

Spectrally-resolved EEG inter-subject correlation reveals distinct cortical oscillatory patterns during free-viewing of affective scenes

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RUNNING HEAD: Emotions trigger inter-brain cortical coherence

ABSTRACT

The analysis of the similarity of the brain response of different individuals using inter-subject correlation (ISC) can be used to uncover the neural mechanisms behind the processing of complex audiovisual stimuli, and to understand how the brain works in real life situations. Previous research on ISC reported anecdotal evidence of larger ISC during emotional scenes compared to neutral ones, but this effect has not been systematically investigated using standardized emotional movies. Moreover, the complex interplay between neuronal populations oscillating at different time-scales was mainly studied through fMRI, thus with limited temporal resolution. This study aimed at showing how emotional movies synchronize brain activity in the main frequency bands characterizing cortical activity. Thirty-nine participants watched 18 movie clips selected from a standardized database of emotional movies (E-MOVIE) while their EEG activity was recorded. Spectrally-resolved ISC was computed based on the coherence of homologous channels for each possible subject pair in the Delta, Alpha and Gamma bands.

Permutation-based statistics revealed that all emotional categories prompted larger ISC compared to the Neutral in each band. Moreover, high arousal erotic and fearful scenes prompted larger Delta-ISC and Gamma-ISC compared to the other categories. Finally, ISC topography followed a spatial gradient. At slower frequencies, ISC involved wider regions of the scalp, becoming more restricted to occipito-parietal regions at higher frequencies.

Taken together, these results show that emotions trigger brain synchronization between individuals at multiple spatial and spectral scales. Different emotional states are reflected in specific topographical patterns of ISC in different frequency bands.

1. INTRODUCTION

In recent years the quest for increasing the ecology of how cognition and its neurobiological foundations are investigated has surged (Spiers & Maguire, 2007). Within this trend, the use of naturalistic audiovisual stimuli like movies has rapidly increased, due to their inherent visual complexity, dynamicity and affective potential which make movies an ideal probe to investigate multiple cognitive domains while avoiding the artificiality that usually characterizes experimental paradigms in cognitive neuroscience (Hasson & Honey, 2012; Nastase, Goldstein, & Hasson, 2020). Indeed, it is very common to investigate cognitive and emotional processes using very simple stimuli, which are easier to control (in terms of their physical and perceptual properties). However, they often represent an over-simplification of what the brain has to process in real-life (Hasson & Honey, 2012; Nastase, Goldstein, & Hasson, 2020).

Besides these advantages, naturalistic paradigms pose non-trivial challenges when it comes to quantifying the brain response to stimuli. Indeed, classical event-related designs represent a sub-optimal approach since naturalistic stimuli do not have discrete events. This prevents the experimenter to characterize brain activity time-locked to specific events, using classical analytical approach. To overcome this issue, Hasson and colleagues (2004) developed a new metric called inter-subject correlation (ISC) which assessed the reliability across participants' brain responses to a movie, rather than quantifying the brain physiological response according to a theoretical model, as in classical event-related designs. The great advantage of this metric is that it allows to uncover specific configurations of brain activity that, due to the uncontrolled nature of a movie, elude the response amplitude modulation typically investigated. Specifically, they showed that watching a movie triggers a strong cortical synchronization between different participants in their primary and secondary sensory cortices (visual and auditory), which also extends beyond these regions and recruits areas involved in higher order cognitive processes, like attention and memory (Hasson et al., 2004).

Since this seminal work, ISC has been explored and refined in a large corpus of studies, demonstrating that ISC is larger during the viewing of professionally-edited movies compared to amateur ones (Herbec, Kauppi, Jola, Tohka, & Pollick, 2015), as well as larger during the presentation of temporally coherent scenes compared to clips scrambled in time (Stephens, Honey, & Hasson, 2013). In addition, in terms of region specific synchronization, it has been shown that brain areas known to respond selectively to some features (i.e., object or faces) are characterized by an increased ISC which is time-locked with the display on the screen of these features (Hasson et al., 2004).

Interestingly, several authors reported that a consistent source of ISC is represented by the emotional information embedded in the stimulus. Using a reverse-correlation strategy, Hasson and colleagues (2004) firstly showed that the global (i.e., non specific to any particular brain region) ISC time course peaks in correspondence of emotionally charged scenes, speculating that this effect might result from the interaction between arousal and attention. Jääskeläinen and colleagues (2008) further suggested that a movie's emotional content might drive increased ISC in frontal regions, especially in the right hemisphere. Using EEG, Dmochowski and colleagues (2012) also reported that ISC is significantly increased during scenes characterized by marked emotional arousal. Their study showed a spectral modulation and a spatial topography which supports the claim that ISC might reflect not only the cortical processing of low-level visual features but also and foremost the cortical signature of increased emotion-laden attention (Ray & Cole, 1985) toward the external environment.

Altogether these studies consistently acknowledged that affective information shapes brain reactivity during ecological stimulation. Nevertheless, they did not formally investigate this effect. The first study that directly addressed this issue (Nummenmaa et al., 2012) showed that ISC varies as a function of the two dimensions underlying emotional experience, namely valence and arousal. Modeling the emotional content of the movies presented to the participants revealed that emotional valence predicts ISC in brain regions belonging to the default mode network (DMN), as well as regions involved in mapping bodily states like insula and anterior cingulate cortex. On the other hand, emotional arousal triggers larger ISC in areas involved in orienting the attention toward external stimuli, like the parietal regions composing the dorsal attentional network (DAN). This latter result provides compelling evidence that when emotionally arousing elements in the environment require attentional orienting, the brain is wired to react rapidly and in a consistent manner across different individuals, to prioritize incoming information processing and eventually coping with environmental requests (Nummenmaa et al., 2012).

Nevertheless, it is the interaction between valence and arousal that subtends the rich variety of emotional states experienced in everyday life. Thus focusing only on the relationship between ISC and subjective ratings, with regard to these dimensions, may limit the characterization of the complex cortical response to emotionally charged scenes. For instance, arousal in the context of negative emotions (i.e., fear) exerts a larger influence on memory compared to appetitive contexts (Mather & Sutherland, 2009). Moreover, negative and arousing stimuli engage visual attention to a larger extent compared to negative but low-arousing information and positive material (Jefferies, Smilek, Eich, & Enns, 2008). An open question that the present paper aims to answer is how affect-

driven ISC can reveal the effect of different emotional states, each occupying a unique portion of the affective space defined by valence and arousal, on cortical activity. This can help to increase our understanding of how affect shapes brain response in a naturalistic setting.

A critical prerequisite to achieve this aim is to leverage the use of stimuli which have a highly standardized and predictable emotional effect, rather than using *ad-hoc* non-standardized film clips as in previous studies (Dmochowski et al., 2012; Nummenmaa et al., 2012). Such stimuli should be able to elicit different affective states each characterized by a unique combination between valence and arousal. This means having stimuli with opposite valence but comparable arousal or, viceversa, stimuli with equal valence but differing in the degree of the arousal induced. Additionally, because valence and arousal represent overarching dimensions along which discrete emotional states can be identified (Cowan and Keltner, 2017), only with the use of standardized emotional movies will it be possible to identify emotion-specific patterns of ISC within these dimensions.

For this study, stimuli were selected from E-MOVIE (Maffei & Angrilli, 2019a), a recently published collection of short film clips with standardized duration, explicitly designed to be used in psychophysiological and neuroimaging experiments. These clips are designed to probe into several affective states to study reactions at both subjective (Maffei, Vencato, & Angrilli, 2015) and physiological level (Maffei & Angrilli, 2019b; Maffei, Spironelli, & Angrilli, 2019). A unique feature of E-MOVIE compared to other existing databases, is that clips are divided in six emotional categories (Erotic, Scenery, Sadness, Compassion and Fear and Neutral condition) arranged along the valence/arousal dimensions. This makes E-MOVIE an ideal tool to study, in detail, how the different combinations of valence and arousal, exert their influence on inter-subject brain synchronization during naturalistic viewing.

A second open question concerning affect-driven ISC, is how it relates to the neurophysiological mechanisms governing cortical activity. A major limitation of fMRI investigation of inter-subject cortical synchronization is that it provides only indirect insights on the actual neural processes occurring during natural viewing. This information is fundamental, since the actual representation of the external world in the brain is the result of integrated activity at multiple time-scales embedded within oscillations occurring at different spectral resolutions and in different cortical regions. Due to the inherent sluggishness of the haemodynamic response, fMRI can provide information only on integrative processes that occur on a very long time scale (Hasson, Yang, Vallines, Heeger, & Rubin, 2008). On the other hand, M/EEG (magneto/electroencephalography) recordings can reveal how ISC occurs in the oscillations that spontaneously characterize brain activity.

Previous studies that looked at ISC in the spectral domain focused mainly on the alpha band, showing that it is modulated by stimulus attentional demand (Dmochowski et al., 2012; Ki, Kelly, & Parra, 2016), as well as by stimulus modality (Cohen & Parra, 2016). Indeed, cortical responses in the alpha range (8-13 Hz) have been repeatedly indicated as a fundamental correlate of the outward allocation of attentional resources (Klimesch, 2012). Changes in alpha amplitude in occipito-parietal cortices are thought to reflect critical mechanisms subtending activation in the visual pathway, required to maximize the processing of external stimuli. In the context of studies employing ISC, Dikker and colleagues also showed that intersubject coherence in the alpha band increases when individual alpha power decreases due to attentional demands from the environment (Dikker et al., 2017). Alpha modulation responds not only to external stimuli in general, but is sensitive to their emotional and motivational significance (De Cesarei & Codispoti, 2011). Specifically, in response to images characterized by high emotional arousal (i.e., erotic pictures or mutilated bodies) alpha band amplitude over posterior sites is usually reduced to larger extent compared to stimuli with no affective valence (De Cesarei & Codispoti, 2011; Sarlo, Buodo, Poli, & Palomba, 2005). This suggests that alpha encodes the motivational salience of a stimulus, and its suppression signals the detection of motivationally relevant information in the environment. Given the distinctive role of posterior alpha, it is possible to hypothesize that the detection and encoding of emotional over neutral information should be reflected in a larger ISC in the alpha range. Moreover, it can be predicted that the greater the intensity (i.e., the arousal) of the emotional experience the larger the alpha ISC.

Besides alpha activity, the complex interplay between attention and emotion involves the oscillatory activity in other cortical rhythms, both slower like Delta and faster like Gamma. Low frequency oscillations in the Delta range (0.5-3.5 Hz) are generally considered a hallmark of cortical idling, since they represent the dominant oscillatory pattern found during stages of deep sleep and after brain damage (Spironelli & Angrilli, 2009). Nevertheless, the topographical distribution of Delta oscillations, spanning over large portions of the cortical surface as well as the evidence that delta activity couples in both amplitude and phase with faster oscillations during complex cognitive activity, like attention and memory (Johnson & Knight, 2015; Morillas-Romero, Tortella-Feliu, Bornas, & Putman, 2015), suggests that delta activity carries more information about cortical computations than just signaling a state of cortical inhibition (Whittingstall & Logothetis, 2009). From an evolutionary perspective, it has been advanced that activity in the delta range reflects the most ancient and phylogenetically preserved cortical modules (Knyazev, 2012). This view is supported by converging evidence that suggest an overlap between cortical and subcortical generators of delta activity with circuits involved in basic motivation and reward (Knyazev, 2012).

Furthermore, abnormalities in delta activity are consistently found in psychopathological conditions characterized by motivational deficits (Knyazev, 2012). Taken together, this evidence suggests that delta activity represents an optimal target for the investigation of the basic mechanisms guiding the detection of emotionally relevant information in the environment. Specifically, it is possible to hypothesize that, within a general trend of larger ISC in the delta band for emotional vs neutral movies, the ISC is expected to be larger in response to scenes with strong biological significance like erotic and threatening clips.

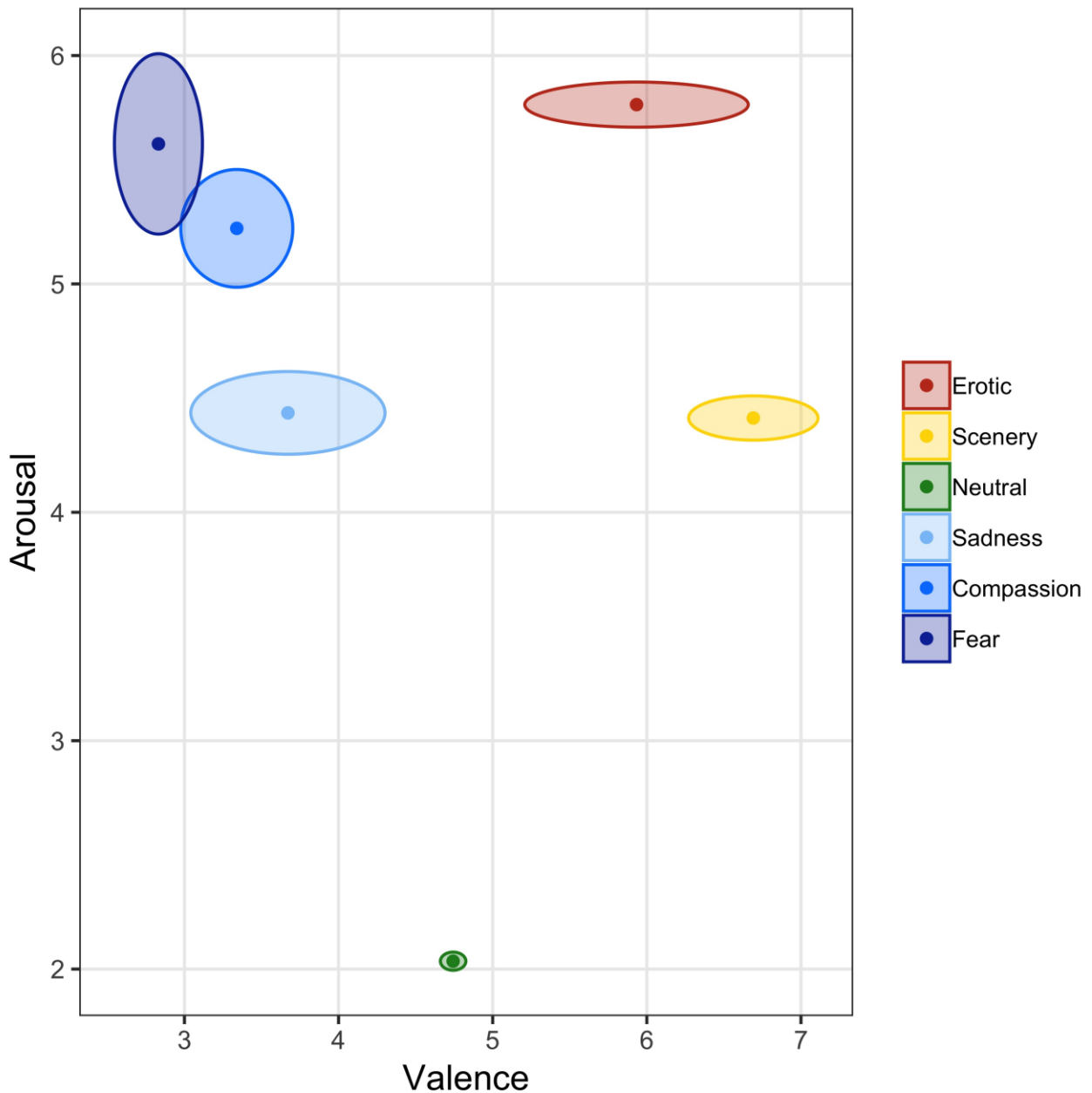
For what concerns faster activity, rapid oscillations in the gamma range are thought to reflect the ongoing integration of converging information which is critical for the emergence of more complex representations from basic sensory information. Comparisons of task-related EEG gamma responses with intra-cortical recordings showed that the former can be considered as a robust correlate of local neural activity (Jerbi et al., 2009). This mechanism has been detailed in the context of visual processing, in which these fast oscillations are recorded in the primary visual cortex, as well as secondary visual cortices and associative parietal regions, during the presentation of either simple or complex visual stimuli. Specifically, visual feature binding, attention, and memory encoding of visual stimuli are all processes that depend on the modulation of gamma activity in both animals and humans (Fries, 2009; Herrmann, Fründ, & Lenz, 2010; Jerbi et al., 2009). Concerning affective information, gamma oscillations proved to be sensitive to the emotional content of visual stimuli. Specifically, gamma power over parietal sites is modulated by both valence and arousal during affective pictures presentation (Keil et al., 2001). This twofold association between gamma activity, emotional valence and arousal has also been also reported during naturalistic viewing (Maffei et al., 2019). Finally, synchronized activity in the gamma range represents a fundamental step during the processing of stimuli with emotional significance and a critical prerequisite for their availability to consciousness (Luo et al., 2009). Taken together, these evidence allow to predict that the inter-subject synchronization in the gamma band during the viewing of emotional movies will be increased compared to a neutral condition, and that gamma-ISC will be larger in response to the Erotic and Fear clips, because these categories are characterized by high arousal and high pleasantness and unpleasantness, respectively.

2. METHODS

2.1. PARTICIPANTS, STIMULI AND PROCEDURES

The sample consisted of thirty-nine healthy participants (19 F, mean age \pm S.D.: 20.71 \pm 2.17) selected from an introductory psychology class who participated in exchange of course credits. All the participants were right-handed and had no history of neurological or psychiatric diseases. The stimuli were eighteen movie clips selected from E-MOVIE (Maffei & Angrilli, 2019a), arranged in six emotional categories, with three clips per category. The categories were Erotic (heterosexual couples engaged in a sexual act), Scenery (stunning views of different natural landscapes), Fear (thrilling scenes of anticipated threat), Sadness (scenes featuring themes of desperation and helplessness), Compassion (scenes of loss, grief and bereavement) and Neutral (scenes drawn from urban documentaries). These categories were selected to cover the whole pleasantness-unpleasantness spectrum and to vary the degree of the arousal elicited within this spectrum. Erotic and Scenery were selected to elicit a pleasant and appetitive response, the former characterized by high arousal while the latter by low arousal. Fear, Sadness and Compassion were instead selected to elicit unpleasant and aversive responses, with both high arousal (Fear) and low arousal (Sadness and Compassion). In the E-MOVIE validation (Maffei & Angrilli, 2019a), each clip was rated by 174 participants on valence and arousal with the Self-Assessment Manikin (Bradley & Lang, 1994), and on how the emotions experienced during each clip fit a series of emotional adjectives to provide a comprehensive assessment of the affective state they elicited¹. The distribution of each film score on valence and arousal is shown in Figure 1.

¹ The E-MOVIE database can be accessed at this link https://osf.io/scrbbp/?view_only=2b3081d3e1a44852a8a0f23ff5f396f7. The clips used were: E-2, E-3, E-4, Sc-3, Sc-4, Sc-6, Sad-1, Sad-2, Sad-3, C-3, C-5, C-6, F-2, F-5, F-6, N-4, N-6, N-7.



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The average duration of the clips was 123 sec (Erotic: $m = 120$ sec, $sd = 0$; Scenery: $m = 119$ sec, $sd = 5$ sec; Neutral: $m = 121$ sec, $sd = 1$ sec; Sadness: $m = 128$ sec, $sd = 3$ sec; Compassion: $m = 124$ sec, $sd = 6$ sec; Fear: $m = 126$ sec, $sd = 4$ sec). The clips were edited, using Adobe Premiere CS5, into a single continuous clip with a resolution of 1280 x 720 pixels, in which the clips were pseudo-randomized, to avoid the consecutive presentation of two clips of the same category.

During the movie presentation, scalp electrical activity was recorded using EEG. The signal was recorded from 38 scalp sites, 31 mounted on an elastic cap (ElectroCap) according the 10-20

International System, and 7 applied below each eye (IO1, IO2), on the external canthus of each eye (F9, F10), on the mastoids (A1, A2) and nasion (Nz). The signal was recorded with a SynAmps RT amplifier and the Curry 7 software (Compumedics Neuroscan, Charlotte, NC, USA), using a sampling rate of 500 Hz, Cz as online reference and keeping the electrode impedances below 5 K Ω . The whole experiment lasted 90 minutes, including skin preparation before sensors application. The study received the ethical clearance from the local Ethics Committee and all the procedures were conformed to the principle expressed by the Declaration of Helsinki for human experiments. All the participants granted their written informed consent to participate in the study.

2.2. EEG PREPROCESSING AND ISC ANALYSIS

EEG data preprocessing consisted of the following steps. First, the continuous data were re-referenced to the average of all channels, and eye artifacts were removed by the MSEC procedure (Ille, Berg, & Scherg, 2002) implemented in the software BESA. Then, the last 30 seconds of each clip were extracted from the continuous data for further analysis, and channels with an average amplitude exceeding ± 150 microVolts were interpolated by spherical spline interpolation. Data from two participants were removed due to an excessive number of artifacts, leading to a total number of 37 participants for the ISC analysis. The choice of restricting the analysis on this time frame was justified by the nature of the clips used, each characterized by containing all the emotional scenes in the last part of the clip, while the first minute serves to introduce the viewer with plot (Maffei & Angrilli, 2019a). Restricting the analysis to this window maximizes the possibility to detect the effect of the emotional content of the movies, since it gives time for the viewers to immerse themselves into the narrative and maximize the ecology of the emotional experience achieved through film watching, as shown also in previous works with E-MOVIE clips (Maffei et al., 2019).

Previous studies investigating inter-subject cortical synchronization with electrophysiological techniques relied on different approaches, ranging from simple correlation of channel time-series (as in BOLD-derived ISC) to multivariate approaches based on blind signal separation algorithms to extract correlated components of activity (Chang et al., 2015; Dmochowski et al., 2012). The main aim of this work was to derive a spectrally-resolved measure of inter-subject cortical synchronization from scalp EEG, thus for each subject pair, ISC has been defined as the magnitude-squared coherence of homologous channel activity.

Given two subjects A and B , the synchrony of their cortical activity at the channel i was computed according to the formula:

$$isc_{i_{AB}}(f) = \frac{|G_{i_A i_B}(f)|^2}{G_{i_A i_A}(f)G_{i_B i_B}(f)}$$

where $G_{i_A i_B}$ represents the cross-spectral density between the signals recorded from channel i in two subjects, and $G_{i_A i_A}$ and $G_{i_B i_B}$ represent the auto-spectral density of the signal from channel i for subject A and B, respectively. The spectral resolution was set at 0.5 Hz, and the ISC in the delta (0.5-4 Hz), alpha (8-13 Hz) and gamma (30 – 49 Hz) bands was derived taking the mean coherence value across all the bins in each band spectral range. The resulting ISC values can range from 0 (no inter-subject coherence) to 1 (perfect inter-subject coherence). Compared to other methods to characterize ISC from EEG recordings, this approach aims at providing a direct assessment at each sensor location of the phase-locked activity between subject pairs, under the assumption that if the oscillatory cortical activity in each band is not synchronized among subjects the ISC will approach to 0. This technique aims to extend the previous knowledge regarding how emotional content modulates cortical oscillatory activity by looking at synchronized spectral changes among participants, which depends on a phase alignment in their cortical activity. On the other hand, techniques based on Canonical Correlation Analysis (Dmochowski et al., 2012) allow only to assess the oscillatory properties of the time-series of the correlated component representing the shared activity among subjects extracted from the recordings. A similar approach to the one employed in the present research has been successfully employed by Dikker and colleagues (2017) to quantify ISC dynamics in a real-life setting.

This analytical strategy resulted in one ISC matrix for each band and channel of the form:

$$ISC^{(n)} = \begin{matrix} & S_1 & S_2 & S_3 & \dots & S_n \\ \begin{matrix} S_1 \\ S_2 \\ S_3 \\ \vdots \\ S_n \end{matrix} & \begin{pmatrix} 1 & isc_{21} & isc_{31} & \dots & isc_{n1} \\ isc_{12} & 1 & isc_{32} & \dots & isc_{n2} \\ isc_{13} & isc_{23} & 1 & \dots & isc_{n3} \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ isc_{1n} & isc_{2n} & isc_{3n} & \dots & 1 \end{pmatrix} \end{matrix}$$

in which the off-diagonal elements represent the ISC for a given band and a given channel between all possible subject pairs. The ISC was computed separately for each film clip, and then derived for each category by computing the median across the three excerpts.

Since the ISC matrix is symmetrical, only the lower triangular portion has been used for statistical analysis. This yielded a total of 666 ISC values per channel, band and film category, representing the observational units for statistical analyses. ISC computation was performed using custom MATLAB scripts.

2.3. STATISTICAL DESIGN

First, the spatial topography of the ISC for each film category was characterized with a non-parametric bootstrap sampling procedure (Chen et al., 2016; Nastase, Gazzola, Hasson, & Keysers, 2019). Because parametric tests (like the one-sample t-test) are not adequate for assessing ISC significance (Nastase et al., 2019), it is necessary to rely on a non-parametrical framework. In this framework, the observed median ISC is compared to an empirical null distribution, estimated from the data, to derive its probability if the null hypothesis is true. The procedure to estimate this empirical null distribution at each scalp site and use it for hypothesis testing consists of three steps. First, a bootstrapped distribution of the median ISC was estimated by resampling subject data 10000 times, and extracting the median ISC in each iteration. Then, a bootstrapped null distribution was obtained by subtracting the actual ISC value from the resampled median distribution (Hall & Wilson, 1991). This bootstrap null distribution was finally used as a reference for comparing the observed median ISC under the null hypothesis of zero inter-subject coherence. To address the simultaneous testing of multiple cortical sites, the resulting p-values were corrected with the Benjamini and Hochberg procedure to control the false-discovery rate. This analysis was performed separately for each EEG band considered.

The second step comprised testing the hypothesis that the content of the emotional categories would trigger a larger cortical inter-subject synchronization compared to the affectively neutral condition. This was accomplished using a permutation-based approach (Chen et al., 2016; Maris & Oostenveld, 2007; Nichols & Holmes, 2002). ISC values at each site were compared between each emotional category and the neutral category with a one-tailed t-test, then values were randomly shifted between the categories and the test recomputed 5000 times in order to construct a null distribution of t-values. This distribution was then used to test the null hypothesis of no difference between emotional categories and the neutral one. The false-discovery rate resulting from multiple testing across electrodes was controlled using the Benjamini and Hochberg procedure to correct the observed probability values. This analysis was performed separately per each EEG band considered.

The use of a non-parametric framework for these analyses was justified by the commonly encountered problem in M-EEG and fMRI experiments of testing hypotheses with multidimensional dataset (i.e., multiple subjects, multiple conditions, multiple electrodes/voxels, multiple frequencies), which prevents to match the strict assumptions of standard parametric statistics. Adopting a non-parametric approach allows the relaxing of these assumptions through the estimation of the null distribution of the test statistic directly from the data, also making straightforward the computation of exact probability values.

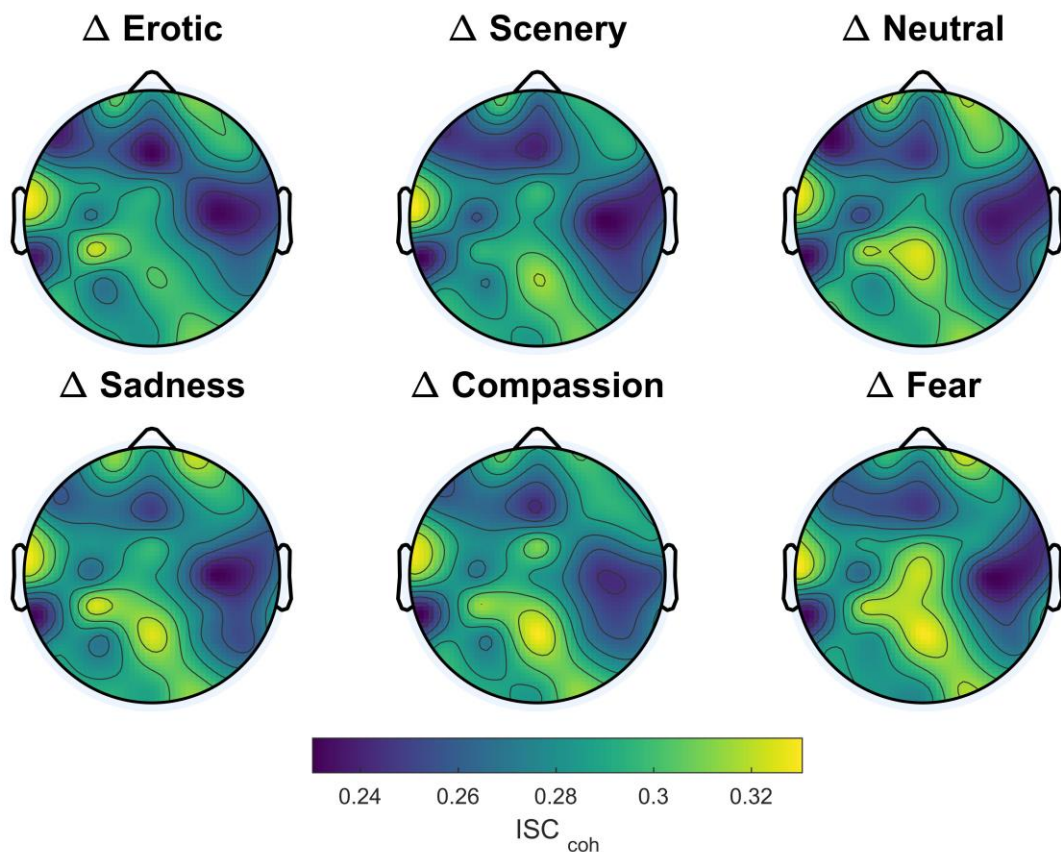
Once identified, for each emotional category, the scalp distribution of larger ISC (compared to the neutral condition), the third and last step consisted in assessing ISC differences among emotional categories. Nine scalp ROIs (Left-Frontal, Fronto-Central, Right-Frontal, Left-Temporal, Central, Right-Temporal, Left-Parietal, Occipital, Right-Parietal) were defined to construct a 3x3 grid covering the scalp along anterior-caudal and left-right axes. The ISC for each ROI was computed by taking the mean ISC of the sensors comprising the ROI. After this step, the delta ISC was computed by subtracting the ISC for the neutral category from the ISC for each emotional category. Finally, the ISC was modeled by fitting a linear mixed-effects model and adopting a model selection strategy based on the Akaike Information Criterion (Maffei & Angrilli, 2018; Maffei et al., 2019; Wagenmakers & Farrell, 2004). Akaike Information Criterion (AIC) is a metric derived from Information Theory that allows to compare models in terms of the amount of information they can explain while controlling for their complexity. It has a very straightforward interpretation, with a lower AIC indexing a better quality of one model compared to another. ISC data were fitted with a full model including three fixed-effect predictors (Film Category, Region and Hemisphere), their interactions and a random intercept to model repeated measurements across subjects. Outlier observations having a standardized residual exceeding 2.5 standard deviations were removed (less than 2 % of the total sample). This model was compared with its simpler instances derived by removing the predictors until reaching an intercept-only model. The best model was identified as the one with the lower AIC, and the significance of its predictors was assessed by means of an F-test using the Satterthwaite approximation for degrees of freedom (Luke, 2016). Significant effects have been further explored by means of post-hoc pairwise contrasts, corrected for multiple comparisons using false discovery rate (FDR).

All the statistical analyses were performed in R (v 3.3.1) with the use of the following packages: *tidyverse*, *lmerTest*, *lsmeans*, *boot*, *permute*, *MuMIn*.

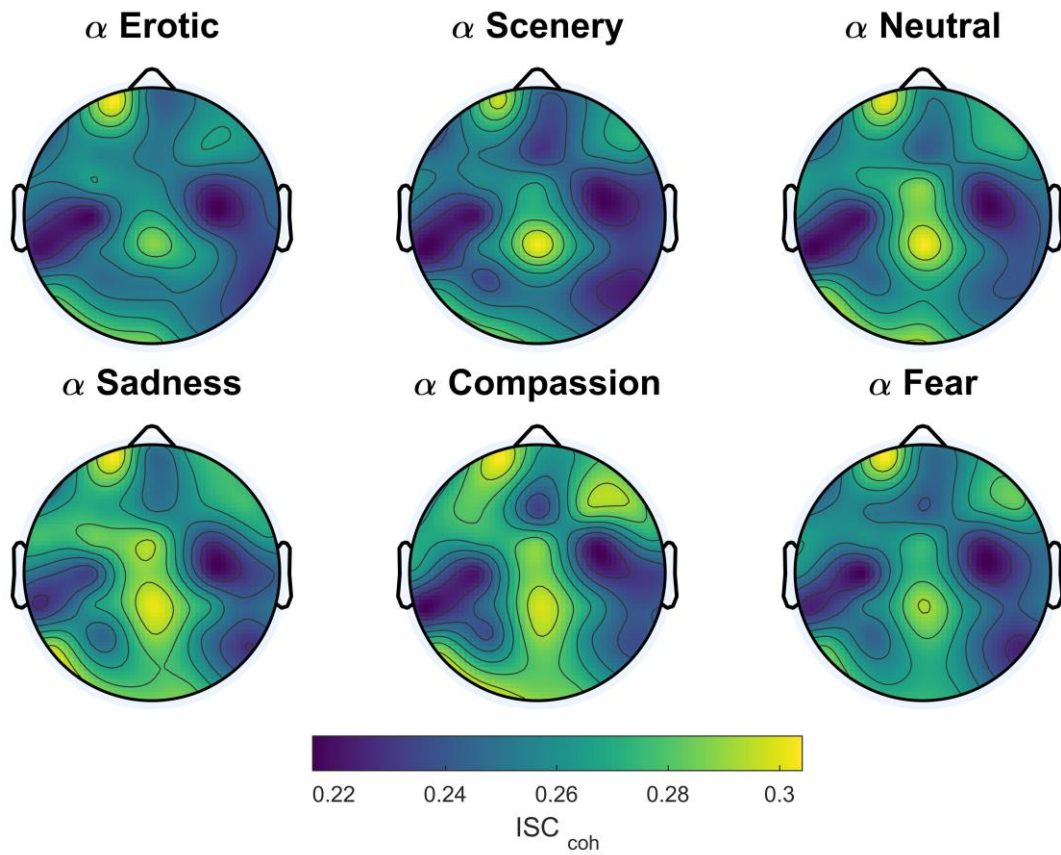
All the figures were generated either in MATLAB using the *topoplot.m* function from EEGLab, or in R using the *ggplot2* package.

3. RESULTS

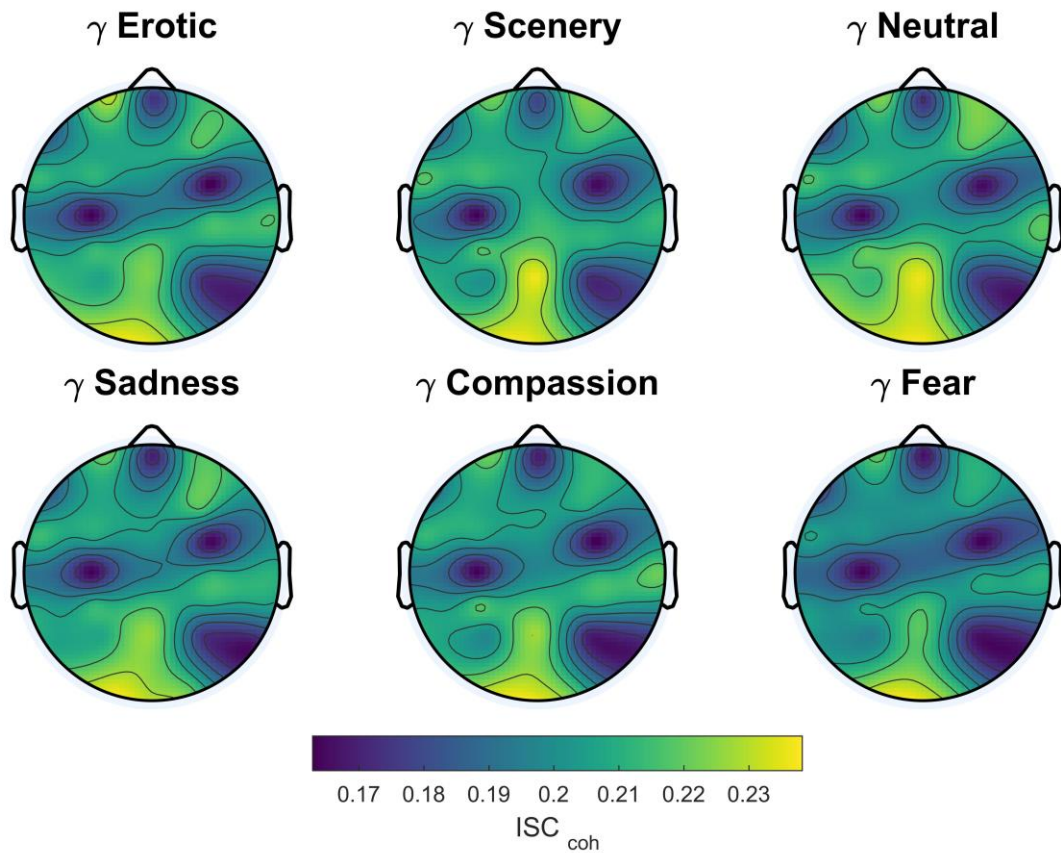
The scalp distribution of ISC was significantly different from zero at all scalp sites in each film category (see Supplementary Material A, for a table with the ISC values for each band and sensor). For the Delta band (Figure 2), the analysis showed that the highest ISC occurs over centro-parietal and occipital sensors, especially in response to clips belonging to the Fear category. A similar pattern was also observed for the Alpha band (Figure 3), although the scalp distribution indicates a stronger ISC over central electrodes than the occipital ones. Finally, analysis of ISC in the Gamma band (Figure 4) revealed a strong inter-subject synchronization over occipital and parietal sensors.



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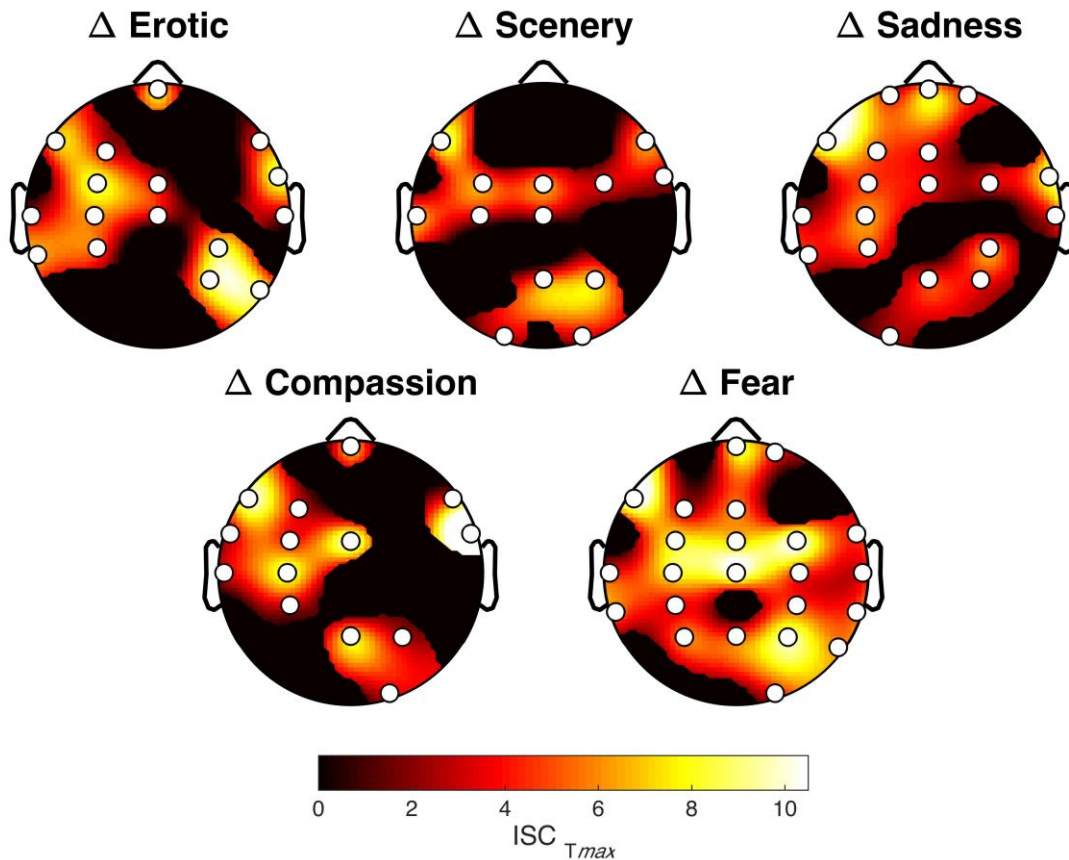


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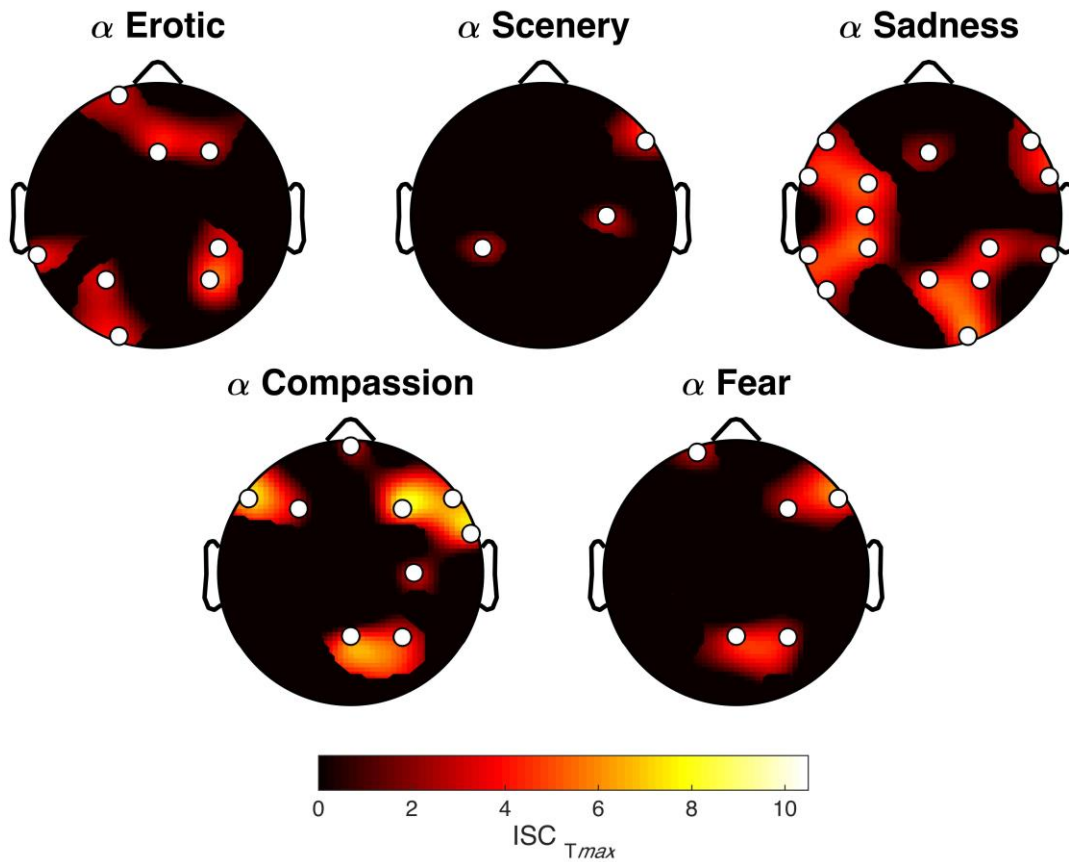
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Concerning the comparison between the ISC driven by emotional content and the ISC triggered by affectively neutral movies, the results for the Delta band showed a larger ISC for each emotional category which extended over wide portions of the scalp (see Table 1 in Supplementary Material B, for the t-values and their associated FDR-corrected *p-values* for each sensor). The comparisons revealed that ISC is significantly increased for the emotional categories in central and parietal sites (Figure 5). In addition, it showed that the emotional content also drove larger ISC in frontal and temporal regions for all categories but Scenery. Furthermore, visual inspection of scalp topography suggests a larger cluster of ISC for Erotic and Fear clips over right parietal electrodes.



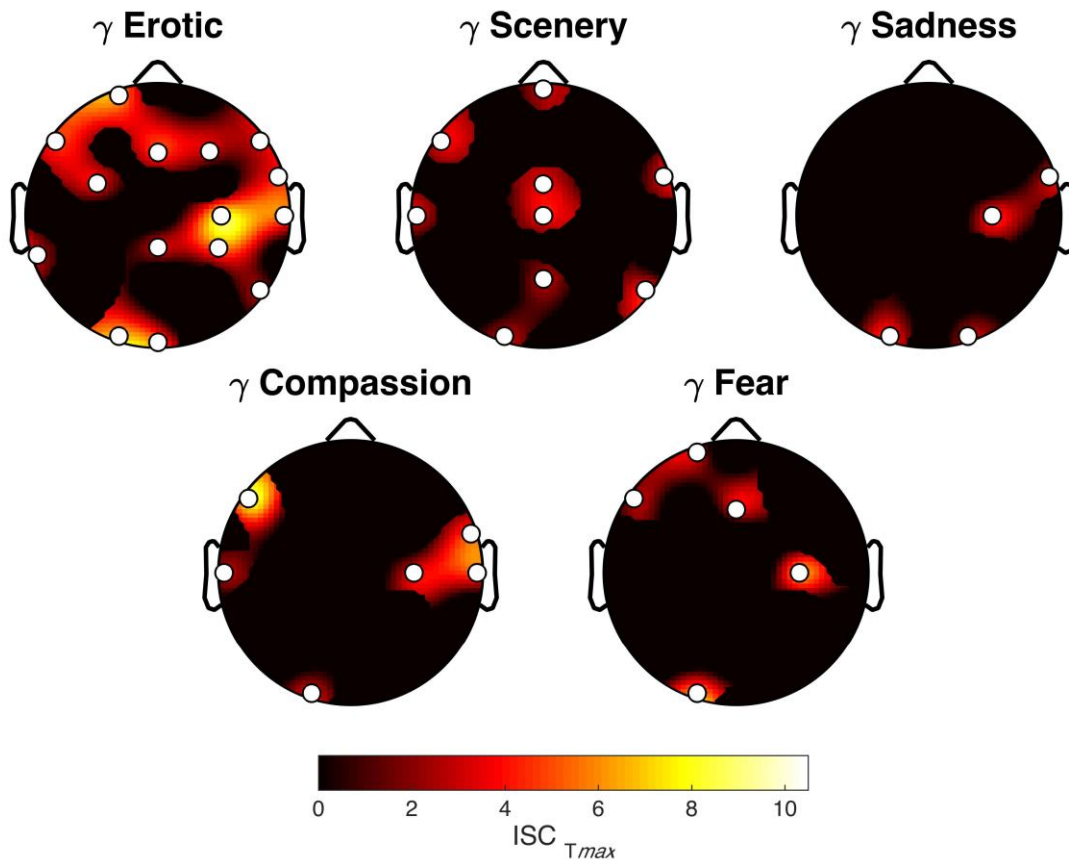
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Analysis of the effect of emotions on the ISC in the Alpha band showed stronger inter-subject cortical synchronization in response to emotional movies (the full results are reported in Table 2 in Supplementary Material B, which contains the t-values and their associated FDR-corrected *p-values* for each sensor). The ISC in the alpha band appears less spread compared to the one observed for the Delta, involving almost exclusively the centro-parietal sites for all categories (Figure 6). Visual inspection of scalp topography suggests that this larger ISC is maximal for Compassion and Sadness clips compared to the other affective categories. In addition, only the Compassion category elicited a specific larger ISC in frontal regions compared to the Neutral clips.



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Gamma band analysis showed that all the emotional movies drove a larger ISC compared to the neutral clip (the full results are reported in Table 3 in Supplementary Material B, which contains the t-values and their associated FDR-corrected *p-values* for each sensor). Larger ISC was observed, consistently across categories, over occipital and parietal sites, although the latter to a lesser extent (Figure 7). In these regions, Erotic and Fear clips that appear to elicit larger ISC than the remaining affective categories. In addition, Erotic movies are characterized by a unique spatial topography compared to the other clips, with larger ISC over central and left frontal sites.



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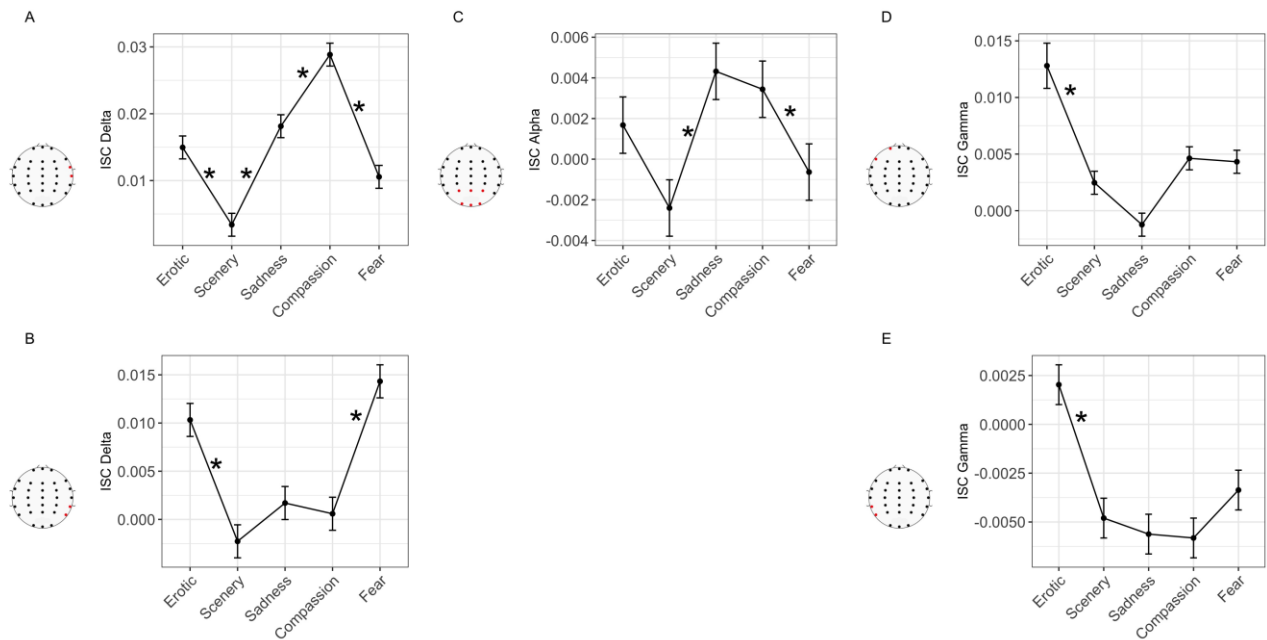
The analysis designed to test the difference in the affect-driven ISC among the five emotional categories showed that, for the Delta band, the best model was the one including all the predictors and their interactions ($AICc = -101883.6$, $\Delta AIC^2 = 110$, $AICw = 1$). The F-test performed to assess the significance of these predictors revealed a significant three-way interaction involving Film Category, Region and Hemisphere ($F_{(16,28745)} = 8.952$, $p < .0001$). Pairwise comparisons on this significant interaction showed that, in the right temporal ROI, Compassion movies elicited a larger ISC compared to other categories (Figure 8A), while Erotic and Fear movies triggered larger ISC in the right parietal ROI (Figure 8B).

Analysis of the Alpha band showed again that the best model was the one including all the predictors and their interactions ($AICc = -113437.2$, $\Delta AIC^2 = 45.2$, $AICw = 1$). The F-test

² The ΔAIC was computed as the difference in AIC between the first and the second ranked model and represents a measure of the difference of the quality between the two best models identified (Wagenmakers & Farrell, 2004)

performed to assess the significance of these predictors revealed a significant three-way interaction involving Film Category, Region and Hemisphere ($F_{(16, 28699)} = 4.83, p < .0001$). Pairwise comparisons revealed, over the occipital ROI, an increase in ISC for the Sadness and Compassion categories, compared to Fear and Scenery ones, and an increase in ISC for Erotic relative to Scenery clips (Figure 8C).

Consistently, analysis of the Gamma band showed that the best model was the one including all the predictors and their interactions ($AICc = -136548.9, \Delta AIC^2 = 65.34, AICw = 1$). The F-test to assess the significance of these predictors revealed a significant three-way interaction involving Film Category, Region and Hemisphere ($F_{(16, 28665)} = 6.09, p < .0001$). Pairwise comparisons showed, an increase in ISC over the left frontal and occipital ROIs for the Erotic clips compared to all the other categories (Figures 8D and 8E).



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4. DISCUSSION

The present paper aims at understanding how the emotional content embedded in a naturalistic stimulus, like a movie clip, modulates the cortical response of the viewer. Previous studies showed that naturalistic stimuli, like movies or audio narratives, trigger a large activation synchronized across viewers in sensory cortices and in regions that integrate low-level sensory information into high-order cognitive representations (Hasson et al., 2004, 2008). Moreover, previous research suggested that this inter-subject synchronization is boosted in the presence of emotionally relevant information (Dmochowski et al., 2012; Hasson et al., 2004; Nummenmaa et al., 2012).

To address this question, a series of film excerpts have been selected from the E-MOVIE database (Maffei & Angrilli, 2019a) arranged in six different categories (Erotic, Scenery, Sadness, Compassion, Fear and Neutral) and cortical response has been collected using EEG. In order to assess the participants' inter-subject synchronization, a new metric based on the coherence between homologous channels was developed to quantify the spectrally-resolved inter-subject correlation in the Delta (0.5-3.5 Hz), Alpha (8-13 Hz) and Gamma (35-48 Hz) bands. The reason to assess inter-subject correlation in the spectral domain stemmed from the need to understand the relative contribution of different oscillatory activities within the cortex, with the final aim to disentangle which band is more sensitive to the different affective states.

The first result of this study is that for each of the three bands considered there is a large degree of ISC in response to a naturalistic stimulus, irrespective of its emotional content. This finding mirrors evidences from fMRI studies that showed that ISC involves, although with a varying strength, all of the cortical surface (Chang et al., 2015; Chen et al., 2016; Hasson et al., 2004), and replicates the evidence that watching a movie prompts a strong ISC also in the electrical activity collected on the scalp (Haufe et al., 2018). The analysis showed different ISC topographies for the three bands considered, with a gradient of reducing topographical spread of the ISC, transitioning from slow to fast activity.

Delta-ISC was characterized by the widest topographical distribution, peaking in posterior electrodes while also involving frontal and temporal sites. This widespread cortical synchronization likely results from the inherent property of this oscillatory rhythm, reflecting the activity of the thalamo-cortical system regulating the relay of incoming sensory information throughout different cortical districts (Steriade, McCormick, & Sejnowski, 1993; Timofeev, Bazhenov, Seigneur, & Sejnowski, 2013). The topography observed for Delta-ISC in this study is also consistent with the topography reported in a recent MEG study employing a single movie (Lankinen, Saari, Hari, &

Koskinen, 2014). The large posterior ISC reflects the response driven by the visual stimulation exerted by movie clips, while the ISC observed over frontal electrodes might reflect the emotional content embedded in the clips mapped in the PFC (Jääskeläinen et al., 2008; Lankinen et al., 2014). On the other hand, Alpha-ISC was characterized by a narrower distribution over the scalp, with a large focus of correlated responses over centro-parietal electrodes and minor foci of ISC in occipital and frontal sites for all the categories. This scalp distribution suggests that the observed Alpha-ISC mostly reflects the deployment of attentional resources towards the stimulus displayed on screen. This interpretation is consistent with major accounts that posit a prominent role of alpha oscillations recorded on the surface of the scalp in tracking the activity of the dorsal attentional network (Capotosto, Babiloni, Romani, & Corbetta, 2009). Indeed, alpha desynchronization in posterior scalp sites is a ubiquitous correlate of outward attention in classical event-related paradigms (Foxe & Snyder, 2011; Klimesch, 2012). In addition, it has been shown using blind-signal separation algorithms that using a naturalistic stimulus like a movie, the most correlated (across participants) EEG component is characterized by desynchronization in the alpha range over centro-parietal electrodes (Dmochowski et al., 2012).

Finally, Gamma-ISC showed a topographical distribution revealing that the greatest coherence across participants' brain activity was confined to occipital and parietal sites. This provides evidence, for the first time using the inter-subject correlation approach, of the role of high-frequency oscillations in the cortical processing of complex visual scenes. Indeed, evidences from surface EEG, ECoG and single cell recordings converge in assigning a fundamental role to fast neural responses in the gamma range in vision (Fries, 2009; Jerbi et al., 2009). Specifically, these fast oscillations are critical for the computations needed for visual information processing and for binding the various features into a coherent perception (Fries, 2009; Fries, Nikolić, & Singer, 2007). This study shows that, for each film category, watching movie clips prompts a strong gamma activation which is highly consistent across viewers' brains, which likely stems from the occipital regions involved in both primary and secondary visual processing and in the parietal regions involved in multisensory integration.

For what concerns the effect of the emotional content of movies, an increased inter-subject coherence was predicted for all the emotional movies compared to the neutral ones. Results support this hypothesized modulation for each of the three bands considered.

In the delta band, the comparison with the neutral condition revealed a strong effect of affective content for each emotional category, with a maximum shared activation in posterior sites. This cluster of activity was common to all the five affective categories, which suggest that this effect

reflects a general increased response to emotionally charged scenes. This supports the idea that this slow oscillatory mode does not passively reflect cortical inhibition, but it rather plays an active role in encoding information from the environment that might be relevant for the organism (Güntekin & Başar, 2016; Knyazev, 2012). Moreover, taken together the pattern observed in this study gives further support to theoretical accounts viewing delta rhythm as an index of the activity within the circuits controlling the motivational state of the organism (Knyazev, 2012). Indeed, the comparisons of the affect-driven ISC in the delta band showed that it increases specifically in response to the three categories characterized by the largest motivational salience and the greatest evolutionary relevance, that are sexual, threatening and crying scenes. Erotic and Fear conditions exerted their influence especially over right parietal sites, suggesting that strong emotional arousal recruits to a large extent parietal regions. This observation might be interpreted as the effect of bottom-up recruitment of these regions by an arousing visual stimulus (Güntekin & Başar, 2014, 2016) a phenomenon in which slow oscillations in the delta range play an important role (Güntekin & Başar, 2014, 2016). Scenes characterized by crying (Compassion) instead elicited a large Delta-ISC in right temporal regions, consistently with previous studies that showed that delta response in these areas is larger for emotional faces and especially for faces for which the viewer has an affiliative response (Başar, Schmiedt-Fehr, Öviz, & Başar-Eroğlu, 2008; Güntekin & Başar, 2016; Sakihara, Gunji, Furushima, & Inagaki, 2012), which is the one subtending the empathic reaction to the sight of another person in tears (Maffei et al., 2019).

In line with the initial prediction, movies with affective content elicited larger ISC in occipito-parietal sites, compared to the neutral clips also in the alpha band, with Compassion and Sadness clips prompting the strongest Alpha-ISC. This specific response was unexpected, since previous investigation of alpha EEG suggested that emotional arousal might be the main source of alpha modulation over occipito-parietal sites (De Cesarei & Codispoti, 2011). Nevertheless, the focus of investigation of previous studies was changes in the power of alpha oscillations, while the present study focused on the amount of correlation of the power within the alpha range. Indeed, previous fMRI studies that used the inter-subject correlation approach reported that parietal regions, which are part of the posterior component of the default mode network, selectively show increased ISC in response to movies eliciting unpleasant and sad emotional states (Nummenmaa et al., 2012). Since alpha activity over occipito-parietal sites has been consistently found to be a reliable index of the activity of the posterior regions of the DMN (Knyazev, Slobodskoj-Plusnin, Bocharov, & Pylkova, 2011; Mo, Liu, Huang, & Ding, 2013), the present findings might reflect the electrophysiological signature of an increased DMN response to stimuli that comprise events with highly relevant socio-emotional information (Nummenmaa et al., 2012).

Affect-driven Gamma-ISC was significant for all the emotional categories compared to neutral clips, with Erotic movies prompting the largest effect, especially in the left hemisphere. This result is in line with the initial prediction of a prominent effect of emotional arousal on the synchronized cortical response of the viewers in this band. It additionally shows that appetitive arousal, the combination of high arousal and high pleasantness, leads to the greatest ISC. Moreover, the strong left lateralization observed in frontal and parietal sites is consistent with very recent findings supporting the “valence hypothesis” of hemispheric asymmetry for emotional processing (Wyczesany, Capotosto, Zappasodi, & Prete, 2018). In this study the authors found a pattern of information exchange that involves frontal, temporal and parietal sites in the left hemisphere, which highly resembles the topographical pattern of ISC found in response to erotic movies in the present study, and suggests the existence of a left-lateralized pathway for processing positive and appetitive emotional information.

5. CONCLUSIONS

Taken together, the present findings provide new insights regarding the cortical mechanisms subtending the processing of emotional information in an ecological context. This study provides new electrophysiological evidence that ISC involves a response which is differentiated in spectral domain, and with partially distinct topographical distribution for each band. Indeed, previous studies that investigated how ISC is able to capture the oscillatory properties of the cortex relied on BOLD-derived inter-subject correlation (Hasson et al., 2008; Kauppi, Jääskeläinen, Sams, & Tohka, 2010; Stephens et al., 2013), or focused on the spectral properties of correlated components extracted from EEG recordings (Cohen & Parra, 2016; Dmochowski et al., 2012; Ki et al., 2016). The fMRI studies showed that high-order brain regions integrate complex audiovisual information at longer timescales, thus showing ISC at slower frequencies, compared to sensory regions, which instead show a response in the upper spectrum of the BOLD signal (Stephens et al., 2013). This study extends this evidence to a direct measurement of the electrical activity of the cortex, showing that the ISC becomes more restricted to sensory regions as the frequency of the activity of interest increases. Low and mid-frequency activity in the delta and alpha bands show a wide ISC that peaks over central electrodes, suggesting a prominent involvement of high-order supramodal regions (Cohen & Parra, 2016). High-frequency activity instead shows a peak ISC over occipital sensors, suggesting a major involvement of modality-specific visual regions. This provides further support

to the existence of receptive window in the human brain that allow the processing of complex, multisensory, information by integrating different features over different time scales.

Moreover, by leveraging for the first time highly standardized emotional movies, this study reveals that different emotional states exert their influence on different oscillatory scales. Low-frequency cortical activity is sensitive mainly to high arousal clips, irrespective of their pleasantness or unpleasantness. On the other hand, alpha is more sensitive to the unpleasantness of the stimuli, especially those related to the displaying of suffering human beings, that is stimuli entailing a strong socio-emotional significance. Finally, high-frequency gamma oscillations reveal a unique response to arousing and appetitive stimuli. These results extend previous findings that suggested that spectrally-resolved ISC can reveal the effect of the emotional content on the processing of naturalistic scenes (Dmochowski et al., 2012). Indeed, the majority of studies that investigated ISC in the spectral domain have largely focused on alpha oscillations (Cohen & Parra, 2016; Dmochowski et al., 2012; Ki et al., 2016). The current study reveals that the effect of emotions on ISC is not restricted to a single oscillatory mode, but instead involves multiple oscillations sensitive to different features of the affective experience.

These results pave the way for future investigation that, combining high-density EEG recordings with source reconstruction algorithms, will go beyond scalp activity and reveal in greater detail the cortical regions involved in the dynamics observed in this research.

Indeed, it is important to acknowledge that the limited coverage of the scalp forbade analysis of EEG inter-subject coherence at source level in this study, thus limiting the interpretation as suggestive in term of the brain areas involved. Nevertheless, the present findings are strongly in accordance with results of studies using fMRI and/or MEG, allowing confidence in their interpretation. It is also important to list other caveats to guide the correct interpretation of these findings. First, these results come from the analysis of the last 30 seconds of film clips, and it might be the case that performing analysis on the entire clip length might reveal a different pattern. Analyzing the entire clip would probably magnify the attentional effect to a dynamic visual stimulus at the cost of shading the effect of the emotional content embedded in it. Indeed, previous studies that quantified ISC on entire film clips (Dmochowski, et al., 2012) revealed a strong ISC in brain regions involved in attention, especially in the spatial orienting of visual attention (like the posterior cingulate cortex). Second, these findings are the results of an aggregated analysis of several clips, in line with previous investigations of the effect of emotions on ISC (Nummenmaa et al., 2012). This choice helped to identify category-specific patterns, but, nonetheless, prevents a finer understanding of the specific features of each clip that contribute to the observed ISC.

Future studies should also try to characterize how the spectral coherence across viewer's brain changes in time, exploiting the metric here presented within a sliding window approach to the analysis of EEG signals. Such time-frequency analysis of inter-subject correlation is expected to reveal how spectral dynamics are affected by discrete and salient events within a continuous ecological narrative (i.e., "jumpscare" moments), and shed new light on the complex cortical interplay between attention and emotion. Finally, future research should also aim at characterizing basic spectral properties of ISC, to quantify how the strength of intersubject coherence changes across different brain rhythms.

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Disclosure Statement

The author reports no potential financial conflict of interest.

Figure Legends

Figure 1: Distribution of each emotional category ratings on the valence/arousal space from E-MOVIE (Maffei and Angrilli, 2019a) normative data. Dots represent mean valence and arousal ratings. The size of the ellipses refers to standard deviations of the ratings on both dimensions.

Figure 2: Scalp map showing the topographical distribution of the inter-subject coherence in the Delta (0.5 – 3.5 Hz) band for each emotional category

Figure 3: Scalp map showing the topographical distribution of the inter-subject coherence in the Alpha (8 – 13 Hz) band for each emotional category

Figure 4: Scalp map showing the topographical distribution of the inter-subject coherence in the Gamma (30 – 49 Hz) band for each emotional category

Figure 5: Scalp map showing the topographical distribution of the significant t-values from the contrasts between the ISC elicited by emotional movies and the ISC elicited by neutral movies in the Delta (0.5 – 3.5 Hz). Hot colors index larger ISC in the emotional conditions. The map shows only sensors for which a significant difference was observed.

Figure 6: Scalp map showing the topographical distribution of the significant t-values from the contrasts between the ISC elicited by emotional movies and the ISC elicited by neutral movies in the Alpha (8 – 13 Hz). Hot colors index larger ISC in the emotional conditions. The map shows only sensors for which a significant difference was observed.

Figure 7: Scalp map showing the topographical distribution of the significant t-values from the contrasts between the ISC elicited by emotional movies and the ISC elicited by neutral movies in the Gamma (30 – 49 Hz). Hot colors index larger ISC in the emotional conditions. The map shows only sensors for which a significant difference was observed.

Figure 8: Pairwise comparisons in affect-driven ISC (emotional minus neutral). Panel A-B show the effect of the emotional content on Delta-ISC in the right temporal and parietal ROIs, respectively. Panel C shows the effect of the emotional content on Alpha-ISC in the central-occipital ROI. Panel D-E show the effect of the emotional content on Gamma-ISC in the left frontal and parietal ROIs, respectively.

* indicate significant effect with $p < 0.05$ and bars represent standard errors.

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