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

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ABSTRACT

Higher cognitive functions depend upon dynamically unfolding brain network interactions. Autobiographical recollection – the autonoetic 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-recollected 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-

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viewed in Spreng et al. (2009) and Svoboda et al. (2006)).[2] There has been growing interest in decomposing the AMN into sub-networks, linking different cognitive components of autobiographic 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.

[2] 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).