Intersubject brain connectivity dynamics encode the stream of affect at multiple timescales

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Abstract

The stream of affect is the result of a constant interaction between past experiences, motivations, expectations and the unfolding of events. How the brain represents the relationship between time and affect has been hardly explored, as it requires modeling the complexity of everyday life in the laboratory. Movies condense into hours a multitude of emotional responses, synchronized across subjects and characterized by temporal dynamics alike real-world experiences.

Here, using naturalistic stimulation, time-varying intersubject brain connectivity and behavioral reports, we demonstrate that connectivity strength of large-scale brain networks tracks changes in affect. The default mode network represents the pleasantness of the experience, whereas attention and control networks encode its intensity. Interestingly, these orthogonal descriptions of affect converge in right temporoparietal and fronto-polar cortex. Within these regions, the stream of affect is represented at multiple timescales by chronotopic maps, where connectivity of adjacent areas preferentially maps experiences in 3- to 11-minute segments.

Introduction

Emotions are intense and immediate reactions of the body and the mind to a precise external or internal event occurring in the present, happened in the past or that may occur in the future (Russell and Barrett, 1999). Over the last years, increasing attention has been devoted to the study of the temporal characteristics of emotions and, more in general, of affective states (Scherer, 2009; Wilson-Mendenhall et al., 2013; Waugh et al., 2015). Studies highlighted factors that influence the timecourse of affect, as the importance of the eliciting event or its physical presence on the scene (see Waugh et al., 2015 and Verduyn et al., 2015 for a review). Moreover, the unfolding over time of affective states is well explained by a constructive process (Barrett, 2006; 2012), which postulates that emotions are the product of a moment-by-moment interaction of physiological, cognitive, social and perceptual components. As the affective experience seems to be intertwined with other mental processes (i.e., perception, cognition and action) the interplay of multiple large-scale networks may be crucial for the representation of emotional states in the brain (Lindquist and Barrett, 2012; Barrett, 2013; Wilson-Mendenhall et al., 2014; Pessoa, 2017; 2018). Of note, a network approach also accounts for the highly dynamic and flexible nature of affective experiences, as the same brain region contributes to different functional networks over time (Pessoa and McMenamin, 2017; Pessoa, 2017; 2018). In line with this, previous studies have identified a distributed set of cortical and subcortical areas consistently involved in the mapping of emotions (Kober et al., 2008; Lindquist et al., 2012; Lindquist and Barrett, 2012). The so-called extended social-affective default network, which comprises the amygdala, the temporoparietal junction, the medial prefrontal cortex and the precuneus among other regions, seems to play a role not only in mentalizing and empathic processing, but also in the representation of affective states (Amft et al., 2015; Satpute and Lindquist, 2019).

Nonetheless, to reveal brain regions involved in the processing of affect, the majority of neuroimaging studies have employed static or relatively brief stimuli (e.g., Posner et al., 2009; Baucom et al., 2012; Kim et al., 2017, but see also Raz et al., 2012; 2016; Résibois et al., 2017) that

may not be adequate to account for the temporal dynamics of the experience (Waugh and Schirillo, 2012). The use of movies in the functional magnetic resonance imaging (fMRI) setting could provide valuable insights instead. In fact, movies are ecological and dynamic stimuli that synchronize brain activity across individuals (Hasson et al., 2004), are able to elicit a wide variety of emotional states (Philippot, 1993; Gross and Levenson, 1995; Schaefer et al., 2010) and allow to track interactions of distinct brain areas over the course of the experience (Nastase et al., 2019). Promising evidence in this regard come from a work that, using relatively brief movie excerpts, demonstrated the association between salience and amygdala-based networks connectivity and the perceived intensity of sadness, fear and anger (Raz et al., 2016).

In the current study, using fMRI and a 2-hour long emotionally charged movie (Forrest Gump; Hanke et al., 2016; Lettieri et al., 2019), we explored the large-scale dynamic reconfigurations of brain networks associated with changes in the subjectively reported affective experience. To estimate variations in brain connectivity, we opted for the time-varying intersubject functional correlation approach (Simony et al., 2016; Najafi et al., 2017), which estimates the coupling of distinct brain regions across different subjects over the course of the stimulation (Figure 1).

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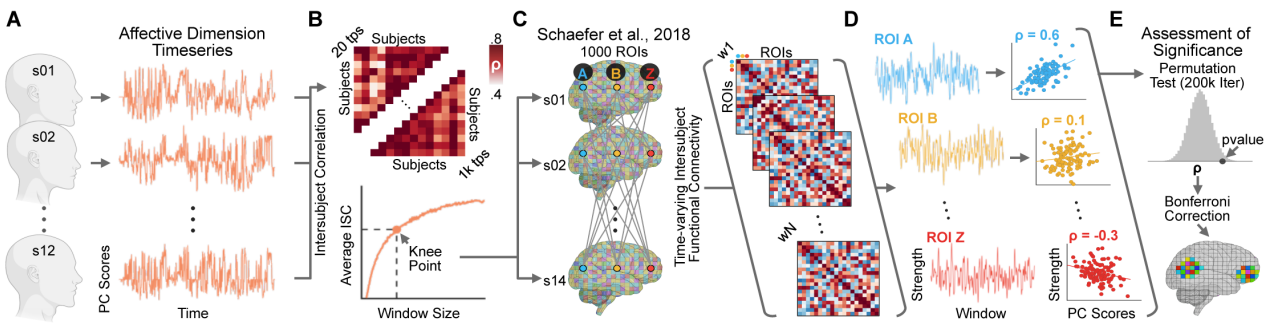

Figure 1 summarizes how we compute the association between affective dimensions extracted from behavioral ratings and time-varying connectivity strength of 1,000 brain regions. Each subject provided ratings of the affective experience during movie watching. We then applied principal component analysis to reveal single-subject affective dimension timeseries (polarity, complexity and intensity; panel **A**). Affective dimensions were correlated across subjects using a sliding window approach with multiple window size, ranging from 20 to 1,000 timepoints. Based on the tradeoff between window size and average intersubject correlation in behavioral ratings we selected the optimal width (i.e., knee point; panel **B**) for the subsequent estimation of brain connectivity dynamics. Brain activity was extracted from 1,000 regions of interest using Schaefer parcellation (2018) and time-varying intersubject functional correlation (tISFC) was computed following Simony et al., 2016 (panel **C**). For each brain area we estimated changes in connectivity strength on the complete graph and correlated (Spearman's ρ) the obtained timeseries with the timecourse of group-level affective dimensions (panel **D**). The assessment of significance was performed using a non-parametric permutation test and Bonferroni correction for multiple comparisons was then applied (n=1,000; critical p-value was 5.0e-5; panel **E**).

Findings demonstrate that reconfigurations of large-scale brain networks follow the changes in the reported affective state. The pleasantness (i.e., polarity) of the experience is primarily represented by connectivity of default mode network nodes, whereas the intensity of emotional events is mainly encoded by connectivity of the dorsal attention, ventral attention and control networks. Of note, connectivity of the right temporoparietal junction and the right fronto-polar cortex represents both polarity and intensity of affective states. In line with topographies of narrative comprehension and memory encoding revealed in high-order associative regions (Baldassano et al., 2017), our results also demonstrate a chronotopic (Protopapa et al., 2019) organization of affect, where distinct brain areas preferentially track changes in the emotional experience at different timescales, ranging from a few to several minutes.

Results

Single-Subject Affective Dimensions obtained from Behavioral Ratings. Affective states elicited by the watching of Forrest Gump are described by three orthogonal affective dimensions (Lettieri et al., 2019): (a) *polarity* (45% of the explained variance) defines whether and to what extent the current experience is perceived as pleasant (negative scores) or unpleasant (positive scores); (b) *complexity* (24% of the explained variance) represents how much the affective state is associated with cognitive processes (positive scores), rather than being characterized by fast and automatic responses (negative scores); (c) intensity (16% of the explained variance) denotes whether the experience is perceived as highly (high positive scores) or mildly (low positive scores) emotional. These three dimensions are consistent across all subjects ($p<0.05$) and explain approximately 85% of the variance in behavioral ratings. For *polarity* scores, median Spearman's correlation across subjects is $\rho=0.580$ (95% CI: 0.560 - 0.615) with an interquartile range of $\rho=0.124$. For *complexity* scores, median Spearman's correlation across subjects is $\rho=0.437$ (95% CI: 0.408 - 0.462) with an interquartile range of $\rho=0.124$. Lastly, for *intensity* ratings, median Spearman's correlation across subjects is $\rho=0.410$ (95% CI: 0.391 - 0.423) with an interquartile range of $\rho=0.089$.

To estimate the association between time-varying intersubject functional correlation (tISFC) and changes in the reported affective experience, we first identified the optimal width of the moving window considering the intersubject correlation of affective dimensions. A tradeoff between the across-participants agreement and window width is reached at 273 timepoints (9m:6s) for polarity, at 205 (6m:50s) for complexity and at 331 (11m:2s) for intensity (for further details please refer to *fMRI Experiment: Intersubject Functional Correlation* in *Methods* section). Affective dimension timeseries were therefore downsampled to this temporal resolution and correlated with brain connectivity dynamics.

Association between tISFC and Polarity of the Emotional Experience. Findings show that connectivity strength of four nodes of the default mode network is significantly associated with changes in the polarity of the affective experience ($p_{Bonf} < 0.05$; Figure 2A and 2B; Supplementary

Table 1). These four regions are the right temporoparietal junction, the right dorsal fronto-polar area, the right dorsomedial prefrontal cortex and the left precuneus. Connectivity of two other brain areas correlates with the perceived pleasantness of events: the right insula, which is part of the ventral attention network and the left middle occipital gyrus, a node of the dorsal attention network. Except for the left middle occipital gyrus, all other significant regions are negatively associated with polarity scores, meaning that the more unpleasant the experience is (i.e., positive scores) the weaker is the connectivity of default mode and ventral attention nodes. Instead, connectivity of the dorsal attention region increases for unpleasant events.

--- Figure 2 about here ---

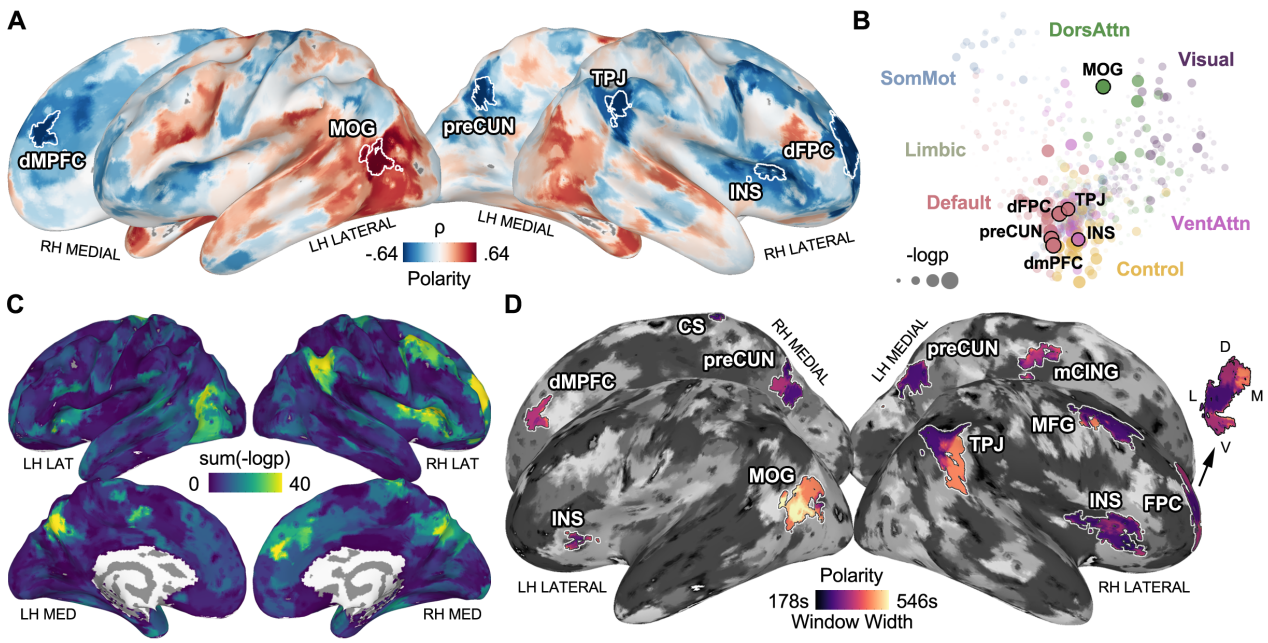

Figure 2. Panel **A** shows results for the correlation (Spearman's ρ) between each brain region tISFC strength and the timecourse of polarity (red colors denote positive, whereas blue colors negative relationships). White outlines define regions surviving the Bonferroni correction for multiple comparisons (n=1,000 regions of interest; critical p-value: 5.0e-5). In panel **B**, the functional distance between brain regions is mapped using multidimensional scaling. Each brain area (i.e., dot) is color-coded depending on network membership, whereas its size and transparency are scaled according to the -log(pvalue) of the relationship with polarity. Of note, the triangular arrangement of brain regions follows the typical transitions between unimodal (i.e, visual and somatomotor) and transmodal (i.e., default mode and control) areas found in Margulies et al., 2016 using resting state connectivity. Panel **C** represents the association between tISFC strength of each brain region and polarity at all explored timescales (from 89 to 273 timepoints). Colors reflect the sum of -log(pvalue) across timescales, ranging from no involvement at any timescale (i.e., dark blue) to consistent recruitment across conditions (i.e., yellow). Lastly, panel **D** depicts the timescale at which connectivity dynamics are maximally associated to changes in polarity for each brain region. White outlines mark areas found to significantly encode polarity at one or more timescales (i.e., logical OR across timescales). LH = left hemisphere; RH = right hemisphere; CS = central sulcus; preCUN = precuneus; TPJ = temporoparietal junction; INS = insula; dFPC = dorsal fronto-polar cortex; mCING = mid cingulate cortex; MFG = middle frontal gyrus; dmPFC = dorsomedial prefrontal cortex; MOG = middle occipital gyrus; FPC = fronto-polar cortex; DorsAttn = dorsal attention network; VentAttn = ventral attention network; SomMot = somatomotor network; D = dorsal; V = ventral; L = lateral; M = medial.

Networks Reconfiguration as function of the Polarity of Emotional Experiences. Figure 3 represents the correlation between significant regions and all other brain areas for events rated either as highly pleasant (i.e., polarity scores below the 10th percentile of the distribution) or highly unpleasant (i.e., polarity scores above the 90th percentile). As compared to unpleasant events, when the experience is perceived as pleasant, right anterior nodes of the default mode network (i.e., dorsal fronto-polar area and dorsomedial prefrontal cortex) show stronger negative correlations with several nodes of the visual network (Figure 3B and 3C). Also, with changes in polarity, the connectivity between these regions and other default mode nodes remains substantially identical. Correlation between the left precuneus and visual areas becomes more negative for pleasant experiences as well (Figure 3D). Moreover, the left precuneus shows a strengthening of negative correlations with dorsal attention regions when the experience is rated as highly unpleasant. The vast majority of connections of the right temporoparietal junction are related to changes in polarity, with an increase in magnitude of both positive and negative correlations moving from unpleasant to pleasant events (Figure 3A). During unpleasant events the right insula is negatively correlated with specific default mode and somato-motor regions. The magnitude of this correlation decreases when subjects are exposed to pleasant events (Figure 3E). The opposite behavior is observed when considering the association between the right insula and areas belonging to the visual network - i.e., weakening of negative correlations for unpleasant as compared to pleasant events. Changes in polarity also modulate the relationship between the right insula and other ventral attention and control network regions. Lastly, for the left middle occipital gyrus, the correlation becomes more positive with other dorsal and ventral attention areas when the experience is unpleasant (Figure 3F). During pleasant events, instead, the coupling of this region with the visual network goes from negative to positive.

--- Figure 3 about here ---

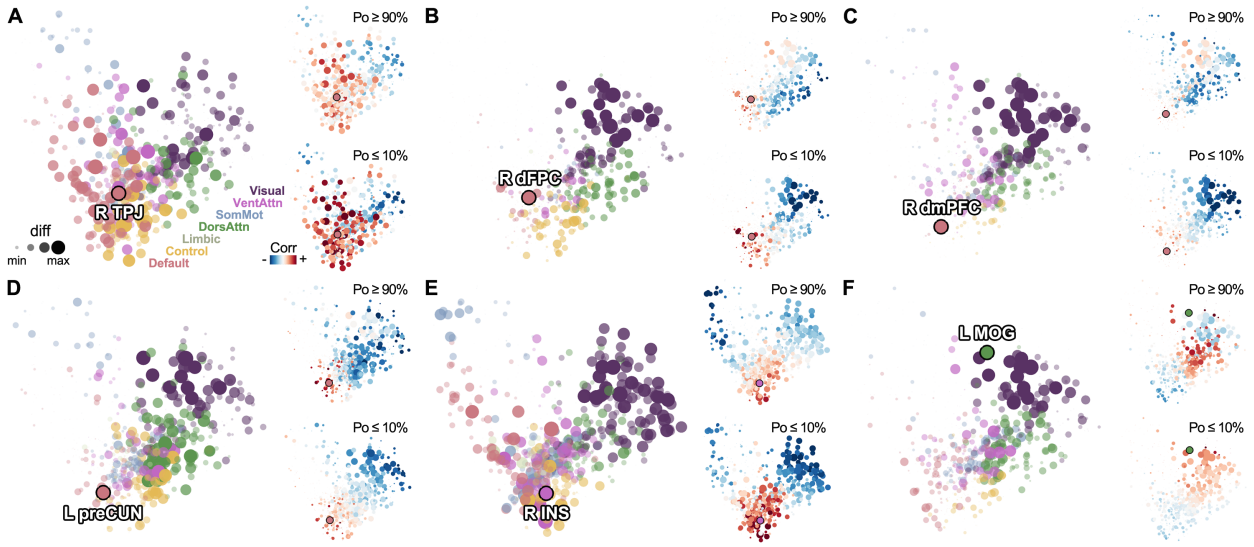

Figure 3 shows reconfigurations of functional connectivity during events rated either as highly pleasant (i.e., polarity scores below the 10th percentile) or highly unpleasant (i.e., polarity scores above the 90th percentile). Within each panel (**A**-**F**), functional distances of the 1,000 brain regions (i.e., dots) are expressed by the spatial arrangement in the multidimensional scaling space. In larger plots, regions are color-coded according to network membership and scaled in size and transparency based on the difference in correlation between the region of interest (i.e., black outlined dot) and the rest of the brain in pleasant and unpleasant events. Similarly, in smaller plots, size and transparency of each dot depends on the difference in correlation as function of polarity values, whereas color indicates the correlation with the region of interest (red positive and blue negative relationships). VentAttn = ventral attention network; DorsAttn = dorsal attention network; SomMot = somatomotor network; R TPJ = right temporoparietal junction; R dFPC = right dorsal fronto-polar cortex; R dmPFC = right dorsomedial prefrontal cortex; L preCUN = left precuneus; R INS = right insula; L MOG = left middle occipital gyrus.

Reliability of the Association between tISFC and Polarity at Multiple Timescales. We replicated the analysis of the relationship between polarity and brain connectivity dynamics at three alternative timescales (see Materials and Methods for further details): 89 timepoints (2m:58s), 143 timepoints (4m:46s) and 239 timepoints (7m:58s). The right dorsal fronto-polar area, the right insula and the left precuneus are associated with changes in *polarity* at all the explored timescales (see Figure 2C and Supplementary Figure 1). Also, connectivity of the right temporoparietal junction, the right dorsomedial prefrontal cortex and the right caudal middle frontal gyrus is significantly related to the pleasantness of the experience at three out of four timescales. Regions as the left middle occipital gyrus, the right precuneus and the right central sulcus track changes in *polarity* at two out of the four time intervals, whereas the left insula and the left mid-cingulate sulcus at a single time window.

Chronotopic Maps of the Polarity of Emotional Experiences. For each of these regions, we report the preferred timescale for the processing of polarity in Figure 2D. Connectivity of the right insula, the right caudal middle frontal gyrus, the right central sulcus and the left precuneus preferentially encodes pleasantness of the events at shorter timescales (~3 minutes), whereas the right dorsomedial prefrontal cortex, the left insula and the left mid-cingulate sulcus at intermediate time windows (~5 minutes). The only brain area showing a marked preference for longer timescales is the left middle occipital gyrus (from ~8 to ~9 minutes). In addition, interesting topographies are highlighted in the right temporoparietal junction, the right dorsal fronto-polar cortex and the right precuneus. Within the temporoparietal junction, connectivity of dorsocaudal territories is associated to *polarity* scores at shorter timescales (~3 minutes), while ventrorostral portions preferentially track pleasantness in ~8-minute segments. For the right precuneus, a rostrocaudal connectivity gradient suggests that, within this region, posterior territories encode *polarity* in 3-minute windows, while its anterior portions in 5-minute segments. Lastly, within the right dorsal fronto-polar area, connectivity is preferentially associated to scores of the *polarity* component at shorter timescales (~3 minutes) in dorsolateral and ventrolateral territories, at intermediate intervals (~5 minutes) in the lateral region and at longer timescales (~8 minutes) in the dorsomedial part.

Association between tISFC and Intensity of the Emotional Experience. Findings demonstrate that connectivity strength of ten brain regions is associated to the perceived intensity of the emotional experience ($p_{Bonf} < 0.05$; Figure 4A and 4B; Supplementary Table 2). Three of these brain areas - the right superior parietal lobule, the right intraparietal sulcus and the left postcentral sulcus - pertain to the dorsal attention network. Two regions belong, instead, to the ventral attention network: the right supramarginal gyrus and the ventral branch of the right precentral sulcus. Also, the caudal part of the right superior frontal gyrus and the pars orbitalis of the right inferior frontal gyrus, which are nodes of the control network, track changes in intensity. Lastly, connectivity of the anterior portion of the right temporoparietal junction, the right ventral fronto-polar area and the

dorsal branch of the right precentral sulcus, respectively part of the default mode, the limbic and the somato-motor network, is associated to the intensity of the emotional experience.

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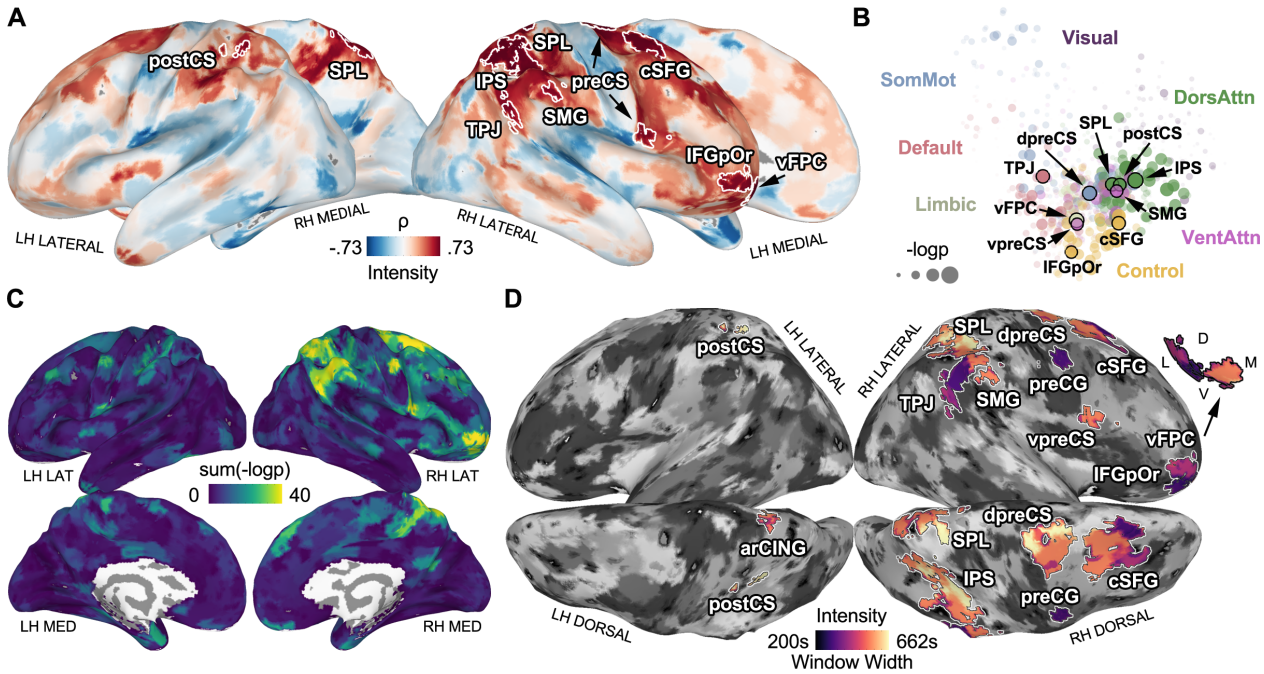

Figure 4. Panel **A** shows results for the correlation (Spearman's ρ) between each brain region tISFC strength and the timecourse of intensity (red colors denote positive, whereas blue colors negative relationships). White outlines define regions surviving the Bonferroni correction for multiple comparisons (n=1,000 regions of interest; critical p-value: 5.0e-5). In panel **B**, the functional distance between brain regions is mapped using multidimensional scaling. Each brain area (i.e., dot) is color-coded depending on network membership, whereas its size and transparency are scaled according to the -log(pvalue) of the relationship with intensity. Panel **C** represents the association between tISFC strength of each brain region and intensity at all explored timescales (from 100 to 331 timepoints). Colors reflect the sum of -log(pvalue) across timescales, ranging from no involvement at any timescale (i.e., dark blue) to consistent recruitment across conditions (i.e., yellow). Lastly, panel **D** depicts the timescale at which connectivity dynamics are maximally associated to changes in intensity for each brain region. White outlines mark areas found to significantly encode intensity at one or more timescales (i.e., logical OR across timescales). LH = left hemisphere; RH = right hemisphere; postCS = postcentral sulcus; SPL = superior parietal lobule; IPS = intraparietal sulcus; TPJ = temporoparietal junction; SMG = supramarginal gyrus; preCS = precentral sulcus; cSFG = caudal superior frontal gyrus; IFGpOr = pars orbitalis of the inferior frontal gyrus; vFPC = ventral fronto-polar cortex; dpreCS = dorsal branch of the precentral sulcus; vpreCS = ventral branch of the precentral sulcus; DorsAttn = dorsal attention network; VentAttn = ventral attention network; SomMot = somatomotor network; D = dorsal; V = ventral; L = lateral; M = medial.

All these regions show a positive relationship with the intensity dimension, meaning that the more the experience is perceived as intense, the stronger the connectivity between these areas and the rest of the brain is.

Networks Reconfiguration as function of the Intensity of Emotional Experiences. Figure 5 and Supplementary Figure 2 detail reconfigurations of functional connectivity during events either perceived as highly emotional (i.e., intensity scores above the 90th percentile of the distribution) or

rated as having modest impact (i.e., intensity scores below the 10th percentile). As compared to low intensity events, those rated as highly emotional are characterized by a strengthening of the negative relationship between nodes of the right dorsal attention network (Figure 5A and 5F and Supplementary Figure 2A) and default mode regions, as well as by an increase in the magnitude of the positive correlation between dorsal attention regions and control and ventral attention nodes. When the experience is rated as highly intense, regions of the ventral attention network, as the inferior branch of the precentral sulcus, become more negatively coupled with visual and default mode regions (Figure 5C and Supplementary Figure 2C). At the same time, these brain areas strengthen their positive relationship with control and dorsal attention nodes. Moving from low to high emotional events, the anterior portion of the right temporoparietal junction increases the within-network positive correlation with other default mode regions and decreases the anti-correlation with dorsal attention areas (Figure 5B). Also, this brain region is negatively related to the somato-motor network during low intensity events, whereas it becomes positively associated with the same areas when the experience is perceived as highly intense. Connectivity of the ventral fronto-polar area shows a clear switch in the coupling with default mode regions (Figure 5D): during low intensity events, this limbic area demonstrates a positive relationship with default mode nodes, which then becomes negative when the experience is rated as highly emotional. In addition, moving from low to high intensity events, the ventral fronto-polar region reinforces the positive relationship with the control network. Similarly, also the pars orbitalis of the right inferior frontal gyrus shows a negative correlation with the default mode and the somato-motor network during intense events (Figure 5E). This relationship is then reversed (i.e., becomes positive) when considering low intensity experiences. Lastly, this control network area becomes decoupled from visual nodes during high, as compared to low, intensity events.

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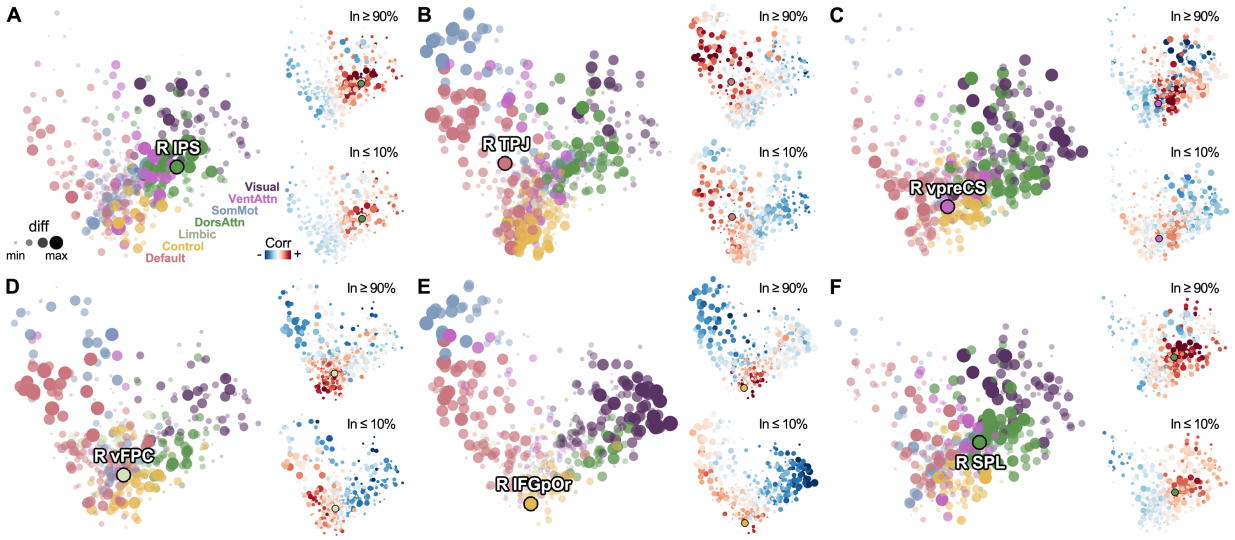

Figure 5 shows reconfigurations of functional connectivity during events perceived as highly emotional (i.e., intensity scores above the 90th percentile) or rated as having modest impact (i.e., intensity scores below the 10th percentile). Within each panel (**A**-**F**), functional distances of the 1,000 brain regions (i.e., dots) are expressed by the spatial arrangement in the multidimensional scaling space. In larger plots, regions are color-coded according to network membership and scaled in size and transparency based on the difference in correlation between the region of interest (i.e., black outlined dot) and the rest of the brain in highly and mildly emotional events. Similarly, in smaller plots, size and transparency of each dot depends on the difference in correlation as function of intensity values, whereas color indicates the correlation with the region of interest (red positive and blue negative relationships). VentAttn = ventral attention network; DorsAttn = dorsal attention network; SomMot = somatomotor network; R TPJ = right temporoparietal junction; R IPS = right intraparietal sulcus; R vpreCS = right ventral branch of the precentral sulcus; R vFPC = right ventral fronto-polar cortex; R IFGpOr = pars orbitalis of right inferior frontal gyrus; R SPL = right superior parietal lobule.

Reliability of the Association between tISFC and Intensity at Multiple Timescales. As in the case of the polarity dimension, we replicated the analysis of correlation between brain connectivity and intensity scores at three additional timescales. Changes in the slope of intersubject agreement in intensity ratings were detected at 100 timepoints (3m:20s), 163 timepoints (5m:26s) and 247 timepoints (8m:14s). The right ventral fronto-polar area and the right caudal superior frontal gyrus are associated with changes in intensity at all explored timescales (see Figure 4C and Supplementary Figure 3). Connectivity of the right temporoparietal junction, the right precentral gyrus, the ventral branch of the right precentral sulcus, the pars orbitalis of the right inferior frontal gyrus and the right superior parietal lobule encodes changes in the intensity of the emotional experience at three out of four timescales. The right intraparietal sulcus, the right supramarginal gyrus and the dorsal branch of the right precentral sulcus are, instead, significantly associated to intensity scores in half of the considered timescales. Lastly, connectivity strength of the right lateral

orbitofrontal cortex and of the left postcentral sulcus significantly correlates with intensity at a specific time range.

Chronotopic Maps of the Intensity of Emotional Experiences. For all these regions, we report the preferred timescale for the processing of intensity of the emotional experience in Figure 4D. As for the polarity results, some regions, as the right temporoparietal junction, the right caudal superior frontal sulcus and a large cluster including the right lateral orbitofrontal cortex, the pars orbitalis of the right inferior frontal gyrus and the right ventral fronto-polar cortex, show interesting timescale topographies. For the right temporoparietal junction, connectivity of the ventral part preferentially encodes intensity in ~5-minute segments (i.e., 163 timepoints), whereas its rostro-dorsal portion favors shorter timescales (~3 minutes). Within the right inferior parietal lobule, moving from the angular gyrus to the posterior region of the supramarginal, we find that the association between connectivity and intensity scores peaks at longer timescales (~8 minutes). As far as the right caudal superior frontal gyrus is concerned, the connectivity of its rostro-medial part preferentially represents the intensity of the experience at shorter timescales (~3 minutes), whereas its rostro-lateral portion achieves the highest significance considering ~5-minute windows. These two regions are separated by a larger cluster preferentially encoding intensity at longer timescales (~8 minutes). In the right ventral prefrontal territories, the connectivity of a large cluster is maximally associated with intensity scores at three distinct timescales: the lateral orbitofrontal cortex shows a preference for shorter time intervals (~3 minutes), the pars orbitalis for intermediate timescales (~5 minutes) and the ventral fronto-polar area for longer segments (~8 minutes).

In addition, results demonstrate that the association between connectivity and intensity of the emotional experience is maximal at longer timescales (~11 and ~8 minutes) for the right superior parietal and intraparietal regions, for the dorsal and ventral branches of the precentral sulcus and for the left postcentral sulcus. Instead, the right precentral gyrus demonstrates its preference for shorter timescales (~3 minutes).

Association between tISFC and Complexity of the Emotional Experience. Lastly, changes in the complexity dimension are not associated to the connectivity of any brain region when considering the optimal window width of 205 timepoints (6m:50s; Supplementary Figure 4D). Nevertheless, results show that connectivity strength of the right mid-cingulate cortex, the right inferior temporal gyrus and the left rostral superior frontal gyrus tracks changes in complexity at shorter timescales (i.e., 88 and 109 timepoints, respectively 2m:56s and 3m:38s; Supplementary Figure 4A-B).

Discussion

In the current study, we show that connectivity strength of default mode nodes, such as the left precuneus, the right dorsomedial prefrontal cortex, the right temporoparietal junction and the right dorsal fronto-polar cortex, is positively associated to the pleasantness of the affective experience. In addition, fronto-parietal regions pertaining to the attention and control networks mainly encode the intensity of the reported experience. Taken together, these findings suggest that the timecourse of orthogonal descriptions of affect (i.e., variations in polarity and intensity) are represented by connectivity strength of distinct brain networks. Besides the dissociation we observe at network-level, changes in polarity and intensity of the experience are both encoded by connectivity of two regions of the right hemisphere: the temporoparietal junction and the fronto-polar cortex. Interestingly, these brain areas encode the dynamics of affect in a chronotopic manner, meaning that distinct regions preferentially represent the stream of affect at different time intervals, ranging from a few to several minutes.

In everyday life, affect varies as function of context, expectations, personal motivations and mechanisms of appraisal. These features are intrinsically related to time, as context and mechanisms of appraisal mainly rely on events and experiences of the past, motivations are built in the present and expectations connect previous knowledge with future outcomes. Nevertheless, it may be difficult to predict the temporal dynamics of affect. When the context is correctly interpreted, and expectations are met there is continuity between past and present states, yet a sudden event may produce a dramatic shift between the current and previous affective states. Moreover, according to experience sampling and retrospective studies, the persistence of affective states can vary significantly with some states lasting on average few minutes and others several hours (Verduyn et al., 2012). The complexity of the relationship between affect and time as it appears to be in real-life situations can be hardly reproduced in the laboratory setting and it can represent a real challenge when researchers are interested in studying how behavioral reports relate to brain activity. This is

presumably one of the main reasons for the scarcity of researches that investigated the temporal dynamics of affect using neuroimaging techniques.

To elicit a variety of affective states, track their evolution in time and maintain relatively high ecological validity in the laboratory setting, an optimal solution may be represented by movie watching (Philippot, 1993; Gross and Levenson, 1995; Schaefer et al., 2010). Movies produce strong affective responses over the course of few hours and mimic everyday life situations with an alternation of sudden and predictable events. Also, changes in affect induced by movies are based on the rich contextual information provided by the narrative and are related to the personal expectations of the viewer.

Building upon this, we collated brain activity data (Hanke et al., 2016) and moment-by-moment affective ratings (Lettieri et al., 2019) acquired during the watching of Forrest Gump, and demonstrated that changes in the subjective emotional experience are explained by dynamic reconfigurations of large-scale brain networks. Differently from previous reports, our study is based on a two-hour movie that elicits several affective responses, with states reported as unpleasant or pleasant, having low or high emotional intensity and being characterized by immediate and spontaneous reactions or by slower cognitive interpretations of movie scenes. Such a variety of states together with a long-lasting stimulation allowed us to identify brain regions tracking changes in affect at different timescales.

Over the course of the last years, researchers have emphasized the importance of moving from a region-based to a network-based approach when studying the neural correlates of emotion and affect (Nummenmaa et al., 2014; Lindquist and Barrett, 2012; Pessoa, 2018, Barrett and Satpute 2013; Wager et al., 2015; Raz et al., 2016; Pessoa, 2017). In this regard, among large-scale brain networks, the default mode is thought to play a crucial role for the construction and representation of emotions (Satpute and Lindquist, 2019). Satpute and Lindquist claim that the conceptualization of emotion categories as patterns of physiological and behavioral responses requires the ability to abstract concrete features (e.g., a smile, the increase in respiration rate) to mental categories (e.g.,

joy, fear) and that the default mode network is the best candidate to carry out such a computation. Indeed, this network includes the temporoparietal junction, the medial prefrontal cortex and the precuneus, which are regions supporting processes of mind wandering and engaged during internally focused states in general (Raichle et al., 2001; Mason et al., 2007; Buckner et al., 2008; Raichle, 2015). This network is also specifically recruited for the integration of emotion and cognition (Gusnard et al., 2001), for the representation of affective states associated with autobiographical memories or theory of mind computations (Spreng et al., 2009), as well as for the combination of sensory inputs coming from internal organs (Kleckner et al., 2017). Our findings support the hypothesis of the central role of the default mode network in the processing of affect, as we demonstrate that its connectivity tracks changes in the subjective judgment of pleasantness during movie watching. This task requires, on the one hand, theory of mind and perspective taking to understand and process emotions, expectations and beliefs of movie characters (e.g., whether something is good or bad for the protagonist) and, on the other hand, that viewers provide subjective descriptions of their own experience (e.g., how one feels about what happens to the protagonist). Importantly, these third- and first-person computations can be both carried out by the default mode network (Schillbach et al., 2008). Our results are also in line with reports that highlighted the role of this network in high paranoia traits or depressed patients, in which negative rumination is intense and related to resting state hyperconnectivity or increased across-subjects synchronization of the default mode network (Whitfield-Gabrieli and Ford, 2012; Finn et al., 2018). Indeed, we find that when healthy subjects experience negative situations, the connectivity of the default mode network with the rest of the brain is actually reduced, whereas it is increased when experiencing positive emotions. Similarly, a recent longitudinal study in a single healthy participant demonstrated that connectivity of the default mode is directly related to positive mood (Mirchi et al., 2019).

With respect to the perceived intensity of affective states, we report a significant association with the connectivity of dorsal and ventral attention networks. Brain regions pertaining to these networks

are involved in the orienting of attention in response to relevant external stimuli (Corbetta et al., 2008). Previous studies have shown a significant interplay between activity of the attention network and emotion regulation processes (Sripada et al., 2014; Lamke et al., 2014), the encoding of affective events (Barnacle et al., 2016) and more generally in the construction of emotional states (Kober et al., 2008; Lindquist et al., 2012; Pessoa, 2018). Other reports found that the connectivity dynamics of the ventral attention network covaried with the perceived intensity of negative affective states (Raz et al., 2016). Our results further expand this evidence, suggesting that the direct relationship between intensity of the emotional experience and connectivity strength of the attention network is not limited to negative emotions. As a matter of fact, our findings demonstrate that the more the experience is perceived as intense the higher is the connectivity of fronto-parietal regions, regardless of the valence of the emotional state. This indicates that brain connectivity encodes the intensity of affect in a similar manner for positive and negative events.

We further show that connectivity of control network nodes is related to the intensity of affect reported by our subjects. The control network is claimed to regulate the activity of the attention and the default mode network, to mediate between potentially conflicting evidence obtained from inner and outer processes (Gao and Lin, 2012) and to be involved in empathy and theory of mind (Bzdok et al., 2012). In the experience of emotions, it has been hypothesized that, together with the default mode, this network is essential in the construction and regulation of the perceived state, as it coordinates the attribution of meaning to the sensation perceived by the individual (Lindquist and Barrett, 2012). Interestingly, in our data, the modulation of intensity of the experience is mediated by the connectivity of the control network with the default mode and the visual network. Specifically, we observe an abrupt change in the sign of connectivity between control and the default mode network, with low intensity events being characterized by a positive coupling between the two and high intensity events being connoted by a negative association. The changes in connectivity between the control network and the default mode are accompanied by changes in connectivity with the network representing the main external drive of brain activity during movie

watching: the visual network. A possible interpretation in this regard is that the weakening of connectivity with the visual network and the strengthening of negative relationships with the default mode network during highly emotional events translates into a reduction of the processing of the incoming stimuli and the enhancement of self-referential processes. Although this may be an intriguing explanation of our data, further studies are needed to demonstrate a causal role of the control network in attenuating the processing of external stimuli and increasing the internal focus of attention in highly emotional events.

Another interesting result that emerges from our study is that - except for the right temporoparietal junction - brain areas significantly encoding polarity differentially relates to visual regions depending on the pleasantness of the experience (Figure 3B-F). In this regard, a recent study that used convolutional neural network to classify emotionally charged images showed that activity of the visual cortex was able to classify distinct emotion categories (Kragel et al., 2019). According to the authors, this evidence supports the existence of emotion schemas, which are patterns of interaction between the environment and the individual, embedded in sensory systems. Even though changes in connectivity of the visual network do not encode changes in affect in our data, our results are not necessarily in contrast with the idea of emotion schemas, as changes in connectivity of default mode regions between highly positive and highly negative events mainly involves the visual network (please see Figure 3).

Moving from a network-level to a region-level description of our results, it is important to note that connectivity strength of the right fronto-polar cortex and of the right temporoparietal junction represents both polarity and intensity of affective states. There is a general consensus on the involvement of the medial and lateral fronto-polar cortex in social cognition abilities, such as perspective taking and empathy (Lawrence et al., 2006; Shamay-Tsoory et al., 2003), theory of mind (Shamay-Tsoory et al., 2005; Roca et al., 2011), emotion processing (Depue et al., 2007; Quirk and Beer, 2006; Lee and Siegle, 2012) and mood (Mirchi et al., 2019). Our results, thus, support the role of this brain area in the cortical representation of affect, demonstrating that

connectivity dynamics of the right fronto-polar region maps changes in the perceived pleasantness and intensity of the emotional experience.

Also the temporoparietal junction is considered one of the core regions of the social brain, given its contribution to theory of mind abilities and its involvement in the regulation of the emotional experience (Kohn et al., 2014; Uchida et al., 2015), in moral decision-making (Reniers et al., 2012; Sevinc and Spreng, 2014) and in empathic processing (Lamm et al., 2007; Kanske et al., 2015). Recent years have been characterized by an increasing interest in understanding the topographic principle of the human cortex and how this organization relates to cognition (Glasser et al., 2016). Indeed, we recently uncovered the existence of orthogonal and spatially overlapping gradients in right temporo-parietal cortex encoding emotion dimensions and demonstrated that the topographic principles lying at the basis of perception and cognition also guide the cortical organization of affect (Lettieri et al., 2019). It is important to note that the central role of the right temporoparietal junction highlighted in the current study is in line with our previous proposal of the topographic organization of affective processing in this region (Lettieri et al., 2019). As hypothesized in our previous study, the right temporoparietal junction may act as a central node of a distributed network of brain regions carrying out distinct computations during processing of affect. Now, we demonstrate that the connectivity of several brain areas is related to changes in affect and that, among these regions, the right temporoparietal junction and the right fronto-polar cortex are the only brain areas encoding multiple orthogonal descriptions of affective states.

In addition to polarity and intensity, we obtained from subjective reports of the emotional experience a third affective dimension that we named complexity. This component maps states cognitively mediated versus instinctual reactions and it seems not to correlate with the connectivity of any brain region, except for the right mid-cingulate cortex, the right inferior temporal gyrus and the left rostral superior frontal gyrus at shorter timescales. Therefore, differently from polarity and intensity, the complexity of affect does not show a specific fingerprint of connectivity dynamics invariant to the definition of the timescale of interest. This may be a peculiar feature of how this

affective dimension is represented in the brain. However, we also cannot exclude that complexity may be better encoded by patterns of activity of specific regions, rather than by the connectivity of large-scale brain networks. In this regard, the activity of the temporoparietal junction may be sufficient to represent the complexity of the emotional experience (Lettieri et al., 2019).

In the current study, we characterize the preferred timescale at which the connectivity of distinct brain regions represents specific descriptions of affect. This seems of particular importance as during everyday life humans automatically segment the continuous stream of thoughts and events into discrete entities. Previous studies on memory and narrative comprehension (Simony et al., 2016; Baldassano et al., 2017; Chen et al., 2016) demonstrated that the brain splits the experience at multiple timescales following a hierarchy in which sensory regions extract information in short segments, whereas high-order areas preferentially encode longer events. We reveal that the same happens for the processing of affect, with chronotopic maps (Protopapa et al., 2019) representing the temporal dynamics of the emotional experience at specific timescales. As compared to studies on narrative comprehension and memory, our results highlight relatively slow dynamics, approximately between 3 and 11 minutes. This is because changes in affect during movie watching are presumably associated with the processing of longer movie excerpts (apart from very unexpected events), which are characterized by temporal dynamics similar to those of major changes in the narrative. In addition, regions encoding affect are generally high-order transmodal cortices (e.g., angular gyrus, precuneus) that are tuned to longer timescales (Baldassano et al., 2017). Interestingly, brain regions coding both changes in polarity and intensity of affect (i.e., right temporoparietal junction and fronto-polar cortex) also show peculiar topographies when considering the preferred timescale. Specifically, within the temporoparietal cortex, preferred timescales for the processing of polarity and intensity are mapped along two orthogonal axes. For polarity, the timescale increases moving from dorsocaudal to ventrorostral territories. For intensity, instead, changes occurring at shorter time intervals are represented by connectivity of ventrocaudal portions, whereas those relative to longer timescales are mapped in rostrodorsal areas. The right

fronto-polar cortex seems to follow a patchier organization, with no clear evidence of linear gradients for the coding of affect at multiple timescales.

Our work is not immune to some criticisms. Firstly, we focused on relatively slow temporal dynamics of affect in the range of few to several minutes. As a matter of fact, the method we selected to reduce the arbitrariness in the definition of the optimal window width favors longer timescales, as the across-subjects correlation increases with the number of timepoints. Also, the temporal resolution of fMRI is suited to capture slower brain dynamics, whereas faster affective reactions may be better studied with other neuroimaging techniques. This intrinsic feature of the method we opted for may have played a role in the results of the complexity dimension, as it represents the contrast between cognitively mediated states and instinctual, presumably faster, reactions. Secondly, to characterize brain connectivity dynamics, we computed the strength on the complete graph. We specifically opted for this procedure to, again, minimize the researcher degrees of freedom, as there is no need to define the thresholding method and level in generating the graph. Also, strength represents a simple measure that expresses the importance of nodes in a network (Rubinov and Sporns, 2010). Thirdly, parcellation of the brain in distinct regions is a crucial point of network analyses. Here, we employed a parcellation based on resting state data (Schaefer et al., 2018), even though a very recent paper argues that the segmentation of the brain in functional units depends on the task (Salehi et al., 2020). In this regard, to limit the impact of a resting state parcellation to extract movie-related brain activity, we chose the most fine-grained parcellation scheme offered by the authors, which comprises 1,000 regions. Lastly, our analysis does not include subcortical regions, as they are not present in the original atlas. Also, these structures usually demonstrate much faster dynamics as compared to those investigated in our study (e.g., Garvert et al., 2014).

In conclusion, we demonstrated that the timecourse of connectivity strength of distinct large-scale brain networks tracks changes in affect. The default mode network represents the pleasantness of the experience, whereas connectivity of attention and control networks encodes its intensity.

Interestingly, these orthogonal descriptions of affective states converge in two cortical regions, as they are both represented by connectivity dynamics of the right temporoparietal and fronto-polar cortex. Within these regions the stream of affect is represented at multiple timescales following chronotopic connectivity maps.

Materials and Methods

Behavioral Experiment: Participants. Twelve Italian native speakers (5F; mean age 26.6 years, range 24–34) provided ratings of their moment-by-moment emotional experience while watching the Forrest Gump movie (R. Zemeckis, Paramount Pictures, 1994). All participants gave their written informed consent to take part in the study after risks and procedures had been explained. They had the right to withdraw at any time and received a small monetary compensation for their participation. All subjects were clinically healthy and had no history of any neurological or psychiatric condition. They also had normal hearing, normal or corrected to normal vision and reported no history of drugs or alcohol abuse. The local Ethical Review Board approved the experimental protocol and procedures (CEAVNO: Comitato Etico Area Vasta Nord Ovest; Protocol No. 1485/2017) and the study was conducted in accordance with the Declaration of Helsinki.

Behavioral Experiment: Stimuli and Experimental Paradigm. Behavioral data have been reported in a previous experiment (see Lettieri et al., 2019 for details) and made freely available at https://github.com/psychoinformatics-de/studyforrest-data-perceivedemotions. Subjects sat comfortably in a silent room facing a 24" Dell™ screen, wore headphones (Sennheiser™ HD201; 21–18,000 Hz; Maximum SPL 108 dB), and were presented with an Italian dubbed and edited version of Forrest Gump. The movie was split into 8 movie segments ranging from 11 to 18 minutes, so to adhere to the fMRI protocol described in Hanke et al., 2016. To collect behavioral reports of the affective experience, subjects were asked to report moment-by-moment (i.e., 10Hz sampling rate) the type and intensity of their inner emotional state using six categories, according to the basic emotion theory (Ekman, 1992): happiness, surprise, fear, sadness, anger and disgust. Importantly, as the complexity of the experience elicited by Forrest Gump cannot be merely reduced to six emotions (Lettieri et al., 2019), we asked subjects not to limit their report to binary choices and use as many combinations of categories as they want, to best describe how they felt at each moment during the movie. This, together with the possibility to indicate the contribution (i.e.,

intensity) of each category to the experienced affective state, ensured that different instances of emotions (Barrett et al., 2007) are captured by our behavioral reports. In addition, we opted for descriptions based on emotion categories as the use of these linguistic labels appear early in life and are easily understandable by the vast majority of people without requiring any specific training (Bretherton and Beeghly, 1982; Ridgeway et al., 1985). The same cannot be for many affective dimensions (Mehrabian and Russell, 1974), such as dominance, certainty or obstruction.

For each subject, the overall duration of the behavioral data acquisition was 120 minutes (72,000 timepoints). Stimulus presentation and recording of the responses were implemented in Matlab (R2016b; MathWorks Inc., Natick, MA, USA) and Psychtoolbox v3.0.14 (Kleiner et al., 2007).

Behavioral Experiment: Single-Subject Affective Dimensions. Starting from categorical descriptions one can obtain the underlying dimensions using factor analysis or principal components. Studies on perception demonstrated that such dimensions are preferentially encoded in the brain (Harvey et al., 2013; Sha et al., 2015) and this may be the case also for the correlates of affective experiences (Nummenmaa et al., 2012; Lettieri et al., 2019). For this reason, by using principal component analysis (PCA) and procrustes rotation, we derived in each subject the timecourse of the affective dimensions explaining behavioral reports of the emotional experience. In brief, timeseries representing the emotional experience of each subject were downsampled to 2-second resolution (3,600 timepoints), matching the temporal characteristics of the fMRI acquisition. Data were then averaged across subjects and PCA was used to reveal group-level affective dimensions. PCA was also performed on single-subject data and the results were aligned to best approximate group-level dimensions using procrustes orthogonal linear transformation (reflection and rotation only). We considered the rotated scores of principal components as single-subject affective dimensions and used these data to inform subsequent fMRI analyses. To assess the agreement across subjects in affective dimensions, we also computed pairwise Spearman's correlation and its significance (see Lettieri et al., 2019 for further details).

fMRI Experiment: Participants. Brain activity elicited by the watching of Forrest Gump was obtained from the studyforrest project - phase II (http://studyforrest.org). Brain data comprise recordings of fourteen healthy German subjects (6F; mean age 29.4 years, range 20–40 years), instructed to simply inhibit any movement and enjoy the movie (see Hanke et al., 2016 for further details). Similarly to the behavioral part of the study, the fMRI acquisition lasted two hours and was split in eight runs (3T Philips Achieva scanner; 32 channels head coil; gradient recall echo-echo planar imaging; 2000ms repetition time, 30ms echo time, 90° flip angle, 3 mm isotropic voxel, 240 mm field of view). Together with the fMRI data, 3D T1w high-resolution anatomical images were also acquired. For further details regarding data acquisition and protocol please refer to Hanke et al., 2016.

fMRI Experiment: Data Pre-processing. AFNI v.17.2.00 (Cox, 1996) and ANTs (Avants et al., 2009) were used to preprocess the MRI data. For each subject, structural images were first skull-stripped (*antsBrainExtraction.sh*) and transformed to match the MNI152 template using non-linear registration (*3dQwarp*). Functional data were corrected for intensity spikes (*3dDespike*), adjusted for slice timing acquisition (*3dTshift*) and corrected for head motion (*3dvolreg*) by computing the displacement between each volume and the most stable timepoint of each run (i.e., the one showing smallest framewise displacement values; Power et al., 2012). Afterwards, the *align_epi_anat.py* and *3dQwarp* software were used to estimate the co-registration between functional and structural data, as well as to correct for phase distortion by allowing non-linear deformations in the y-direction (i.e., phase acquisition direction) only. Linear (i.e., motion correction, co-registration) and non-linear (i.e., phase distortion and MNI152 registration) transformations were then concatenated and applied (*3dNwarpApply*) to the functional data, so to obtain standard-space single-subject timeseries with a single interpolation step (i.e., sinc interpolation method), maintaining also the original spatial resolution (3mm isotropic voxel). In addition, data were iteratively smoothed until 6mm full-width

at half maximum level was reached (*3dBlurToFWHM*) and rescaled (*3dcalc*) so that changes in activity were expressed as percentage with respect to the average voxel intensity in time (*3dTstat*). Lastly, we used *3dDeconvolve* to regress out from brain activity signal drifts (*polort* in *3dDeconvolve*) and physiological confounds following the recommendations in Ciric et al., 2017. Therefore, we used a model with 36 regressors of no interest to reduce the possibility that results of intersubject functional correlation could be explained by factors other than neurovascular coupling. Specifically, we created (*Atropos*; Avants et al., 2011; *3dmask_tool*) binary masks of the white matter (WM) and cerebrospinal fluid (CSF) and extracted the timeseries of the average WM and CSF activity. Global signal (GS), which is the average activity across all voxels, was also calculated. For each of the three obtained timeseries (i.e., GS, WM, CSF) we computed their temporal derivatives, the quadratic terms and squares of derivatives, resulting in 12 regressors. The remaining 24 comprised the six head motion parameters estimated with *3dvolreg*, their temporal derivatives, their quadratic terms and the squares of derivatives. All regressors of no interest were then de-trended using the same degree of polynomial (*polort*) employed in *3dDeconvolve* to remove slow drifts from voxels activity. The model was then fitted in brain activity using a mass-univariate general linear model. The residuals of this fitting were considered the single-subject brain activity associated to the watching of Forrest Gump and used in subsequent analyses.

fMRI Experiment: Intersubject Functional Correlation. The intersubject functional correlation (ISFC) method measures brain inter-regional covariance induced by stimulation, as it computes the correlations between signal change of a specific brain region in one subject with activity of all other regions in other subjects (Simony et al., 2016). When compared to other measures of functional connectivity, ISFC demonstrates higher signal-to-noise ratio as it inherently filters out activity not related to stimulus processing and artifacts not correlated across brains. In addition, similarly to other functional connectivity methods, ISFC can be used to study dynamic reconfigurations of brain networks using a moving-window approach. We estimated the static and time-varying ISFC (tISFC)

associated with the watching of Forrest Gump using custom MATLAB scripts that we made freely available at URL.

As a first step, we selected the atlas provided by Schaefer and colleagues (2018) and parcellated the brain of each subject into 1,000 cortical regions of interest (ROIs; Figure 1C). We opted for this atlas as it provides a fine-grained segmentation of the cerebral cortex that, at the same time, reflects the 7 resting state networks identified by Yeo and collaborators (2011): visual, somato-motor, ventral attention, dorsal attention, limbic, control and default mode network. To compute static ISFC, the timecourse of brain activity was extracted from each ROI of one subject and correlated using Pearson's product-moment coefficient with the remaining 999 regions of all other subjects. By repeating this procedure for all the 14 subjects, we generated 91 (i.e., number of all possible combinations of subjects) correlation matrices having 499,500 cells each (i.e., number of all possible combinations of ROIs). We then applied Fisher z-transformation and averaged correlation values across subjects to produce a group-level ISFC map.

To compute tISFC, one has first to determine the width of the moving-window (i.e., how many timepoints in a single window) and the degree of overlap between adjacent windows (i.e., how many timepoints are shared by two subsequent windows). Both parameters are often chosen arbitrarily, even though they may significantly affect the results. To limit the arbitrariness of this choice, we estimated the optimal window width as function of the intersubject correlation in affective dimensions (obtained from the behavioral experiment). Specifically, we computed the average intersubject correlation of affective dimension timeseries for all possible window widths, ranging from 20 to 1000 timepoints (i.e., from 40s to ~33m) and having 33% of overlap (Figure 1A and 1B). We considered the optimal window size the point at which the intersubject correlation curve starts to flatten (i.e., knee point), namely the point representing a reasonable trade-off between the agreement across participants and window width (Figure 1B). This procedure was repeated for all the affective dimensions separately. Once the optimal window width was established, we computed the tISFC as the Pearson's correlation between each ROI of one subject

and all other ROIs of other subjects, across all windows (Figure 1C). By repeating this procedure for all the 14 subjects, we generated for each window 91 correlation matrices having 499,500 cells each (i.e., number of all possible combinations of ROIs). We then applied Fisher z-transformation and averaged correlation values across subjects to produce a group-level timeseries of brain connectivity (i.e., tISFC) associated with movie watching.

fMRI Experiment: Association between tISFC and Changes in Affective Dimensions. The primary aim of our study was to relate changes in tISFC to variations in the perceived affective state during movie watching. Therefore, for each ROI we computed connectivity strength as the sum of the Z-transformed correlation values at each timepoint (Figure 1D). We thus obtained 1,000 timeseries expressing the relationship of each ROI with the rest of the brain throughout the movie. These timeseries were then correlated using Spearman's ρ coefficient with the group-level timecourse of affective dimensions, after the latters being downsampled to the temporal resolution determined by the optimal window (see above) using a moving-average procedure. To assess the significance of the association (Figure 1E), we used a non-parametric permutation test based on timepoint shuffling of affective dimensions (200,000 iterations; minimum two-tailed p-value: 1.0e-5). At each iteration, the randomized affective dimensions were correlated with each of the 1,000 timeseries of ROI connectivity strength, providing null distributions of Spearman's correlation values. The position of the actual association in the null distribution determined the two-tails level of significance, which was then corrected for multiple comparisons using the Bonferroni method (n=1,000; critical p-value was 5.0e-5).

fMRI Experiment: Network Reconfigurations Related to Affective Dimensions. The parcellation proposed by Schaefer and colleagues (2018) is based on the 7 resting state networks identified by Yeo and collaborators (2011). This allowed us to better characterize the relationship between changes in affective dimensions and functional characteristics of brain networks. Specifically, node

strength summarizes the connectivity of a specific region with the rest of the brain, yet it does not provide any information about how brain networks reorganize as function of the affective experience and which associations between ROIs are changing to a greater extent. To overcome this limitation, we first used classical Multi-Dimensional Scaling (MDS; Torgerson, 1952) on the group-level ISFC to measure and graphically represent functional distances of the 1,000 brain regions during movie watching. In the MDS plot, each region was color-coded in accordance with network membership and scaled in size and transparency depending on the log p-value of the association between connectivity strength and changes in affective dimensions. Results of this procedure are represented in Figure 2B and Figure 4B.

Moreover, we considered as a seed region each ROI found to be significant in previous analyses (see the *Association between Time-Varying ISFC and Changes in Affective Dimensions* paragraph) and represented its correlation with all other ROIs at tISFC timepoints corresponding to affective dimension scores either greater than the 90th percentile or smaller than the 10th percentile. Lastly, to better highlight how brain networks did reorganize at timepoints having opposite affective dimension scores, for each target region we computed the difference of correlation values and scaled its size and transparency accordingly. Results of this procedure are represented in Figure 3, Figure 5 and Supplementary Figure 2.

fMRI Experiment: Timescales of the Relationship between Connectivity Strength and Affective Dimensions. Recent studies on narrative comprehension and memory encoding demonstrated that distinct brain regions segment and process information at specific timescales, with early and mid sensory areas preferring short events, and fronto-parietal association regions encoding hundreds of seconds of information (Baldassano et al., 2017; Chen et al., 2016; Hasson et al., 2015). Starting from this evidence, we measured the preferred timescale at which brain regions process affective information. First, we repeated the estimate of the optimal window width (see *Time-varying Intersubject Functional Correlation* paragraph) at three additional timescales: from 20 to 250, to

500 and to 750 timepoints. After the optimal width was determined for each range, we calculated the tISFC and correlated the connectivity strength of each ROI with the downsampled version of the affective dimensions. We then estimated the significance of the associations at additional timescales following the same procedure described above and applied a winner-takes-it-all criterion on the log-transformed p-value maps to establish the preferred timescale of each brain region. Results of this procedure are presented in Figure 2D and Figure 4D.

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Author Contributions

G.L., G.H. and L.C., conceived the study, designed the behavioral experiment, developed the code, performed behavioral and fMRI data analysis, interpreted the obtained results and drafted the manuscript. G.L., G.H., E.R., P.P. and L.C. critically revised the manuscript. All the authors approved the final version of the manuscript.

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