

# The spatiotemporal substrates of autobiographical recollection: Using event-related ICA to study cognitive networks in action

Chris Tailby<sup>a,c,\*</sup>, Genevieve Rayner<sup>a,c,1</sup>, Sarah Wilson<sup>a,c</sup>, Graeme Jackson<sup>a,b,d</sup>

<sup>a</sup> The Florey Institute of Neuroscience and Mental Health, Austin Campus, Melbourne, VIC, Australia

<sup>b</sup> Florey Department of Neuroscience and Mental Health, The University of Melbourne, Melbourne, VIC, Australia

<sup>c</sup> Melbourne School of Psychological Sciences, The University of Melbourne, VIC, Australia

<sup>d</sup> Department of Neurology, Austin Health, Melbourne, VIC, Australia

## ARTICLE INFO

### Keywords:

Functional magnetic resonance imaging  
Autobiographical memory  
Default mode network  
Independent components analysis  
Brain networks

## ABSTRACT

Higher cognitive functions depend upon dynamically unfolding brain network interactions. Autobiographical recollection – the autoegetic re-experiencing of context rich, emotionally laden, personally experienced episodes – is an excellent example of such a process. Autobiographical recollection unfolds over time, with different cognitive processes engaged at different times throughout. In this paper we apply a recently developed analysis technique – event related independent components analysis (eICA) – to study the spatiotemporal dynamics of neural activity supporting autobiographical recollection. Participants completed an in-scanner autobiographical recollection paradigm in which the recalled episodes varied in chronological age and emotional content. By combining eICA with these cognitive manipulations we show that the brain-wide response to autobiographical recollection comprises brain networks with (i) different sensitivities to psychological aspects of the to-be-recalled material and (ii) distinct temporal profiles of activity during recollection. We identified networks with transient activations (in language and cognitive control related regions) and deactivations (in auditory and sensorimotor regions) to each autobiographical probe question, as well as networks with responses that are sustained over the course of the recollection period. These latter networks together overlapped spatially with the broader default mode network (DMN), indicating subspecialisation within the DMN. The vividness of participants' recollection was associated with the magnitude of activation in left dorsolateral prefrontal cortex and deactivation in visual association cortices. We interpret our results in the context of current theories of the spatial and temporal organisation of the human autobiographical memory system. Our findings demonstrate the utility of eICA as a tool for studying higher cognitive functions. The application of eICA to high spatial and temporal resolution datasets identifies in a single experimental protocol spatially specific networks that are recruited during cognitive activity, as well as the temporal order of activation of these networks.

## Introduction

Autobiographical memory enables the rich recollection of personally-experienced episodes from across the lifespan, incorporating details such as time, place, and emotions into a continuous sense of self (Tulving, 1983). It therefore relies upon a range of cognitive operations, including episodic memory, self-reflection, emotional processing, visual imagery, executive functions, and semantic processes (Svoboda et al., 2006). Subjective complaints of poor autobiographical memory are common in the clinical setting where they present in a variety of guises, ranging from a frustrating sense of forgetfulness, through to the complete loss of isolated recent events (transient global amnesia:

Hunter (2011); transient epileptic amnesia: Zeman and Butler (2010)) or even an entire life history (fugue: amnesia for one's life and loss of personal identity; Kihlstrom (2005)).

Functional neuroimaging has identified an extensive brain network that is consistently recruited during autobiographical recollection, the autobiographical memory network (AMN) (Andrews-Hanna et al., 2014; Buckner and Carroll, 2007; Svoboda et al., 2006). This network overlaps substantially with the resting-state 'default mode network' (DMN) (Raichle et al., 2001), and includes midline regions (medial prefrontal cortices, medial temporal cortex, retrosplenial/posterior cingulate cortex), lateral cortical regions (ventrolateral prefrontal cortex, anterolateral temporal cortex, temporoparietal junction), and the cerebellum (re-

\* Correspondence to: Melbourne Brain Centre, The Florey Institute of Neuroscience and Mental Health, 245 Burgundy Street, Heidelberg, VIC 3084, Australia.

E-mail address: [chris.tailby@florey.edu.au](mailto:chris.tailby@florey.edu.au) (C. Tailby).

<sup>1</sup> These authors contributed equally to this work.

viewed in Spreng et al. (2009) and Svoboda et al. (2006)).<sup>2</sup> There has been growing interest in decomposing the AMN into sub-networks, linking different cognitive components of autobiographical recall to different circuits within the AMN in order to better understand how the network operates as a whole (Andrews-Hanna et al., 2010; e.g. Andrews-Hanna, 2012; Andrews-Hanna et al., 2014; Bar, 2007, 2009; Binder et al., 2009; Buckner et al., 2008; Buckner and Carroll, 2007; Hassabis and Maguire, 2009; Kim, 2012; Leech et al., 2011; Schacter et al., 2007; Seghier and Price, 2012; Smallwood et al., 2012; Spreng et al., 2009). For instance, mesial temporal components of the network have traditionally been associated with memory functions *per se* (Squire et al., 2004), lateral parietal regions have been hypothesised to relate to attentional processes that operate during memory search and retrieval (Cabeza, 2008; Cabeza et al., 2008; Ciaramelli et al., 2008; Wagner et al., 2005), anterolateral temporal regions are thought to support semantic contributions to autobiographical recollection (Irish and Piguet, 2013), and medial prefrontal cortex is postulated to support social and self-referential processes and emotional function (Gusnard et al., 2001; Raichle, 2015; Van Overwalle, 2009).

A variety of experimental approaches have been used in an effort to parcellate the AMN. For instance, Piefke et al. (2003) showed that manipulation of the recency and emotional valence of autobiographical memories resulted in differences in the topology of fMRI-measured activation patterns. Conversely, by explicitly considering the temporal dynamics of evoked activity, Daselaar et al. (2008, using subjective reports of the timing of cognitive processes) and Addis et al. (2004, using a multivariate analysis technique, partial least squares) have sought to use response timing information to disentangle different neural contributions to the autobiographical recollection process.

The primary aim of the present work was to delineate subsystems within the broader AMN by applying a novel multivariate analysis technique, event-related independent components analysis (eICA, Masterton et al., 2013), to BOLD data acquired while participants completed an in-scanner autobiographical memory paradigm modelled on those of Piefke et al. (2003) and Rekkas and Constable (2005). We originally developed eICA in order to investigate spatiotemporal patterns of neural activity associated with EEG identified epileptiform events. The technique, however, is applicable to any event-related data; we apply it here, for the first time, to cognitive event-related data. eICA first estimates the event-related response at each voxel (via deconvolution), then identifies networks by applying spatial ICA to the set of estimated event-related responses. Thus, unlike univariate analysis methods, eICA makes no prior assumptions about the shape of the hemodynamic response. It therefore has the potential to offer important insights into the spatiotemporal structure of neurocognitive functions. We hypothesise that the broader AMN will decompose into a set of discrete sub-networks subserving emotional valence, recency, and other recollection-related cognitive processes, each with their own distinct temporal signature.

## Materials and methods

### Participants

12 healthy, right-handed individuals participated in this study (8 females and 4 males; mean age=30.33 ± 9.34 years). None had any history of neurological or psychiatric illness. All participants provided written informed consent in accordance with the Declaration of Helsinki, with the study approved by the relevant Human Research Ethics Committees.

<sup>2</sup> For convenience we refer to the AMN and DMN as distinct entities, although acknowledge that they show extensive overlap. We use AMN to refer to the network identified through activation studies of autobiographical recollection, and DMN to refer to the network identified via methods such as resting state connectivity and task-related deactivation.

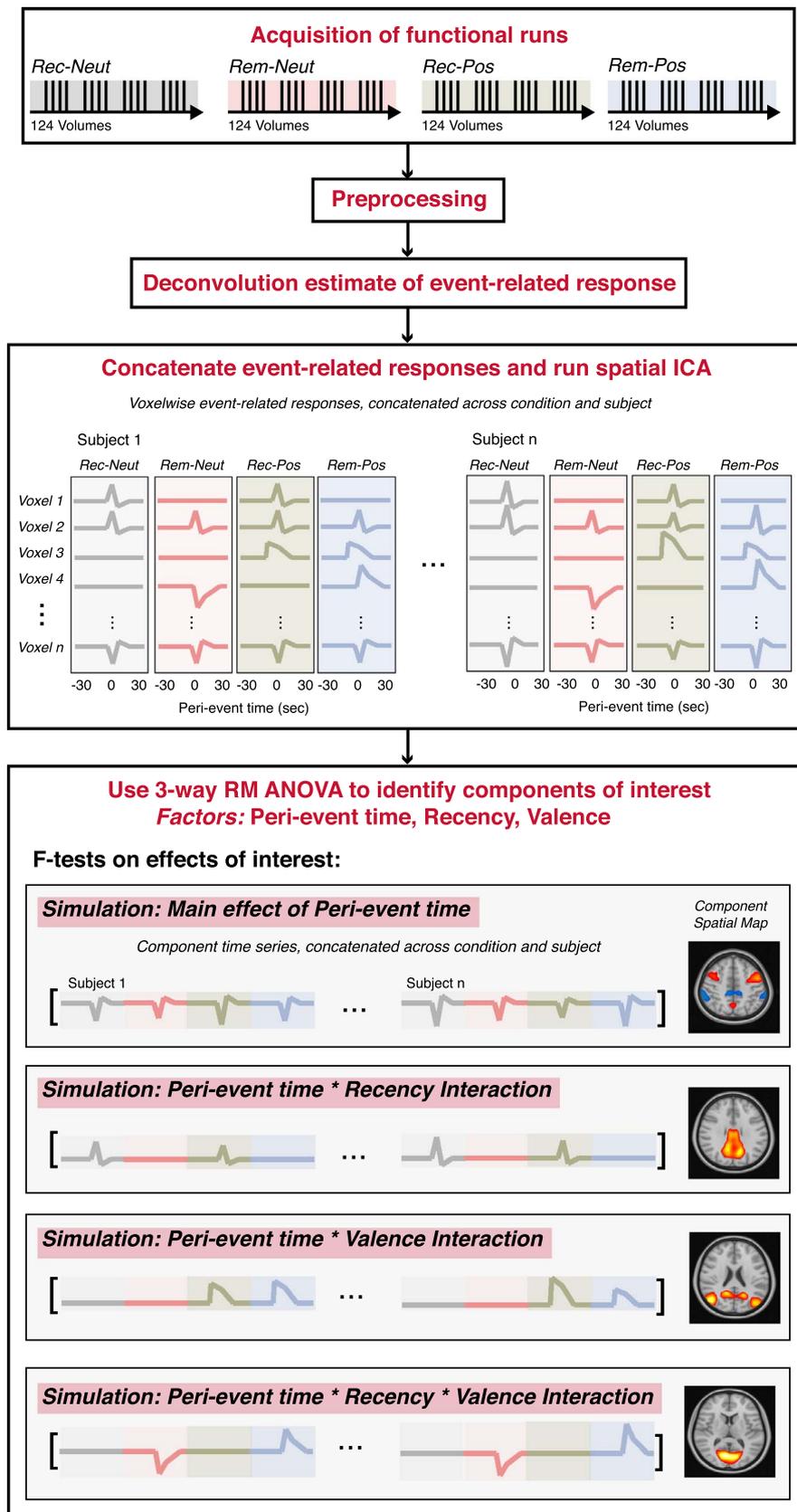
### Autobiographical memory paradigm

The autobiographical memory paradigm used probe questions to stimulate autobiographical recollection. To separate elements of the AMN sensitive to the recency and emotional valence of autobiographical memories, we constructed a set of probe questions designed to manipulate these factors: *Recency* (two levels: *Recent* and *Remote*) and *Emotional Valence* (referred to hereafter simply as *Valence*; two levels: *Neutral* and *Positive*). One of the difficulties in studying autobiographical memory has been controlling for the different life experiences of individual participants. To overcome this, in the present study the examiner covertly orchestrated a standardised set of experiences for the 24 h preceding the scan (adapted from Rekkas and Constable (2005)). The day before the scan the examiner phoned the participant and introduced scripted topics of conversation (e.g. MR safety questions, directions to Institute, parking options, confirm details of scan time), and on the day of the scan the examiner greeted the participant and several scripted exchanges again took place (e.g., telling a joke, offering a baked good, asking about hobbies, asking about music preferences). The pre-scan protocol and the full set of in-scanner probe questions are available as [Supplementary material](#).

In-scanner probe questions interrogated scripted elements of these interactions (such as where the examinee was when they received the phone call, being offered a baked good, et cetera), thereby tapping *recent* autobiographical memories common to all participants. For *remote* autobiographical memories, probe questions related to generic aspects from the primary and high school years (~5–15 years of age), such as birthday parties, school teachers, and the examinee's bedroom as a teenager.

In order to manipulate *Valence*, 50% of the *Recent* and *Remote* autobiographic memories were designed not to elicit any strong emotion (*Neutral* valence) and 50% were designed to elicit positive emotion (*Positive*). *Neutral* questions targeted presumptively mundane matters, such as a *Recent-Neutral* memory where examinees were asked where they were when the examiner phoned them, and what they did after the phone call. *Positively*-valenced questions targeted presumptively pleasurable life experiences such as a primary school birthday party (*Remote-Positive*). As in Rekkas and Constable (2005), participants were instructed to “retrieve specific events involving the particular person, place, or thing referenced by the probes and to mentally reflect or put themselves back in those situations to the best of their ability”, and to use the full duration of each trial to “mentally explore and visualise each particular situation” to recall as many details as possible. Participants were advised that the questions were there to serve as a general guide, rather than define or limit the retrieval experience. To control for basic cognitive factors considered *a priori* to be unrelated to autobiographical memory *per se* (such as visual stimulation, reading, et cetera) participants were presented with ‘baseline’ semantic questions designed to evaluate the retrieval of ‘factual’ knowledge (e.g. “Is a carrot orange?”).

All stimuli were presented using white font against a black background. A given run began with presentation of six baseline semantic knowledge questions, each displayed for 6 s (36 s total). This was then followed by four autobiographical memory questions, each presented for 5 s with an additional 7 s period (during which the screen was black) provided for exploration and elaboration of the probed recollection (i.e. 12 s inter-question-interval, 48 s total). The first question in each block of four established a general topic for which the participant was asked to recall a particular autobiographical memory (e.g. recall ‘... a high school party or social?’), and the subsequent three questions were designed to promote more detailed exploration of this memory (e.g. recall ‘...where it was held?’). Five baseline blocks of semantic questions were alternated with four task-active blocks of autobiographical memory questions, yielding a run length of 372 s (124 volumes; see Fig. 1, panel 1).



**Fig. 1.** Experimental design and analysis. Top: each of four experimental runs comprised a series of autobiographical memory probe questions (black vertical lines) interspersed with baseline semantic knowledge questions. Each run was then preprocessed within SPM12 using a standard pipeline (see text). The event-related response was then estimated in each voxel via deconvolution using a Fourier Basis Set, with autobiographical questions specified as the events of interest. The collection of voxelwise event-related responses was then concatenated across conditions and participants, and spatial ICA performed on this concatenated data. Note that the concatenated data are shown here arranged as voxels by time, facilitating visualization of the event-related responses, however in the ICA equation itself the concatenated data are arranged as time by voxels (see Eq. (4)). The resulting components (hypothetical examples of which are shown in the bottom panel) were analysed via three way repeated measures ANOVA. Note that for the components shown in the bottom panel, hot and cool colours in the spatial maps denote positive and negative weightings on their associated time courses, respectively. For instance, the component shown at bottom is anchored in medial occipital cortex, with the weighting map indicating deactivation in response to *Remote-Neutral* memories (pink trace) and activation in response to *Remote-Positive* memories (blue trace).

### Image acquisition and preprocessing

Images were acquired on a 3 T Siemens Skyra scanner (Siemens, Erlanger, Germany) using a 20 channel head coil. A whole brain gradient-echo single shot echo-planar T2\*-weighted sequence was used to acquire data sensitive to the BOLD signal (repetition time=3000 ms; echo time=30 ms; field of view=216 mm×216 mm; 72×72 imaging matrix; 44 contiguous slices). Resolution was 3 mm×3 mm in-plane, with 3-mm thick axial slices.

Pre-processing was performed using Statistical Parametric Mapping software (SPM8; Wellcome Department of Imaging Neuroscience, University College London, UK) and included: slice-timing correction; rigid-body realignment to correct for subject motion (Friston et al., 1995); coregistration to T1; non-linear spatial normalization to SPM standard space (“MNI space”; Montreal Neurological Institute, McGill University, Canada) using (Ashburner et al., 1999); re-sampling into 2 mm isotropic voxels; and spatial smoothing with an isotropic Gaussian kernel (FWHM=8 mm).

### eICA analysis

The details of eICA analysis have been published previously (Masterton et al., 2013). Here, we use group eICA, performed upon temporally concatenated data as described therein. The first step of the analysis uses deconvolution to estimate the event-related response at each voxel; this initial deconvolution step is performed separately for each condition in each participant. Spatial independent components analysis (ICA) is then applied to the collection of voxel-wise event-related responses, temporally concatenated across participants and conditions. This yields a set of spatially independent networks (components), each with an associated set of event-related temporal responses (concatenated across participants and conditions). Note the distinction from most conventional applications of ICA to fMRI: in eICA the ICA is not applied to the entire (concatenated) fMRI time-series; it is only applied to the (concatenated) event-related time-courses at each voxel. This will yield a relatively small number of independent components. The deconvolution step is required to parse out the event-related response from the temporally overlapping responses to separate events (the temporal overlap, due to HRF “smearing”, precludes the use of a procedure such as averaging of temporally aligned events to estimate the event-related response).

For a given condition in a given participant, the deconvolution at each voxel,  $i$ , is performed by fitting the following general linear model (GLM):

$$y_i = \mathbf{X}\boldsymbol{\beta}_i + \boldsymbol{\eta}_i,$$

where,  $\mathbf{y}_i$  is a column vector containing the time-course of BOLD signal intensities measured at voxel  $i$ ;  $\mathbf{X}$  is a design matrix;  $\boldsymbol{\beta}_i$  is the vector of weighting parameters and  $\boldsymbol{\eta}_i$  is Gaussian noise with variance,  $\sigma_i^2$ , and autocorrelation matrix,  $\mathbf{R}_i$ , i.e.  $\boldsymbol{\eta}_i \sim \mathcal{N}(0, \sigma_i^2 \mathbf{R}_i)$ . The design matrix implements a linear deconvolution with the columns containing regressors created by convolving a stick function representing the event-timings with a set of linear basis functions (Henson, 2003). Each autobiographical memory probe question was specified as an event. The event-related response was estimated over a 33 s *Peri-event time* window (11 TRs), beginning 2 TRs (6 s) prior to event onset and extending 9 TRs (27 s) from event onset. The deconvolution at each voxel was estimated using a Fourier Basis Set of order 5 (corresponding to 11 basis functions, yielding  $p=11$  parameter estimates of interest), specified using the *fMRI model specification* module in SPM12. The design matrix also included the six estimated motion parameters, their square, their temporal derivative, and the square of their temporal derivatives (Friston et al., 1996). High motion volumes (frame wise displacement > 1 mm), and the subsequent two volumes, were also modelled in the design matrix, as stick functions at the corresponding time points (Lemieux et al., 2007). Model estimation included a high-

pass filter (cut-off=128 s) to remove low-frequency signal fluctuations.

Whitening is performed on the parameter estimates ( $\boldsymbol{\beta}_i$ ) to make the errors independent and identically distributed. This requires a voxel-wise estimate,  $\hat{\sigma}_i^2$ , of the noise variance which can be obtained from the residuals after the GLM fit. A whitening filter,  $(\hat{\sigma}_i \mathbf{K})^{-1}$ , is then formed via the Cholesky decomposition of this estimated error covariance matrix:

$$\mathbf{K}\mathbf{K}^T = \text{pinv}(\mathbf{R}_i)\text{pinv}(\mathbf{R}_i)^T, \quad (1)$$

which is used to provide whitened parameters estimates,  $\hat{\mathbf{b}}_i$ , for each voxel (where  $\text{pinv}(\mathbf{R}_i)$  denotes the pseudoinverse of  $\mathbf{R}_i$ ):

$$\hat{\mathbf{b}}_i = (\hat{\sigma}_i \mathbf{K})^{-1}(\mathbf{I} - \mathbf{D})\hat{\boldsymbol{\beta}}_i + \mathbf{D}\hat{\boldsymbol{\beta}}_i = (\hat{\sigma}_i \mathbf{K})^{-1}(\mathbf{I} - \mathbf{D})\boldsymbol{\beta}_i + \mathbf{D}\boldsymbol{\beta}_i + (\hat{\sigma}_i \mathbf{K})^{-1}\mathbf{e}_i = \mathbf{b}_i + \mathbf{e}_i, \text{ where } \mathbf{D}_{ij} = p^{-1} \text{ for all } i \text{ and } j, \text{ and } \mathbf{e}_i \sim \mathcal{N}(0, \mathbf{I}).$$

These whitened parameter estimates provide columns for the estimate,  $\hat{\mathbf{B}}$ , of the event related BOLD signal changes, i.e.:

$$\hat{\mathbf{B}} = [\hat{\mathbf{b}}_1 \hat{\mathbf{b}}_2 \dots \hat{\mathbf{b}}_n] = \mathbf{B} + \mathbf{E}, \text{ where } \mathbf{B} = [\mathbf{b}_1 \mathbf{b}_2 \dots \mathbf{b}_n] \text{ and } \mathbf{E} = [\mathbf{e}_1 \mathbf{e}_2 \dots \mathbf{e}_n]. \quad (2)$$

Mathematically, the BOLD signal changes,  $\mathbf{B}$ , concatenated across conditions and participants, are modelled as a  $(p \times c \times s) \times n$  matrix representing the event-related signal captured by  $p$  basis function parameter estimates  $\times c$  conditions  $\times s$  participants and  $n$  voxel locations. This event-related signal is assumed to reflect a mixture of a small (unknown) number,  $q$ , of independent spatial sources (with the requirement that  $q < (p \times c \times s)$ ). This model is represented as:

$$\mathbf{B} = \mathbf{A}\mathbf{S} + \mathbf{M}, \text{ where } \mathbf{M} = \mathbf{m} \times \mathbf{1} \quad (3)$$

where  $\mathbf{S}$  is a  $q \times n$  matrix of (zero-mean) spatial sources;  $\mathbf{A}$  is a  $(p \times c \times s) \times q$  mixing matrix,  $\mathbf{m}$  is a  $(p \times c \times s) \times 1$  vector of spatial means across all voxels at each time-point, and  $\mathbf{1}$  is a  $1 \times n$  vector of all ones.

Substituting Eq. (2) into Eq. (3) gives:

$$\hat{\mathbf{B}} = \mathbf{A}\mathbf{S} + \mathbf{M} + \mathbf{E}. \quad (4)$$

Probabilistic ICA (Beckmann and Smith, 2004) is then used to provide estimates,  $\hat{\mathbf{A}}$  and  $\hat{\mathbf{S}}$ , of the spatial sources and mixing matrix in Eq. (4). This yields a set of component spatial weighting maps, each with an associated time course comprising a set of event-related responses that have been concatenated across participant and condition. Given our experimental design (4 conditions) and analysis approach (a peri-event time window of 11 TRs; 12 participants), the time course estimated for each component is a vector that is  $11 \times 4 \times 12 = 528$  elements long. Each 528-element group-component time-course vector can be rearranged to yield each participant's event-related response for each condition. This data can then be fed into a repeated measures ANOVA to assess for effects of *Peri-event time*, *Recency*, *Valence*, and their interactions (see below).

The eICA procedure was implemented in Matlab (R2013a, The Mathworks, Natick, MA, USA) using SPM12 to perform the GLM parameter estimation, and the FastICA and ICASSO toolboxes (Himberg et al., 2004; Hyvärinen, 1999) to perform the ICA decomposition. The number of independent components ( $n=35$ ) was estimated using Bayesian model-order selection based upon the eigenvalues of the sample covariance matrix (Minka, 2000), and principle component analysis (PCA) was used to project the data into this signal sub-space. The FastICA algorithm used the symmetric approach and hyperbolic tangent as the contrast function. The ICASSO procedure, which minimises the variability that is inherently associated with FastICA estimation due to the stochastic nature of the algorithm, ran 30 iterations of the algorithm with bootstrap re-sampling and randomisation of initial conditions.

### Identification of components reflecting consistent event-related responses across participants

The output of ICA is a set of components, some of which are presumed to reflect “meaningful” brain networks, others to reflect noise. In order to identify “meaningful” group-level components we start with the assumption that such components will show a relatively consistent event-related response that varies systematically across participants as a function of time and condition, whereas artefactual noise-related components will not (Masterton et al., 2013). Therefore to test our hypothesis that distinct sub-networks subserve different aspects of autobiographical recollection (such as emotional valence and recency), each with its own distinct temporal signature, we performed a 3-way repeated measures ANOVA (factors: *Recency*, 2 levels; *Valence*, 2 levels; *Peri-event time*, 11 levels) on each component, using as inputs the condition specific time-courses estimated for that component in each participant (see Fig. 1). For each component we tested for the following effects of interest:

- (1) a main effect of *Peri-event time*: would indicate a time varying response, the shape of which is unaffected by *Recency* or *Valence* (Fig. 1, bottom panel, top row).
- (2) a *Recency\*Peri-event time* interaction: a time-varying response that varies in shape as a function of *Recency* irrespective of *Valence* (Fig. 1, bottom panel, second row);
- (3) a *Valence\*Peri-event time* interaction: a time-varying response that varies in shape as a function of *Valence* irrespective of *Recency* (Fig. 1, bottom panel, third row); and
- (4) a *Recency\*Valence\*Peri-event time* interaction: this would indicate that the estimated event-related response varies (consistently across participants) as a function of *Recency*, *Valence*, and *Peri-event time* (Fig. 1, bottom panel, bottom row);

[As we were *a priori* only interested in effects manifesting as BOLD signal fluctuations varying systematically as a function of peri-event time, we did not examine for main effects of *Recency* (averaged across *Valence* and *Peri-event time*) or *Valence* (averaged across *Recency* and *Peri-event time*)] We used Bonferroni correction ( $p < 0.05$ ) in order to control for multiple comparisons in assessing these F-tests (140 tests total: 35 components multiplied by four F-tests per component;  $p_{crit}=0.00036$ ). Repeated measures ANOVAs were performed in Matlab (R2014b, The Mathworks, USA) using the *fitrm* function, applying the Greenhouse-Geisser correction for violations of sphericity. Significant effects of interest were followed up using the Matlab command *multcompare*, specifying ‘ComparisonType’ as ‘tukey-kramer’ and ‘Alpha’ as 0.00036. For those components in which there was a significant *Recency\*Peri-event time* interaction we use asterisks to identify the TRs for which the estimated response in the Recent condition is significantly different from that in the Remote condition (see Fig. 3). To avoid clutter in the figures, for components with a main effect of *Peri-event time* we do not indicate which time bins are significantly different from one another (there are 55 possible comparisons, as many as 16 of which are significant for a given component in our data). We used dual regression (Beckmann et al., 2009; Filippini et al., 2009) to threshold, for display purposes, the spatial weighting maps of those components with significant effects of interest (feature threshold:  $p < 0.001$ ; FDRc  $< 0.00036$ ).

### Calculation of composite z-maps combined across components

To enable visualisation of the collection of networks for which a given effect of interest was significant we created a composite component map by combining the dual regression cluster thresholded t-maps from the relevant components. These composite t-maps were created by taking, at each voxel, the signed maximum absolute t-value across the individual cluster thresholded t-maps.

### Correlation analysis between visual imagery and fMRI measures

Following scanning participants completed a modified version of the Vividness of Visual Imagery Questionnaire (VVIQ; Amedi et al., 2005) that quantifies the subjective vividness of participants' mental imagery (Score range=16–80). To identify brain regions where task-evoked BOLD signal fluctuations were significantly correlated with the vividness of recollection we conducted Pearson product-moment correlational analyses between VVIQ scores and an estimate of the BOLD response in each participant. We estimated the BOLD response for participant  $x$  in component  $y$  as the integral, from 3 to 15 s following presentation of the probe question (corresponding to the mauve shaded region in the time course of Fig. 5), under that participant's estimated event-related response (averaged across conditions) for that component.

### Results

Of the 35 components recovered by eICA, 11 had significant effects of interest (see Methods). Three components had significant *Peri-event time\*Recency* interactions. Two of these components also exhibited a significant main effect of *Peri-event time*. An additional eight components had a significant main effect of *Peri-event time* in the absence of any interactions. No components had significant *Peri-event time\*Valence* or *Peri-event time\*Recency\*Valence* interactions.

Fig. 2A shows the composite map derived by combining the 10 components with a significant main effect of *Peri-event time*. The map reveals an activation pattern with a strong resemblance to the AMN (as defined by activation studies, Andrews-Hanna et al. (2014)), as well as to the DMN (as defined by task-related deactivation and resting state studies, reviewed in Raichle (2015)). There are major hubs of activation bilaterally in posterior cingulate cortex, precuneus, retrosplenial cortex, parahippocampal gyrus, hippocampus, medial and ventrolateral prefrontal cortex, lateral inferior parietal cortex, superior temporal sulcus, and cerebellum. There is also notable task-related deactivation, primarily in primary sensory and motor areas.

Fig. 2B shows the composite map of the three components showing significant *Recency\*Peri-event time* interactions (each of these components showed stronger responses for *Recent* memories, see below). This map has strong activation within posterior regions of the AMN (medially in posterior cingulate cortex and precuneus; laterally in the vicinity of the TPO junction), as well as in bilateral superior temporal sulcus and right cerebellum.

In the following sections we consider the different components contributing to the composite maps shown in Fig. 2.

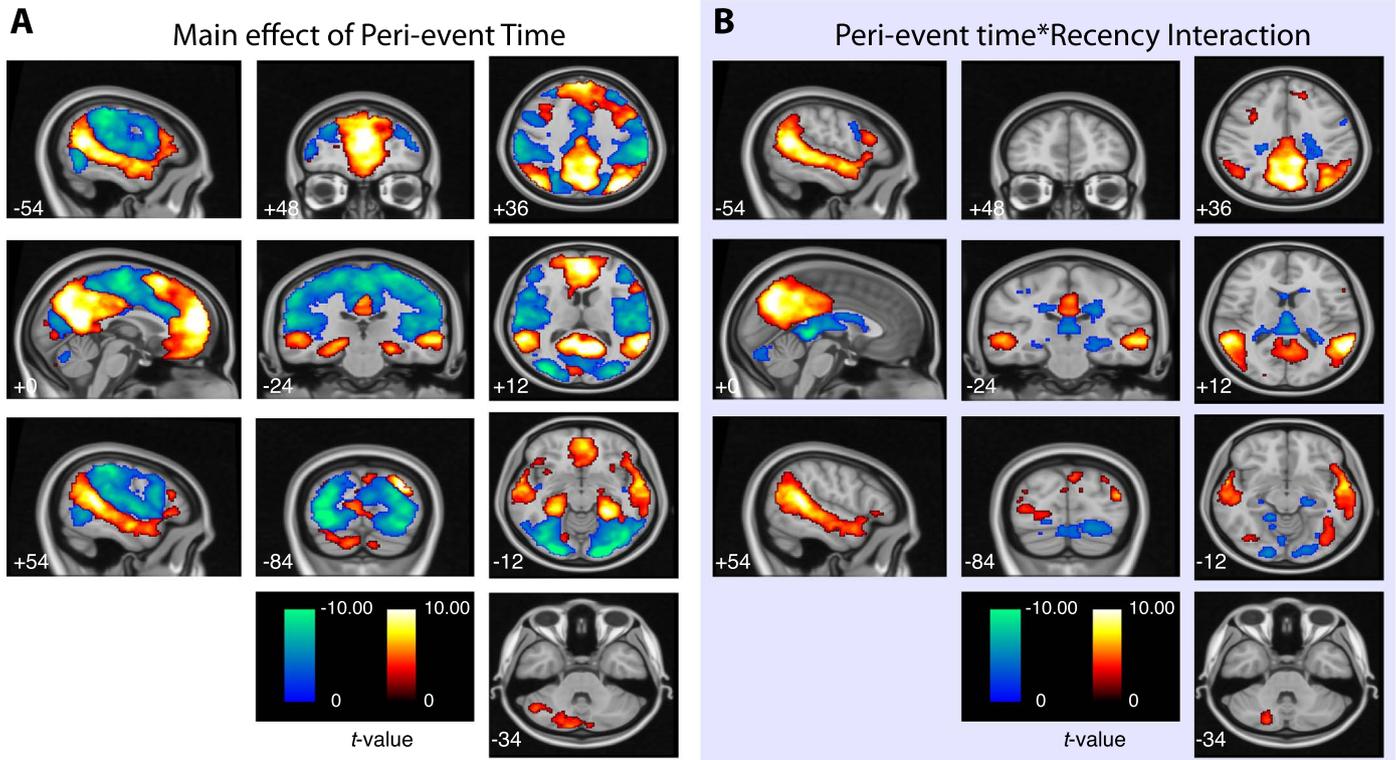
### Recent memories evoke stronger activation in superior temporal sulcus and posterior AMN

The three components for which there was a significant *Recency\*Peri-event time* interaction are shown in Fig. 3. The component in panel A, with bilateral (left greater than right) activation along the length of superior temporal sulcus, shows relatively transient activation for both *Recent* (red curve) and *Remote* (blue curve) memories, with the activation being greatest for *Recent* memories. The components in panels B and C, on the other hand, exhibit relatively sustained responses to *Recent* memories with negligible BOLD signal change for *Remote* memories. Together, the components in B and C show considerable overlap with posterior regions of the AMN (medially in posterior cingulate and precuneus; laterally near TPO junction).

### Other sub-networks to emerge have a distinct temporal signature during autobiographic recollection

Fig. 4 shows the remaining eight significant components, all of which were characterised by a significant main effect of *Peri-event time*. Some familiar network components are apparent, including

## Composite IC Maps



**Fig. 2.** Composite eICA maps. *A*: composite effect map (see Methods) from 10 components with a significant main effect of *Peri-event time*. Selected slices shown in sagittal (left column), coronal (middle column) and axial slices (right column). Hot/cool colours show regions with an initial increase/decrease in BOLD signal following presentation of autobiographical probe questions. The network shown in hot colours resembles the AMN as identified in previous meta-analyses (Andrews-Hanna et al., 2014; Svoboda et al., 2006). *B*: composite effect map for the three components with a significant *Recency\*Peri-event time* interaction. The individual component spatial maps contributing to the composite map were thresholded, via dual regression, at feature threshold  $p < 0.001$ , FDR  $< 0.00036$  (see Methods).

activation in a left-biased language-like network (opposed to deactivation in bilateral supramarginal gyrus and precuneus) (Fig. 4A), deactivation in sensorimotor cortex (C), deactivation in a frontoparietal and lateral occipitotemporal attentional network (E), and deactivation in visual networks (F,H). The components in Fig. 4D and G comprise subregions of the AMN: medial prefrontal cortex (G), and a network of areas including retrosplenial cortex extending bilaterally down through lingual and parahippocampal gyri into hippocampus (along with superior parietal lobule and superior frontal sulcus, see Supplementary material, D). The component in Fig. 4B shows deactivation in auditory and opercular somatosensory cortices opposed to activation in an attention-like network involving bilateral superior and middle frontal gyri plus right cerebellum (Fig. 4B).

*Event-related responses in AMN regions are more sustained than those in primary cortical and attention-related regions*

As well as describing components in terms of their topology, eICA also provides detailed information about the temporal dynamics of the response. In Figs. 3 and 4 the components have been arranged vertically on the basis of approximate latency to peak amplitude, to facilitate comparisons of both the latency and the transience of event related responses. For instance the components in Fig. 3A and Fig. 4A,B,F,H are relatively transient, whereas those in Fig. 3B,C and Fig. 4C,D,E,G appear more sustained. All of the component time courses are shorter than would be predicted by convolving the HRF with a boxcar function modelling the 12 s recollection period (thin grey line on time-course plots in Fig. 4). Broadly speaking, the most sustained activations are observed in those components that overlap the AMN (Fig. 3B,C and Fig. 4D,G), and deactivations in somatomotor regions and a frontoparietal attention-like network (Fig. 4C and E).

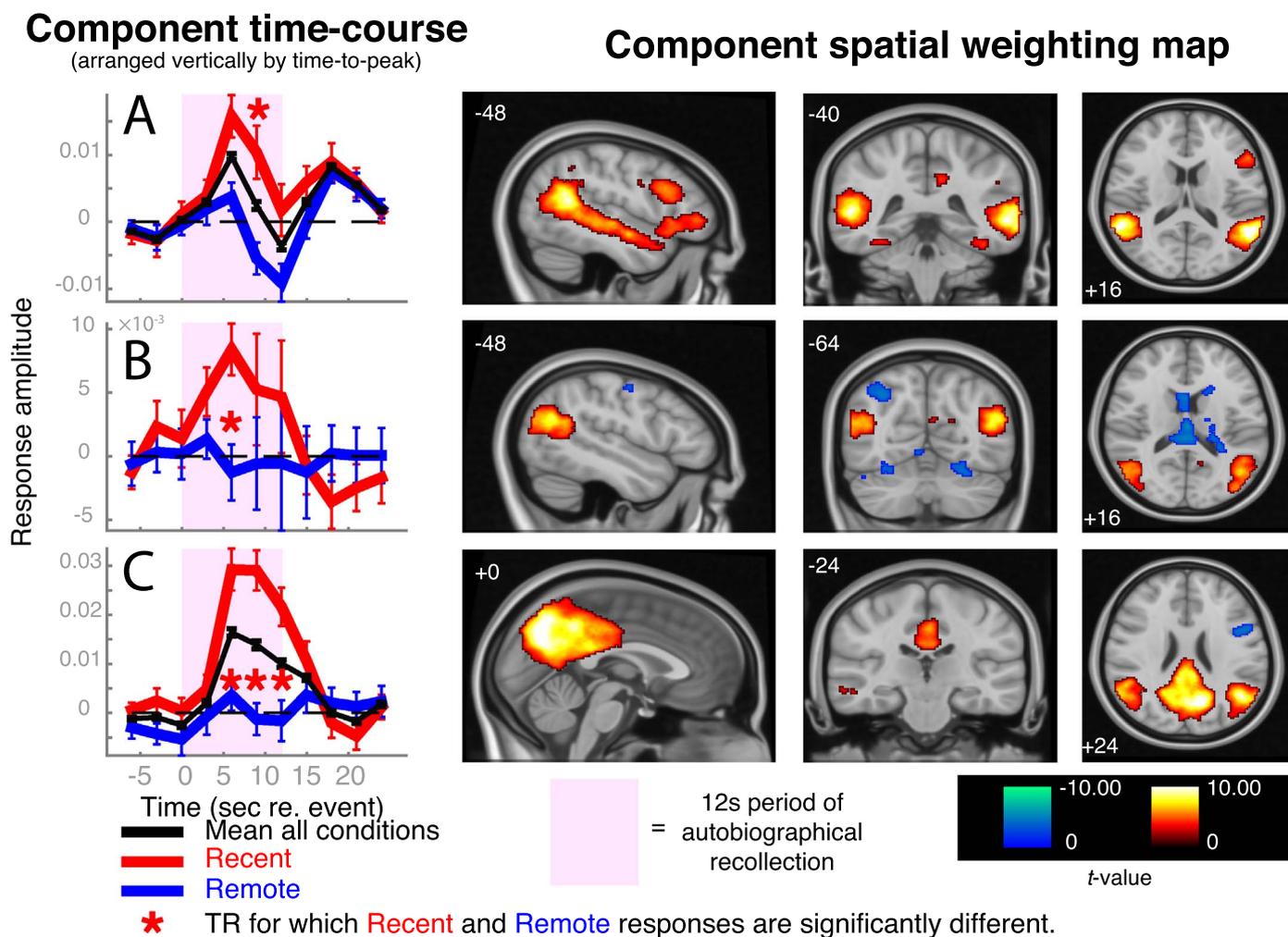
*Better visual imagery is associated with deactivation in association visual cortex*

We regressed participants' VVIQ scores against the estimated BOLD response observed in the 11 components with a significant effect of interest. One component, that shown in Fig. 4F, exhibited a significant ( $p < 0.0045$  [0.05/11]) positive correlation ( $r = 0.81$ ,  $p = 0.0014$ ; 95% confidence interval:  $0.44 < r < 0.94$ ). Additional slices through this component are shown in Fig. 5. As noted above, in relation to Fig. 4, this component shows significant deactivation throughout visual association cortex. It also exhibits activation in left middle frontal gyrus. The positive correlation indicates that as the BOLD response increases in this frontal region and decreases in visual association areas, the vividness of visual imagery increases.

## Discussion

This study applied eICA to brain activity measured during a high level cognitive operation – autobiographical recollection. The technique was able to capture the broader AMN as described in previous studies (Andrews-Hanna et al., 2014; Buckner and Carroll, 2007; Svoboda et al., 2006). It did so, however, in a purely data-driven manner, parcellating brain-wide patterns of recollection-related neural activity into a set of brain networks with distinct spatiotemporal profiles of task-related activity. The collection of networks recovered by eICA includes some that were activated during recollection (e.g., networks for introspection, language, memory, social processing), some that were deactivated during recollection (sensory and motor networks; networks for externally-oriented attention), and some that were sensitive to the recency of the to-be-recalled material.

The broader AMN, as described here and elsewhere (Andrews-



**Fig. 3.** Time-courses (left), and their associated spatial weighting maps (right), for the three components in which there is a significant *Peri-event time\*Recency* interaction ( $p < 0.00036$ ). Components have been arranged so that the time-to-peak of the event related response increases going from top to bottom. Error bars show standard errors of the mean. All time courses are signed such that the initial post-event response has a positive slope (event onset is at peri-event time=0, shown by the left edge of the purple-shaded region). Thus, as hot and cool colours in the spatial maps indicate positive and negative weightings on the component time course, they can be interpreted as “activations” and “deactivations”, respectively. Mauve shaded vertical bar shows timing of the autobiographical question (0=question onset; 12 s allowed for question-cued recollection). Spatial maps have been thresholded, via dual regression, at feature threshold:  $p < 0.001$ ,  $FDRc < 0.00036$ .

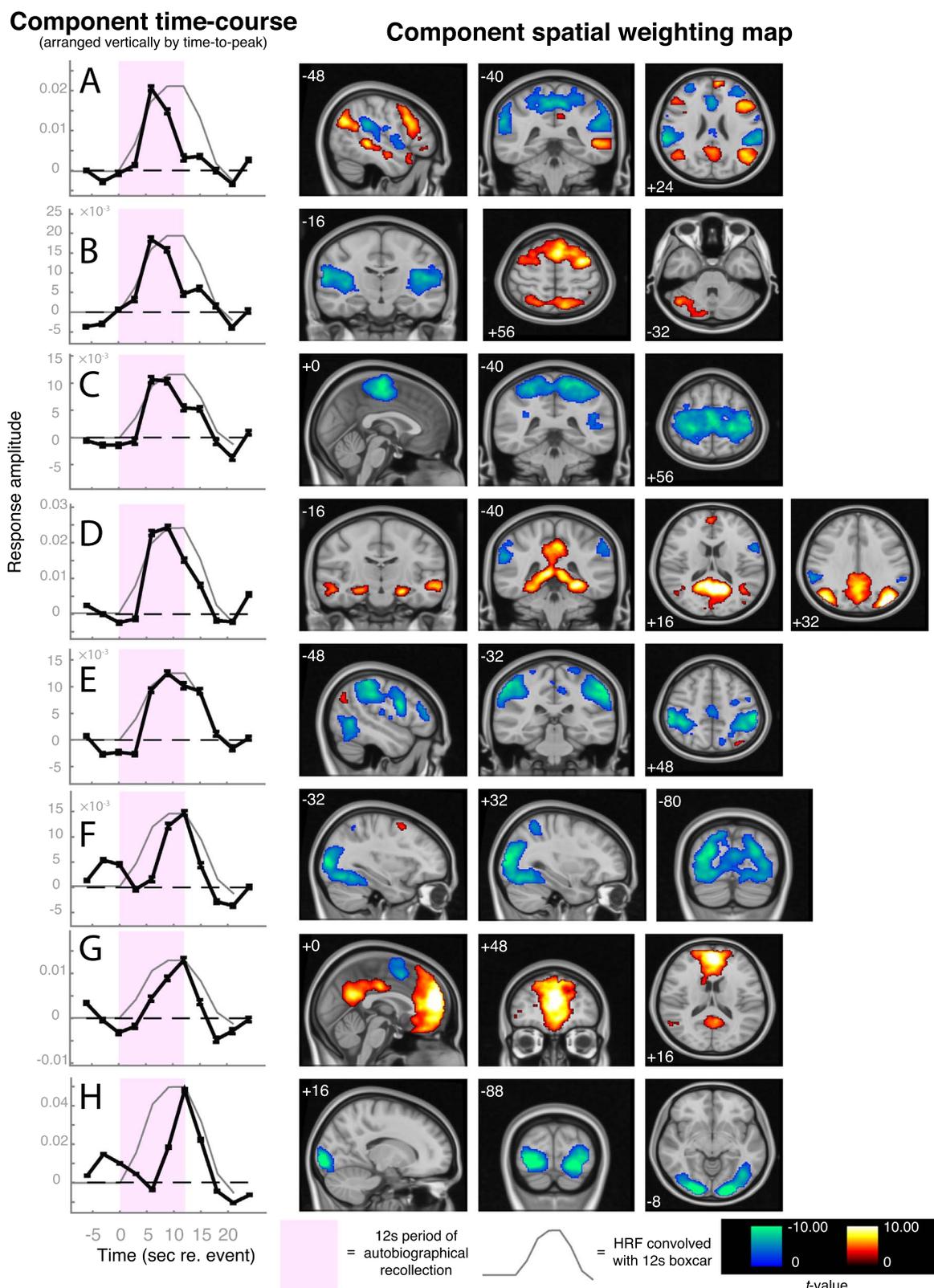
Hanna et al., 2014; Buckner and Carroll, 2007; Piefke et al., 2003; Steinworth et al., 2006; Svoboda et al., 2006), overlaps substantially with the DMN (Raichle et al., 2001). Our data indicate that the larger AMN – and, therefore, the DMN – can be fractionated into separate subnetworks on the basis of the *Recency* of autobiographical memories recalled, and the dynamics of activity during recollection. This suggests functional specialisation within different elements of the AMN. Such functional specialisation within this collection of brain regions is also implied by recent task- (Andrews-Hanna et al., 2010, 2014; Buckner and Carroll, 2007; Sestieri et al., 2011; Spreng et al., 2009) and rest-based (Andrews-Hanna et al., 2010, 2014; Buckner et al., 2008; Uddin et al., 2009) analyses of the DMN. In the following we consider the potential roles of the different networks that contribute to the broader AMN, as revealed by our analyses.

#### *Posterior, but not anterior, midline DMN activation depends upon the recency of the memory*

Two midline DMN components extracted from the AMN show dissociable contributions to autobiographic recall. The posterior component shown in Fig. 3C includes a major hub anchored in precuneus, posterior cingulate cortex, and retrosplenial cortex, the postero-medial core of the DMN. This component was activated by Recent, but not

Remote, memories, consistent with previous reports of recency effects in these regions (Niki and Luo, 2002; Piefke et al., 2003; Rekkas and Constable, 2005; Steinworth et al., 2006). Sheldon and Levine (2013) (see also Niki and Luo (2002)) have argued that greater activation for recent memories may relate more to vividness than age of the memory per se, with recent memories being recovered with richer sensory detail than their remote counterparts, which may instead rely upon more schema-like or semanticised representations (Cabeza and St Jacques, 2007; Piolino et al., 2002; Sheldon and Levine, 2013) supported outside of this posteromedial hub.

The other major midline hub of the DMN is located anteriorly, in medial prefrontal cortex (Gusnard et al., 2001; Raichle et al., 2001), and corresponds closely to the component shown in Fig. 4G. Activation in this component of the DMN dissociated from that in posteromedial DMN (Fig. 3C) in that it was not sensitive to the recency of the recollected material, and it engaged in the retrieval process slowly, rising to a late peak ~3 TRs following the probe question. This suggests a slow unfolding recruitment of this region during the recollection process. Medial prefrontal cortex has been implicated in social cognition (Van Overwalle, 2009), self-referential processing (Aminoff et al., 2013; Andrews-Hanna et al., 2014; Heatherton et al., 2006; Raichle, 2015), and emotion processing (Gusnard et al., 2001), all intimately involved in autobiographical recollection.

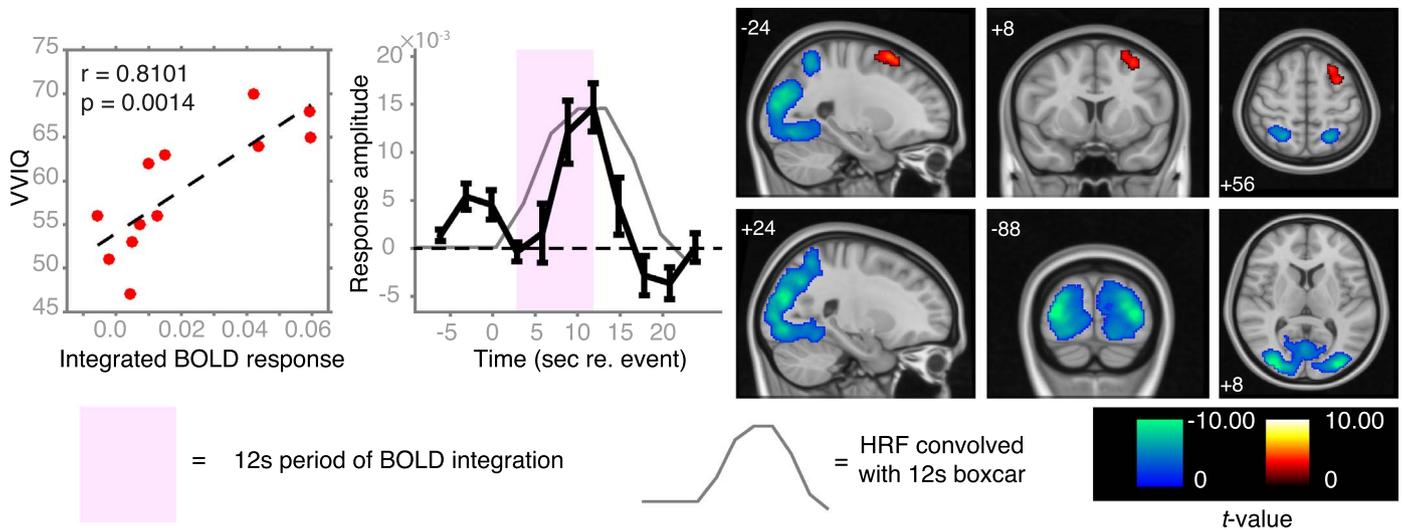


**Fig. 4.** Time-courses (left), and their associated spatial weighting maps (right), for components in which there is a significant main effect of *Peri-event time* ( $p < 0.00036$ ). Conventions as in Fig. 3. Thin grey lines on time-course plots show canonical HRF convolved with a 12 s boxcar. Spatial maps have been thresholded, via dual regression, at feature threshold:  $p < 0.001$ ,  $FDRc < 0.00036$ .

*A unified parahippocampal/retrosplenial system supporting efficient encoding of context*

The component shown in Fig. 4D extends from retrosplenial cortex down through lingual gyrus to medial temporal cortex bilaterally, along

with activation in lateral parieto-occipital cortex. The medial elements of this component have been considered to form an hierarchical functional unit representing successively higher degrees of contextual association (Aminoff et al., 2013; Saling, 2009). Within this interpretive framework hippocampus and parahippocampal cortex are



**Fig. 5.** Regression of visual imagery score (VVIQ) against estimated BOLD response. VVIQ was significantly positively correlated (left) with the integrated BOLD signal in one component, that shown in Fig. 4F, displayed here with additional planes showing frontal activation accompanying extensive deactivation in visual association cortices. Spatial maps have been thresholded, via dual regression, at feature threshold:  $p < 0.001$ ,  $FDRc < 0.00036$ .

conceptualised as representing associations between environmental stimuli (e.g. a mixing bowl, a cake tin, and an oven), while retrosplenial cortex is thought to represent a higher-level amalgamation of these lower level contextual associations into schemas or prototypes (e.g. a schema governing the behavioural and cognitive actions involved in cooking) (Aminoff et al., 2013; Salig, 2009). These schemas/prototypes provide efficient representations that guide our expectations and inform our interactions with the world. Concurrent activation of these regions as a functional unit (component) during recollection is understandable when we consider that contextual and schematic representations provide a means of gaining access to specifically probed autobiographical events, acting as a substrate upon which to “fill-in” the recovered event details (Irish and Piquet, 2013).

#### *Lateral parietal cortex may co-ordinate the search of autobiographical recollections*

The components in Figs. 3B and 4D show prominent activation in parietal cortex bilaterally. While these regions are not considered in traditional accounts of human memory (see Berryhill et al. (2007), Price et al. (1999), Squire and Bayley (2007)) recent studies of focal lesion patients (Berryhill et al., 2007; Davidson et al., 2008) and studies of recollection-related brain activity (Cabeza, 2008; Cabeza et al., 2008; Ciaramelli et al., 2008) have led to an hypothesised attentional role for this region during recollection. By this account strategic (top-down) search of the autobiographical store is implemented by dorsal parietal cortex (Fig. 4D), with ventral parietal cortex (Fig. 3B) signalling successful retrieval of suitable candidate memories (Cabeza, 2008; Cabeza et al., 2008; Ciaramelli et al., 2008; Wagner et al., 2005). A functional role for the component of Fig. 4D in strategic memory search would also explain the unification of this region into the component encompassing prominent activation in parahippocampal and retrosplenial cortex; as argued above these latter regions are thought to support a hierarchy of contextual associations (Aminoff et al., 2013), and as such would seem to offer an ideal entry point for strategically guided search of the autobiographical store.

#### *Recency effects in superior temporal sulcus*

Strong bilateral—but left-dominant—activation was observed along the length of the superior temporal sulcus (STS) during autobiographical recollection (Fig. 3A). Linguistic processing has been shown to produce activation in these regions (left > right), especially for ex-

tended passages of text/speech (Hein and Knight, 2008; Redcay, 2008). The STS component in Fig. 3A responded transiently to all conditions, with a larger response during recollection of recent memories. The transient, short latency response may simply reflect the brief period of time taken to read the probe questions. The effect of *Recency* may reflect that a linguistic strategy is used more heavily during the recall of recent autobiographical memories (Lloyd-Jones et al., 2008).

The activations and recency effect observed for the component in Fig. 3A may also relate to the purported role(s) of the STS in multisensory integration and social processing (Beauchamp, 2005; Deen et al., 2015; Hein and Knight, 2008). The autobiographical recollections probed here encompassed personal and interpersonal interactions, and therefore drew upon functions such as theory of mind and social judgments. Multisensory integration would be expected given the multimodal richness of autobiographical recollection, especially the more vivid recollections associated with recent events (Sheldon and Levine, 2013). The transient response of the component of Fig. 3A may reflect an initial phase of recollection in which an event is recalled in rich polymodal detail, followed by subsequent elaboration of specific attributes of the recalled episode.

#### *What is the role of cerebellum in autobiographical recollection?*

One of the recovered components exhibited right lateralised cerebellar activation (accompanied by left predominant activation in cortex) that was comparable across all memory conditions (Fig. 4B). Right lateralised cerebellar activity has been noted in a previous study of autobiographical recollection (Svoboda et al., 2006). The cerebellum is connected widely with contralateral cortex, especially with prefrontal and parietal regions associated with cognitive networks (Habas et al., 2013; Stoodley, 2012; Strick et al., 2009). While the cerebellum has been broadly linked to cognition and emotional functioning (Schmahmann, 2004), the right cerebellum seems to be involved in verbal aspects of cognition traditionally lateralised to the left cerebral cortex (O'Halloran et al., 2012; Stoodley, 2012). Its precise role in recollection is not yet fully understood and warrants further investigation.

#### *Deactivation of primary sensory and motor cortices during autobiographical recollection*

In addition to revealing widespread activation within the AMN, the composite IC map of Fig. 2A is notable for revealing deactivations throughout sensory (visual, auditory and somatosensory) and motor

regions (Fig. 4B,C,F,H), and in areas thought important for the detection of/orienting to external stimuli (e.g. right TPJ and right middle and inferior frontal gyri, Fig. 4E) (Corbetta et al., 2008; Corbetta and Shulman, 2002). This can be interpreted as withdrawal from the processing of “irrelevant” sensory and movement related information during internally focused processing (Amedi et al., 2005).

#### *Emotional processing is revealed using salient emotional cues*

Contrary to expectation, we did not observe any components with a significant *Peri-event time\*Valence* interaction. Previous studies have used participant specific questions, tailored to each individual's personal history (Addis et al., 2004, 2007a; Fink et al., 1996; Greenberg et al., 2005; Maguire et al., 2001; Steinworth et al., 2006). In contrast, our use of the same set of probe questions for all participants may not have adequately elicited or constrained the actual emotional content (*Positive* or *Negative*) of the memories recovered. For example, a nominally *Neutral* probe question (for instance, about one's school playground) may have produced mild *Positive* emotions in one participant, *Neutral* recollection in another, and strongly *Negative* emotions in a third.

#### *The temporal dynamics of the processing of autobiographical recollection*

Cued autobiographical recollection is a process that unfolds over seconds: the memory cue initiates a search process, leading to recovery of a target memory, and subsequent elaboration of that memory (see, for instance, Addis et al. (2007b) and Daselaar et al. (2008)). We observed relatively transient activations with early peaks in supero-lateral and supero-medial prefrontal cortex (Fig. 4B), a left language-like network (Fig. 4A), and bilateral STS (Fig. 3A). These could represent early cognitive state setting in response to the cue questions, reading of the cue questions themselves, and an early multisensory representation of a recalled episode, respectively. Deactivations in primary sensorimotor and auditory regions also occur transiently and early (Fig. 4B and C), consistent with internally directed processing (except for the visual activity required for cue reading, which results in later deactivation in visual areas: Fig. 4F and H). Interestingly, the magnitude of the delayed activation in mesial superior frontal cortex and left dorsolateral prefrontal cortex, and of the delayed deactivation in visual association areas (component in Figs. 4F and 5) was associated with the vividness with which participants were able to recollect the autobiographical episodes. This may suggest that those participants who were readily able to utilise the visually presented cues to trigger recall, thereby switching from an external (cue reading) to internal attentional (recollection) state, were those most able to engage deeply with the task.

Relatively more sustained activations were observed in more traditional AMN/DMN regions (components in Fig. 3B,C and Fig. 4D). These regions therefore are likely involved in the selection, generation, and elaboration of autobiographical recollections, processes that occur over extended periods. While speculative, the late peak in mesial prefrontal activity (Fig. 4G) could reflect the gradual emergence of personal salience in the recollected experiences.

#### *Considerations in applying eICA*

In our initial paper introducing eICA (Masterton et al., 2013) we discussed a number of issues pertinent to the technique, and to ICA approaches more broadly. These include the importance of the initial deconvolution step (Friston et al., 1998; Jacobs et al., 2008; Josephs et al., 1997; Penny et al., 2011), selection of the peri-event time window, estimation of the number of sources in the data (Beckmann and Smith, 2004; Minka, 2000), the ICA algorithm used (Hyvärinen, 1999), the stochastic nature of ICA itself (Cole et al., 2010), and the influence of these factors on the obtained results (Calhoun et al., 2003;

Cole et al., 2010; Li et al., 2007). The spatial independence assumption of spatial ICA has been the subject of some criticism (for instance, in limiting the types of processes that can be identified, see Friston (1998)), however it has also been noted that spatial independence is consistent with the localisationist approach of clinical neuropsychology and neurology (Beckmann, 2012).

ICA is a data driven method, with interpretation necessarily occurring *post hoc*. The brain regions unified in any given component recovered by eICA share a common temporal relationship to the event upon which the ICA is conditioned (here, autobiographical probe questions). This unification need not imply homogeneity of function throughout that component. The unification could, for instance, reflect transient cooperation between functionally distinct brain areas for the purposes of the cognitive task at hand (autobiographical recollection), or similar event-related response shapes in different brain areas without any direct interaction between them. In the present work we have qualitatively interpreted attributes of the event-related responses across components, such as their relative latency and shape. Such comparisons could, in principle, be made quantitative by extending our eICA approach to include bootstrapping of the participant specific time courses (and fitting smooth functions to these, from which estimates of parameters such as latency and FWHM could be derived; e.g. Lindquist et al., 2009). Short TR acquisitions (e.g. Feinberg et al., 2010), and/or jittering of stimulus timings (Josephs et al., 1997) would be advantageous in such an extension.

#### *Conclusion*

Autobiographical recollection, like other higher-order cognitive processes (Park and Friston, 2013), is supported by complex, time-varying interactions between multiple brain networks (Addis et al., 2004; Daselaar et al., 2008). Using eICA we have shown that the neural system recruited during autobiographical recollection, the AMN, comprises a system of subnetworks that can be separated on the basis of their differential sensitivity to mnemonic features such as the chronological age of the to-be-retrieved memories, as well as on their unique response dynamics during autobiographical retrieval. Our findings are consistent with recent work arguing that the DMN actually comprises a collection of networks that co-activate or interact during complex forms of cognition such as autobiographical recollection, episodic future simulations, and mentalising (Andrews-Hanna, 2012; Andrews-Hanna et al., 2014; D'Argembeau et al., 2013; Kim, 2012; Schacter et al., 2012; Szpunar et al., 2013). Our analyses (herein, and Masterton et al., 2013) demonstrate that eICA is capable of uncovering, in a data driven manner, event-related network responses embedded within large collections of space- and time-varying signals (e.g., fMRI, EEG, MEG). Further, they show that the recovered network responses can be related to overt measures of cognition. eICA therefore offers a powerful, generalised, data-driven analysis tool for studying the neurocognitive architecture of the human brain.

#### **Acknowledgements**

This study was supported by the National Health and Medical Research Council (NHMRC) of Australia (Program Grant 628952, Project Grant 1081151) and the Victorian Government Operational Infrastructure Support Program. Additional support was provided by a Rebecca L. Cooper Medical Research Foundation grant to CT, and an Austin Health Medical Research Foundation Grant awarded to GR and SW at The University of Melbourne. GJ is supported by an NHMRC Practitioner Fellowship (1060312).

#### **Appendix A. Supplementary material**

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.neuroimage.2017.02.088.

## References

- Addis, D.R., McIntosh, A.R., Moscovitch, M., Crawley, A.P., McAndrews, M.P., 2004. Characterizing spatial and temporal features of autobiographical memory retrieval networks: a partial least squares approach. *NeuroImage* 23, 1460–1471.
- Addis, D.R., Moscovitch, M., McAndrews, M.P., 2007a. Consequences of hippocampal damage across the autobiographical memory network in left temporal lobe epilepsy. *Brain* 130, 2327–2342.
- Addis, D.R., Wong, A.T., Schacter, D.L., 2007b. Remembering the past and imagining the future: common and distinct neural substrates during event construction and elaboration. *Neuropsychologia* 45, 1363–1377.
- Amedi, A., Malach, R., Pascual-Leone, A., 2005. Negative BOLD differentiates visual imagery and perception. *Neuron* 48, 859–872.
- Aminoff, E.M., Kveraga, K., Bar, M., 2013. The role of the parahippocampal cortex in cognition. *Trends Cogn. Sci.* 17, 379–390.
- Andrews-Hanna, J.R., 2012. The brain's default network and its adaptive role in internal mentation. *Neuroscientist* 18, 251–270.
- Andrews-Hanna, J.R., Reidler, J.S., Sepulcre, J., Poulin, R., Buckner, R.L., 2010. Functional-anatomic fractionation of the brain's default network. *Neuron* 65, 550–562.
- Andrews-Hanna, J.R., Saxe, R., Yarkoni, T., 2014. Contributions of episodic retrieval and mentalizing to autobiographical thought: evidence from functional neuroimaging, resting-state connectivity, and fMRI meta-analyses. *NeuroImage* 91, 324–335.
- Ashburner, J., Friston, K.J., et al., 1999. Nonlinear spatial normalization using basis functions. *Hum. Brain Mapp.* 7, 254–266.
- Bar, M., 2009. The proactive brain: memory for predictions. *Philos. Trans. R. Soc. B: Biol. Sci.* 364, 1235–1243.
- Bar, M., 2007. The proactive brain: using analogies and associations to generate predictions. *Trends Cogn. Sci.* 11, 280–289.
- Beauchamp, M.S., 2005. See me, hear me, touch me: multisensory integration in lateral occipital-temporal cortex. *Curr. Opin. Neurobiol.* 15, 145–153.
- Beckmann, C.F., 2012. Modelling with independent components. *NeuroImage* 62, 891–901.
- Beckmann, C.F., Mackay, C.E., Filippini, N., Smith, S.M., 2009. Group comparison of resting-state fMRI data using multi-subject ICA and dual regression. *NeuroImage* 47, S148.
- Beckmann, C.F., Smith, S.M., 2004. Probabilistic independent component analysis for functional magnetic resonance imaging. *IEEE Trans. Med. Imaging* 23, 137–152.
- Berryhill, M.E., Phuong, L., Picasso, L., Cabeza, R., Olson, I.R., 2007. Parietal lobe and episodic memory: bilateral damage causes impaired free recall of autobiographical memory. *J. Neurosci.* 27, 14415–14423.
- Binder, J.R., Desai, R.H., Graves, W.W., Conant, L.L., 2009. Where is the semantic system? A critical review and meta-analysis of 120 functional neuroimaging studies. *Cereb. Cortex* 19, 2767–2796.
- Buckner, R.L., Andrews-Hanna, J.R., Schacter, D.L., 2008. The brain's default network. *Ann. N. Y. Acad. Sci.* 1124, 1–38.
- Buckner, R.L., Carroll, D.C., 2007. Self-projection and the brain. *Trends Cogn. Sci.* 11, 49–57.
- Cabeza, R., 2008. Role of parietal regions in episodic memory retrieval: the dual attentional processes hypothesis. *Neuropsychologia* 46, 1813–1827.
- Cabeza, R., Ciaramelli, E., Olson, I.R., Moscovitch, M., 2008. The parietal cortex and episodic memory: an attentional account. *Nat. Rev. Neurosci.* 9, 613–625.
- Cabeza, R., St Jacques, P., 2007. Functional neuroimaging of autobiographical memory. *Trends Cogn. Sci.* 11, 219–227.
- Calhoun, V.D., Adali, T., Hansen, L.K., Larsen, J., Pekar, J.J., 2003. ICA of functional MRI data: an overview.
- Ciaramelli, E., Grady, C.L., Moscovitch, M., 2008. Top-down and bottom-up attention to memory: a hypothesis (AtoM) on the role of the posterior parietal cortex in memory retrieval. *Neuropsychologia* 46, 1828–1851.
- Cole, D.M., Smith, S.M., Beckmann, C.F., 2010. Advances and pitfalls in the analysis and interpretation of resting-state fMRI data. *Front. Syst. Neurosci.* 4, 8.
- Corbetta, M., Patel, G., Shulman, G.L., 2008. The reorienting system of the human brain: from environment to theory of mind. *Neuron* 58, 306–324.
- Corbetta, M., Shulman, G.L., 2002. Control of goal-directed and stimulus-driven attention in the brain. *Nat. Rev. Neurosci.* 3, 201–215.
- D'Argembeau, A., Cassol, H., Phillips, C., Baletau, E., Salmon, E., Van der Linden, M., 2013. Brains creating stories of selves: the neural basis of autobiographical reasoning. *Soc. Cogn. Affect. Neurosci.* (nstd028).
- Daselaar, S.M., Rice, H.J., Greenberg, D.L., Cabeza, R., LaBar, K.S., Rubin, D.C., 2008. The spatiotemporal dynamics of autobiographical memory: neural correlates of recall, emotional intensity, and reliving. *Cereb. Cortex* 18, 217–229.
- Davidson, P.S., Anaki, D., Ciaramelli, E., Cohn, M., Kim, A.S., Murphy, K.J., Troyer, A.K., Moscovitch, M., Levine, B., 2008. Does lateral parietal cortex support episodic memory?: evidence from focal lesion patients. *Neuropsychologia* 46, 1743–1755.
- Deen, B., Koldewyn, K., Kanwisher, N., Saxe, R., 2015. Functional organization of social perception and cognition in the superior temporal sulcus. *Cereb. Cortex* (bhv111).
- Feinberg, D.A., Moeller, S., Smith, S.M., Auerbach, E., Ramanna, S., Glasser, M.F., Miller, K.L., Uğurbil, K., Yacoub, E., 2010. Multiplexed echo planar imaging for sub-second whole brain fMRI and fast diffusion imaging. *PLoS One* 5, e15710.
- Filippini, N., McIntosh, B.J., Hough, M.G., Goodwin, G.M., Frisoni, G.B., Smith, S.M., Matthews, P.M., Beckmann, C.F., Mackay, C.E., 2009. Distinct patterns of brain activity in young carriers of the APOE-ε4 allele. *Proc. Natl. Acad. Sci. USA* 106, 7209–7214.
- Fink, G.R., Markowitsch, H.J., Reinkensmeyer, M., Bruckbauer, T., Kessler, J., Heiss, W.-D., 1996. Cerebral representation of one's own past: neural networks involved in autobiographical memory. *J. Neurosci.* 16, 4275–4282.
- Friston, K.J., 1998. Modes or models: a critique on independent component analysis for fMRI. *Trends Cogn. Sci.* 2, 373–375.
- Friston, K.J., Ashburner, J., Frith, C.D., Poline, J.B., Heather, J.D., Frackowiak, R.S.J., 1995. Spatial registration and normalization of images. *Hum. Brain Mapp.* 3, 165–189.
- Friston, K.J., Josephs, O., Rees, G., Turner, R., 1998. Nonlinear event-related responses in fMRI. *Magn. Reson. Med.* 39, 41–52.
- Friston, K.J., Williams, S., Howard, R., Frackowiak, R.S., Turner, R., 1996. Movement-related effects in fMRI time-series. *Magn. Reson. Med.* 35, 346–355.
- 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, 659–674.
- Gusnard, D.A., Akbudak, E., Shulman, G.L., Raichle, M.E., 2001. Medial prefrontal cortex and self-referential mental activity: relation to a default mode of brain function. *Proc. Natl. Acad. Sci. USA* 98, 4259–4264.
- Habas, C., Shiner, W.R., Greicius, M.D., 2013. Delineation of cerebrocerebellar networks with MRI measures of functional and structural connectivity. In: *Handbook of the Cerebellum and Cerebellar Disorders*. Springer, 571–585.
- Hassabis, D., Maguire, E.A., 2009. The construction system of the brain. *Philos. Trans. R. Soc. B: Biol. Sci.* 364, 1263–1271.
- Heatherington, T.F., Wyland, C.L., Macrae, C.N., Demos, K.E., Denny, B.T., Kelley, W.M., 2006. Medial prefrontal activity differentiates self from close others. *Soc. Cogn. Affect. Neurosci.* 1, 18–25.
- Hein, G., Knight, R.T., 2008. Superior temporal sulcus—it's my area: or is it? *Cogn. Neurosci.* 20, 2125–2136.
- Henson, R.N.A., 2003. Analysis of fMRI time series. In: Frackowiak, R.S.J., Friston, K.J., Frith, C.D., Dolan, R.J., Price, C.J., Zeki, S., Ashburner, J.T., Penny, W.D. (Eds.), *Human Brain Function*. Academic Press.
- Himberg, J., Hyvärinen, A., Esposito, F., 2004. Validating the independent components of neuroimaging time series via clustering and visualization. *NeuroImage* 22, 1214–1222.
- Hunter, G., 2011. Transient global amnesia. *Neurol. Clin.* 29, 1045–1054.
- Hyvärinen, A., 1999. Fast and robust fixed-point algorithms for independent component analysis. *IEEE Trans. Neural Netw.* 10, 626–634.
- Irish, M., Piguet, O., 2013. The pivotal role of semantic memory in remembering the past and imagining the future. *Front. Behav. Neurosci.* 7.
- Jacobs, J., Hawco, C., Kobayashi, E., Boor, R., LeVan, P., Stephani, U., Siniatchkin, M., Gotman, J., 2008. Variability of the hemodynamic response as a function of age and frequency of epileptic discharge in children with epilepsy. *NeuroImage* 40, 601–614.
- Josephs, O., Turner, R., Friston, K., 1997. Event-related fMRI. *Hum. Brain Mapp.* 5, 243–248.
- Kihlstrom, J.F., 2005. Dissociative disorders. *Annu. Rev. Clin. Psychol.* 1, 227–253.
- Kim, H., 2012. A dual-subsystem model of the brain's default network: self-referential processing, memory retrieval processes, and autobiographical memory retrieval. *NeuroImage* 61, 966–977.
- Leech, R., Kamourieh, S., Beckmann, C.F., Sharp, D.J., 2011. Fractionating the default mode network: distinct contributions of the ventral and dorsal posterior cingulate cortex to cognitive control. *J. Neurosci.* 31, 3217–3224.
- Lemieux, L., Salek-Haddadi, A., Lund, T.E., Laufs, H., Carmichael, D., 2007. Modelling large motion events in fMRI studies of patients with epilepsy. *Magn. Reson. Imaging* 25, 894–901.
- Li, Y.-O., Adali, T., Calhoun, V.D., 2007. Estimating the number of independent components for functional magnetic resonance imaging data. *Hum. Brain Mapp.* 28, 1251–1266.
- Lindquist, M.A., Loh, J.M., Atlas, L.Y., Wager, T.D., 2009. Modeling the hemodynamic response function in fMRI: efficiency, bias and mis-modeling. *NeuroImage* 45, S187–S198.
- Lloyd-Jones, T.J., Brandimonte, M.A., Bäuml, K.-H., 2008. Verbalising visual memories. *Eur. J. Cogn. Psychol.* 20, 387–395. <http://dx.doi.org/10.1080/09541440701755543>.
- Maguire, E.A., Henson, R.N., Mummery, C.J., Frith, C.D., 2001. Activity in prefrontal cortex, not hippocampus, varies parametrically with the increasing remoteness of memories. *NeuroReport* 12, 441–444.
- Masterton, R.A.J., Jackson, G.D., Abbott, D.F., 2013. Mapping brain activity using event-related independent components analysis (eICA): specific advantages for EEG-fMRI. *NeuroImage* 70, 164–174. <http://dx.doi.org/10.1016/j.neuroimage.2012.12.025>.
- Minka, T.P., 2000. Automatic choice of dimensionality for PCA. In: *Proceedings of the NIPS*. pp. 598–604.
- Niki, K., Luo, J., 2002. An fMRI study on the time-limited role of the medial temporal lobe in long-term topographical autobiographic memory. *J. Cogn. Neurosci.* 14, 500–507.
- O'Halloran, C.J., Kinsella, G.J., Storey, E., 2012. The cerebellum and neuropsychological functioning: a critical review. *J. Clin. Exp. Neuropsychol.* 34, 35–56. <http://dx.doi.org/10.1080/13803395.2011.614599>.
- Park, H.-J., Friston, K., 2013. Structural and functional brain networks: from connections to cognition. *Science* 342, 1238411. <http://dx.doi.org/10.1126/science.1238411>.
- Penny, W.D., Friston, K.J., Ashburner, J.T., Kiebel, S.J., Nichols, T.E., 2011. *Statistical Parametric Mapping: the Analysis of Functional Brain Images*. Academic press.
- Piefke, M., Weiss, P.H., Zilles, K., Markowitsch, H.J., Fink, G.R., 2003. Differential remoteness and emotional tone modulate the neural correlates of autobiographical memory. *Brain* 126, 650–668.
- Piolino, P., Desgranges, B., Benali, K., Eustache, F., 2002. Episodic and semantic remote autobiographical memory in ageing. *Memory* 10, 239–257.
- Price, C.J., Mummery, C.J., Moore, C.J., Frackowiak, R.S.J., Friston, K.J., 1999.

- Delineating necessary and sufficient neural systems with functional imaging studies of neuropsychological patients. *J. Cogn. Neurosci.* 11, 371–382.
- Raichle, M.E., 2015. The brain's default mode network. *Annu. Rev. Neurosci.*
- Raichle, M.E., MacLeod, A.M., Snyder, A.Z., Powers, W.J., Gusnard, D.A., Shulman, G.L., 2001. A default mode of brain function. *Proc. Natl. Acad. Sci. USA* 98, 676–682.
- Redcay, E., 2008. The superior temporal sulcus performs a common function for social and speech perception: implications for the emergence of autism. *Neurosci. Biobehav. Rev.* 32, 123–142.
- Rekkas, P.V., Constable, R.T., 2005. Evidence that autobiographic memory retrieval does not become independent of the hippocampus: an fMRI study contrasting very recent with remote events. *J. Cogn. Neurosci.* 17, 1950–1961.
- Saling, M.M., 2009. Verbal memory in mesial temporal lobe epilepsy: beyond material specificity. *Brain*, (awp012).
- Schacter, D.L., Addis, D.R., Buckner, R.L., 2007. Remembering the past to imagine the future: the prospective brain. *Nat. Rev. Neurosci.* 8, 657–661.
- Schacter, D.L., Addis, D.R., Hassabis, D., Martin, V.C., Szpunar, K.K., 2012. The future of memory: remembering, imagining, and the brain. *Neuron* 76, 677–694.
- Schmahmann, J.D., 2004. Disorders of the cerebellum: ataxia, dysmetria of thought, and the cerebellar cognitive affective syndrome. *J. Neuropsychiatry Clin. Neurosci.* 16, 367–378. <http://dx.doi.org/10.1176/appi.neuropsych.16.3.367>.
- Seghier, M.L., Price, C.J., 2012. Functional heterogeneity within the default network during semantic processing and speech production. *Front. Psychol.*, 3.
- Sestieri, C., Corbetta, M., Romani, G.L., Shulman, G.L., 2011. Episodic memory retrieval, parietal cortex, and the default mode network: functional and topographic analyses. *J. Neurosci.* 31, 4407–4420.
- Sheldon, S., Levine, B., 2013. Same as it ever was: vividness modulates the similarities and differences between the neural networks that support retrieving remote and recent autobiographical memories. *NeuroImage* 83, 880–891.
- Smallwood, J., Brown, K., Baird, B., Schooler, J.W., 2012. Cooperation between the default mode network and the frontal–parietal network in the production of an internal train of thought. *Brain Res.* 1428, 60–70.
- Spreng, R.N., Mar, R.A., Kim, A.S., 2009. The common neural basis of autobiographical memory, prospection, navigation, theory of mind, and the default mode: a quantitative meta-analysis. *J. Cogn. Neurosci.* 21, 489–510.
- Squire, L.R., Bayley, P.J., 2007. The neuroscience of remote memory. *Curr. Opin. Neurobiol.* 17, 185–196.
- Squire, L.R., Stark, C.E., Clark, R.E., 2004. The medial temporal lobe. *Annu. Rev. Neurosci.* 27, 279–306.
- Steinworth, S., Corkin, S., Halgren, E., 2006. Ecphory of autobiographical memories: an fMRI study of recent and remote memory retrieval. *NeuroImage* 30, 285–298.
- Stoodley, C.J., 2012. The cerebellum and cognition: evidence from functional imaging studies. *Cerebellum* 11, 352–365.
- Strick, P.L., Dum, R.P., Fiez, J.A., 2009. Cerebellum and nonmotor function. *Annu. Rev. Neurosci.* 32, 413–434.
- Svoboda, E., McKinnon, M.C., Levine, B., 2006. The functional neuroanatomy of autobiographical memory: a meta-analysis. *Neuropsychologia* 44, 2189–2208.
- Szpunar, K.K., Jacques, P.L.S., Robbins, C.A., Wig, G.S., Schacter, D.L., 2013. Repetition-related reductions in neural activity reveal component processes of mental simulation. *Soc. Cogn. Affect. Neurosci.*, (nst035).
- Tulving, E., 1983. *Elements of Episodic Memory*. Clarendon, Oxford.
- Uddin, L.Q., Clare Kelly, A.M., Biswal, B.B., Xavier Castellanos, F., Milham, M.P., 2009. Functional connectivity of default mode network components: correlation, anticorrelation, and causality. *Hum. Brain Mapp.* 30, 625–637.
- Van Overwalle, F., 2009. Social cognition and the brain: a meta-analysis. *Hum. Brain Mapp.* 30, 829–858.
- Wagner, A.D., Shannon, B.J., Kahn, I., Buckner, R.L., 2005. Parietal lobe contributions to episodic memory retrieval. *Trends Cogn. Sci.* 9, 445–453.
- Zeman, A., Butler, C., 2010. Transient epileptic amnesia. *Curr. Opin. Neurol.* 23, 610–616.