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Article *in* Social Cognitive and Affective Neuroscience · June 2015

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doi: 10.1093/scan/nsv073
Original article

Memory and reward systems coproduce 'nostalgic' experiences in the brain

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Abstract

People sometimes experience an emotional state known as 'nostalgia', which involves experiencing predominantly positive emotions while remembering autobiographical events. Nostalgia is thought to play an important role in psychological resilience. Previous neuroimaging studies have shown involvement of memory and reward systems in such experiences. However, it remains unclear how these two systems are collaboratively involved with nostalgia experiences. Here, we conducted a functional magnetic resonance imaging study of healthy females to investigate the relationship between memory-reward co-activation and nostalgia, using childhood-related visual stimuli. Moreover, we examined the factors constituting nostalgia and their neural correlates. We confirmed the presence of nostalgia-related activity in both memory and reward systems, including the hippocampus (HPC), substantia nigra/ventral tegmental area (SN/VTA), and ventral striatum (VS). We also found significant HPC-VS co-activation, with its strength correlating with individual 'nostalgia tendencies'. Factor analyses showed that two dimensions underlie nostalgia: emotional and personal significance and chronological remoteness, with the former correlating with caudal SN/VTA and left anterior HPC activity, and the latter correlating with rostral SN/VTA activity. These findings demonstrate the cooperative activity of memory and reward systems, where each system has a specific role in the construction of the factors that underlie the experience of nostalgia.

Key words: nostalgia; autobiographical memory; reward; resilience; fMRI

Introduction

When something that is physically or mentally encountered cues memory retrieval, we sometimes experience a distinct emotional state called nostalgia. This term was originally introduced by a Swiss physician, Johannes Hofer (1688/1934), as a Greek compound consisting of *nostos* (return) and *algos* (pain). He conceptualized nostalgia as a neurological disease characterized by adverse psychological and physiological symptoms, including persistent thinking of home, anxiety, irregular heartbeat, anorexia and insomnia, as displayed by many Swiss mercenaries who went on an expedition to foreign shores (Wildschut *et al.*, 2006). In the modern era, nostalgia has been regarded as a predominantly (but not exclusively) positive emotional experience that is described as positive sentiment or bittersweet and wistful pleasure, an experience that accompanies autobiographical memory (AM) retrieval (Davis, 1979; Wildschut *et al.*, 2006). Although the affective signature of

Received: 28 October 2014; **Revised:** 20 May 2015; **Accepted:** 4 June 2015

nostalgia is rather mixed, nostalgia is now thought to serve a psychologically adaptive function. For example, recent behavioral and psychophysiological studies of nostalgia have revealed that nostalgic experiences can decrease dysphoric states such as loneliness, depression and rumination about death (Wildschut *et al.*, 2006; Yamagami *et al.*, 2007; Routledge *et al.*, 2008; Zhou *et al.*, 2008), and can also decrease levels of peripheral proinflammatory cytokines such as the tumor necrosis factor-α and interferon-γ (Matsunaga *et al.*, 2013). Furthermore, nostalgia can increase self-esteem, self-positivity and sense of social connectedness in young people (Sedikides et al., 2006), as well as sense of self-worth and desire to live in older adults who participate in reminiscence therapy, a clinical intervention that relies heavily on evoking nostalgic experiences (Yamagami *et al.*, 2007). Such findings suggest that nostalgia can play a role in psychological resilience and everyday well-being.

One conceptual model of nostalgia proposes that nostalgic experiences are in fact a combination of autobiographical and affective experiences (Barrett *et al.*, 2010), as theoretical studies of emotion have suggested that emotion can be constructed using information provided by memory, interoceptive information from inside one's body and sensory inputs from the outside world (Barrett, 2006; Moriguchi and Komaki, 2013). Previous studies have shown that a nostalgic experience can be triggered by remembering AMs, such as through sensory inputs (smell, music and visual stimuli related to the past), conversation about the past and the experience of similar events (Davis, 1979; Wildschut *et al.*, 2006; Chrea *et al.*, 2009; Barrett *et al.*, 2010). Although it is very important to clarify the neural basis of nostalgia, there have been only a few neuroimaging studies. Among them, one functional magnetic resonance imaging (fMRI) study examined the neural substrates of listening to music that evokes emotions such as tenderness, peacefulness and nostalgia, showing that experiencing these high valence/low arousal emotions activates various brain regions, including the hippocampus (HPC), parahippocampus, ventral striatum (VS) and ventromedial prefrontal cortex (VMPFC), as well as the subgenual/rostral anterior cingulate cortex, somatosensory cortex and medial motor cortex (Trost *et al.*, 2012). In addition, a positron emission tomography study examined odor-evoked AMs that accompany a sense of nostalgia, showing that such AMs are accompanied by activation of the precuneus and medial orbitofrontal cortex (Matsunaga *et al.*, 2013). This study also showed a positive correlation between both sources of activation, indicating a memory-reward relationship. Although these studies show activation of memory and reward systems as well as their co-activation during nostalgia experiences, it has not been clarified how the strength of such memory-reward relationships is actually correlated with the subjective experience of nostalgia.

To address this issue, we conducted an fMRI study and performed the following analyses using visual stimuli related to childhood and highly likely to evoke nostalgic feelings, and that are not inherently rewarding like food, money and sexual stimuli. First, we sought to confirm activity of memory and reward-related areas during nostalgia. That is, we specifically assessed HPC activity during nostalgic experiences, given that a previous fMRI study (Trost *et al.*, 2012) reported the involvement of HPC and that this region is crucial for the retrieval of autobiographical events (Fink *et al.*, 1996; Ryan *et al.*, 2001; Maguire and Frith, 2003; Markowitsch *et al.*, 2003; Addis *et al.*, 2004; Cabeza *et al.*, 2004; Gilboa *et al.*, 2004; Piolino *et al.*, 2004; Svoboda *et al.*, 2006; Cabeza and St Jacques, 2007; Schacter and Addis, 2007; Viard *et al.*, 2007). Concerning reward-related areas, we investigated VS, VMPFC and substantia nigra/ventral tegmental area (SN/VTA) activity, because positive affect should be associated with these reward-system activations, which has already been demonstrated with numerous research paradigms (Diekhof *et al.*, 2012; Kuhn and Gallinat, 2012). We also investigated the co-activation (positive correlation between brain activities in two regions) of the HPC and reward-related areas to confirm interregional relationships during nostalgic experiences. Then, to examine the relationship between the memory-reward collaborative activity and the subjective experience of nostalgia, we investigated whether individual patterns of memory-reward co-activation are correlated with the 'nostalgia tendency', or the extent to which one tends to experience a remembrance as subjectively more nostalgic. If the co-operative activity of memory-reward systems is actually important for constructing nostalgia experiences, its strength should be correlated with the nostalgia tendency across individuals.

In addition to memory-reward co-activation in nostalgia, we also examined the factors constituting nostalgia and their neural correlates. We asked participants to rate their emotions and memories during the experimental task, including the temporal remoteness of memory, thought to be an important factor in nostalgia (Davis, 1979) but one that has been underemphasized in previous psychological studies (Wildschut *et al.*, 2006; Barrett *et al.*, 2010). Based on ratings data, we performed an exploratory factor analysis to extract the factors constituting nostalgia, and conducted parametric modulation analyses with each factor.

Materials and methods

Participants

Fifteen right-handed healthy young female undergraduates were recruited and completed the fMRI experiment as described below. One participant was removed from data analysis, as she reported that she had fallen asleep during the fMRI experiment. All statistical analyses were conducted using data from the remaining 14 participants (mean age $\pm$ s.d. $= 22{\cdot}1 \pm 0{\cdot}6$ years). Participants had no history of psychiatric or neurological disorders. Only female participants were recruited because females have previously been shown to recall emotional AMs at a faster and higher rate than males (Davis, 1999), and because there are sex differences at the neural level related to emotional AM retrieval (Piefke *et al.*, 2005). All participants provided their written informed consent prior to their participation. This study was approved by the Research Ethics Committee of Tokyo Metropolitan University and conducted in accordance with the Declaration of Helsinki.

fMRI experiment

We assumed that nostalgia would be induced by triggers common to a relatively homogeneous subset of individuals within the same culture, age and sex groupings. For instance, most Japanese people experience similar events during the 6 years of compulsory education in elementary school. Memories of these times should contain common features, irrespective of the specific place in which participants grew up. All such individuals spent large amounts of time in a school building with a typical appearance, used certain types of school stationery typically depicting animated characters, and spent this unique period with friends of the same age. Almost all of these experiences are limited to elementary school, and people seldom have the same experiences after graduation. We therefore created visual stimuli

for the fMRI task that depicted objects and scenes that are emotionally neutral by their nature but would be expected to induce nostalgic experiences once the stimuli were associated with the participants' childhood (nostalgic pictures), as well as similar control pictures that should not induce nostalgia (Figure 1). For stimulus preparation details, see Supplementary information.

During the fMRI experiment, pictures falling into the four categories shown in Figure 1 were randomly presented for 8 s each. All pictures were presented only once and were interleaved with 8 s fixation crosses. Participants were not explicitly informed that they would be shown pictures specifically designed to arouse nostalgia, but were only instructed to view the pictures attentively. By this means, we could show that the induction of nostalgia can be a very basic and automated mental process, such that it can be triggered implicitly. Presentation software (Neurobehavioral Systems) was used to display the pictures and to control presentation timing.

Scanning was conducted using a 3T MRI scanner (Achieva Quasar Dual, Philips). Blood oxygenation level-dependent (BOLD) T2*-weighted MR signals were measured using a gradient echo-planar imaging (EPI) sequence. Two hundred and ten volumes with nineteen contiguous slices of 6 mm thickness were acquired (TR = 4000 ms, TE = 35 ms, flip angle = 90°, FOV = 230 mm^2, scan matrix = 128 × 128, total scan time = 840 s).

Post-scanning ratings

Immediately after the fMRI scan, participants were asked to again view all of the pictures on a computer screen and to retrospectively evaluate their experiences during scanning. These evaluations included: (i) two items pertaining to the object or scene depicted in each stimulus ['How much do you know about the object/scene depicted in the picture?' (recognizability) and 'How familiar are you with the object or scene depicted in the picture?' (familiarity)], (ii) four items assessing the emotional experience that occurred when participants saw each picture during scanning ['How much nostalgia did you feel?' (nostalgia), 'How happy did you feel?' (happiness), 'How much did you feel attachment to the object or the scene?' (attachment) and 'How sentimental did you feel?' (sentimentality)] and (iii) four items assessing AMs retrieved in the scanner ['How important was the remembered AM?' (personal significance), 'How vivid was the remembered AM?' (vividness), 'How long ago did the remembered event occur?' (age of memories) and 'When did you last recall the AM?' (age of last recall)]. These items were created based on previous behavioral studies of nostalgia (Davis, 1979; Wildschut *et al.*, 2006; Barrett *et al.*, 2010) to assess the psychological properties of nostalgia. All items were rated on a 5-point scale (1: not at all, 2: not much, 3: slightly, 4: quite, 5: extremely), except for the last two items which were each rated on a 6-point scale [1: before entering elementary school (under 6 years old), 2: early elementary grades (7–9 years old), 3: late elementary grades (10–12 years old), 4: junior high school (13–15 years old), 5: high school (16–18 years old), 6: university (19–present years old)]. Scores for the last two items were transformed into years prior to the day of the experiment.

Fig. 1. Examples of experimental stimuli. The upper row shows nostalgic pictures and the lower row shows control pictures (left column: object pictures, right column: scene pictures). All pictures were given a short title in order to ensure visual recognition and facilitate memory access (written in Japanese). Note that both nostalgia and control pictures were emotionally neutral, and were matched on their visual features such as content and angle.

Behavioral data analysis

To identify the separate qualitative aspects of the nostalgic experience, we first conducted a multiple regression analysis with subjective nostalgia intensity as the dependent variable and the nine items mentioned above as independent variables, using forward stepwise selection ($n = 728$; 52 pictures × 14 participants). We then selected significant explanatory variables on the basis of this analysis, and performed an exploratory factor analysis to convert these variables into uncorrelated factors and extract interpretable subsets constituting the nostalgia construct. The maximum-likelihood method was used for factor extraction and the resulting factors were subjected to Promax rotation. We also calculated mean nostalgia scores (responses to the question 'How much nostalgia did you feel?') for all stimuli (52 pictures in total), for each participant, and deemed this value to represent an individual's 'nostalgia tendency', as such values should reflect a broad tendency to experience subjective feelings of nostalgia. All behavioral data analyses were performed using SPSS statistical software version 17.0 (IBM SPSS).

fMRI data analysis

Image preprocessing and statistical analyses were performed using SPM8 (Wellcome Department of Cognitive Neurology, http://www.fil.ion.ucl.ac.uk/spm/). Functional images were realigned to the first volume to correct interscan movements. The slice timing in each volume shot was corrected. Functional images were then spatially normalized to the Montreal Neurological Institute (MNI) EPI template and smoothed with a Gaussian filter of 8-mm full width at half maximum.

Before conducting analyses of the fMRI data, we redefined the categorical membership of each picture according to participants' post-scanning nostalgia ratings, such that nostalgic pictures had scores of ≥ 3 (i.e. slightly/quite/extremely nostalgic) and control pictures had scores of ≤ 2 (i.e. not/not at all nostalgic). To analyse the fMRI time series data, we modeled hypothetical hemodynamic event-related transient and sustained responses (Krendl *et al.*, 2012). In the transient model, effects of interest were modeled by convolving each stimulus onset with the canonical hemodynamic response function (HRF), whereas in the sustained model, effects were modeled with the boxcar function convolved with the HRF. The former is useful for detecting fast neural responses from task-onset, while the latter is useful for detecting lasting responses over the task-block. We used this approach because midbrain dopamine neurons show

transient activity increases in response to salient rewarding and novel events (Schultz, 1998; Shohamy and Adcock, 2010), whereas the HPC shows rather sustained activity during AM retrieval (Ryan *et al.*, 2001). The convolved hypothetical hemodynamic curves in response to the four kinds of stimulus (nostalgic object, nostalgic scene, control object and control scene) were entered into the two types of GLM model as explanatory variables, with motion parameters and discrete cosine filter models as a high-pass filter with a 128 s cut-off period as nuisance covariates. The two models were estimated to fit the time-series BOLD signals at each voxel. We then averaged the estimated parameters (beta values) into the nostalgia (object and scene) and control (object and scene) conditions.

Region of interest analysis

The bilateral HPC region of interests (ROIs) were first created using the automated anatomical labeling (AAL) atlas (Tzourio-Mazoyer *et al.*, 2002). We then separated the HPC into anterior and posterior portions in reference to a study examining the antero-posterior functional specialization of the HPC (Poppenk *et al.*, 2013). Neuroimaging studies of AM retrieval have shown that the anterior HPC plays a role in the pattern completion of gist-like representations of an autobiographical event, whereas the posterior HPC is involved in the retrieval of spatially and temporally specific (pattern separated) representations (Nadel *et al.*, 2013; Poppenk *et al.*, 2013). The limit between anterior and posterior portions corresponded to $y = -21$ mm (MNI coordinates) (Poppenk *et al.*, 2013). In total, we generated four hippocampal ROIs: left anterior (L.aHPC), left posterior (L.pHPC), right anterior (R.aHPC) and right posterior (R.pHPC) portions.

Reward-related ROIs were identified by referring to a previous meta-analysis of the neural substrates of reward processing (Diekhof *et al.*, 2012). This meta-analysis has shown that the SN/VTA plays a role in reward anticipation, whereas the VMPFC functions during the reward outcome or reward receipt) phase, and the VS is involved during both anticipation and outcome phases. We defined the SN/VTA ROI as the intersection of the 8-mm radius sphere centered at (−4, −16, −14) and the midbrain mask as identified using PickAtlas software (Maldjian *et al.*, 2003). As for the VMPFC ROI, we generated an 8-mm radius sphere centered at (−2, 64, −2). For the VS ROIs, we calculated the centroid of the two VS coordinates reported in the meta-analysis, resulting in an 8-mm radius sphere centered at (−10, 11, −4) and (14, 13, −8). These eight ROIs are depicted in Figure 2A.

We used MarsBaR software (version 0.42, http://marsbar.sourceforge.net/) to extract the mean parameter estimate within each of the eight ROIs from individual beta images for nostalgia and control conditions (estimated by the transient and sustained hemodynamic GLM model), and we compared these using paired *t*-tests of estimates for nostalgia *vs* control

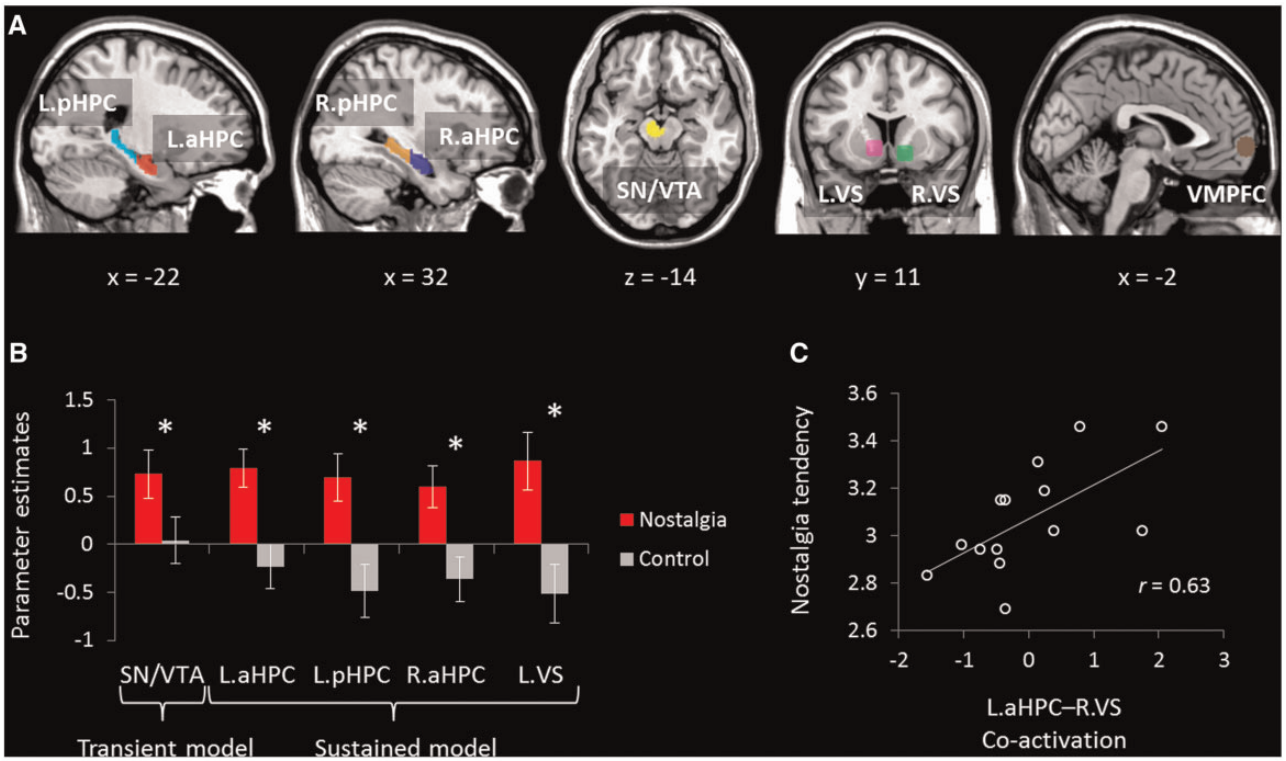

Fig. 2. ROI analyses of brain activity for nostalgia *vs* control events. (A) The eight ROI masks used in this study. The four hippocampus ROIs [L.aHPC (red), L.pHPC (cyan), R.aHPC (blue) and R.pHPC (orange)] were created by dividing the AAL HPC masks into anterior and posterior portions ($y = -21$ mm, MNI coordinates), and four reward-related ROIs [SN/VTA (yellow), L.VS (purple), R.VS (green) and VMPFC (brown)] were created using coordinates reported in a meta-analysis concerning reward processing (for more details, see the Region of interest analysis section). (B) HPC and reward-related ROIs that showed significant activity differences between the nostalgia and control conditions. The mean parameter estimates (beta values) for each ROI were extracted from each condition and compared using paired *t*-tests ($P < 0.05$, FWE corrected by Holm method). Error bars show individual differences (SEM). Asterisks (*) denote a significant difference between conditions. (C) Among the HPC and reward-related ROIs, the L.aHPC and R.VS were co-activated and the L.aHPC-R.VS co-activation index was significantly correlated with nostalgia tendency ($r(12) = 0.63$, $P = 0.047$). The co-activation index was defined as the first eigenvalue of these two ROIs' activity (parameter estimates) that represents co-activation strength. Nostalgia tendency was defined as the individual mean nostalgia score across all experimental stimuli in this study (52 pictures). L, left; R, right; aHPC, anterior hippocampus; pHPC, posterior hippocampus; FWE, family wise error.

events (i.e. we ran two *t*-test comparisons on the eight ROIs using estimates from both transient and sustained models, resulting in a total of 16 *t*-tests). Because we ran multiple comparison analyses, the statistical threshold was corrected as the family wise error rate [family wise error; the Holm method (Holm, 1979)]. In addition to this hypothesis-driven ROI approach, we also performed a conventional whole-brain voxel-by-voxel analysis comparing the nostalgia and control conditions ($P < 0.001$ uncorrected, $k \geq 10$).

Relationships between memory-reward co-activation and nostalgia tendency

To demonstrate whether and how nostalgia-related neural activities in the memory and reward systems were related to one another, we investigated their co-activation. Co-activation means the positive correlation of brain activity between two regions, indicating interregional relationships in terms of the magnitudes of activity (Greenberg *et al.*, 2005).

We first regressed individual hippocampal activity (beta estimates of the HPC subregional ROIs that showed significant nostalgia-control differences) on the beta estimates of the four reward-related ROIs. We then ran multiple forward stepwise regression analyses in which HPC ROI activity was set as the dependent variable and activities in the four reward-related ROIs were set as the independent variables ($P < 0{\cdot}05$, FWE corrected via the Holm method). We used these regression analyses to obtain most significant reward-related regions that showed co-activation with each subregion in the HPC (i.e. the L/R aHPC/pHPC).

We then conducted correlational analyses between the strength of interregional relationships and individual nostalgia tendency scores (averaged nostalgia ratings of the pictures; see Behavioral data analysis) to demonstrate that memory-reward interrelationships are important in the generation of nostalgic experiences. We first calculated individuals' 'memory-reward co-activation index' by computing the first eigenvalue through a principal component analysis of the individual activation (beta estimates) in the hippocampal and reward-related regions. We then correlated these individual co-activation indices with participants' nostalgia tendency scores.

Correlation between neural activity and factors constituting nostalgia

To confirm the role of the selected ROIs in the generation of nostalgic experiences, we performed correlational (parametric modulation) analyses of the activation using the summed scores of each factor that composes nostalgia, as revealed by the aforementioned factor analysis (see Behavioral data analysis). In this analysis, as well as the ROI analyses, we modeled two hypothetical hemodynamic responses (transient and sustained), and tested which ROI activation was correlated with each nostalgia factor. The search volume was restricted to the 8-mm radius sphere, centered at the peak coordinates within the ROI mask that showed differential brain activity in the voxel-by-voxel nostalgia *vs* control contrast [$P < 0{\cdot}05$, FWE corrected in small volume correction (SVC)].

Results

Psychological aspects of nostalgic experiences

On the basis of post-scanning ratings of the pictures, participants reported that they had experienced nostalgia during scanning, such that the nostalgic pictures were in fact rated to be highly nostalgic, ($M = 4.5$, s.d. $= 0.6$), and the control pictures rated as low on this dimension ($M = 1.7$, s.d. $= 0.9$). This was a statistically significant difference, $t\ (50) = 28.6$, $P < 0.01$. This confirms that genuine nostalgic experiences were evoked in the scanner despite the fact that participants received no explicit guidance or warnings in this regard. We also confirmed that nostalgic pictures reminded participants of their remote past. Participants viewing the nostalgic pictures recalled events they experienced around 12.1 (s.d. $= 1.4$) years ago (around when participants were in elementary school), while they reported that the control pictures were associated with reminiscing back to an average of 5.4 (s.d. $= 2.7$) years ago (around when participants were in high school) ($t\ (13) = 15.8$, $P < 0.01$).

A multiple regression analysis ($n = 728$) showed that age of memories ($\beta = 0.35$), happiness ($\beta = 0.31$), attachment ($\beta = 0.135$), sentimentality ($\beta = 0.134$), personal significance ($\beta = 0.085$) and age of last recall ($\beta = 0.092$) were significant predictors of nostalgia (adjusted $R^2 = 0.77$, $P < 0.05$), whereas recognizability ($\beta = 0.028$), vividness ($\beta = 0.002$) and familiarity ($\beta = -0.027$) were not. A subsequent exploratory factor analysis including the six significant predictors of nostalgia scores revealed that these predictors converged on two factors (Table 1). The first contained the four items of attachment, happiness, personal significance and sentimentality, and was termed 'emotional and personal significance'. The second contained age of memories and age of last recall, and was termed 'chronological remoteness'. This result is consistent with the notion that nostalgia is predicted by mixed but predominantly positive emotions, and is associated with 'getting back to old times' (Davis, 1979; Wildschut *et al.*, 2006; Barrett *et al.*, 2010).

Neural activity for the nostalgia *vs* control contrast

As predicted, hypothesis-driven ROI analysis revealed significant HPC and reward-related area activity for the nostalgic *vs* control pictures comparison (Table 2 and Figure 2B). There was a significant activity difference between nostalgia and control events ($t\ (13) = 4.96$, $P = 0.0042$, FWE corrected by Holm method) for the transient model in which we predicted reward-related SN/VTA activity. In this transient model, the other seven ROIs did not show significant activity differences between the two events (Table 2). For the sustained model in which we predicted activation of both the memory-related HPC subregions and reward-related regions, significant differential activity was observed between the two events in the L.aHPC ($t\ (13) = 4.76$, $P = 0.0056$), L.pHPC ($t\ (13) = 3.85$, $P = 0.028$), R.aHPC ($t\ (13) = 3.63$, $P = 0.036$), and in the L.VS (a reward-related region, $t\ (13) = 3.68$, $P = 0.036$). Other regions did not show significant activity after correction for multiple comparisons, including the SN/VTA ($t\ (13) = -2.09$), R.VS ($t\ (13) = 1.30$), VMPFC ($t\ (13) = 2.49$) and R.pHPC ($t\ (13) = 3.00$) (Table 2). These results support our hypothesis that nostalgia experiences involve both reward and memory systems.

The additional whole-brain voxel-by-voxel analysis ($P < 0.001$ uncorrected, $k \geq 10$) revealed transient activity in the SN/VTA, right perirhinal cortex, right supplementary motor area and right cerebellum, and sustained activity in the right aHPC/parahippocampal cortex, left aHPC, left thalamus, left dorsolateral prefrontal cortex, right hypothalamus and bilateral cerebellum (Table 3).

Relationships between the HPC-VS co-activation and the nostalgia tendency

As expected, we found HPC and VS activation to be interrelated across individuals, such that individual differences in R.VS

Table 1. Exploratory factor structure of nostalgia

Items	Factor 1: Emotional and personal significance	Factor 2: Chronological remoteness
	Factor loadings	
Attachment	0·898	−0·087
Happiness	0·862	0·058
Personal significance	0·748	0·046
Sentimentality	0·518	0·083
Age of memories	−0·02	0·996
Age of last recall	0·062	0·734
	Correlation	
Factor 1	–	
Factor 2	0·557	–

Extraction method: maximum-likelihood method; Rotation method: Promax with Kaiser normalization.

Table 2. ROI analysis results

	ROI	T	P	P (corrected)
Transient model				
L	aHPC	1·214	0·246	
R		1·887	0·082	
L	pHPC	−0·856	0·407	
R		−0·784	0·447	
L	SN/VTA	4·958	0·000	0·004*
L	VS	−0·169	0·868	
R		0·015	0·989	
L	VMPFC	−0·474	0·643	
Sustained model				
L	aHPC	4·760	0·000	0·006*
R		3·633	0·003	0·036*
L	pHPC	3·849	0·002	0·028*
R		3·002	0·010	
L	SN/VTA	−2·085	0·057	
L	VS	3·684	0·003	0·036*
R		1·295	0·218	
L	VMPFC	2·488	0·027	

R, right; L, left; aHPC, anterior hippocampus; pHPC, posterior hippocampus. Asterisk (*) shows significant difference for activity between the nostalgia and control conditions ($P < 0.05$, FWE corrected by Holm method).

activity predicted such differences in bilateral aHPC activity (t (12) = 2.68, $P = 0.02$ for L.aHPC-R.VS and t (12) = 3.40, $P = 0.01$ for R.aHPC-R.VS), and that individual differences in L.VS activity predicted such differences in L.pHPC activity (t (12) = 4.60, $P = 0.002$, $P < 0.05$ FWE corrected by the Holm method), in the multiple regression analysis in which the activity of each HPC ROI (bilateral aHPC and L.pHPC) was regressed by the activity estimates for the four reward-related regions. The HPC and VS showed concurrent, interrelated patterns of activity during the experience of nostalgia. Furthermore, to test for collaborative activity of memory-reward systems in nostalgia, we calculated the individual strengths of the HPC-VS co-activations (first eigenvalue of each HPC-VS pairs' activity), and correlated these with individual nostalgia tendency scores. L.aHPC-R.VS co-activation scores were correlated with nostalgia tendency (Figure 2C, r (12) = 0.63, $P = 0.047$), while the co-activations of L.pHPC-L.VS and R.aHPC-R.VS were not significant (r (12) = 0.48, $P = 0.079$, r (12) = 0.52, $P = 0.112$, respectively, FWE corrected using Holm method). This result indicates that HPC-VS co-activation makes an important contribution to the experience of nostalgia.

Table 3. Whole-brain analysis results

Brain region	BA	MNI Coordinates x	y	z	Peak T	Cluster k
Transient model						
L SN/VTA		−4	−20	−20	5.75	50
		−6	−16	−10	4.86	
R Perirhinal cortex	38	34	−2	−22	4.66	17
R Cerebellum		40	−52	−34	4.53	26
R Supplementary motor area	6	6	14	68	4.41	22
Sustained model						
R aHPC/parahippocampal cortex		32	−8	−22	8.12	205
		34	4	−16	5.18	
		30	−18	−20	4.19	
R Cerebellum		50	−56	−46	6.51	45
		42	−52	−44	4.77	
L Cerebellum		−20	−74	−42	5.83	54
L Thalamus		−16	−10	6	5.22	39
L aHPC		−22	−10	−22	5.12	40
L Dorsolateral prefrontal cortex	8	−20	32	52	5.03	15
R Hypothalamus		8	0	−4	4.64	19
L Cerebellum		−22	−50	−40	4.53	35
		−28	−58	−38	4.28	
R Cerebellum		30	−64	−34	4.48	19
R Cerebellum		8	−36	−14	4.46	28

BA, Brodmann area; aHPC, anterior hippocampus. $P < 0.001$ uncorrected, $k \geq 10$

Factor-specific nostalgia-related neural activity

We confirmed via the aforementioned factor analysis that nostalgia consists of two factors: emotional and personal significance and chronological remoteness. Although emotional and personal significance scores were correlated with transient activity in the caudal portion of the SN/VTA, Chronological remoteness scores were correlated with rostral SN/VTA activity [Table 4 and Figure 3, parametric modulation analyses; t (13) = 4.28, $P = 0.023$ and t (13) = 4.48 $P = 0.024$, respectively, with the SVC within a sphere region centered at the peak coordinates found at voxel-by-voxel analyses of the nostalgia *vs* control contrast; (−4, −20, −20) and (−6, −16, −10)]. Furthermore, emotional and personal significance scores were correlated with both transient and sustained L.aHPC activity [parametric modulation analyses; t (13) = 4.26, $P = 0.024$, and t (13) = 5.81, $P = 0.003$, respectively, with spherical SVC centered at L.aHPC coordinate (−22, −10, −22)], while there was no such relationship for chronological remoteness scores. Thus, nostalgia appears to be composed of two different factors, and these different aspects of nostalgia are underpinned by a differential and fine spatial pattern of neural activation within the memory- and reward-related brain regions.

Discussion

Using multiple regression analysis, we demonstrated that nostalgia intensity is predicted by age of memories, happiness,

Table 4. Correlational analysis (parametric modulation analysis) of neural activation and nostalgia factors

Brain region		MNI coordinates x	y	z	Peak T	Cluster k	SVC P (FWE-cor)
Factor 1: Emotional and personal significance							
Transient							
L	Caudal SN/VTA	−6	−20	−18	4·28	6	0·023
L	aHPC	−22	−10	−20	4·26	2	0·024
Sustained							
L	aHPC	−24	−4	−24	5·81	46	0·003
Factor 2: Chronological remoteness							
Transient							
L	Rostral SN/VTA	−8	−10	−6	4·48	6	0·024
Sustained							
	None						

FWE, family wise error; aHPC, anterior hippocampus. $P < 0·05$ FWE corrected in SVC.

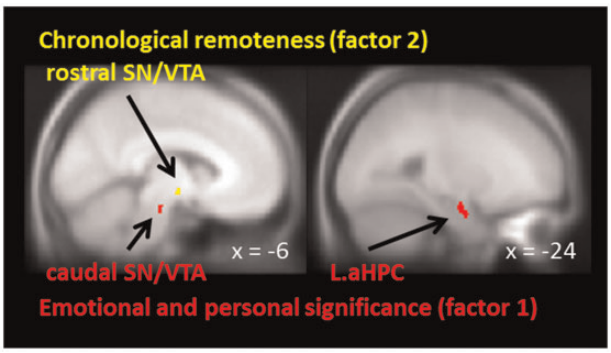

Fig. 3. Neural activation correlated with two different aspects of nostalgia. Emotional and personal significance (factor 1) was correlated with activation of the caudal portions of the SN/VTA and L.aHPC (shown in red), whereas Chronological remoteness (factor 2) was correlated with activation of the rostral SN/VTA (shown in yellow). aHPC, anterior hippocampus.

attachment, sentimentality, personal significance and age of last recall. This result indicates that nostalgia is not merely positive but instead has a rather mixed emotional profile (happiness accompanying sentimentality), and also indicates that remote and personally significant AMs, which dated from around elementary school in this study, are related to nostalgic experiences. On the other hand, vividness scores did not predict nostalgia intensity. This is probably because we used generic (rather than specific) visual stimuli to trigger nostalgic experiences and did not explicitly ask participants to remember specific AMs from elementary school. A more speculative interpretation of this finding may be that nostalgic experiences can be triggered by retrieval of gist-like AM representations (for lifetime periods and/or general events), which is modeled at an early stage of the AM reconstructive process (Conway and Pleydell-Pearce, 2000), before vivid and specific AM remembering occurs. In addition, we found that the nostalgic experience can be parsed into two dimensions, emotional and personal significance (factor 1) and chronological remoteness (factor 2). The 'emotional and personal significance' factor would be analogous to the conceptual model of nostalgia (Barrett *et al.*, 2010) that emphasizes both affective and memory-related experiences. In addition to this factor, 'chronological remoteness' emerged here as a distinct factor in the construction of nostalgic experiences. Interestingly, we found different patterns of neural activity corresponding to these two factors within the nostalgia-related brain areas. The L.aHPC and caudal SN/VTA play a key role in emotional and personal significance, whereas rostral SN/VTA activity is correlated with chronological remoteness. A previous neuroimaging study supports a possible functional differentiation of the SN/VTA along its rostro-caudal axis, such that caudal SN/VTA activity is modulated by reward whereas activation of the more rostral portion of the SN/VTA is modulated by novelty (Krebs *et al.*, 2011). Based on this, rostral SN/VTA activity implicates the involvement of novelty detection during nostalgic experiences (i.e. the retrieval of long-forgotten remote memories should be experienced as novel relative to the retrieval of recent past). With regards to the L.aHPC, this region appears to play a specific role in the retrieval of emotionally and personally significant information, as shown in a previous study in which HPC activity was modulated by the emotionality and personal significance of AMs (Addis *et al.*, 2004).

Given that the HPC plays a crucial role in AM retrieval (Fink *et al.*, 1996; Ryan *et al.*, 2001; Maguire and Frith, 2003; Markowitsch *et al.*, 2003; Addis *et al.*, 2004; Cabeza *et al.*, 2004; Gilboa *et al.*, 2004; Piolino *et al.*, 2004; Viard *et al.*, 2007), along with evidence that our participants did recall their remote past and feel strong nostalgic feelings in the scanner, the HPC activity we observed suggests that nostalgia requires more AM retrieval than does observing non-nostalgic (control) events. Such HPC activity without intentional retrieval demand suggests involvement of involuntary AM retrieval (Berntsen and Hall, 2004) in nostalgic experiences. Furthermore, rather anteriorly biased HPC activation (bilateral aHPC) is compatible with our behavioral results such that most of the objects and scenes depicted in the stimuli had been long forgotten and stored in long-term memory, and that associated details were therefore relatively degraded, in agreement with previous findings that the aHPC plays a role in the pattern completion of gist-like representations (Nadel *et al.*, 2013; Poppenk *et al.*, 2013). Of course, we assume that detailed AM representations triggered by personalized stimuli (such as family photographs) can also induce nostalgia, and in such cases we speculate that both gist-like and detailed AM retrieval processes would be involved in the involuntary induction of nostalgia and subsequently more detailed AM recollection.

We could also confirm interregional relationships between the memory and reward systems, as a co-activated pattern across participants for the HPC (bilateral anterior and left posterior) and VS. Furthermore, the strength of individual memory-reward interrelationships was correlated with individual subjective experience of nostalgia (a correlation of the nostalgia tendency with the L.aHPC-R.VS co-activation). This result shows that the memory and reward systems coproduce subjective nostalgic experiences. Such interregional relationships during nostalgic experiences may be based on the intrinsic memory-reward network, that is, the hippocampal-VTA loop (Lisman and Grace, 2005) that enables hippocampal signals to activate the nucleus accumbens (a component of the VS) and the SN/VTA dopaminergic system. Although our data cannot show the direction of signal processing, the HPC, VS and SN/VTA activity and the HPC-VS co-activation suggest the possibility that memory retrieval via the HPC can trigger a series of reward processing through the hippocampal-VTA loop. Moreover, some studies have shown that reward-triggered involvement of this

loop can enhance memory consolidation (Wittmann *et al.*, 2005; Adcock *et al.*, 2006). Although these studies have primarily focused on memory encoding processes, it has recently been suggested that involvement of this loop in retrieval could provide modulatory effects such as the re-encoding of the retrieved memory in accord with its expected utility and reinforcement learning (Scimeca and Badre, 2012). Based on this function of the hippocampal-VTA loop, we speculate that the memory and reward systems (i.e. the nostalgia-related network) might be involved in resilience, as follows. Whenever nostalgia occurs, the association between the retrieved AM and its reward value as represented in the nostalgia-related network would be reinforced by dopamine transmission, such that the AM would be re-encoded and re-stored in the network. Such reinforced associations are expected to induce more positive and rewarding experiences than before when nostalgia occurs again after the reinforcement of their association, suggesting that such experiences act as resilience to overcome adversity and providing support for strong motivation to live (Routledge *et al.*, 2008; Zhou *et al.*, 2008).

Conclusions

This study confirmed activation of memory (bilateral aHPC and L.pHPC) and reward (SN/VTA and L.VS) related areas, as well as their co-activation (L.aHPC-R.VS, R.aHPC-R.VS and L.pHPC-L.VS), during nostalgia experiences elicited by visual stimuli. Furthermore, we revealed a positive correlation between memory-reward co-activation (L.aHPC-R.VS) and the nostalgia tendency, indicating that the memory and reward systems coproduce subjective experiences of nostalgia. We also found that the two dimensions of nostalgic experiences—emotional and personal significance and chronological remoteness—have differential neural correlates, such that the caudal SN/VTA and L.aHPC are involved in the former and the rostral SN/VTA is involved in the latter. Taken together, these results show that cooperative activity of memory and reward systems, where each of them has a specific role in the construction of the factors that produce the experience of nostalgia.

Acknowledgements

We thank Ai Matsuoka for assisting with the experiments and Dr Kazuo Mishima for helpful discussions and comments.

Supplementary data

Supplementary data are available at *SCAN* online.

Conflict of interest. None declared.

References

Adcock, R.A., Thangavel, A., Whitfield-Gabrieli, S., Knutson, B., Gabrieli, J.D. (2006). Reward-motivated learning: mesolimbic activation precedes memory formation. *Neuron*, **50**(3), 507–17.

Addis, D.R., Moscovitch, M., Crawley, A.P., McAndrews, M.P. (2004). Recollective qualities modulate hippocampal activation during autobiographical memory retrieval. *Hippocampus*, **14**(6), 752–62.

Barrett, F.S., Grimm, K.J., Robins, R.W., Wildschut, T., Sedikides, C., Janata, P. (2010). Music-evoked nostalgia: affect, memory, and personality. *Emotion*, **10**(3), 390–403.

Barrett, L.F. (2006). Solving the emotion paradox: categorization and the experience of emotion. *Personality and Social Psychology Review*, **10**(1), 20–46.

Berntsen, D., Hall, N.M. (2004). The episodic nature of involuntary autobiographical memories. *Memory & Cognition*, **32**(5), 789–803.

Cabeza, R., Prince, S.E., Daselaar, S.M., *et al.* (2004). Brain activity during episodic retrieval of autobiographical and laboratory events: an fMRI study using a novel photo paradigm. *Journal of Cognitive Neuroscience*, **16**(9), 1583–94.

Cabeza, R., St Jacques, P. (2007). Functional neuroimaging of autobiographical memory. *Trends in Cognitive Sciences*, **11**(5), 219–27.

Chrea, C., Grandjean, D., Delplanque, S., *et al.* (2009). Mapping the semantic space for the subjective experience of emotional responses to odors. *Chemical Senses*, **34**(1), 49–62.

Conway, M.A., Pleydell-Pearce, C.W. (2000). The construction of autobiographical memories in the self-memory system. *Psychology Review*, **107**(2), 261–88.

Davis, F. (1979). *Yearning for Yesterday: A Sociology of Nostalgia*. New York: Free Press.

Davis, P.J. (1999). Gender differences in autobiographical memory for childhood emotional experiences. *Journal of Personality and Social Psychology*, **76**(3), 498–510.

Diekhof, E.K., Kaps, L., Falkai, P., Gruber, O. (2012). The role of the human ventral striatum and the medial orbitofrontal cortex in the representation of reward magnitude—an activation likelihood estimation meta-analysis of neuroimaging studies of passive reward expectancy and outcome processing. *Neuropsychologia*, **50**(7), 1252–66.

Fink, G.R., Markowitsch, H.J., Reinkemeier, M., Bruckbauer, T., Kessler, J., Heiss, W.D. (1996). Cerebral representation of one's own past: neural networks involved in autobiographical memory. *The Journal of Neuroscience*, **16**(13), 4275–82.

Gilboa, A., Winocur, G., Grady, C.L., Hevenor, S.J., Moscovitch, M. (2004). Remembering our past: functional neuroanatomy of recollection of recent and very remote personal events. *Cerebral Cortex*, **14**(11), 1214–25.

Greenberg, D.L., Rice, H.J., Cooper, J.J., Cabeza, R., Rubin, D.C., LaBar, K.S. (2005). Co-activation of the amygdala, hippocampus and inferior frontal gyrus during autobiographical memory retrieval. *Neuropsychologia*, **43**(5), 659–74.

Holm, S. (1979). A simple sequentially rejective multiple test procedure. *Scandinavian Journal of Statistics*, **6**, 65–70.

Krebs, R.M., Heipertz, D., Schuetze, H., Duzel, E. (2011). Novelty increases the mesolimbic functional connectivity of the substantia nigra/ventral tegmental area (SN/VTA) during reward anticipation: evidence from high-resolution fMRI. *Neuroimage*, **58**(2), 647–55.

Krendl, A.C., Kensinger, E.A., Ambady, N. (2012). How does the brain regulate negative bias to stigma?. *Social Cognitive and Affective Neuroscience*, **7**(6), 715–26.

Kuhn, S., Gallinat, J. (2012). The neural correlates of subjective pleasantness. *Neuroimage*, **61**(1), 289–94.

Lisman, J.E., Grace, A.A. (2005). The hippocampal-VTA loop: controlling the entry of information into long-term memory. *Neuron*, **46**(5), 703–13.

Maguire, E.A., Frith, C.D. (2003). Lateral asymmetry in the hippocampal response to the remoteness of autobiographical memories. *The Journal of Neuroscience*, **23**(12), 5302–7.

Maldjian, J.A., Laurienti, P.J., Kraft, R.A., Burdette, J.H. (2003). An automated method for neuroanatomic and cytoarchitectonic atlas-based interrogation of fMRI data sets. *Neuroimage*, **19**(3), 1233–9.

Markowitsch, H.J., Vandekerckhove, M.M., Lanfermann, H., Russ, M.O. (2003). Engagement of lateral and medial prefrontal areas in the ecphory of sad and happy autobiographical memories. *Cortex*, **39**(4-5), 643–65.

Matsunaga, M., Bai, Y., Yamakawa, K., *et al.* (2013). Brain-immune interaction accompanying odor-evoked autobiographic memory. *PLoS One*, **8**(8), e72523.

Moriguchi, Y., Komaki, G. (2013). Neuroimaging studies of alexithymia: physical, affective, and social perspectives. *Biopsychosocial Medicine*, **7**(1), 8.

Nadel, L., Hoscheidt, S., Ryan, L.R. (2013). Spatial cognition and the hippocampus: the anterior-posterior axis. *Journal of Cognitive Neuroscience*, **25**(1), 22–8.

Piefke, M., Weiss, P.H., Markowitsch, H.J., Fink, G.R. (2005). Gender differences in the functional neuroanatomy of emotional episodic autobiographical memory. *Human Brain Mapping*, **24**(4), 313–24.

Piolino, P., Giffard-Quillon, G., Desgranges, B., Chetelat, G., Baron, J.C., Eustache, F. (2004). Re-experiencing old memories via hippocampus: a PET study of autobiographical memory. *Neuroimage*, **22**(3), 1371–83.

Poppenk, J., Evensmoen, H.R., Moscovitch, M., Nadel, L. (2013). Long-axis specialization of the human hippocampus. *Trends in Cognitive Sciences*, **17**(5), 230–40.

Routledge, C., Arndt, J., Sedikides, C., Wildschut, T. (2008). A blast from the past: the terror management function of nostalgia. *Journal of Experimental Social Psychology*, **44**(1), 132–40.

Ryan, L., Nadel, L., Keil, K., *et al.* (2001). Hippocampal complex and retrieval of recent and very remote autobiographical memories: evidence from functional magnetic resonance imaging in neurologically intact people. *Hippocampus*, **11**(6), 707–14.

Schacter, D.L., Addis, D.R. (2007). The cognitive neuroscience of constructive memory: remembering the past and imagining the future. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, **362**(1481), 773–86.

Schultz, W. (1998). Predictive reward signal of dopamine neurons. *Journal of Neurophysiology*, **80**(1), 1–27.

Scimeca, J.M., Badre, D. (2012). Striatal contributions to declarative memory retrieval. *Neuron*, **75**(3), 380–92.

Sedikides, C., Wildschut, T., Arndt, J., Routledge, C. (2006). *Affect and the Self*. New York: Psychology Press.

Shohamy, D., Adcock, R.A. (2010). Dopamine and adaptive memory. *Trends in Cognitive Sciences*, **14**(10), 464–72.

Svoboda, E., McKinnon, M.C., Levine, B. (2006). The functional neuroanatomy of autobiographical memory: a meta-analysis. *Neuropsychologia*, **44**(12), 2189–208.

Trost, W., Ethofer, T., Zentner, M., Vuilleumier, P. (2012). Mapping aesthetic musical emotions in the brain. *Cerebral Cortex*, **22**(12), 2769–83.

Tzourio-Mazoyer, N., Landeau, B., Papathanassiou, D., *et al.* (2002). Automated anatomical labeling of activations in SPM using a macroscopic anatomical parcellation of the MNI MRI single-subject brain. *Neuroimage*, **15**(1), 273–89.

Viard, A., Piolino, P., Desgranges, B., *et al.* (2007). Hippocampal activation for autobiographical memories over the entire lifetime in healthy aged subjects: an fMRI study. *Cerebral Cortex*, **17**(10), 2453–67.

Wildschut, T., Sedikides, C., Arndt, J., Routledge, C. (2006). Nostalgia: content, triggers, functions. *Journal of Personality and Social Psychology*, **91**(5), 975–93.

Wittmann, B.C., Schott, B.H., Guderian, S., Frey, J.U., Heinze, H.J., Duzel, E. (2005). Reward-related FMRI activation of dopaminergic midbrain is associated with enhanced hippocampus-dependent long-term memory formation. *Neuron*, **45**(3), 459–67.

Yamagami, T., Oosawa, M., Ito, S., Yamaguchi, H. (2007). Effect of activity reminiscence therapy as brain-activating rehabilitation for elderly people with and without dementia. *Psychogeriatrics*, **7**(2), 69–75.

Zhou, X., Sedikides, C., Wildschut, T., Gao, D.G. (2008). Counteracting loneliness: on the restorative function of nostalgia. *Psychological Science*, **19**(10), 1023–9.