

Pre-stimulus default mode activity influences depth of processing and recognition in an emotional memory task

Leila M. Soravia^{*1}, Joëlle S. Witmer^{*1,4}, Simon Schwab¹, Masahito Nakataki³, Thomas Dierks¹, Roland Wiest², Katrin Henke⁴, Andrea Federspiel^{1,‡}, Kay Jann^{1,5,‡¶}

¹*Department of Psychiatric Neurophysiology, University Hospital of Psychiatry, University of Bern, Bolligenstrasse 111, 3000 Bern, Switzerland*

²*Department of Diagnostic and Interventional Neuroradiology, Inselspital, University Hospital of Bern, Freiburgstrasse 4, 3010 Bern, Switzerland*

³*Department of Psychiatry, The University of Tokushima, Japan*

⁴*Department of Psychology, University of Bern, Fabrikstrasse 8, 3012 Bern, Switzerland*

⁵*Brain Mapping Center, Department of Neurology, University of California Los Angeles, 660 Charles E Young Dr South, 90095 Los Angeles, CA, USA*

*shared first authorship

‡shared senior authorship

¶Correspondence and requests for material should be addressed to:

Kay Jann, Ahmanson-Lovelace Brain Mapping Center, Department of Neurology, University of California Los Angeles, 660 Charles E Young Dr South, 90095 Los Angeles, CA, USA.
Phone: 310-206-2200; Fax: 310-794-7406; Email: kayjann@ucla.edu

The number of text pages: 11; number of figures: 2; number of tables: 2

The number of words in the abstract: 226; total number of words in the paper: 3258

Key Words: fMRI, DMN, encoding, memory, pre-stimulus activity

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 – 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 deeper encoding and enhanced consolidation and retrieval performance even one week later. Even small pre-stimulus lapses of attention influence consolidation and subsequent recognition performance.

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(1), by cognitive control functions (2), by emotional valence(3) and by depth of processing. The elaboration of stimulus material is crucial for memory formation even if the encoding is incidental (4). Emotional contents are remembered better than non-emotional contents (3). Thus, even with incidental encoding, differences at encoding, consolidation or retrieval enhanced participants' long-term retention for the negative relative to the neutral information (5). According to neuroimaging studies, the amygdala is the crucial structure for emotional memory (6), while recognition memory is associated with encoding-dependent modulation of activity in frontal brain regions(7, 8) and the medial temporal lobes (MTLs) (9, 10), 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 (11, 12). 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 to not-remembered words (8). Thus, the level of activity within the frontal cortex during encoding predicts subsequent consolidation (7, 8, 13, 14). 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 (15, 16). Furthermore, recent studies indicate that the default mode network (DMN) activity influences emotional perception and recognition (17). In healthy subjects the DMN is involved in self-referential mental explorations (18-20) including mind-wandering (21), remembering the past and envisioning future events(17, 22-24). Mason and colleagues (21) 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 due to efficient suppression of internally-oriented thoughts (25-27)and an

activation of the DMN during retrieval of past episodic events (28). However, van Buuren and colleagues (20) 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 sub-functions of self-referential processing. Besides brain activity during stimulus encoding, an influence of pre-stimulus activation patterns on subsequent performance has been demonstrated (29-31). These findings indicate that brain activity just before a stimulus, predicted whether the stimulus would be remembered in a subsequent memory test (32-34). 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 (35). 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 (3, 29, 36). 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 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, 7 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. (37). It consisted of 80 photographs of four emotional categories (negative, neutral, animal (positive), spider (disgust)), partly selected from the International Affective Picture System (IAPS; (38)). 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 [38].

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 x 64, field of view (FOV) = 230 mm x 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 (39): 176 sagittal slices, TR/TE = 7.92/2.48 ms, flip angle = 16°, matrix size = 256 x 256, FOV = 256 mm x 256 mm, yielding a nominal isotropic resolution of 1 mm³ (i.e. 1 mm x 1 mm x 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.

Field Code Changed

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) (40). 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. To assess differences between remembered vs. non-remembered stimuli and emotional vs. non-emotional ratings a nonparametric Wilcoxon-test was conducted. Interaction effects between recognition and emotional rating were computed with pairwise comparisons

Wilcoxon-tests and a repeated measure ANOVA with recognition and emotion as within-subject factors. A probability of $< .05$ 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, coregistration, 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.

i) 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 $p < .05$ and corrected for multiple comparisons using a cluster-size statistical threshold estimated by Monte-Carlo simulations (41). 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.

ii) 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

Field Code Changed

fluctuations, a concatenated group level ICA approach was applied using the Group ICA (GICA) of fMRI Toolbox (GIFT) (42, 43). The individual BOLD signal time series were first demeaned and a gray matter (GM) mask was applied before running the ICA infomax algorithm (44). 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 (45, 46) as well as by assessing the similarity between components and predefined template network maps. Individual subject DMN maps and activity timecourses 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 pre-stimulus DMN activity was extracted for each subject from its normalized DMN time course. Pre-stimulus periods (2.5sec) for each trial of remembered respectively non-remembered 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 pre-stimulus DMN activity for remembered and non-remembered stimuli was then computed by multiplying the participant's normalized DMN timecourse with either predictor (binarized applying a threshold of 2 standard deviations above the mean).

Interaction of brain activity and behavioral variables: Brain activity for either encoding (ROI individual averaged beta-values) respectively pre-stimulus DMN activity was analyzed using nonparametric Wilcoxon-tests to assess differences between remembered vs. non-remembered stimuli. Furthermore, interaction effects between DMN activation before stimulus onset, emotional rating and recognition were computed with pairwise comparisons Wilcoxon-tests and a repeated measure ANOVA with recognition and emotion as within-subject factors. A probability of $< .05$ was considered statistically significant.

Field Code Changed

Field Code Changed

Field Code Changed

Field Code Changed

Results

Recognition performance: Analysis of the recognition rate showed that the recognition performance was above chance level according to the Signal Detection Theory (SDT) (40) 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 supplements Tables S1, S2; Figures S1, S2).

Emotional rating: A Wilcoxon test was conducted to elucidate differences for recognized vs. non-recognized and emotional vs. non-emotional pictures. Three of the four tested contrasts were statistically significant ($p \leq .05$ (two-tailed)). The contrast between “NoEmotion” & “recognition” vs. “NOemotion” & “NOrecognition” was not significant ($U=-0.227$, $p=.82$ (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 ($t(23) = 5.18$; $p < .0001$), cuneus ($t(23) = 4.32$; $p < .0001$), superior temporal gyrus ($t(23) = 4.79$; $p < .0001$), posterior cingulate gyrus ($t(23) = 3.87$; $p < .0001$), superior frontal gyrus ($t(23) = 3.93$; $p < .0001$) and middle temporal gyrus ($t(23) = 5.11$; $p < .0001$) during encoding of subsequent recognized pictures as compared to subsequent not-recognized pictures (see supplements Table S3, Figure S3).

Default mode network activation: ICA analysis of pre-trial activity identified the default mode network (Table 1 and Figure 1) with synchronized activation in the posterior cingulate ($z\text{-ICA}=8.05$), the anterior cingulate ($z\text{-ICA}= 7.51$) and the bilateral inferior parietal lobes (right $z\text{-ICA}=2.23$, left $z\text{-ICA}=2.87$). 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 timecourse in the DMN 2.5 sec before the encoding of pictures ($t(23) = -12.58$, $p < .0001$ (two-tailed)), which were recognized one week later.

Interaction between Default Mode Network activation and stimulus induced emotions:

A Wilcoxon 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 ($p \leq .01$) (see Table 2 Figure 2).

Because an interaction effect requires a parametric routine, the data was additionally analyzed with a 2 x 2 (Emotion [yes, no] x Recognition [yes, no]) repeated measures ANOVA. The analysis indicated a main effect of recognition ($F(1,22) = 15.75, p < .001$), a significant main effect emotion ($F(1,22) = 5.1, p < 0.001$) and no significant recognition x emotion interaction effect ($F(1,22) = 0.67, p = .88$), showing that recognition performance and emotional perception together were influenced by the strength of DMN activation.

Analysis of the means revealed a significant difference (by Wilcoxon test) between "NOrecognition" & "emotion" and "recognition" & "NOemotion" pictures ($z(23) = 4.53, p < .001$), a significant difference between "NOrecognition" & "emotion" and "NOrecognition" & "NOemotion" pictures ($z(23) = -3.59, p < .001$), a significant difference between "recognition" & "emotion" and "recognition" & "NOemotion" pictures ($z(23) = -3.01, p < .002$), a significant difference between "recognition" & "emotion" and "NOrecognition" & "emotion" pictures ($z(23) = 3.02, p < .002$) and a significant difference between "recognition" & "NOemotion" and "NOrecognition" & "NOemotion" pictures ($z(23) = 2.77, p < .006$), no significant difference between "recognition" & "emotion" and "NOrecognition" & "NOemotion" pictures ($z(23) = -1.04, p = 0.3$), (Fig. 2)

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 to neutral pictures (3, 5, 47, 48) and studies revealing higher brain activation in MTL while encoding subsequent recognized pictures (6, 9, 36). 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) (3, 5, 47). Especially the amygdala influences other brain regions such as the hippocampus, striatum and neocortex (49) 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 (17). Further

Field Code Changed

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 (50, 51). Only a few recent studies investigated the question whether activation patterns shortly before stimulus onset could predict if the stimulus would be subsequently remembered (29, 31, 32). 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 pre-stimulus DMN activation and perceived emotionality of the pictures and high pre-stimulus 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 (17, 20, 52) and mind-wandering (21). 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),

Field Code Changed

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.

Acknowledgements

This study was supported by grants from the Swiss National Science Foundation (Soravia, de Quervain, Heinrichs, Strik: Nr. 32003B_124947) and the Medical Faculty of the University of Bern (Nr. 520.10). Sincere thanks are given to PhD M. Fislser, MSc B. Preisig and MSc C. de Buman for excellent research assistance.

References

1. Craik FIM, Govoni R, Naveh-Benjamin M, Anderson ND. The effects of divided attention on encoding and retrieval processes in human memory. *Journal of Experimental Psychology*. 1996;125(2):159-80.
2. Reas ET, Brewer JB. Effortful retrieval reduces hippocampal activity and impairs incidental encoding. *Hippocampus*. 2013;23(5):367-79.
3. Buchanan TW, Adolphs R. The role of the human amygdala in emotional modulation of long-term declarative memory. In: Oaksford SMM, editor. *From brain to behavior*. London, U. K.: Benjamins; 2002. p. 9-34.
4. Craik FIM, Tulving E. Depth of Processing and the Retention of Words in Episodic Memory. *Journal of Experimental Psychology*. 1975;3(104):268-94.
5. Kensinger EA, Corkin S. Effect of Negative Emotional Content on Working Memory and Long-Term Memory. *Emotion*. 2003;3(4):378-93.
6. McGaugh JL. Memory--a Century of Consolidation. *Science*. 2000;287(5451):248-51.
7. Brewer JB, Zhao Z, Desmond JE, Glover GH, Gabrieli JDE. Making memories: Brain activity that predicts how well visual experience will be remembered. *Science*. 1998;281:1185 – 7.
8. Buckner RL, Wheeler ME, Sheridan MA. Encoding Processes during Retrieval Tasks. *Journal of Cognitive Neuroscience*. 2001;13(3):406-15.
9. Stark CEL, Okado Y. Making Memories without Trying: Medial Temporal Lobe Activity Associated with Incidental Memory Formation during Recognition. *The Journal of Neuroscience*. 2003;23(17):6748-53.
10. Squire LR, Stark, C. E. L., & Clark, R. E. The Medial Temporal Lobe. *Annual Review of Neuroscience*. 2004;27:279-306.
11. Wagner AD, Schacter DL, Rotte M, Koutstaal W, Maril A, Dale AM, et al. Building Memories: Remembering and Forgetting of Verbal Experiences as Predicted by Brain Activity. *Science*. 1998;281(5380):1188-91.
12. Brewer JB, Zhao Z, Desmond JE, Glover GH, Gabrieli JDE. Making Memories: Brain Activity that Predicts How Well Visual Experience Will Be Remembered. *Science*. 1998;281(5380):1185-7.
13. Kelley WM, Miezin FM, McDermott KB, Buckner RL, Raichle ME, Cohen NJ, et al. Hemispheric Specialization in Human Dorsal Frontal Cortex and Medial Temporal Lobe for Verbal and Nonverbal Memory Encoding. *Neuron*. 1998;20:927-36.
14. Wagner AD, Schacter DL, Rotte M, Koutstaal W, Maril A, Dale AM, et al. Building Memories: Remembering and Forgetting of Verbal Experiences as Predicted by Brain Activity. *Science*. 1998;281:1188-91.
15. Fransson P, Marrelec G. The precuneus/posterior cingulate cortex plays a pivotal role in the default mode network: Evidence from a partial correlation network analysis. *NeuroImage*. 2008;42(3):1178-84.
16. Owen A, McMillan K, Laird A, Bullmore E. N-back working memory paradigm: a meta-analysis of normative functional neuroimaging studies. *Hum Brain Mapp*. 2005;25(1):46-59.

17. Buckner RL, Andrews-Hanna JR, Schacter DL. The brain's default network: anatomy, function, and relevance to disease. *Annals of the New York Academy of Sciences*. 2008;1124:1-38.
18. Gusnard DA, Akbudak E, Shulman GL, Raichle ME. Medial prefrontal cortex and self-referential mental activity: Relation to a default mode of brain function. *Proceedings of the National Academy of Sciences*. 2001;98(7):4259-64.
19. Andrews-Hanna JR, Reidler JS, Sepulcre J, Poulin R, Buckner RL. Functional-Anatomic Fractionation of the Brain's Default Network. *Neuron*. 2010;65(4):550-62.
20. van Buuren M, Gladwin TE, Zandbelt BB, Kahn RS, Vink M. Reduced functional coupling in the default-mode network during self-referential processing. *Human Brain Mapping*. 2010;31:1117-27.
21. Mason MF, Norton MI, Van Horn JD, Wegner DM, Grafton ST, Macrae CN. Wandering minds: The default network and stimulus-independent thought. *Science*. 2007;315:393-5.
22. Northoff G, Bermpohl F. Cortical midline structures and the self. *Trends in Cognitive Sciences*. 2004;8(3):102-7.
23. Buckner RL, Carroll DC. Self-projection and the brain. *Trends in Cognitive Sciences*. 2007;11:49-57.
24. Spreng RN, Mar RA, Kim ASN. The Common Neural Basis of Autobiographical Memory, Prospection, Navigation, Theory of Mind, and the Default Mode: A Quantitative Meta-analysis. *Journal of Cognitive Neuroscience*. 2009;21(3):489-510.
25. McKiernan KA, Kaufman JN, Kucera-Thompson J, Binder JR. A Parametric Manipulation of Factors Affecting Task-induced Deactivation in Functional Neuroimaging. *Journal of Cognitive Neuroscience*. 2003;15(3):394-408.
26. Daselaar SM, Prince SE, Cabeza R. When less means more: deactivations during encoding that predict subsequent memory. *Neuroimage*. 2004;23:921-7.
27. Daselaar SM, Prince SE, Dennis NA, Hayes SM, Kim H, Cabeza R. Posterior midline and ventral parietal activity is associated with retrieval success and encoding failure. *Frontiers in Human Neuroscience*. 2009;3:1-10.
28. Huijbers W, Pennartz CMA, Cabeza R, Daselaar SM. The Hippocampus Is Coupled with the Default Network during Memory Retrieval but Not during Memory Encoding. *PLoS ONE*. 2011;6(4):e17463.
29. Otten LJ, Quale AH, Akram S, Dietwig TA, Rugg MD. Brain activity before an event predicts later recollection. *Nature Neuroscience*. 2006;9(4):489-91.
30. Weissman DH, Roberts KC, Visscher KM, Woldorff MG. The neural bases of momentary lapses in attention. *Nature Neuroscience*. 2006;9(7):971-8.
31. Galli G, Choy TL, Otten LJ. Prestimulus brain activity predicts primacy in list learning. *Cognitive Neuroscience*. 2012;3(3-4):160-7.
32. Adcock RA, Thangavel A, Whitfield-Gabrieli S, Knutson B, Gabrieli JDE. Reward-Motivated Learning: Mesolimbic Activation Precedes Memory Formation. *Neuron*. 2006;50(3):507-17.
33. Mackiewicz KL, Sarinopoulos I, Cleven KL, Nitschke JB. The effect of anticipation and the specificity of sex differences for amygdala and hippocampus

function in emotional memory. *Proceedings of the National Academy of Sciences of the United States of America*. 2006;103(38):14200-5.

34. Padovani T, Koenig T, Brandeis D, Perrig WJ. Different brain activities predict retrieval success during emotional and semantic encoding. *Journal of Cognitive Neuroscience*. 2011;23:4008-21.

35. Eichele T, Debener S, Calhoun VD, Specht K, Engel AK, Hugdahl K, et al. Prediction of human errors by maladaptive changes in event-related brain networks. *Proceedings of the National Academy of Sciences*. 2008;105(16):6173-8.

36. Buckner RL. Frontal cortex contributes to human memory formation. *Nature Neuroscience*. 1999;4(2):311-4.

37. Rasch B, Spalek K, Buholzer S, Luechinger R, Boesiger P, Papassotiropoulos A, et al. A genetic variation of the noradrenergic system is related to differential amygdala activation during encoding of emotional memories. *Proceedings of the National Academy of Sciences*. 2009;106(45):19191-6.

38. Lang PJ, Bradley MM, Cuthbert BN. *International Affective Picture System (IAPS): affective ratings of pictures and instruction manual*. Gainesville, FL: : University of Florida. ; 2005.

39. Deichmann R, Schwarzbauer C, Turner R. Optimisation of the 3D MDEFT sequence for anatomical brain imaging : technical implications at 1.5 and 3 T. *NeuroImage*. 2003;24:757-67.

40. Banks WP. Signal detection theory and human memory. *Psychological Bulletin*. 1970;2(74):81-99.

41. Forman SD, Cohen JD, Fitzgerald M, Eddy WF, Mintun MA, Noll DC. Improved assessment of significant activation in functional magnetic resonance imaging (fMRI): Use of a cluster-size threshold. *Magnetic Resonance in Medicine*. 1995;33(5):636-47.

42. Esposito F, Scarabino T, Hyvarinen A, Himberg J, Formisano E, Comani S, et al. Independent component analysis of fMRI group studies by self-organizing clustering. *Neuroimage*. 2005;25:193-205.

43. Calhoun VD, Adali T, Pearlson GD, Pekar JJ. A method for making group inferences from functional MRI data using independent component analysis *Human Brain Mapping*. 2001;14:140-51.

44. Jann K, Gee DG, Kilroy E, Schwab S, Smith RX, Cannon TD, et al. Functional connectivity in BOLD and CBF data: Similarity and reliability of resting brain networks. *NeuroImage*. 2015;106(0):111-22.

45. Smith SM, Miller KL, Moeller S, Xu J, Auerbach EJ, Woolrich MW, et al. Temporally-independent functional modes of spontaneous brain activity. *Proceedings of the National Academy of Sciences of the United States of America*. 2012;109(8):3131-6.

46. Beckmann CF, DeLuca M, Devlin JT, Smith SM. Investigations into resting-state connectivity using independent component analysis. *Philosophical Transactions of the Royal Society B: Biological Sciences*. 2005;360(1457):1001-13.

47. Reisberg D, Heuer F. Remembering the details of emotional events. In: Neisser WU, editor. *Affect and Accuracy in Recall: Studies of 'Flashbulb' Memories*. Cambridge: University Press; 1992. p. 162-90.

48. Hamann S. Cognitive and neural mechanisms of emotional memory. *Trends in Cognitive Sciences*. 2001;5(9):394-400.
49. Cahill L, McGaugh JL. Mechanisms of emotional arousal and lasting declarative memory. *Trends in Neurosciences*. 1998;21:294-9.
50. Raichle ME, MacLeod AM, Snyder AZ, Powers WJ, Gusnard DA, Shulman GL. A default mode of brain function. *Proceedings of the National Academy of Sciences*. 2001;98(2):676-82.
51. Greicius MD, Supekar K, Menon V, Dougherty RF. Resting-state functional connectivity reflects structural connectivity in the default mode network. *Cerebral Cortex*. 2009;19:72-8.
52. Gusnard DA, Akbudak E, Shulman GL, Raichle ME. Medial prefrontal cortex and self-referential mental activity : relation to a default mode of brain function. *PNAS*. 2001;98:4259-64.

Figures

Figure 1: The default mode network (DMN) identified by independent component analysis (ICA). ICA analysis of pre-trial rest activity (2.5 seconds before stimulus encoding (pre-state)) identified the default mode network with synchronized activation in the anterior- and posterior- cingulate and the bilateral parietal lobes (areas indicated in hot-color).

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). Circles represent the outliers between 1.5 and 3 IQR, stars 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 [38].

Table 1:Independent Component Analysis (ICA). The ICA analysis identified the default mode network (DMN).The statistical map of the DMN was corrected for multiple comparisons (FWE<.01).

Region	BA	coordinates (SD)			Cluster size [voxel]	t-test of z-ICA values
		x	y	z		
Anterior cingulate	n.a.	-2.1(6.3)	46.2(8.3)	-6.4 (6.2)	1097	14.3
Posterior cingulate	23	0.1 (10.1)	-50.0(12.4)	29.3 (15.9)	11010	30.4
Inferior parietal lobe, left	39	-38.0 (26.7)	-66.2 (3.2)	42.7 (3.9)	2347	23.3
Inferior parietal lobe, right	39	46.0 (31.5)	-64.0 (5.1)	36. (5.9)	1772	21.2

Note. BA = Brodmann Area; SD =standard deviation

Table 2: Mean DMN activation before stimulus onset between the recognition and emotion conditions. 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 [38]. A Wilcoxon rank-sum 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 ($p \leq .01$).

	recognition_emotion		NOrecognition_NOemotion	
	z	p	z	p
recognition_NOemotion	-10.03	.0001	4.41	.001
NOrecognition_emotion	4.41	.001	-8.57	.0001

Note. N = 24.