Accepted version

Licence CC BY-NC-ND

Wyczesany, M., Capotosto, P., Zappasodi, F., & Prete, G. (2018). Hemispheric asymmetries and emotions: Evidence from effective connectivity. Neuropsychologia, 121, 98-105.

Doi: https://doi.org/10.1016/j.neuropsychologia.2018.10.007

*Manuscript
Click here to view linked References

Hemispheric asymmetries and emotions: evidence from effective connectivity

Miroslaw Wyczesany [1,2*]

Paolo Capotosto [2,3]

Filippo Zappasodi [2,3]

Giulia Prete [4]

[1] Institute of Psychology, Jagiellonian University, Ingardena 6, PL-30060 Krakow
m.wyczesany@uj.edu.pl; ORCID: 0000-0003-1091-5485

[2] Department of Neuroscience, Imaging and Clinical Sciences, "G. d'Annunzio" University of Chieti-Pescara, Via dei Vestini 33, IT-66100 Chieti

[3] Institute for Advanced Biomedical Technologies, "G. d'Annunzio" University of Chieti-Pescara, Via Luigi Polacchi 11, IT-66100 Chieti

[4] Department of Psychological, Health and Territorial Sciences, "G. d'Annunzio" University of Chieti-Pescara, Via dei Vestini 32, IT-66100 Chieti

* corresponding author

Keywords: Electroencephalography; Emotions; Hemispheric asymmetries; Right Hemisphere Hypothesis; Valence Hypothesis.

Abstract

The Right Hemisphere Hypothesis (RHH) posits that the right hemisphere is specialized in processing all emotions; the Valence Hypothesis (VH) suggests a left/right-hemispheric specialization for positive/negative emotions, respectively. Behavioural, neuroimaging and physiological investigations alternatively support either the RHH or the VH, but connectivity analyses have been hardly exploited in this field. In the present study, unilateral and bilateral presentations of positive (happy) and negative (angry) emotional faces were used during electroencephalographic (EEG) recordings, and estimation of effective connectivity was performed using the Directed Transfer Function, to estimate causal influences between brain regions (Granger causality approach). The results show a strong pattern of connectivity among different frontal areas (orbitofrontal and dorsolateral prefrontal cortex), attentional network (frontal eye field, intraparietal sulcus), visual occipital areas and temporal sites, mainly lateralized in the right hemisphere for all emotions, in accordance with the RHH. Moreover, a stronger pattern of connectivity is evident when stimuli are presented in accordance with the VH (positive/negative emotions to the left/right hemisphere, respectively). Finally, the results suggest a crucial role of the right dorsolateral prefrontal cortex in a top-down regulation toward different areas involved in emotional processing. We conclude that the RHH and the VH are not mutually exclusive, but they seem to coexist during affective perception.

1 Introduction

The question of how both hemispheres contribute to emotional processing has been extensively studied. However, the results are still partly discrepant and the neural underpinnings of affective processes are yet to be fully recognized. The most acknowledged theories in this frame, suggesting a different pattern of hemispheric specialization for positive and negative valence emotions, are alternatively supported by a number of studies (for a meta-analysis see Fusar-Poli et al., 2009). According to the Right Hemisphere Hypothesis (RHH; Gainotti, 2012, 1972) the right hemisphere (RH) would be superior to the left hemisphere (LH) in processing all emotional stimuli, disregarding of their emotional valence. According to the Valence Hypothesis (VH; Baijal and Srinivasan, 2011; Davidson et al., 1987; Wyczesany et al., 2009) the left and the right hemisphere would be specialized in processing positive and negative emotions, respectively. Each of these theories has been confirmed by means of different paradigms, but the most useful to investigate hemispheric asymmetry is the divided visual field paradigm. In this task the participant is asked to fixate the gaze ahead and a stimulus is presented laterally in one visual hemifield for a period shorter than that needed to make a saccadic movement (150 ms). In this way, the visual information presented in a visual field directly reaches the contralateral hemisphere, allowing researchers to evaluate the specific response of each hemisphere to the emotional content of the stimulus presented laterally. Using this paradigm, however, contrasting findings emerged concerning hemispheric asymmetries for positive and negative emotions; some studies providing support for the RHH (e.g., Prete et al., 2015b, 2015b; Torro-Alves et al., 2011) some others supporting the VH (e.g., Jansari et al., 2011; Prete et al., 2014), mainly depending upon the unilateral or bilateral presentation of emotional faces. Moreover, it has to be remarked that a motivational account has also been proposed (Poole and Gable, 2014), according to which cerebral lateralization for emotions is dependent upon the motivational content of the stimulus, rather than its valence, with a left-hemispheric superiority for approach-related emotions (e.g., happiness or anger) and a right-hemispheric superiority for avoidance-related emotions (e.g., fear). The crucial point of the motivational model is considered the hemispheric asymmetry for anger, which is a negative valence emotion, but it is approaching-related: Harmon-Jones, Gable and Peterson (Harmon-Jones et al., 2010) reviewed a number of studies showing that state and trait anger lead to a strong left-hemispheric activity, compared to the right-hemispheric activity, mainly in the frontal areas. Neither neuroimaging, nor electrophysiological investigations have been sufficient to disentangle this issue, revealing alternative pattern of results. For instance, event-related brain potentials (ERPs) provided alternative support for either the RHH (e.g., Prete et al., 2015a) or for the VH (e.g., Baijal and Srinivasan, 2011).

The number of already published EEG studies does not usually provide cortical localization for observed lateralization effects, and this issue was rarely raised in the literature. Some scarce data suggest the dorsolateral cortex as a possible substrate of EEG asymmetry observed with spectral methods (Pizzagalli et al., 2005). Undoubtedly, this cortical area remains crucial for a variety of emotional processes, including motivation, emotional perception and learning, and response control. It can be regarded as a key region for cognitive / emotional interactions, which integrate signals from vast number of subcortical and cortical areas (especially orbitofrontal, and posterior cortices) (Barbas, 2000; Davidson, 2004; Ligeza et al., 2016). On the other hand, fMRI studies often fail to replicate EEG findings regarding hemispheric specialization and asymmetry, which can be caused by a number of factors, including data preprocessing, reference, and the choice of parameters for estimating inter-hemispheric balance. The fMRI results are also affected by unnatural conditions during the measurement (uncomfortable, noisy environment and supine position which interferes with embodied emotional state; (Harmon-Jones and Peterson, 2009). Nevertheless, also fMRI results are inconclusive concerning hemispheric asymmetries for emotions. On one hand, Narumoto and colleagues (2001) found that emotional compared to non-emotional faces enhanced activity in the right superior temporal sulcus. Similarly, Sato and co-workers (2004) found an increased activity in the occipital and temporal areas for emotional faces, mainly lateralized to the right hemisphere. On the other hand, in a review on this issue, Bass and colleagues (2004) highlighted the main role of the left amygdala in emotional processing, suggesting a crucial role of the left hemisphere in emotions. Finally, Killgore and Yurgelun-Todd (2007) presented chimeric faces, constituted by half emotional face (happy or sad) and half neutral face, finding a posterior right-hemispheric activity for both positive and negative emotional valence. The authors also found that this right-hemispheric activity was stronger for negative than for positive emotions. Importantly, results also revealed a valence-specific asymmetry in the anterior region, with a stronger left-hemispheric involvement for happiness and right-hemispheric involvement for sadness.

We expect that the overall image of the hemispheric specialization is quite complex and our knowledge on this phenomenon would benefit from more advanced methods of brain imaging, which provide information beyond the classic techniques. Growing interest in network approach to the working brain brings a promise of significant advances in understanding neural substrates of mental functions. An important advantage of connectivity methods is the analysis of mutual relationships between functionally interconnected structures which can provide more comprehensive image of underlying brain processes and lateralization of their neural substrates. The role of brain oscillations in emotional processing is a relatively new field of research. Oscillatory activity in particular frequency bands underlies different aspects of communication between cortical areas (von Stein and Sarnthein, 2000). This communication constitutes a crucial substrate of brain functions including emotional processing. For instance, beta band is more influenced by negative (e.g., angry) than positive (e.g., happy) and neutral emotions, possibly representing a fast and automatic reaction to potentially aversive stimuli. Moreover, as suggested by Güntekin and Başar, (2014), even if spontaneous EEG studies lead to expect a relative right-alpha activity associated with negative emotions and relative left-alpha activity associated to positive emotions (in accordance with the VH), evoked/event-related oscillation studies did not confirm this expectation (Harmon-Jones et al., 2010; Pönkänen and Hietanen, 2012). It is thus possible, that by inferring on brain processes only by observing changes in EEG spectral power, an important functional aspect is neglected, which is the role of oscillations in internal brain communication. Hence, the connectivity analysis has become increasingly important in recent years, using variety of measurement techniques and derived parameters. For instance, in a recent study (Dasdemir et al., 2017) EEG functional connectivity was analyzed by means of phase locking value during the presentation of positive and negative stimuli. They found a bilateral activity for positive emotions and an activation mainly involving the right hemisphere for negative emotions. In the study using emotional imagery tasks and effective connectivity measurement (Wyczesany et al., 2014), it has been shown that positive condition was associated with increased activity of the right parietal source with flows reaching bilateral temporal areas. On the other hand, negative recollections were related to increased activity of right temporal sources, sending information in beta band towards number of cortical regions, including bilateral posterior but left shifted anterior regions. This latter pattern was similarly observed in another study, where functional connectivity estimated from spontaneous EEG recording was correlated with self-report of emotional state (Wyczesany et al., 2011). In a study where effective connectivity was assessed during perception of emotional pictures, the reports of more negative subjective state was associated with increased information flow from the frontal areas towards wide parietal and occipital areas, which was interpreted as a increased top-down control of the prefrontal cortex (PFC) over the perceptual and attentional areas during the state of emotional tension (Wyczesany et al., 2015). The investigation of face perception in regard to cortical connectivity was performed by (Li et al., 2015), where coherence between electrodes was calculated in patients with depression compared to healthy controls. Patients were shown to have generally higher coherence values in prefrontal and occipital brain regions, however more detailed effects were possibly obscured by the lack of specificity of the coherence measure. The brain connectivity patterns during face perception was also studied by Jamal et al. (2015), who provided an insight into stimuli driven dynamics in communication between cortical regions, however no effects of emotions were checked. The emotional faces were used as stimuli in another study, where inter-hemispheric communication was investigated using the Directed Transfer Function method. It was described that watching negative (sad) expressions caused stronger links between bilateral frontal regions in lower frequencies (Vecchio et al., 2013). Unfortunately, a more systematic review of connectivity studies of emotional processing is not possible, as the existing data are scarce and heavily fragmentary.

In the present study, using emotional faces in unilateral and bilateral presentation in a divided visual field paradigm, we apply effective connectivity method to explore the dynamics of network communication during processing of emotional content. Starting from the literature described above, we decided to exploit a divided visual field paradigm in which positive approach-related (happy; HA) and negative, approach-related (angry; AN) faces were presented. We intended to disentangle the possible effect of single or double positive/negative emotional faces on cerebral asymmetries (VH and RHH), by using two approach-related expressions (thus controlling for the possible effect of the motivational account). We avoided to use neutral expression or other emotional expressions because we aimed to directly disentangle the hypotheses concerning hemispheric asymmetries (RHH, VH). Stimuli were presented either in one visual field at time (during the simultaneous presentation of a black and white checkerboard in the opposite visual field: unilateral presentation of emotional faces) or in the two visual fields simultaneously (bilateral presentation of two emotional faces). In the unilateral condition a checkerboard was used instead — for instance — of a neutral face, in order to obtain a real "unilateral" presentation of an emotional face, and thus to prevent possible effects related to the non-target face. Similarly, we avoided exploiting a unilateral presentation in which one visual hemifield remained empty in order to control for the low-level perceptual effects (size, luminance and position of the checkerboard was equated to those of facial stimuli). In the analysis we included a number of crucial regions involved in perception of visual stimuli, its evaluation, and emotional responding. Apart of the occipital visual areas, also the temporal regions (further visual processing as well as emotional functions), and these covering the dorsal attentional network (parietal as well as the frontal areas) were observed. In the prefrontal cortex, both orbitofrontal (emotional and motivational stimuli estimation) and dorsolateral areas were also considered. These areas formed a network of regions of interests, whose communication was a subject of our study. They partly correspond to the visual, attentional, and executive 'big' functional networks. We were considering both alpha and beta bands, with the aim to verify the expected stronger beta response to negative valence emotions, and to disentangle the possible hemispheric asymmetries for alpha band according to the positive and negative emotional stimuli. In particular, starting from the two main theories on hemispheric asymmetry for emotions we expected to find:

- According to the RHH: presentation of emotional stimuli to the right hemisphere comparing to the left hemisphere presentation will intensify cortical communication (including increased flow from the occipital cortex and parietal attentional areas to the frontal regions), comparing to left hemisphere presentation, despite the valence. This result should be evident in the unilateral presentation conditions, where one emotional face is presented in isolation to a single hemisphere: in this case we expected that the presentation of an emotional face to the RH leads to a greater connectivity among emotional areas than the presentation of an emotional face to the LH;

- According to the VH: presentation of stimuli according to the postulated specialization (left-hemispheric specialization for happy faces, right-hemispheric specialization for angry faces) with respect to the reversed presentation will be associated with increased processing reflected by heightened flow from the occipital to the frontal areas and increased involvement of attentional regions; also, the dorsolateral cortex will specifically increase its activity as a source, depending on the emotion presented. In particular, we expected to find greater overall connectivity when a happy face is presented to the LH and/or a angry face is presented to the RH, with respect to the opposite pattern (a happy face presented to the LH and/or an angry face presented to the RH).

In order to explore the possible hemispheric asymmetries for emotional faces, we firstly compared the connectivity for a happy face presented to the RH vs a happy face presented to the LH (unilateral presentation). The same comparisons were carried out for angry faces. We expected that, according to the RHH, for both happy and angry expressions a stronger pattern of connectivity would be evident in the right than in the left hemisphere, and/or when the emotional face was presented to the RH, showing a stronger right-hemispheric involvement for all emotions. Otherwise, according to the VH, we expected to find a stronger pattern of connectivity in the left hemisphere for happy faces and in the right hemisphere for angry faces, and/or a higher level of connectivity for happy faces presented to the LH and for angry faces presented to the RH, revealing a valence-dependent pattern of hemispheric asymmetry. Then, we used bilateral presentations to disentangle the possible hemispheric asymmetries: we expected to find a higher level of connectivity during the presentation of the positive emotion to the LH and the contemporary presentation of the negative emotion to the RH, with respect to the opposite pattern, thus supporting the VH. Alternatively, we expected that if the RHH is true, a greater right-hemispheric activity should be evident independently of the side of presentation of positive and negative faces. To test these hypothesis, we compared the two pattern of presentation one another (angry to the RH and happy to the LH vs happy to the RH and angry to the LH). Finally, we also used the bilateral presentations of two congruent emotional expressions (both happy or both angry faces) to further confirm either a right-hemispheric involvement for all emotions (RHH) or a left/right-hemispheric involvement for positive/negative emotions, respectively (VH). In this case, we compared the presentation of two angry faces vs two happy faces and two happy faces vs two angry faces, expecting to find a right-hemispheric and a left-hemispheric connectivity, respectively, according to the VH, or an overall right-hemispheric activity, in accordance with the RHH.

2 Material and methods

2.1 Procedure

The procedure was carried out in accordance with the principles of the Declaration of Helsinki, and was approved by the Ethics Committee for Biomedical Research of the University “G. d’Annunzio” of Chieti and Pescara. Sixteen volunteers (9 females), same sample as in (Prete et al., 2018), participated in the experiment. Photographs in frontal view of 15 female and 15 male faces in happy and angry poses were used. Moreover, a black and white checkerboard was also presented. All stimuli were equated for size and luminance and were presented in gray scale. Stimuli were presented either unilaterally (one facial stimulus to the RH, in the left visual field: LVF, or to the LH, in the right visual field: RVF, whereas the checkerboard was presented in the opposite visual field), or bilaterally (two faces presented together at the same time, one in each visual field). In unilateral presentation, the face was either a happy or an angry face (4 conditions: angry-LH, angry-RH, happy-LH, happy-RH). In the bilateral conditions the two stimuli could show the same emotion or the two different emotions (4 conditions: LH-RH = happy-happy, angry-angry, happy-angry, angry-happy). In each trial, after the presentation of a black fixation cross in the center of the screen (500 ms), the stimulus was presented lateralized for 125 ms. In the following ISI, randomized between 1200 and 1800 ms, a fixation cross was presented (see Figure 1). The 8 conditions (4 unilateral and 4 bilateral) were repeated 120 times each, in which no response was required. In the original task (Prete et al., 2018), further 128 trials were used to collect behavioural response: in these trials the central cross presented during the ISI was red, and this meant that a response was required: participants were instructed to judge the emotional expression (using a 5-points Likert scale, from1 = very angry, to 5 = very happy), only in those trials in which the cross was red (these trials are not analyzed here). For more details on stimuli and procedure see (Prete et al., 2018).

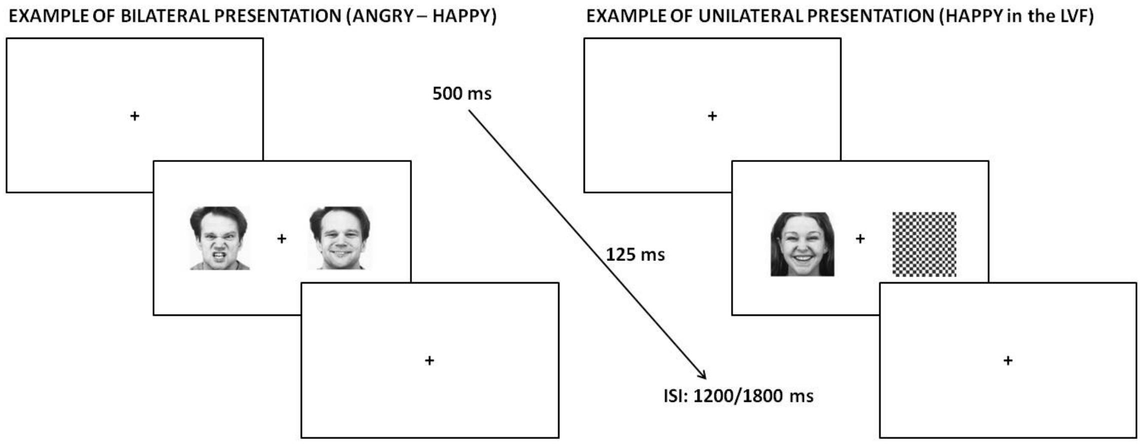

Fig. 1. Experimental procedure: bilateral (left panel) and unilateral (right panel) presentations.

During the entire procedure, EEG was recorded by means of a 128 electrode net (Electrical Geodesic, Version 1.1), placed according to an augmented 10–20 system, with the skin-electrode impedance kept below 50 kΩ.

2.2 Connectivity Analysis

Estimation of effective connectivity was performed using the Directed Transfer Function (DTF; Blinowska et al., 2004). The method is based on the autoregressive modelling of time series data. As biological signals display a sort of oscillatory properties, these oscillations can be considered as regularities which allows for predicting (with a limited reliability) the given signal by observing its nearest past and estimating the parameters of autoregressive model. Thus, each data sample *X(t)* can be represented as a weighted sum of *p* previous samples with a random component *E(t)* added:

$$X(t)=c+\sum_{i=0}^{p} A(i)X(t-i)+E(t)$$

where *A(t)* is the model coefficient matrix. This formula is valid also when multichannel data is considered, and *X(t)* becomes a vector representing a set of multiple channels values. Causal influences between sources of signals can then be estimated using Granger causality approach, which defines a signal *S2* as causal for a signal S*1* only if S*1* can be better predicted using previous values of both signals than using past values of signal S*1* alone. This approach, applied to EEG signal, allows for estimating the strength of information flow and direction of influence between brain regions. As a result, we can determine the dynamics of functional cortical networks related to particular cognitive processes. After transforming into a frequency domain, the above equation can be written as:

$$X(f) = A^{-1}(f)E(f) = H(f)E(f)$$

where *H(f)* can be considered as a form of linear filter:

$$H(f) = \left(\sum_{m=0}^{p} A(m)\exp(-2\pi i m f \Delta t)\right)^{-1}$$

Finally, non-normalized DTF function that describes the flow from channel *j* to channel *i* at frequency *f* is defined:

$$\gamma_{\mathrm{ij}}^{2}(f) = |H_{\mathrm{ij}}(f)|^{2}$$

2.3 *EEG data processing*

Data preprocessing was performed using EEGLab toolbox. The signal was referenced to Cz electrode and filtered with 5Hz high-pass and 45Hz low-pass filters and downsampled to 128 Hz. Oculomotor artefacts were corrected using custom procedure, which fitted individual shape of eye blink and removed its envelope without affecting high frequency components and disturbing original correlation structure of the dataset. Then, the signal was segmented in a time window 0 to 1 sec relative to stimuli onset. Epochs in which the amplitude on any of the electrodes exceeded 30 μV were further rejected. We decided to carry out sensor-level analysis, since additional source reconstruction may present a risk of disrupting the correlation structure of analysed signals (Kaminski and Blinowska, 2014). It should be noted, that the correspondence between electrodes locations and underlying structures are approximate, and the risk of spurious connection is present to some extent. Hence, the results should be treated with some caution. Our approach, however, can be justified by the fact that autoregressive methods (including DTF) are at least partly insensitive to volume conduction, which provides increased spatial accuracy comparing to classic EEG techniques (Kaminski and Blinowska, 2017). More on the ongoing debate regarding pros and cons of sensor vs source level analysis can be found in (Van de Steen et al., 2016). Based on 10-20 montages atlas (Koessler et al., 2009) and following electrodes were selected to create following regions of interest (ROIs): the occipital visual cortex (Occ): O1, O2; left (L) / right (R) intraparietal sulci (L/R IPS): P3 / P4; left / right frontal eye field (L/R FEF): FC3 / FC4; left / right anterior temporal area (L/R Tmp): FT9 T7 / FT10 T8; dorsolateral prefrontal cortex (L/R DLPFC): F1 F3 / F2 F4; orbitofrontal cortex (L/R OFC): F7 Fp1 / F8 Fp2. DTF calculations were carried out using Multar software (University of Warsaw). The MVAR model order was set to eight, according to the Akaike criterion (AIC). Non-normalized DTF values were estimated for each condition separately in both alpha (8-12 Hz) and beta band (14-25Hz). The frequencies were selected to cover middle- and long-distance cortical communication responsible for both bottom-up and top-down influences (Bastos et al., 2012; Vossel et al., 2013). Using the interquartile range procedure (Tukey, 1976), extremes values in DTF distributions were rejected (below Q1-1.5*IQR or above Q3 +1.5*IQR (Ligeza et al., 2016).

2.4 Statistical analysis

Statistical analysis was carried out with linear mixed models using *lme4* R package (Bates et al., 2015). For unilateral stimuli presentation, a statistical model with face valence and hemisphere as fixed factors and subjects as a random factor was used to compare the effects of valence and presentation side on DTF connectivity estimations between considered ROIs. The exact formula of the model was: DTF ~ valence + hemisphere + 1|subject + ε (where ε is the error term). For bilateral stimuli presentation, a model with four valence-side conditions (HA-AN, AN-HA, HA-HA, AN-AN, where the left abbreviation denotes emotion presented to the left hemisphere, while the right one denotes emotions presented to the right hemisphere) as fixed factor and subjects as random factor was used to investigate the effects on DTF measures during mixed-valence (HA-AN and AN-HA i.e. happiness presented to the LH and anger presented to the RH versus anger presented to the LH and happiness presented to the RH), as well as same-valence presentation (AN-AN and HA-HA). In this case the model formula could be written as: DTF ~ condition + 1|subject + ε. Both alpha and beta band connectivity were separately analyzed. The significance of the effects were estimated using the Satterthwaite's method for approximating degrees of freedom by means of the *lmerTest* library (Kuznetsova et al., 2017) with alpha level set to more conservative criterion of $p<0.01$. To infer about changes in connectivity rate, particular contrasts were created depending on the presentation condition. For unilateral presentation two opposite cases were considered: RH>LH (directions where flows were higher during presentation to the right comparing to the left hemisphere) and LH>RH (the opposite pattern). For bilateral presentation following contrasts were considered: HA-AN>AN-HA and AN>HA>HA-AN (for incongruent emotions presentation), as well as AN-AN>HA-HA, and HA-HA>AN-AN (for congruent emotion faces). All scalps were visualized using Trans3D package (Department of Physics, University of Warsaw).

3 Results

3.1 Unilateral presentation

A first set of comparisons was carried out considering the unilateral presentation of one emotional face (angry or happy) to the RH vs LH. All results are reported in Table 1 and significant comparisons are shown in Figure 2. Presenting an angry (AN) face to the right hemisphere (RH) comparing to the left hemisphere (LH) increased alpha flows originating mostly from the right dorsolateral prefrontal cortex (RDLPFC), reaching the left DLPFC, bilateral orbitofrontal cortex (OFC), and bilateral temporal (Tmp) areas. Also, the left frontal eye field (LFEF) increased flow to RTmp and LDLPFC. Finally, increased transfer from the left intraparietal sulcus (LIPS) to the ROFC was observed. In the beta band, the only increase was seen from RDLPFC to LOFC. Presenting an angry face to the LH comparing to the RH did not reveal any significant increase of information flow in alpha band. In the beta range, increase from the ROFC to LOFC was observed and bilateral strengthening of communication between the occipital (Occ) and LDLPFC areas.

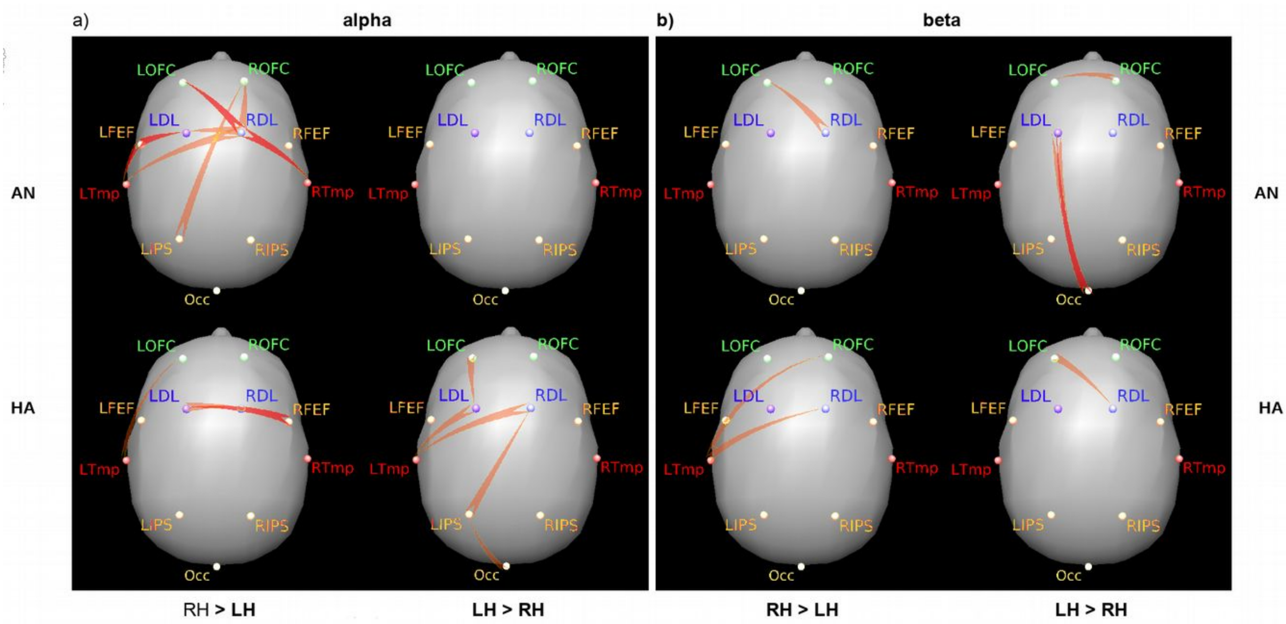

Fig. 2. Significant effects of hemisphere on DTF connectivity estimates for simple emotion comparisons in unilateral presentation condition in alpha (a) and beta (b) band. The upper row shows presentation of angry (AN) expression, while the lower one presentation of happy (HA) expression. The left columns for each of the frequency band show flows greater for the right hemisphere presentation comparing to the left hemisphere presentation. The right columns show reversed contrast, with greater flows in the left vs right hemisphere presentation. Orange arrows: p<0.01, red arrows: p<0.001

Presentation of a happy (HA) face to the left comparing to the right hemisphere caused increase of effective connectivity in the following directions: from Occ to LIPS, from LIPS to RDLPFC, from bilateral DLPFC to LTmp, from LOFC to LDLPFC in alpha band; from LOFC to RDLPFC in beta band. Reversed presentation, i.e. a happy face to the right comparing to the left hemisphere, was associated with increase of flow from RFEF to LDLPFC, from LDLPFC to RDLPFC, and from LTmp to LOFC in the alpha band; from LTmp to ROFC and to RDLPFC in the beta band.

comparison	freq range	direction	std beta	p value
angry: RH > LH	alpha	RDLPFC → LTmp	0.21	0.009
		RDLPFC → RTmp	0.32	<0.001
		RDLPFC → LOFC	0.26	<0.001
		RDLPFC → ROFC	0.24	0.004
		LFEF → LTmp	0.38	<0.001
		LFEF → LDLPFC	0.37	<0.001
		LIPS → ROFC	0.26	0.003
	beta	RDLPFC → LOFC	0.21	0.006
angry: LH > RH	beta	Occ → LDLPFC	0.29	<0.001
		LDLPFC → Occ	0.23	0.002
		ROFC → LOFC	0.23	0.010
happy: RH > LH	alpha	LTmp → LOFC	0.25	0.003
		RFEF → LDLPFC	0.42	<0.001
		LDL → RDLPFC	0.21	0.004
	beta	LTmp → ROFC	0.23	0.002
		LTmp → RDLPFC	0.16	0.005
happy: LH > RH	alpha	Occ → LIPS	0.36	0.003
		LIPS → RDLPFC	0.24	0.007
		RDLPFC → LTmp	0.24	0.003
		LDLPFC → LTmp	0.26	0.003
		LOFC → LDLPFC	0.25	0.004
	beta	LOFC → RDLPFC	0.28	0.001

Table 1: Significant comparisons during unilateral presentations of one happy (HA) or one angry (AN) face to the left hemisphere (LH) and to the right hemisphere (RH).

3.2 Bilateral presentation: incongruent emotions (different faces)

As reported in Table 2 the presentation of incongruent faces according to the valence hypothesis comparing to the opposite pattern (HA-AN vs AN-HA contrast, i.e. HA→LH and AN→RH vs AN→LH and HA→RH) revealed significant increase of RDLPFC source activity in the alpha band which increased information transfer to the bilateral OFC and LTmp, as well as increase of flow from the LIPS and RIPS to the ROFC and LOFC, respectively (Figure 3). No significant effects of reversed contrast (contrary to valence hypothesis: AN-HA vs HA-AN) were observed. Also, no significant effects of comparisons for beta band were found.

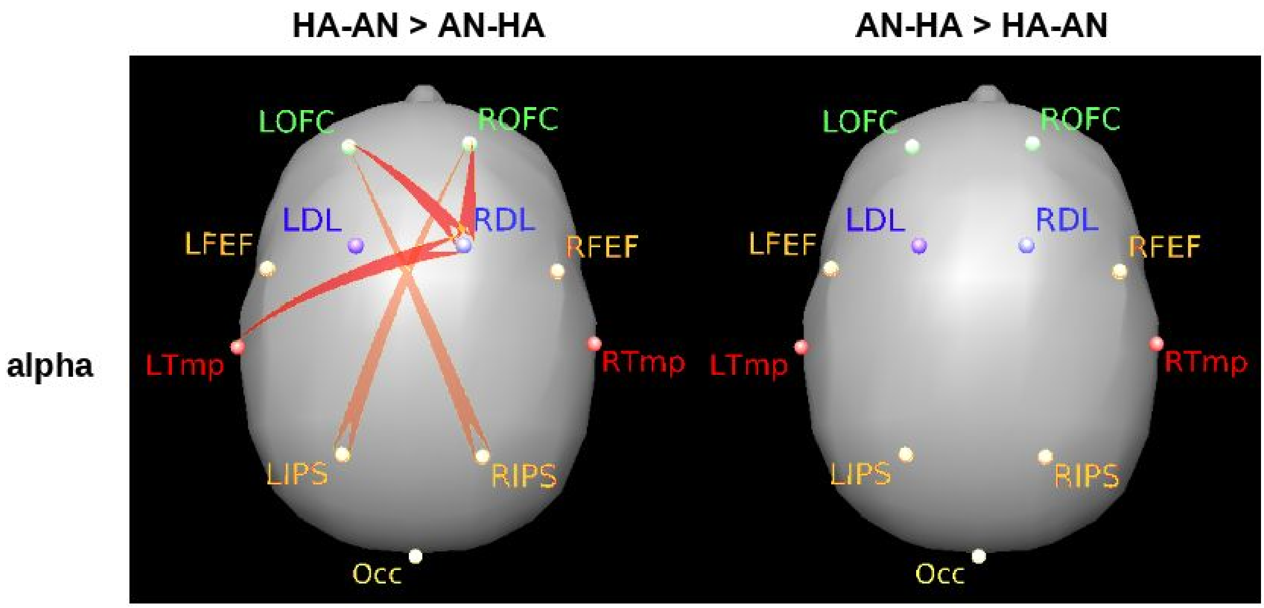

Fig. 3. Significant differences in DTF connectivity estimates during the presentation of incongruent faces composed of happy (HA) and angry (AN) expressions. The HA-AN > AN-HA contrast shows the directions, where flows increased for the presentation, according to the VH (HA→LH and AN → RH) comparing to the reversed presentation, contrary to the VH (AN→LH and HA → RH). The second contrast (AN-HA > HA-AN) yield no signifcant increases of DTF values. Orange arrows: p<0.01, red arrows: p<0.001

comparison	freq range	direction	std beta	p value
HA-AN > AN-HA	alpha	RDLPFC → LTmp	0.25	<0.001
		RDLPFC → LOFC	0.32	<0.001
		RDLPFC → ROFC	0.27	<0.001
		LIPS → ROFC	0.30	0.006
		RIPS → LOFC	0.13	0.010

Table 2: Effects of comparisons for bilateral presentations of incongruent faces composed of happy (HA) and angry (AN) expressions. Only one contrast is presented, for which significant effects were found: increase of flows for the

presentation accordant with the valence hypothesis (HA-AN i.e. HA→LH and AN → RH) comparing to the reversed pattern (AN-HA, i.e AN→LH and HA → RH).

3.3 Bilateral presentation: congruent emotions (same faces)

As described in Table 3, the bilateral presentation of two angry comparing to two happy faces revealed increased flows from the Occ to both RDLPFC and LTmp, and from the LDLPFC to LTmp in the alpha band, and from ROFC to RDLPFC in the beta band (Figure 4). The presentation of two happy comparing to two angry faces was associated with an increased flow from LFEF to RDLPFC, and LOFC to LTmp flows in the alpha band, while in the beta band only RFEF to LDLPFC transfer was significantly heightened.

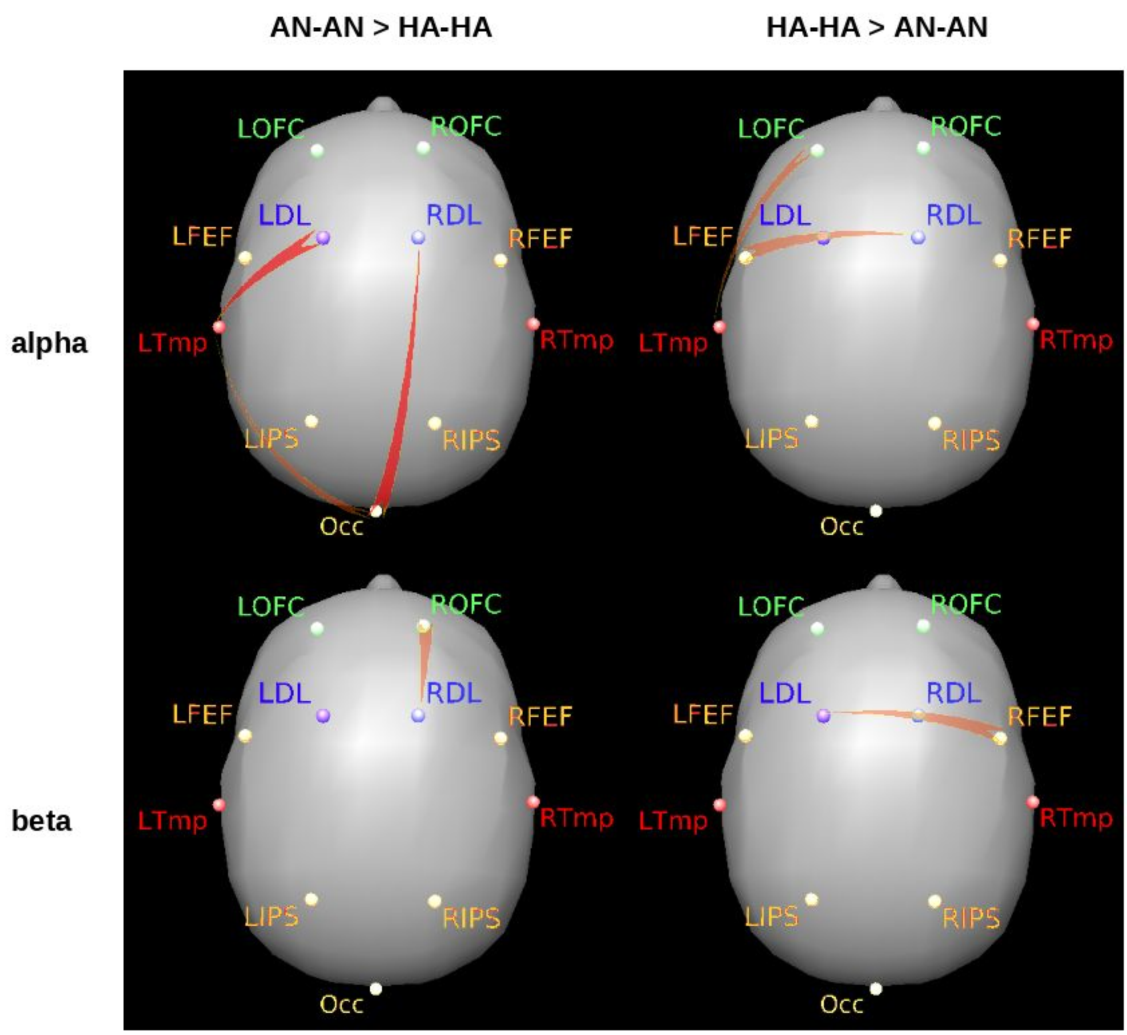

Fig. 4. Significant differences of DTF connectivity estimates during bilateral presentation of congruent emotional faces (either happy or angry). The left column shows flows that were greater for angry comparing to happy faces, while the

right one shows the opposite contrast, where happy faces evoked greater flow than angry faces. Orange arrows: p<0.01, red arrows: p<0.001

<table>
<tr><th>comparison</th><th>freq range</th><th>direction</th><th>std beta</th><th>p value</th></tr>
<tr><td rowspan="4">AN-AN > HA-HA</td><td rowspan="3">alpha</td><td>LDLPFC → LTmp</td><td>0.31</td><td><0.001</td></tr>
<tr><td>Occ → LTmp</td><td>0.24</td><td>0.008</td></tr>
<tr><td>Occ → RDLPFC</td><td>0.32</td><td><0.001</td></tr>
<tr><td>beta</td><td>ROFC → RDLPFC</td><td>0.22</td><td>0.009</td></tr>
<tr><td rowspan="3">HA-HA > AN-AN</td><td rowspan="2">alpha</td><td>LOFC → LTmp</td><td>0.23</td><td>0.007</td></tr>
<tr><td>LFEF → RDLPFC</td><td>0.18</td><td>0.006</td></tr>
<tr><td>beta</td><td>RFEF → LDLPFC</td><td>0.16</td><td>0.002</td></tr>
</table>

Table 3: Statistics for significant diferences during bilateral presentations of two happy (HA-HA) and two angry (AN-AN) faces.

4 Discussion

The main aim of the present study was to assess the possible hemispheric asymmetries for positive and negative emotions, starting from a controversial frame of reference proposing two contrasting theories: the RHH, suggesting a right-hemispheric superiority for all emotions, and the VH, suggesting a left/right-hemispheric superiority for positive/negative emotions, respectively. We exploited a divided visual field paradigm in which happy (positive) and angry (negative) emotional expressions were presented either to one hemisphere at time (unilateral presentation) or to the two hemispheres simultaneously (bilateral presentation). The present results revealed that during the unilateral presentations of an emotional face (Figure 2) the right hemisphere responds with increased information exchange (mostly in the alpha band) involving especially the dorsolateral area. Hence, this region seems to be crucial in processing all emotions, which is in line with the RHH. Nevertheless, it has to be highlighted that apart from the right hemisphere, the left one showed also increased communication when the emotional content was positive, according to the VH. The fact that the RDLPFC during processing of emotional information is strongly connected with several different areas suggests a kind of control function played by this region over the others (what is in line with the RHH), and the connectivity including DLPFC, IPS and FEF could be referred to the involvement of the Dorsal Attentional Network (DAN, Corbetta and Shulman, 2002) in emotional processing, confirming previous evidence (e.g., Ligeza et al., 2016). Moreover, limbic (temporal) structures are known to be associated to facial emotional detection (e.g., (Johnson, 2005), and the fact that the temporal activity is mainly lateralized to the left hemisphere could also be a sign of a linguistic processing, maybe due to an implicit verbal labelling of the emotions carried out by participants.

In the bilateral presentation of mixed emotional faces (Figure 3) only the presentation in accordance with the VH shows the connectivity among the same areas as those involved in unilateral presentation, further suggesting that when a positive emotion is presented to the left hemisphere and a negative emotion is (simultaneously) presented to the right hemisphere, there is a significant intensification of brain oscillations. Importantly, the opposite comparison (presentation contrary to the VH) yielded no single effect of increased flow. This can be considered as more efficient communication among the emotional-related brain areas (i.e., RDLPFC, bilateral OFC and IPS) when the left hemisphere is presented with positive and the right hemisphere is presented with negative content, which again strengthens their postulated specialization, especially in the perceptual domain. It should be noted, however, that this congruence with the VH applies to the effects observed in the anterior part of the brain, specifically in the dorsolateral region. That is where most of the hemisphere-specific effects were coherently observed. In this view, the fact that we did not find a stronger left- than right-hemispheric connectivity for emotional faces prevents us to support the motivational model, according to which both happy and angry emotional expressions should lead to a frontal left-hemispheric involvement, due to the approaching-related motivational content. The posterior areas, including parietal and occipital regions do not display pronounced hemispheric specialization, and it can be concluded that early stages are processed bilaterally by both hemispheres. Connections from the parietal, attentional regions to the orbitofrontal part seem to be equally affected, with no regard to the hemisphere.

Finally, a last comparison has been carried out between the two bilateral congruent conditions (Figure 4) and the results seem to confirm the VH, at least in the beta band: negative emotions leads to connectivity between right-hemispheric areas (from OFC to DLPFC), whereas positive emotions involved also left-hemispheric areas (DLPFC). Caution is needed concerning this latter point because the conditions included in these comparisons could differ in some features, including arousal level.

The present study investigated alpha and beta band oscillations during the passive viewing of emotional faces. By means of the same paradigm it has been previously shown that the emotion-related ERP components P1, N170 and P2 at parietal sites were generally larger in the right than in the left hemisphere, independently of the emotional content of the stimuli, thus supporting the RHH (Prete et al., 2018). In the same study, however, behavioural responses provided support for the VH. Thus, the overall conclusion was that ERP evidence is not necessarily congruent with behavioural evidence, at least in the field of asymmetries for positive and negative emotions.

Our findings confirm previous evidence (Balconi and Lucchiari, 2008; Ligeza et al., 2016) showing a crucial role of the right dorsolateral prefrontal cortex as a structure directly involved in the perceptual processing of all emotions, and it reveals connectivity in both alpha and beta bands which starts from this area to reach a number of areas involved in emotional detection, such as orbitofrontal cortex, temporal structures, frontal eye field and intraparietal sulcus. Importantly, if on one hand the right hemisphere – especially its anterior part – appears to be directly involved in all emotion processing, thus supporting the RHH, on the other hand it has to be highlighted that brain connectivity is stronger when a positive emotion directly reaches the left hemisphere and a negative emotion directly reaches the right hemisphere, thus providing support for the VH.

We can conclude that the two main theories on hemispheric asymmetries for emotions are not mutually exclusive but they coexist in a complex pattern of connectivity within and between the two hemispheres. We should also point that our results were based mostly on a visual presentation task with emotional stimuli, and our effects on brain connectivity and hemispheric lateralization patterns should be primarily interpreted in regard to perceptual processes. Moreover, our results are based on a paradigm in which only two emotional expressions have been used (angry and happy faces), and further studies are needed to verify the possibility to generalize these results to different emotional expressions (e.g., sadness or fear), and to different stimuli than faces (e.g., complex scenes). Finally, due to the fact that we mainly aimed at directly compare the VH and the RHH, in the present study a positive and a negative approach-related emotions have been selected. Starting from the possible different arousal level associated to happy and angry faces (e.g., Picardo et al., 2016), further studies are needed to disentangle this possible confounding effect. In this view, hemispheric asymmetries should be explored for approach-related (e.g., happiness or anger) vs avoidance-related (e.g., fear) emotions, in order to test the validity of the motivational model (Poole and Gable, 2014), and the possible influence of the arousal level of the stimuli.

5 Conclusions

In the present study we exploited unilateral and bilateral presentations of positive (happy) and negative (angry) emotional faces during EEG recordings. Starting from the unresolved field of cerebral asymmetries for positive and negative emotions, we were aimed at clarifying the involvement of each hemisphere in positive and negative emotion perception, by means of estimation of effective connectivity used to estimate causal influences between brain regions. We found that the majority of interconnected brain areas for both positive and negative emotions were lateralized to the right hemisphere, independently of the visual field of presentation, thus supporting the RHH. Moreover, the right-hemispheric activity was stronger when the presentation of the emotional stimuli was congruent with the VH (angry faces presented to the RH and happy faces presented to the LH). We found higher connectivity among prefrontal cortex, attentional network (frontal eye field, intraparietal sulcus), visual areas and temporal sites. In accordance with previous studies, results seem to suggest a core role of the right dorsolateral prefrontal cortex, possibly involved in a top-down regulation toward different areas involved in emotional processing. The present study showed that the RHH and the VH coexist during emotional perception, as shown by means of a Directed Transfer Function analysis.

References

Baas, D., Aleman, A., Kahn, R.S., 2004. Lateralization of amygdala activation: a systematic review of functional neuroimaging studies. Brain Research Reviews 45, 96–103.

Baijal, S., Srinivasan, N., 2011. Emotional and hemispheric asymmetries in shifts of attention: An ERP study. Cognition and Emotion 25, 280–294.

Balconi, M., Lucchiari, C., 2008. Consciousness and arousal effects on emotional face processing as revealed by brain oscillations. A gamma band analysis. International Journal of Psychophysiology 67, 41–46.

Barbas, H., 2000. Connections underlying the synthesis of cognition, memory, and emotion in primate prefrontal cortices. Brain research bulletin 52, 319–330.

Bastos, A.M., Usrey, W.M., Adams, R.A., Mangun, G.R., Fries, P., Friston, K.J., 2012. Canonical Microcircuits for Predictive Coding. Neuron 76, 695–711. https://doi.org/10.1016/j.neuron.2012.10.038

Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting Linear Mixed-Effects Models Using lme4 | Bates | Journal of Statistical Software. Journal of Statistical Software 67. https://doi.org/10.18637/jss.v067.i01

Blinowska, K.J., Kuś, R., Kamiński, M., 2004. Granger causality and information flow in multivariate processes. Physical Review E 70, 050902.

Corbetta, M., Shulman, G.L., 2002. Control of goal-directed and stimulus-driven attention in the brain. Nature Reviews Neuroscience 3, 201–215. https://doi.org/10.1038/nrn755

Dasdemir, Y., Yildirim, E., Yildirim, S., 2017. Analysis of functional brain connections for positive–negative emotions using phase locking value. Brain Cogn 11, 487–500.

Davidson, R.J., 2004. What does the prefrontal cortex “do” in affect: Perspectives on frontal EEG asymmetry research. Biological psychology 67, 219–234.

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 and Cognition 6, 403–411.

Fusar-Poli, P., Placentino, A., Carletti, F., Allen, P., Landi, P., Abbamonte, M., Barale, F., Perez, J., McGuire, P., Politi, P.L., 2009. Laterality effect on emotional faces processing: ALE meta-analysis of evidence. Neuroscience Letters 452, 262–267.

Gainotti, G., 2012. Unconscious processing of emotions and the right hemisphere. Neuropsychologia 50, 205–218.

Gainotti, G., 1972. Emotional behavior and hemispheric side of the lesion. Cortex 8, 41–55.

Güntekin, B., Başar, E., 2014. A review of brain oscillations in perception of faces and emotional pictures. Neuropsychologia 58, 33–51.

Harmon-Jones, E., Gable, P.A., Peterson, C.K., 2010. The role of asymmetric frontal cortical activity in emotion-related phenomena: A review and update. Biological Psychology 84, 451–462. https://doi.org/10.1016/j.biopsycho.2009.08.010

Harmon-Jones, E., Peterson, C.K., 2009. Supine Body Position Reduces Neural Response to Anger Evocation. Psychol Sci 20, 1209–1210. https://doi.org/10.1111/j.1467-9280.2009.02416.x

Jamal, W., Das, S., Maharatna, K., Pan, I., Kuyucu, D., 2015. Brain connectivity analysis from EEG signals using stable phase-synchronized states during face perception tasks. Physica A: Statistical Mechanics and its Applications 434, 273–295. https://doi.org/10.1016/j.physa.2015.03.087

Jansari, A., Rodway, P., Goncalves, S., 2011. Identifying facial emotions: Valence specific effects and an exploration of the effects of viewer gender. Brain Cogn 76, 415–423.

Johnson, M.H., 2005. Subcortical face processing. Nature Reviews Neuroscience 6, 766.

Kaminski, M., Blinowska, K., 2014. Directed Transfer Function is not influenced by volume conduction—inexpedient pre-processing should be avoided. Frontiers in Computational Neuroscience 8, 61.

Kaminski, M., Blinowska, K.J., 2017. The Influence of Volume Conduction on DTF Estimate and the Problem of Its Mitigation. Frontiers in computational neuroscience 11.

Killgore, W.D., Yurgelun-Todd, D.A., 2007. The right-hemisphere and valence hypotheses: could they both be right (and sometimes left)? Social cognitive and affective neuroscience 2, 240–250.

Koessler, L., Maillard, L., Benhadid, A., Vignal, J.P., Felblinger, J., Vespignani, H., Braun, M., 2009. Automated cortical projection of EEG sensors: Anatomical correlation via the international 10–10 system. NeuroImage 46, 64–72. https://doi.org/10.1016/j.neuroimage.2009.02.006

Kuznetsova, A., Brockhoff, P.B., Christensen, R.H.B., 2017. lmerTest package: tests in linear mixed effects models. Journal of Statistical Software 82.

Li, Y., Cao, D., Wei, L., Tang, Y., Wang, J., 2015. Abnormal functional connectivity of EEG gamma band in patients with depression during emotional face processing. Clinical Neurophysiology 126, 2078–2089. https://doi.org/10.1016/j.clinph.2014.12.026

Ligeza, T.S., Wyczesany, M., Tymorek, A.D., Kamiński, M., 2016. Interactions Between the Prefrontal Cortex and Attentional Systems During Volitional Affective Regulation: An Effective Connectivity Reappraisal Study. Brain Topogr 29, 253–261. https://doi.org/10.1007/s10548-015-0454-2

Narumoto, J., Okada, T., Sadato, N., Fukui, K., Yonekura, Y., 2001. Attention to emotion modulates fMRI activity in human right superior temporal sulcus. Cognitive Brain Research 12, 225–231.

Picardo, R., Baron, A.S., Anderson, A.K., Todd, R.M., 2016. Tuning to the positive: Age-related differences in subjective perception of facial emotion. PloS one 11, e0145643.

Pizzagalli, D.A., Sherwood, R.J., Henriques, J.B., Davidson, R.J., 2005. Frontal Brain Asymmetry and Reward Responsiveness A Source-Localization Study. Psychological Science 16, 805–813.

Pönkänen, L.M., Hietanen, J.K., 2012. Eye contact with neutral and smiling faces: effects on autonomic responses and frontal EEG asymmetry. Frontiers in human neuroscience 6, 122.

Poole, B.D., Gable, P.A., 2014. Affective motivational direction drives asymmetric frontal hemisphere activation. Experimental brain research 232, 2121–2130.

Prete, G., Capotosto, P., Zappasodi, F., Laeng, B., Tommasi, L., 2015a. The cerebral correlates of subliminal emotions: an electroencephalographic study with emotional hybrid faces. European Journal of Neuroscience 42, 2952–2962.

Prete, G., Capotosto, P., Zappasodi, F., Tommasi, L., 2018. Contrasting hemispheric asymmetries for emotional processing from event-related potentials and behavioral responses. Neuropsychology.

Prete, G., D’ascenzo, S., Laeng, B., Fabri, M., Foschi, N., Tommasi, L., 2015b. Conscious and unconscious processing of facial expressions: Evidence from two split-brain patients. Journal of neuropsychology 9, 45–63.

Prete, G., Laeng, B., Tommasi, L., 2014. Lateralized hybrid faces: evidence of a valence-specific bias in the processing of implicit emotions. Brain Cogn 19, 439–454.

Sato, W., Kochiyama, T., Yoshikawa, S., Naito, E., Matsumura, M., 2004. Enhanced neural activity in response to dynamic facial expressions of emotion: an fMRI study. Cognitive Brain Research 20, 81–91.

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. Psicologia USP 22, 181–196.

Tukey, J.W., 1976. Exploratory data analysis. 1977. Massachusetts: Addison-Wesley.

Van de Steen, F., Faes, L., Karahan, E., Songsiri, J., Valdes-Sosa, P.A., Marinazzo, D., 2016. Critical comments on EEG sensor space dynamical connectivity analysis. Brain topography 1–12.

Vecchio, F., Babiloni, C., Buffo, P., Rossini, P.M., Bertini, M., 2013. Inter-hemispherical functional coupling of EEG rhythms during the perception of facial emotional expressions. Clinical Neurophysiology 124, 263–272.

von Stein, A., Sarnthein, J., 2000. Different frequencies for different scales of cortical integration: from local gamma to long range alpha/theta synchronization. International Journal of Psychophysiology 38, 301–313. https://doi.org/10.1016/S0167-8760(00)00172-0

Vossel, S., Geng, J.J., Fink, G.R., 2013. Dorsal and Ventral Attention Systems Distinct Neural Circuits but Collaborative Roles. Neuroscientist 1073858413494269. https://doi.org/10.1177/1073858413494269

Wyczesany, M., Ferdek, M., Grzybowski, S., 2014. Cortical functional connectivity is associated with the valence of affective states. Brain Cogn 90, 109–115. https://doi.org/10.1016/j.bandc.2014.06.001

Wyczesany, M., Grzybowski, S., Barry, R., Kaiser, J., Coenen, A., Potoczek, A., 2011. Covariation of EEG synchronization and emotional state as modified by anxiolytics. J Clin Neurophysiol 28, 289–296. https://doi.org/10.1097/WNP.0b013e31821c34f7

Wyczesany, M., Kaiser, J., Barry, R., 2009. Cortical lateralization patterns related to self-estimation of emotional state. Acta Neurobiol Exp (Wars) 69, 526–536.

Wyczesany, M., Ligeza, T., Grzybowski, S., 2015. Effective connectivity during visual processing is affected by emotional state. Brain Imaging and Behavior 9, 717–728. https://doi.org/10.1007/s11682-014-9326-8