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Original Article

Mood congruency effects are mediated by shifts in salience and central executive network efficiency

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Abstract

Emotions are not confined to short momentary states but carry on over time, facilitating the perception and interpretation of the environment in mood-congruent ways. Yet, the (neural) mechanism linking affective stimulation at a certain time-point to such altered, mood-congruent processing of stimuli presented at a subsequent time-point remains unknown. Recent research suggests that such a link could be explained by transient effects of affective stimulation on the organization of intrinsic macro-scale neural networks. It remains, however, unclear whether these changes in network organization are influencing subsequent perception in a mood-congruent way. Addressing this gap the current study investigated whether changes in network organization, measured in terms of network efficiency, mediate the relation between mood induction and mood-congruent processing as measured by reaction times during an emotional Stroop task. The results demonstrated that negative mood induction increased the efficiency of the salience network and decreased the efficiency of the central executive network. This modulation of network efficiency fully mediated the effects of mood induction on reaction times to negative words. These findings indicate that transient shifts in the organization of macro-scale neural networks are an essential part of the emotional response and can help to explain how affect shapes our interaction with the environment.

Key words: efficiency; emotional Stroop task; executive network; mood congruency; salience network

Introduction

The emotions we experience are not confined to short momentary states but carry on over time and shape the perception, interpretation and interaction with our environment (e.g. Clore and Huntsinger, 2007). Especially the tendency of emotions to facilitate processing of stimuli in a mood-congruent manner has received considerable attention (for example MacLeod and Mathews, 1988; Tamir and Robinson, 2007; Isaac *et al.*, 2012; Forgas, 2017). On the upside, such mood-congruent processing is considered to reflect a core functional feature of emotions, helping us to navigate the threats and opportunities in our environment (for example Schwarz, 1990; Eldar *et al.*, 2016). On the downside, when such mood-congruent processing becomes inflexible and difficult to regulate, it is considered to play a crucial role in the development of affective disorders (for example Koster *et al.*, 2005). Despite its central role for adaptive and maladaptive functioning, the (neural) mechanisms linking affective stimulation, at a certain time-point, to the processing of novel stimuli at a subsequent time point are not fully understood.

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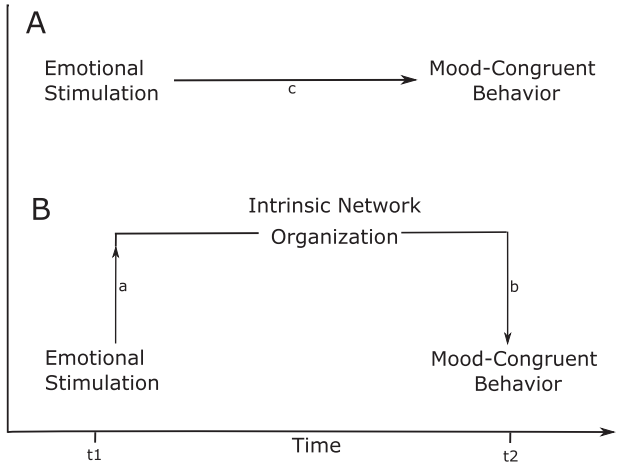


Fig. 1. Overview over research questions. Testing the hypothesis that the effect of emotional stimulation at a certain time-point (t1) to mood-congruent behavior at a subsequent time point (t2) (A) is linked by transient shifts in intrinsic network organization (B), we will, as a first aim, replicate the findings of a relation between emotional stimulation and subsequent mood-congruent behavior (c) as well as emotional stimulation and shifts in intrinsic network organization (a). As a second aim we will test for a relation of shifts in intrinsic network organization and mood-congruent shifts in behavior (b), and finally as a third aim, we will test if these shifts in intrinsic network organization are mediating the relation of emotional stimulation on mood-congruent behavioral shifts (B).

Outlining a potential neural mechanism of how affective stimulation might shape the processing of subsequently presented novel stimuli, recent research has shown that mood induction is related to transient and sustained shifts of functional connectivity within macro-scale neural networks involved in emotional processing. Indeed, it is becoming increasingly clear that neural responses to mood induction are not confined to the duration of such stimulation but carry on and modulate neural activity and connectivity within the salience network (SN), the default mode network (DMN) as well as the central executive network (CEN) (Harrison *et al.*, 2008; Eryilmaz *et al.*, 2011, Borchardt *et al.*, 2017). The transient character of these changes (see for example Eryilmaz *et al.*, 2011) as well as the links between transient changes in network organization and behavior (Tambini *et al.*, 2016; see also Spoorns, 2010; Raichle, 2015) are making them a promising candidate for orchestrating the effects of emotions on subsequent processing of novel stimuli (see also Pessoa, 2017; Pessoa, 2018). However, to our knowledge, no study has yet examined whether affect-induced changes of macro-scale neural networks are related to mood-congruent processing of novel stimuli and whether these changes can indeed explain (mediate) the relationship between emotional stimulation and mood-congruent processing of novel stimuli.

Accordingly, the overall aim of the present study is to test the potential role of changes in network organization in connecting affective stimulation with subsequent mood-congruent processing of novel stimuli. For this purpose we first aim to replicate the findings that affective stimulation results in mood-congruent processing of novel stimuli (see arrows c in Figure 1) and in changes in the intrinsic organization of the DMN, CEN and SN (see arrow a in Figure 1). The second aim is to test a possible relation between changes in the organization of these networks and (mood-congruent) processing of novel stimuli (see arrow b in Figure 1). Finally, the third aim is to test whether changes in the intrinsic organization of the DMN, CEN and SN mediate the effect of affective stimulation on mood-congruent processing of novel stimuli (see Figure 1).

To realize these aims, we conducted a functional magnetic resonance imaging (fMRI) study consisting of nine sessions. Each session started with a mood induction (positive *vs* negative *vs* neutral), followed by a resting state period and a measurement of mood-congruent processing. To induce affective experience we made use of emotional movie clips as they have been shown to be highly effective at eliciting emotions (Gross and Levenson, 1995; see also Lench *et al.*, 2011). Resting-state periods after negative and positive mood induction were used to estimate network integration in terms of network efficiency (Latora and Marchiori, 2001), indicating the capacity of a network to support rapid, efficient and integrated communication. This topological feature of network organization has been shown to be sensitive to the affective context (McMenamin *et al.*, 2014) and such emotion-dependent reconfiguration of network integration have been argued to be a central aspect in linking emotions to changes in perception and behavior (see for example Pessoa, 2017). Finally, the emotional Stroop task (Williams *et al.*, 1996) is presented at the end of each session to capture mood-congruent behavioral changes in the processing of novel emotional stimuli (see also Gilboa-Schechtman *et al.*, 2000).

Based on previous work we formulated the following hypotheses. Related to our first goal, we expected to replicate the mood congruency effect on reaction times in the emotional Stroop task with negative mood induction increasing the reaction times to negative and positive mood induction to positive words (as for instance shown in Gilboa-Schechtman *et al.*, 2000). Moreover we expected that the mood induction would impact the functional organization of the SN and CEN. In particular, we expected to find increased SN efficiency after negative mood induction (compared to positive mood induction), replicating the relationship between coupling of SN regions and negative emotional states (see Harrison *et al.*, 2008; Eryilmaz *et al.*, 2011; see also van Marle *et al.*, 2009; Raz *et al.*, 2012; Raz *et al.*, 2016). In contrast, we expected, in line with findings of reduced CEN efficiency in negative emotion contexts (McMenamin *et al.*, 2014; see also Hermans *et al.*, 2014), decreased CEN efficiency after negative mood induction (compared to positive mood induction).

Related to our second goal, we expected changes in efficiency of both networks to impact subsequently presented emotional stimuli. On the one hand we predicted the SN to be involved in facilitating the processing of negative emotional stimuli. This prediction is mainly based on previous research showing that negative mood induction modulates the responses of key SN regions to subsequently presented stimuli (for example Wang *et al.*, 2006; Qiao-Tasserit *et al.*, 2018). On the other hand we expected alterations in the CEN to be connected to facilitating processing of positive stimuli after positive mood induction (as compared to negative mood induction). This prediction is mainly based on findings of increased activity in a key CEN region—the dorsolateral prefrontal cortex (dlPFC)—in response to positive stimuli being associated to increased sensitivity to these stimuli, resulting in a larger change of the affective state of the subjects (Mak *et al.*, 2009) as well as reduced dlPFC responses to positive stimuli after negative-mood induction (Ossewarde *et al.*, 2011).

Finally, no directed predictions were formulated regarding the DMN as most studies report a modulation of the DMN by mood but the direction of these effects are highly inconsistent (see Harrison *et al.*, 2008; Borchardt *et al.*, 2017; Clemens *et al.*, 2017), making it difficult to formulate specific hypothesis about the affect-dependent changes in network efficiency as well as the effects of such potential changes on subsequent emotional stimuli.

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Related to our third goal, we expect that changes in network efficiency are able to explain the mood induction effects on changes in the processing of subsequently presented words. Accordingly, we expected that the effects of affective stimulation on reaction times in the emotional Stroop task are fully mediated by changes in network efficiency that are outlasting the mood induction.

Materials and methods

Participants

An initial sample of 287 participants was recruited through online advertisements and flyers in which they were asked to fill out an online screening questionnaire. From this participant pool, 38 participants were selected based on their suitability to undergo an fMRI scan and additional criteria including no color blindness, no history of psychiatric or neurological disorders and right handedness. The selection process was further guided to achieve an approximately equal distribution of scores on the BFI-2 neuroticism scale (Soto and John, 2017). This procedure ensured that the sample of participants represented a wide range of trait emotionality and is not biased toward well-adapted participants scoring low on neuroticism, which would possibly limit the generalizability of the findings. To achieve this, the original participant pool was divided into five groups, representing five distinct sections of neuroticism scores (very low [< 2], low [2–2.5], middle [2.5–3], high [3–3.5] and very high [>3.5]). An approximately equal number of participants from every section were invited to participate in the study. Of those who agreed to participate, one participant was excluded from the analysis because of low compliance during the fMRI session (40% answered questions compared to 99.1% in the overall sample). Additionally two fMRI trials (see design section below) had to be removed from the analysis because of failed registration during preprocessing. This resulted in a total of 331 trials (109 negative, 111 neutral and 111 positive) nested within 37 subjects.

The final sample consisted of 17 male and 20 female healthy participants between 18 and 32 years of age (M = 24.03). The study was approved by the Ethics Committee Research UZ/KU Leuven (S59871).

Design

Every participant underwent nine task sessions (see Figure 2) inside the scanner, each consisting of a mood induction followed by a short resting period and an emotional Stroop task (see Williams et al., 1996). To make sure to avoid position effects of the mood inductions as well as avoid more than two mood inductions with the same valence following each other, the order of the session was determined via randomly grouping one session with a positive, one session with negative and one session with neutral mood induction into three blocks and then randomizing the order of the presentation of these blocks.

Mood induction. Each participant was exposed to three positive, three negative and three neutral emotional movie clips. The neutral movie clip lasted for ∼30 s while the emotional movie clips lasted for ∼90 s (for further information about the movie clips see Supplementary Table S1).

Participants indicated their mood state using a 7-item Likert scale (from very positive to very negative) before the movie and after the resting period. These ratings allowed for checking the effectiveness of the mood induction to induce prolonged changes in mood that sustained until after the resting state period. Furthermore, to obtain additional data on the mood state experienced during mood induction, participants were asked to watch and rate all the emotional movie clips again after the fMRI session (for the ratings on specific emotion categories see Supplementary Figure S1).

Resting phase. Every emotional movie clip was followed by a short eye-open resting period of 130 s. Since no analysis of the resting period after neutral movies were planned, and to reduce total scanning time, the resting phase after neutral movies was reduced to 10 s.

Emotional Stroop task. During this task, participants were shown positive, negative and neutral words in red, green, blue or yellow and had to indicate the color of the word by pressing a button corresponding to the color. The relative position of the colored buttons on the button boxes that participants were holding in their hands was indicated by color–words on the screen. For example, if the button at the extreme left of the button box corresponded to green, the word 'green' was situated on the extreme left of the screen. Each word was shown until a button press (maximum 2 s) and then followed by a fixation cross until the total presentation time of the word and the fixation cross was 2.5 s.

In every task session 50 Dutch words were shown, equaling 450 in total. Of these, 150 words were unique—50 positive, 50 negative and 50 neutral—and each word was repeated three times (once after neutral, once after negative and once after positive mood inductions). The words were selected from a normed list of Dutch words (Moors et al., 2012) so that they approximately matched in regard to arousal (negative: M = 3.98, SD = 1.09; neutral: M = 3.68, SD = 0.50; positive: M = 4.09, SD = 0.62) and word length (negative: M = 7, range = 5–10; neutral: M = 6, range = 5–8; positive: M = 7, range = 5–8) while showing clear differences in their valence (negative: M = 2.09, SD = 0.31; neutral: M = 4.42, SD = 0.47; positive: M = 6.10, SD = 0.23) (for the specific words see Supplementary Table S2).

Image acquisition

All scans were acquired with 3T MRI scanner (Philips Medical Systems). For all functional scans T2∗-weighted multiband sequences containing 40 slices (TR/TE = 1200/30 ms, voxel size = 2.7 × 2.7 × 3 mm, FOV = 216 × 120 × 216) were acquired. High-resolution T1-weighted structural images were acquired containing 184 slices (TR/TE = 9.75/4.6 ms, voxel size = 1 × 1 × 1 mm, FOV = 256 × 256 × 184).

Image preprocessing

Structural MRI. Preprocessing of the structural MRI data, including intensity normalization, removal of non-brain tissue and calculating ventricle and white matter tissue masks, was performed with Freesurfer (http://surfer.nmr.mgh.harvard.edu) (Fischl et al., 2002; Fischl, 2012; Fischl, 2004).

Resting state. Preprocessing of the resting state periods after the movies was performed using AFNI (http://afni.nimh.nih.gov/afni) (Cox, 2012) using standard procedures, including de-spiking, co-registration, normalization to MNI-space and

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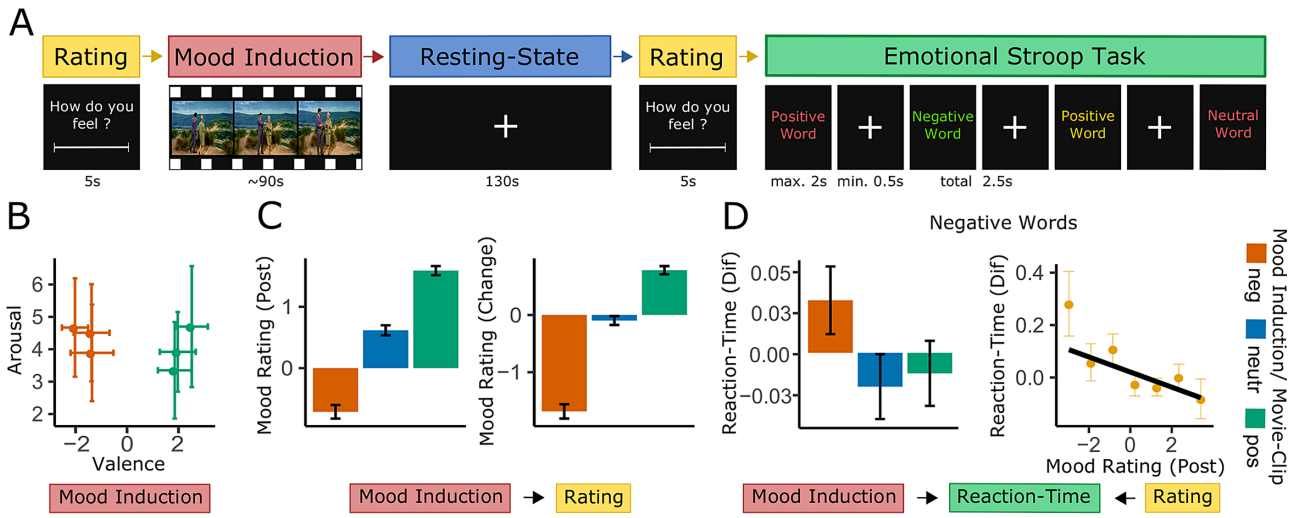


Fig. 2. Overview of the study design. (A) The general outline of the single-task sessions is depicted. Each session started with rating the current affective state on a scale from very negative to very positive followed by a short movie clip as mood induction. After that, an eye-open resting-state period and a second (post) rating of the current affective state followed. Finally participants were confronted with an emotional Stroop task. Each participant underwent nine task sessions with in total three negative, three positive and three neutral mood inductions/movie clips. The graphs in the lower panel depict basic visualizations of data characterizing participants response to this design including (B) valence and arousal ratings of the emotional movies used as mood induction (as rated during the second viewing of the movie clips after the scanning session) and (C) effectiveness of the mood induction on both the mood ratings after the mood induction and resting state period (mood rating post) and the change in indicated mood before and after the mood induction. In (D) the effect of the mood induction (valence of the movie-clips) as well as subjective mood ratings (post) on group mean centered reaction times toward negative words in the emotional Stroop task are shown.

smoothing using a 6 mm full-width half-maximum Gaussian kernel. Additionally images were band-passed filtered (0.008–0.15) and censored (Euclidean norm, >0.3; outlier, >0.1). Motion parameters as well as tissue-based regressors (ANATICOR; Jo *et al.*, 2010)—estimated from Freesurfer ventricles as well as white matter masks—were regressed out (3dDeconvolve) of the fMRI time series. To prevent spill-over effects from the movie clips shown before the resting period, the first 10 s of the resting period were removed from the analysis. Preprocessing of these resting state periods was done separately for every subject and session.

Network parameters

Regions of interest. Network nodes were defined as 5 mm radius spheres around 36 regions of interest (ROIs) described in previous studies as being part of the DMN ($n = 12$, Fox *et al.*, 2005), SN ($n = 13$, Hermans *et al.*, 2011) and CEN ($n = 11$, Seeley *et al.*, 2007) (for the detailed description of the used ROIs see Supplementary Table S3; also see Najafi *et al.*, 2017). For every session and subject the mean time series of the voxels within every ROI sphere was extracted and used to construct a 36×36 Pearson correlation matrix.

Network efficiency. A global threshold of $r = 0.25$ was applied to all matrices to account for noise as well as to remove all negative (Pearson) correlations (see also Supplementary Figure S2 for stability of effect sizes over different thresholds). Network efficiency, defined as the inverse of the sum of shortest paths (as implemented in the Brain Connectivity Toolbox, Rubinov and Sporns, 2010), was calculated for the DMN, SN and CEN for each participant and session (220 sessions: 109 negative, 111 positive) separately (for a similar approach see McMenamin *et al.*, 2014; see also Supplementary Figure S3 for visualization of the distribution of efficiency parameters).

Manipulation check: mood induction

In order to check the effectiveness of the mood induction procedure, we examined the influence of the valence of the mood induction (i.e. valence of the shown movie clips) on experienced mood (i.e. the subjective mood ratings) after the mood induction (i.e. after the resting state phase). Taking into account the nested structure of the data (331 sessions nested within 37 subjects), these effects were modeled with random-intercept multilevel models (nlme-package; Pinheiro *et al.*, 2019). To reduce the number of analyses we first calculated an omnibus *F*-test for mood induction differences followed by planned *t*-tests comparing positive, negative and neutral mood inductions. Two sessions from one subject had to be removed from the analysis because of missing mood ratings. These sessions were subsequently removed from all analysis including the subjective mood ratings.

Data-analytic strategy for aim 1: the effect of mood induction on reaction times in the emotional Stroop task and network efficiency during rest

Impact of mood induction on reaction times in the emotional Stroop task. To capture reaction time differences between sessions, the reaction times were first normalized for each button (to control for differences in mean and variance between buttons) and then aggregated by calculating the median reaction time differences (positive words–neutral words and negative words–neutral words) within each task session. Mood effects on these median reaction time differences were analyzed with a random-intercept multilevel model (nlme-package; Pinheiro *et al.*, 2019). Specifically, we calculated omnibus *F*-tests for effects of mood induction on negative (contrasted with neutral) as well as positive (contrasted with neutral) words followed by planned *t*-tests comparing positive, negative and neutral mood induction. Subsequently, in order to additionally estimate the effect of subjectively experienced mood (as rated by the participants after the resting phase), an additional random-intercept multilevel model

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including the group-mean centered mood ratings as predictor of reaction times was fitted. Five sessions (of five different subjects) had to be removed from the analysis because of errors in reaction time recordings or technical problems with button boxes during the sessions.

Impact of mood induction on network efficiency. Taking into account the nested structure of the data (sessions nested in subjects), multilevel models (nlme-package; Pinheiro *et al.*, 2019) were estimated to separately examine the effect of the positive and negative mood induction on the efficiency of the CEN, SN and DMN. These models included a random intercept for subjects as well as valence of the mood induction (positive or negative) as a binary level one predictor. Sessions with neutral mood induction were not included in the analysis.

In a subsequent set of analyses, we added the subjectively experienced (and rated) valence after mood induction as a predictor of network efficiency. The rationale behind this was that, especially in the context of investigating the influence of affect, an important distinction pertains to whether the relationship with mood is linear (i.e. linearly changing with the valence of the mood) or quadratic (i.e. changing both with increased positive and negative mood, suggesting changes driven by general emotionality or valence-independent arousal). To distinguish these effects, orthogonal polynomials of the indicated mood after the mood induction (of the first and second degree, i.e. linear and quadratic trend) were estimated (using the 'poly ()' R-function) and included into the multilevel models for network efficiency as continuous first-level predictors. Since we were solely interested in within-person relationships, the mood ratings were person-mean centered before being entered into the model. Additionally, to ensure that the modeling of sub-network specific effects was not driven by unspecific changes of the global network, the efficiency of the global network (i.e. SN, CEN and DMN) was added as a nuisance predictor to all models. Resulting *P* values were corrected for multiple comparisons using family-wise error correction (Holm–Bonferroni method; Holm, 1979).

Data-analytic strategy for aim 2: relation between network efficiency at rest and reaction times in the emotional Stroop task

Next we investigated the possible functional role of the affect-induced network changes on the subsequent processing of emotional information. More precisely, separate single random-intercept multilevel models were estimated predicting reaction times during the emotional Stroop by means of network efficiency of the SN, DMN and CEN (nlme-package, Pinheiro *et al.*, 2019). Resulting *P* values were corrected for multiple comparisons using family-wise error correction (Holm-Bonferroni method; Holm, 1979).

Data-analytic strategy for aim 3: mediation of the relation between mood induction and reaction times in the emotional Stroop task by network efficiency

For aspects of the network organization that were significantly associated with behavior outcomes (aim 2), we then estimated 1-1-1 hierarchical mediation models including (a) the valence of the mood induction (positive *vs* negative; independent variable), (b) the session specific reaction time trends (dependent variable) and (c) network efficiency (mediator). This (level 1) mediation model allows to estimate the within subject mediation effects while taking into account the nested structure of the data. The mediation models were estimated using the boot package (Canty and Ripley, 2019) in R and customized R-scripts, in order to estimate indirect multilevel model effects (Elizabeth Page-Gould, http://www.page-gould.com/r/indirectmlm/; see Zhang *et al.*, 2009) with bootstrapped confidence intervals (1000 bootstrap samples).

Results

Manipulation check: mood induction

We found strong differences in mood ratings after positive, negative and neutral mood induction ($F(2, 295) = 194.83$, $P < 0.001$). Valence ratings were higher (i.e. more positive) for positive than negative ($\beta = 2.30$, 95% CI [2.06–2.55], $t(184) = 18.55$, $P < 0.001$) and neutral mood inductions ($\beta = 0.97$, 96% CI [0.77–1.17], $t(185) = 9.60$ $P < 0.001$), and higher for neutral compared to negative mood induction ($\beta = 1.33$, 95% CI [1.11–1.56], $t(184) = 11.62$, $P < 0.001$). Investigating the ratings of positive and negative movie clips after the fMRI part of the study (outside the scanner after re-watching these movie clips) revealed that, while there were strong differences in valence ratings between positive and negative movie clips ($\beta = 4.08$, 95% CI [3.87–4.29], $t(184) = 37.50$, $P \leq 0.001$), arousal ratings showed significant but, based on the very low effect size, only marginally relevant differences ($\beta = -0.37$, 95% CI [−0.73 to −0.01], $t(184) = -2.02$, $P = 0.045$) (see Figure 2).

To further characterize the mood induction, we additionally investigated how the mood induction changed the experience of specific emotions (for further information see Supplementary Figure S1). The results revealed that positive mood induction consistently increased the experience of positive emotions (happy, amused and relaxed) and decreased the experience of negative emotions (sadness, anger, anxiety and stress). In contrast negative mood induction, while consistently decreasing all positive emotions, only increased the experience of sadness (but not anger, anxiety or stress).

Aim 1: the effect of mood induction on reaction times in the emotional Stroop task and on network efficiency at rest

Impact of mood induction on reaction times in the emotional Stroop task. Reaction times during the emotional Stroop task for negative ($F(2, 282) = 4.69$, $P = 0.010$), but not positive words ($F(2, 282) = 1.17$, $P = 0.311$), were significantly influenced by mood induction. Further, comparing the effects of single mood inductions on reaction times to negative words revealed a significant increase in reaction times after negative compared to positive mood induction ($\beta = 0.12$, 95% CI [0.02–0.21], $t(177) = 2.37$, $P = 0.019$) and compared to the neutral mood induction ($\beta = 0.142$, 95% CI [0.04–0.24], $t(177) = 2.83$, $P = 0.005$). There was no difference in reaction times after neutral and positive mood induction ($P = 0.6$) (for better comparability with previous studies, significant effects of mood induction on reaction-times are additionally shown in milliseconds in Supplementary Figure S4).

The relationship between negative mood and increased reaction times to negative words was further confirmed testing for effects of continuous mood ratings, showing an increase of reaction times with decreasing (more negative) mood rating

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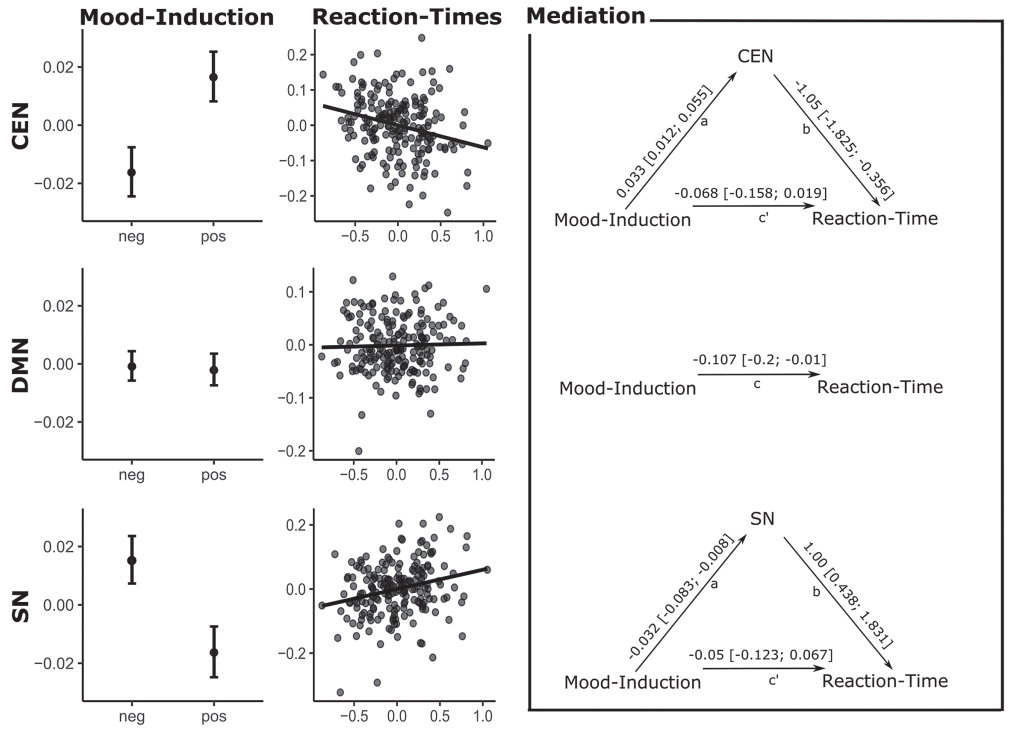


Fig. 3. Overview of mood-dependent changes in the functional organization of intrinsic networks as well as downstream behavioral consequences. Changes in network organization are depicted in on the left panel as average person-mean centered network efficiency parameters after positive and negative mood induction. The downstream consequences of network organization on behavior are depicted as scatterplots between the efficiency of each sub-network and reaction times to negative words in the emotional Stroop task in the middle panel. Finally the paths estimated within the hierarchical mediation analysis (1-1-1) of the relation between mood induction (positive, negative) and reaction times to negative words (arbitrary units) during the emotional Stroop task, including SN as well as CEN efficiency (inverse sum of shortest paths) as mediators, are shown on the left panel.

($\beta = -0.04$, 95% CI [−0.07 to −0.003], $t(284) = -2.18$, $P = 0.030$) (see Figure 3).

Impact of mood induction on network efficiency. Investigating the mood-dependent changes in network efficiency, we found an increased efficiency of the SN after negative compared to positive mood induction ($\beta = -0.04$ (0.01), 95% CI [−0.06 to −0.01], $t(157) = -2.63$, $P = 0.009$, $P_{FWE} = 0.027$). Furthermore the SN efficiency increased linearly with decreasing (more negative) subjectively experienced mood ($\beta = -0.20$ (0.1), 95% CI [−0.39 to −0.01], $t(155) = -2.10$, $P = 0.037$).

In contrast, the efficiency of the executive network (CEN) was higher after positive compared to negative mood induction ($\beta = 0.03$ (0.01), 95% CI [0.01–0.06], $t(157) = 2.59$, $P = 0.011$, $P_{FWE} = 0.027$) and showed a linear increase with more positive subjectively experienced mood ($\beta = 0.22$ (0.1), 95% CI [0.03–0.42], $t(155) = 2.23$, $P = 0.027$). There was no significant association between mood induction or mood ratings with the DMN Efficiency ($P > 0.48$) and none of the quadratic effects of continuous mood ratings reached significance (all $P > 0.49$).

Aim 2: relation between network efficiency and reaction times in the emotional Stroop task

Examining possible relations between changes in network organization after mood induction and mood-congruent reaction times in the emotional Stroop task (see Figure 3), we found that increasing SN efficiency predicted longer reaction times to negative words ($\beta = 1.04$ (0.3), 95% CI [0.11–0.87], $t(157) = 3.47$, $P < 0.001$, $P_{FWE} = 0.001$). Higher CEN efficiency was in contrast related to reduced reaction times to negative words ($\beta = -1.06$ (0.3), 95% CI [0.11–0.87], $t(157) = -3.59$, $P < 0.001$, $P_{FWE} = 0.001$). DMN efficiency was not related to reaction times to negative words during the emotional Stroop task ($P = 0.53$) and there were no associations between any of the network efficiency scores (i.e. SN, CEN and DMN) and reaction times to positive words (all $P > 0.4$).

Aim 3: mediation of the relation between mood induction and reaction times in the emotional Stroop task by network efficiency

Further investigating the role of changes in network efficiency in the relationship of the mood induction (positive *vs* negative) and subsequent reaction times two hierarchical multilevel within-subject mediation analysis (1-1-1) were estimated. The first model involved SN efficiency, the second CEN efficiency as mediators. No mediation with DMN efficiency was carried out because of the lack of found relations with DMN efficiency.

The analyses revealed that there was a significant indirect effect (ab-path: −0.032, 95% CI [−0.083 to −0.008]) from mood induction over SN efficiency (a-path: −0.031, 95% CI [−0.051 to −0.010]) to reaction times to negative words (b-path: 1.00, 95% CI [0.438–1.831]) that fully mediated the relationship between mood induction and reaction times (c-path: −0.107, 95% CI [−0.2 to −0.01]; c'-path −0.05, 95% CI [−0.123 to 0.067]). Similarly also E_{CEN} was found to be linking mood induction to reaction times to negative words (ab-path: −0.035, 95% CI [−0.075 to −0.008]; a-path: 0.033, 95% CI [0.012–0.055]), fully mediating their relation-

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ship (c-path: −0.107, 95% CI [−0.2 to −0.01]; c'-path −0.068, 95% CI [−0.158 to 0.019]). Accordingly the reduced efficiency of the CEN as well as the increased efficiency of the SN after negative mood induction (compared to positive mood induction) were able to fully explain the effect of mood induction on reaction times to negative words in the emotional Stroop task (i.e. increased reaction times after negative compared to positive mood induction; see also Figure 3).

Discussion

The overall aim of the present study was to test a potential mediating role of network efficiency in connecting affective stimulation with subsequent mood-congruent processing of novel stimuli. For this purpose we investigated mood effects on network efficiency of the SN, CEN and DMN and reaction times in response to emotional stimuli (aim 1). Subsequently we tested whether these changes in networks efficiency were related to reaction times in response to emotional stimuli (aim 2) and finally whether network efficiency mediated the relation between mood induction and reaction times in response to emotional stimuli (aim 3).

As a first main result and in accordance with our hypotheses and previous results, converging evidence from both the mood induction manipulation and subjective mood ratings pointed to a central valence-dependent dynamic of increasing SN efficiency (E_{SN}) and a decrease in the efficiency of the CEN (E_{CEN}) with increasing negative mood. This finding is especially interesting since the SN and CEN are two closely related intrinsic networks that interact dynamically to guide interactions with the external environment. Within this interaction both networks have been described to take over complementary roles in cognitive control (see for example Corbetta *et al.*, 2008). While the CEN has been especially associated with goal-directed processes, and biasing attentional and perceptual processes based on pre-existing information (Corbetta and Schulman (2002); Dosenbach *et al.*, 2008), the SN is usually connected to stimulus-driven processes, detecting salient cues in the environment, interrupting ongoing activity in the CEN (Corbetta *et al.*, 2008) and coordinating neural resources in response to such cues (Uddin, 2014; Seeley *et al.*, 2007).

Interestingly, shifts in the balance of these two networks have been proposed to be a central feature in the adaptation to aversive environments. In this context, downregulating the CEN and upregulating the SN would bias the interaction with the environment toward a facilitated detection of and response to potentially threatening stimuli at the cost of pursuing long-term goals and integrating pre-existing information (Hermans *et al.*, 2014, see also van Oort *et al.*, 2017). Accordingly shifts in the efficiency of the SN and CEN could facilitate the processing of negative information and take over a central role in in enabling congruency processes connected to negative emotional states.

Indeed, in line with previous results (Gilboa-Schechtman *et al.*, 2000), we found negative mood (and negative compared to positive mood induction) to increase the reaction times in response to negative words in the emotional Stroop task. Furthermore, both SN and CEN efficiency were related to reaction times to negative words. While E_{SN} was positively associated with increased reaction times to negative words, increases in E_{CEN} were connected to reduced reaction times to negative words.

Finally testing the specific role of those shifts in network efficiency, we were able to show that both fully mediated the relationship between mood manipulation and reaction times in response to negative words. Accordingly there was a significant indirect effect from negative mood induction, over increasing E_{SN} and decreasing E_{ECN} to facilitating the processing of negative stimuli that could fully explain the direct effect of negative mood induction on the reaction times of negative words.

The observed effects of shifts in network efficiency were limited to negative words. Accordingly, in contrast to supporting a general hypervigilant state, increased E_{SN} and decreased E_{CEN} seem to have a valence-specific effect, facilitating the processing of negative but not positive words. More in general, while successfully inducing positive mood, we did not observe a mood congruency effect on positive words. One possible explanation for these results could be that the fMRI environment added too much noise to the behavior in the task to detect the mood-congruency effect on positive words. Indeed these effects were, in previous studies (see Gilboa-Schechtman *et al.*, 2000), much smaller compared to the negative congruency effects and could be more susceptible to effects of a noisy and uncomfortable environment (see also van Maanen *et al.*, 2016). Another possible explanation could be that positive mood congruency effects are more complex than simply the enhancement of positive information. Indeed there are some indications that the mood-congruent enhancement of the processing of positive emotional information might depend on additional affect dimensions, such as the reward character of the stimuli (Tamir and Robinson, 2007) or the self-relatedness if the information (Grol *et al.*, 2012). Furthermore positive affect might be more generally connected to an increased broadening of attention as well as increased cognitive flexibility (Vanlessen *et al.*, 2016; Fredrickson *et al.*, 2001). Consequently not finding any relationship with positive words has to be interpreted carefully. Future studies specifically designed to detect effects on the processing of positive stimuli are needed to further clarify this relationship.

In contrast to the SN and CEN we did not find any relation between DMN efficiency and mood induction or subjective valence ratings. This finding is difficult to interpret given the inconsistent literature concerning the DMN after aversive/negative stimulation showing no effect (for example Eryilmaz *et al.*, 2011), decreased connectivity (for example Harrison *et al.*, 2008) or increased connectivity (for example Clemens *et al.*, 2017) within the DMN. Possible explanations might be that the DMN is sensitive to aspects of the specific content of the mood induction, like self-relevance or social context (for a discussion see van Oort *et al.*, 2017) or that organizational differences of the DMN in context of emotion are rather representing trait differences (for example Perkins *et al.*, 2015) that are not captured with our strictly within-subject design. However, given the important role of the DMN in affective disorders (see for example Kaiser *et al.*, 2015) and the possible involvement of the DMN in aberrant emotional processing (Ho *et al.*, 2015) elucidating the role of the DMN in emotion and emotional behavior will clearly be another important future direction.

In conclusion we found that increased efficiency of the SN and decreased efficiency of CEN after affective stimulation are linking negative mood induction to subsequent mood-congruent behavioral changes to negative emotional information. This demonstrates that transient affect-dependent shifts in network organization are functional underlying core aspects of the emotional response. Accordingly our findings are pointing to transient and sustained shifts in macro-scale neural networks being an essential part of the emotional response driving the interaction between affective experience and environment.

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Supplementary data

Supplementary data are available at SCAN online.

Conflict of interest

None declared.

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