Prestimulus Default Mode Activity Influences Depth of Processing and Recognition in an Emotional Memory Task

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Abstract: Low self-referential thoughts are associated with better concentration, which leads to deeper encoding and increases learning and subsequent retrieval. There is evidence that being engaged in externally rather than internally focused tasks is related to low neural activity in the default mode network (DMN) promoting open mind and the deep elaboration of new information. Thus, reduced DMN activity should lead to enhanced concentration, comprehensive stimulus evaluation including emotional categorization, deeper stimulus processing, and better long-term retention over one whole week. In this fMRI study, we investigated brain activation preceding and during incidental encoding of emotional pictures and on subsequent recognition performance. During fMRI, 24 subjects were exposed to 80 pictures of different emotional valence and subsequently asked to complete an online recognition task one week later. Results indicate that neural activity within the medial temporal lobes during encoding predicts subsequent memory performance. Moreover, a low activity of the default mode network preceding incidental encoding leads to slightly better recognition performance independent of the emotional perception of a picture. The findings indicate that the suppression of internally-oriented thoughts leads to a more comprehensive and thorough evaluation of a stimulus and its emotional valence. Reduced activation of the DMN prior to stimulus onset is associated with

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deeper encoding and enhanced consolidation and retrieval performance even one week later. Even small prestimulus lapses of attention influence consolidation and subsequent recognition performance. *Hum Brain Mapp* 37:924–932, 2016. © 2015 Wiley Periodicals, Inc.

Key words: fMRI; DMN; encoding; memory; pre-stimulus activity

INTRODUCTION

There is extensive evidence that encoding of new information and whether strong or weak memory traces are formed is modulated by the amount of attention [Craik et al., 1996], by cognitive control functions [Reas and Brewer, 2013], by emotional valence [Buchanan and Adolphs, 2002], and by depth of processing. The elaboration of stimulus material is crucial for memory formation even if the encoding is incidental [Craik and Tulving, 1975]. Emotional contents are remembered better than non-emotional contents [Buchanan and Adolphs, 2002]. Thus, even with incidental encoding, differences at encoding, consolidation or retrieval enhanced participants' long-term retention for the negative relative to the neutral information [Kensinger and Corkin, 2003]. According to neuroimaging studies, the amygdala is the crucial structure for emotional memory [McGaugh, 2000], while recognition memory is associated with encoding-dependent modulation of activity in frontal brain regions [Brewer et al., 1998; Buckner et al., 2001] and the medial temporal lobes (MTLs) [Stark and Okado, 2003; Squire et al., 2004], which comprise a complex network of interconnected nuclei including the amygdala, hippocampus, and surrounding structures. Studies observed that the amount of MTL activity during the incidental encoding of stimuli predicted the performance in a subsequent recognition test [Brewer et al., 1998; Wagner et al., 1998]. This is in line with findings of a further fMRI study showing that regions along the inferior frontal gyrus are higher activated while encoding later remembered words compared with not-remembered words [Buckner et al., 2001]. Thus, the level of activity within the frontal cortex during encoding predicts subsequent consolidation [Brewer et al., 1998; Buckner et al., 2001; Kelley et al., 1998; Wagner et al., 1998]. Summarized, it seems that the frontal lobes as well as the MTLs are crucially involved in forming memories but the mechanisms of their cooperation and the underlying networks remain unanswered [Fransson and Marrelec, 2008;

Owen et al., 2005]. Furthermore, recent studies indicate that the default mode network (DMN) activity influences emotional perception and recognition [Buckner et al., 2008]. In healthy subjects the DMN is involved in self-referential mental explorations [Andrews-Hanna et al., 2010; Gusnard et al., 2001; van Buuren et al., 2010] including mind-wandering [Mason et al., 2007], remembering the past and envisioning future events [Buckner and Carroll, 2007; Buckner et al., 2008; Northoff and Bermpohl, 2004; Spreng et al., 2009]. Mason et al. [2007] proposed that mind-wandering represents a psychological “baseline state” supported by activity in the DMN that only emerges when the brain is not occupied by any task that requires attention. Therefore, during tasks with high cognitive demand such as encoding of stimuli, the DMN regions show deactivation because of efficient suppression of internally-oriented thoughts [Daselaar et al., 2004, 2009; McKiernan et al., 2003] and an activation of the DMN during retrieval of past episodic events [Huijbers et al., 2011]. However, van Buuren et al. [2010] related activity in the DMN to self-referential processing, such as thinking about one's preferences and personality traits. The results of their study support the functional specialization within the DMN and its involvement in different subfunctions of self-referential processing. Besides brain activity during stimulus encoding, an influence of prestimulus activation patterns on subsequent performance has been demonstrated [Galli et al., 2012; Otten et al., 2006; Weissman et al., 2006]. These findings indicate that brain activity just before a stimulus, predicted whether the stimulus would be remembered in a subsequent memory test [Adcock et al., 2006; Mackiewicz et al., 2006; Padovani et al., 2011]. Weissman et al. [2006] demonstrated that momentary lapses in attention are associated with reduced task-induced deactivation of the DMN before stimulus presentation, which can further lead to erroneous responses [Eichele et al., 2008]. Summarized, there is evidence that being focused in the external environment is associated with reduced DMN activity and leads to open mind, which enhances concentration and promotes comprehensive stimulus evaluation including emotional categorization. This, in turn, leads to deeper stimulus processing and better long-term retention [Buchanan and Adolphs, 2002; Otten et al., 2006; Buckner, 1999]. However, the interactions of these components have not yet been studied in detail.

The aim of the present fMRI experiment was to explore the influence of DMN activity on the emotional evaluation of pictures and the pictures' mnemonic fate as assessed through

Abbreviations

DMN	default mode network
EPI	echo planar imaging
FOV	field of view
fMRI	functional magnetic resonance imaging
MDL	maximum description length
MDEFT	modified driven equilibrium fourier transformation

recognition one week later. Thirty-one subjects were exposed to 80 pictures of different emotional valence during functional magnetic resonance imaging (fMRI) and asked to complete an online recognition task one week later to test recognition performance of the incidentally encoded pictures.

METHOD

Subjects

Thirty-one right-handed healthy subjects were recruited via advertisement. Exclusion criteria included previous history of neurologic or psychiatric disorders, history of head injury, acute or chronic medical conditions, psychotropic drug treatment, current drug or alcohol abuse, or any contraindication to MRI (metallic objects, pregnancy). After complete description of the study to the subjects, written informed consent was obtained. The study was approved by the ethics committee of the Canton of Bern, Switzerland (Nr. 161/07). Out of the thirty-one subjects that were tested in the MR, seven subjects had to be excluded from the analysis because of missing data of the online experiment. The final sample consisted of 24 subjects (11 women, 13 men, mean age $\pm$ SD 27.16 $\pm$ 5.59 years; age range 21–46 years).

fMRI-Task

The fMRI-task was an adapted version of the picture task published by Rasch et al. [Rasch et al, 2009]. It consisted of 80 photographs of four emotional categories (negative, neutral, animal (positive), spider (disgust)), partly selected from the International Affective Picture System (IAPS; [Lang et al., 2005]). To assess the emotional valence each picture was rated on a scale ranging from 1 (no valence) to 4 (maximal valence) during the scanning session. The pictures were presented for 5 seconds followed by a fixation cross for 1 second and the rating with a maximal time range of 3 seconds. Each block (picture, fixation, rating) lasted 9 seconds and was randomly jittered with 3–5 seconds to the next block. The stimulus presentation and response registration was performed using E-Prime 2.0 (Psychology Software Tools Inc., Pittsburgh, USA). For the statistical analysis, we dichotomized the responses into the categories “NOemotion” vs. “emotion”. These categories were based on the subjects’ ratings of the emotional valence of each picture. “NOemotion” consists of pictures that were evaluated with the value 1 (no emotional valence), while “emotion” category consists of pictures evaluated with the values 2, 3 or 4 (little to maximum emotional valence) on the Self-Assessment Manikin (SAM) scale [Lang et al., 2005].

Recognition Task

The recognition task was an online experiment, which presented the same 80 photographs of the fMRI-task and

80 additional photographs of the same four categories (negative, neutral, animal (positive), spider (disgust)). The photographs were presented in a randomized order. The subjects were asked to rate each picture regarding recognition.

Data Acquisition

The experiments were performed at the Department of Neuroradiology of the University Hospital of Bern between 8 am and 10 am on a 3T Siemens Trio unit (Erlangen, Germany). Prior to the MRI experiment, participants received a short instruction about the picture task and were asked to absolve a short exercise on the computer to become familiar with the ratings. fMRI data was acquired during the performance of the picture task with a BOLD T2*-weighted echo planar imaging (EPI) sequence (37 slices. TR/TE = 2500/30 ms, flip angle = 90°, slice thickness = 3 mm, inter slice gap thickness = 0 mm, matrix size = 64 $\times$ 64, field of view (FOV) = 230 mm $\times$ 230 mm, 579 volumes in 24:14 min. In addition, high-resolution T1-weighted structural images were obtained with a 3D Modified Driven Equilibrium Fourier Transformation (MDEFT) sequence [Deichmann et al., 2003]: 176 sagittal slices, TR/TE = 7.92/2.48 ms, flip angle = 16°, matrix size = 256 $\times$ 256, FOV = 256 mm $\times$ 256 mm, yielding a nominal isotropic resolution of 1 mm³ (i.e. 1 mm $\times$ 1 mm $\times$ 1 mm), 13:43 min total acquisition time. After the scanning session participants were asked to absolve the online experiment one week later on a private computer with internet access.

Behavioral Data Analysis

Statistical analyses were conducted with the statistical software package SPSS version 22. The recognition performance was analyzed according to the Signal Detection Theory (SDT) [Banks, 1970]. The discrimination sensitivity (d') was calculated (z (hit rate) – z (false alarm rate)) for every single subject and all four picture categories (neutral, negative, animal, spider) separately as well as across all categories. Zero values were set to 0.01. To check if the d' value is significantly greater than 0, which means significantly above chance level, the differences were analyzed with a one-sample t -test and test value of 0. All behavioral ratings were first tested for non-normality by using the Shapiro–Wilk statistic. The null hypothesis is that the rating values follow a normal distribution. All rating variables remembered ($W = 0.95$; $P = 0.31$) and non-remembered ($W = 0.94$; $P = 0.19$) were not different from a normal distribution. To assess differences between remembered vs. non-remembered stimuli and emotional vs. non-emotional ratings a paired-samples t -test was conducted. Interaction effects between recognition and emotional rating were computed with paired-samples t -test and a repeated measure ANOVA with recognition and emotion as within-subject

factors. A probability of less than 0.05 was considered statistically significant.

fMRI Data Analysis

The preprocessing and analysis of the fMRI data was performed using Statistical Parametric Mapping, version 8 (SPM8) software (Wellcome Department of Imaging Neuroscience, University of London). To allow for T1 equilibration effect, the first two volumes of the functional data were discarded. The preprocessing of the images included slice scan time correction, realignment, co-registration, normalization to the Montreal Neurological Institute (MNI) coordinate system and spatial smoothing with an 8-mm full width at half maximum Gaussian kernel. Two analyses were performed on the MRI data, (i) the brain activation pattern during encoding of subsequently remembered stimuli vs. non-remembered stimuli, (ii) the brain activity within the DMN immediately before presentation of subsequently remembered vs. non-remembered stimuli.

Brain activation during stimulus encoding

A design matrix containing two predictors coding for the time points of stimulus encoding of afterwards remembered respectively non-remembered pictures was created. Stimulus category (remembered vs. non-remembered) was defined by the subsequent online recognition task and stimuli were combined across emotional valence categories. These two predictors were convolved with a double gamma hemodynamic response function to account for delays in BOLD responses. Voxel-wise statistics and contrasts between the two predictors were computed. Significance levels were set at $P < 0.05$ and corrected for multiple comparisons using a cluster-size statistical threshold estimated by Monte-Carlo simulations [Forman et al., 1995]. Activity in areas showing differences between encoding of remembered vs. non-remembered stimuli was assessed by extracting the GLM beta-values from the brain regions that revealed significant contrast between the two predictors.

Pre-stimulus DMN activity

Pre-stimulus DMN activity was extracted from the data by means of Independent component analysis (ICA): To identify the Default Mode Network, and its ongoing intrinsic fluctuations, a concatenated group level ICA approach was applied using the Group ICA (GICA) of fMRI Toolbox (GIFT) [Calhoun et al., 2001; Esposito et al., 2005]. The individual BOLD signal time series were first demeaned and a gray matter (GM) mask was applied before running the ICA infomax algorithm [Jann et al., 2015]. Next we estimated the optimal number of component that best describes the data using the maximum description length (MDL) criterion. A total of 28 components were found to be the optimal number of components. The component representing the default mode

network (DMN) was identified by visual comparison to published distributions [Beckmann et al., 2005; Smith et al., 2012] as well as by assessing the similarity between components and predefined template network maps. Individual subject DMN maps and activity time courses were then computed using back-reconstruction with GICA. The group maps and the subject maps were stored as z-maps. To display the DMN a one-sample *t*-test across individuals' DMN z-maps was performed and thresholded at $P(\text{FEW}) < 0.01$. The prestimulus DMN activity was extracted for each subject from its normalized DMN time course. Prestimulus periods (2.5 sec) for each trial of remembered respectively nonremembered stimuli were defined by creating two new predictors coding for this pre-stimulus periods in either category. These predictors were again convolved with a HRF. Individual mean prestimulus DMN activity for remembered and non-remembered stimuli was then computed by multiplying the participant's normalized DMN time-course with either predictor (binarized applying a threshold of 2 standard deviations above the mean).

Statistical Analyses

Brain activity for either encoding (ROI individually averaged beta-values) respectively prestimulus DMN activity was analyzed using *t*-tests to assess differences between remembered vs. non-remembered stimuli. Furthermore, we computed the relation between the average prestate DMN activity and subsequent stimulus-induced activity (separately for remembered and non-remembered). This was done for two ROIs in the temporal lobe as revealed by analysis (i) above. We then compared the correlation coefficients between the two categories of stimuli using activity using Fisher's test to evaluate whether prestate DMN activity differentially influences subsequent stimulus related activity in the two conditions. Finally, interaction effects between DMN activation before stimulus onset, emotional rating and recognition were computed with *t*-test and a repeated measure ANOVA with recognition and emotion as within-subject factors. A probability of less than 0.05 was considered statistically significant.

RESULTS

Recognition performance: Analysis of the recognition rate showed that the recognition performance was above chance level according to the signal detection theory (SDT) [Banks, 1970] and that animal (positive) ($M(d') = 1.33$), negative ($M(d') = 1.26$) and spider (disgust) ($M(d') = 0.74$) pictures were better recognized than neutral pictures ($M(d') = 0.65$) (for detailed information see Supporting Information Tables S1, S2; Figs. S1, S2).

TABLE I. Independent component analysis (ICA)

Region	BA	Coordinates (SD)			Cluster size (voxel)	I-Test of z-ICA values
		x	y	z		
Anterior cingulate	n.a.	-2.1 (6.3)	46.2 (8.3)	-6.4 (6.2)	1,097	14.3
Posterior cingulate	23	0.1 (10.1)	-50.0 (12.4)	29.3 (15.9)	11,010	30.4
Inferior parietal lobe, left	39	-38.0 (26.7)	-66.2 (3.2)	42.7 (3.9)	2,347	23.3
Inferior parietal lobe, right	39	46.0 (31.5)	-64.0 (5.1)	36 (5.9)	1,772	21.2

The ICA analysis identified the default mode network (DMN). The statistical map of the DMN was corrected for multiple comparisons (FEW < 0.01)

Note. BA = Brodmann Area; SD = standard deviation.

Emotional Rating

Results of the ANOVA show significant main effects of recognized vs. non-recognized ($F(1,22)=8.1, P < 0.009$) and emotional vs. non-emotional ($F(1,22)= 24.57, P < 0.001$) pictures as well as a significant interaction effect ($F(1,22) = 9.18, P < 0.006$). Paired-samples t -tests were conducted to elucidate differences for recognized vs. non-recognized and emotional vs. non-emotional pictures. Five of the seven tested contrasts were statistically significant ($P \leq 0.05$ (two-tailed)): "recognition" & "emotion" and "recognition" & NOemotion" pictures ($t(22) = -2.74, P < 0.02$), "recognition" & "emotion" and "NOrecognition" & emotion" pictures ($t(22) = 4.72, P < .001$), "NOrecognition" & "emotion" and "recognition" & NOemotion" pictures ($t(22) = -9.6, P < 0.001$), "NOrecognition" & "emotion" and "recognition" & emotion" pictures ($t(22) = -4.72, P < 0.001$), "NOrecognition" & "emotion" and "NOrecognition" & NOemotion" pictures ($t(22) = -6.31, P < 0.001$).

The two contrast between "NoEmotion" & "recognition" vs. "NOemotion" & "NOrecognition" ($t(22)=0.642, P=0.52$) and "recognition" & "emotion" and "NOrecognition" & NOemotion" pictures ($t(22) = -1.59, P = 0.13$) were not significant ($t(22)=0.642, P = 0.52$ (two-tailed)).

Subsequent Memory Effect

A General Linear Model (GLM) was conducted to examine differences of brain activation pattern in memory relevant brain regions during encoding of recognized and not recognized pictures. Analysis show higher activation in the right fusiform gyrus ($t(23)=5.18; P < 0.0001$), cuneus ($t(23)=4.32; P < 0.0001$), superior temporal gyrus ($t(23)=4.79; P < 0.0001$), posterior cingulate gyrus ($t(23)=3.87; P < 0.0001$), superior frontal gyrus ($t(23)=3.93; P < 0.0001$) and middle temporal gyrus ($t(23)=5.11; P < 0.0001$).

Figure 1.

The default mode network (DMN) identified by independent component analysis (ICA). ICA analysis of pretrial rest activity (2.5 seconds before stimulus encoding (prestate)) identified the default mode network with synchronized activation in the anterior- and posterior- cingulate and the bilateral parietal lobes (areas indicated in hot-color). [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

TABLE II. Mean DMN activation before stimulus onset between the recognition and emotion conditions

	Recognition_emotion		NOrecognition_NOemotion	
	<i>t</i>	<i>p</i>	<i>t</i>	<i>p</i>
Recognition_NOemotion	-10.03	0.0001	4.41	0.001
NOrecognition_emotion	4.41	0.001	-8.57	0.0001

N = 24

The category 'NOemotion' consists of pictures that were evaluated with the value 1 ('no arousal'), the 'emotion' category of pictures evaluated with the values 2, 3 or 4 (little to maximum arousal) on the Self-Assessment Manikin (SAM) scale [Lang et al., 2005].

Paired-samples *t*-test was conducted to elucidate differences on the DMN activation for recognized vs. non-recognized and emotional vs. non-emotional pictures. Two of the four tested contrasts of mean DMN activation 2.5 seconds before stimulus onset was statistically significant ($P \leq 0.01$)

0.0001) during encoding of subsequent recognized pictures as compared with subsequent not-recognized pictures (Supporting Information Table S3, Fig. S3).

Default Mode Network Activation

ICA analysis of pre-trial activity identified the default mode network (Table I and Fig. 1) with synchronized activation in the posterior cingulate (z -ICA=8.05), the anterior cingulate (z -ICA= 7.51) and the bilateral inferior parietal lobes (right z -ICA=2.23, left z -ICA=2.87). A General Linear Model was conducted to examine differences between DMN activation 2.5 seconds prior of encoding of later recognized and not-recognized pictures. Results show significant synchronized BOLD time course in the DMN 2.5 sec before the encoding of pictures ($t(23) = -12.58$, $P < 0.0001$ (two-tailed)), which were recognized one week later.

A paired-samples *t*-test was conducted to elucidate differences on the DMN activation for recognized vs. non-recognized and emotional vs. non-emotional pictures. Each of the four tested contrasts of mean DMN activation before stimulus onset was statistically significant ($p \leq .01$) (Table II and Fig. 2).

Because an interaction effect requires a parametric routine, the data was additionally analyzed with a 2×2 (Emotion [yes, no] $\times$ Recognition [yes, no]) repeated measures ANOVA. The analysis indicated a main effect of recognition ($F(1,22) = 15.75$, $P < 0.001$), a significant main effect emotion ($F(1,22) = 5.1$, $P < 0.001$) and no significant recognition $\times$ emotion interaction effect ($F(1,22) = 0.67$, $P = 0.88$), showing that recognition performance and emotional perception together were influenced by the strength of DMN activation.

Analysis of the means revealed a significant difference between "NOrecognition" & "emotion" and "recognition" & NOemotion" pictures ($t(23) = 8.33$, $P < 0.022$), a significant difference between "NOrecognition" & "emotion" and "NOrecognition" & "NOemotion" pictures ($t(23) = -8.58$, $P < 0.001$), a significant difference between "recognition" & "emotion" and "recognition" & NOemotion" pictures ($t(23) = -10.04$, $P < 0.001$), a significant difference between

"recognition" & "emotion" and "NOrecognition" & "emotion" pictures ($t(23) = 4.41$, $P < 0.001$) and a significant difference between "recognition" & "NOemotion" and "NOrecognition" & "NOemotion" pictures ($t(23) = 4.42$, $P < 0.001$), and a significant difference between "recognition" & "emotion" and "NOrecognition" & "NOemotion" pictures ($t(23) = -2.44$, $P = 0.03$), (Fig. 2)

Figure 2.

Proceeding default mode network (DMN) activation of the recognition and emotion condition before stimulus onset. The central box shows the data between 25th and 75th quartiles, with the median represented by the line. The whiskers extend from the upper and lower quartiles to a distance of 1.5 interquartile range (IQR). Crosses represent the outliers over 3 IQR below the 25th or above the 75th quartile. The category 'NOemotion' consists of pictures that were evaluated with the value 1 ('no arousal'), the 'emotion' category of pictures evaluated with the values 2, 3 or 4 (little to maximum arousal) on the Self-Assessment Manikin (SAM) scale [Lang et al., 2005]. ANOVA showed significant main effects of recognition ($F(1,22) = 15.75$, $P < 0.001$) and a significant main effect emotion ($F(1,22) = 5.1$, $P < 0.001$). [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

Relation Between Prestate Activity and Stimulus-Induced Activity

The relation between the average pre-state DMN activity in each subject and the subsequent stimulus induced activity did not reveal a significant correlation, however the observed relation was at trend level, suggesting a general association between prestate-DMN activity and activity in task related areas during task execution (Supporting Information Fig. S4). Furthermore, the relation was opposite for remembered and non-remembered stimuli, respectively, as would be expected. Comparing the correlation coefficients, we found that both ROI exhibit significantly different correlations under the assumption that the correlation for the two conditions should have opposite direction: Left temporal ROI difference between correlations $z = -1.73$ $P(\text{one-tailed}) = 0.042$; Right temporal ROI difference between correlations $z = -2.15$ $P(\text{one-tailed}) = 0.016$.

DISCUSSION

In the present study, we investigated the brain activity preceding and during the encoding of pictures of different emotional valence and their subjective rating on a later recognition performance. Results indicate that a high activity of the DMN just before encoding leads to a slightly poorer recognition performance and a less emotional perception of a picture. DMN activity preceding not recognized and not emotional pictures differed from either recognized or emotional pictures. Furthermore, we found significantly higher activation in the MTL during encoding of later recognized pictures and an enhanced recognition for emotional pictures compared to neutral pictures. The results support our hypothesis, that low self-referential activity is associated with low activity in the default mode network (DMN) promoting better concentration, which leads to deeper encoding and increases learning and subsequent retrieval. Thus, the suppression of internally-focused thoughts (reduced DMN activity) leads to enhanced concentration, more comprehensive stimulus evaluation including emotional categorization and deeper stimulus processing promoting better long-term retention over one whole week. The results are further supported by studies showing that emotional pictures are better recognized compared with neutral pictures [Buchanan and Adolphs, 2002; Hamann, 2001; Kensinger and Corkin, 2003; Reisberg and Heuer, 1992] and studies revealing higher brain activation in MTL while encoding subsequent recognized pictures [Buckner, 1999; McGaugh, 2000; Stark and Okado, 2003]. The fact that emotional pictures are remembered better than neutral pictures suggests a more differentiated encoding process for emotional stimuli leading to a stronger memory trace (or enhanced/deeper consolidation) [Buchanan and Adolphs, 2002; Kensinger and Corkin, 2003; Reisberg and Heuer, 1992]. Especially the amygdala influences other brain regions such as the hip-

pocampus, striatum, and neocortex [Cahil and McGaugh, 1998] whenever the nature of the encoded material is perceived as emotional. This is supported by the present findings showing a higher activation in the right amygdala, parahippocampal gyrus, hippocampus, fusiform gyrus and inferior parietal lobe, in the medial frontal and anterior cingulate gyrus and the precuneus for remembered versus forgotten pictures.

In addition to the brain activation during encoding, the present study yielded a synchronized neural network shortly before stimulus onset along the medial frontal gyrus, the posterior cingulate, and the lateral parietal cortices constituting the DMN [Buckner et al., 2008]. Further analysis of the DMN revealed a connection between its activation preceding stimulus encoding and subsequent recognition performance. This connection has been demonstrated in different studies investigating DMN activation at the time of encoding [Greicius et al., 2009; Raichle et al., 2001]. Only a few recent studies investigated the question whether activation patterns shortly before stimulus onset could predict if the stimulus would be subsequently remembered [Adcock et al., 2006; Galli et al., 2012; Otten et al., 2006]. The present findings revealed that reduced DMN activation preceding stimulus encoding is associated with better recognition performance. However this was independent of the emotional valence of the stimuli. Preceding DMN activity for not recognized stimuli rated as emotional was comparable to the recognized stimuli and differed from the non-emotional not recognized stimuli, thus suggesting that being in a state of preparedness for encoding as evidenced by reduced activation of the DMN prior to stimulus onset leads to a qualitatively better encoding. The difference between low prestimulus DMN activation and perceived emotionality of the pictures and high prestimulus DMN activation and the perception of the pictures as neutral can be understood by taking into account that the DMN is highly activated during mental explorations referenced to oneself [Buckner et al., 2008; Gusnard et al., 2001; van Buuren et al., 2010] and mind-wandering [Mason et al., 2007]. During rumination, the hippocampus and the memory system was activated and therefore not available during the presentation of the pictures, which should be encoded. Therefore, strong DMN activation has negative consequences for learning because the individual is engaged in internally focused tasks. Nevertheless, the findings accentuate the crucial role of DMN activation preceding incidental encoding and the role of emotional perception and increase the scientific knowledge of the DMN functioning and its impact on memory formation. Furthermore, the results provide relevant evidence for declarative learning and recognition theories. To optimize learning, it is important to have a free mind: the results indicate that for best learning outcomes one should be focused on the external environment without being engaged in a task to be ready to process new information. Thus, before starting learning one should

solve problems or practice meditation or relaxation to free the mind actively. The findings might further have clinical impact for psychiatric disorders with deficits in encoding and emotional evaluation of stimuli (e.g. schizophrenia and depression), which might be related to changes in DMN activation respectively an impaired ability to deactivate it before stimulus perception and processing. Rumination or self-referential thinking and the inability to stop it, is a core symptom of depression which is often treated with psychotherapy or antidepressant medication. Goal of the treatment is that patients learn strategies to stop rumination which in turn is associated with better well-being. Summarized, the findings give new insight in the neuronal correlates of learning and recognition processes as well as direct input for the optimization of learning strategies and have clinical relevance.

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