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

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

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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.

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., 1983) 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 non-conscious 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).

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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 inter-hemispheric 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, 2013; 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). 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) 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