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Impact of transient emotions on functional connectivity during subsequent resting state: A wavelet correlation approach

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ABSTRACT

The functional properties of resting brain activity are poorly understood, but have generally been related to self-monitoring and introspective processes. Here we investigated how emotionally positive and negative information differentially influenced subsequent brain activity at rest. We acquired fMRI data in 15 participants during rest periods following fearful, joyful, and neutral movies. Several brain regions were more active during resting than during movie-watching, including posterior/anterior cingulate cortices (PCC, ACC), bilateral insula and inferior parietal lobules (IPL). Functional connectivity at different frequency bands was also assessed using a wavelet correlation approach and small-world network analysis. Resting activity in ACC and insula as well as their coupling were strongly enhanced by preceding emotions, while coupling between ventral-medial prefrontal cortex and amygdala was selectively reduced. These effects were more pronounced after fearful than joyful movies for higher frequency bands. Moreover, the initial suppression of resting activity in ACC and insula after emotional stimuli was followed by a gradual restoration over time. Emotions did not affect IPL average activity but increased its connectivity with other regions. These findings reveal specific neural circuits recruited during the recovery from emotional arousal and highlight the complex functional dynamics of default mode networks in emotionally salient contexts.

Introduction

Some brain regions are spontaneously more active during the awake-resting state than during cognitive tasks. These regions constitute the so-called 'default mode network' (DMN) and are thought to relate at least partly to introspective processes and homeostasis regulation (Raichle et al., 2001; Greicius et al., 2003; Buckner and Vincent, 2007; Fox and Raichle, 2007). This network includes the posterior and anterior cingulate cortices (PCC, ACC), medial and inferior parietal lobules (IPL), ventro-medial prefrontal cortex (vMPFC), and lateral temporal areas, all being consistently deactivated during demanding cognitive tasks such as working memory, language, or attention (Greicius et al., 2003; Greicius and Menon, 2004; Fox et al., 2005), relative to rest. Although the amount of decreases in DMN may depend on the task difficulty (Esposito et al., 2006) or the nature of preceding cognitive activity (Waites et al., 2005; Buckner et al., 2008), it is unknown how resting conditions are modified by particular states of mind or moods that are likely to have an impact on interoceptive processes and homeostasis. This issue is crucial to better understand the functional significance of the default mode (Raichle, 2009), as well as the pathological changes observed in neuropsychiatry conditions (Zhang and Raichle, 2010).

Here we investigated how prior emotions (positive or negative) alter spontaneous brain activity and large-scale network connectivity during subsequent rest. Emotions are pervasive in daily life and exert long-lasting effects on cognition, attention, and motivation (Dolan, 2002). Thus, emotional experiences and moods are likely to influence the way we process information through attentional, perceptual, or mnesic biases (Vuilleumier, 2005). However, unlike moods, emotions are defined as transient physiological events (Scherer, 2005), and their impact on subsequent mental activity is poorly known. Most neuroimaging studies on emotion processing have typically focused on phasic responses to brief emotional stimuli (pictures, faces), but it is intuitively evident that even transient emotions can have lingering effects on mental and physiological states. Recent findings suggest that sad mood may decrease connectivity between areas belonging to the DMN (Harrison et al., 2008), whereas prior exposure to emotionally arousing pictures may reduce the magnitude of activation in parietal areas during rest (Pitroda et al., 2008). However, the pattern and dynamics of changes induced by transient emotions on activity and connectivity of the extended DMN still remain unclear.

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Measures of functional connectivity (based on temporal correlations between distant regions) are particularly useful to evaluate spontaneous fluctuations throughout the brain (Greicius et al., 2003; van de Ven et al., 2004; Achard et al., 2006), and have commonly been used to study the DMN in healthy controls and neurological disorders (Greicius et al., 2004, 2007).

The main goal of our study was to determine the effects of positive (joy) and negative (fear) emotions induced by short movie excerpts on subsequent brain activity and interregional connectivity within the DMN. Specifically, we used fMRI with wavelet correlation analysis and small-world connectivity methods to investigate how the 'resting state' is altered and then returns to a spontaneous 'default mode' after emotional movies, and to determine whether such changes differ depending on the preceding emotion type.

Materials and methods

Participants

We recruited 15 volunteers (4 male) without any history of neurological or psychiatric disorders, age between 18 and 36 years (mean = 23.8), and right-handed. All participants signed a consent form approved by the local ethics committee.

Emotional stimuli

The experimental protocol consisted of short video clips alternating with resting periods (see below for details of the procedure). In order to induce different emotions before each resting period, we created a series of video clips by editing popular movies or TV pieces. Most of these clips were selected from a standard database in which longer versions are available, and were previously assessed in terms of valence, arousal, and type of emotions (Schaefer et al., 2005). Table 1 lists the movie titles from which our clips were generated, together with the corresponding emotion type and duration. The original movies were edited using Adobe Premiere Pro CS3 in order to obtain the desired effect within an average duration of 50 s per movie. A total of 34 clips were created and then validated in a preliminary study in which healthy volunteers ($n = 6$) rated the pleasantness, intensity, and type of elicited emotion for each stimulus. Then, based on these ratings, we selected 18 movie excerpts (6 joyful, 6 neutral, and 6 fearful) for the actual fMRI experiment so as to obtain reliable differences in valence ratings but comparable intensity between the positive and negative emotional conditions (see Table 1). The final movies were compared in terms of low-level features (sound level, luminance, spatial frequency and motion), but showed no significant differences between the three emotion conditions (ANOVA, all $p > .194$) except for marginally higher luminance in joyful movies than others ($p = .045$).

Table 1
Movie excerpts used in the fMRI experiment. Duration and emotion type are shown for each movie, together with their average emotional ratings. Pleasantness and intensity (arousal) were rated by 6 volunteers (not involved in the fMRI study) in a preliminary study using a continuous scale from 1 to 6. For pleasantness, 1 indicates 'very pleasant' and 6 'very unpleasant'; for intensity, 1 represents 'very emotional' and 6 'not at all emotional.'

Movie excerpt from	Duration	Pleasantness	Intensity
Fearful movies			
The Piano	42 s	5.33	1.67
Copycat	52 s	3.33	2.33
Scream 1	53 s	3.67	2
It	55 s	4.17	2.17
Léon	61 s	3.17	3.5
The Shining	61 s	3.33	1.67
Mean (±SD)	54 ± 7.04	3.83 ± 0.82	2.22 ± 0.68
Joyful movies			
Benny & Joon	42 s	1.67	2.67
Gags—Just for Laughs 1	50 s	2.17	3.17
Gags—Just for Laughs 2	55 s	1.67	2.83
When Harry Met Sally	58 s	1.83	2.83
There's Something About Mary	62 s	2.5	3.33
Gags— Just for Laughs 3	65 s	2.17	2.67
Mean (± SD)	55.3 ± 8.38	2 ± 0.33	2.92 ± 0.27
Neutral movies			
The Lover	37 s	3.5	6
Three colors: Blue	47 s	3.5	5.83
La Petite Jérusalem	48 s	3	5
Documentary—Ancient Rome	49 s	3.17	5.83
Les Mystères du Cosmos	53 s	2.67	6
Le Mystère de l'Horloge	57 s	2.83	5.67
Mean (±SD)	48.50 ± 6.75	3.11 ± 0.34	5.72 ± 0.37

Data acquisition

MRI was performed on a Siemens 3T Trio TIM system. Functional images were acquired in two scanning runs (2598 volumes in total) with the following parameters: repetition time (TR) 1100 ms, echo time (TE) 27 ms, flip angle 90°, 21 axial slices, in-plane resolution of 3.75 × 3.75 mm (64 × 64 matrix), and slice thickness 4.2 mm with a 1.05 mm gap. In addition, for each participant, we acquired field-map scans and a high resolution T1-weighted anatomical image with the parameters as follows: MPRAGE sequence, TR 1900 ms, TE 2.32 ms, flip angle 9°, 192 axial slices, voxel sizes 0.90 × 0.90 × 0.90 mm (256 × 256 matrix). Note that the short TR used here allowed us to obtain a high sampling rate, which helped us determine dynamic fluctuations in brain activity and also minimize aliasing of non-neuronal physiological activity in resting state fMRI acquisition.

Experimental procedure

The experiment was implemented using the EPRIME v2.0 software and consisted of 18 alternating cycles, each including a movie excerpt followed by a resting period as illustrated in Fig. 1. Participants watched the movies projected on a white screen through a mirror mounted on the head coil, and listened to the soundtrack through MRI-compatible headphones. In each cycle, participants first watched a movie clip lasting about 50 s, followed by a resting period of 90 s. The order of the different movies and emotion conditions was pseudo-randomized across the participants. Each cycle started by a central gray screen that warned the participants about the upcoming movie. After the movie was finished, the participants were instructed to close their eyes, and let their mind freely wander for the next 90 s (the exact instruction given in French was 'fermez les yeux et laissez le cours de vos pensées défiler librement'). At the end of this resting period, a short beep sound was presented to prompt them to open their eyes, and a question screen was shown to inquire about the dominant content of their thoughts during the rest interval that had just finished. Four options were proposed: a) movie content, b) personal issues, c) experiment environment, such as MRI noise or setting, and d) sleepiness or struggling against sleep. Answers were given by pressing one of four possible keys. This response was followed by the gray screen for 3 s, which warned them to get ready for the following movie. These instructions were presented to the participants as a means to ensure that they did not fall asleep during rest, without requiring any explicit report or memory about the movie contents.

The same loop continued for all different clips. The scanning session included 2 successive runs (23 min each), each containing 9 movie and 9 resting blocks (3 different movies for each of the 3 emotion conditions: joyful, fearful, and neutral). Onset times, response accuracy, and response times were collected via EPRIME.

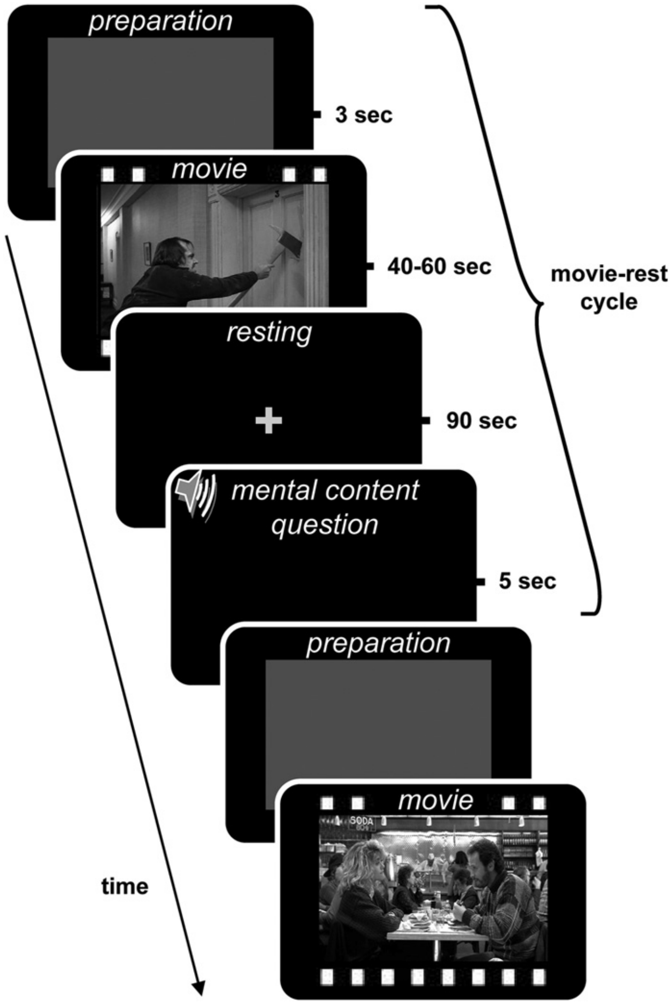

Fig. 1. Illustration of the experimental paradigm. Each movie-rest cycle began with the presentation of a warning panel indicating to the subjects that the next movie was about to start. The movie excerpt was then played, immediately followed by a 90-s rest period. A short beep sound was played at the end of the resting period, and the subjects indicated the nature of their thoughts during the preceding rest interval: a) movie content, b) personal issues, c) experiment environment, such as MRI noise or setting, and d) sleepiness or struggling against sleep.

Preprocessing of fMRI data

All functional images were field-map corrected and realigned to the first acquired image; corrected for slice timing, normalized to the MNI template (reslicing $3 \times 3 \times 3$ mm voxel size), and smoothed using an 8 mm (FWHM) kernel. Each subject's anatomical image was also normalized to the MNI template with a voxel size of $1 \times 1 \times 1$ mm.

General linear model analysis with SPM

Preprocessed fMRI data were first analyzed using the General Linear Model as implemented in the SPM5 software (www.fil.ion.ucl.ac.uk/spm/). A design matrix was constructed for each individual participant, including three covariates of interest in the regression analysis for the three types of movies (fearful, joyful, and neutral), as well as separate regressors for the different types of resting periods following each movie condition (post-fearful, post-joyful, post-neutral). Each resting period was divided into three equal parts (30 s time bins), so as to model different time intervals during which brain activity may gradually change after the end of the emotional movie. In addition, the period corresponding to questions about spontaneous mental content (after each resting period) was added to the design matrix as another covariate of no interest. All these 13 regressors were then convolved with a hemodynamic response function (HRF) according to a block design for the univariate regression analysis. We added the realignment parameters to the design matrix to account for movement confounds. The design matrix also accounted for low-frequency drifts (cutoff frequency at 1/256 Hz). Parameter estimates and standard errors were computed in a voxel-wise manner for each regressor in each subject.

These estimated parameters were then entered into a second-level random-effect group analysis. T-tests were performed on the main contrasts of interest in order to determine the main condition effects (movie, rest) as well as the specific emotional effects (fear, joy, neutral) during either the movie or resting periods. For the main effects comparing movie to rest (and vice versa) and the contrasts between different emotional movies (relative to neutral movies), we used a statistical threshold of $p = 0.01$ corrected for false discovery rate (FDR) across the whole-brain and a cluster extent threshold of 20 voxels. For specific contrasts comparing different emotional effects and different time bins during resting periods with each other, we used an uncorrected p value $= 0.001$ at the voxel level with an extent threshold of 10 voxels. All regions that survived these thresholds were considered as activated and reported.

Functional connectivity analysis using wavelet transform

We performed a functional connectivity analysis using temporal correlations between regional brain activity for predefined sub-bands of a wavelet decomposition. This method has previously been shown to be useful to evaluate spontaneous fluctuations in brain activity and has been used as a measure for decoding brain states (Achard et al., 2006; Richiardi et al., in press). The wavelet transform provides compact time-frequency decomposition into an orthonormal basis. Here, we applied the orthogonal cubic B-spline wavelet transform in the temporal domain (Battle, 1987; Mallat, 1989). Each time-course was decomposed in a sum of dilated and shifted wavelet functions; in the latter, the associated weights are the wavelet coefficients $w_j[k]$, where j is the scale and k is the index. We computed correlations between the wavelet coefficients of a given sub-band for all regions of interest (ROIs) that were identified in the GLM contrasts (Supplementary Fig. 1). Then, we evaluated the cross-correlation matrices (CM) between these regions, for each condition and for four different wavelet sub-bands that included the typical resting state frequency range (~0.01–0.1 Hz).

In order to compute the normalized correlation between any pair of regions, the time-courses corresponding to all the blocks of a specific condition (e.g., fearful movies) were extracted for both regions. Then, a discrete wavelet transform separated the signal into four different frequency bands: i) 0.03–0.06 Hz, ii) 0.06–0.11 Hz, iii) 0.11–0.23 Hz, iv) 0.23–0.45 Hz. The first two frequency intervals are known to correspond to typical default mode bands and constituted our main ‘bands of interest.’ We will therefore report results from these two bands only. The two other bands are usually related to other non-neuronal physiological oscillations like respiration and heart beat, and did not show reliable effects in our study. As a result of the wavelet transform, a set of wavelet coefficients was obtained for each region and the cross-correlations between the coefficients of all possible pairs of regions were calculated. Thus, we could obtain correlation matrices for each block in the experiment (e.g., each movie clip or each resting period). In order to statistically test for differences between two resting conditions (e.g., rest post-fearful>rest post-neutral), the correlation matrices corresponding to the blocks of each of the two conditions (12 per condition for each participant) were compared by nonparametric permutation testing (Nichols and Holmes, 2002). To obtain the distribution, under the null hypothesis, of the subject-averaged difference between the two conditions, the labels of the correlation matrices were randomly permuted many times. By repeatedly applying 5000 relabelings we found that this gives a reliable estimate of the rejection probability of our measure of interest. The p value of the difference between conditions obtained for the connection between each pair of regions was then converted into an equivalent z-score. Significant connections with $z>2$ are marked by * (corresponding to $p<0.01$ one-tailed uncorrected) and those with $z>2.30$ by ** (corresponding to $p<0.0005$ one-tailed uncorrected).

Small-world model of network connectivity

A network analysis was also performed based on the thresholded correlation matrices. The wavelet correlation matrices, defined for each condition and each sub-band, were thresholded using false discovery rate at 0.2. Several node measures based on small-world models were computed on these thresholded matrices. In a small-world network model, each region is considered as a "node" and, after appropriate thresholding, various measures can be computed for each node, such as its clustering coefficient, mean minimum path length, and degree (Watts and Strogatz, 1998). Clustering coefficient is the fraction of existing links that connect a node's neighbors to each other out of the maximum possible number of such links. The minimum path length is the number of connections that forms the shortest path between two nodes, whereas the mean minimum path length for a specific node is the average of all minimum path lengths between that node and all other nodes. The degree of a node is defined as the number of connections it makes with the other nodes of the network. Based on these measures, the hubs of a network are defined as the nodes with largest degree. Eventually, these parameters can be averaged over different participants to obtain a single value per condition and sub-band.

Results

Behavioral results

After each resting period, the participants classified their predominant mental activity during the preceding 90 s of rest by choosing among four possible options: a) movie content, b) personal issues, c) experiment environment such as MRI noise and settings, and d) sleepiness or struggle against sleep. There were 6 resting blocks for each emotion type, after which this question was asked. Fig. 2 shows the mean number of each possible response for each resting condition averaged across our 15 participants.

Following neutral movies, personal issues dominated spontaneous thoughts, with only infrequent reference to the movie clip. After joyful movies, the participants tended to think equally about personal issues and movie content. By contrast, during the resting periods following fearful clips, personal issues were reduced and movie content was the most common concern present in their thoughts. We performed a repeated-measure ANOVA on these numbers with emotion (3 levels) and thought content (4 levels) as factors, which revealed a significant interaction of emotion and thought content [$F(6,78)=5.94$, $p<0.001$], as well as a main effect of thought content [$F(3,39)=22.85$, $p<0.001$]. Post-hoc t-tests confirmed that reports of thoughts related to 'movie content' and 'personal issues' were respectively increased and reduced during resting after fearful clips, relative to neutral movies (both $p<0.02$); thoughts related to 'movie content' were also increased after joyful clips relative to neutral clips (Fig. 2). There were no significant changes for the amount of thoughts related to scanner environment or struggle against sleep (all $p>0.05$).

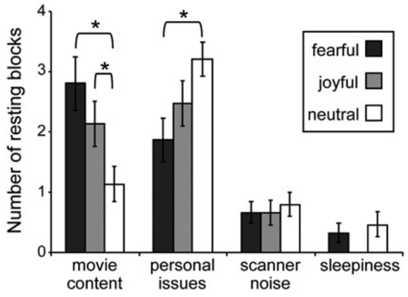

Fig. 2. Behavioral results during fMRI. The content of spontaneous thoughts reported after each resting period is shown for conditions following fearful, joyful, and neutral movies (group-averaged number of periods after which subjects reported a specific content, out of a total of 6 movies for each emotion type; $n=15$ subjects). Thoughts about 'movie content' were increased in both the post-fearful and post-joyful condition, relative to the post-neutral condition. In contrast, thoughts about 'personal issues' were reduced in the post-fear condition compared to the neutral condition.

GLM results in SPM

Our main interest was to compare the resting periods that followed different types of emotional movies, but for completeness we also examined the main effects of resting and movie-watching as well as the differential effects of emotional movie content.

Main effects of movie and rest

Fig. 3 shows the main effects of movie-watching (across all types of emotion content) and resting state (across all types of preceding movie), respectively, at the group level.

During movies (Fig. 3A), as expected, widespread increases in activity were observed in visual, auditory, and multisensory regions as compared with the eye-closed resting periods (all $p<0.01$ FDR corrected). In addition to early occipital and higher-level extrastriate visual areas in ventral temporal cortex, these sensory-driven activations involved the motion-related V5/MT complex in posterior temporal cortex, auditory areas in lateral temporal cortex, and multisensory areas in superior temporal sulcus (STS), plus dorsolateral prefrontal areas, and subcortical peaks in lateral (visual) and medial (auditory) geniculate nuclei of the thalamus.

The opposite contrast resting>movies (across all emotion conditions) revealed several brain regions typically associated with DMN (Fig. 3B). These regions included the posterior and anterior cingulate cortices (PCC and ACC, respectively), bilateral anterior insula, and bilateral inferior parietal lobules (IPL). The left putamen, precentral and postcentral gyri were also activated in this contrast. Table 2 shows the anatomical coordinates and statistical information about these brain regions.

Emotion effects during movies

To ensure that the emotional content of movies was effective, we also compared the two emotional conditions (joyful and fearful pooled together) relative to the neutral movies (Supplementary Fig. 2, Supplementary Table 1). This contrast revealed increased activation in mid-occipitotemporal cortex, fusiform cortex, superior temporal gyrus, precentral gyrus, dorsal precuneus, left thalamus, and left amygdala (all $p<0.01$ FDR corrected). Although the right amygdala did not survive this threshold, it was also found to be activated and survived when using a 8 mm-small volume correction centered on a symmetric peak ($p=0.031$ FWE-corrected), confirming the impact of the movie clips on emotional brain response. Differential activation was found in left amygdala, bilateral temporal poles, and occipital cortex for joyful>fearful movies, and in bilateral parieto-occipital cortex and right PCC for fearful>joyful movies.

Lingering emotion effects during subsequent resting

The most important comparisons in our study concerned the resting periods preceded by different types of movies (initially collapsing across the 3 successive time bins of each period). For rest intervals following fearful movies, as compared with those following neutral movies, we observed increased activity in the pallidum, anterior thalamus, as well as a medial region of hypothalamus

(Fig. 4A, Table 3A). In the reverse contrast, i.e., rest post-neutral > rest post-fearful, we found significant increases in vMPFC, rostral ACC, cuneus and superior temporal regions (Fig. 4B, Table 3B). Thus, some regions typically implicated in default mode (DM) activity were less active during resting after exposure to fearful than neutral events.

Next, to determine the effect of positive emotional events, we computed similar contrasts for the resting periods following joyful movies. For rest post-joyful > rest post-neutral, we found no supra-threshold activity (at $k > 10$ and $p < 0.001$ uncorrected). However, for the opposite contrast, i.e., rest post-neutral > rest post-joyful, we observed greater activity in several brain regions, including both ventral and dorsal medial prefrontal cortices (vMPFC, dMPFC), ACC, parietal operculum, and precuneus (Fig. 4C, Table 4). These data again indicate a relative reduction of typical resting activity following the emotional condition, compared to the neutral condition.

We also compared resting activity across the different emotions during each of the 3 successive time bins of rest periods. Similar results were found, with additional changes in left thalamus for post-fearful vs. post-neutral during the first time bin, but no additional effect observed for post-joyful condition.

Time-course of changes in resting state brain activity

In order to better understand the lingering effects of emotions elicited by movies on the subsequent resting state, we divided the 90 s

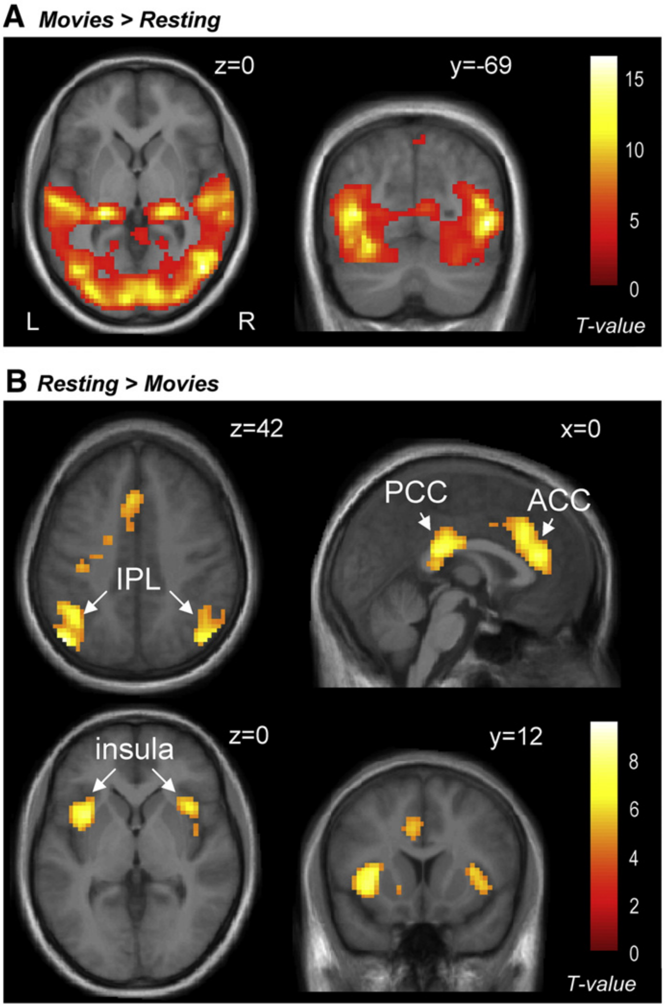

Fig. 3. Brain activation in the main experimental conditions. A) SPM contrasts showing enhanced activity in visual, auditory, and multisensory regions during movies compared to resting periods (all emotion conditions collapsed). B) Opposite contrast showing activation in posterior cingulate cortex (PCC), anterior cingulate cortex (ACC), bilateral insula, and bilateral inferior parietal lobules (IPL) during resting periods compared to movies. Threshold $k > 20$ voxels, $p < 0.01$ FDR corrected in both cases.

Table 2
Regions significantly activated during resting > movie (all emotion conditions collapsed).

Region	Side	*x*	*y*	*z*	*Z*-score	Cluster size
IPL	L	−51	−69	36	5.2	235
	L	−42	−54	42	4.49	
Insula	L	−36	9	3	4.82	206
IPL	R	48	−69	39	4.79	138
	R	57	−63	30	4	
	R	60	−57	36	3.93	
PCC		0	−33	21	4.73	169
		0	−33	12	3.91	
ACC		0	36	18	4.7	667
	L	−3	24	30	4.61	
	R	9	30	21	4.42	
Insula	R	39	15	−3	4.39	166
	R	33	18	6	4.36	
	R	54	3	12	4.16	
PrCG	R	27	−15	57	4.27	26
PoCG	L	−36	−18	30	3.96	201
	L	−36	−24	45	3.88	
	L	−27	−6	30	3.81	
Putamen	L	−18	6	−6	3.95	20

Abbreviations: IPL: inferior parietal lobule, PCC: posterior cingulate cortex, ACC: anterior cingulate cortex, PrCG: precentral gyrus, PoCG: postcentral gyrus, L: left, R: right.
All regions survived the statistical threshold of $p < 0.01$ FDR corrected, cluster size $k > 20$ voxels.

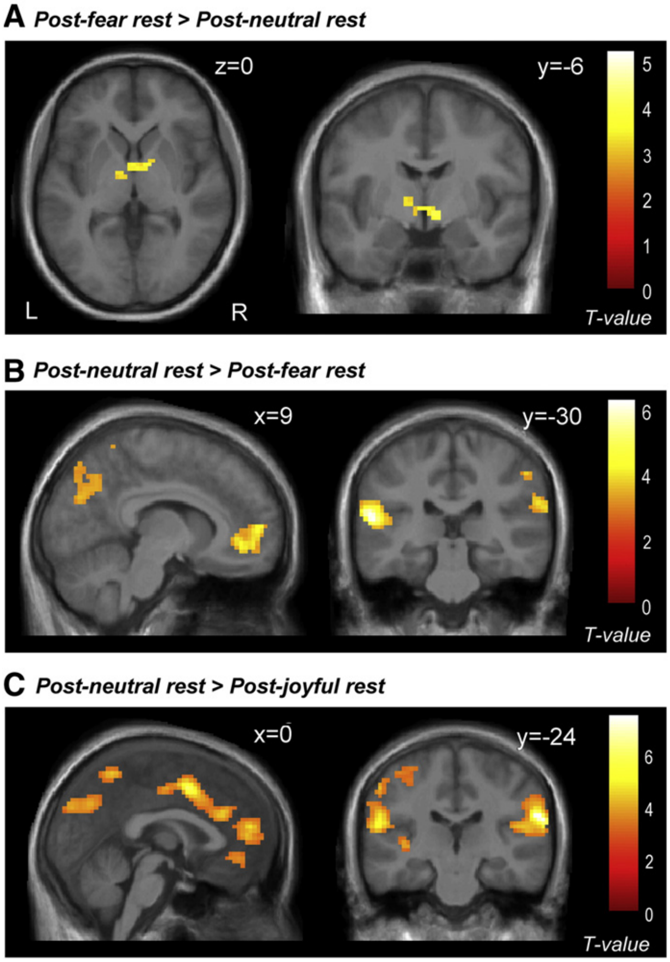

Fig. 4. Effects of emotions on subsequent resting state. A) Regions more active during rest post-fearful > rest post-neutral movies, including thalamus, striatum, and hypothalamus. B) Regions more active during rest post-neutral compared to rest post-fearful movies, including vMPFC, superior temporal gyrus. and precuneus. C) Regions more active during rest post-neutral > rest post-joyful, including vMPFC, dMPFC, precuneus, mid ACC, and supramarginal gyrus. All peaks significant at $p > 0.001$ at the voxel level. Threshold $k > 20$, $p < 0.005$ uncorrected for illustration purpose.

Table 3
Brain regions activated during resting periods following fearful vs. neutral movies.

Region	Side	*x*	*y*	*z*	*Z*-score	Cluster size
(A) Rest post-fearful vs. rest post-neutral movies						
Hypoth	R	6	−9	−9	3.79	13
	R	6	−3	−3	3.77	
Pallidum	R	12	0	0	3.1	
Thalamus *	L	−12	−6	0	3.27	11
(B) Rest post-neutral vs. post-fearful movies						
STG	L	−57	−30	12	4.2	76
	L	−45	−21	9	3.49	
SupMG	L	−54	−42	33	3.76	46
	L	−60	−54	24	3.4	
ACC	L	−9	48	0	3.73	50
	L	−3	42	6	3.25	
vMPFC	R	12	51	−9	3.7	44
	R	6	57	3	3.36	
	R	9	42	−6	3.31	
MidFG	L	−36	51	18	3.46	16
Cuneus	L	−6	−87	36	3.4	13

Abbreviations: Hypoth: hypothalamus, STG: superior temporal gyrus, SupMG: supramarginal gyrus, ACC: anterior cingulate cortex, vMPFC: ventral medial prefrontal cortex, MidFG: middle frontal gyrus, L: left, R: right.
All regions survived a statistical threshold of $p<0.001$ (uncorrected), cluster size $k>10$. * Thalamus: only found in contrast RF1>RN1 (comparison of the first 30 s time bin of resting periods).

of each resting interval into three time bins of 30 s in our GLM analysis. This allowed us to examine more precisely the temporal dynamics of changes in the DM regions that were more active during resting periods than during movies. To this aim, for the main regions showing DM activity (rest>movie) or persistent suppression by preceding emotion conditions (rest post-neutral>rest post-joyful + rest post-fearful) in the SPM analysis above, we extracted the parameter estimates of activity (beta values) computed for their activated clusters and determined by the GLM for each of the three successive time bins of resting activity. Averaging over the three 30-s time bins provided better signal-to-noise ratio than looking at the true time-series, without additional noise due to the intrinsic scan-by-scan variability in BOLD contrast and more general signal drift effects.

Table 4
Regions significantly activated during resting periods following neutral>joyful movies.

Region	Side	*x*	*y*	*z*	*Z*-score	Cluster size
ParOp	R	66	−24	21	4.62	220
	R	63	−15	30	3.98	
	R	45	−30	15	3.38	
SPL	L	−18	−57	57	4.55	304
	L	−9	−54	54	4.46	
	L	−33	−48	60	3.96	
SMA		0	3	45	4.11	82
MidFG	L	−36	51	18	4.1	99
	L	−24	54	24	3.78	
SFG	R	30	−9	57	4.04	16
ParOp	L	−57	−24	18	3.8	92
Prec	L	−9	−72	42	3.79	224
	R	18	−69	45	3.73	
	R	9	−66	39	3.67	
IPL	L	−57	−42	36	3.75	37
IOcC	L	−51	−69	−3	3.73	16
MidFG	R	24	45	33	3.67	47
dMPFC	L	−3	48	12	3.62	88
	R	9	54	0	3.56	
PrCG	L	−57	3	36	3.58	17
ROp	R	54	6	3	3.57	40
	R	54	9	−6	3.55	
ACC		0	30	24	3.36	11

Abbreviations: ParOp: parietal operculum, SPL: superior parietal lobule, SMA: supplementary motor area, MidFG: middle frontal gyrus, SFG: superior frontal gyrus, Prec: precuneus, IPL: inferior parietal lobule, IOcC: inferior occipital cortex, dMPFC: dorsal medial prefrontal cortex, PrCG: precentral gyrus, ROp: rolandic operculum, ACC: anterior cingulate cortex, L: left, R: right.
All regions survived the statistical threshold of $p<0.001$ (uncorrected), cluster size $k>10$ voxels.

As shown on Fig. 5, different activity profiles were observed among these regions. The PCC showed no significant variation in activity between the neutral and emotional rest conditions (Fig. 5A). Thus, this region showed similar increases during rest regardless of the preceding movie type. The inferior parietal lobule (IPL), bilaterally, also showed strong increases during resting state, although return to resting activity appeared slightly less complete or less rapid after emotional than neutral movies (Fig. 5B).

By contrast, a much stronger emotional effect was observed on the level and time-course of activity during rest for the insula and ACC. Both ACC and insula bilaterally showed a typical DM pattern with a strong deactivation during the movies (Figs. 5C and D). However, activation during resting periods clearly differed depending on whether the preceding movie was emotional or not. After neutral movies, resting state activity recovered immediately to a stable level, whereas it exhibited a more gradual restoration after both joyful and fearful movies. Finally, the vMPFC and precuneus exhibited a marked initial reduction during rest after emotional movies, which then recovered gradually during the remaining period of rest (Fig. 5E and F). In addition, these two regions showed no reduction following neutral movies.

In order to examine more precisely these dynamic changes over the successive 30-s time bins in the different resting periods, we measured the recovery slopes for each region using linear regression with time bins as the independent variable and parameter estimates from each ROI and each period (i.e., rest post-joyful) as a dependent variable. This analysis revealed no significant slope for PCC and IPL, whereas a significant effect was found for the condition "rest post-joyful" in ACC and right insula ($F(1,43)=5.89$, $p<0.019$ and $F(1,43)=8.05$, $p<0.007$, respectively); the positive slopes during rest post-fearful did not reach significance ($p=0.16$ and $p=0.13$, respectively). Significant slopes were observed for both conditions of "rest post-joyful" and "rest post-fearful" in the vMPFC ($F(1,43)=6.63$, $p<0.014$ and $F(1,43)=4.18$ $p<0.047$, respectively) and precuneus ($F(1,43)=10.02$ $p<0.003$ and $F(1,43)=5.90$ $p<0.019$, respectively).

Note that these effects of emotion on the return to resting state did not seem to depend on the effects of emotion during the movie period itself, because most of the DMN regions above showed differential responses to the movie content, with generally larger deactivation to emotional than neutral situations (Fig. 5). A repeated-measure ANOVA on parameter estimates of activity from these ROIs during the movie periods showed a highly significant effect of emotion (3 levels) for PCC ($F(2,28)=15.66$, $p<0.0001$) and IPL ($F(2,28)=9.67$, $p<0.001$), although these two regions showed no reliable modulation of resting activity by emotion condition (Fig. 5AB). The effect of emotional content on activation to the movies was marginal for precuneus ($F(2,28)=3.14$, $p<0.059$) and ACC ($F(2,28)=2.66$, $p<0.088$), but did not reach significance in insula ($F(2,28)=2.42$, $p<0.108$) and VMPFC ($F(2,28)=1.84$, $p<0.177$). Moreover, in all cases, these effects were generally similar for positive and negative movies.

Functional connectivity results

Regions identified by contrasts of interest in SPM were then selected to examine their functional connectivity during rest periods, and to test for changes in connectivity induced by the different emotion conditions. The selected regions of interest and the contrasts from which they were obtained are indicated in Table 5. These ROIs corresponded to brain areas typically associated with the DMN and/or emotion processing, which were found to be differentially activated when comparing either rest vs. movie, emotional vs. neutral movies, or different rest conditions with each other (periods following neutral vs. emotional movies), as described in our analyses above. Note that

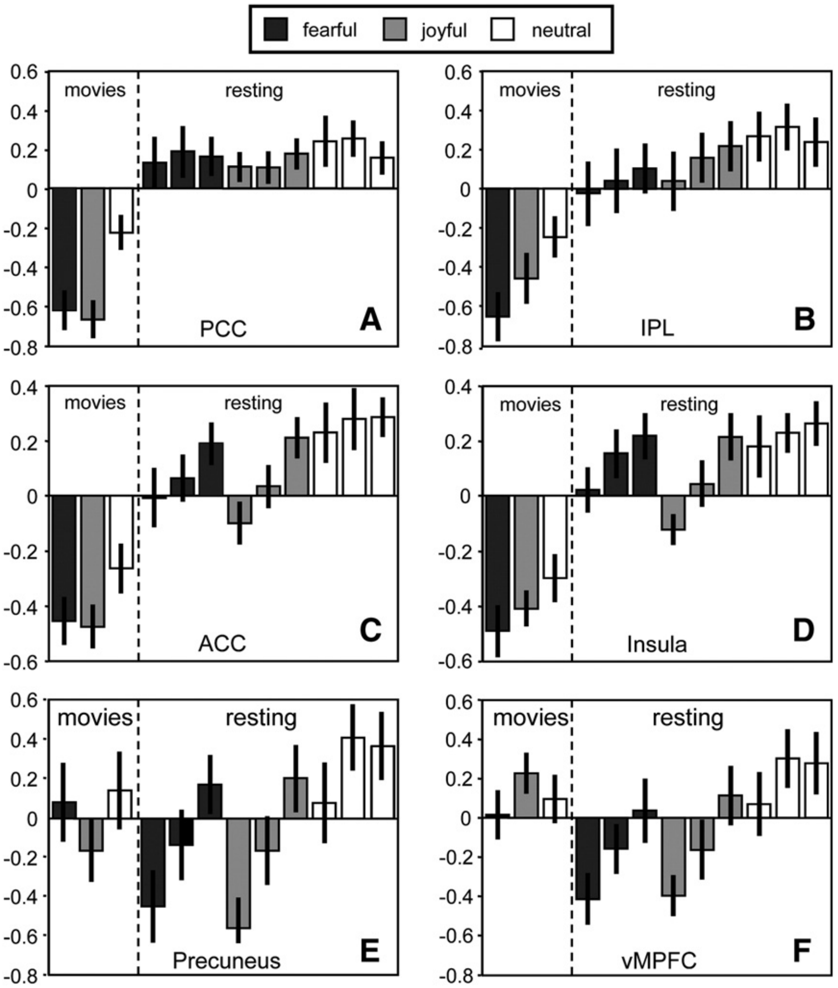

Fig. 5. Magnitude and time-course of activity (parameter estimates) for the main regions differentially activated during resting periods, across three successive 30-s periods and three emotion conditions. The first three bars represent activity during movie-watching, with the different emotion types depicted in different colors (black = fearful, gray = joyful, white = neutral movies). The other bars represent the resting periods, with each successive time bins of 30 s shown for the periods following fearful (three leftmost black bars), joyful (three central gray bars), and neutral movies (three rightmost white bars). These three successive time bins in each emotion condition correspond to the 0–30 s, 30–60 s, and 60–90 s of rest following the end of the movie. Activity in (A) posterior cingulate cortex and (B) inferior parietal lobule, showing global increases during rest but regardless of the preceding emotion condition. Activity in (C) ACC and (D) right insula, showing marked deactivations during movies, with a steep increase in activity during rest after neutral movies but more gradual restoration of rest activity after joyful and fearful movies. Unlike typical default mode regions, activity in (E) left precuneus and (F) vMPFC was not reduced during movies, but during the first part of resting periods following emotional movies, and it then progressively increased to a complete restoration level. All regions showed symmetric pattern in the two hemispheres, but only one side is illustrated here for left IPL and right insula, and other activation clusters spanned across the midline.

the results remained similar when we added other regions that were not differentially activated by rest and movie conditions.

Correlation matrices for main contrasts among different resting periods

We used the time-courses associated with the peak of each ROI to compute wavelet correlations between all pairs of regions. Statistical comparisons of correlation matrices from different conditions were performed using nonparametric permutation tests (see Materials and Methods section). On the statistical correlation matrix plotted in Fig. 6, significant changes in connections are marked as * (corresponding to $p < 0.01$ one-tailed uncorrected) or ** (corresponding to $p < 0.0005$ one-tailed uncorrected).

Wavelet correlation comparisons for resting in post-fear against post-neutral periods are shown in Fig. 6AB (rest post-fearful > rest post-neutral), for two frequency ranges typically associated with DM activity. Different patterns of significant changes in connectivity were observed for these two different frequency bands. In the 0.03–0.06 Hz sub-band (Fig. 6A), connections were specifically enhanced between IPL and ACC, two regions showing a DM behavior with more activity during resting. Significant increase in correlation was observed between left insula and thalamus. Conversely, the right amygdala showed reduced coupling with ACC and precuneus. In the 0.06–0.11 Hz sub-band (Fig. 6B), the left insula was more strongly coupled to several regions of the DMN including ACC, PCC, bilateral IPL and left precuneus, as well as subcortical structures like left thalamus and right pallidum. These two subcortical regions are also more strongly connected to each other for this specific contrast. Again, the amygdala showed reduced coupling with precuneus as well as vMPFC. Similar correlation matrices were also computed for two higher frequency bands (0.11–0.23 Hz and 0.23–0.45 Hz), but are not reported here since they did not reveal any statistically significant correlations and consistent pattern.

The same comparison of resting after joyful movies and after neutral movies (rest post-joyful > rest post-neutral) revealed significant changes in connectivity patterns for the same two frequency bands (Fig. 6CD). In the lower band (0.03–0.06 Hz), we found again stronger coupling between areas of the DMN, particularly for right IPL with PCC, left IPL, and subcortical regions in thalamus and pallidum (Fig. 6C). The left insula was also significantly more connected to the left IPL and the same subcortical structures. In the higher band (0.06–0.11 Hz), significant increases in correlations were observed for bilateral insula with the right pallidum, and for left insula with the

Table 5

Regions of interest selected from relevant contrasts in SPM and used for connectivity analyses. The contrast from which the peak activation was defined is shown in the leftmost column.

Contrast	Region label	Side	Coordinates		
			x	*y*	*z*
Rest>movie	Insula	Left	−36	9	3
	Insula	Right	39	15	−3
	ACC		0	36	−18
	PCC		0	−33	21
	IPL	Left	−42	−54	42
	IPL	Right	45	−54	42
RN>RJ+RF	Precuneus	Left	−12	−69	36
	Precuneus	Right	12	−63	39
	vMPFC	Right	9	39	−3
EmoMovie>NeutMovie	Amygdala	Left	−15	−3	−15
	Amygdala	Right	12	−6	−15
RF>RN	Hypothalamus	Right	6	−9	−9
	Pallidum	Right	12	0	0
	Thalamus*	Left	−12	−6	0

Abbreviations: RN: rest post-neutral, RJ: rest post-joyful, RF: rest post-fearful, EmoMovie: emotional movies, NeutMovie: neutral movies.

* Left thalamus was selected from the contrast comparing only the first 30-s time bin of the corresponding resting periods (RF1>RN1).

left IPL, left precuneus, and left thalamus (Fig. 6D). Decreases in correlations were found only between vMPFC and left amygdala and only for the high sub-band (0.06–0.11 Hz). Again, the two highest frequency bands (0.11–0.23 Hz and 0.23–0.45 Hz) showed no significant and reliable effects.

Small-world parameters across different resting conditions

Finally, we calculated three measures (degree, clustering coefficient, and path length) derived from a small-world network model (Watts and Strogatz, 1998), based on the correlation matrices for the same set of ROIs. In a small-world network, the node (region) with the highest number of surviving connections after thresholding of the correlation matrices (FDR corrected) has the highest degree, and is considered as the hub for that network. By averaging the degree values across all participants for each of the 15 ROIs, and then ranking them according to their magnitude, we identified three consistent hubs for this network (i.e., regions with the three highest degrees for the different sub-bands and resting conditions). These hubs are listed in Table 6 with their group-averaged degree values in the two frequency sub-bands of interest (0.03–0.06 and 0.06–0.11 Hz). The precuneus was the dominant hub in the post-neutral resting periods, followed by PCC, whereas the latter was dominant in both the post-fear and post-joyful resting periods, together with ACC and precuneus (as well as the right pallidum in the 0.06–0.11 Hz range post-fear). This result converges with the modulation of functional connectivity found for the same regions in the wavelet correlation analysis above.

We also performed a repeated-measures ANOVA on the three small-world parameters, taking the 3 resting conditions and 2 frequency sub-bands as factors ('emotion' and 'sub-band'). Our analysis revealed that the values of cluster coefficient [$F(1,14)=14.37$, $p<0.002$] and degree [$F(1,14)=10.86$, $p<0.005$] were significantly larger in the higher sub-band, i.e. 0.06–0.11 Hz. We did not find any significant main effect of emotion and no interaction of the two factors for any of the parameters.

Discussion

We examined brain activity and functional connectivity during different rest conditions, following exposure to situations with varying emotional content. Because complex mental states like emotions may have lingering effects and can influence the processing of subsequent information through perceptual or memory biases (Dolan, 2002), our study aimed at determining the impact of transient (positive and negative) emotions on the following resting states. Our findings show that emotions induced by short movies strongly modulate the pattern of activity in regions associated with the "default mode" network (DMN) and their functional connectivity at rest. These data are consistent with behavioral evidence of lasting consequences of short-lived emotions on subsequent cognitive performance, sleep, and mood (Thayer et al., 1994; Baumeister et al., 1998; Sonnentag et al., 2008; Dunn et al., 2009). Thus, although emotions are defined as transient mental events (Scherer, 2005), they can produce significant changes in brain states even after the return to rest.

Differential effects during and after emotional movies

Both positive and negative movies evoked widespread activations in sensory and limbic brain regions, including amygdala, clearly showing that movies engaged attention and produced emotional responses as expected. Furthermore, not only did we observe a deactivation of several regions of the DMN during movie periods, including IPL, PCC, ACC, and insula, but we also found that most of these regions were more strongly deactivated during emotional than neutral movies. This pattern suggests that the multisensory events and emotions conveyed by the emotional movies constituted a more demanding or absorbing stimulation for the participants, as compared to the neutral condition. This is consistent with studies reporting that task-related deactivations in DMN are stronger for higher cognitive loads (Esposito et al., 2006).

However, we found no direct relation between a differential recruitment of these brain areas during emotional movies and their modulation by emotion during subsequent rest. No effect of preceding fear or joy was observed for IPL and PCC, despite their stronger deactivation during emotional than neutral movies. By contrast, significant emotion effects on subsequent resting activity were seen in ACC and insula, as well as in the precuneus and vMPFC. Taken together, these data point to a functional dissociation between these different regions within the DMN (Mantini et al., 2007), and indicate that modulations of resting state by preceding emotions could not be explained by simple metabolic consequences or non-specific carry-over of the sensory-driven BOLD changes. Rather, our results suggest a distinct role for some regions in DMN in the regulation of affect and return to homeostasis after transient emotional events.

The aftermath of fear and joy

The lingering effects of induced emotions on subsequent brain states are supported by the behavioral results obtained during fMRI in our participants, when they reported the content dominating their thoughts during each resting period. After neutral movies, spontaneous thoughts were mainly related to personal issues (e.g., daily events in their agenda), but movie content dominated after fearful movies and thus appeared to "stick" to their mind. By contrast, both personal issues and movie content were equally reported after joyful movies, whereas thinking about scanner environment or 'feeling sleepy' were practically not present in their thoughts in any condition. Overall, these reports suggest that, at least subjectively, emotions (especially negative) tended to have a systematic persistent effect on subsequent mental states and reduced the frequency of purely self-referential thinking. However, like in other studies of resting state, it is difficult to verify the exact mental content of participants in these conditions since any systematic sampling procedure would inevitably bias the nature and intensity of imagery and introspective processes that spontaneously take place during rest (Mason et al., 2007). Here we chose to ask only a general question after each rest period to our participants, allowing us to probe for a possible behavioral correlate of changes in brain activity, but without requiring explicit attention to the movie content.

Our functional imaging results revealed the neural underpinnings of these differential effects of emotion on following rest periods. Both the GLM analysis and connectivity measures converged to delineate a

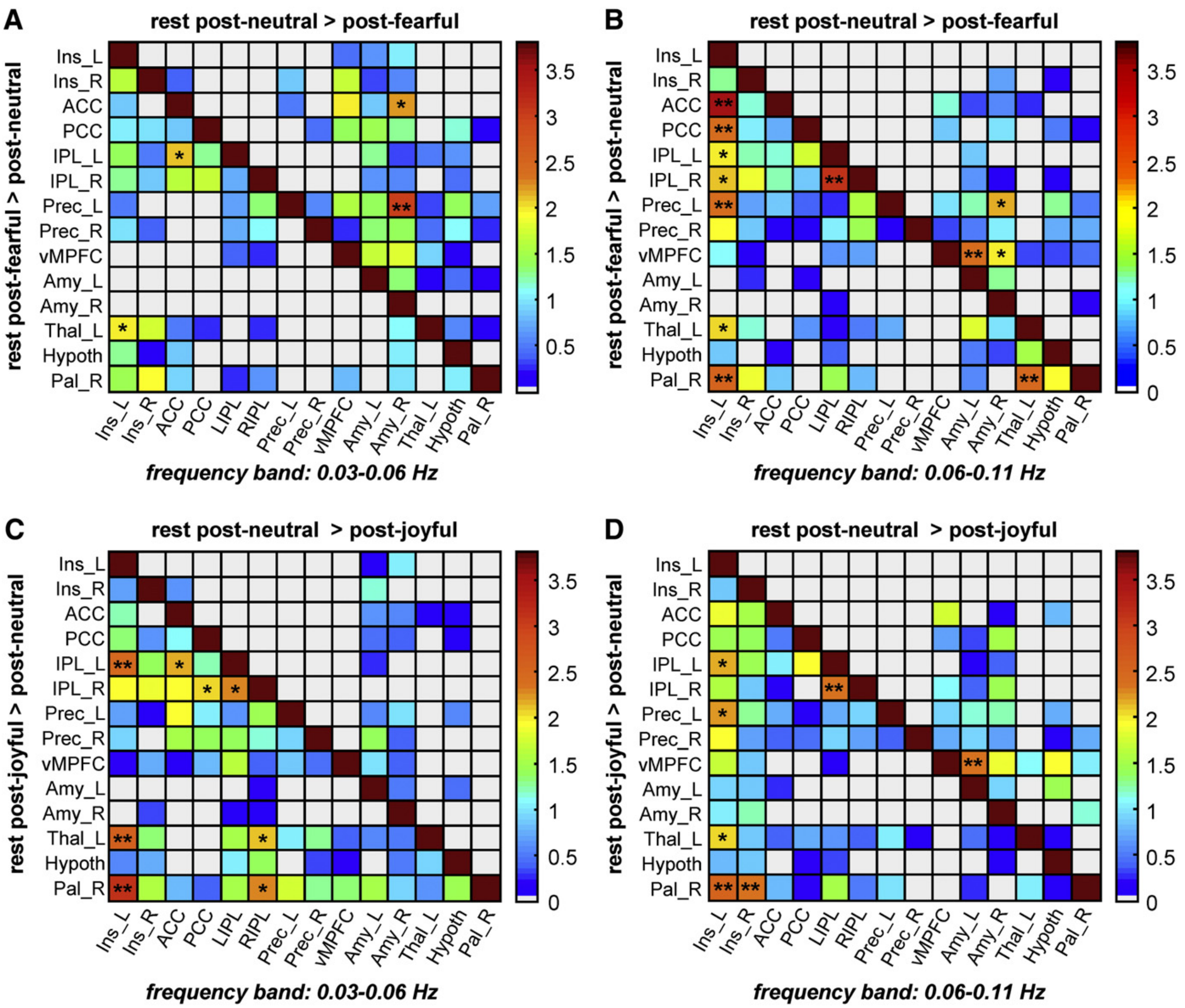

Fig. 6. Statistical correlation matrices between pairs of ROIs for the different resting conditions. Left and right halves of the matrices with respect to the negative diagonal show the values for inverse contrasts (e.g., rest post-fearful > rest post-neutral and rest post-neutral > rest post-fearful). Significant connections with $z > 2$ are marked by * (corresponding to $p < 0.01$ one-tailed uncorrected) and those with $z > 2.30$ by ** (corresponding to $p < 0.0005$ one-tailed uncorrected). Direct contrast between correlation matrices for rest post-fearful vs. rest post-neutral movies is depicted for (A) the frequency band 0.03–0.06 Hz, and (B) the frequency band 0.06–0.11 Hz. Direct contrasts between correlation matrices for rest post-joyful vs. rest post- neutral movies, are depicted (C) for the frequency band 0.03–0.06 Hz and (D) for the higher band 0.06–0.11 Hz. Abbreviations: Ins: insula, ACC: Anterior Cingulate cortex, PCC: posterior cingulate cortex, IPL: inferior parietal lobule, Prec: precuneus, vMPFC: ventral medial prefrontal cortex, Amy: amygdala, Thal: thalamus, Hypoth: hypothalamus, Pal: pallidum.

series of sub-networks within DM regions that were consistently modulated by the preceding movie type. Distinct patterns were observed for each of these sub-networks in terms of overall changes in activity, time-course of modulation (e.g., progressive or immediate), and functional connectivity.

Table 6
Hubs of the network for the different resting conditions.

Sub-band	Rest post-fear		Rest post-joyful		Rest post-neutral	
0.03–0.06 Hz	PCC	5.20	PCC	4.60	Precuneus_R	4.13
	Precuneus_L	4.20	ACC	4.53	Precuneus_L	4.00
	ACC	4.07	Precuneus_L	4.47	PCC	3.60
0.06–0.11 Hz	PCC	6.60	PCC Precuneus_L	5.80	Precuneus_L	5.33
	Pallidum_R	6.00	ACC	5.53	Precuneus_R	5.13
	Precuneus_R	5.93		5.07	PCC	4.93

Abbreviations: ACC: anterior cingulate cortex, PCC: posterior cingulate cortex, Precuneus_L: left precuneus, Precuneus_R: right precuneus, Pallidum_R: right pallidum. Regions listed here are those with the highest group-averaged degree values (given next to the region names), as derived from the small-world network analysis, for each condition and each sub-band.

A first large-scale network was centered on the insula, which showed strong functional correlations with ACC, precuneus, and IPL, as well as subcortical regions in thalamus and pallidum. A striking resemblance in the activation patterns of insula and ACC was seen during both the movie and resting periods, and for both emotion types (fear and joy). These two regions showed a large relative deactivation during movies (the strongest for fearful movies and the weakest for neutral movies), but also a global reduction in the post-emotion rest periods, and only gradual increases over successive time bins of post-emotion resting. This was unlike the post-neutral periods where resting activity was immediately restored. This pattern clearly demonstrates long-lasting effects of transient emotions on both of these regions. In addition, the precuneus also showed a gradual return to "normal" resting state levels. Remarkably, all these regions showed an increased functional connectivity with the insula that occurred specifically in the higher portion of the resting state frequency band (0.06–0.11 Hz), not in the lower band (0.03–0.06 Hz). In addition, an increase in left IPL-ACC connectivity was also selectively observed in the low band after fearful movies. Thus, in small-world network analyses, ACC became one of the three main hubs in brain networks after emotional movies.

This increased coupling may reflect the role of insula and ACC in the integration and regulation of interoceptive information about bodily states and arousal to form a representation of current affect and motivation state (Craig, 2002; Critchley et al., 2004). Anatomical studies have shown direct projections from insula to ACC, and a strong connectivity between these two regions has already been reported in resting state without any emotional stimulation (Seeley et al., 2007; Taylor et al., 2008). Our findings confirm this connectivity and provide direct support for its involvement in affective state representations. In addition, ACC is implicated in top-down control mechanisms allowing the suppression of interference by negative emotional information (Bishop et al., 2004), an ability that contributes to emotion regulation and is altered in people with anxiety (Salkovskis, 1996; Bishop, 2007) or dysphoria (Gilboa and Gotlib, 1997) who show reduced ability to recover from acute stressors and persistence of negative affect. The networks identified here may therefore constitute a central brain system for behavioral adjustment and interoceptive monitoring subsequent to emotional arousal, particularly when fear-related. Furthermore, reduced ACC activity during recovery from transient emotions may accord with findings that executive control and error monitoring abilities associated with ACC functions are impaired in healthy participants after exposure to negative material (Baumeister et al., 1998; Inzlicht and Gutsell, 2007), an effect attributed to depletion of self-control resources due to prior emotion regulatory demands. Our data show for the first time changes in ACC activity and connectivity that may account for these striking effects of emotion regulation on the performance of subsequent cognitive tasks.

A second sub-network of regions affected by previous emotions was centered on vMPFC and amygdala. Unlike insula and ACC, these regions were not generally modulated by rest compared to movie periods in neutral conditions, but vMPFC showed a large deactivation immediately after emotional movies, followed by gradual increases until the end of the resting period, and connectivity analyses revealed a selective reduction of coupling with bilateral amygdala during the post-emotion compared to post-neutral rest (predominating in the high frequency-band). These effects were similar for fear and joy, but fear induced additional reduction in coupling between right amygdala with precuneus and ACC (predominating in the low-frequency band). No variation in activity across time bins was seen in vMPFC during neutral rest. Because vMPFC is involved in self-referential processes (Gusnard et al., 2001; D'Argembeau et al., 2007), and in extinction of conditioned fear through interactions with amygdala circuits (LeDoux, 2000; Phelps et al., 2004), its suppression during post-emotion periods dovetails to our behavioral findings that self-focused thoughts were reduced in emotional resting periods, particularly after fearful movies. Moreover, a similar combination of diminished vMPFC activity and increased amygdala activity during an affective reappraisal task was shown to correlate with individual tendency to ruminate on negative information (Ray et al., 2008), suggesting that reduced vMPFC control of emotion processing in the amygdala may contribute to sustain negative interpretations evoked by unpleasant or threatening stimuli (Bishop, 2007). Thus, in our study, decreased connectivity between vMPFC and amygdala might reflect the persistence of negative movie content and suppression of self-related thoughts in the post-fear resting periods, perhaps due to reduced interactions with ACC and other brain regions involved in emotion regulation. Future studies could employ a similar procedure to examine whether these effects are amplified in individuals with anxiety or mood disorders who are prone to ruminations.

As the self-reports of the participants suggest, it is possible that some mental and/or emotional imagery took place during rest periods after emotional movies, which might have contributed to the effects reported above. There is no easy way to separate this factor from the emotional processing due to the lingering effects of the movies. However, most of the regions showing differential connectivity during the post-emotion rest periods are typically implicated in emotional perception and regulation, suggesting that changes observed in the rest period did concern affective processes rather than imagery alone. On the other hand, because emotion regulation was not explicitly manipulated in this experiment (e.g., by instructions), we cannot definitely conclude that participants used emotion regulation strategies (voluntarily or not) in order to get over the emotional (disturbing or amusing) effect of the movie and return to a more balanced neutral state. Nonetheless, it is likely that connectivity changes reflected neural processes contributing to cope with emotional reactions elicited by the previous movies. Follow-up studies manipulating regulation explicitly, e.g., using instructions of up/down regulation or reappraisal, might be valuable to further investigate the nature of these effects.

Imperturbability of rest

A final set of regions included PCC and IPL, which showed typical DM activity with strong increases during rest and decreases during movies, but no significant modulation across the different emotion conditions or time bins of rest. Moreover, small-world parameters indicated that PCC remained a major hub of the brain for all conditions and all bands. This finding is compatible with the idea of PCC as a "pivotal" region in DM (Fransson and Marrelec, 2008). Likewise, IPL activity was increased during rest with no (or weak) effects of the preceding emotions. However, functional connectivity analysis revealed higher coupling of left and right IPL with each other and with the insula and ACC (in higher and lower bands, respectively), during emotional compared to neutral resting periods.

Both IPL and PCC are core regions of the DMN that have been associated with "intrinsic" activity, typically decoupled from external stimulation (Golland et al., 2007). While the function of these regions remain unclear, they are usually attributed to internally directed processes and self-awareness (Fox and Raichle, 2007) (Goldberg et al., 2008). Their activity and connectivity during rest might reflect a general role in controlling attention to different mental contents in the absence of sensory inputs (Corbetta et al., 2008), and could thus imply flexible cross-links with different brain networks based on the current state, including those implicated in affect and interoceptive awareness (e.g., insula-ACC) that were modulated by previous movie content in our experiment.

Resting frequency matters

More generally, our results demonstrate that connectivity measures may uncover the network architecture of resting activity more precisely than changes in BOLD contrast alone, since some areas showed strong modulations of their functional coupling without any change in overall activity. Furthermore, different changes in connectivity patterns were seen across different frequency bands. For example, for post-fearful rest, the higher (0.06–0.11 Hz) resting state band revealed important correlations between regions involved in emotional processing (e.g., insula-ACC, vMPFC-amygdala) that were not seen in the lower (0.03–0.06 Hz) band. Differences between sub-bands were also observed in the small-world analysis, with significantly higher average cluster coefficient and degree values in the high than low range. These findings highlight the need to consider different frequency bands and the usefulness of wavelets in functional connectivity analyses of resting state fMRI. Whether there is a lower limit for frequencies contributing to spontaneous BOLD changes is still debated, but our findings suggest a clear distinction between the low and high frequencies of typical resting state fluctuations (<0.1 Hz) and indicate that the upper band resembles more a small-world network and has more connections.

Conclusion

In summary, by demonstrating that short emotional events may have prolonged effects on spontaneous brain states at rest, our study highlights the dynamic structure of DMN and reveals specific networks associated with emotion regulation mechanisms. These findings have important implications for understanding the functional role of the DMN and investigating the impact of emotional stressors in psychopathological conditions, but also call for careful control of emotional context in imaging studies of resting state.

Supplementary materials related to this article can be found online at doi:10.1016/j.neuroimage.2010.10.021.

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