutral faces ($p=0.054$). The main effect of Position was significant ($F_{(2, 112)}=9.6$, $MSE=0.63$, $p < 0.001$, $\eta^2=0.15$; center: 2.88 ± 0.019; left: 2.73 ± 0.019; right: 2.79 ± 0.019). Post-hoc comparisons indicated that stimuli presented centrally were judged as more friendly than those presented both in the left visual field ($p < 0.001$) and in the right visual field ($p=0.012$), and that stimuli presented in the LVF were judged as slightly less friendly than those presented in the RVF ($p=0.072$). The main effect of Sex of face was significant ($F_{(1, 56)}=66.78$, $MSE=2.62$, $p < 0.001$, $\eta^2=0.54$; female: 3.04 ± 0.014; male: 2.56 ± 0.014), female faces being judged as more friendly than male faces. The main effect of Time was not significant ($F_{(2, 112)}=1.33$, $p=0.268$; 28 ms: 2.82 ± 0.019; 85 ms: 2.8 ± 0.019; 128 ms: 2.78 ± 0.019).

2.3. Discussion

Experiment 1 revealed that 28 ms were sufficient to processing hybrid faces, strengthening the evidence that low spatial frequencies influence the social evaluation of emotional stimuli, even if a longer exposure time allows for more differentiated friendliness evaluations. This pattern of results contrasts with that of Bar et al. (2006) who found that observers needed at least 39 ms to judge the threat of faces, whereas 26 ms were not sufficient (all stimuli were followed by a mask consisting in black lines on a gray and white background). A possible explanation for the difference between these two studies is the fact that Bar et al. asked participants to evaluate the threatening level of neutral (unfiltered) faces only, thus testing for the presence of "first impressions", whereas in the present study, besides unfiltered neutral faces, the hybrid stimuli did contain an emotional expression though "invisible". However, the two studies are in agreement concerning the central role of the low spatial frequencies in social evaluation of faces. Moreover, the results of Experiment 1 confirmed and extended those of with hybrid faces: stimuli presented in the left visual field (right hemisphere) were judged as less friendly than those presented in the right visual field (left hemisphere), confirming the validity of the VH, and this effect was stronger for female happy faces and for male neutral and angry faces (see Fig. 2). Importantly, the effects obtained could not be ascribed to trace phenomena ensuing presentation (buffering, afterimages, etc.) as demonstrated by the fact the results were not influenced by masking. To conclude, the hypothesis according to which the very rapid presentation time could disconfirm the VH, possibly supporting the RHH, can be excluded on the basis of the present results.

3. Experiment 2

Differently from results of Experiment 1, supporting the VH, a previous study making use of bilateral presentations of two hybrid faces had provided support for the RHH (Prete et al., 2013). In an attempt to resolve this contradiction, in Experiment 2 we manipulated the composition of stimuli, taking advantage of a peculiar type of bilateral presentation, chimeric faces. We tested the possibility that presenting a chimeric face in the center of the screen, thus associating two identical or different emotional hybrid hemifaces to the two hemifields, could provide useful hints for settling the dispute between the right hemisphere and the valence hypothesis in the domain of implicit emotion processing. In fact, previous studies showed that the presentation of two emotional hemifaces in the two visual hemifields (parafoveal presentation) showed no asymmetries with unfiltered stimuli (Prete et al., 2014a,b), whereas the bilateral presentation of two separate emotional filtered or unfiltered faces (extrafoveal presentation), supported the right hemisphere hypothesis (Prete et al., 2013). Considering these types of evidence together, it could be hypothesized that the right-hemispheric superiority found by means of the bilateral presentation paradigm was due to a form of "bilateral redundancy effect": the simultaneous extrafoveal presentation of two stimuli could be the reason *per se* of cerebral asymmetries, possibly due to an attentional bias more than to a cerebral asymmetry in emotion processing (Kim et al., 1990). On the other hand, if the right-hemispheric superiority in subliminal emotion processing found with the bilateral presentations is consistent, it should also occur in the case of hybrid chimeric faces. Thus, in this experiment, we expected that in the case a right-hemispheric supremacy in the processing of hybrid chimeric faces would be found the RHH would be supported, whereas, the VH would be supported, by finding a hemispheric asymmetry in a valence-specific fashion (as in Experiment 1, and in Prete et al., 2014a,b). Furthermore, we tested the effect of disrupting the configural processing of emotional faces, by presenting the stimuli either in upright canonical orientation or upside-down.

3.1. Material and methods

3.1.1. Participants

The task was administrated to a new group of 54 volunteers (28 female and 26 male; age: 21.57 ± 0.39). All participants were right-handers and their mean handedness score was 61.57 (± 2.35), as assessed by a short version of the Edinburgh Handedness Inventory (Oldfield, 1971). All participants had normal or corrected-to-normal vision and they were unaware of the purpose of the study. All other aspects were the same as in the previous experiment.

3.1.2. Stimuli

Source faces used to create chimeras were the same as those used in Experiment 1. In the present experiment, the faces of 4 females and 4 males in neutral pose and the hybrid happy and hybrid angry images corresponding to the same individuals were selected. Each of these 24 faces was divided into two halves (left and right neutral, happy and angry hemifaces) and each hemiface was coupled with all of the other hemifaces belonging to the same individual, thus forming 9 chimeric faces for each identity, three of which were in fact non-chimeric (left hemiface/right hemiface: HA/HA, AN/AN, NE/NE, HA/AN, AN/HA, HA/NE, NE/HA, AN/NE, NE/AN). In order to reduce the sense of strangeness due to the juxtaposition of two hemifaces, a thin white stripe was inserted between the two halves (width: 0.02° of visual angle). All images were then digitally rotated upside-down in order to obtain the inverted version.

3.1.3. Procedure

Participants were tested individually, sitting in a dark room at a distance of about 72 cm from the computer screen. The structure of each trial was the following: after a blank screen lasting 1 s, a black fixation cross (0.02° × 0.02° of visual angle) was presented centrally for 1 s, then the stimulus appeared for 128 ms in the center of the screen, and after its disappearance the screen remained blank until the participant gave her/his rating. Immediately thereafter, the next trial started.

Participants were asked to keep their gaze at the fixation cross in the center of the screen, they were informed that face images would be presented upright and upside-down, and that they would be required to evaluate how much each face appeared friendly, using the same 5-point Likert scale as in Experiment 1, in which 1 corresponded to "very unfriendly" and 5 corresponded to "very friendly".

All participants performed two sessions, one for each responding hand, and the order of the sessions was counterbalanced among participants. In each session, half stimuli were presented in canonical orientation (upright) and the other half were presented in inverted orientation (upside-down); the presentation order of stimuli was randomized across and within participants. Before starting the experimental sessions, participants were presented with 6 stimuli used to familiarize with the task and with the friendliness scale. Between the two sessions, participants were allowed to make a short break and they were asked to change the responding hand.

The task was presented by means of E-Prime software (Psychology Software Tools, Inc., Pittsburgh, PA) and it lasted about 20 min.

3.2. Results

Statistical analyzes were conducted by means of the software Statistica 8.0.550 (StatSoft. Inc., Tulsa, USA). A repeated measures ANOVA was carried out using Orientation (upright, upside-down), Condition (left hemiface/right hemiface: HA/HA, AN/AN, NE/NE,
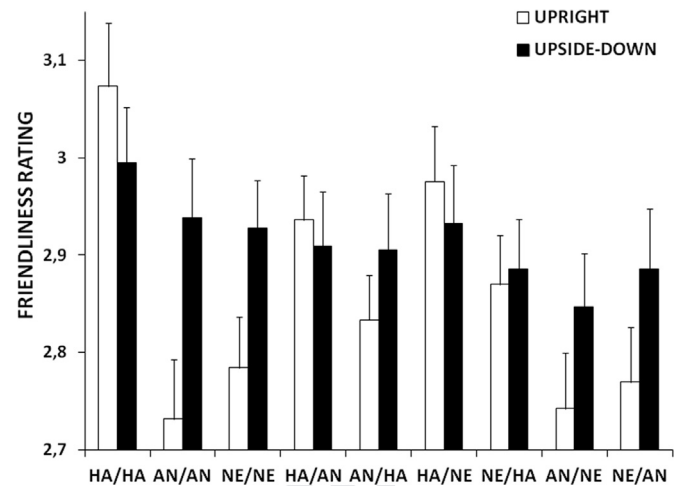
Fig. 3. Interaction Orientation X Condition: mean ratings of hybrid chimeric faces in canonical (white bars) and inverted (black bars) orientation on the friendliness scale (range: 1–5). Error bars represent standard errors.

HA/AN, AN/HA, HA/NE, NE/HA, AN/NE, NE/AN) and Sex of face (female, male) as within-subject factors, and the friendliness ratings of stimuli as dependent variable. Post-hoc comparisons were carried out by Duncan tests.

In a preliminary split-plot ANOVA Sex of participants (female, male) was used as between-subject factor, and Hand used to respond (left, right) was used as additional within-subject factor, but they were not significant as main effects (Sex of participants: $F_{(1, 49)} = 0.23$, $p = 0.634$; Hand used to respond: $F_{(1, 49)} = 0.02$ $p = 0.888$), nor in interaction with any other factors, so they were excluded from further analyzes. Furthermore, three participants were excluded from the analysis because their mean scores were above 2 standard deviations from the sample mean (2 female and 1 male).

The interaction Orientation X Condition was significant ($F_{(8, 400)} = 4.93$, $MSE = 0.09$, $p < 0.001$, $\eta^2 = 0.09$, Fig. 3). Post-hoc comparisons showed that the ratings for upside-down presented stimuli were randomly assigned, whereas the upright HA/HA face was judged as more friendly than all others except the upside-down HA/HA face, and that the upright AN/AN face was judged as less friendly than all others except the upright NE/NE, AN/NE and NE/AN faces. All post-hoc results are reported in Table 2, the main results concerning the higher friendliness judgments for upright HA/AN than AN/HA face and for upright HA/NE than NE/HA face, showing the greater weight of the face presented in the left visual field (right hemisphere) for the final friendliness evaluation.

The interaction Sex of face X Orientation was significant ($F_{(1, 50)} = 4.66$, $MSE = 0.21$, $p = 0.036$, $\eta^2 = 0.09$). Post-hoc comparisons revealed that female faces were judged as more friendly than male faces, in both upright ($p = 0.005$) and inverted orientations ($p < 0.001$), and that only female faces were judged as more friendly when presented upside-down than upright ($p = 0.001$).

The main effect of Condition was significant ($F_{(8, 400)} = 10.44$, $MSE = 0.11$, $p < 0.001$, $\eta^2 = 0.17$, see Table 3 for all post-hoc results), whereas the main effects of Orientation and Sex of face failed to reach statistical significance (Orientation: $F_{(1, 50)} = 1.41$, $p = 0.240$; upright faces: 2.857 ± 0.019, upside-down faces: 2.914 ± 0.018; Sex of face: $F_{(1, 50)} = 1.87$, $p = 0.179$; female faces: 2.954 ± 0.028, male faces: 2.817 ± 0.025).

3.3. Discussion

The results of Experiment 2 showed that the upside-down presentation of the hybrid faces prevented the modulation of

Table 2
Results of Duncan's post-hoc comparisons for the interaction Orientation X Condition (the mean friendliness ratings for each condition are represented in Fig. 3).

ORIENTATION X CONDITION		UPRIGHT ORIENTATION									UPSIDE-DOWN ORIENTATION								
		HA/HA	AN/AN	NE/NE	HA/AN	AN/HA	HA/NE	NE/HA	AN/NE	NE/AN	HA/HA	AN/AN	NE/NE	HA/AN	AN/HA	HA/NE	NE/HA	AN/NE	NE/AN
UPRIGHT ORIENTATION	HA/HA	–																	
	AN/AN	<0.001	–																
	NE/NE	<0.001	0.270	–															
	HA/AN	0.003	<0.001	0.002	–														
	AN/HA	<0.001	0.033	0.254	0.043	–													
	HA/NE	0.030	<0.001	<0.001	0.394	0.004	–												
	NE/HA	<0.001	0.004	0.068	0.198	0.425	0.038	–											
	AN/NE	<0.001	0.798	0.365	<0.001	0.053	<0.001	0.007	–										
	NE/AN	<0.001	0.409	0.732	0.001	0.163	<0.001	0.035	0.531	–									
UPSIDE-DOWN ORIENTATION	HA/HA	0.068	<0.001	<0.001	0.217	0.001	0.649	0.013	<0.001	<0.001	–								
	AN/AN	0.003	<0.001	0.002	0.955	0.040	0.393	0.186	<0.001	<0.001	0.219	–							
	NE/NE	0.002	<0.001	0.003	0.853	0.061	0.332	0.250	0.001	0.001	0.176	0.819	–						
	HA/AN	<0.001	<0.001	0.011	0.576	0.132	0.185	0.427	0.004	<0.001	0.086	0.553	0.669	–					
	AN/HA	<0.001	<0.001	0.012	0.536	0.146	0.167	0.460	0.005	<0.001	0.077	0.513	0.633	0.932	–				
	HA/NE	0.003	<0.001	0.002	0.932	0.050	0.371	0.219	0.001	<0.001	0.201	0.895	0.909	0.614	0.576	–			
	NE/HA	<0.001	0.001	0.033	0.326	0.270	0.080	0.711	0.015	0.003	0.031	0.309	0.399	0.629	0.671	0.355	–		
	AN/NE	<0.001	0.016	0.172	0.080	0.754	0.010	0.588	0.102	0.029	0.003	0.074	0.107	0.211	0.230	0.091	0.394	–	
	NE/AN	0.001	0.001	0.036	0.318	0.284	0.077	0.730	0.017	0.003	0.030	0.302	0.385	0.614	0.649	0.345	1.000	0.414	–

friendliness judgments (e.g., happy/happy face was not differently evaluated than angry/angry face), confirming that the emotional processing of hybrid faces is based on a configural analysis of stimuli. Moreover, only female faces were judged as more friendly when presented upside-down than upright. A possible explanation for this unexpected result could be that when presented in canonical orientation, chimeric and hybridized faces could appear 'strange' and thus they could be evaluated as relatively unfriendly. When presented in upside-down orientation the sense of strangeness could disappear specifically because the presence of shadows (due to the overlap of two images) and the difference between the two hemifaces could be ignored in inverted orientation, leading to a more positive judgment. This process occurs only for female faces possibly because female faces are generally evaluated as more friendly than male faces (i.e., Prete et al., 2014a,b), so that the reduced relevance of 'negative' aspects due to inversion could be enough to increase friendliness judgments for female but not for male faces. Importantly, for the upright presentation, the friendliness judgments of hybrid chimeric faces confirmed the validity of the right hemisphere hypothesis. In fact, the main friendliness modulations were obtained depending on the emotional expression of the left hemiface: the happy/angry face was evaluated as more friendly than the angry/happy face, as well as the happy/neutral face was evaluated as more friendly than the neutral/happy face (higher friendliness evaluations when the happy hemiface was presented in the left than in the right hemifield). Similarly, the neutral/neutral face was judged as less friendly than the happy/neutral face, but not less friendly than the neutral/happy face.

Thus, Experiment 2 supports the RHH, whereas Experiment 1 had provided validity for the VH. Presentation time of stimuli does not seem to be a plausible reason for this difference, because the same duration as in Experiment 2 (128 ms) was also used in Experiment 1, in which presentation time was neither a main effect, nor interacted in a three-way interaction with emotion and position of the stimuli. Moreover, hemispheric asymmetries in chimeric faces paradigm had been found also in free viewing, without any limitation of presentation time (Levy et al., 1983a,b; Levine and Levy, 1986; Bourne, 2008).

4. Experiment 3

Experiments 1 and 2 lend support to the VH and the RHH, respectively. Despite the role of each hemisphere in implicit emotion processing as shown by the two tasks cannot be generalized, these contrasting results recapitulate those already found by means of analogous paradigms (unilateral tachistoscopic presentations: Prete et al., 2014a,b; bilateral presentations: Prete et al., 2013). One preliminary conclusion is that each account is typically supported depending on whether unilateral or bilateral presentations of facial stimuli are used. To better investigate whether such hemispheric asymmetries and interhemispheric dominance/suppression mechanisms could be made apparent in these tasks, we decided to test A.P., an anterior callosotomized patient, whose partial disconnection, saving the splenium, would ensure interhemispheric communication between visual regions and at the same time would avoid the spatial extinction typically found in split-brain patients (Hausmann et al., 2003; Corballis et al., 2005).

In Experiment 3, patient A.P. performed a similar paradigm as that described in Experiment 1. We hypothesized that a split-brain patient with an intact splenium, which is responsible of occipital cortex interconnection (Aboitiz and Montiel, 2003), ensured that the patient could see stimuli presented in both visual hemifields, without the risk of a potential extinction for lateralized stimuli,

Table 3

Results of Duncan's post-hoc comparisons for the main effect of Condition (the 'Mean' column contains the mean friendliness ratings for each condition).

CONDITION	Mean	HA/HA	AN/AN	NE/NE	HA/AN	AN/HA	HA/NE	NE/HA	AN/NE	NE/AN
HA/HA	3.03	–								
AN/AN	2.83	< 0.001	–							
NE/NE	2.86	< 0.001	0.518	–						
HA/AN	2.92	< 0.001	0.013	0.057	–					
AN/HA	2.87	< 0.001	0.319	0.676	0.119	–				
HA/NE	2.95	0.012	< 0.001	0.005	0.332	0.014	–			
NE/HA	2.88	< 0.001	0.230	0.523	0.165	0.790	0.024	–		
AN/NE	2.79	< 0.001	0.239	0.082	< 0.001	0.368	< 0.001	0.021	–	
NE/AN	2.83	< 0.001	0.819	0.414	0.007	0.244	< 0.001	0.169	0.305	–

depending on the hand used to respond (contralateral hemispheric activation). A.P. had been previously tested in a bilateral visual field paradigm using hybrid faces (Prete et al., 2013): in that study, A.P.'s performance provided support for the right hemisphere hypothesis, as did the control group.

4.1. Material and methods

4.1.1. Participants

A.P. is a 49-year-old man, who underwent the surgical resection of a large anterior portion of the corpus callosum (CC) to reduce the spread of epileptic seizures. The surgery was carried out in 1993 and it left intact only the splenium (Fig. 4).

A.P.'s postoperative IQ was 87, as measured by means of the Wechsler Adult Intelligence Scale (WAIS), and his laterality quotient was $+10$, according to the Edinburgh Handedness Inventory (Oldfield, 1971). A.P. had no visual impairments or psychiatric symptoms, and he was tested at the Epilepsy Center of the Polytechnic University of Marche (Torrette, Ancona), during a pause between routine neurological examinations.

4.1.2. Stimuli and procedure

The patient was tested with the same paradigm as that described in Experiment 1. In particular, A.P. performed the same task as the 'Non-Mask group', and he was presented stimuli using only the presentation time of 85 ms (the intermediate time used
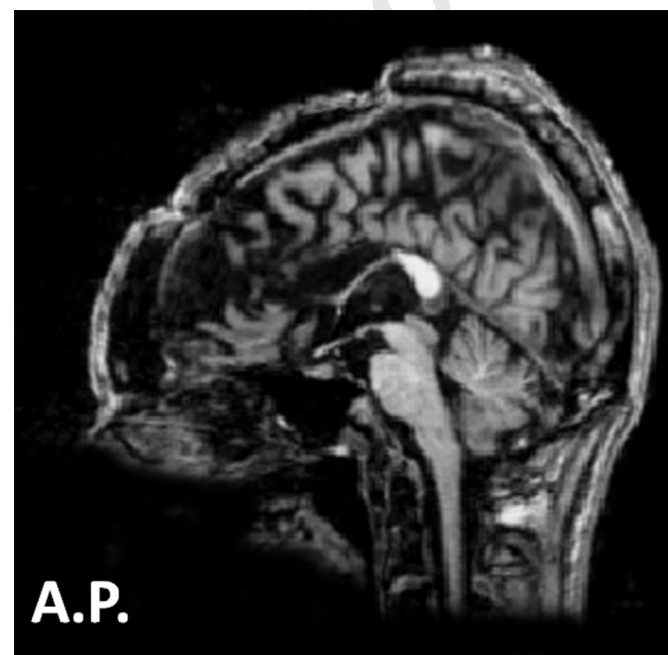
Fig. 4. Midsagittal MRI of A.P.'s brain, showing the section of the corpus callosum, which saves the splenium.

with healthy participants). He responded with the left hand in a first session and with the right hand in a second session.

4.2. Results

The friendliness scores of A.P. in each session (left hand and right hand) were compared with the 95% confidence intervals of healthy participants who responded with the same hand (left and right, respectively) in Experiment 1. In particular, the comparisons were carried out between A.P.'s responses and healthy participants' responses in the 'Non-Mask group' ($N=14$, for each hand), to stimuli presented for 85 ms (from the sample of healthy participants, both left-handers and outliers were excluded, as in Experiment 1).

Comparisons for the left hand session showed that the mean friendliness scores of A.P. were above the cut-off of the 95% confidence intervals of the healthy participants when an angry face was shown in each position, and a neutral face was shown centrally and in the right visual field (Fig. 5).

Importantly, t-tests showed that A.P. did not differentiate between the three different emotional expressions (happy: 3.22 ± 0.15, neutral: 3.14 ± 0.14, angry: 3.19 ± 0.14; happy versus angry: $t_{(5)}=0.20$, $p=0.849$; happy versus neutral: $t_{(5)}=0.50$, $p=0.635$; neutral versus angry: $t_{(5)}=-0.20$, $p=0.846$) independently of their position, whereas his judgments were slightly lower for stimuli presented in the left visual field than in the right visual field, although the difference did not reach statistical significance ($t_{(5)}=-2.10$, $p=0.089$; left visual field: 2.97 ± 0.16, right visual field: 3.28 ± 0.12, center: 3.30 ± 0.14), independently of their emotional content.
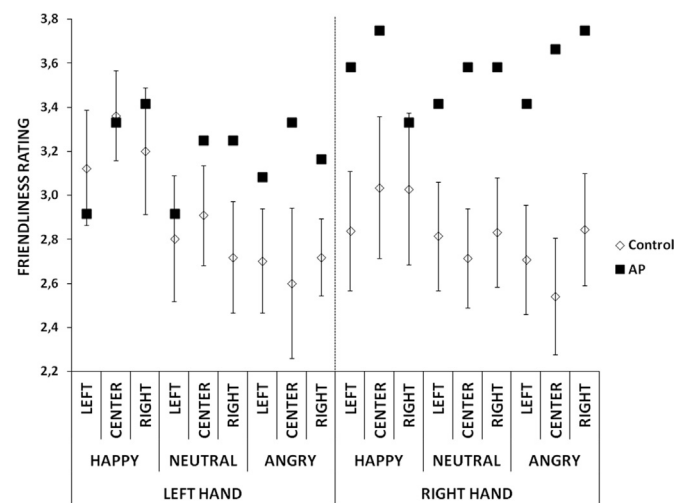

Fig. 5. 95% confidence intervals of the healthy participants (lines) and A.P.'s means (squares) on the friendliness scale (range: 1–5) for happy, neutral and angry faces, presented in the left visual field, centrally, and in the right visual field, in the left hand (left panel) and in the right hand (right panel) session.

The comparisons of the right hand session showed that A.P.'s friendliness scores were above the cut-off of the 95% confidence intervals in all conditions, except for the condition in which a happy face was shown in the right visual field (Fig. 5).

Also in this session, t-tests showed that the patient did not differentiate between happy, neutral and angry faces (happy: 3.55 ± 0.09, neutral: 3.53 ± 0.09, angry: 3.61 ± 0.10; happy versus angry: $t_{(5)} = -1.00$, $p = 0.363$; happy versus neutral: $t_{(5)} = 0.41$, $p = 0.695$; neutral versus angry: $t_{(5)} = -1.46$, $p = 0.203$), regardless of their position, and that his judgments were slightly lower for stimuli presented in the left visual field (3.47 ± 0.09) than in the right visual field (3.55 ± 0.09) and centrally (3.66 ± 0.10), regardless of their emotional content, again without reaching statistical significance (left versus right: $t_{(5)} = -0.88$, $p = 0.41$; center versus left: $t_{(5)} = 1.56$, $p = 0.18$; center versus right: $t_{(5)} = 1.08$, $p = 0.33$).

Thus, the mean scores of A.P. for stimuli presented in the three positions, independently from their emotional content and from the hand used to respond, were computed and compared with the 95% confidence intervals of healthy participants. At all positions, the mean scores of A.P. were above the cut-off of the 95% confidence intervals of healthy participants (Fig. 6).

Moreover, considering the means of A.P. for responses given with both hands, the t-tests showed that his friendliness judgments were lower for stimuli presented in the left than in the right visual field ($t_{(11)} = -2.18$, $p = 0.05$) and centrally ($t_{(11)} = -2.02$, $p = 0.068$).

Finally, A.P.'s responses were significantly lower when he used his left hand than when he used his right hand ($t_{(5)} = -4.38$, $p = 0.007$, left hand: 3.185 ± 0.11, right hand: 3.565 ± 0.10).

4.3. Discussion

The results of A.P. could be view as in line with the valence hypothesis: although he did not attribute different friendliness scores to the hybrid faces, he judged as less friendly the stimuli presented in the left visual hemifield (right hemisphere) than those presented in the right visual hemifield (left hemisphere). Similarly, his judgments were lower when he responded using the left hand (right hemisphere), than the right hand (left hemisphere). All these evidence seem to support the fact that the left-hemispheric activation (due to both the RVF presentation and the right hand response) leads to a more positive emotional judgments than the right-hemispheric activation (due to both the LVF presentation and the left hand response), as proposed by the VH. It should be noted, however, that A.P.'s responses were not
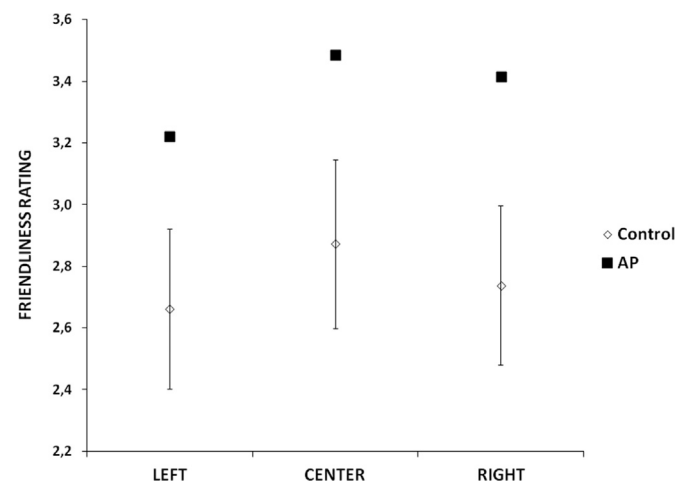
influenced by the emotional content of the images.

5. Experiment 4

In Experiment 3, the results of A.P. confirmed those of healthy participants: stimuli presented in the LVF were judged as less friendly than those presented in the RVF, supporting the valence hypothesis. However, results of healthy participants in Experiment 2 provided support for the right hemisphere hypothesis. Thus, in the present experiment we tested A.P. with the same paradigm used in Experiment 2. We expected that the results of the callosotomized patient in this paradigm may further clarify the dispute between the valence and the right hemisphere hypotheses.

5.1. Material and methods

5.1.1. Stimuli and procedure

A.P. performed the same paradigm as described in Experiment 2. He performed the first session using the right hand, and the second session using the left hand.

5.2. Results

The friendliness scores of A.P. in each session (left hand and right hand) were compared with the 95% confidence intervals of healthy participants tested in Experiment 2 ($N = 51$). Comparisons for each session were carried out considering upright and upside-down faces, separately.

For the left hand session, A.P.'s friendliness scores for upright faces were above the 95% confidence intervals of healthy participants for all chimeric faces, except for the HA/AN face (Fig. 7). The patient's friendliness judgments were not modulated by the emotional content of upright hybrid chimeric faces: for example, his highest judgment was that given to the NE/AN face, and his evaluation of the AN/AN face was higher than that of the HA/HA face, showing that his evaluations were not attributed according to the emotional content of faces.

A.P.'s friendliness scores for upside-down faces, in the left hand session, were above the 95% confidence intervals of healthy participants for the HA/AN, NE/HA and AN/NE faces, and they were below them for the HA/HA, AN/AN, HA/NE and NE/AN faces
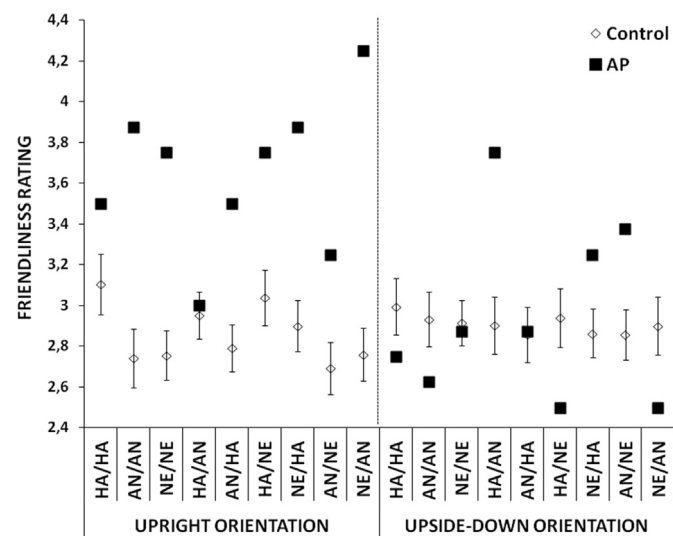

Fig. 6. 95% confidence intervals of the healthy participants (lines) and A.P.'s means (squares) on the friendliness scale (range: 1–5) for hybrid faces presented in the left visual field, centrally and in the right visual field.

Fig. 7. Left hand session: 95% confidence intervals of the healthy participants (lines) and A.P.'s means (squares) on the friendliness scale (range: 1–5) for upright (left panel) and upside-down (right panel) chimeric hybrid faces.
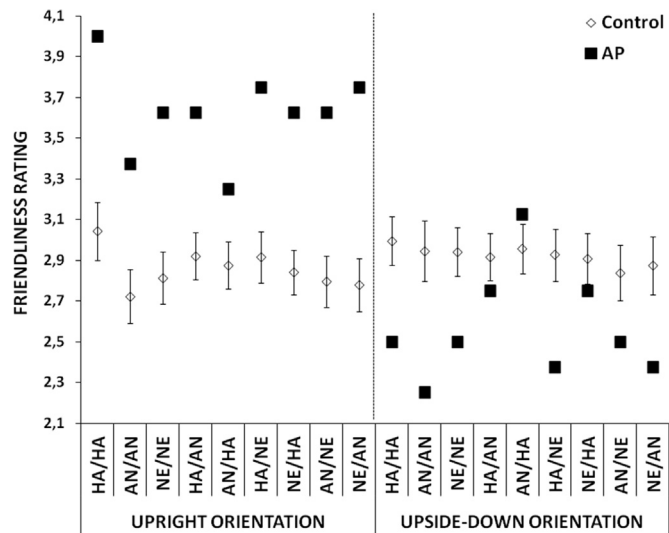
Fig. 8. Right hand session: 95% confidence intervals of the healthy participants (lines) and A.P.'s means (squares) on the friendliness scale (range: 1–5) for upright (left panel) and upside-down (right panel) chimeric hybrid faces.

(Fig. 7). Also for stimuli presented upside-down, A.P. did not attribute congruent friendliness scores to the hybrid faces, using the left hand: for example, his rating was higher for the HA/AN face than for the HA/HA face.

In the right hand session, A.P.'s friendliness scores for upright faces were above the 95% confidence intervals of healthy participants for all chimeric faces (Fig. 8).

Importantly, in this session the pattern of results of A.P. was very similar to that of the healthy participants: his friendliness ratings were higher for HA/HA and lower for AN/AN faces with respect to the NE/NE condition. The friendliness judgments were higher for HA/AN than for AN/HA face, and for HA/NE than for NE/HA face. Moreover, they were lower for AN/NE than for NE/AN faces.

Finally, in the right hand session, A.P.'s friendliness scores for upside-down faces were below the 95% confidence intervals of healthy participants in all conditions, except in the AN/HA condition, in which they were above them (Fig. 8). The friendliness ratings of A.P. seem to be randomly distributed in this session: his judgments were higher for both the AN/HA and the HA/AN face than for the HA/HA face.

T-tests showed a trend in favor of higher friendliness scores when A.P. used the left than the right hand ($t_{(3)}=2.61$, $p=0.079$; left hand: 3.29 ± 0.04; right hand: 3.09 ± 0.08). For the left hand session, his judgments were higher for upright than for upside-down faces ($t_{(3)}=4.00$, $p=0.028$; upright: 3.638 ± 0.12; upside-down: 2.94 ± 0.14), and the same is true for the right hand session ($t_{(3)}=6.45$, $p=0.007$; upright: 3.625 ± 0.16; upside-down: 2.569 ± 0.12). However, the *t*-test comparing the scores given to upright faces using the left or the right hand was not significant ($t_{(3)}=0.24$, $p=0.824$), but it was significant for upside-down faces ($t_{(3)}=4.08$, $p=0.026$).

5.3. Discussion

Results of Experiment 4 indicated that A.P. was not able in discriminating among upside-down hybrid faces, in both left and right hand sessions. This can be interpreted as due to the impossibility of processing faces as a configuration because of the upside-down presentation of faces. Moreover, A.P.'s judgments were better when he used the left hand (right hemisphere) than the right hand but only for the upside-down stimuli, possibly indicating a higher right-hemispheric ability in face processing or a more positive right-hemispheric appreciation for emotional face in general. Importantly, A.P. seemed to attribute appropriate evaluations to the upright hybrid faces, only when he was required to respond with the right (dominant) hand. In this condition, the sole in which his friendliness ratings were congruent with the emotional content of stimuli and with the responses of healthy participants, A.P.'s results added support for the right hemisphere hypothesis, as healthy participants' results. Specifically, the friendliness judgments of chimeric faces were mainly modulated by the emotional content of the left hemifaces (right hemisphere), showing a dominant role of the right hemisphere in detecting both positive and negative emotional content of stimuli. Similar results, supporting the RHH, were described in the processing of unfiltered emotional chimeric faces in a previous study with A.P. (Prete et al., 2014a,b).

6. General discussion

Regarding the unconscious effects of the emotional hybrid faces, the present study confirms first of all that social judgments about faces can be systematically influenced by low spatial frequency information of the visual stimuli, despite these being blended with the high spatial frequencies of neutral faces, resulting in "hybrid faces". Secondly, also in these hybrid emotional faces, the central role of a global analysis based on low spatial frequency was shown by the disruption of the typical social judgments when these faces were shown in inverted orientation. Thirdly, we found that the social judgments occurred very rapidly, with a presentation time of just 28 ms, and that this was not imputable to image persistence because the results were not influenced by the presence of a mask following the stimulus.

Regarding laterality effects, the present study confirmed the occurrence of effects predicted by both the right hemisphere hypothesis and the valence hypothesis. Specifically, the unilateral presentation of hybrid faces showed that the friendliness judgments of stimuli depended on presentation side, with more positive evaluation of stimuli presented in the right visual hemifield (left hemisphere) than in the left visual hemifield (right hemisphere). On the other hand, the presentation of chimeric hybrid faces led to better appreciate the emotional content of the left hemiface, regardless of its emotional valence. This pattern of results seems to be robust and holds true both with healthy participants and the callosotomized patient A.P., confirming previous results (e.g. Prete et al., 2014a,b, 2013).

Experiment 1 revealed one of the most surprising results of the study, namely the rapidity of the detection of the low spatial frequency: while Bar et al. (2006) found that 26 ms were not sufficient to address an evaluation of the threatening level of neutral faces, the present study showed that 28 ms were enough to attribute a friendliness scores to hybrid faces. A difference between these two studies is the position of stimuli presentation on the screen: Bar et al. presented all stimuli centrally, whereas in the present study stimuli were presented laterally as well as centrally. However, the interaction found in the present study between emotion content and position of stimuli showed that the friendliness scores for different hybrid expressions remained significant even in the case of central presentation, excluding the possibility to justify the difference in this way. Importantly, in the present study, the hybrid stimuli contained an emotional core hidden in low spatial frequency, whereas Bar et al. presented all stimuli as neutral faces. Thus, the difference between the results of these two studies could depend upon this aspect: emotional low frequencies could be subliminally processed through a rapid subcortical route, receiving the magnocellular input (Schiller and Malpeli, 1977;

Tamietto and de Gelder, 2010), including amygdala, pulvinar and superior colliculus (Morris et al., 1999), and engaging orbito-frontal and cingulate cortices (Pessoa and Adolphs, 2010; Tamietto and De Gelder, 2010) possibly responsible for the hemispheric asymmetry, whereas non-emotional information probably exploit the relatively slow, cortical route receiving the parvocellular input (Livingstone and Hubel, 1988).

Gainotti (2012) recently reviewed a number of studies showing the role of this subcortical pathway in subliminal emotion processing. In particular, the author highlighted the right-hemispheric lateralization in unconscious (masked) emotional processing, opposite to the left-hemispheric specialization in conscious (cognitive) processing of emotional stimuli (see Spence et al., 1996).

In contrast to the right-hemispheric dominance in unconscious emotional processing proposed by , the present results (Experiments 1 and 3) supported the VH. In particular, Experiment 1 confirmed the results of : hybrid faces influenced the friendliness evaluation of observers, with higher scores attributed to happy than neutral faces and lower scores attributed to angry than neutral faces, and – importantly – stimuli presented in the left visual field were evaluated as less friendly than those presented in the right visual field, as it would be predicted by the VH. We highlight that the interactive effects indicated that happy faces were judged as more friendly when presented in the right than in the left visual field, and angry faces were judged as less friendly when presented in the left than in the right visual field. This pattern could be viewed in support of the VH, according to which the left hemisphere better encodes positive emotions, and the right hemisphere better encodes negative emotions. This association is reinforced by the evidence that for neutral faces there was no hemifield asymmetry, confirming that results found for happy and angry faces were not dependent upon aspects other than the emotional content of the stimuli. Finally, in the comparison between female and male faces, the results of Experiment 1 confirmed the association between female faces and positive emotions, on one hand, and that between male faces and negative emotions, on the other hand, as already found by Prete et al. (2014a,b). In fact, the three-way interaction showed that the support for the VH was stronger with female faces in happy pose, and with male faces in angry and neutral poses.

Support for the VH derived also from A.P.'s results in Experiment 3: the patient did not attribute different judgments to hybrid faces, but his scores were compatible with the pattern supporting the VH, for two reasons: they were higher when stimuli were presented in the right than in the left visual field, and they were higher when he used the right hand (left hemisphere) than the left hand. The fact that A.P. did not distinguish among hybrid faces could be due to the rapid presentation of such stimuli. In fact, in a previous study making use of the bilateral presentation of two identical or different hybrid faces, he was able to process these stimuli (Prete et al., 2013), attributing higher and lower friendliness scores to happy and angry hybrid faces, respectively. In that study, however, two faces could be presented simultaneously, increasing the difficulty of the task demand, but stimuli were presented for a longer time (250 ms). In the present study the short duration of stimuli could have hindered emotional processing.

Despite the mentioned evidence in support of the VH, Experiments 2 and 4 provided support for the RHH, confirming the results of Prete et al. (2013): hybrid faces were better discriminated by the right hemisphere (left hemifaces), disregarding their emotional content. In fact, friendliness scores were congruent with the left hemiface disregarding of their emotional positive or negative content, as shown by the higher friendliness scores attributed to the happy/neutral and the happy/angry faces, compared to the respective mirror reversed chimeras. Also in this case, the results of A.P. in Experiment 4 for upright faces were congruent with

those of the healthy participants, in the case of the right hand responses. As regard the left hand session, A.P.'s results seemed to disclose his inability in the evaluation of hybrid faces. This effect could be dependent upon his difficulty in responding with the left non-dominant hand. Another possibility is the "diagonistic dyspraxia" (Akelaitis, 1945) often observed in anterior callosotomy patients, according to which a kind of competition between the dominant and the non-dominant hand could interfere with the correct execution of unimanual actions (Berlucchi, 2012). Otherwise, this pattern indirectly provided further support for the validity of the RHH: in fact when A.P. used the right (dominant) hand, the left hemisphere should have been more activated, and this should have led to shift the attention on the contralateral (right) hemifield. Nevertheless, his judgments were congruent with the left-sided hemifaces, showing a right-hemispheric dominance in this task. Moreover, in Experiments 2 and 4, the stimuli presented upside-down received friendliness scores that seemed randomly assigned by both healthy participants and A.P. This result was not surprising, but it confirmed the literature showing that the processing of the low spatial frequency exploits a configural analysis of the faces, which is disrupted by face inversion (Maurer et al., 2002).

Thus, the chimeric faces paradigm, in contrast to the divided visual field paradigm, provides evidence for a right-hemispheric superiority in emotion detection. A possible explanation for the difference pattern of results obtained by means of the two paradigms could be ascribed to the eccentricity of the stimuli. In the chimeric faces paradigm, the lateralized presentation consists of two hemifaces presented besides the center of the visual field (parafoveal presentation), whereas in the divided visual field paradigm, a face was presented at 2.4° of visual angle laterally from the center of the visual field (extrafoveal presentation). The tachistoscopic presentation of stimuli used in both paradigms should have avoided possible eye movements, thus the best candidate explanation for the obtained effects could indeed be the different position of faces in the types of presentation. However, previous studies using hybrid faces showed that the results obtained in the chimeric faces paradigm perfectly overlap with those obtained by means of bilateral presentation of two extrafoveal hybrid faces (Prete et al., 2013).

A more acceptable explanation for the results could be associated with the number of (hemi)faces seen at a time. Specifically, in both chimeric faces and bilateral presentation paradigms, two faces (or hemifaces) were simultaneously presented, increasing the perceptual/cognitive load of each trial. In fact, in all the paradigms discussed, participants were required to give a single friendliness judgment, both in the case of chimeras (see Experiments 2 and 4) and in the case of bilateral presentation of two separate and lateralized faces (as in Prete et al., 2013). Excluding other possible effects, as the presentation time, the eccentricity of faces and the task demands – which remained similar in all these studies – the sole difference between paradigms in which results supported the VH and those in which they supported the RHH was the number of faces shown in a trial. Thus, we hypothesized that when a stimulus is presented in isolation (one face), each hemisphere shows its superiority in a valence-specific manner, supporting the VH; when two faces have to be processed simultaneously, the left-hemispheric superiority in positive emotions disappears and the right hemisphere seems 'dominant' in processing all emotions. In this view a central role could be played by the possible decisional processes occurring in the case of presentations involving different emotions. In fact, the valence-specificity could be considered as the 'default' hemispheric emotional asymmetry, whereas the right-hemsipheric dominance could be observed in all the cases in which decision-making is invoked due to the presentation of multiple (and different) visual emotional

stimuli. In this perspective, the contrasting results present in the literature concerning the two main theories of cerebral asymmetry in emotion processing, could be reconsidered in the light of the paradigm adopted from time to time.

It is worth briefly recalling that cerebral asymmetries have been proposed by a number of hypotheses in the study of attention, independently from emotional content of stimuli. Of note, the hypothesis of a right-hemispheric attentional bias was proposed in studies in which hemispheric biases were systematically considered in different tasks and it was named 'characteristic perceptual asymmetry' (Kim et al., 1990), intended as a kind of index of hemispheric arousal. Concerning face processing, it has been shown that a right-hemispheric superiority exists for both tachistoscopic lateralized faces, and for chimeric faces in free vision presentation (thus, for both unilateral and bilateral presentations, Kim et al., 1990; Levy et al., 1983a,b), suggesting that it was not due to a sort of sensory pathway dominance, but possibly to a lateralized attentional activation. Moreover, this asymmetry has proven to be stimulus-dependent (for example, a left-hemispheric bias was shown for linguistic stimuli; Levine et al., 1984), and it remains uncertain whether it could be considered as related or independent from gender and handedness of observers (see Eviatar et al., 1997 and Kim et al., 1990 for contrasting results; see also Marzoli et al., 2014 for a recent review on perceptual asymmetries and handedness).

Thus, even if the literature about hemispheric specialization in emotion analysis had alternatively supported either the VH or the RHH in a mutually exclusive fashion, the present study could be interpreted as evidence for the 'modified valence hypothesis', namely the coexistence of the two hypotheses. It could also be proposed that the subliminal emotion content of lateralized stimuli reaches the contralateral hemisphere, in which a valence-specific response takes place. Any model of the possible subcortical and cortical routes for stimuli processing should assume that after a very rapid contralateral analysis, callosal fibers transfer the information from one hemisphere to the other. However, the rather unique opportunity to test a callosotomized patient, allowed us to conclude that callosal connections are very little involved in this asymmetric activity: A.P.'s performance is very comparable to that of healthy participants, even if he lacks the corpus callosum, with the exception of the posterior portion (splenium). Thus, based upon the knowledge that the splenium ensures the cortical striate and extrastriate exchange of visual information about lateralized stimuli, we might hypothesize that the anterior connections between hemispheres are not included in this exchange. So, it is possible that all the main dynamics happen subcortically, where the hemispheric asymmetries should be better-established. In this regards, it is important to pay attention to studies in which the subcortical asymmetry in (subliminal) emotion processing have been investigated. The amygdala could play a crucial role in this model, and a number of studies have focused on its asymmetric activation during subliminal emotion detection: even in the case of amygdala activation, however, different patterns of asymmetries are alternatively supported by contrasting results (Baas et al., 2004; Öhman, 2002), suggesting another evidence in favor of coexistence of the VH and the RHH.

To conclude, we propose to consider the two main hypotheses on hemispheric asymmetry in emotion processing as complementary, rather than competing, at least in the case of implicit emotion processing. Our results suggest that the two models could be supported in alternative ways depending on the specific paradigm used. In particular, we propose that the specific hemispheric superiority in positive/negative emotion analysis could disappear in the case in which two subliminally emotional (hemi)faces have to be processed simultaneously. In other words, the present results seem to justify the hypothesis according to which when more than one subliminal emotional 'unit' have to be processed at the same time, the relative dominance of the right hemisphere appears clearer, thus suggesting the coexistence of both types of cerebral organization for subliminal emotion processing.

Uncited references

Laeng and Rouw (2001), Leknes et al. (2012)

Acknowledgments

References

Aboitiz, F., Montiel, J., 2003. One hundred million years of interhemispheric communication: the history of the corpus callosum. Braz. J. Med. Biol. Res. 36 (4), 409–420. http://dx.doi.org/10.1590/S0100-879X2003000400002.

Adolphs, R., Tranel, D., Damasio, H., Damasio, A., 1994. Impaired recognition of emotion in facial expressions following bilateral damage to the human amygdala. Nature 372 (6507), 669–672. http://dx.doi.org/10.1038/372669a0.

Akelaitis, A.J., 1945. Studies on the corpus callosum IV. Diagonistic dyspraxia in epileptics following partial and complete section of the corpus callosum. Am. J. Psychiatry 101 (5), 594–599.

Baas, D., Aleman, A., Kahn, R.S., 2004. Lateralization of amygdala activation: a systematic review of functional neuroimaging studies. Brain Res. Rev. 45 (2), 96–103. http://dx.doi.org/10.1016/j.brainresrev.2004.02.004.

Baijal, S., Srinivasan, N., 2011. Emotional and hemispheric asymmetries in shifts of attention: an ERP study. Cogn. Emot. 25, 280–294. http://dx.doi.org/10.1080/02699931.2010.492719.

Bar, M., Neta, M., Linz, H., 2006. Very first impressions. Emotion 6 (2), 269. http://dx.doi.org/10.1037/1528-3542.6.2.269.

Berlucchi, G., 2012. Frontal callosal disconnection syndromes. Cortex 48 (1), 36–45. http://dx.doi.org/10.1016/j.cortex.2011.04.008.

Borod, J.C., 1993. Cerebral mechanism underlying facial, prosodic and lexical emotional expression: a review of neuropsychological studies and methodological issues. Neuropsychology 7, 445–463. http://dx.doi.org/10.1037/0894-4105.7.4.445.

Bourne, V.J., 2008. Chimeric faces, visual field bias, and reaction time bias: have we been missing a trick? Laterality 13 (1), 92–103. http://dx.doi.org/10.1080/13576500701754315.

Collishaw, S.M., Hole, G.J., 2000. Featural and configurational processes in the recognition of faces of different familiarity. Perception 29 (8), 893–910. http://dx.doi.org/10.1068/p2949.

Corballis, M.C., Corballis, P.M., Fabri, M., Paggi, A., Manzoni, T., 2005. Now you see it, now you don't: variable hemineglect in a commissurotomized man. Cogn. Brain Res. 25, 521–530. http://dx.doi.org/10.1016/j.cogbrainres.2005.08.002.

Davidson, R.J., 1984. Affect, cognition, and hemispheric specialization. In: Izard, C.E., Kagan, J., Zajonc, R. (Eds.), Emotion, Cognition, and Behaviour. Cambridge University Press, New York.

Davidson, R.J., Mednick, D., Moss, E., Saron, C., Schaffer, C.E., 1987. Ratings of emotion in faces are influenced by the visual field to which stimuli are presented. Brain Cogn. 6, 403–411. http://dx.doi.org/10.1016/0278-2626(87)90136-9.

Demaree, H.A., Everhart, D.E., Youngstrom, E.A., Harrison, D.W., 2005. Brain lateralization of emotional processing: historical roots and a future incorporating "dominance". Behav. Cogn. Neurosci. Rev. 4 (1), 3–20. http://dx.doi.org/10.1177/1534582305276837.

Eviatar, Z., Hellige, J.B., Zaidel, E., 1997. Individual differences in lateralization: effects of gender and handedness. Neuropsychology 11 (4), 562. http://dx.doi.org/10.1037/0894-4105.11.4.562.

Fusar-Poli, P., Placentino, A., Carletti, F., Allen, P., Landi, P., Abbamonte, M., Politi, P.L., 2009. Laterality effect on emotional faces processing: ALE meta-analysis of evidence. Neuroscience letters 452 (3), 262–267. http://dx.doi.org/10.1016/j.neulet.2009.01.065.

Gainotti, G., 1972. Emotional behavior and hemispheric side of the lesion. Cortex 8 (1), 41–55. http://dx.doi.org/10.1016/S0010-9452(72)80026-1.

Gainotti, G., 2012. Unconscious processing of emotions and the right hemisphere. Neuropsychologia 50 (2), 205–218. http://dx.doi.org/10.1016/j.neuropsychologia.2011.12.005.

Gao, X., Maurer, D., 2011. A comparison of spatial frequency tuning for the recognition of facial identity and facial expressions in adults and children. Vis.

Res. 51, 508–519. http://dx.doi.org/10.1016/j.visres.2011.01.011.

Han, S., Weaver, J.A., Murray, S.O., Kang, X., Yund, E.W., Woods, D.L., 2002. Hemispheric asymmetry in global/local processing: effects of stimulus position and spatial frequency. Neuroimage 17 (3), 1290–1299. http://dx.doi.org/10.1006/nimg.2002.1255.

Hausmann, M., Corballis, M.C., Fabri, M., 2003. Line bisection in the split brain. Neuropsychology 17 (4), 602–609. http://dx.doi.org/10.1037/0894-4105.17.4.602.

Hellige, J.B., 1996. Hemispheric asymmetry for visual information processing. Acta Neurobiol. Exp. 56, 485–497.

Kim, H., Levine, S.C., Kertesz, S., 1990. Are variations among subjects in lateral asymmetry real individual differences or random error in measurement?: Putting variability in its place. Brain Cogn. 14 (2), 220–242. http://dx.doi.org/10.1016/0278-2626(90)90031-I.

Làdavas, E., Cimatti, D., Del Pesce, M., Tozzi, G., 1993. Emotional evaluation with and without conscious stimulus identification: evidence from a split-brain patient. Cogn. Emot. 7, 95–114. http://dx.doi.org/10.1080/02699939308409179.

Laeng, B., Rouw, R., 2001. Canonical views of faces and the cerebral hemispheres. Laterality: Asymmetries Body Brain Cogn. 6 (3), 193–224. http://dx.doi.org/10.1080/13576500042000115.

Laeng, B., Profeti, I., Saether, L., Adolfsdottir, S., Lundervold, A.J., Vangberg, T., Øvervoll, M., Johnsen, S.H., Waterloo, K., 2010. Invisible expressions evoke core impressions. Emotion 10 (4), 573–586. http://dx.doi.org/10.1037/a0018689.

Laeng, B., Sæther, L., Holmlund, T., Wang, C.E., Waterloo, K., Eisemann, M., Halvorsen, M., 2013a. Invisible emotional expressions influence social judgments and pupillary responses of both depressed and non-depressed individuals. Front. Psychol. 4, http://dx.doi.org/10.3389/fpsyg.2013.00291.

Laeng, B., Saether, L., Holmlund, T., Wang, C.E.A., Waterloo, K., Eisemann, M., Halvorsen, M., 2013b. Invisible emotional expressions influence social judgments and papillary responses of both depressed and non-depressed individuals. Front. Psychol. 4, 1–7. http://dx.doi.org/10.3389/fpsyg.2013.00291.

Leknes, S., Wessberg, J., Ellingsen, D.M., Chelnokova, O., Olausson, H., Laeng, B., 2012. Oxytocin enhances pupil dilation and sensitivity to 'hidden' emotional expressions. Soc. Cogn. Affect. Neurosci. nss062, http://dx.doi.org/10.1093/scan/nss062.

Leknes, S., Wessberg, J., Ellingsen, D.M., Chelnokova, O., Olausson, H., Laeng, B., 2013. Oxytocin enhances pupil dilation and sensitivity to 'hidden' emotional expressions. Soc. Cogn. Affect. Neurosci. , http://dx.doi.org/10.1093/scan/nss062.

Levine, S.C., Levy, J., 1986. Perceptual asymmetry for chimeric faces across the life span. Brain Cogn. 5 (3), 291–306. http://dx.doi.org/10.1016/0278-2626(86)90033-3.

Levine, S.C., Banich, M.T., Koch-Weser, M., 1984. Variations in patterns of lateral asymmetry among dextrals. Brain Cogn. 3 (3), 317–334. http://dx.doi.org/10.1016/0278-2626(84)90024-1.

Levy, J., Heller, W., Banich, M.T., Burton, L., 1983a. Are variations among right-handers in perceptual asymmetries caused by characteristic arousal differences between hemispheres? J. Exp. Psychol.: Hum. Percept. Perform. 9, 329–359. http://dx.doi.org/10.1037/0096-1523.9.3.329.

Levy, J., Heller, W., Banich, M.T., Burton, L.A., 1983b. Asymmetry of perception in free viewing of chimeric faces. Brain Cogn. 2, 404–419. http://dx.doi.org/10.1016/0278-2626(83)90021-0.

Levy, J., Trevarthen, C., Sperry, R.W., 1972. Perception of bilateral chimeric figures following hemispheric deconnexion. Brain 95, 61–78.

Livingstone, M., Hubel, D., 1988. Segregation of form, color, movement, and depth: Anatomy, physiology, and perception. Science 240, 740–749.

Lundqvist, D., Flykt, A., Öhman, A., 1998. The Karolinska Directed Emotional Faces (KDEF). CD ROM from Department of Clinical Neuroscience, Psychology section, Karolinska Institutet, pp. 91–630.

Marzoli, D., Prete, G., Tommasi, L., 2014. Perceptual asymmetries and handedness: a neglected link? Frontiers in psychology 5, http://dx.doi.org/10.3389/fpsyg.2014.00163.

Maurer, D., Grand, R.L., Mondloch, C.J., 2002. The many faces of configural processing. Trends Cogn. Sci. 6 (6), 255–260. http://dx.doi.org/10.1016/S1364-6613(02)01903-4.

Morris, J.S., Öhman, A., Dolan, R.J., 1999. A subcortical pathway to the right amygdala mediating "unseen" fear. Proc. Natl. Acad. Sci. 96 (4), 1680–1685. http://dx.doi.org/10.1073/pnas.96.4.1680.

Najt, P., Bayer, U., Hausmann, M., 2013. Models of hemispheric specialization in facial emotion perception—a reevaluation. Emotion 13 (1), 159. http://dx.doi.org/10.1037/a0029723.

Öhman, A., 2002. Automaticity and the amygdala: nonconscious responses to emotional faces. Curr. Dir. Psychol. Sci. 11 (2), 62–66. http://dx.doi.org/10.1111/1467-8721.00169.

Oldfield, R.C., 1971. The assessment and analysis of handedness: The Edinburgh inventory. Neuropsychologia 9, 97–114. http://dx.doi.org/10.1016/0028-3932(71)90067-4.

Pessoa, L., Adolphs, R., 2010. Emotion processing and the amygdala: from a 'low road' to 'many roads' of evaluating biological significance. Nat. Rev. Neurosci. 11 (11), 773–783. http://dx.doi.org/10.1038/nrn2920.

Peyrin, C., Chauvin, A., Chokron, S., Marendaz, C., 2003. Hemispheric specialization for spatial frequency processing in the analysis of natural scenes. Brain Cogn. 53, 278–282. http://dx.doi.org/10.1016/S0278-2626(03)00126-X.

Prete, G., D'Ascenzo, S., Laeng, B., Fabri, M., Foschi, N., Tommasi, L., 2013. Conscious and unconscious processing of facial expressions: evidence from two split-brain patients. J. Neuropsychol. , http://dx.doi.org/10.1111/jnp.12034.

Prete, G., Laeng, B., Tommasi, L., 2014. Lateralized hybrid faces: Evidence of a valence-specific bias in the processing of implicit emotions. Laterality: Asymmetries Body Brain Cogn. 19 (4), 439–454. http://dx.doi.org/10.1080/1357650X.2013.862255.

Prete, G., Marzoli, D., Brancucci, A., Fabri, M., Foschi, N., Tommasi, L., 2014. The processing of chimeric and dichotic emotional stimuli by connected and disconnected cerebral hemispheres. Behav. Brain Res. 271, 354–364. http://dx.doi.org/10.1016/j.bbr.2014.06.034.

Proverbio, A.M., Zani, A., Avella, C., 1997. Hemispheric asymmetries for spatial frequency discrimination in a selective attention task. Brain Cogn. 34, 311–320. http://dx.doi.org/10.1006/brcg.1997.0901.

Schiller, P.H., Malpeli, J.G., 1977. Properties and tectal projections of monkey retinal ganglion cells. J. Neurophysiol. 40, 428–445.

Schyns, P.G., Oliva, A., 1999. Dr. Angry and Mr. Smile: when categorization flexibly modifies the perception of faces in rapid visual presentations. Cognition 69 (3), 243–265. http://dx.doi.org/10.1016/S0010-0277(98)00069-9.

Sergent, J., 1982. The cerebral balance of power. Confrontation or cooperation? J. Exp. Psychol.: Hum. Percept. Perform. 8, 253–272. http://dx.doi.org/10.1037/0096-1523.8.2.253.

Spence, S., Shapiro, D., Zaidel, E., 1996. The role of the right hemisphere in the physiological and cognitive components of emotional processing. Psychophysiology 33 (2), 112–122. http://dx.doi.org/10.1111/j.1469-8986.1996.tb02115.x.

Sperry, R.W., Gazzaniga, M.S., Bogen, J.E., 1969. Interhemispheric relationships: the neocortical commissures; syndromes of hemisphere disconnection. Handb. Clin. Neurol. 4, 273–290.

Stone, V.E., Nisenson, L., Eliassen, J.C., Gazzaniga, M.S., 1996. Left hemisphere representations of emotional facial expressions. Neuropsychologia 34, 23–29. http://dx.doi.org/10.1016/0028-3932(95)00060-7.

Tamietto, M., De Gelder, B., 2010. Neural bases of the non-conscious perception of emotional signals. Nat. Rev. Neurosci. 11 (10), 697–709. http://dx.doi.org/10.1038/nrn2889.

Tamietto, M., Adenzato, M., Geminiani, G., de Gelder, B., 2007. Fast recognition of social emotions takes the whole brain: interhemispheric cooperation in the absence of cerebral asymmetry. Neuropsychologia 45 (4), 836–843. http://dx.doi.org/10.1016/j.neuropsychologia.2006.08.012.

Tanaka, J.W., Farah, M.J., 1993. Parts and wholes in face recognition. Q. J. Exp. Psychol. 46 (2), 225–245. http://dx.doi.org/10.1080/14640749308401045.

Thomas, N.A., Wignall, S.J., Loetscher, T., Nicholls, M.E., 2014. Searching the expressive face: Evidence for both the right hemisphere and valence-specific hypotheses. Emotion 14 (5), 962. http://dx.doi.org/10.1037/a0037033.

Torro-Alves, N., de Sousa, J.P.M., Fukusima, S.S., 2011. Assimetrias hemisféricas na percepção de expressões faciais: um estudo com a técnica de campo visual dividido. Psicol. USP 22 (1), 181–196.

Torro-Alves, N., Fukusima, S.S., Aznar-Casanova, J.A., 2008. Models of brain asymmetry in emotional processing. Psychol. Neurosci. 1 (1), 63–66. http://dx.doi.org/10.1590/S1983-32882008000100010.

Turk, D.J., Heatherton, T.F., Kelley, W.M., Funnell, M.G., Gazzaniga, M.S., Macrae, C.N., 2002. Mike or me? Self-recognition in a split-brain patient. Nat. Neurosci. 5, 841–842. http://dx.doi.org/10.1098/rstb.2008.0293.

Uddin, L.Q., Rayman, J., Zaidel, E., 2005. Split-brain reveals separate but equal self-recognition in the two cerebral hemispheres. Conscious. Cogn. 14, 633–640. http://dx.doi.org/10.1016/j.concog.2005.01.008.

Vuilleumier, P., Armony, J.L., Driver, J., Dolan, R.J., 2003. Distinct spatial frequency sensitivities for processing faces and emotional expressions. Nat. Neurosci. 6, 624–631. http://dx.doi.org/10.1038/nn1057.