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Functional anatomy of temporal organisation and domain-specificity of episodic memory retrieval

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ABSTRACT

Episodic memory provides information about the "when" of events as well as "what" and "where" they happened. Using functional imaging, we investigated the domain specificity of retrieval-related processes following encoding of complex, naturalistic events. Subjects watched a 42-min TV episode, and 24 h later, made discriminative choices of scenes from the clip during fMRI. Subjects were presented with two scenes and required to either choose the scene that happened earlier in the film (Temporal), or the scene with a correct spatial arrangement (Spatial), or the scene that had been shown (Object). We identified a retrieval network comprising the precuneus, lateral and dorsal parietal cortex, middle frontal and medial temporal areas. The precuneus and angular gyrus are associated with temporal retrieval, with precuneal activity correlating negatively with temporal distance between two happenings at encoding. A dorsal fronto-parietal network engages during spatial retrieval, while antero-medial temporal regions activate during object-related retrieval. We propose that access to episodic memory traces involves different processes depending on task requirements. These include memory-searching within an organised knowledge structure in the precuneus (Temporal task), online maintenance of spatial information in dorsal fronto-parietal cortices (Spatial task) and combining scene-related spatial and non-spatial information in the hippocampus (Object task). Our findings support the proposal of process-specific dissociations of retrieval.

1. Introduction

Episodic memory provides information about our personal experiences of "when" and "where" events occur as well as "what" happens. In order to simulate the complexity of the processes involved in autobiographical memory, recent studies on episodic memory retrieval have endeavoured to employ real-life-like materials for learning. These range from photographs taken from a first-person perspective (St. Jacques, Rubin, LaBar, & Cabeza, 2008), to documentary videos of people engaged in everyday life activities (Fujii et al., 2004; Mendelsohn, Chalamish, Solomonovich, & Dudai, 2008; Mendelsohn, Furman, & Dudai, 2010), to videos showing navigation through a house (Hayes, Ryan, Schnyer, & Nadel, 2004), or navigating in virtual environments (Burgess, Maguire, Spiers, & O'Keefe, 2001; Ekstrom & Bookheimer, 2007; Ekstrom, Copara, Isham, Wang, & Yonelinas, 2011; King, Hartley, Spiers, Maguire, & Burgess, 2005).

A defining characteristic of episodic memories is that they allow us to relive our past as it has unfolded over extended time windows (Tulving, 1985). In order to be accessible for future retrieval, the different elements of an event have to be associatively linked into a durable memory trace (Staresina & Davachi, 2009). The organisation of temporal memory can be classified in "distance", "location", and "relative times" theories (Friedman, 1993). For example, distance-based explanations are dependent on processes that are correlated with the time between encoding and retrieval. A subgroup of distance-based theories, namely "chronological organisation theories", holds that representations of events are organised in the memory store by their order of occurrence. Friedman (1993) reasoned that if memory is organised according to the order of occurrence, memories laid down at adjacent points in time would prime one another (see also Estes, 1985). Behavioural findings in long-term memory recall support this prediction (Barsalou, 1988; Bruce & Van Pelt, 1989; Huttenlocher, Hedges, & Prohaska, 1988; Linton, 1986). In these studies, subjects frequently reported having thought of other events that were close to the target event in time (Friedman, 1987; Friedman & Wilkins, 1985). Similarly, serial position recall experiments (on a time scale of minutes) provide evidence that even when unordered recall is required, subjects show a strong unprompted tendency to recall temporally adjacent items together (e.g., Laming, 1999). These findings are consistent with the proposal that memories are laid down and recalled according to the order of occurrence.

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However, a large body of behavioural evidence gave the opposite pattern of results. Studies on serial recall and free recall have found that items that are near to one another in time are more confusable (Brown & Chater, 2001; Yntema & Trask, 1963). Behavioural experiments that manipulated the temporal distance between items by increasing or decreasing the rate of presentation of items in a list showed that temporally adjacent items tend to have their positions recalled in the wrong order after short delays (e.g., Neath & Crowder, 1990, 1996), and even after 24 h (Nairne, 1992). Neuropsychological studies associated deficits in temporal order retrieval with damage to the prefrontal cortex (e.g., Butters, Kaszniak, Glisky, Eslinger, & Schacter, 1994; McAndrews & Milner, 1991; Shimamura, Janowsky, & Squire, 1990). Specifically, Milner, Corsi, and Leonard (1991) reported demand for temporal order retrieval was greater when the temporal distance of a stimuli pair was shorter.

Functional neuroimaging techniques provide an additional means to assess the neural correlates of temporal memory and the effect of temporal distance. Behavioural measures (i.e., accuracy and RT) provide us with the end result of a set of processes. This set is likely to engage multiple brain regions, each of which may contribute differentially to temporal retrieval performance. Previous fMRI studies on temporal distance have found that the higher difficulty for items closer in time is associated with activation of prefrontal cortex. For example, in temporal order judgements prefrontal activations increased with decreasing temporal distance between word pairs [with 3 vs. 8 intervening words] (Konishi et al., 2002), between line-drawing pictures [within vs. across lists] (Suzuki et al., 2002) or in verbal recency judgements (Zorrilla, Aguirre, Zarahn, Cannon, & D'Esposito, 1996).

Unlike these previous studies, in this investigation we adopted a paradigm that employed rich stimuli entailing a large amount of interrelated events (i.e., happenings within a TV episode). We investigated whether the parameterised temporal distance between encoded events led to a modulatory effect on brain activity which can be associated with the retrieval of such temporal information. Of particular relevance is St. Jacques et al. (2008) study when subjects made temporal order judgements to pairs of photographs they had personally taken. They found that events separated by shorter temporal distance led to activations in left prefrontal, parahippocampal, precuneus, and visual cortices. Given the effect of temporal distance on retrieval performance, St. Jacques et al. (2008)'s parametric analysis controlled for task difficulty by taking into account subject-specific accuracy as a potential confounding effect. However, this procedure only copes with between-subject performance differences but not for the critical difference between trial-types (i.e., shorter vs. longer distances). This makes it harder to interpret their parametric effects given that retrieval demands tend to increase with shorter temporal distances (Christoff et al., 2001; Konishi et al., 2002).

Together with these temporal aspects, episodic memories are characterised by complex content experiences that typically involve multiple types of elements. According to Tulving (1972), this construct can be conceptually broken down into the three elements: "when", "what" and "where", each of which can be assessed behaviourally. As loss of the connections between the different elements of an event is commonplace (Burgess & Shallice, 1996), it is possible that processes related to the retrieval of these different elements may be subserved by dissociable anatomical structures of a wider retrieval network. Several previous studies made use of fMRI or PET to disentangle the functional contributions of these elements (Burgess et al., 2001; Ekstrom & Bookheimer, 2007; Ekstrom et al., 2011; Fujii et al., 2004; Hayes et al., 2004; Nyberg et al., 1996). For example, in a spatial navigation paradigm, Ekstrom and Bookheimer (2007) had subjects play a taxi-driver game, in which they freely searched for passengers and delivered them to specific landmark stores. Subjects were then scanned with fMRI as they retrieved landmarks, spatial, and temporal associations from their navigational experience. The authors attributed perirhinal cortex activations to landmark retrieval, hippocampal/striatal activations to temporal order retrieval, and parahippocampal activations to spatial association retrieval, respectively. In a subsequent study, Ekstrom et al. (2011) dissociated brain regions involved in the retrieval of spatial and temporal information. Again, participants first navigated a virtual city, experiencing unique routes in a specific temporal order and learning about the spatial layout of the city. At retrieval, subjects made discrimination judgments either about the spatial distance between two landmarks or about the temporal order in which they came across the two. fMRI analyses revealed comparable hippocampal activity during these two tasks, and confirmed greater parahippocampal activity during spatial retrieval, and greater prefrontal activity during temporal order retrieval.

We aimed to address several issues with respect with these earlier studies. First, these studies have focussed on probing temporal order (or recency) judgements of two independent events, which did not occur one after the other among a string of similar events (e.g., "which store did you visit first?"). Second, they have not directly compared spatial ("where") and temporal ("when") and object ("what") retrieval tasks following the encoding of a single experience (here, the viewing of the TV episode). Third, the durations between encoding and retrieval in these studies, which ranged from seconds (e.g., Ekstrom et al., 2011) to an average of 83 min in Fujii et al. (2004), were considerably shorter than the one-day period used in our current study.

In light of these considerations, our experiment was designed to employ rich, semantically contiguous/continuous stimuli for encoding (cinematic material) and to require a longer retention period (24 h). Given the advantages of naturalistic cinematic material (e.g., Hasson, Furman, Clark, Dudai, & Davahi, 2008), we employed a specific TV series involving complex features characteristic of real-life-like events. The choice of a long movie with a very large amount of interrelated events differs from other studies that have chosen to use short, action/goal-oriented clips (e.g., Swallow et al., 2011; Swallow, Zacks, & Abrams, 2009). As critically, the 42-min episode contained one hour of movie plot that related to real-world events, and accordingly provided an almost one-to-one temporal correspondence between the time of the events in the movie plot and the "real" time experienced by the viewer. Twenty-four hours after encoding, subjects were tested with a two-choice discrimination test of scenes extracted from the film, while undergoing functional magnetic resonance imaging. On each trial, the subject was either required to choose the scene that happened earlier in the film (Temporal trials), or the scene with a correct spatial arrangement when it was contrasted with a mirror-image foil (Spatial trials), or the scene that had been shown in the film as opposed to a novel scene (Object trials).

This study had two main aims. First, within our paradigm we asked whether decreasing the temporal distance between encoded events would improve (e.g., Friedman, 1993) or weaken (e.g., Konishi et al., 2002) retrieval performance on temporal trials, and so enable us to assess the effect of temporal distance on retrieval-related brain activity. Second, we examined whether the domain-specificity of the components of "what", "where" and "when" would lead to different patterns of activation during the retrieval tasks.

2. Materials and methods

2.1. Subjects

Fifteen right-handed native Italian speakers participated in this study (mean age: 25.9, 18–37 years; 9 females). All had normal or corrected-to-normal (contact lenses) visual acuity and were screened by their naivety about the TV series utilised in the study. No participants reported neurological impairments and all