Neural Substrates Related to Constructing Novel Events

by

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Abstract

This dissertation explored the cognitive processes and neural substrates underlying the simulation and construction of novel mental representations, by manipulating factors influencing construction ability. Across four experiments, subjects constructed novel events by relating multiple cue words to a single context word in order to make a coherent representation. Experiments 1 and 2 tested whether memory deficits related to age and amnesia due to medial temporal lobe lesions affect event construction performance. Both older adults and patients with amnesia showed deficits in event construction, with poorer performance at increasing mnemonic loads. Moreover, older adults' construction ability was associated with memory performance, suggesting that associative encoding processes are crucial for simulation tasks.

Experiments 3a and 3b examined whether semantic congruency between items and context influences event construction and subsequent memory. In Experiment 3a, younger adults constructed imagined events with from cue words that were typically or atypically related to the context word. Atypical events were less coherent, and were rated as poorer in quality and more difficult to construct. Experiment 3b also showed an advantage for typical trials on a cued recall test, suggesting the congruency of an imagined event with prior knowledge has a strong influence on its subsequent retrieval.

Experiment 4 used fMRI to determine the neural correlates of imagining. Constructing imagined events activated the hippocampus, medial prefrontal regions, and default mode network regions in comparison to a baseline condition. Moreover, clusters of activation in the anterior hippocampus were positively correlated with construction task performance across all task conditions, whereas activity in the medial frontal poles varied with individual differences in the typicality of imagined events. Posterior hippocampus was associated with the novelty of imagined events, but did not correlate strongly with the anterior hippocampus or task performance.

Taken together, these studies suggest that these regions are crucial when constructing a novel imagined event, regardless of the nature of the stimuli. In particular, the hippocampus may be necessary to bind items during the construction process, especially as representations become increasingly complex.

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1 Chapter 1: General Introduction

A recent topic of investigation concerns how humans construct novel mental representations of fictitious events, commonly referred to as imagination or future simulation. Converging evidence from studies of healthy adults and patients with focal lesions with behavioural and functional neuroimaging measures suggests that future simulation is largely associated with episodic memory and its underlying neural correlates (Addis & Schacter, 2012; Thomas Suddendorf & Corballis, 2007; Szpunar, Addis, McLelland, & Schacter, 2013). However, future simulation is a complex task involving several cognitive processes: consequently, the contributions of specific brain regions to different processes implicated in future simulation are not well-delineated. The purpose of this dissertation is to use different manipulations in order to elucidate the cognitive processes that may contribute to the construction of future simulations, and to determine how different neural substrates may be related to these processes.

The first sets of experiments use a novel paradigm to show that changes in episodic memory performance directly affect the ability to construct a novel mental representation. Moreover, these studies establish that how an event is constructed influences its subsequent memory, and that memory deficits primarily affect the ability to construct mental representations once they are sufficiently complex. The second set of experiments show that the semantic relatedness of the information during event construction affects the quality of the mental representation, and influences the likelihood of recalling that simulation subsequently. The last experiment provides functional neuroimaging data showing that the hippocampus and medial prefrontal cortex are associated with constructing simulations in general, and also are associated with different aspects of task performance.

The first chapter of this dissertation reviews the literature on episodic memory and event construction. Specifically, it reviews the theoretical rationale underlying the study of future simulation and the several putative processes and associated neural substrates contributing to event construction. It highlights unresolved questions regarding the types of paradigms used to study event construction, and the means of measuring task performance.

1.1 The properties of episodic memory and their utility

Although the ability to encode, retain, and retrieve information is not unique to humans, there are aspects of episodic memory that are particularly evident in humans. Specifically, the recall of our personal past can be associated with a special subjective sense of re-experiencing, what Tulving referred to as *autonoetic consciousness* (Tulving, 1972). That is, when recalling a past event, we may sometimes experience a sense of "mental time travel", allowing us to re-live those past events in a way that parallels our original experience at the time the memory was experienced. Also, episodic memory retrieval is a reconstructive process: that is, a stored memory is not retrieved as an exact copy of the original experience, but is reworked according the pre-existing schemas, inferences, motivation and so on (Bartlett, 1932). One manifestation of this property is that episodic memories seem to maintain a level of compositionality, wherein individual items and any associations between them are represented as separate entities (Cohen & Eichenbaum, 1993). Consequently, a particular memory can be conjured up by multiple cues that help compose it: that is, given an event with several items, any one item can hypothetically serve as a successful retrieval cue for that event (Bunsey & Eichenbaum, 1996; Moscovitch, 1994; Schacter, Norman, & Koutstaal, 1998). The reconstructive nature of memory retrieval also renders our memory prone to error, mediated by factors such as the nature of the cue. For example, in the Deese-Roediger-McDermott (DRM) paradigm, participants are asked to learn a list of semantically-related words. At recall, the list words and semantically-related lures are presented for recognition. Consistently, participants tend to endorse semantically-related lures as being part of the original study list, suggesting that memory for previous information is subject to bias based on the nature of the cue and the semantic network to which it is related (Roediger, & McDermott, 1995; see also Bartlett, 1932).

Finally, related to the idea that any given memory can be retrieved flexibly by various cues, so too can new information be flexibly encoded (Dusek & Eichenbaum, 1997; Henke, 2010). That is, if we experience two items, A and B, simultaneously, and associate them into a memory, we can later associate either of those stimuli with a new item (i.e., A with C or B with D): thus, our ability to encode new information is not restricted entirely by past experience, although prior experiences can benefit memory for new items, given a high degree of similarity between stored and incoming information (Craik & Tulving, 1975; Kan, Alexander, & Verfaellie, 2009; Staresina, Gray, & Davachi, 2009). It is clear that the ability to acquire lasting memories from previous experience, and reliably retrieve that information has high utility value: salient information regarding objects, situations, or individuals can be stored for future reference. For example, an unpleasant experience at a certain restaurant or a comfortable ride in a specific car may become experiences we cache, which may subsequently guide our behavior, in this case future spending. Similarly, the ability to encode items flexibly also allows for an updating of stored information as situations change, a necessary consequence of living in a dynamic environment. Although one may learn initially that a friend enjoys pomegranates, if that friend develops an allergy to the fruit, the association between the friend and fruit must be altered to avoid disaster. The flexible natures of memory at both retrieval and encoding serve to provide a means for humans to access and acquire information based on changing demands (Suddendorf & Corballis, 2007).

1.2 Episodic memory and additional utilities

In addition to the obvious uses for different attributes of memory, there exist several lines of evidence that show the contributions of these aspects of memory on non-mnemonic tasks. In terms of autonoetic consciousness and re-experiencing personal past events, Pillemer (2003) describes the potential impact of very memorable personal events, as providing guidance in probabilistically-rare situations, or helping form how we view ourselves as individuals. These special or “self-defining” memories may often be referenced at later time points to frame current issues, such as difficult life decisions (Conway & Pleydell-Pearce, 2000; Singer, 2004). Indeed, McAdams (2001) notes that one crucial aspect of an individual’s personality exists at the level of the life story, or the continual construction of one’s life experiences into a coherent narrative, to derive a sense of identity and meaning. Finally, evolutionary psychology accounts for the utility of mental time travel suggest that personal experiences with high utility value tend to be affectively charged, and that the ability to re-experience such events allows for the simulation of outcomes beyond the present moment, allowing for delay of gratification or the avoidance of major long-term loss in the face of immediate gains (Benoit, Gilbert, & Burgess, 2011; Boyer, 2008).

Parallel findings suggest less personally-relevant memories are also used for non-mnemonic tasks. Chen, Mo, & Honomichl (2004) presented vignettes of ill-defined problems to two groups of individuals: one Chinese group and one North American group. Crucially, some of the problems were analogously similar to Chinese and North American fables, and thus both groups should have more familiarity with some problems that may aid their performance for those specific problems. Indeed, the groups showed higher success rates for solving problems that were analogous to previous childhood fables, compared to the other problems. Moreover, although never explicitly stated, many subjects reported being reminded of the useful fable during the problem-solving process. Notably, success rate for solving any problem was above 0%, suggesting that although memory for related stories and solutions facilitated performance, it was not strictly necessary. Similarly, when participants were asked to predict how much they would enjoy a certain mundane event in the near future (i.e., going to a baseball game or riding the subway), their predicted enjoyment was mediated by more memorable previous instances of the same event, even if such instances were not statistically likely (Morewedge, Gilbert, & Wilson, 2005).

With respect to encoding, one notable function of the ability to associate information flexibly seems to be the resultant ability to draw inferences between memories that share common elements. That is, because items and their associations are thought to be encoded as separate units, if an item exists as part of several memories, one can also form associations between the separate elements of those memories. For example, in the associative inference task, pairs of items are learned (i.e., A-B, B-C, X-Y, Y-Z) during one phase, and then, new pairs with one overlapping item are judged for their correctness (i.e., A-C, X-Z). The ability to infer correctly these second-order associations requires that the initial memory for pairs not exist as a single, “unitized” entity, but rather, as separate elements which form part of a whole. The hippocampus is associated with these types of judgments, in addition to encoding the initial inter-item pairs (Bunsey & Eichenbaum, 1996; Shohamy and Wagner, 2008;Zeithamova & Preston, 2010).

These sets of findings suggest that the nature of memory has additional utility beyond its contents: a retrieved memory is referenced and interpreted according to current task demands, a feat possible due to the flexible nature of how experiences are stored. In addition, the sense of re-experiencing helps bestow affective valence to certain important experiences, possibly aiding in their retrieval at subsequent points to guide behaviour. Finally, parts of an existing memory may be re-encoded in new combinations, allowing for associations to be formed between unrelated elements, enabling the emergence of reasoning between existing memories, and the generation of increasingly novel events to be retained.

1.3 Episodic memory and simulation

Combining the notions of autonoetic consciousness and the flexible nature of memory, some researchers have suggested that a powerful function of human memory systems is to go beyond the immediate present, and ‘simulate’ or ‘imagine’ other scenes or scenarios. By these accounts, the ability to travel mentally back in our personal past also applies to travelling forward to a predicted future: the fact that memory retrieval is reconstructive suggests that we may recombine or retrieve elements from disparate events in order to simulate a future outcome. Such ability would confer the benefit of pre-experiencing or “simulating” future outcomes, so that more adaptive decisions can be made without experiencing any potentially negative effects (Atance & O’Neill, 2001; Boyer, 2008; Gilbert & Wilson, 2007; Schacter & Addis, 2007; Schacter et al., 2012; Suddendorf & Corballis, 2007).

Behaviourally, there are several lines of evidence to suggest humans indeed engage in such future simulations. Within the personality field, the notion of “possible selves” has emerged as one way in which humans regulate behaviour according to prior knowledge (Markus & Nurius, 1986; Oyserman & Markus, 1990). During life, we acquire different schemas regarding various types of people and roles, and simulate ourselves in a future context partially according to these templates. For example, a future self who is frightening (i.e., “feared self”), may serve as a warning not to engage in behaviours that may lead to such an individual. In a similar vein, simulation can also be a self-regulation strategy for accomplishing a personal goal, particularly when that simulation includes estimating the means to attain such goals, rather than merely the desired outcome (Oyserman, Bybee, & Terry, 2006; Pham & Taylor, 1999; Taylor, Pham, Rivkin, & Armor, 1998). Such phenomena are not rare occurrences in the context of daily life. McVay, Kane, & Kwapii (2009) took an experience-sampling approach to estimate the prevalence of task-unrelated thoughts (including thinking about future events) in a sample of undergraduates over a period of 1 week. Subjects reported being in a task-unrelated thought during 30% of the time points that were sampled, suggesting a good portion of their mental time is spent thinking about times other than the present. Other studies have reported the frequency of future-related thoughts to be as high as 59 instances per day (Argembeau, Renaud, & van der Linden, 2011).

Developmentally, the emergence of episodic memory in children appears at approximately 3 or 4 years of age, and seems to coincide with other abilities associated with the notion of future simulation (Atance, 2008). For example, Suddendorf & Busby (2005) asked 3-, 4-, and 5-year old children questions about what they did yesterday and what they will do tomorrow. Approximately 30% of 3-year olds could produce plausible answers to either past or future questions, whereas 50% of 4- or 5-year olds responded with plausible answers. Similarly, Richmond & Pan (2013) had 3- and 5-year old children recall past events or imagine new events using pictures of personal items, as well as perform an age-appropriate associative inference task (i.e., learn A-B, B-C, and test on A-C or B-D). They found that the ability to simulate future events was correlated with associative inference task performance, suggesting that the ability to encode items together flexibly is associated with future simulation in children.

In sum, such findings suggest that the development of episodic memory allows for the ability to consider or simulate future outcomes, and that we as humans take advantage of this throughout a good portion of our life.

1.4 Processes and neural substrates underlying simulation

Perhaps the strongest support for an association between episodic memory and future simulation, comes from evidence of the underlying neural substrates of both processes. Early findings of patients with amnesia due to hippocampal lesions suggested some parallels between remembering past events and simulating future ones (Klein, Loftus, & Kihlstrom, 2002; Tulving, 1985). For example, Klein et al. (2002) asked amnesic patient D. B. to imagine personal events and general issues that may occur in the near future. Although D. B. was not able to describe any specific events that may occur in his personal future, he could nonetheless give reasonable descriptions of future issues in a general, semantic sense, such as those concerning greenhouse gases and urban transportation. Such an effect would suggest that brain structures implicated in episodic memory, particularly the hippocampus, would play a role in imagining future events.

Recent evidence from studies of patients with brain lesions (Addis, Sacchetti, Ally, Budson, & Schacter, 2009; Hassabis, Kumaran, Vann, & Maguire, 2007; Rosenbaum, Gilboa, Levine, Winocur, & Moscovitch, 2009), functional neuroimaging of healthy people (Addis, Pan, Vu, Laiser, & Schacter, 2009; Hassabis & Maguire, 2007; Okuda et al., 2003; Spreng, Mar, & Kim, 2008) and even of electrophysiological studies in rats (Johnson & Redish, 2007), have suggested that the hippocampus is implicated in imagining future events. Specifically, one key process underlying episodic memory and future simulation is retrieving information from episodic memory. When retrieving an item, either via free recall or in response to a cue, the hippocampus provides traces or “pointers” to retrieve information related to that memory, stored in perceptual neocortical regions (Moscovitch, 2008; Moscovitch et al., 2005, following Teyler and DiScenna, 1986). Given that simulations must be based on existing memories, simulation likely samples from episodic memory, particularly if simulating a personal future event. Thus, the hippocampus should be implicated during future simulation, in a manner paralleling its role during episodic memory retrieval.

Indeed, Hassabis et al. (2007) asked patients with hippocampal lesions to imagine themselves in different scenes in response to a cue (i.e. beach), and noted that patients reported fewer details, and less coherent scenes, compared to controls. Also, patients with Alzheimer's disease, who show a decrease in the number of internal "episodic-like" details during autobiographical memory retrieval, show a similar deficit when simulating future events (Addis et al., 2009). Finally, there is some evidence to suggest that patients with developmental amnesia due to perinatal neural insult can also show impairments in future simulation that mirror their deficits in episodic memory((Kwan, Carson, Addis, & Rosenbaum, 2010) but see (Hurley, Maguire, & Vargha-Khadem, 2011)).

In terms of neuroimaging evidence, structures implicated in autobiographical memory recall, including the medial temporal lobes, medial prefrontal cortex, and medial and lateral parietal cortices, also tend to be recruited during future simulation (Andrews-Hanna, Reidler, Sepulcre, Poulin, & Buckner, 2010; Spreng & Grady, 2010). Studies using similar paradigms to the aforementioned patient studies have found that subjective ratings of how detailed an imagined event was, correlated positively with hippocampal activity (Addis & Schacter, 2008), a pattern that is paralleled in studies of autobiographical memory recall (Cabeza & Jacques, 2007; Gilboa, 2004). In addition, varying the personal significance of imagined events also modulates activity in the autobiographical memory network, paralleling the role of personal significance in past experiences (A. D'Argembeau et al., 2010). Finally, recent studies examining the role of autobiographical memory systems across various tasks show a common core network implicated in autobiographical memory, future simulation, prospective memory, and even ToM (theory of mind; Spreng & Grady, 2010; Spreng et al., 2009)

In terms of the frontal lobe contributions to future simulation, the most consistently implicated region in future imagining is the medial prefrontal cortex, with reported activation encompassing the frontal poles (BA 10), ventromedial prefrontal cortex (BA 25 & 32), and dorsomedial prefrontal cortex (BA 9). These regions of medial prefrontal cortex have been implicated in a wide variety of tasks, ranging from self-referential processing (Craik et al., 1999; Mitchell, 2009), to autobiographical memory recall (Cabeza & Jacques, 2007; Svoboda, McKinnon, & Levine, 2006), ToM (Frith & Frith, 2006), and even some forms of reasoning (Green, Kraemer, Fugelsang, Gray, & Dunbar, 2010; Raposo, Vicens, Clithero, Dobbins, & Huettel, 2011; Volle, Gilbert, Benoit, & Burgess, 2010). Also, medial prefrontal activity during future simulation is associated with various factors, including emotional significance, the amount of reported detail, and how self-referential the simulation is. The precise role of the medial prefrontal cortex in these simulations, however, is not clear.

1.5 Construction as a key aspect of simulation

In addition to retrieval, another key aspect to imagining a novel event is the construction of the mental representation itself (i.e. event construction). Because an imaginary event has not been previously experienced, it cannot be evoked in its entirety merely by retrieving items from memory. To imagine a novel, coherent event, these items must be recombined or reordered in new ways (Addis & Schacter, 2012; Rosenbaum et al., 2009; Suddendorf & Corballis, 2007), and it is presumably the coherence of a constructed event (or lack thereof) that would dictate whether imagined items in consciousness are perceived as a unified scene/event, or merely unrelated mental images (Addis & Schacter, 2012; Blumenfeld, Parks, Yonelinas, & Ranganath, 2011; Hassabis, Kumaran, Vann, & Maguire, 2007). Furthermore, given the flexible nature of episodic memory with respect to retrieval and encoding, it is reasonable to expect that constructing/recombining information into a coherent mental representation is an important aspect of imagination (Bartlett, 1932; Martin, Schacter, Corballis, & Addis, 2011; Roediger, & McDermott, 1995; Schacter & Addis, 2007; Schacter et al., 1998).

There is some evidence to suggest that imagination performance depends partially on event construction ability. Studies of patients with hippocampal lesions have shown that in addition to being sparsely detailed, the imagined scenes produced by patients are also rated as less spatially-coherent by the patients themselves and by raters ((Hassabis et al., 2007; Rosenbaum et al., 2009; though see (Squire et al., 2010)). It is not clear, however, whether the patients' deficit in retrieving details from memory precluded them from constructing spatially coherent scenes, or whether two separate deficits exist. Indeed, in a recent review, Addis & Schacter (2012) identify initial construction and elaboration as two of the many process involved in imagination, noting that less is known about the processes and neural substrates governing event constructions.

Drawing on Hassabis et al.'s findings regarding the importance of coherence in scene construction, I posit that coherence is an important aspect of event construction. Theoretically, the notion of coherence is important for simulating future events, because such events are less constrained in terms of their content or structure: whereas recalling past memories is bound by what we have actually experienced, we may imagine new experiences that are based less on our past experience, and more on semantic memories. Theoretically, although the flexible nature of memory is a key prerequisite for constructing new imagined scenarios, such memories must be constrained within conceptual knowledge abstracted from numerous situations, in order to avoid an overload of specific information (J. R. Anderson & Schooler, 1991). Imagination, then, must be a combination of previous episodic and semantic memories, particularly since autobiographical memories are situated within a semantic framework (Conway & Pleydell-

Pearce, 2000; Suddendorf & Corballis, 2007), requiring integrating different types of information, and the relative coherence of the resultant mental representation would be one manner to judge the relative success of such a task.

However, no studies to date have provided a systematic investigation of event construction during imagination, the factors that affect the coherence of an imagined event, and how such factors modulate activity in associated brain regions. For example, as future simulations are necessarily based on both episodic and semantic memory, one dimension with which simulations can vary is their congruence with pre-existing schemas or general knowledge. It has long been observed that prior knowledge can facilitate performance on a variety of tasks. For example, information congruent with pre-existing schemas is recalled better than incongruent information (Craik & Tulving, 1975; Kan et al., 2009; Staresina, Gray, & Davachi, 2009). Also, the amount of information one can maintain in working memory is increased if such information can be organized or ‘chunked’ into fewer items (Bor & Owen, 2007; Cowan, 2001; Miller, 1956). Furthermore, factors that affect complex cognitive processes in general should also affect event construction. Increasing the amount of information to be processed (i.e., set size) increases task demands across a variety of paradigms, such as relational reasoning, visual attention, and working memory (Awh & Jonides, 2001; Cowan, 2001; Viskontas, Morrison, Holyoak, Hummel, & Knowlton, 2004). However, previous studies on future simulation have typically provided a single cue, allowing participants to elaborate in an open-ended fashion: consequently, differences in the amount of information to be processed have varied as a function of participant performance, rather than being directly manipulated. Summerfield et al. (2008) conducted a scene construction task involving a manipulation of set size: however, the impetus of their study was to examine the imagining of a single object vs. objects that comprise a scene. Thus it is unclear to what extent manipulating factors such as the semantic associations between items or the number of items to be processed, affects the ability to construct a novel simulation, and/or modulates neural activity during future simulation tasks.

1.6 Overview of the current research

The present line of work seeks to understand the processes underlying the construction of novel events during future simulation, and the role of specific brain regions during event construction. To this end, four experiments examined coherence in event construction for non-personal events using a novel paradigm, across several subject groups. Specifically, Experiment 1 tested whether event construction may be associated with the hippocampus, by measuring the impact of age-related changes in long-term memory on event construction, given that these changes have been linked to decreases in hippocampal functioning in healthy older adults (Noble et al., 2012). Event construction demand was varied by manipulating set size, to see the impact of increased mnemonic load on performance. In addition, I also tested the association between how well an event was constructed, and subsequent memory of that event, and whether other potential variables could account for such findings. In Experiment 2, the same paradigm was applied to patients with lesions to the medial temporal lobes, to test directly whether the hippocampus and surrounding medial temporal regions are necessary to construct a novel simulation, and how abilities on event construction affect subsequent memory.

Experiments 3a, 3b, and 4 used a modified version of the previous paradigm to test the influence of the semantic-relatedness of items (i.e., typicality), and the influence of the number of items (set size) on event simulation performance, subsequent memory, and neural activity. Specifically, Experiment 3a examined the effect of typicality and set size on event construction performance. In addition, the association between event construction performance and measures associated with prefrontal function were examined, to explore the putative role of these brain regions on event construction. Experiment 3b replicated the findings regarding the role of typicality on event construction performance, and explored the effect of typicality on subsequent memory using a modified paradigm suitable for fMRI. Experiment 4 examined the neural correlates of event construction and subsequent memory: specifically, the contributions of the hippocampus and medial prefrontal cortex to event construction, and how activity in these regions may be affected by the typicality and/or the complexity of a constructed simulation.

Chapter 2: Event construction and age-related changes in long-term memory

2 Experiment 1: Introduction

Although it is clear that future simulation involves both the initial construction of the representation, and subsequent elaboration of the event, the processes that govern the former aspect are still poorly understood. A limitation of studies of future simulation has been the use of open-ended cueing paradigms: the subject is usually given a general cue and is asked to generate an imagined event based on such information. Such a task would require both retrieving episodic and semantic elements from long-term memory (LTM) in response to a general cue (e.g. imagine a beach scene), and then constructing the imagined event from those elements. Consequently, variations in task performance may be due to differences in the ability to search memory and retrieve the requisite elements from LTM (e.g. umbrella, beach balls, people playing volleyball, etc.), and/or from differences in recombining and binding of retrieved elements into a coherent representation.

Addis and colleagues recently developed an experimental recombination procedure, whereby participants produce items from their personal past in one session, which are then randomly recombined by the experimenters and presented as items to be imagined in a new future event (Addis, Musicaro, Pan, & Schacter, 2010; Addis, Pan, et al., 2009). Such a task allows for the measurement of behaviour and neural activity in response to having to imagine a novel event, particularly if analysis is focused during the early time period of imagining trials, where subjects must be initially constructing their simulations. Indeed, using this paradigm, neural activity implicated in construction and elaboration of simulations has been identified (Schacter & Addis, 2009). Studies have also compared simulations that are relevant to personal goals vs. non-relevant, more specific vs. more general, and those that are more or less probabilistically likely (Addis, Cheng, Roberts, & Schacter, 2011; D'Argembeau et al., 2010; Weiler, Suchan, & Daum, 2010). Summerfield et al. (2008) presented subjects with 3 – 6 household objects and construct a scene with the elements. The nature of the task, however, was always similar - to assimilate items in order to create a mental image of a scene - so construction demands were present, but still limited to placing objects in canonical locations. Thus, such manipulations vary mostly the nature of the simulations, rather than the amount of constructive effort required during simulation.

To this end, I developed a novel paradigm to examine construction ability during imagination of novel, non-personal events (hereby referred to as *event construction*), which was used in four Experiments to assess event construction across a variety of conditions. In Experiment 1, I examined whether aging is associated with changes in event construction ability, and whether the coherence of an imagined event mediates its subsequent memory. Younger and older adults were shown a "context" word and 3 - 6 "item" words on a computer screen, and were asked to construct an imaginary event by relating the presented item to one another in the target context. With the words still visible on the screen, the event was then described out loud, and the responses were recorded, and later transcribed and scored. Providing items for the to-be-imagined events for the duration of the trial ensured that differences in event construction performance would be based largely on differences related to the construction process itself; that is, the effect of LTM demands during the task were reduced, since the participant did not have to hold these items in memory during the construction phase. Group differences in performance were compared at different set sizes, to determine whether event construction varies as a function of age.

To determine whether event construction ability plays a role in subsequent memory for constructed events, I used a cued recall paradigm to probe memory of the stimulus items 10 min following the task. If the coherence of the imagined events enhances memory for the individual items, then creating more relations between or among items within an imagined event should be associated with recall of those items.

Since coherence in scene construction is reduced in people with amnesia related to MTL damage (Hassabis et al., 2007), I hypothesized that age-related memory decline would affect event construction coherence in a similar manner. This led to the prediction that the events older adults construct would be less coherent, given the deterioration of the MTL with age, and thus memory for the constructed events would be worse than that of young adults. Moreover, given that older adults do show deficits in future simulation, it is reasonable to predict that part of this effect is due to poor event construction (Addis, Wong, & Schacter, 2008; Addis et al., 2010)

However, it was possible that older adults' performance would be superior to that of young adults because of other factors that improve with age, such as older adults' proficiency in telling coherent stories (Pratt, Boyes, Robins, & Manchester, 1989), intact ability to construct and comprehend a narrative (Radvansky & Copeland, 2001), and their well-developed semantic memory (Craik & Salthouse, 2000). Thus, it may be that under the conditions of the current paradigm, older adults can successfully use the provided items efficiently to complete the task, as providing environmental support has been shown to decrease age effects on cognitive function (Craik, 1986).

2.1 Method

2.1.1 Participants

Twenty-four younger adults and 26 older adults participated in the study. All participants were native-English speakers and had no prior history of any major neurological or psychological illness. Group demographics are listed in Table 2.1. All older adults were living independently within the greater Toronto area, and were recruited through ads in the local newspaper. All younger adults were first-year psychology students at the University of Toronto. Testing took place over a single session, lasting approximately two hours. Participants gave informed consent prior to their participation in the study. For their participation, older adults were remunerated $20, and younger adults were awarded course credit. This study was approved by the Research Ethics Board at the University of Toronto.

Table 2.1. Demographics and neuropsychological test scores for younger and older adults

	Young Adults	Older Adults	*p*-value
n	24	26	
Age	18.5 (1.35)	74.15 (6.47)	
# Right-handed	22	23	
Years of education	12.92 (.57)	15.28 (3.14)	
Word span	4.70 (.70)	4.35 (.63)	= 0.07
Alpha span	4.13 (.69)	3.69 (.68)	< .05
Letter-number sequencing (max = 21)	-	9.8 (2.08)	
Logical memory immediate recall (max = 75)	-	40.54 (10.93)	
Logical memory delay recall (max = 50)	-	25.54 (9.39)	

Standard deviations (*SD*) listed in parentheses.

2.1.2 Design

The experimental session consisted of one block of 24 trials, with six trials per set size. On each trial, following a fixation cross, participants were shown a context word (i.e. STADIUM), which was paired with a varying number of item words (set size: 3, 4, 5, or 6 words). Participants were told to imagine the items together within the event or scene described by the context, and to describe that event out loud. Specifically, participants were told to imagine as many relations between the items as possible, and to be sure to state those relations explicitly out loud. For example, for items ‘APPLE, DESK, PENCIL, BOOK’ and the context ‘SCHOOL’, participants should say something like, “Inside a school room, there’s a desk with a book on it. On top of the book is an apple with a pencil sticking out of it.” Participants were told that it was not sufficient to just say the words out loud or just form a sentence with the items (viz. "Inside the school there was a desk, a book, an apple and a pencil”); they must try to imagine the event or scene, and how the items are related. Participants were given no time limit to describe their event or scene. All words were presented on the screen for the duration of the trial. When the imagined event or scene was described in full, the participant pressed a key to end the trial. Following this, participants made self-report judgments on a 5-point Likert scale of the perceived difficulty of imagining the event or scene, and its subjective overall coherence.

Scoring

The imagined events and scenes were recorded via digital recorder and transcribed verbatim for scoring purposes. For each trial, the number of explicitly mentioned relations between item words was tallied, to give a measure of how related the constituent items were (i.e.

relational coherence) as an index of event or scene construction ability. The rationale for this scoring was based on previous reports of associative deficits within older adults (Mitchell, Johnson, Raye, Mather, & D'esposito, 2000; Old & Naveh-Benjamin, 2008), and by studies establishing the roles of the hippocampus in relational memory processes and imagination (Hassabis et al., 2007; Zeithamova & Preston, 2012). I assumed that if participants produced a coherent imagined event or scene during the task, the relations between items should be available to verbal report. Moreover, highly coherent imagined events and scenes would have a larger number of relations between constituent elements, compared to those that are less coherent.

For example, for the items "BIRD, EDGE, MAILBOX, GRASS" and context 'YARD', the description "In my front yard, there was a bird at the edge of the grass. The bird was looking at the mailbox" would be scored as having four relations: yard-bird, bird-edge, edge-grass, bird-mailbox. In contrast, the description "There's a yard outside, and inside the yard there's a bird, and I also see a mailbox and some grass by the edge" would be scored as having two relations: yard-bird, grass-edge. The latter description would not be as coherent as the former, having fewer relations amongst the items. The description, "I see a yard, and some grass, and a mailbox, and an edge" would be scored as having no relations, because it is unclear how the items are present within the imagined scene. Moreover, in line with task instructions, only relations formed between stimulus words were counted in the scoring: relations between stimulus words and other items spontaneously included by the participant were not counted. This ensured that the measure of relational coherence is based only on event construction ability for the given stimuli, and is not influenced by whether or not participants differed in the amount of detail incidentally retrieved from memory during the task.

Examples of types of relations are listed in Table 2.2. For a relation to be counted between items, the participant must have explicitly stated the relation between them: assumed or inferred relations were not counted unless it was impossible to interpret the phrase any other way. Repetitions of relations between two item words were not counted. Also, any item word could have a described relation with multiple other item words, as long as they were stated explicitly. Scoring was done by the author and a research assistant. Inter-rater reliability was tested by selecting 25 events at random and comparing scoring criteria: percent agreement between scorers was high (Cronbach's alpha = .95). Because of the contents of the transcribed narratives, it was not always possible to be blind to group membership. However, because the scoring criteria involved very little subjective judgment, scoring bias was not an issue.

Table 2.2. Examples of relations for scoring of the construction task for all Experiments

Relation Type	Description	Example	Related Words
Spatial	Two items and their location to one another	"Then our **boat** got caught in some **seaweed**. We tried using a…"	BOAT-SEAWEED
		"I was climbing a **tree** in the **park**, when I saw a bunch of geese…"	TREE-PARK
Temporal	Two items and their temporal proximity or sequence	"My boyfriend decided to read me a passage from his favourite **poetry** book, and then he proposed to me with a **diamond** ring…"	POETRY-DIAMOND
		"While they're staring at the **moon**, a **frog** jumps onto the girl's face…"	MOON-FROG
Causal	Causal effect or inference between two items	"I handed the **camera** to my mother so that she could take a picture of the **pony**…"	CAMERA-PONY

		"I won a **prize** for shooting an **arrow** through a balloon…"	PRIZE-ARROW
Indirect	An explicit relation between two items via a third item	"The **uniformed** clerk took our luggage on the **trolley**…"	UNIFORM-TROLLEY (via luggage)
		"The **umbrellas** were shading a small little boy playing with his **ball**…"	UMBRELLA-BALL (via boy)

In addition, the word count of each trial response was measured, to determine whether groups would differ in terms of verbosity. The number of item words per trial that were omitted across groups was tallied, to determine whether or not subjects were prone to forgetting of recent responses during the imagination task. The rationale for this measure was that if older adults had somewhat poor memory for recent responses, they may also forget whether or not a given item word was already incorporated into their narrative, and thus fail to mention it altogether.

2.1.3 Materials

A total of 132 words were taken from the MRC psycholinguistics database (Coltheart, 1981), of which 24 were used for context descriptions (i.e. BEACH), and the remaining 108 words were used as items to be imagined within each context. All context lists were approximately equivalent in terms of word length (range = 4 – 8 letters, *M* = 5.43, *SD* = 1.27), frequency (range = 1 - 125 per million, *M* = 30.08, *SD* = 28.12), concreteness (range = 425 – 637, *M* = 581.90, *SD* = 39.26), imageability (range = 454 – 642, *M* = 579.91, *SD* = 39.04), and familiarity (range = 381 – 644, *M* = 531.34, *SD* = 51.91).

Item words were not counterbalanced or randomized for each context word because doing so would have resulted in highly implausible combinations of items and contexts, despite the fact that all word stimuli were highly familiar. Instead, item words were yoked to context words such that every item word could plausibly occur within the given context, but would not be found exclusively within that context (i.e. a jacket in a basement, vs. a polar bear in the Arctic). Context and item word sets were presented randomly to avoid order effects. To test for potential word differences across set size conditions, several one-way ANOVAs were conducted using the mean frequency, imageability, and familiarity, and word length for each set size. There were no significant differences for any of the word attributes [frequency, $F(3,104) = 1.27$, $p = .29$; imageability, $F(3,104) < 1$; familiarity, $F(3,104) = 1.68$, $p = .18$; word length, $F(3,104) < 1$].

2.1.4 Procedure

Participants were tested individually in a quiet testing room. Following informed consent, participants were given the construction task. Approximately 10 minutes following completion of the construction task, participants completed cued recall of the item words used in the construction task, using the context words as a cue. In addition, all participants were given word span and alpha span, simple span measures of working memory (Craik, 1986) and older adults were given additional measures of WM (Letter-number sequencing) and LTM (Logical memory) from the Wechsler Memory Scales—3rd Edition (Wechsler, 1997). These additional measures were not given to the younger adults because of concerns regarding restricted variance of scores within this age group, which may limit the likelihood of detecting meaningful correlations. Both logical memory and letter-number sequencing were administered following cued recall of items from the construction task, to avoid interference effects from those items.

2.2 Results

All statistical results were computed using IBM SPSS version 19.

2.2.1 Event Construction Task Performance

Number of Relations

To determine whether age groups differed in terms of the relational coherence of their imagined events and scenes, we submitted the mean number of explicit relations in the construction task to an ANOVA with age (younger, older) as a between-subjects factor and set size (3, 4, 5, 6) as a within-subjects factor. This analysis revealed a main effect of set size, $F(3, 144) = 56.10$, $p < .001$, with more relations being formed as the number of items increased (Figure 2.1). The main effect of age was also significant, $F(1,48) = 9.14$, $p < .005$, with older adults producing fewer relations ($M = 51.92$, $SD = 17.35$) during their imagined events and scenes compared to younger adults ($M = 64.33$, $SD = 9.29$). The group by set size interaction was also significant, $F(3, 144) = 11.10$, $p < .001$. *T*-tests of simple effects showed that younger adults produced significantly more relations when constructing an event with five or six item words, $t(48) = 2.05$, $p = .05$ and $t(48) = 4.87$, $p < .05$, respectively. Other set sizes showed a trend toward group differences in performance (3 words: $t(48) = 1.13$, $p = .26$; 4 words: $t(48) = 1.91$, $p = .06$).

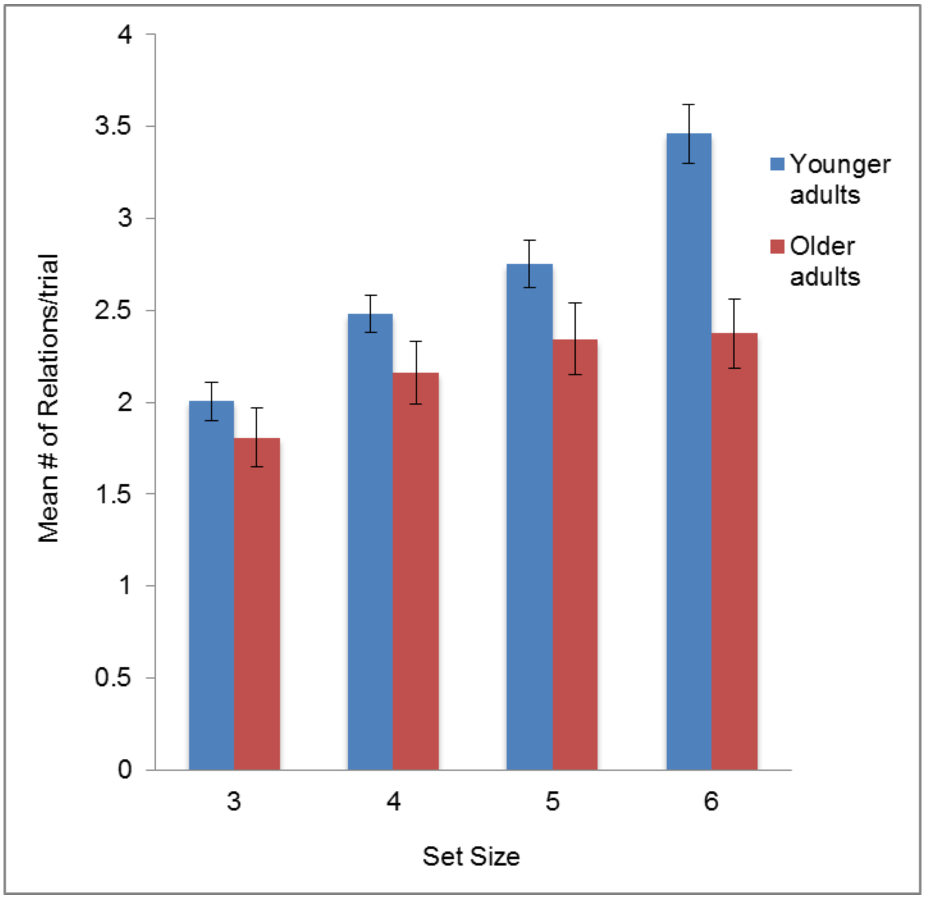

Figure 2.1. Mean number of relations/trial (coherence score) at set sizes from 3-6 for older and younger adults in Experiment 1.

2.2.2 Omissions

The rate of word omissions was very low in both groups at lower set sizes, resulting in non-normal distributions. Thus, group differences were compared at each set size using nonparametric statistics. Data from one older adult was an outlier (> 2 SDs from the mean) and was excluded from the analysis. Mann-Whitney *U*-tests indicated that older adults were more likely to omit item words from their imagined scenes only at a set size of 6 ($U = 288$, $p = .69$, $U = 262.5$, $p = .15$, $U = 270$, $p = .45$, and $U = 177.5$, $p < .05$ for set size 3, 4, 5, and 6, respectively). This occurred despite the fact that the item words were present on the screen for the duration of the trial (Figure 2.2).

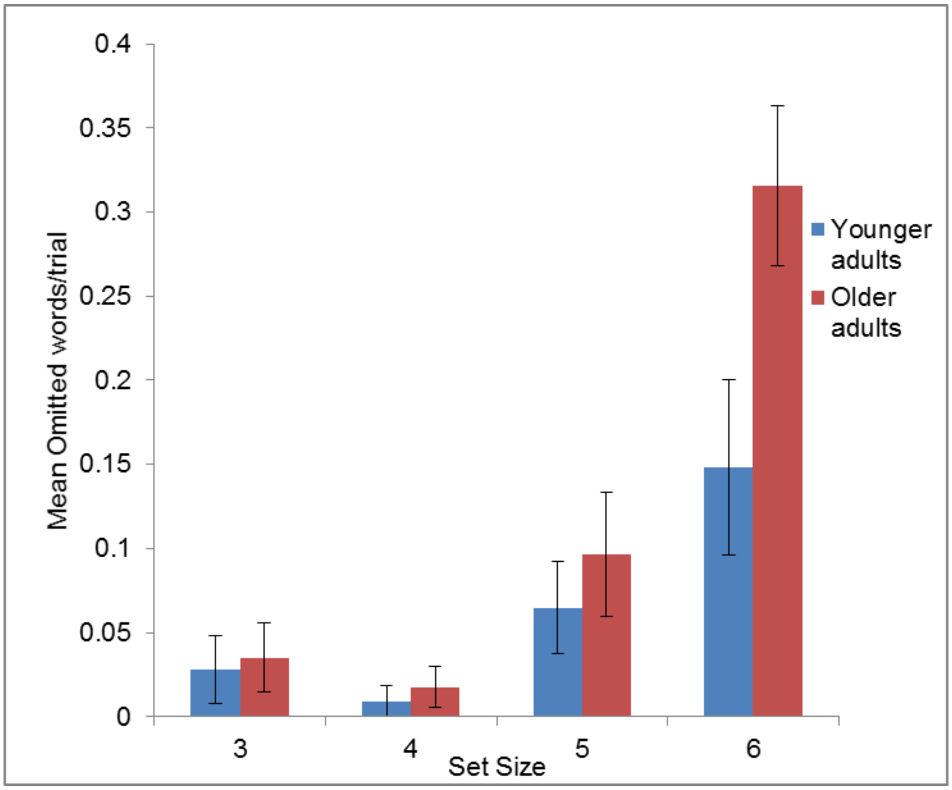

Figure 2.2. Omission rates at set sizes from 3-6 for older and younger adults in Experiment 1.

2.2.3 Subjective Ratings

Ratings of coherence and difficulty were entered into a mixed ANOVA with age and set size as between and within-subjects variables, respectively. There was a main effect of set size, $F(3,144) = 4.69$, $p < .05$: with increasing set size, imagined events and scenes were rated as slightly less coherent, $M = 3.39$, 3.21, 3.21, and 3.15 for set sizes 3, 4, 5, and 6, respectively. The main effect of age was not significant, $F < 1$. The age by set size interaction was significant, $F(3,144) = 2.67$, $p = .05$. With increasing set size, younger adults tended to report lower levels of coherence (Young: $M = 3.38$, 3.14, 3.13, and 2.95 for set sizes 3, 4, 5, and 6, respectively), compared to older adults (Older: $M = 3.40$, 3.28, 3.30, and 3.35 for set sizes 3, 4, 5, and 6, respectively). However, t-tests of simple effects at all set sizes failed to reach statistical significance ($t < 1$ for set sizes 3, 4, and 5; $t(48) = 1.45$, $p = .15$ for set size 6).

For difficulty, there was a main effect of age, with younger adults rating the task as more difficult (Young: $M = 2.42$, 2.54, 2.85, and 3.09 for set sizes 3, 4, 5, and 6, respectively), compared to older adults (Older: $M = 1.67$, 1.89, 2.05, and 2.10 for set sizes 3, 4, 5, and 6, respectively; $F(1,48) = 12.06$, $p = .001$). The main effect of set size was also significant $F(3,144) = 21.08$, $p < .001$, with trials at higher set sizes being rated as more difficult ($M = 2.05$, 2.21, 2.45, and 2.60 for set sizes 3, 4, 5, and 6, respectively) . The interaction was not significant, $F(3,144) = 1.84$, $p = .15$.

2.2.4 Word Count

To test the possibility that performance on the construction task was confounded by verbal output, we calculated word counts for each participant's responses on each trial. Preliminary analysis suggested the distributions of word counts at all set sizes violated assumptions of normality (Kolmogorov-Smirnov *Z*s = 1.82, 1.79, 1.51, and 1.73 for set sizes 3, 4, 5, and 6, respectively; all *p*s < .05). Thus, we log-transformed the word count data and submitted it to a mixed ANOVA with group and set size as the between- and within-subjects variables, respectively. The main effects of set size and age were significant, with larger set sizes eliciting more lengthy verbal responses, and older adults producing more words than younger adults (F(3, 144) = 131.07, $p < .001$ and $F(1,48) = 12.82$, $p < .005$, respectively). The group by set size interaction was also significant, $F(3, 144) = 11.38$, $p < .001$. Inspection of Figure 2.3 clearly indicates that older adults were more verbose compared to younger adults, the difference varying as a function of set size. To investigate the contribution of verbosity to task performance, the average word count/trial was also computed for each participant, log transformed, and used as a covariate in the earlier ANOVA on relational coherence scores. Both the main effects of group and set size remained significant after accounting for individual levels of verbosity, *F*(1, 47) = 12.78, *p* = .001, and *F*(3, 139) = 8.48, *p* < .001, respectively. The group by set size interaction also remained significant, *F*(3, 139) = 5.40, *p* = .002. Thus, the age differences in task performance could not be explained by differences in verbosity between groups.

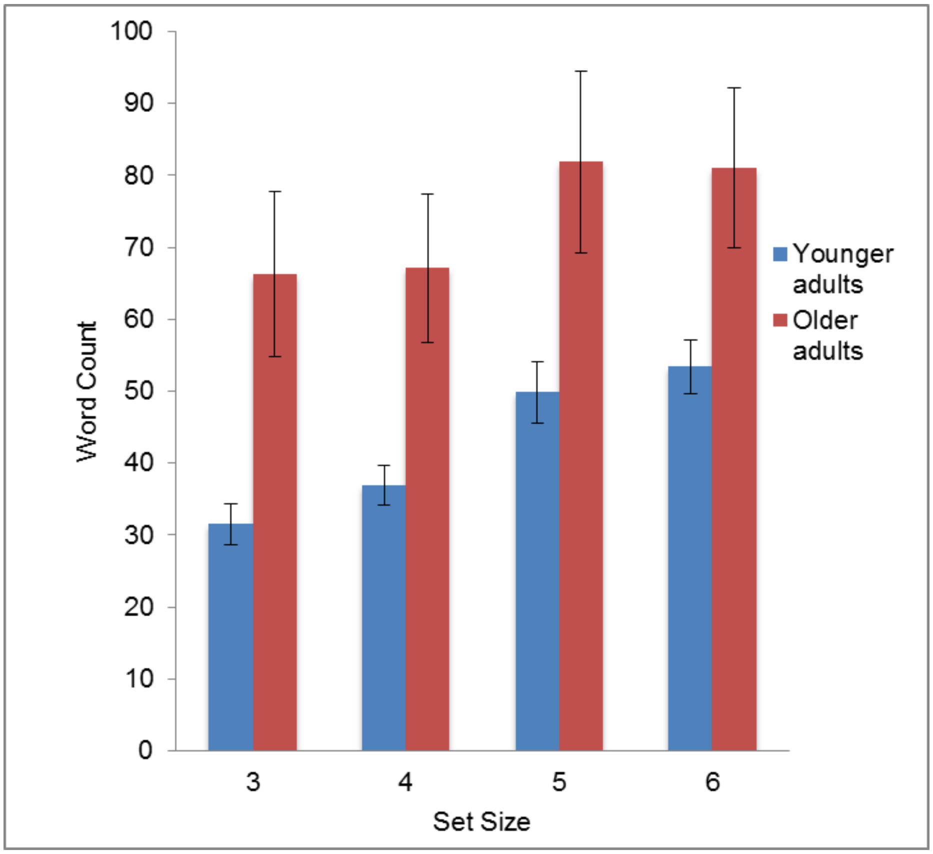

Figure 2.3. Word count of responses during the construction task at set sizes from 3-6 for older and younger adults in Experiment 1.

2.2.5 Cued Recall

The number of words recalled from the construction task after a delay was entered into an ANOVA, again with age as a between-subjects variable, and set size as a within-subjects variable. There were significant main effects of set size and age, $F(3, 144) = 77.53$, $p < .001$ and $F(1, 48) = 31.97$, $p < .001$, respectively (Figure 2.4). Not surprisingly, more words were recalled on trials with a larger set size, and older adults recalled fewer words ($M = 56.38$, $SD = 21.94$) compared to younger adults ($M = 83.38$, $SD = 10.30$). The interaction was also significant, $F(3, 144) = 9.72$, $p < .001$. Tests of simple effects revealed that younger adults recalled more words compared to older adults for all set sizes, with this difference increasing at higher set sizes (3 words: $t(48) = 3.39$, $p = .008$; 4 words: $t(48) = 4.19$, $p < .001$; 5 words: $t(48) = 5.47$, $p < .001$; 6 words: $t(48) = 5.10$, $p < .001$).

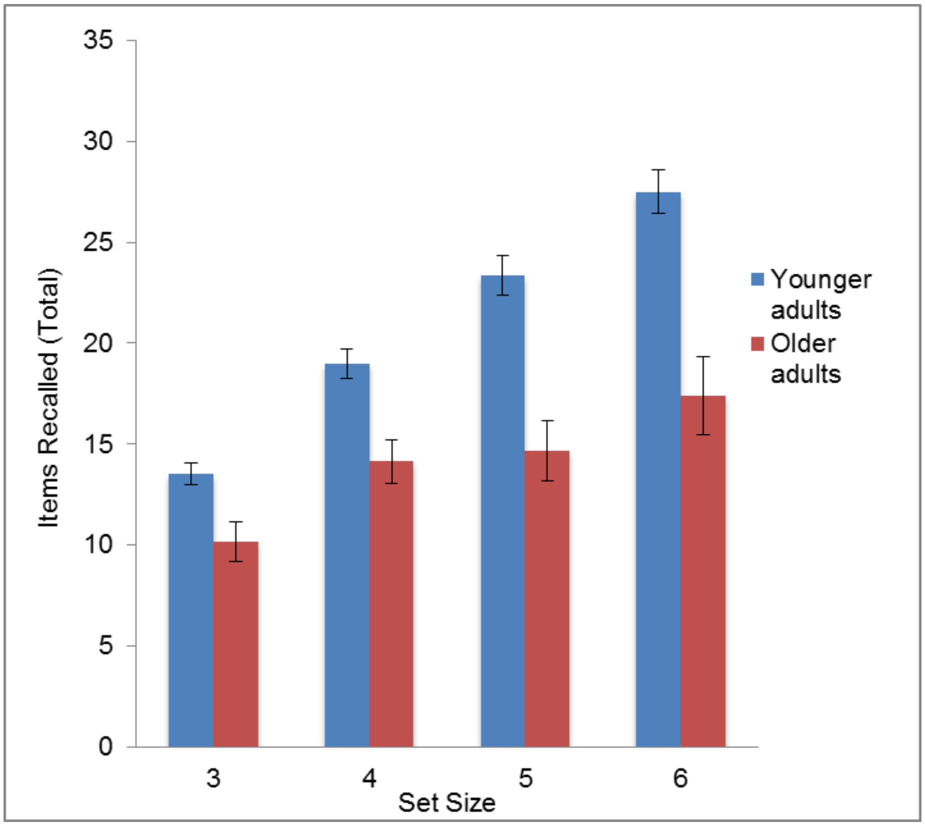

Figure 2.4. *Cued recall performance of task stimuli at set sizes from 3-6 for older and younger adults in Experiment 1.*

Recall performance was also calculated as the proportion of words correctly recalled for each set size. Across conditions, younger adults recalled roughly 80% of item words, whereas older adults recalled roughly 60% at best (i.e. 3 words condition, *M* = .56), showing a non-significant decline in performance with more words (6 words condition, *M* = .48) (Figure 2.5).

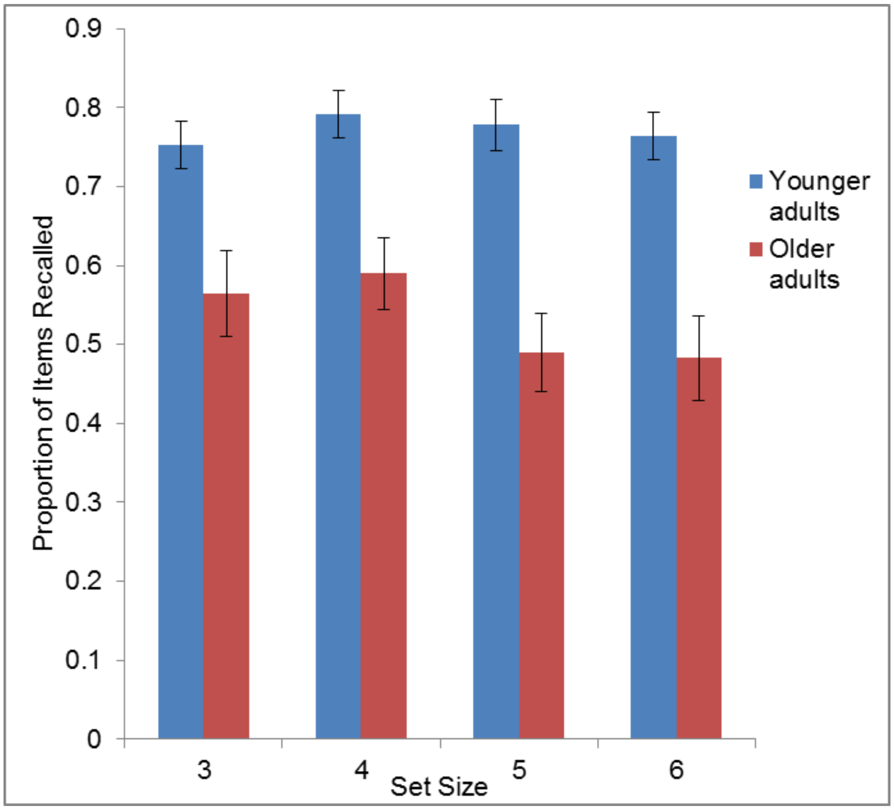

Figure 2.5. Proportion of stimuli recalled at set sizes from 3-6 for older and younger adults in Experiment 1.

To determine if words that were successfully bound during the task were more likely to be subsequently recalled, I re-analyzed cued recall performance by calculating the proportion of recalled words that were part of an inter-item relation that was used during the event construction task (Figure 2.6). The main effect of group was significant, with younger adults showing a higher proportion of recalled words as part of an inter-item relation, compared to older adults, *F*(1,48) = 12.65, $p < .005$. The main effect of set size was also significant, *F*(3,144) = 3.21, $p < .05$. The interaction was not significant, *F*(3,144) = 1.48, $p = .22$.

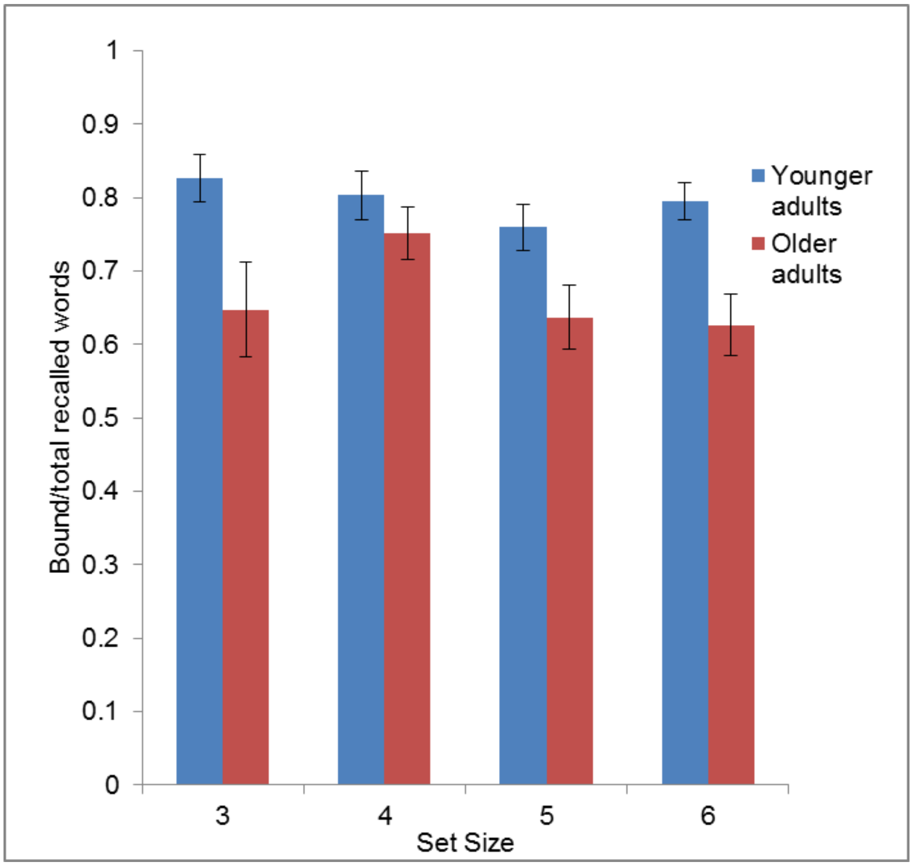

Figure 2.6. Proportion of bound versus total recalled words at set sizes from 3-6 for older and younger adults in Experiment 1

I also computed overall task performance and recall performance for each individual to examine individual differences in task performance and recall. Across age groups, forming more relations during the construction task was associated with higher recall scores (younger adults $r = .47$, $p < .05$; older adults, $r = .52$, $p < .05$), suggesting that creating more inter-item relations during the task improved subsequent memory for the items. In addition, within older adults, the total number of relations formed across trials (i.e. total coherence) was positively correlated with long term memory test scores (i.e. logical memory; $r = .41$, $p < .05$), but not with the two working memory measures (i.e. alpha span and letter-number sequencing; $r = .15$ and $r = .05$, respectively).

2.3 Discussion

In this experiment, I investigated whether older adults would show deficits in constructing novel events/scenes when the primary elements were provided and while varying set size. Using this paradigm, one may have predicted that older adults would show deficits in performance compared to younger adults, due to age-related changes in cognitive functioning (Addis et al., 2010; Craik & Salthouse, 2000; Hasher et al., 1999; Mitchell et al., 2000; Old & Naveh-Benjamin, 2008). However, it is possible that older adults' performance may have been superior to that of young adults because of other factors that improve with age, such as older adults' proficiency in telling coherent stories (Pratt, Boyes, Robins, & Manchester, 1989), intact ability to construct and comprehend a narrative (Radvansky & Copeland, 2001), and their well-developed semantic memory (Craik & Salthouse, 2000). Consistent with the former prediction, we found that older adults created fewer relations between items in their imaginary constructions compared to younger adults, reaching significant differences at higher set sizes (i.e. set sizes 5 and 6). With larger sample sizes and more statistical power, it is likely that group differences would have reached significance at the lower set sizes as well. These results could not be explained by differences in overall words used or task difficulty, as older adults were more verbose and rated the task as less difficult, compared to younger adults. For older adults, the relational coherence was correlated with performance on standard tests of LTM, but not of tests of simple working memory span.

The age-related deficits in relational coherence parallel those reported in other studies showing relational processing deficits in older adults, due to declining hippocampal function (Mitchell et al., 2000; Old & Naveh-Benjamin, 2008). For example, Ryan, Moses, & Villate (2009) reported age-related deficits in forming propositional relations on a transitive inference task. Older adults showed poorer performance in terms of acquiring the propositional relations, which was also correlated with neuropsychological measures sensitive to hippocampal function. Similarly, in our study, performance on a neuropsychological test of LTM in older adults was also positively correlated with relational coherence ability (see also Addis et al., 2008; 2010). At the other end of the lifespan, future simulation performance in children is associated with both the relative onset of episodic memory ability, and with individual differences in episodic memory encoding, providing further evidence for the association between relational processing and event construction (Richmond & Pan, 2013). Thus, decreases in associative binding were the likely source for the age effects in this experiment.

Also, the coherence of a constructed event affected subsequent memory for the items, as relational coherence scores were correlated positively with cued recall of test items across both age groups. Importantly, items that were relationally bound were more likely to be recalled, and older adults recalled a lower proportion of bound items, suggesting that decreased ability to create associations between item words influenced their recall. It is well-established that the depth to which information is processed affects its subsequent memory, and that mental imagery and semantic elaboration are two types of deep processing (Bower, 1970; Craik & Tulving, 1975). Thus, it is reasonable to infer that imagining items within a novel event/scene combines these forms of deep processing, and thus influences subsequent memory. Indeed, recent neuroimaging evidence suggests that the quality of an imagined event, which implicates the right anterior hippocampus, influences subsequent memory of an imagined event via the interaction between anterior and posterior regions of the right hippocampus (Martin et al., 2011).

Notably, the observed deficits in relational coherence cannot fully account for the age-related deficit in subsequent memory. Specifically, we observed that although subsequent memory for the constructed event was related to relational coherence in both older and younger adults, the proportion of bound items that were recalled was lower in older than in younger adults, indicating that poor retention was an added problem for the older group. This is supported by the finding that older adults showed an increased propensity to omit item words at the highest set size, suggesting that they had difficulty monitoring whether or not items had already been mentioned (Petrides & Milner, 1982). One possibility is that these omissions were also due to deficits in retention: that is, at high mnemonic loads, older adults had deficits retaining all the information over time. Results compatible with this interpretation were obtained recently by Gallo, Korthauer, McDonough, Teshale, & Johnson, (2011) who tested younger and older adults on a future imagining paradigm, and measured memory for both the details of each event and source memory (i.e. task condition), one day later. Not surprisingly, older adults showed poorer memory for both source information and specific event details. Notably, however, older adults still showed poorer source memory for those events that they could recall in detail, suggesting that they had difficulty retaining information over time, be it specific event details, source information, or both.

Despite these clear patterns of age-related deficits in performance, subjective ratings of coherence and task difficulty did not parallel these objective measures of task performance. The fact that older adults rated the present task as less difficult despite showing poorer performance, suggests that their subjective perceptions of the task may be influenced by other factors. In this case, there are two possibilities. The first is that older adults' increased familiarity with such tasks was responsible for their lower ratings of difficulty. Anecdotally, many older adults reported that the task reminded them of reading to their children, and that they found the task easy to understand. Moreover, older adults would have had more experience engaging in prospection, as people may use this strategy in decision-making and problem solving (Boyer, 2008; Buckner & Carroll, 2007; Suddendorf & Corballis, 2007), particularly in their 30's and 40's, when major life goals require frequent future planning (i.e. relationships, family, work productivity; Conway & Holmes, 2004). A second possibility is that older adults' poor metamemory abilities (Dunlosky & Connor, 1997; Shaw & Craik, 1989) lead them to underestimate task demands and prevents them from exerting the necessary effort needed to perform well (see also Hertzog & Dunlosky, 2011). Gallo et al. (2011) also found that subjective ratings of task performance were not related to source memory in older adults who completed a future imagining task, providing further evidence that such ratings in older adults may reflect other processes.

Although the findings from Experiment 1 fit well with other studies of age-related deficits in event construction and retention, other interpretations are possible. One is that age-related deficits in executive control or working memory, as opposed to some relational deficit, are driving the effects (Cabeza, Dolcos, Graham, & Nyberg, 2002; Velanova, Lustig, Jacoby, & Buckner, 2007).That is, deficits in the ability to organize and combine information during the construction task were the source of poor performance (Simons & Spiers, 2003). Performance, however, was always self-paced with no response deadline demands, and items were always presented within a plausible context that provided a general schema for organization, thereby minimizing strategic organizational demands that typically implicate the prefrontal cortex (Blumenfeld & Ranganath, 2007). Indeed, older adults show reduced deficits in memory performance when relevant contextual information is provided (Craik & Schloerscheidt, 2011; McGillivray & Castel, 2010). Performance also did not correlate with a measure of working memory, a test of frontal function, though correlations may have be found with tests of frontal function that were not investigated in this study. Despite this, it is important to note that these findings do not rule out the contributions of executive control processes on event construction performance in older adults, but merely that they did not seem to be a limiting factor under the current task parameters. Under different conditions, it is possible that older adults' performance also would reflect the operation of executive components associated with WM.

Another possibility is that group differences arose from age differences in narrative style, communicative goals, or some other factor that altered the nature of the responses in younger vs. older adults. Recent evidence suggests that accounting for differences in description performance, or inducing more detailed styles of description, is sufficient to eliminate age-related deficits in future imagining performance (Gaesser, Sacchetti, Addis, & Schacter, 2011; Madore, Gaesser, & Schacter, in press). To the extent that these differences are reflected in verbosity, such effects may be discounted as the group differences remained after covarying out word count. Moreover, whereas other studies have found age differences in the amount of detail provided in future events, this paradigm used a relational coherence measure using provided items, a different measure of imagination ability. Furthermore, there is some evidence to suggest differences in narrative style are caused by age-related changes in LTM, suggesting a common link between narrative style and event construction (Chapman et al., 2002; Fleming & Harris, 2008)

Furthermore, it is possible that age-related deficits were due to older adults retrieving less conceptually-rich representations when given the cue words. That is, when shown an item word such as ‘portrait’, younger adults may bring to mind more conceptual associations, compared to older adults. However, aging is typically associated with slight increases in crystallized knowledge, suggesting that older adults have more conceptual information at their disposal (Craik & Salthouse, 2000). Thus, it is not likely that age-related change in the conceptual richness of mental representations can fully account for the present findings.

2.4 Conclusion

The results favour the interpretation that age differences in relational processing and LTM were the source of the older adults’ deficit on the event construction task. Given the central role of the hippocampus and medial temporal lobes in LTM, it is reasonable to suggest that these structures may indeed contribute to the age-related changes in event construction and subsequent memory. However, aging is associated with various neurological changes, affecting numerous regions in terms of both gray and white matter: thus, to obtain stronger evidence that the MTLs are indeed crucial for event construction, one needs to test such a paradigm on patients with damage to the MTL, who have severely impaired LTM but relatively preserved functions in other cognitive domains, including WM. If this is correct, the deficits observed in older adults should be manifested to an equal or greater degree in patients, even though the material necessary for construction is readily available to them on the screen throughout the task. In addition, given the theoretical role of the MTL in creating coherent mental representations (Addis & Schacter, 2012), testing patients with MTL damage using our paradigm can determine whether indeed event construction is dependent on MTL structures.

Chapter 3: The role of the medial temporal lobes in event construction

As discussed in the General Introduction, previous studies showing future imagining deficits in patients have used open-ended cueing paradigms, which do not allow for distinguishing whether poor performance is due to deficits in retrieving the elements that form the core of the constructed event, or due to some deficit in forming a coherent mental representation using those elements (Addis et al., 2009; Hassabis et al., 2007; Squire et al., 2010). Race et al. (2011) tested patients with hippocampal lesions on a future imagining task, and included a narrative construction control task, in which subjects had to describe a complex picture in great detail. They found that patients had less-detailed future scenarios but showed no deficits in producing a narrative of the picture compared to controls, suggesting narrative construction was not a factor in patients' future imagining performance. Although their task would appear similar to this paradigm, there are a few key differences. In this task, patients have to construct a new event, rather than describe an existing one, and although the items are always present on the screen, the relational, internal representations they form during construction of the event/scene must be held online in WM and/or encoded into LTM as the task proceeds. By also varying the number of elements that need to be included in the event, I could determine whether the deficit in amnesic patients is exacerbated by the ensuing complexity of the construction.

If MTL-mediated LTM processes are indeed implicated in event construction, one would expect that patients would show larger deficits in event construction compared to controls. In addition, because of their large deficits in LTM, patients may be more prone to deficits in monitoring their performance, as they would have difficulty encoding their imagined events, and thus would not recall earlier portions of their description (Squire et al., 2010, though it should be noted the authors found no overall deficits in amnesics vs. controls). If this is the case, then patients should show increased omission rates at lower set sizes, compared to older adults, as well as much poorer memory for the stimuli, even if tested immediately following the task.

3 Experiment 2

3.1 Method

3.1.1 Participants

Six patients (one female) with damage to the MTL from the greater Toronto area participated in this study. All were native English speakers and had isolated impairments in long-term memory, with no deficits in visual perception, language, executive functioning, attention, or simple measures of working memory. Group demographics and neuropsychological test performance are listed in Table 3.1. In terms of etiology, two patients suffered damage to the MTL due to epileptic seizures, and one of these patients had surgical resection of the right MTL. Two patients sustained damage due to viral encephalitis, one patient suffered from suspected Whipple's encephalopathy, and the final patient suffered anoxic damage due to an MCA infarction. To confirm that damage was localized to the MTL, T1- and T2-weighted structural MRIs were obtained. Five out of the 6 patients received scans, with one patient dying before structural scans could be obtained (See Appendix 1 for representative structural slices).

Twelve controls (six females) that were matched as closely as possible to patients for age and education were recruited from the greater Toronto area. None of the controls had a history of major neurological or psychological illnesses.

3.1.2 Design

Experiment 2 used a similar paradigm to Experiment 1. Participants were presented with a context word and 3 – 6 item words and asked to imagine an event with those words, relating the items as much as possible. Dependent measures included the number of inter-item relations, the number of omitted trial words, word count, subjective ratings of coherence and difficulty, and cued recall of the items.

3.1.3 Materials and Procedure

The materials and testing procedure were similar to those of Experiment 1. For patients, the testing session lasted 1 hour, consisting of the construction task, followed by cued recall of the objects. In addition, information on performance on some neuropsychological tests was obtained prior to the experiment from clinical files. For the control participants, testing also took place over a single session, lasting approximately 2 hours, with the construction task occurring in the first hour, followed by neuropsychological testing. All participants gave informed consent prior to their participation, and were remunerated for their participation. This study was approved both by the Research Ethics Board at the University of Toronto and the Research Ethics Board at Baycrest Centre for Geriatric Care.

3.1.4 Results

All statistical results were computed using IBM SPSS version 19.

3.1.5 Neuropsychological Tests

Neuropsychological testing of the groups confirmed LTM deficits in all patients (*Table 3.1*). Notably, there were no other significant cognitive deficits between groups, suggesting that any group differences in task performance are due to memory-related factors, and not to other functions.

Table 3.1. Demographics and neuropsychological performance for patient and control groups in Experiment 2

Patients	Age	Yrs Ed	D.S. Fwd	D.S. Bwd	D.S. Tot	LM 1	LM 2	FAS	Animal
			(/14)	(/14)	(/28)	(/75)	(/50)		
1001	56	12	11	6	17	17	0	29	16
1003	37	12	11	8	19	28	8	29	19

1004	60	16	9	9	18	27	0	61	23
1005	58	16	9	6	15	38	18	47	25
1006	58	12	7	6	13	20	12	26	18
1007	56	16	-----	-----	12	-----	-----	-----	-----
Control (Mean)	50.85	15.67	11	7.17	16.4	47	29.5	49.55	23.73
t-test (*p* value)	0.47	0.16	0.11	0.6	0.71	**< . 01**	**< . 01**	0.19	0.12

Note: Yrs Edu = years of education; D. S. Fwd = Digit span forward; D.S. Bwd = Digit span backward;
D.S. Tot = Digit Span total; LM 1 = Logical memory immediate recall; LM 2 = Logical memroy delayed recall;
FAS = Phonemic fluency; Animals = Semantic fluency

3.1.6 Event Construction Task Performance

Relational Coherence

The mean number of explicit inter-item relations formed during the construction task was entered into a mixed ANOVA with group (patient, control) and set size (3, 4, 5, 6) as the between- and within-subjects factors, respectively. This analysis revealed a main effect of group, with patients producing fewer relations on average compared to controls, $F(1, 16) = 6.84$, $p < .05$, and a main effect of set size, indicating more relations were formed on trials with larger set sizes, $F(3, 48) = 24.79$, $p < .001$. The group by set size interaction was significant, $F(3, 48) = 2.86$, $p < .05$ (Figure 3.1). Tests of simple effects showed that patients produced significantly fewer relations on trials of set size 3, 5, and 6, with a similar trend at a set size of 4 ($t(14) = 2.44$, $p < .05$, $t(14) = 1.90$, $p = .08$, $t(14) = 3.73$, $p < .01$, and $t(14) = 3.13$, $p < .01$ for set sizes 3, 4, 5, and 6, respectively).

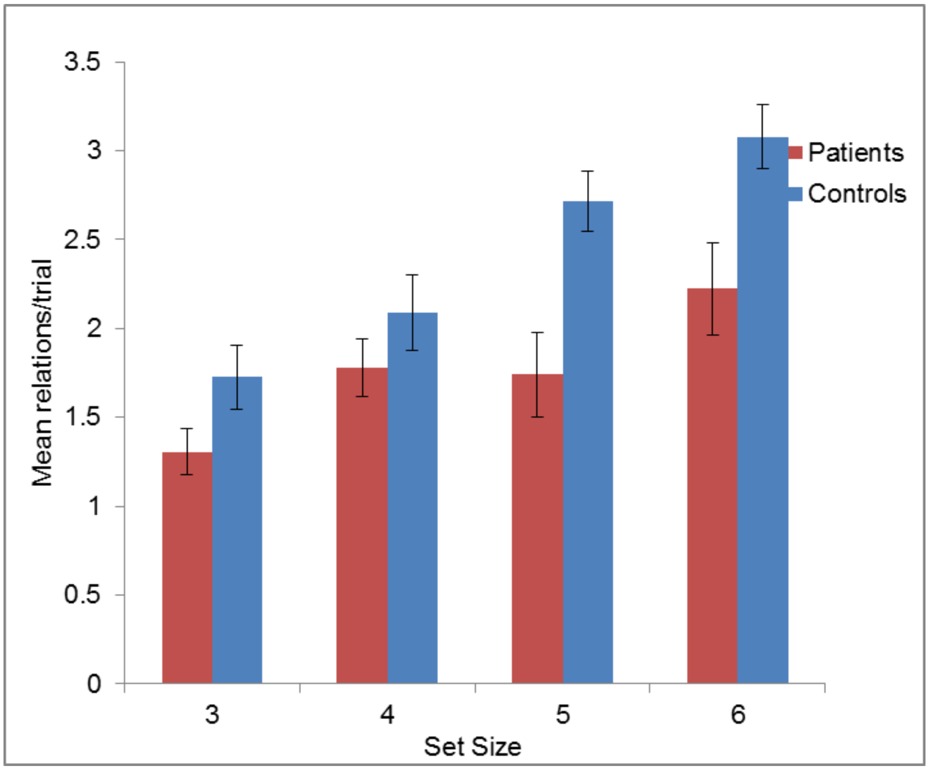

Figure 3.1. *Mean number of relations/trial (coherence score) at set sizes from 3-6 for patients and controls in Experiment 2.*

Omissions

The mean number of item words that were shown on screen but omitted from the imagined scenes was submitted to a similar mixed ANOVA. The main effects of group and set size were significant, $F(1, 16) = 16.30$, $p < .01$ and $F(3, 48) = 9.43$, $p < .001$, respectively. In addition, the group by set size interaction was also significant, $F(3, 48) = 4.92$, $p < .01$ (Figure 3.2). Tests of simple effects showed that patients omitted more words compared to controls at set sizes 4 and 5 (3 words: $t(16) < 1$, 4 words: $t(16) = 3.97$, $p < .005$, 5 words: $t(16) = 4.44$, $p < .005$, 6 words: $t(16) = 1.25$, $p = .23$). Generally, patients were more likely to omit item words from their imagined scenes, compared to controls. This occurred despite the fact that the item words were present on the screen for the duration of the trial.

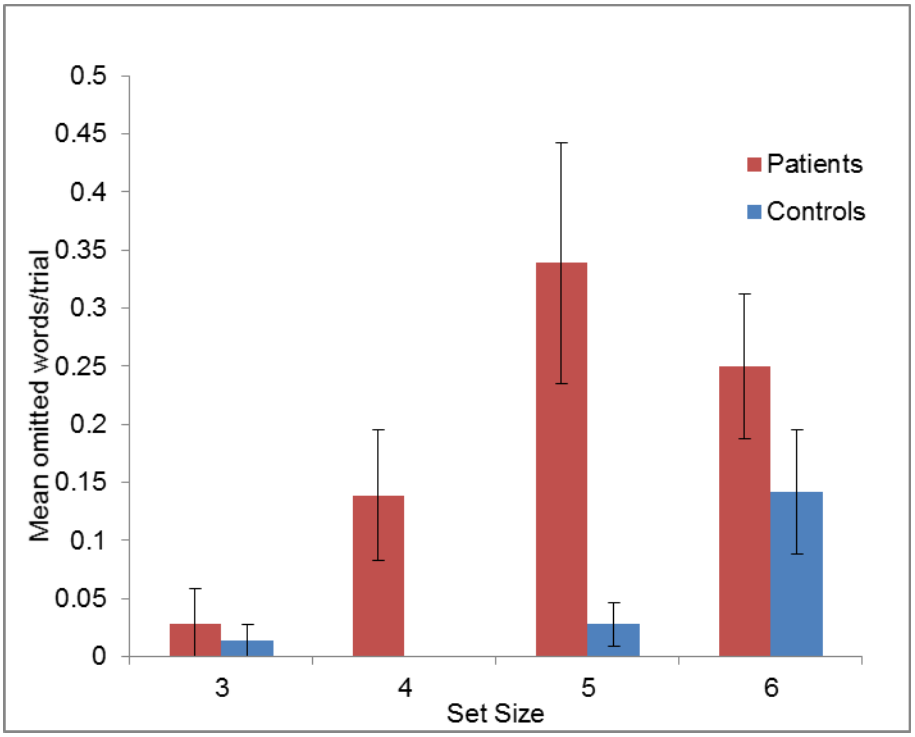

Figure 3.2. Omission rates at set sizes from 3-6 for patients and controls in Experiment 2.

3.1.7 Subjective Ratings

Ratings of coherence and difficulty were analyzed across groups in a mixed ANOVA. For coherence, the main effect of set size was not significant, $F(3,45) = 1.11$, $p = .35$, and the main effect of group was also not significant, $F(1, 16) = 1.11$, $p = .31$. However, the group by set size interaction was significant, $F(3,48) = 2.82$, $p < .05$. Tests of simple effects revealed that there was a trend for controls rating their events/scenes as more coherent at a set size of 3 only, $t(16) = 2.11$, $p = .05$. None of the other set sizes approached significance ($t(16) < 1$ for set sizes 4, 5, and 6).

In terms of subjective difficulty, neither the main effect of set size, $F(3,48) < 1$, nor the main effect of group, $F(1,16) = 2.48$, $p = .14$, was significant. Similarly, the group by set size interaction was not significant, *F*(3,48) = 1.53, *p* = .22, suggesting that although patients performed more poorly compared to controls, they did not consider the task to be more difficult.

3.1.8 Word Count

To examine whether the observed effects were due to differences in verbal output across groups, we calculated word counts for each trial, and submitted the average word count per condition into an ANOVA using the same between- and within- subject factors. There was a significant effect of set size, with longer responses being produced at higher set sizes, *F*(3, 48) = 24.68, *p* < .001. Neither the main effect of group nor the group by set size interaction was significant (*F*s < 1.02). Thus, verbal output per se could not account for patients' deficits in task performance.

3.1.9 Cued Recall

Cued recall performance could not be collected for one patient, who had to leave the testing session early. Not surprisingly, the main effect of group was significant, with patients recalling fewer items compared to controls, *F*(1, 15) = 25.21, *p* < .001. In addition, the main effect of set size was significant *F*(3, 45) = 18.73, *p* < .001. The group by set size interaction was not significant, *F*(3, 45) = 2.01, *p* = .15 (Figure 3.3). Inspection of Figure 3.3 indicates that patients' performance at the cued recall task was close to floor for all set sizes. Consequently, analysis of the proportion of recalled words that were successfully bound was not calculated.

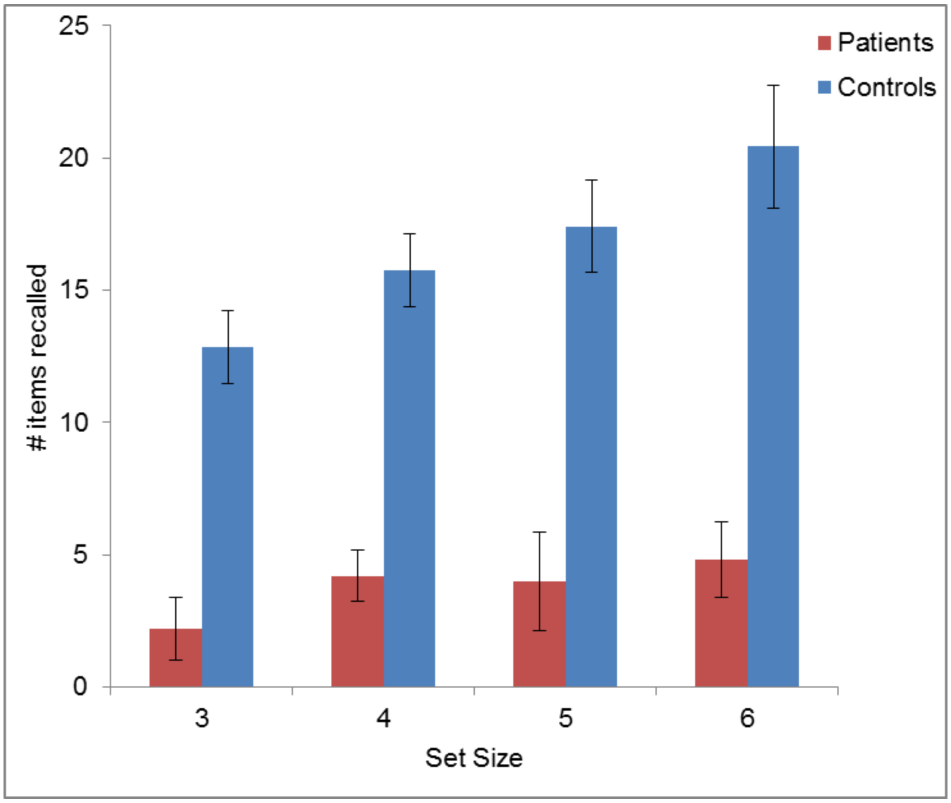

Figure 3.3. *Cued recall of task stimuli at set sizes from 3-6 for patients and controls in Experiment 2.*

3.2 Discussion

In this experiment, I sought to obtain more direct evidence that LTM processes, mediated by the MTL, are implicated in event construction. Consistent with the predictions, patients with MTL lesions, whose deficits were restricted to LTM, formed fewer inter-item relations than did control participants. These findings are consistent with the notion that patients with hippocampal lesions have difficulty creating spatially coherent scenes (Hassabis et al., 2007), formulating coherent narratives overall (Rosenbaum et al., 2009), and maintaining coherence over conversational discourse, perhaps due to poor retention over time. Moreover, these results are not due to differences in verbosity, as there were no group differences in terms of the length of descriptions. Thus, these findings confirm that LTM memory processes dependent on the MTL are implicated during the construction of a novel mental representation.

Not surprisingly, patients performed at floor for subsequent memory of items immediately following the task, reflecting their impairment in declarative memory (Scoville & Milner, 1957). Interestingly, patients were prone to omit items even at lower set sizes (i.e. 4), suggesting they had difficulty constructing an event beyond a certain mnemonic load. I posit that patients can initially construct an event to some extent, but have difficulty encoding and retaining this information. Consequently, this information was not reliably available to be referenced as they continued their descriptions, resulting in fewer inter-item relations, and deficits in monitoring whether or not item words had been mentioned. Interestingly, Squire et al. (2010) also found that patients with hippocampal lesions were prone to repetitions when imagining the future, which would also be consistent with deficits in retention: if previously mentioned information cannot be reliably retained, it may either be mentioned again or not mentioned at all. Taken together, these findings suggest that successfully imagining a novel event requires the on-line retention of the mental representation during the construction process.

Recently, Zeithamova & Preston (2010) found that the ability to draw inferences from overlapping memories was associated with the anterior hippocampus. In their task, subjects were presented with pairs of pictures during a learning phase (e.g., A-B, X-Y, B-C) some of which contained a common or overlapping element. Subjects were subsequently tested for memory of previously presented pairs (i.e., A-B, X-Y), as well as for inferences between pairs of items that shared a common element (i.e., A-C, from A-B, B-C). Increased hippocampal activity was observed when subjects had to infer a relation between items from overlapping pairs, compared to previously presented pairs. In addition, at encoding, hippocampal activity was also greater when subjects were presented with the second pair from an overlapping pair (i.e., when presented with B-C, having seen A-B earlier in the list). The authors suggest that one function of the hippocampus is to allow for flexible encoding between previously encoded events, such that when items from disparate events are presented simultaneously, retrieval of associated information also occurs, resulting in the encoding of those sets of information into a new ensemble. Such a function seems consistent with the notion that patients had difficulty appending subsequent information to an initially constructed representation.

| Another possibility is that patients show deficits in the perceptual representation of scenes (Hassabis & Maguire, 2009; Lee, Yeung, & Barense, 2012). That is, the deficit may have occurred at earlier stages of processing, such that patients' inability to accurately represent an imagined representation precluded their ability to bind subsequent information. This perspective would also predict fewer relations formed during the task, as well as increased omission rates.

The current data cannot conclusively differentiate between these two possibilities. Because patients did not give lower ratings of coherence, and increased omissions were only evident at a set size of 4, one could argue that initial mental representations were sufficient to constitute a scene, but patients were unable to bind additional information to that representation. Moreover, a perceptual representation deficit account would suggest that processing limits would be reached at lower set sizes for patients, and thus might predict that their performance would resemble an asymptotic curve; however, this was not the case. Race et al (2011) tested whether deficits in narrative construction could account for amnesics' deficit in future imagining, by having patients with MTL lesions imagine future events, and also describe a picture in as much detail as possible. Whereas patients showed deficits in future imagining, they did not show any deficits on describing the picture, suggesting that they could sufficiently perceive the picture, at least enough to keep track of their descriptions. However, these pictures were relatively simple, and not as complex as a naturalistic scene. Nevertheless, accurate estimation of the perceptual fidelity of subjects' imagined events would be required, in order to rule out a perceptual account of the present data.

In contrast to task performance, patients did not show a consistent difference from controls in terms of their subjective ratings of coherence and difficulty. Damage to the MTL does not typically impair insight into general cognitive function or metamemory judgments, although accurate judgment on specific aspects of cognition may be more variable (Parkin, Bell, & Leng, 1988; Seelye, Schmitter-Edgecombe, & Flores, 2010; Shimamura & Squire, 1986). Given the nature of the present task, it is possible that because the items were provided and patients were generally able to complete the task, they may have adopted a different criterion in judging their performance, compared to controls. Future imaging studies in which patients report poorer ratings of performance (Hassabis et al., 2007) used an open-ended cueing paradigm, which has significant LTM retrieval demands. This element of retrieval would presumably influence patients' perceived task performance, perhaps accounting for the discrepancies between previous findings and our own.

3.3 Interim Summary

Across 2 experiments, I found evidence that LTM binding processes are implicated in event construction: Experiment 1 showed the effect of age-related memory changes on event construction, both in terms of between group effects and in terms of individual differences in LTM within age groups. Experiment 2 showed that such processes are dependent on the hippocampus, as patients with lesions to the medial temporal lobes showed poorer performance compared to age-matched controls. In addition, across experiments, set size was a contributing factor to event construction performance, such that both older adults and patients produced fewer inter-item relations and were prone to omitting items at larger set sizes.

Within healthy younger and older adults, the coherence of constructed events had a direct association with subsequent memory of the items, suggesting that how well an event is constructed positively influences subsequent memory for that representation. Some investigators have argued that the ability to remember simulations extends their utility beyond the present: that is, if we retain the hypothetical events we imagine, such information may prove useful should an analogous event arise down the road (Martin et al., 2011; Szpunar et al., 2013). It is well-established that processing information more deeply, via semantic elaboration, visual imagery, or relating information to oneself, increases memory for those items (Bower, 1970; Craik & Tulving, 1975; Symons & Johnson, 1997). Event construction may encompass all of these processes, and the extent to which one successfully engages this processing may predict the benefit to memory performance.

It is worth noting that although patients with MTL damage showed impairments in the construction task, the magnitude of their construction deficits was much smaller than their deficits in memory. The nature of the construction paradigm was to minimize retrieval demands and mnemonic load by providing the items on the screen for the duration of the trial. Less supportive task conditions would likely compound the magnitude of patient deficits, as shown in previous studies (Addis et al., 2009; Hassabis et al., 2007; Kwan et al., 2010). Nevertheless, if the MTLs are critical for event construction, one might have expected the patient group to perform even more poorly compared to older adults in Experiment 1. Although patients showed deficits at lower set sizes compared to older adults, they were still able to create some inter-item relations during the task. It may be that some inter-item relations generated by patients could be supported primarily by semantic memory, and these relations would still be counted in the scoring. However, these associations represented only a small percentage (i.e. approximately 10%) of the responses produced by subjects, as the ability to create further inter-item relations requires the hippocampally-dependent, flexible recombination of information. Moreover, although patients with MTL lesions do show deficits in semantic tasks under some conditions (Greenberg, Keane, Ryan, & Verfaellie, 2009; Sheldon & Moscovitch, 2012), these effects are minor in comparison to the patients' deficits in LTM (see Table 3). Thus, it is unlikely that deficits in semantic memory account for the differences between patients and controls.

Nonetheless, the extent to which pre-existing knowledge (i.e., schemas) influences event construction performance remains an open question. Given the unconstrained nature of imagining novel events, having pre-existing schemas as scaffolds upon which to base behaviour is advantageous, and much of human cognition shows a performance advantage when the stimuli are based on prior knowledge. In addition, the design of the current paradigm downplayed the contributions of higher order executive functions to event construction, which would likely also be relevant, particularly in conditions with minimal support from prior schemas. The broader influences of pre-existing knowledge and executive functioning on event construction are investigated in Chapter 4.

Chapter 4: The Effects of Typicality on Event Construction

As imagining novel events is inherently open-ended, individuals can draw upon different strategies to complete the task: although there is an established link between imagining and autobiographical memory, event construction is likely to draw upon information from both episodic memory and semantic memory (Irish, Hodges, & Piguet, 2013; Suddendorf & Corballis, 2007). Consequently, event construction may evoke different cognitive functions and neural substrates, depending on task demands. One factor that may affect the coherence of an imagined event is the congruency of the to-be-imagined event with a pre-existing schema (i.e., *typicality*). Because imagining new events imposes fewer constraints than recalling past experiences, we may imagine events that are very unlikely or impossible, which would not have the benefit of being based on a general schema (Irish & Piguet, 2013). Thus, having to imagine a coherent event that is relatively atypical would be more difficult than imagining a coherent typical event. It is well-documented that information that can be organized into meaningful structures (i.e. ‘chunks’) can be processed more efficiently than a similar amount of information that is unrelated (Bor & Owen, 2007; Cowan, 2001; MIller, 1956). Moreover, the presence of prior knowledge or structure typically benefits LTM performance, both during encoding (Castel, 2005; Craik & Tulving, 1975; Staresina et al., 2009) and during retrieval (Baddeley & Wilson, 2002; Giovanello, Keane, & Verfaellie, 2006)

Specific to imagining novel events, the notion of varying levels of typicality actually occurs naturally: for example, when simulating a novel event, such data must be placed within the context of existing knowledge. Even autobiographical memories seem to exist within a nested hierarchy of semantic themes, spanning different lengths of time (Conway & Pleydell-Pearce, 2000; Gilboa, 2004). If one considers the notion that a core function of the ability to simulate is to anticipate future outcomes, it is clear that such a simulation is necessarily a combination of episodic and semantic features. For example, Suddendorf & Corballis (2007) give the example of engaging in mental time travel to prepare for a job interview, suggesting that previous job interview experiences (episodic memories), in addition to questions one might anticipate getting (episodic and/or semantic memories), combine to produce the simulation of what may occur.

Recent findings have suggested that semantic memory and its associated neural substrates are also crucial for imagining (Irish, Addis, Hodges, & Piguet, 2012; Race, Keane, & Verfaellie, 2013). For example, Irish et al. (2012) compared patients with Alzheimer's disease who have impairments in episodic memory and relative sparing of semantic memory, patients with semantic dementia who have impaired semantic memory and relative sparing of episodic memory, and healthy controls on a future imagining task. Both patient groups showed poorer future imagining performance, but notably, different patterns of gray matter atrophy predicted performance for both groups, suggesting that their performance may be driven by different neural systems. It is not clear whether more subtle differences between groups exist in terms of the nature of their simulations. Regardless, disruption of either episodic memory or semantic memory is sufficient to produce future simulation deficits, suggesting both contribute to such mental representations.

Whether typicality affects the event construction stage of imagining non-personal events is not clear. In terms of general imagination performance and related neural correlates, there is some evidence to suggest that the hippocampus is more active when imagining less plausible, compared to more plausible, future events (Weiler et al., 2010). Also, the hippocampus shows different patterns of connectivity with other brain regions during the imagination of general, well-repeated events, versus specific, unique future events (Addis et al., 2011). One way of characterizing such findings is that they reflect a dimension of typicality, such that imagining events that are specific or less plausible are more atypical, whereas repeated or highly plausible or events would be more typical.

If constructed events can vary in terms of typicality, it is likely that atypical events place greater demands on executive control processes as compared to typical events. Although there are several models of the processes implicated in executive functioning, a common theme of executive dysfunction is the inability to apply appropriate behaviour in situations without well-defined schemas (Burgess, Alderman, Volle, Benoit, & Gilbert, 2009; Friedman & Miyake, 2000; Goel, 2010; Wood & Grafman, 2003). To what extent variation in executive functioning affects event construction is not clear. Some evidence indicates that patients with mild executive dysfunction do show future simulation deficits: however, these studies have examined the more elaborative aspects of future simulation, rather than construction (Berryhill, Picasso, Arnold, Drowos, & Olson, 2010a; de Vito et al., 2012).

To this end, I modified the existing event construction paradigm to investigate the effects of atypicality on event construction performance. Specifically, the context-item pairings were designed so that the items would be relatively typical or atypical for a given context. In addition, the manipulation of set size remained, in order to explore whether mnemonic load and typicality interact. Furthermore, a response deadline was introduced to increase task demands during the construction task, and time to completion was measured to add another indicator of construction performance, which may be more sensitive to individual differences in performance, and the manipulation of typicality. To explore the potential contributions of different facets of executive functioning, subjects were also given tests of verbal fluency and relational reasoning, to see if individual differences in these measures track event construction performance.

4 Experiment 3a

4.1 Method

4.1.1 Participants

Twenty-two healthy younger adults (7 Males; *M* age = 21.5, *SD* = 1.40), participated in this study for course credit. All were native-English speakers, and did not have a history of neurological/psychological illness.

4.1.2 Design

The general event construction task was used, with similar instructions. Subjects viewed a context word and 2 or 4 item words, and were told to imagine an event with those items, while trying to relate the items explicitly as much as possible. However, on half of the trials the item words were things not typically associated with the context (e.g. a context “lawn” with the items “cocktail” and “camera”), whereas the other half of trials contained items that were fairly typical for that context (e.g. “beach” with “tide” and “sandal”). Thus, the experiment consisted of a 2 x 2 crossed design with typicality and set size as independent variables. There were 16 construction trials in each condition, resulting in 64 trials overall.

Context-item pairings in the typical condition were chosen such that the items were reasonably associated with the context, but were not exclusively associated with that context: this was done to ensure subjects were simulating a novel event, and not merely describing well-known semantic associations with a given context. Also, atypical pairings were chosen to be unlikely, but not extremely bizarre or nonsensical, to ensure subjects could complete the task within the time period.

4.1.3 Materials

A total of 264 words were taken from the MRC psycholinguistics database (Coltheart, 1981) to be used as item words in the task: word length (range = 4 – 8 letters, *M* = 5.14, *SD* = 1.38), frequency (range = 1 - 847 per million, *M* = 46.41, *SD* = 90.75), concreteness (range = 402 - 670, *M* = 554.05, *SD* = 60.27), imageability (range = 401 - 635, *M* = 525.89, *SD* = 51.45), and familiarity (range = 407 - 655, *M* = 553.10.34, *SD* = 53.69). One hundred twenty-eight common contexts were chosen and split into two lists of 64 contexts, and paired with 2 or 4 items deemed to be fairly typical or atypical for each context. Subjects completed the task with one of the two lists. There were no significant differences between the two lists in terms of word length, frequency, concreteness, or familiarity (all *F*s < 1).

4.1.4 Tests & Procedure

Event Construction Task

On each trial, subjects were shown a context and item words, and were given 20 s to imagine an event with those items in the specific context, relating the items together as much as possible. Subjects were told to press a key once they had successfully constructed the event. Afterward, subjects provided subjective ratings on a 5-point Likert scale (1 = low, 5 = high) for 1) the coherence of the imagined event, 2) the amount of detail, and 3) the perceived level of difficulty in constructing the event. The trials were split into 4 blocks of 16 trials, with the conditions presented randomly. A 2 min rest occurred between blocks. Following the task, participants completed a description phase: for each trial, they were shown the context-item pairings, and had to describe what they imagined with those items. Then, subjects provided ratings on a 5-point scale (1 = low, 5 = high) for the typicality of the event they constructed, and their confidence that they had remembered all the details. Descriptions were self-paced with no time limits. Subjects were explicitly told to describe what they had simulated before, and not to come up with a new event on the spot. The responses were recorded, transcribed, and scored for the number of explicitly mentioned inter-item relations, as per previous experiments.

Analogical reasoning task: People pieces test

The people pieces test is an analogical reasoning task, designed to measure relational reasoning across stimuli with similar visual complexity (Cho et al., 2010; Viskontas et al., 2004). In this task, two pairs of cartoon people are presented, and the relation between the pairs can be analogous along 4 perceptual dimensions: gender, height, width, and colour of clothing. On each trial, the subject was presented with both pairs, and was asked to evaluate whether the pairs are analogous along 1 - 4 of these dimensions. For example, if asked to evaluate along two dimensions, the screen might show the stimuli and the words "height?" and "colour?" Subjects provided yes/no responses, and were given 8 s to respond. The pairs matched along the proposed dimensions on half of the trials. The people pieces test allowed for the measurement of relational reasoning ability by directly manipulating the number of relations the subject had to evaluate: such abilities are associated with being able to draw associations between increasingly disparate information (Bunge, Wendelken, Badre, & Wagner, 2005; Green, Fugelsang, Kraemer, Shamosh, & Dunbar, 2006; Green et al., 2010) . Performance measures included reaction time and accuracy.

Verbal Fluency

In addition, subjects completed phonemic and semantic fluency tasks. In phonemic fluency, subjects are asked to generate as many words as possible starting with the letters F, A, and S, with a 1 minute time limit for each letter. In semantic fluency, subjects are asked to generate as many animals as possible for 1 minute. The former task is thought to measure top-down retrieval from LTM, and is sensitive to frontal lobe injury, whereas the latter test is more strongly associated with semantic knowledge, and is sensitive to temporal lobe damage (Milner, 1964; Newcombe, 1967; Troyer, Moscovitch, Winocur, Alexander, & Stuss, 1998). For both phonemic and semantic fluency, the total number of words generated, the number of switches, and the mean cluster size were calculated (Troyer, Moscovitch, Winocur, Alexander, & Stuss, 1998).

Procedure

After informed consent was obtained, subjects first completed the verbal fluency test, to avoid potential contaminating effects from the event construction task. Next, they completed either the event construction task with description phase, or the people pieces task, with the order randomized across subjects. Prior to completing the event construction task, subjects completed six practice trials with the experimenter present. In this practice version, subjects described their imagined events after each trial, in order to ensure task compliance. The entire testing session lasted approximately 90 minutes, and occurred in a quiet room.

4.2 Results

All statistical results were computed using IBM SPSS version 20. Tests of simple effects were computed with Bonferroni correction for multiple comparisons, as implemented in SPSS.

4.2.1 Event Construction Task Performance

Relational Coherence

The average number of inter-item relations per trial was submitted to a repeated-measures ANOVA with set size and typicality as within-subjects factors. The main effects of set size and typicality were significant ($F(1,21) = 157.45$, $p < .001$ and $F(1,21) = 32.39$, $p < .001$, respectively), with typical trials having more relations than atypical trials, and set size 4 trials having more relations than set size 2 trials. The set size x typicality interaction was significant ($F(1,21) = 14.45$, $p < .001$). Inspection of Figure 4.1 shows a greater number of relations formed for typical vs. atypical events at a set size of 4 (paired *t*(21) = 5.61, *p* < .001), compared to a set size of 2 (paired *t*(21) = 1.42, *p* = .17).

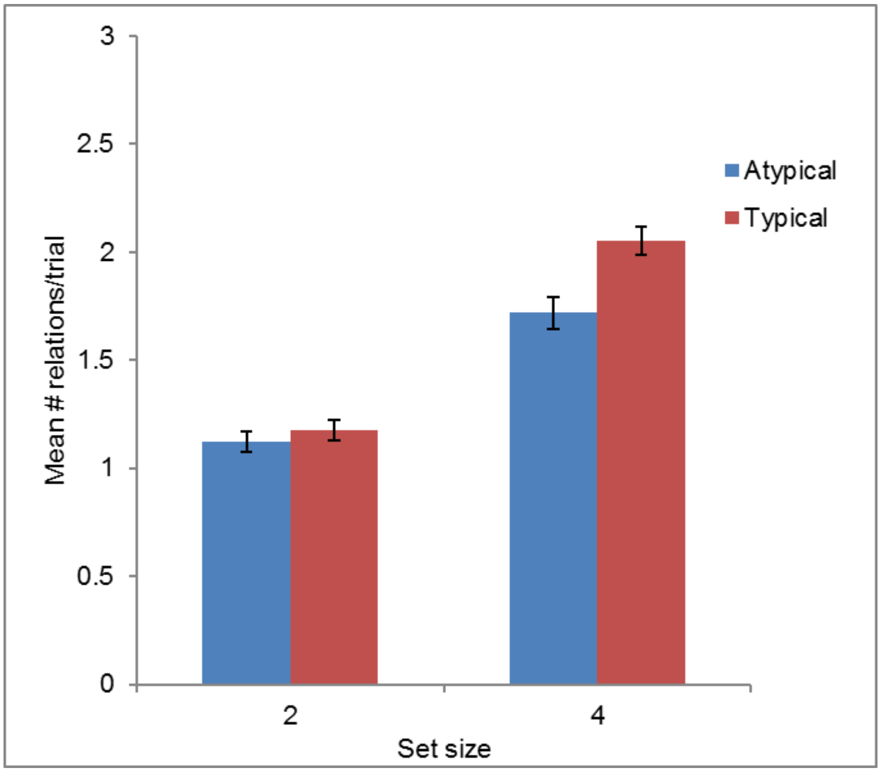

Figure 4.1. Mean number of relations/trial (coherence score) for set sizes 2 and 4 and for typical and atypical context-item pairings in Experiment 3a

Completion Time

The average time to construct each event was similarly submitted to a repeated-measures ANOVA on set size and typicality. The main effects of set size and typicality were significant (*F*(1,21) = 96.03, *p* < .001 and *F*(1,21) = 78.73, *p* < .001, respectively), with 4 item trials taking longer to complete than trials with 2 items, and atypical trials requiring a longer completion time than typical trials. In addition, there was a statistical trend for the set size x typicality interaction (*F*(1,21) = 3.28, *p* = .09), with a greater discrepancy between atypical and typical latencies at a set size of 4 (Figure 4.2).

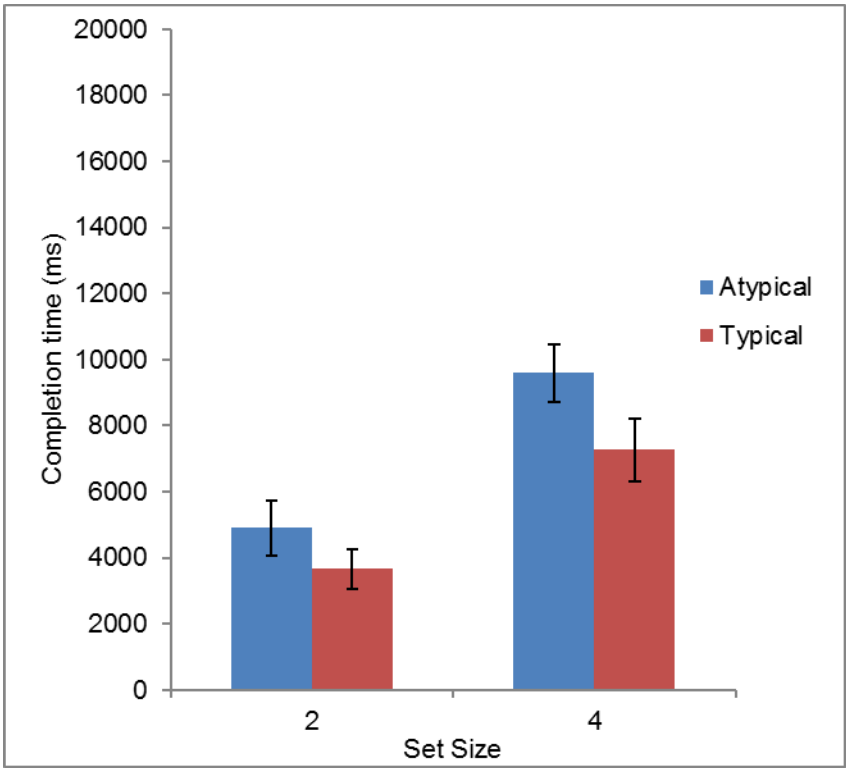

Figure 4.2. Mean completion time per trial for set sizes 2 and 4 and for typical and atypical context-item pairings in Experiment 3a

Subjective Ratings

Subjective ratings of coherence, detail, and difficulty were collected after each imagining trial: mean scores are listed in Table 4.1. In general, during the construction phase of the task, there was a main effect of typicality on ratings of coherence ($F(1,21) = 73.71$, $p < .001$), detail ($F(1,21) = 23.84$, $p < .001$), and difficulty ($F(1,21) = 89.82$, $p < .001$) such that atypical events were rated as less coherent, less detailed, and more difficult compared to typical events. There was also a significant main effect of set size for ratings of coherence ($F(1,21) = 12.11$, $p < .005$) and difficulty ($F(1,21) = 18.85$, $p < .001$), with 4-item trials being rated as less coherent and more difficult than 2-item trials. The interactions approached significance for coherence ($F(1,21) = 4.21$, $p = .053$) and detail ($F(1,21) = 4.31$, $p = .05$) ratings, showing an increased discrepancy between atypical and typical trials at a set size of 4.

Ratings of typicality showed a main effect of condition, confirming that atypical trials evoked simulations that were less typical ($F(1,21) = 113.04$, $p < .001$). In addition, there was a main effect of set size, with imagined events with 2 items being rated as more typical than 4 items ($F(1,21) = 55.85$, $p < .001$).

In terms of subjects' confidence that all the elements of previously imagined events were recalled, there was a main effect of condition and set size on memory confidence, with atypical trials and set size 4 trials being rated lower ($F(1,21) = 20.02$, $p < .001$ and $F(1,21) = 17.03$, $p < .001$, respectively). The interaction was not significant, $F(1,21) < 1$. Despite differences across conditions, it should be noted that the mean scores were all above 4 on a 5-point scale, indicating that subjects were generally very confident that all imagined information had been recalled during the delayed scene descriptions.

Table 4.1. Subjective ratings of coherence, detail, difficulty, typicality, and memory confidence for imagined events at set sizes 2 and 4, and atypical and typical conditions in Experiment 3a

Rating Type (1 - 5)	Atypical		Typical	
	2	4	2	4
Coherence	3.47 (.78)	3.07 (.64)	4.44 (.58)	4.25 (.56)
Detail	3.61 (.70)	3.39 (.60)	4.00 (.95)	3.96 (.64)
Difficulty	2.23 (.53)	2.90 (.63)	1.51 (.34)	2.03 (.58)
Typicality	3.27 (.71)	2.65 (.72)	4.3 (.62)	3.72 (.63)
Memory Confidence	4.43 (.58)	4.08 (.73)	4.72 (.41)	4.40 (.55)

SD are in parentheses

4.2.2 Executive Functions Measures

People pieces test

Performance on the people pieces test is listed in Table 4.2. In general, reaction times increased and performance decreased as the number of relations to evaluate increased. Moreover, subjects were slightly slower on incorrect trials compared to correct trials. Similarly, accuracy also decreased slightly with an increasing number of relations, consistent with previous studies using the same measure (Viskontas et al., 2004).

Table 4.2. Analogical reasoning performance in Experiment 3a

	Number of Relations			
People Pieces Task	1	2	3	4
Accuracy (%)	83 (13)	80 (14)	73 (16)	74 (11)
Reaction Time (ms)	2586 (1210)	3694 (906)	4511 (1217)	5077 (1313)

SD are in parentheses

Verbal fluency

Verbal fluency data from one subject could not be collected due to time constraints. In general, subjects were able to generate a mean of 14.76 (*SD* = 4.15) items per letter during phonemic fluency, and 25.95 (*SD* = 5.31) items during semantic fluency, in line with previous findings in healthy adults that semantic fluency is easier than phonemic fluency (Tombaugh, Kozak, & Rees, 1999) (Table 4.3).

Table 4.3. Verbal fluency performance in Experiment 3a

	Fluency	
	Phonemic	Semantic
# words generated	44.24 (12.41)	25.95 (5.31)
# switches	30.24 (6.57)	9.57 (3.47)
Mean cluster size	0.41 (.30)	1.83 (1.60)

SD are in parentheses

4.2.3 Correlations

To determine whether event construction preferentially taxed certain executive functions, Pearson correlations were computed between the total number of relations formed at a set size of 4, and total accuracy on the people pieces test, as well as the total number of items generated on phonemic and semantic fluency. Event construction at a set size of 4 was chosen because of the restricted variance in performance across individuals at a set size of 2. Interestingly, objective relational coherence scores were positively correlated with relational reasoning performance on the people pieces task ($r = .52$, $r^2 = .27$, $p < .01$, 95% CI = [.12, .78]). In contrast, relational coherence scores were not associated with the number of words generated for either phonemic or semantic fluency ($r = .24$, $r^2 = .06$, $p = .29$ and $r = .21$, $r^2 = .04$, $p = .36$, respectively). Similarly, relational coherence scores were not correlated with switching and clustering for either phonemic (switching: $r = .31$, $p = .17$; clustering: $r = -.06$, $p = .81$) or semantic fluency (switching: $r = -.02$, $p = .94$; clustering: $r = .18$, $p = .45$). Thus, the ability to compare multiple relations simultaneously was associated with the ability to form multiple inter-item relations during event construction, but not general retrieval ability or semantic memory.

4.3 Discussion

The results from Experiment 3a show that typicality affects event construction performance: compared to simulating relatively typical events, atypical events were objectively less coherent, and subjectively rated as less coherent and less detailed. Moreover, atypical events were more difficult to construct, as indexed by increased latency and by subjective ratings of difficulty. Finally, event construction seemed to depend to a greater extent on the ability to process multiple associations, compared to verbal fluency ability.

In terms of objective measures of coherence, the effect of typicality only emerged at a set size of 4. This is likely due to the restricted number of inter-item relations that can be formed amongst 3 words (context + 2 items), particularly within the given time limit. Latency and subjective ratings data suggest that atypical items take longer to construct and are rated as more difficult, even at a set size of 2, suggesting typicality did modulate performance irrespective of mnemonic load. Thus, the ability to construct an imagined event is sensitive to the congruency between context and items. It is well-established that prior knowledge confers a benefit to task performance across a variety of domains (Awh & Jonides, 2001; Castel, 2005;Craik & Tulving, 1975). In this case, in the typical condition, it is reasonable to suppose that the contextual schema can act as a semantic scaffold, making it easier to generate associations between items to form a particular simulation. However, in the atypical condition, potential scripts associated with that context are insufficient to provide an appropriate scaffold for the items, and so the subject must generate an association between items with less semantic support, resulting in longer latencies and less successful performance (see also Irish & Piguet, 2013).

The correlation between reasoning and construction performance suggests that one facet of event construction is the ability to draw associations between sets of information. That is, in order to truly simulate events, the information amongst items must be organized and bound into a meaningful gestalt. Measures of analogical reasoning require the subject to extract the associations amongst objects, and then compare those associations through a 2nd order relation. This type of task has similar requirements as novel event construction: the items must be processed such that they can be related to one another, particularly if there is no canonical semantic association with which to relate them. Such abilities are thought to be a measure of fluid intelligence, and are associated with creativity and real-world problem solving (Blanchette & Dunbar, 2001; Green, Kraemer, Fugelsang, Gray, & Dunbar, 2012). An interesting implication of this finding is that individuals who rank higher on measures of fluid intelligence may be able to simulate more nuanced or unlikely scenarios, which may aid them in solving certain classes of problems, or provide them with a greater repertoire of possible experiences on which to draw. Indeed, Sheldon, McAndrews, & Moscovitch(2011) found that the ability to provide detailed solutions to ill-defined social problems was associated with autographical memory performance, suggesting that both problem solving and event construction may share some underlying cognitive processes.

In terms of subjective ratings of task performance, there were independent effects of set size and typicality, which were consistent across ratings. As predicted, typical events were easier to produce, and had a higher quality of mental representation, mirroring the objective performance measures. Interestingly, set size also had an effect: providing more items resulted in lower ratings of coherence and higher ratings of difficulty. The typicality by set size interactions also suggested that this negative influence of set size was larger for atypical trials, compared to typical trials. These findings suggest that the influence of prior knowledge on event construction is more noticeable at higher mnemonic loads, as it is increasingly difficult to process information without an appropriate schema.

It is worth noting that although significant effects of typicality emerged, differences between typical and atypical events only reflected approximately 1 point on a 5-point scale. Similar differences occurred for ratings of coherence, detail, and difficulty, suggesting that atypical events were still judged as fairly coherent and detailed events. Moreover, difficulty ratings were at most an average of 2.90 in the atypical condition with 4 items, suggesting that the task was not too difficult.

One limitation of this study is that subsequent memory of the items was not measured. Thus, it is not known to what extent the effects of typicality on event construction also apply to subsequent memory for those simulated events. Given the association between event construction and cued recall of those items in Experiment 1, it is possible that typicality will exert similar effects on event construction and subsequent memory. This possibility is explored in Experiment 3b.

4.4 Experiment 3b

A common finding is that information congruent with preexisting knowledge shows a memory benefit, compared to information that is incongruent. For example, Craik & Tulving (1975) demonstrated a congruency effect for words in a sentence, namely, that studying items in a sentence to which the answer was yes (e.g., “Is a CHERRY a fruit?”) were better remembered than words in a question to which the answer was no. Similarly, Castel (2005) found that older adults memory for a list of grocery items is better if the items are paired with realistic prices, as compared to unrealistic prices, a finding that is mirrored even in patients with hippocampal amnesia (Kan et al., 2009).

However, such a benefit for knowledge congruency and memory is not universal. Studies of memory for stories show that inserting atypical events in narrative sometimes produces better memory for the atypical events, as they must be more deeply processed to produce a coherent representation of the text (Erdfelder & Bredenkamp, 1998). Moreover, when a low number of atypical items is studied in the context of typical items, the atypical items are particularly distinct and thus show a mnemonic benefit (i.e. von Restorff effect; Kohler & von Restorff, 1933). Finally, imagining interactions between pairs of studied items confers equivalent memory benefits to associative memory, regardless of whether the interactions are bizarre (i.e. a piano smoking a cigar) vs. nonbizarre (i.e. a cigar sitting on top of a piano; Wollen, Weber, & Lowry, 1972). Thus, it is possible that either typical or atypical constructed events can show a mnemonic advantage at recall.

The purpose of Experiment 3b was threefold: 1) to replicate findings from Experiment 3a with respect to event construction and typicality; 2) to investigate the potential contribution of typicality on subsequent memory for simulated events, and 3) to determine whether manipulating task parameters to be appropriate for an fMRI study affects the general pattern of results from Experiment 3a. To this end, healthy younger adults were given a similar event construction task, in which 2 or 4 items were shown with a context that was relatively typical or atypical for those items, and were given a limited time to construct an event while relating the items as much as possible. In addition, a separate working memory task was introduced as a potential control task for an fMRI study. Following the construction task, subjects completed a 2-step recall/description task, where they were first shown the context word and had to recall the items, and then shown both context and item words and had to describe the event they had constructed.

4.5 Method

4.5.1 Participants

Twelve healthy younger adults (5 men, *M* age = 22.33, *SD* = 6.12) participated for course credit. All were native-English speakers and had no history of neurological or psychological illness. Prior to the experiment, informed consent was obtained from all subjects. The studies were approved by the Research Ethics Board at the University of Toronto.

4.5.2 Design

As in Experiment 3a, subjects were shown a context word and 2 or 4 item words, with the context being relatively typical or atypical with the items. In addition, on some trials, subjects completed a separate working memory task, where 2 or 4 words were shown, and subjects had to order the words in reverse alphabetical sequence. Thus, the experiment was a 3 x 2 crossed design, with task (imagine-atypical; imagine-typical; control) and set size (2 or 4 words) as within-subjects factors. Subjects completed 20 trials per condition, resulting in 120 trials overall.

4.5.3 Materials

A total of 360 words were taken from the MRC psycholinguistics database (Coltheart, 1981) to be used as item words in the task: word length (range = 4 – 8 letters, *M* = 5.17, *SD* = 1.35), frequency (range = 1 - 847 per million, *M* = 47.73, *SD* = 86.11), concreteness (range = 402 - 670, *M* = 555.06, *SD* = 57.29), imageability (range = 401 - 635, *M* = 554.49, *SD* = 52.71), and familiarity (range = 407 - 655, *M* = 523.90, *SD* = 52.85). Two hundred forty words were assigned to the event construction condition: sets of 2 or 4 words were paired with 80 common contexts deemed to be fairly typical or atypical for each context. The remaining 120 words were assigned to the working memory condition, 40 words for the set size 2 condition, and 80 words for the set size 4 condition.

4.5.4 Tests and Procedure

In the first phase, subjects completed the event construction task and working memory task, with trials intermixed in a random fashion (Figure 4.3).

On each trial, subjects were cued for 1.25 s about which task to perform, imagining or working memory, followed by a fixation for 500 ms. On event construction trials, subjects saw 2 or 4 item words paired with typical or atypical contexts for 12 s: Subjects had to imagine an event with those items, relating them together as much as possible. They were instructed to press a key when they had successfully constructed an event, and to maintain that event in mind until the 12 s had elapsed. The response deadline was shortened from 20 s to 12 s based on inspection of latency data from Experiment 3a, which showed that the vast majority of trials could be completed within 12 s. Also, because subsequent memory was a dependent measure, the stimuli remained on the screen for 12 s to control for exposure time. After the 12 s had elapsed, subjects had 3.5 s to rate the subjective coherence of their imagined event on a 5-point Likert scale.

In the working memory condition, subjects were shown 2 or 4 words for 12 s, and had to put those words in reverse alphabetical order (i.e., from Z to A), pressing a key once the new order was computed. Once completed, they were told to rehearse that new order subvocally until the 12 s had elapsed. Afterward, subjects were probed about which word should appear in the 2nd or 4th position, and had 3.5 s to respond. Half of the probes were correct, and half the probes were incorrect. The tasks were completed in 4 blocks of 30 trials, with a 2 min break between blocks.

Then, after a 5-min delay, subjects completed a self-paced cued recall/description phase. First, subjects were shown a context word, and had to recall all the item words that were presented with that context word during the construction task. Then, subjects pressed a button and all the items appeared on the screen with the context word, at which time subjects were told to describe the event they imagined with those words, describing all the relations they had formed earlier. Subjects were instructed specifically to describe what they had imagined before, not create a new event on the spot. This design allows for a measure of relational coherence, without contaminating subsequent memory performance.

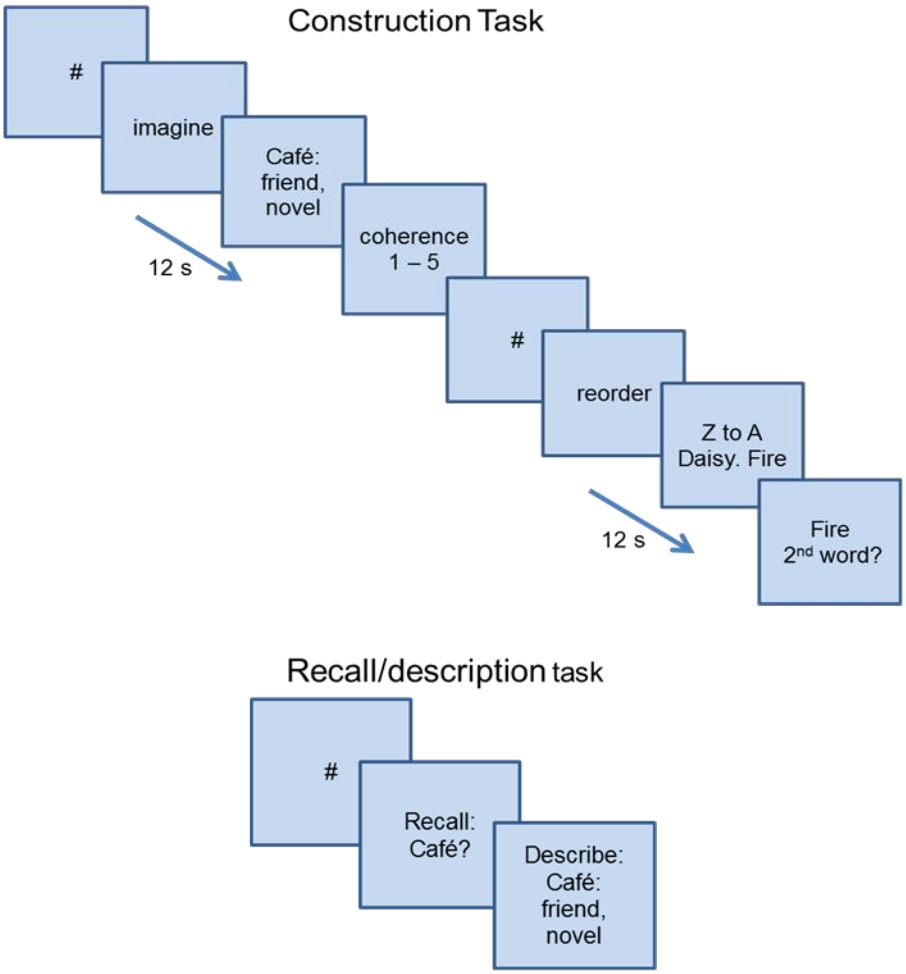

Figure 4.3 Schematic of the event construction task and recall/description task in Experiment 3b

4.6 Results

All statistical results were computed using IBM SPSS version 20. Tests of simple effects were computed with Bonferroni correction for multiple comparisons, as implemented in SPSS.

4.6.1 Event Construction Task Performance

Relational Coherence

The mean number of relations/trial was entered into a 2 x 2 repeated-measures ANOVA with set size and typicality as within-subjects variables. There were main effects of typicality and set size, with more relations being formed on typical trials ($F(1,11) = 8.72$, $p < .05$), and at a set size of 4 (*F*(1,11) = 83.23, $p < .001$). The set size by typicality interaction was also significant (*F*(1,11) = 8.98, $p < .05$). T-tests of simple effects showed a significant difference between typical and atypical trials at a set size of 4 (paired *t*(11) = 3.14, $p < .01$), but not at a set size of 2 (paired *t*(11) = 1.02 $p = .33$) (Figure 4.4).

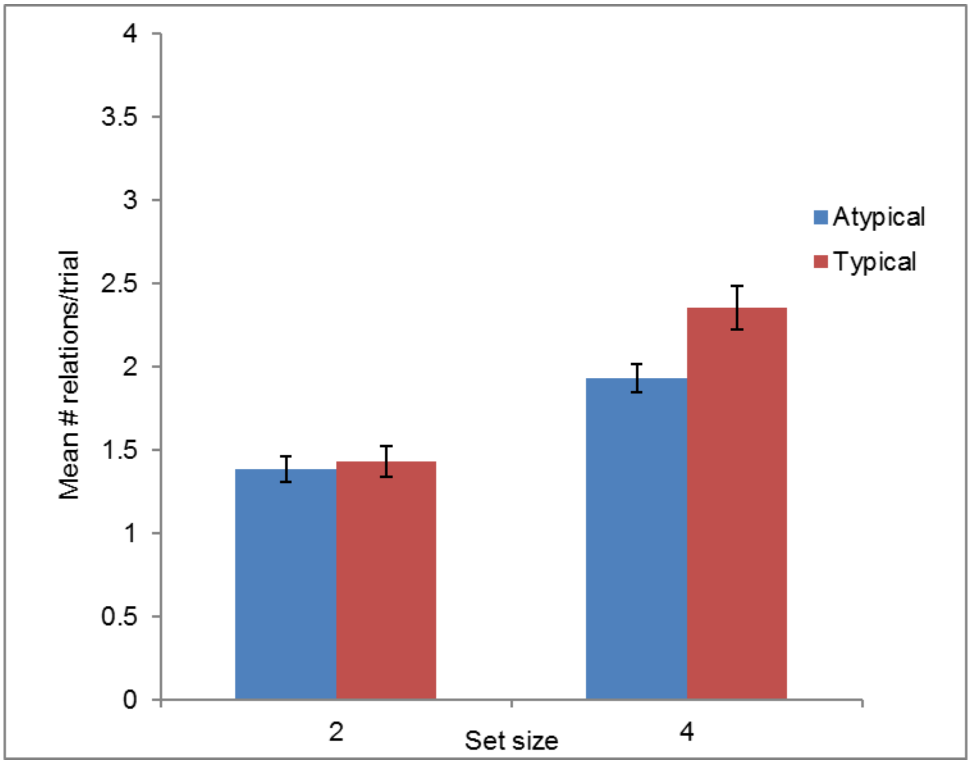

Figure 4.4. Mean number of relations/trial (coherence score) for set sizes 2 and 4 and for typical and atypical context-item pairings in Experiment 3b

Completion Time

Latency data across both event construction and working memory conditions was submitted to a 3 x 2 repeated-measures ANOVA with condition and set size as within-subjects variables (Figure 4.5). There were significant main effects of typicality (*F*(1,22) = 24.40, $p < .001$) and set size (*F*(1,11) = 41.14, $p < .05$). The interaction was not significant, *F*(1, 22) < 1.

Post-hoc tests comparing conditions showed the atypical condition was significantly slower than the typical condition (*p* < .001), which was in turn slower than the control condition (*p* < .05).

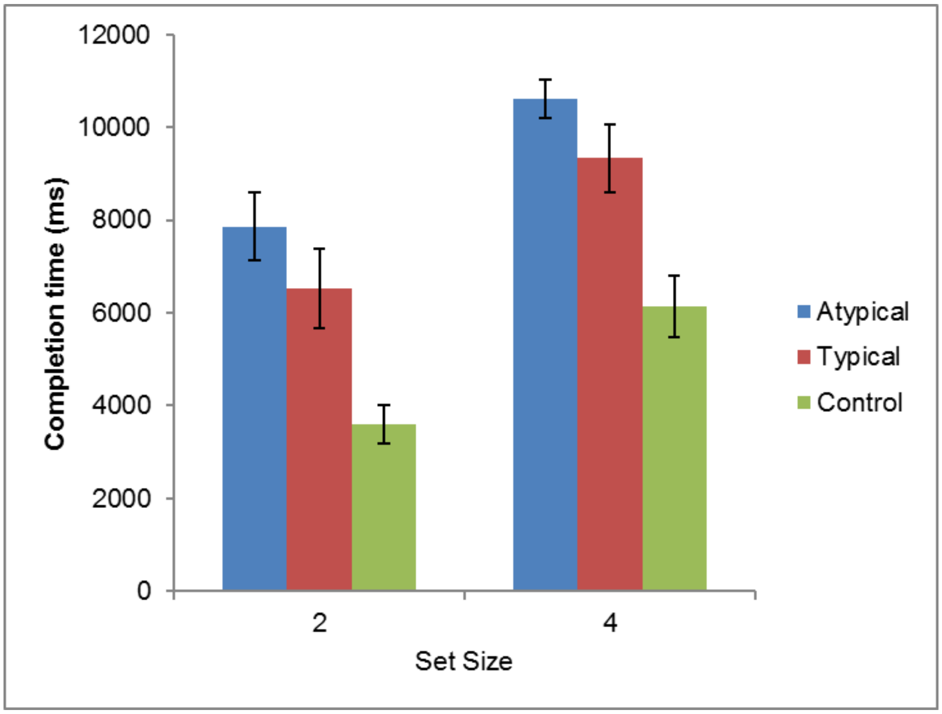

Figure 4.5. Mean completion time per trial for typical imagining, atypical imagining, and working memory conditions at set sizes 2 and 4 in Experiment 3b

4.6.2 Working Memory Task Performance

Accuracy on the working memory task was very high, with 94 % accuracy in at a set size of 2 (*SD* = .06), and 94 % accuracy at a set size of 4 (*SD* = .07).

4.6.3 Subjective Ratings

Ratings of coherence were entered into a 2 x 2 repeated measures ANOVA with condition and set size as factors. There were significant main effects of condition and set size (*F*(1,11) = 62.48, *p* < .001 and *F*(1,11) = 13.84, *p* < .005, respectively), with typical and 2-item conditions being rated as more coherent. The interaction was not significant, *F*(1,11) < 1 (Table 4.4).

Table 4.4. Subjective ratings of coherence for imagined events at set sizes 2 and 4 and atypical and typical conditions in Experiment 3b

Rating Type (1 - 5)	Atypical		Typical	
	2	4	2	4
Coherence	3.57 (.60)	3.10 (.42)	4.68 (.30)	4.30 (.49)

SD are in parentheses

4.6.4 Cued Recall

The number of trials in which at least one item was recalled (Recall success) is presented in Figure 4.6. This measure of memory was used because the different number of items across conditions meant that comparing the raw number of recalled words across set sizes was not meaningful. Recall success was entered into a 2 x 2 repeated measures ANOVA with condition and set size as factors. There was a significant effect of condition (*F*(1,11) = 33.80, *p* < .001) but not set size (*F*(1,11) < 1). The interaction showed a trend toward significance (*F*(1,11) = 3.62, *p* = .08), with subjects showing larger recall success in the typical condition vs. atypical condition at set size 4.

For completeness, the total number of recalled words was also compared within each set size (Figure 4.7). There was a main effect of typicality both at set size of 2 (paired *t*(11) = 2.73, *p* < .05) and at a set size of 4 (paired *t*(11) = 5.42, *p* < .001), with an advantage for typical items. Taken together, these findings suggest that typical events show a mnemonic advantage, both in terms of likelihood of retrieval, and in terms of number of items recalled per event.

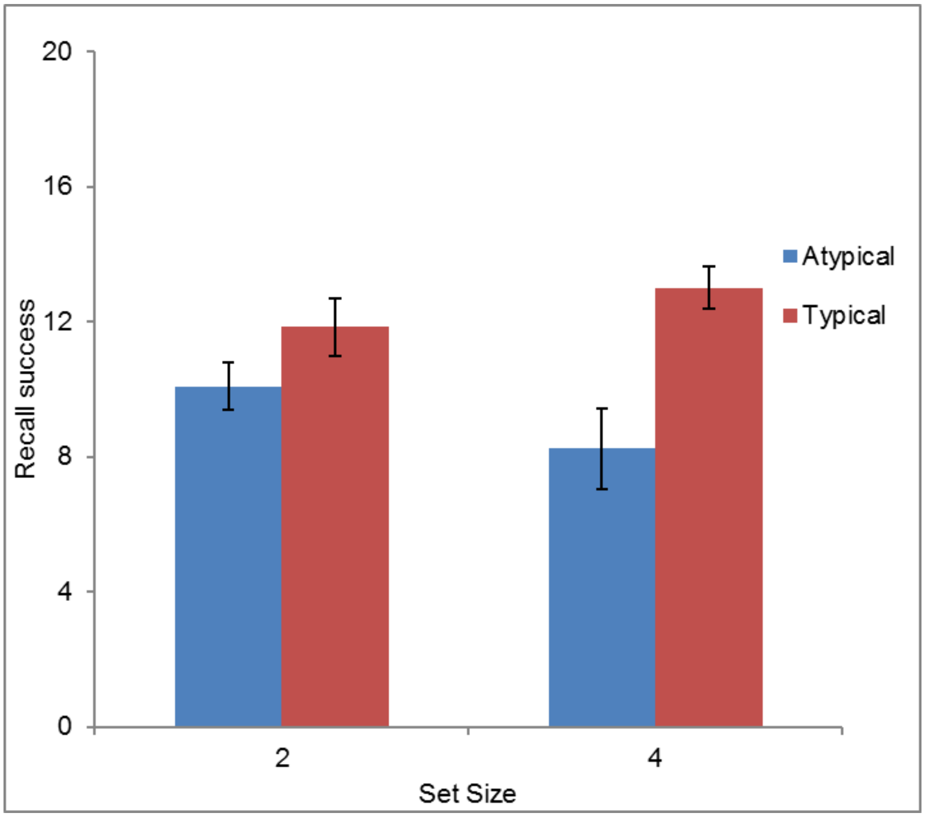

Figure 4.6. *Likelihood of recalling at least one item given the context cue at set sizes 2 and 4 and for typical and atypical context-item pairings in Experiment 3b*

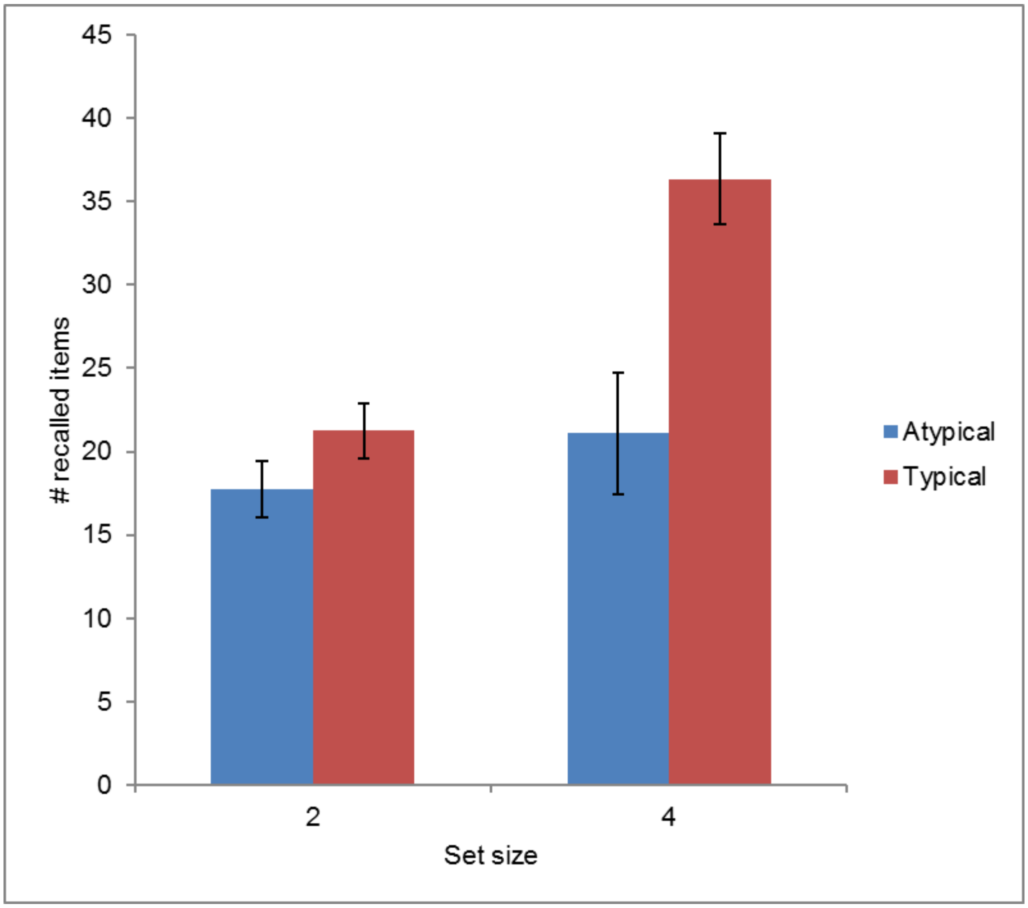

Figure 4.7 Total number of recalled item words given the context cue at set size 2 and 4 and for typical and atypical context-item pairings in Experiment 3b

4.7 Discussion

Despite using a slightly modified paradigm, Experiment 3b yielded similar results to those of Experiment 3a: compared to events imagined with typical items, those with atypical items were less coherent and took longer to construct. Moreover, at recall, typical contexts showed a memory performance advantage, both in terms of the raw number of recalled words, and the likelihood of recalling any item. Across several domains, processing is facilitated when supported by prior knowledge, whereas having to process novel, odd, or implausible information tends to result in increased completion time, and weaker inter-item associations (Worthen, 2006). Thus, semantic context can impart a powerful influence on the ability to simulate a novel event, particularly when the items or perhaps the events occurring in that context do not match with pre-existing knowledge.

In addition, there was a memory advantage for typical items, both in terms of whether any item word was recalled, and in terms of the raw number of items recalled. A common finding is that information congruent with existing knowledge shows a memory benefit compared to information that is incongruent (Craik & Tulving, 1975). However, this is not always the case. Studies of memory for prose show that inserting atypical events in narrative sometimes produces better memory for the atypical events, as they must be more deeply processed to produce a coherent representation of the text (Erdfelder & Dredenkamp, 1998). Nevertheless, in Experiments 3a and 3b, atypical trials showed poorer memory, despite being rated as more difficult, less coherent, and taking longer to process.

Although the results demonstrated the influence of typicality on memory, the source of the effect is not clear. In this study, the memory benefit most likely occurred at retrieval: that is, with a list of 80 trials, typical contexts are generally a more effective retrieval cue for the items. This is not surprising given that atypical contexts were chosen precisely because they were not strongly associated with the items. Consequentially, these findings suggest that once imagined events are encoded into memory, they are similarly affected by factors that govern the general accessibility of memory (Szpunar, 2010). Given a particular cue, memories, either real or imagined, that are congruent with prior knowledge are more easily accessed, and thus are more likely to be recalled. This is conceptually inconsistent with the notion that future imagining is useful as a means to create simulations, which are encoded for later reference (Szpunar et al., 2013): If we tend to recall more typical events when trying to predict a future outcome, this would limit the utility of memorizing imagined events to times when the future is consistent with prior knowledge. Thus, although the ability to combine disparate memories into new simulations is conceptually useful due to its flexibility, it is pragmatically limited by the subsequent accessibility of those simulations.

Consequentially, factors that further enhance the accessibility of semantic memories will also bias memory for imagined events. For example, semantic facts show faster retrieval if they are associated with a previous episodic memory (Westmacott, Black, Freedman, & Moscovitch, 2004).When this is applied to event construction, despite the participants' ability to imagine events that have not been directly experienced, those events that match previous experiences may still show a mnemonic advantage. Moreover, if certain generalized cognitive schemas become more accessible in conscious awareness, they could influence the retrieval of schema-consistent information. For example, a common finding in major depressive disorder is the presence of maladaptive cognitive schemas (i.e. "no matter how hard I try, I'm just a failure") that bias the retrieval of past experiences, as well as the interpretation of those experiences (Clark & Beck, 2010). In fact, a primary goal of cognitive-behavioural therapy is to highlight alternative interpretations of events or positive, schema-inconsistent past events, in order to "disprove" the cognitive schema as a hypothesis. One may speculate that a difficulty in treating depression may lie in the fact that although alternative, more adaptive interpretations of past events may be constructed during therapy sessions, such simulations are not as accessible as those mental events consistent with the more prominent cognitive distortions (Witheridge, Cabral, & Rector, 2010).

4.7.1 Summary

Across 2 experiments, I demonstrated that typicality, in addition to mnemonic load, also can affect event construction and subsequent memory. Relatively atypical events take longer to construct, are not as coherent, and are rated as less detailed and more difficult. Also, atypical events are less likely to be remembered when memory is tested using cued recall. In addition, the ability to construct a simulation initially is associated with relational reasoning performance, suggesting common cognitive processes and neural substrates to both tasks. The issue of neural substrates underlying event construction is explored more thoroughly in Chapter 5.

5 Chapter 5: Medial Temporal Lobe and Prefrontal Cortex Contributions to Event Construction

Despite work showing significant overlap between cognitive processes and neural correlates involved in autobiographical recall, and in future simulation (Addis, Pan, et al., 2009; Schacter et al., 2012; Spreng & Grady, 2010), there are unique behavioural effects and patterns of neural activity during future simulation, suggesting additional cognitive processes. Phenomenological reports of future simulation suggest that compared to past events, future events are perceived with fewer sensory details, a decreased sense of re-experiencing, and longer task completion times (A. D'Argembeau & Van der Linden, 2004, 2006). In terms of neural activity, early studies comparing autobiographical recall and future imagining found greater activity during future imagining in the hippocampus and the medial prefrontal cortex, including the medial frontal poles (Okuda et al., 2003). Similarly, Addis et al. (2007) directly compared future imagining, autobiographical recall, and a semantic definition and object imagery control tasks, and found increased activity in the future imagining conditions in the right frontal pole, right hippocampus, bilateral inferior frontal gyri, and bilateral middle temporal gyri. Activity in these regions, however, also varied by the phase of simulation or recall: increased activity for future events during the construction phase was noted in all these regions except for the right middle temporal gyrus, which was more active during the elaboration phase.

As future events are relatively novel, there is an additional construction demand during future simulation that is not present to the same extent in autobiographical recall. Both the hippocampus and frontal poles have shown increased activation during future simulation, compared to autobiographical recall. Yet, the contributions of these during the construction phases of future simulation are not yet clear. The cognitive processes associated with these regions and their putative contributions to event construction are briefly reviewed.

5.1.1 The hippocampus and event construction

Addis & Schacter(2012) posited three hippocampally-related processes that are crucial for future simulation: retrieval of information, recombination/construction of the simulation, and encoding of the stimulation. Specific to recombination/construction, converging evidence suggests that the hippocampus is needed when combining information in novel ways. For example, hippocampal integrity is necessary for the ability to make inferences across sets of related stimuli (i.e. transitive inference), and to infer associations between items and related information during encoding (Zeithamova & Preston, 2010) . Moreover, the hippocampus seems necessary to help initially form a coherent spatial representation of a location for the purposes of navigation (Johnson & Redish, 2007; Spiers & Maguire, 2007). Taken together, it seems that the hippocampus is implicated when subjects process a sufficiently complex mental representation that involves explicit, unique relational associations amongst the items.

In general, hippocampal activity has been observed both during the initial construction phase of future simulation (i.e., between 2 – 8 s after item onset), and during subsequent elaboration of the simulated event (Addis et al., 2009). There are several factors that modulate hippocampal activity during future simulation. Addis & Schacter (2008) found that the subjective ratings of detail parametrically modulated hippocampal activity when elaborating on future simulations, suggesting an additional role for the hippocampus in retrieving information to embellish the mental representation. Increased hippocampal activity has also been noted when imagining increasingly implausible future events (Weiler et al., 2010), perhaps suggesting that imagining a less likely occurrence involves having to retrieve more disparate details together. However, these increases in activity were all observed during the elaboration phase of the task, so it is not known to what extent, if any, this effect occurs at initial event construction.

Factors that affect hippocampal activity during the initial construction phase are less consistent. Summerfield, Hassabis, & Maguire, (2010) used a scene construction task where subjects had to incorporate 3 – 6 objects, one at a time, into a coherent imagined scene. Increased hippocampal activity was observed when imagining the first and 3rd object, but no further activity occurred with increasing set size, suggesting increased construction demands do not track with hippocampal activity beyond a certain threshold. However, Addis et al. (2011) had subjects imagine specific vs. general future events, reasoning that the former had additional construction demands due to the novelty of a specific scenario, compared to a more generalized, prototypical scenario. Increased activity in the right anterior hippocampus was found when imagining specific future events, consistent with previous studies showing anterior hippocampus during the construction phase of future simulation (Addis et al., 2009).

Similarly, studies of hippocampal lesion patients have shown mixed evidence of construction deficits during future simulation. Hassabis et al. (2007) found that hippocampal lesion patients imagined scenarios that were less spatially-coherent, but noted that one patient’s performance was equivalent to controls, and could utilize residual hippocampal tissue in service of scene construction (Mullally, Hassabis, & Maguire, 2012) . Rosenbaum et al. (2009) found that the amnesic patient K.C. had difficulty reproducing well-known narratives in a coherent fashion, making sequencing errors for the events, suggesting deficits in the re-construction of well-learned, complex narratives. However, Squire et al. (2010) found no impairment in amnesic patients with hippocampal lesions, although their performance deficits approached statistical significance in some conditions. Finally, Race et al. (2011) gave amnesic patients a picture description task, and noted that patients were unimpaired at describing a picture, although they could not imagine future events, suggesting that future imagining performance is not due to deficits constructing a complex narrative. Overall, although hippocampal activity during event construction has been reported, the precise contribution of the hippocampus to event construction, and thus the factors that modulate hippocampal activity, are unclear.

5.1.2 The Frontal Poles and Event Construction

The frontal poles correspond approximately to Brodmann Area (BA) 10, and encompass both medial and lateral portions of the most anterior portions of the frontal cortex. Consequently, BA 10 is the largest Brodmann area, and thus a definitive theoretical account of its function(s) is still under development (Ramnani & Owen, 2004). Patient studies suggest that damage to the frontal poles results in a number of deficits, including prospective memory (Volle, Gonen-Yaacovi, Costello, Gilbert, & Burgess, 2011) , multitasking (Dreher, Koechlin, Tierney, & Grafman, 2008), future planning (Burgess & Shallice, 1991), and a poor metacognitive sense of self (Hoffmann & Bar-On, 2012; Stuss & Alexander, 2007): however, as these lesions are often quite widespread, it is difficult to ascribe specific functions and processes to discrete regions.

Recent neuroimaging data has suggested a dissociation of function between the medial aspects and the more lateral regions of the frontal poles. The medial frontal poles tend to show activity during any task involving the consideration of one's own mental state, the mental state of others, or both. For example, medial frontal pole activity occurs when judging the relevance of trait words to one self (Craik et al., 1999), and also during memory tests with self-referential items must be encoded (Gutchess, Kensinger, & Schacter, 2010), suggesting a role in considering any self-referential information. However, these regions are also active when engaging in theory of mind (ToM) tasks (Amodio & Frith, 2006), considering social dilemmas (Moll, De Oliveira-Souza, & Zahn, 2008; Van Overwalle, 2009), or reading narratives (Yarkoni, Speer, & Zacks, 2008), suggesting they are also sensitive to tasks involving the mindsets of others. These findings have prompted the notion that the medial prefrontal cortex is implicated in 'mentalizing', or the consideration of one's mental state or another's in a simulated context.

Conversely, the lateral portions of the frontal poles are active when processing complex material, or when multiple tasks must be completed. In one example, diPisapia, Slomski, & Braver (2007) had subjects maintain one number in WM, while engaging in serial math problems. Crucially, in some conditions, the maintained number had to be incorporated into the math problems in order to come to a solution, or merely reported after the math problem. Compared to when the information was reported separately, the lateral frontal poles were more active when the maintained number had to be integrated into the existing task, suggesting that this region is implicated when multiple tasks must be combined. Thus, tasks involving relational reasoning (i.e. analogical reasoning; Bunge, Wendelken, Badre, & Wagner, 2005; Christoff, Ream, Geddes, & Gabrieli, 2003; Prabhakaran, Smith, Desmond, Glover, & Gabrieli, 1997), or tasks involving a main goal and additional subgoals (Braver & Bongiolatti, 2002; Koechlin, Basso, Pietrini, Panzer, & Grafman, 1999) activate the lateral frontal poles, relative to other complex tasks.

Recent structural and functional connectivity findings also support the dissociation between medial and lateral frontopolar regions. Specifically, Gilbert et al., (2006) conducted a meta-analysis of the different types of tasks that activated BA 10, and found that the medial portions were preferentially involved during mentalizing, whereas the lateral frontal poles were engaged largely during working memory and episodic memory retrieval. Liu et al. (2013) found that the medial frontal poles are typically connected with the medial prefrontal cortex and areas of the default mode network, whereas lateral frontal poles are more connected with regions in the lateral prefrontal cortex and lateral superior parietal cortex. Interestingly, these dissociations in functional connectivity do not appear to be absolute, and regions that are typically active with the lateral frontal poles can also be co-active with the medial frontal poles, when subjects engage in mentalizing-type tasks (Gilbert, Gonen-Yaacovi, Benoit, Volle, & Burgess, 2010). Indeed, medial frontopolar activity has been observed during analogical reasoning tasks (Green et al., 2010; Volle, Gilbert, Benoit, & Burgess, 2010), and also when reasoning about socially-relevant stimuli (Raposo et al., 2011). Similarly, engaging in a working memory task for socially-relevant stimuli also tends to activate the medial frontal poles rather than the lateral frontal poles (Meyer, Spunt, Berkman, Taylor, & Lieberman, 2012), suggesting that although functionally distinct, these regions, and any functional networks with which they are associated, may engage with one another, depending on the nature of the task.

The frontal poles and adjacent medial prefrontal cortex show reliable activity during future imagining, but there are several factors that modulate frontal pole activation, with no obvious common element. For example, in one of the earliest neuroimaging studies on future imagining, Okuda et al., (2003) found several medial prefrontal peaks more active when imagining far future events compared to near future events, but also several peaks showing the opposite effect. Addis & Schacter (2008) found that the amount of subjective detail parametrically modulated right medial frontal pole activity during future imagining, and suggested perhaps the amount of extra processing to imagine a detailed, novel event might modulate frontal pole activity. In addition, D’Argembeau et al., (2010) found that imagining future events consistent with one’s personal goals increases frontal pole activity, compared to imagining goal-irrelevant or routine activities. Similarly, imagining future events with positive-valence, or associated with greater long-term gains, are also associated with increased medial prefrontal activity (D’argembeau et al., 2008). Whether common factors underlie these various effects remains unknown. Recently, Andrews-Hanna (2012) has argued that a core network of regions commonly engaged during future simulation (i.e. the default mode network; DMN) consists of two interacting subsystems. The first is a medial temporal lobe ‘construction’ network, composed of the hippocampus, posterior cingulate cortex, inferior parietal lobules, and ventromedial prefrontal cortex, and is thought to be implicated in the construction of simulated events. The other is a dorsomedial prefrontal cortex ‘mentalizing’ network, involving the dorsomedial prefrontal cortex (including the medial frontal poles), lateral temporal cortices, and angular gyrus, and is thought to be involved in mentalizing in general. Interaction between these networks is thought to occur in a region of the medial frontal poles, between the ventromedial prefrontal cortex of the construction subsystem, and the dorsomedial prefrontal cortex of the mentalizing subsystem. Under this model, the hippocampus and frontal poles would both contribute to construction in general, though they may be functionally connected to distinct brain regions.

Finally, it is worth noting that patients with lesions to the prefrontal cortex or associated regions also show deficits in future simulation, which tend to correspond with poor executive functioning (Berryhill, Picasso, Arnold, Drowos, & Olson, 2010; de Vito et al., 2012). However, these studies used patients with lesions outside medial prefrontal regions, and so do not address the direct impact of medial frontal poles on future simulation abilities. The only study to provide relevant data has been conducted by Irish et al. (2012), who used voxel-based morphometry to obtain measures of gray matter atrophy in Alzheimer’s dementia and semantic dementia patients, in order to measure whether changes in cortical thickness correlated with future thinking performance. Interestingly, within Alzheimer’s patients, future thinking scores were negatively correlated with the amount of atrophy in the frontal poles, suggesting they may indeed be necessary for future simulation.

5.1.3 Typicality, Set Size, and Neural Responses during Event Construction

Given the effects of typicality and set size on event construction performance, and the increased hippocampal and frontopolar activity during future simulation, it is possible that these factors might modulate activity in these regions during future simulation.

Hippocampus

With respect to typicality, neuroimaging studies of associative memory find that during associative encoding tasks (i.e. learning of word pairs), the hippocampus and surrounding medial temporal lobes are active regardless of whether such items are semantically-related or unrelated (Achim, Bertrand, Montoya, Malla, & Lepage, 2007; Addis & McAndrews, 2006; Davachi & Wagner, 2002; Staresina & Davachi, 2006). However, studies of patients with hippocampal lesions show that tasks that are thought to be hippocampally-dependent (i.e., transitive inference, recollection of word pairs), can be performed following hippocampal damage if the pair of words is semantically-related, or can be “unitized” to support performance (Giovanello et al., 2006; Quamme, Yonelinas, & Norman, 2007). Moreover, although transitive inference is usually impaired in patients, their performance is greatly improved if the pairs of items to be compared have a prior semantic relation (Moses, Ostreicher, Rosenbaum, & Ryan, 2008). In this case, the relational hierarchy needed to ascertain various inferences between cards is already well-known, and thus does not likely require the same type of process that is dependent on the hippocampus. Thus, it is possible that greater hippocampal activity would be found when constructing atypical vs. typical events.

An interesting parallel is found in patients with developmental amnesia, who show inconsistent findings of future simulation impairments (Cooper, Vargha-Khadem, Gadian, & Maguire, 2011; Kwan et al., 2010). One idea proposed to explain the discrepant findings is that given certain task parameters, patients are able to use established schemas in semantic memory to aid their performance, thus minimizing their episodic simulation impairment. Under these conditions, it appears that the hippocampus is not necessary when imagining typical events, as they may be completed using schema-consistent semantic information.

However, some studies have found hippocampal activity during imagination of non-personal, and presumably relatively schematic, imagined events. D'Argembeau et al. (2009) found that imagining events not relevant to one's personal goals also activated the hippocampus. Race et al. (2013) had patients with MTL lesions imagine semantic future events, such as important issues facing society and their effects on individuals. The authors found that even for these relatively semantic imagined events, amnesic patients could not produce detailed descriptions, suggesting that it is the nature of the imagining task, rather than the semantic associations of the information, that implicated the hippocampus. Nevertheless, based on the literature showing the role of the hippocampus in encoding novel inter-item associations, one would predict that during event construction, the hippocampus would be more active when simulating atypical events, as compared to typical events.

In terms of set size, results from Experiment 2 clearly indicate that the contribution of the hippocampus to event construction is sensitive to mnemonic load. In addition, recent evidence suggests that the hippocampus is important for working memory when the stimuli are novel and/or sufficiently complex, and thus difficult to rehearse mentally (Hannula, Tranel, & Cohen, 2006; Olson, Page, Moore, Chatterjee, & Verfaellie, 2006; Ranganath & Blumenfeld, 2005; Rose, Olsen, Craik, & Rosenbaum, 2012). Thus, in addition to greater hippocampal activity during event construction vs. a control condition, I would predict that hippocampal activity during event construction would increase as a function of mnemonic load: that is, greater hippocampal involvement when imagining more items.

Frontal poles

There is evidence to suggest that typicality might modulate frontopolar activity during future simulation. For example, Green et al. (2009) found that during an analogical reasoning task, increasing abstractness of the association between word pairs (i.e. decreasing typicality) was associated with increased left medial frontal pole activity, even when accounting for task difficulty. Such findings parallel the increased frontal pole activity when imagining detailed future events (Addis & Schacter, 2008), which would also involve forming more disparate associations, as future events tend to be more semantic and generalized in nature (Anderson, 2012; Szpunar, Chan, & McDermott, 2009). Also, activity in the medial frontal poles tends to be greater when viewing self-relevant information, compared to information not associated with oneself (Craik et al., 1999; Mitchell, Macrae, & Banaji, 2006), which could be interpreted along a continuum of semantic similarity or typicality with oneself. Indeed, activity in the medial frontal poles is also observed when considering another person who is close (i.e. family, close friends) vs. a stranger (Mitchell, 2009). Thus, I predict increased medial frontal pole activity when constructing typical vs. atypical events.

In terms of set size, neither medial nor lateral frontopolar regions typically show a direct modulation with set size during tasks (Braver & Bongiolatti, 2002), whereas more caudal frontal areas such as the ventrolateral prefrontal cortex are sensitive to mnemonic load (Rottschy et al., 2012). However, lateral frontopolar regions are active when task demands require maintaining information online and additional processing. For example, having to generate or evaluate an analogical pair of items across an increasing number of dimensions, integrating the product of one cognitive operation into another, or detecting a target while doing another task, are associated with increased lateral frontopolar activity (Braver & Bongiolatti, 2002; De Pisapia et al., 2007; Christoff & Gabrieli, 2000; Prabhakaran et al., 1997). Given that event construction involves integrating information into a coherent representation, it may be that increasing mnemonic load in this task would modulate lateral frontopolar activity.

5.1.4 Current Study

To explore the contributions of the hippocampus and frontal poles to event construction, I compared neural activity while subjects completed the event construction task from Experiment 3b. Subjects saw a context word with 2 or 4 items that were relatively typical or atypical, and had to imagine an event, relating those items as much as possible. Specifically, I predict that the hippocampus would be more active when imagining atypical events, and when imagining events with higher vs. lower mnemonic load. In terms of the frontal poles, I predict increased medial frontopolar activity for typical vs. atypical events, and an effect of mnemonic load for the lateral frontal poles.

6 Experiment 4

6.1 Method

6.1.1 Participants

Nineteen right-handed volunteers participated in the study. All were native-English speakers, with no history of neurological or psychological illness. Prior to participating, all subjects gave informed consent in accordance with the Research Ethics Board at the University of Toronto, and were paid $45 for their participation. Three subjects had to be removed from analysis: two for excessive head movement, and one for extremely low performance, who could not recall any information pertaining to the task. The remaining 16 subjects (7 males, *M* age = 22.3, *SD* = 4.16) were analyzed in the study.

6.1.2 Design and Procedure

Subjects completed tasks similar to those in Experiment 3b, involving two tasks, an imagining task and a working memory control task. In the imagining task (IMAGINE), subjects were shown a context word with 2 or 4 item words, and was instructed to imagine an event with those items in that context, relating the items explicitly as much as possible. In addition, the context-item pairing could be relatively typical (e.g. ‘tide’, ‘sandal’ with ‘beach’) or atypical (‘salad’, ‘clown’ with ‘cruise ship’). In the working memory control task (REORDER), subjects were also shown 2 or 4 words, but had to reorder them in their mind in reverse alphabetical sequence (i.e. Z to A). Thus, the experiment was comprised of a 3 x 2 design with condition (IMAGINE-atypical, IMAGINE-typical, REORDER) and set size (2, 4) as within-subjects variables.

Prior to the fMRI scanning session, subjects completed a practice session, in which the task instructions were specified, and two examples given. Subjects completed one block of 20 trials, 10 IMAGINE and 10 REORDER trials. The experimenter was present during the practice session to answer any questions about the task.

During the scanning session, on each trial, a task cue appeared for 1.25 s indicating the task that was to follow. On IMAGINE trials, subjects saw a context word and 2 or 4 item words simultaneously for 12 s, and had to imagine an event with all the items related. Once they had constructed the event, they pressed a button, and were told to mentally rehearse the event until the 12 s had elapsed. Then, they had 3.5s to rate the coherence of the imagined event on a 4-point scale (1 = not coherent at all, 4 = very coherent). On REORDER trials subjects were shown 2 or 4 words, and had 12 s to put the words in reverse alphabetical order, pressing a key once the order was determined. Subjects had to rehearse that new order mentally until the 12 s elapsed. Then, subjects were shown a probe word, and had 3.5 s to answer whether it appeared in the 2nd or 4th position in reverse alphabetical sequence. The probe word was in the correct position on 50% of the trials. Following each trial, a fixation cross appeared for 1.5 to 7.5 s, to allow for inter-trial jitter.

Subjects completed 24 trials/condition, resulting in 144 trials overall. Trials were divided into 6 runs with 4 trials/condition in each run, with conditions presented in random order. Each run lasted approximately 8.5 min, with 30 – 60 s in between runs to reiterate instructions. The entire scanning session lasted approximately 90 min.

Following the scanning session, subjects completed a 2-step recall/description task in a separate testing room with the experimenter present. Subjects were shown a context word, and had to recall all the words that were presented with the context word in the scanner. Then, subjects pressed a key, and all associated item words were shown, at which point the subject was to describe what he/she imagined with those items, noting the relations between them. Subjects then provided ratings from 1 – 4 (1 = low, 4 = high) for the typicality of the event they imagined, and how much the event reminded them of a past personal experience (remindingness) (Figure 6.1).

Performance for both phases was self-paced. For the recall phase, subjects were encouraged to produce words even if they weren’t entirely confident. For the description phase, the experimenter provided no probes, other than to remind the subjects to describe the event they had imagined in the scanner. The descriptions were recorded, and later transcribed and scored according to the criteria in previous experiments. In addition, for recall, the number of words recalled per trial was measured (total recall), as well as the number of trials per condition where at least one item word was recalled (recall success).

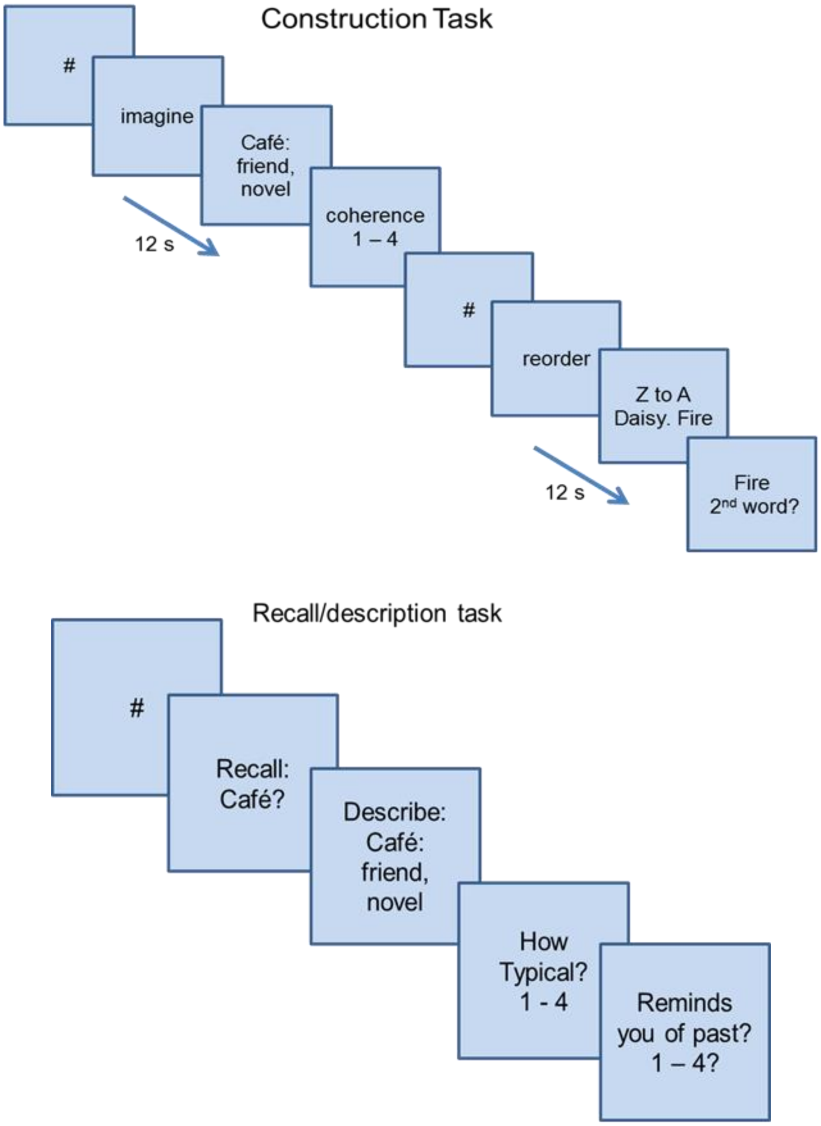

Figure 6.1 Schematic of the event construction task and recall/description task in Experiment 4

6.1.3 fMRI Data Acquisition & Preprocessing

Data was acquired using a Siemens Tim Trio 3.0 T MRI scanner using a 12-channel head coil, at the Rotman Research Institute, Baycrest Centre, Toronto, Ontario. T2-weighted images were acquired in the axial oblique plane using a gradient echo-planar imaging (EPI) sequence (repetition time [TR] = 2000 ms, echo time [TE] = 30 ms, field of view = 200 mm, voxel size = 3 x 3 x 3.5 mm^3). Each volume contained 30 slices acquired in an interleaved fashion, covering the entire cerebral cortex. High resolution T1-wieghted images were acquired prior to the functional scans using an MPRAGE sequence (TR = 2000 ms TE = 2.63 ms, field of view = 256 mm, voxel size = 1mm^3, 160 slices).

For each run, the first 4 scans were discarded for scanner equilibration. Data were preprocessed and analyzed using SPM5 (Wellcome Department of Imaging Neuroscience, http://www.fil.ion.ucl.ac.uk/spm/software/spm5). The functional volumes were corrected for slice acquisition times, realigned to the mean image, and coregistered with each subject's structural image. The resulting parameters were then used to spatially normalize the images to the MNI template brain provided in SPM5, resampling to 2 mm^3 isotropic voxels. Finally, the images were smoothed with an 8 mm isotropic Gaussian kernel.

6.1.4 fMRI Data Analysis

The fMRI BOLD signal was decomposed using the general linear model (Friston et al., 1995) separately for each run. Activity for the entire duration of stimulus presentation (i.e. 12 s) was modeled using the canonical hemodynamic response function. Six separate regressors were modeled for each task condition, as well as 6 regressors corresponding to the realignment parameters for each subject, to correct for motion artifacts. A 1/128 Hz high-pass filter was applied to the data and model. Parameters for each regressor were estimated using a least-mean-squares fit of the model to the functional data. Parameter estimates for all 6 task conditions were entered into a flexible factorial ANOVA at the 2nd level using a random-effects analysis and a non-sphericity correction. To test the main effect of imagining, activity across all IMAGINE task conditions was contrasted with activity across all REORDER conditions. To test the effect of typicality, within the IMAGINE conditions, the atypical and typical conditions were contrasted, collapsing across set sizes. Finally, to test the effect of set size, the IMAGINE conditions at a set size of 4 and 2 were contrasted, collapsing across typicality.

Also, a separate model was created to examine subsequent memory effects across conditions. Within the atypical and typical conditions, trials were sorted according to whether any word was remembered or forgotten (i.e. recall success), thus creating 4 regressors (Atypical-remembered, Typical-remembered, Atypical-forgotten, Typical-forgotten). Memory performance was collapsed across set size because of insufficient trials to model the effects of set size on memory. In addition, there was no effect of set size on memory performance (see Results). Parameter estimates for all 4 task conditions were entered into a flexible factorial ANOVA at the 2nd level using a non-sphericity correction. To test subsequent memory effects, all remembered trials were contrasted with all forgotten trials ([Atypical-remember + Typical-remembered] – [Atypical-forgotten + Typical-forgotten]). In addition, contrasts were created to compare Typical-remembered and Atypical-remembered trials.

Furthermore, because the hippocampus and frontal poles were of interest, I conducted a region of interest (ROI) analysis by extracting mean-level activity within the defined regions for all conditions using MarsBar (Brett et al., 2002) (see Appendix 2 for ROIs). For the hippocampus, anatomical ROIs of anterior (Volume = 7740 mm^3) and posterior hippocampi (Volume = 7320 mm^3) were defined using the standard AAL atlas (Tzourio-Mazoyer et al., 2002). For the main analysis, activity across both left and right hippocampi were combined, as there were no strong laterality predictions. However, activity for left and right hippocampi individually showed similar effects (see Appendix 4). For the frontal poles, functional ROIs were defined as bilateral 10 mm spheres drawn around activity peaks of medial (Volume = 7968 mm^3) and lateral frontal pole regions (Volume = 7968 mm^3), based on a meta-analysis of frontal pole activity across a variety of tasks (Gilbert et al., 2006). These peaks have previously been used to examine separate medial and lateral frontal pole activity in other cognitive tasks (Volle et al., 2010). Activity was extracted from bilateral spheres, as there was no a prior predictions for laterality effects in the frontal poles (Appendix 3).

To test whether behavioural measure of task performance correlates with brain activity, I conducted a behavioural partial-least squares (PLS) analysis on brain activity during all IMAGINE conditions (McIntosh & Lobaugh, 2004). In general, behavioural PLS is a multivariate, data-driven technique, designed to investigate individual differences in brain-behaviour associations. Specifically, behavioural PLS identifies a set of latent variables (LVs), which maximally explain the association between brain activity and task performance, across conditions and across subjects. The results reveal whole-brain patterns of activity that correlate positively or negatively with task performance, across subjects.

PLS first calculates correlations between brain activity and mean behavioural performance per condition, creating a vector for the behavioural measure for each subject. These vectors are stacked into a single matrix and decomposed using single value decomposition, yielding LVs that express the commonalities and differences in networks of brain regions across all task conditions. The result is an extraction of functional networks that are positively or negatively associated with task performance, which may differ according to task conditions (i.e. typicality and set size). Moreover, there is no assumption of the shape of the hemodynamic response and no explicit contrast of activity across task conditions. Instead, the algorithms calculate the hemodynamic response that best explains the association between brain activity and behaviour across all conditions.

In PLS, the statistical significance of each LV is assessed by permutation testing, in which behavioural observations are shuffled within subjects, to calculate the probability of each LV occurring by chance alone. The reliability of each voxel’s contribution to the LVs is determined through bootstrap resampling, whereby subjects are randomly resampled and replaced, and the standard errors computed, in order to obtain an estimate of the standard error for each voxel. The result is a bootstrap ratio (BSR) for each voxel that is proportional to a z-score. Because calculation of the LVs is done simultaneously, there is no need to correct for multiple statistical comparisons. For this analysis, 500 permutations were run, and the data were resampled 100 times.

Three separate analyses were conducted, measuring the association between brain activity and 1) relational coherence, 2) subjective ratings of typicality, and 3) subjective ratings of remindingness.

6.2 Behavioural Results

All behavioural and ROI data were analyzed using IBM SPSS 20. Coherence ratings for 4 subjects, and typicality and remindingness ratings for 2 subjects were not recorded due to computer malfunction. Data for 1 run from one participant had to be excluded due to an unforeseen task interruption. Nineteen recall trials from another subject were not recorded due to computer malfunction, and these trials were not included in the fMRI analyses.

6.2.1 Task Performance

Relational Coherence

The number of relations formed during the IMAGINE conditions was entered into a 2 x 2 repeated-measures ANOVA with typicality and set size as within-subjects variables. The main effect of typicality approached significance, with typical items having more relations ($F(1,15) = 3.30$, $p = .09$). There was a main effect of set size, with trials having 4 items containing more relations than trials with 2 items ($F(1,15) = 33.19$, $p = .001$). The interaction was not significant ($F < 1$). These results generally replicated the behavioural findings from Experiments 3a and 3b, suggesting that typicality and set size can impact event construction performance: however, in this particular case, the effect of typicality was not as large as in Experiment 3b (Figure 6.2).

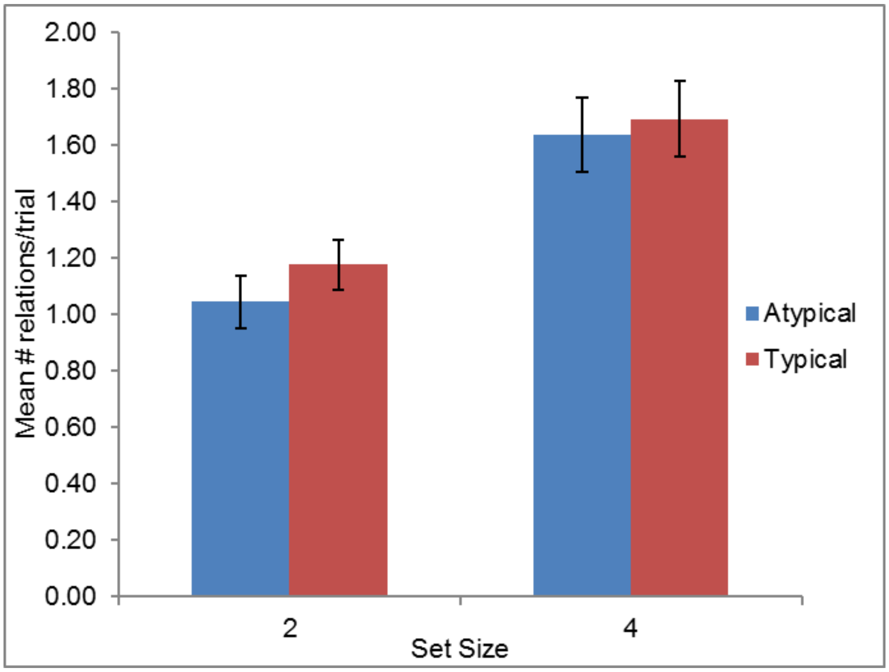

Figure 6.2. Mean number of relations/trial (coherence score) for set sizes 2 and 4 and for typical and atypical context-item pairings in Experiment 4

Completion time

Latency for all conditions was entered into a 3 x 2 repeated-measures ANOVA with task and set size as factors. There was a main effect of task ($F(2,30) = 28.27$, $p < .001$): tests of simple effects showed that times in the atypical condition were significantly slower than the typical condition ($p < .001$), and the typical condition was significantly slower than the control condition ($p < .005$). There was also a main effect of set size ($F(1,30) = 88.14$, $p < .001$), with 4 items taking longer than 2 items in general. The interaction was also significant ($F(2,30) = 7.94$, $p < .005$). Post hoc tests determined that at a set size of 2, the atypical condition was slower than the typical condition ($p < .001$), the typical and atypical conditions were each slower than the control condition (*p* < .001. At a set size of 4, the atypical condition was slower than the typical condition (*p* < .001) and control condition (*p* < .005), but the typical condition was not different from the control condition (*p* = .13) (Figure 6.3).

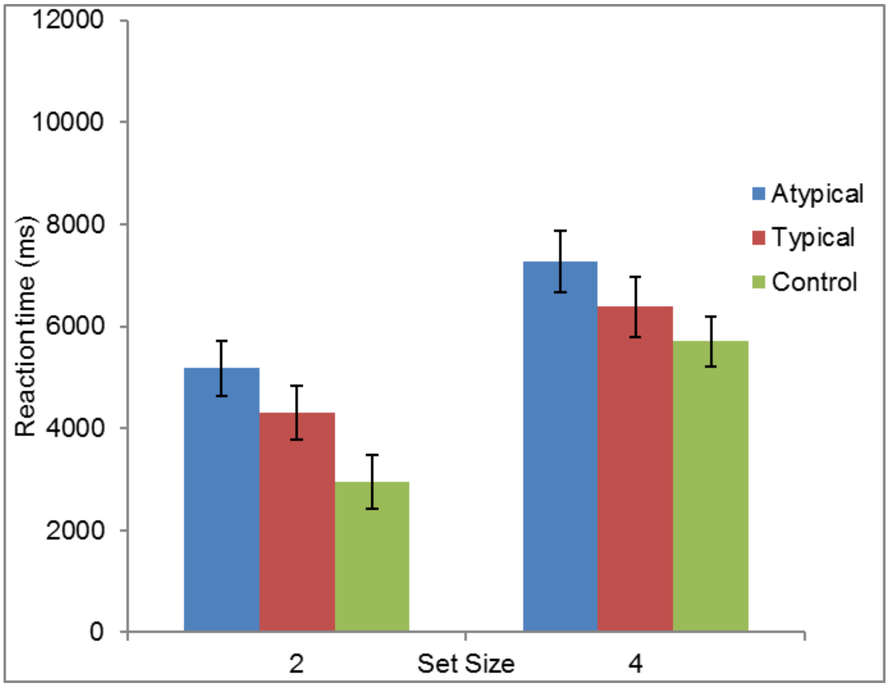

Figure 6.3. Mean completion time per trial for typical imagining, atypical imagining, and working memory conditions at set sizes 2 and 4 in Experiment 4

Subjective Ratings

In terms of subjective ratings of coherence obtained in the scanner, there was a main effect of typicality (*F*(1,11) = 37.47, *p* < .001), with typical items being rated as more coherent, and a main effect of set size (*F*(1,11) = 14.06, *p* < .005), with set size 2 trials being rated as more coherent than 4 item trials. The interaction was not significant (*F* < 1).

For ratings of typicality, both the main effects of typicality (*F*(1,13) = 100.38, *p* < .001) and the effect of set size (*F*(1,13) = 30.86, *p* < .001) were significant. As expected, typical trials were rated as more typical and set size 2 trials were rated as more typical than set size 4 trials. The interaction was not significant (*F* < 1). For ratings of the extent to which imagined events reminded subjects of a past personal experience (remindingness), there was a main effect of typicality (*F*(1,13) = 64.32, *p* < .001) and set size (*F*(1,13) = 12.21, *p* < .005), with typical events and events with 2 items being more likely to remind subjects of a past event. The interaction was marginally significant (*F*(1,13) = 4.39, *p* = .056), with a greater discrepancy between typical and atypical trials at a set size of 2, compared to set size 4 (Table 6.1).

Table 6.1. Subjective ratings of coherence, typicality, and remindingness for imagined events at set sizes 2 and 4 and atypical and typical conditions in Experiment 4

Rating Type (1 - 4)	Atypical		Typical	
	2	4	2	4
Coherence	2.89 (.49)	2.62 (.55)	3.66 (.22)	3.41 (.24)
Typicality	2.06 (.48)	1.79 (.30)	3.28 (.50)	3.04 (.60)
Remindingness	1.47 (.30)	1.35 (.31)	2.38 (.59)	2.13 (.50)

SD are in parentheses

6.2.2 Cued Recall

The number of trials where any word was recalled (i.e. recall success) was entered into a similar ANOVA. There was a main effect of condition, with typical trials being more frequently recalled than atypical trials (*F*(1,15) = 44.18, *p* < .0001). Neither the main effect of set size, nor the interaction, was significant (all *F*s < 1) (Figure 6.4).

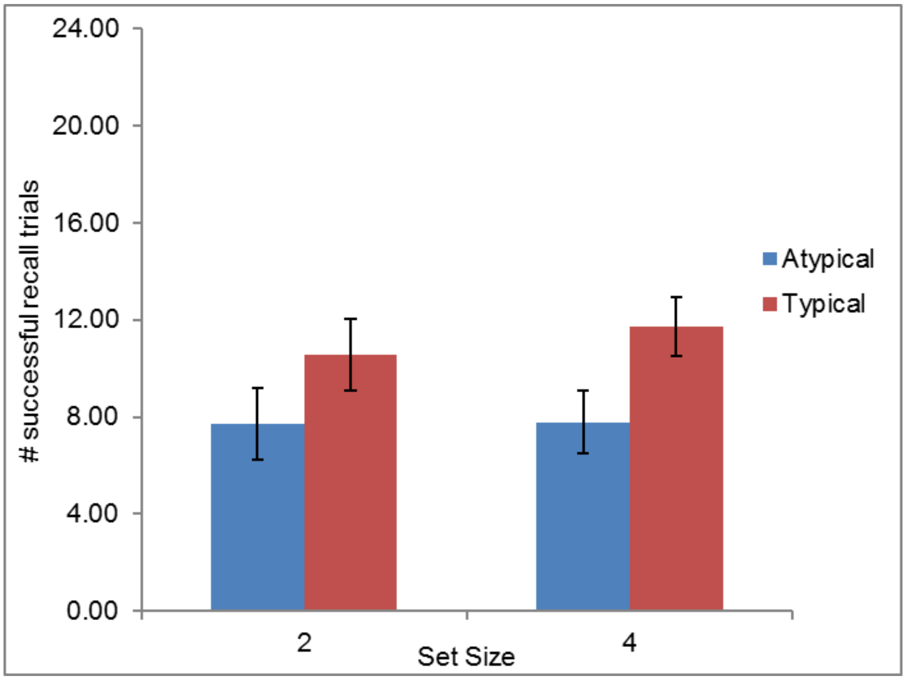

Figure 6.4. Likelihood of recalling at least one item given the context cue at set sizes 2 and 4 and for typical and atypical context-item pairings in Experiment 4

Also, the total number of recalled words was compared within set sizes. There was a significant advantage for typical trials at both set size 2 ($F(1,15) = 15.77$, $p < .005$) and set size 4 ($F(1,15) = 18.65$, $p < .005$).

6.3 fMRI Results

6.3.1 Whole Brain Analyses

All whole brain analysis contrasts were corrected for multiple comparisons using a false detection rate approach, *FDR* < .05 (Genovese, Lazar, & Nichols, 2002), and all figures show regions of activation that survive an *FDR* $p < .05$, with a minimum cluster size of 20, unless otherwise specified.

Task Effects

To examine neural activity associated with event construction, I compared activity in all IMAGINE conditions to all REORDER conditions (Figure 6.5). Constructing a novel event in general activated regions of the default mode network that have been previously implicated in future imagining tasks (Addis et al., 2007; Andrews-Hanna, 2012), including the bilateral medial frontal poles, medial parietal regions, and the parahippocampal gyri extending into the anterior hippocampus. In addition, imagining was also associated with a large cluster in the right ventrolateral prefrontal cortex (VLPFC) and right dorsolateral prefrontal cortex (DLPFC), bilateral lateral temporal cortices and bilateral cerebellum (Table 6.2).

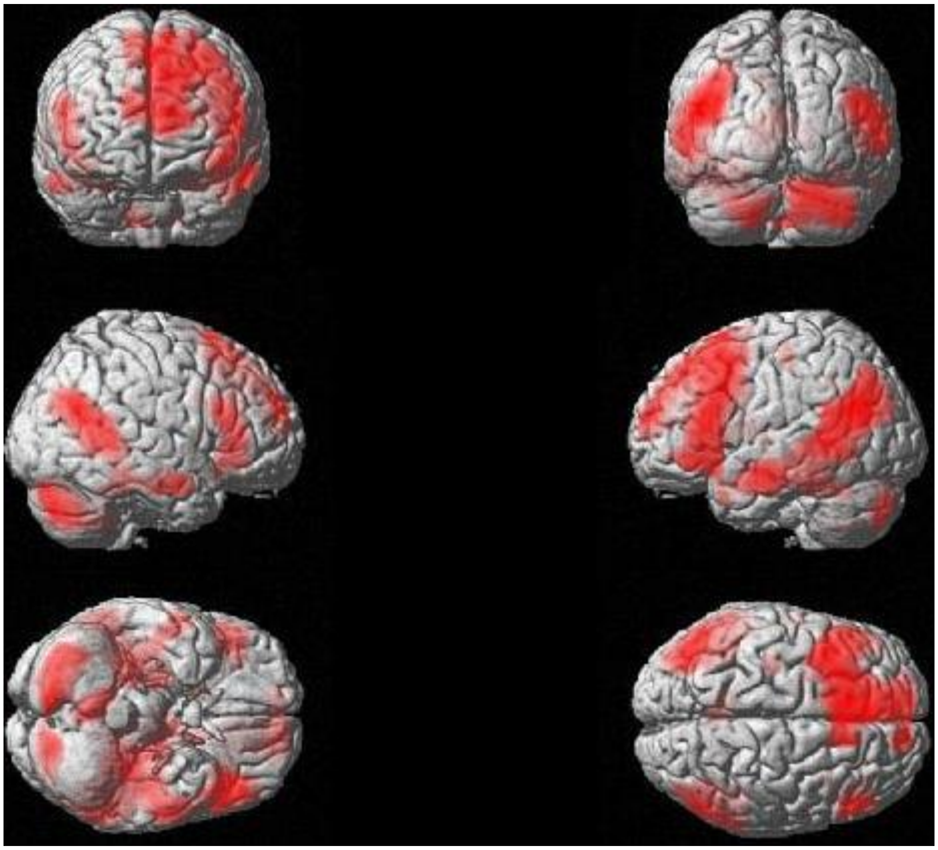

Figure 6.5. Whole brain activation contrasting IMAGINE conditions with CONTROL conditions, collapsing across typicality and set size.

For the reverse contrast, regions more active during the verbal working memory task included a large frontoparietal network that is typically associated with working memory tasks in general (Nee et al., 2012; Rottschy et al., 2012). Specifically, large clusters bilaterally in the DLPFC, extending medially into the anterior cingulate cortex, a large cluster with a peak in the left precentral gyrus encompassing the left inferior parietal cortex, a cluster in right inferior parietal cortex, and right lateral temporal cortex. In addition, separate clusters in the left supplementary motor area, and left cerebellum were also significant (Table 6.2).

Table 6.2. Regions of increased activation comparing IMAGINE and REORDER conditions. Peak of activation are denoted in MNI coordinates

Imagine vs. Re-order

	Brain Region	BA*	MNI coordinates	Cluster Size	Z Score
	Frontal		x, y, z		
L	Superior Medial Frontal Cortex	10	-6 58 24	19744†	>7.99
R	Inferior Frontal Gyrus	45	56 24 22	1016	5.92
		47	48 30 -6	Same cluster	5.03
		45	54 34 6	Same cluster	4.84
	Temporal				
L	Middle temporal gyrus	39	-46 -68 24	19744†	>7.99
R	Middle temporal gyrus	39	46 -62 22	2296	6.82
			62 -52 2	Same cluster	6.1
			44 -46 12	Same cluster	4.2
L	Parahippocampal/Fusiform Gyrus	37	-28 -34 -20	19744†	>7.99
R	Parahippocampal/Fusiform Gyrus	30	26 -32 -20	1630	6.29
		37	32 -36 -16	Same cluster	6.03
L	Hippocampus		-20 -16 -16	Same cluster	4.85
R	Hippocampus		22 -14 -22	Same cluster	4.15
		20	42 -16 -28	Same cluster	5.06
	Parietal				
L	Precuneus	31	-12 -48 38	95	3.58
L	Postcentral Gyrus	4	-32 -24 50	134	2.95
L	Precentral Gyrus	6	-30 -22 58	Same cluster	2.72
	Other				
R	Cerebellum		12 -84 -36	2042	>7.99
			18 -72 -28	Same cluster	7.52
			36 -78 -40	Same cluster	7.36

R	Cerebellum		8 -54 -46	500	5.12
L	Cerebellum		-16 -86 -36	552	5.41

Re-order vs. Imagine

Hemisphere	Brain Region	BA*	MNI coordinates	Cluster Size	Z Score
	Frontal		x, y, z		
R	Middle Frontal Gyrus	46	38 42 26	3604	4.77
		46	36 34 36	Same cluster	4.52
		11	24 52 6	Same cluster	4.43
R	Middle Frontal Gyrus	8	26 18 56	27	2.79
L	Middle Frontal Gyrus	46	-34 38 22	89	3.22
L	Anterior Cingulate Cortex	24	-12 8 36	25	3.17
L	Supplementary Motor Area	6	-4 2 60	26	3.03
	Temporal				
L	Precentral Gyrus	6	-50 -6 48	24258†	6.97
R	Precentral Gyrus	6	54 0 38	620	4.48
		6	54 4 20	Same cluster	3.37
R	Temporal Pole	48	54 6 0	Same cluster	2.87
R	Middle Temporal Gyrus	21	60 -22 -12	125	4.29
	Parietal				
R	Precuneus	23	16 -60 30	24258†	7.29
R	Inferior Parietal Lobule	40	46 -44 48	Same cluster	6.77
	Other				
L	Cerebellum	-	-34 -42 -42	31	2.97
			-42 -50 -44	Same cluster	2.85

†These regions are part of the same activation cluster

*Brodmann areas are approximate

Typicality effects

I contrasted atypical with typical IMAGINE trials, collapsing across set size, to determine what brain regions are more active when constructing an atypical event. There were no regions that survived the multiple comparisons correction. However, at a threshold of $p < .001$ and a minimum cluster size of 20 voxels, regions in the left dorsal anterior cingulate cortex and left cerebellum emerged.

Similarly, the reverse contrast comparing activity associated with typical vs. atypical events yielded no regions surviving multiple comparisons correction. However, at a threshold of

$p < .001$ and 20 voxels, one cluster in the right supramarginal gyrus showed increased activity when constructing typical events.

Table 6.3. Regions of increased activation comparing typical and atypical IMAGINE conditions. Peak of activation are denoted in MNI coordinates

Imagine Atypical vs. Imagine Typical

Hemisphere	Brain Region	BA*	MNI coordinates	Cluster Size	Z Score
			x, y, z		
	Frontal				
L	Anterior Cingulate Cortex	32	-6 18 48	66	3.52
	Other				
L	Cerebellum	-	-14 -86 -30	53	3.53

Imagine Typical vs. Imagine Atypical

Hemisphere	Brain Region	BA*	MNI coordinates	Cluster Size	Z Score
			x, y, z		
R	Supramarginal Gyrus	40	66 -32 32	68	3.61

*Brodmann areas are approximate

Set Size effects

Next, to investigate the effect of set size on neural activity during event construction, I contrasted IMAGINE trials with 4 items with trials containing 2 items, collapsing across typicality conditions. Regions with significant clusters included the left VLPFC, bilateral hippocampus, bilateral fusiform gyrus, right precuneus and lateral parietal cortices, as well as a large cluster of activity bilaterally in the visual cortex, with activity extending into the superior parietal lobes on the left. In addition, the left thalamus, right caudate nucleus, and right cerebellum were also more active when imagining events with 4 items.

The reverse contrast comparing imagining trials with 2 items vs. 4 items revealed significant clusters in the left anterior cingulate cortex, as well as bilateral activity in the supramarginal gyri, and left inferior parietal lobule. Additional activity was also found bilaterally in the insula and visual cortex (Table 6.4).

Table 6.4. Regions of increased activation comparing IMAGINE conditions at a set size of 4 and 2. Peak of activation are denoted in MNI coordinates

Imagine 4 vs. Imagine 2

Hemisphere	Brain Region	BA*	MNI coordinates	Cluster Size	Z Score
			x, y, z		
	Frontal				
L	Inferior Frontal Gyrus	44	-40 12 22	6792	5.65
L			-40 4 30	Same cluster	5.54
L			-40 20 20	Same cluster	5.5
	Temporal				
L	Hippocampus	27	-20 -30 -4	124	3.91
R	Hippocampus	37	24 -28 -6	26	3.11
R	Fusiform Gyrus	19	42 -64 -20	18	2.91
	Fusiform Gyrus	37	40 -42 -18	45	2.91
		37	46 -52 -14	Same cluster	2.79
	Parietal				
R	Angular Gyrus	7	28 -54 44	1414‡	5.55
R	Precuneus	23	8 -54 46	1414‡	3.17
	Occipital				
R	Middle Occipital Cortex	19	32 -66 28	1414‡	4.4
L	Inferior Occipital Gyrus	18	-20 -90 -6	4872	6.57
L			-30 -88 -8	Same cluster	6.54
L	Fusiform Gyrus	37	-42 -60 -12	Same cluster	6.43
R	Inferior Occipital Gyrus	18	20 -90 -2	658	5.95
R			30 -96 -6	Same cluster	4.68
R			36 -88 -10	Same cluster	3.67
R	Striate Cortex	17	12 -68 12	15	2.81
	Other				
L	Thalamus	-	-8 -14 2	215	3.58
			12 -18 16	Same cluster	3.08
			8 -12 0	Same cluster	3.05
L	Brain Stem	-	-2 -30 -4	77	3.39
R	Caudate	-	4 6 12	113	3.29
			6 8 20	Same cluster	3.19
R	Cerebellum		8 -72 -26	907	5.62
			10 -78 -36	Same cluster	5.5

R	Cerebellum	-	30 -66 -50	38	3.89
			-2 -54 -34	175	3.7
R	Cerebellum	-	0 -50 -18	12	2.73

Imagine 2 vs. Imagine 4

Hemisphere	Brain Region	BA*	MNI coordinates	Cluster Size	Z Score
	Frontal		x, y, z		
L	Anterior Cingulate Cortex	10	-4 50 8	194	4.37
L	Medial Orbitofrontal Cortex	10	-2 54 -4	Same cluster	3.52
	Temporal				
L	Insula	48	-44 -2 6	35	3.94
R	Insula	48	48 0 10	13	3.63
	Parietal				
R	Supramarginal Gyrus	48	58 -22 28	349	4.71
L	Supramarginal Gyrus	42	-58 -24 18	20	3.62
L	Inferior Parietal Lobule	40	-52 -54 44	25	3.68
L	Postcentral Gyrus	3	-20 -40 72	34	3.83
	Occipital				
L	Cuneus	18	-8 -76 34	175	4.35
R	Cuneus	19	12 -86 34	87	4.2
R	Lingual Gyrus	19	22 -62 -8	14	3.73

‡These regions are part of the same functional cluster
*Brodmann areas are approximate

6.3.2 Regions of Interest Analyses

Hippocampus

To provide an additional test of the contributions of the hippocampus to event construction, mean-level activity in the anterior and posterior hippocampi were analyzed in separate 3 x 2 repeated measures ANOVA with condition and set size as within-subjects variables. For the anterior hippocampus, there was a main effect of condition ($F(2,30) = 4.65$, $p < .05$), with increased activity in the IMAGINE conditions relative to the REORDER conditions. Post-hoc tests revealed no difference between the two imagining conditions ($p = .9$), no significantly increased activity when imagining atypical events compared to the control task ($p = .18$), and significantly increased activity when imagining typical events, compared to the control task ($p < .05$). There was no significant effect of set size, and no interaction (all *F*s < 1). Thus, it appears that the anterior hippocampi are implicated in event construction in general, irrespective of set size or the typicality of the events.

Conversely, the posterior hippocampi showed a significant effect of set size ($F(1,30) = 4.63$, $p < .05$), with increased activity when processing 4 items compared to 2 items. Neither the effect of condition, nor the interaction, was significant (all *F*s < 1). Thus, the posterior hippocampal regions seem to be sensitive to the amount of information, irrespective of task demands (Figure 6.6).

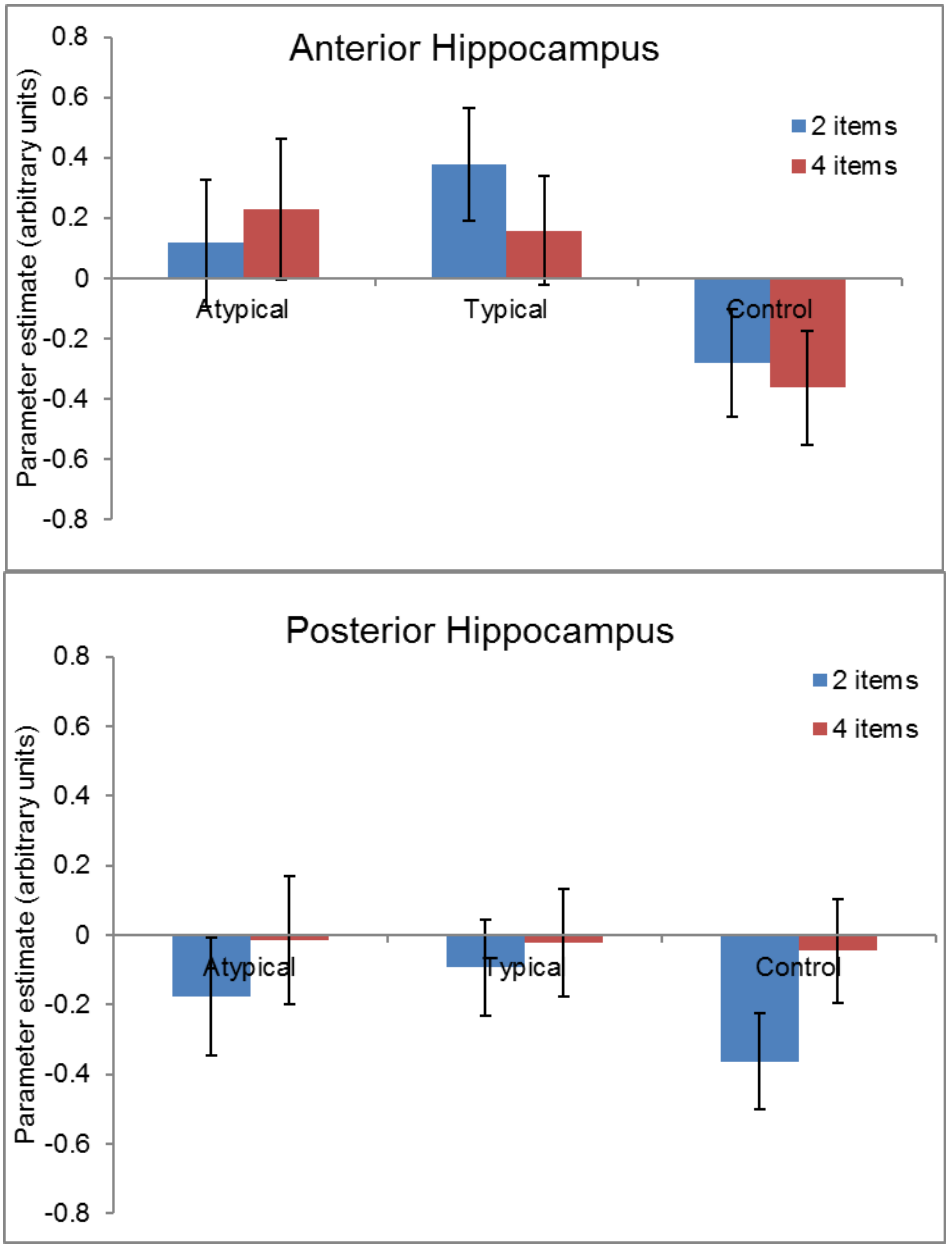

Figure 6.6. Mean level activity from the bilateral anterior and posterior hippocampus for all task conditions.

Frontal Poles

The medial and lateral frontal poles were separately submitted to similar ANOVAs. For the medial frontal poles, there was a significant effect of condition ($F(2,30) = 17.17$, $p < .001$), with increased activity in the IMAGINE conditions compared to the REORDER conditions. Tests of simple effects revealed that activity in the medial frontal poles for atypical and typical events did not differ significantly ($p = .96$), whereas activity was higher when imagining atypical events compared to the control task ($p < .005$), and activity for typical events was also higher compared to the control task ($p < .005$). In addition, there was a significant effect of set size ($F(1,30) = 19.92$, $p < .001$), and a significant interaction ($F(2,30) = 10.49$, $p < .001$). Inspection of Figure 6.7 shows the effect of set size being driven largely by increased activity at a set size of 2 compared to 4 in the REORDER condition and the typical IMAGINE condition. For the interaction, post-hoc tests indicated that at a set size of 2, the atypical and typical conditions did not differ from each other ($p = .89$), whereas activity was greater for the atypical condition compared to the control condition ($p = .06$), and activity was greater for the typical condition compared to the control condition ($p < .01$). At a set size of 4, activity during the atypical conditions was higher than the typical condition ($p < .05$), and activity was greater for the atypical condition compared to the control condition ($p < .005$.

Conversely, the lateral frontal poles showed a marginally significant effect of condition, ($F(2,30) = 2.78$, $p = .078$), with greater activity in the REORDER condition, relative to both IMAGINE conditions. The main effect of set size was not significant ($F < 1$). However, the interaction was significant ($F(2,30) = 6.11$, $p < .01$). Post-hoc tests revealed that no conditions were significantly different at a set size of 2: however, at a set size of 4, the control condition showed greater activity, compared to either the atypical ($p = .06$) or typical ($p < .05$) conditions (Figure 6.7).

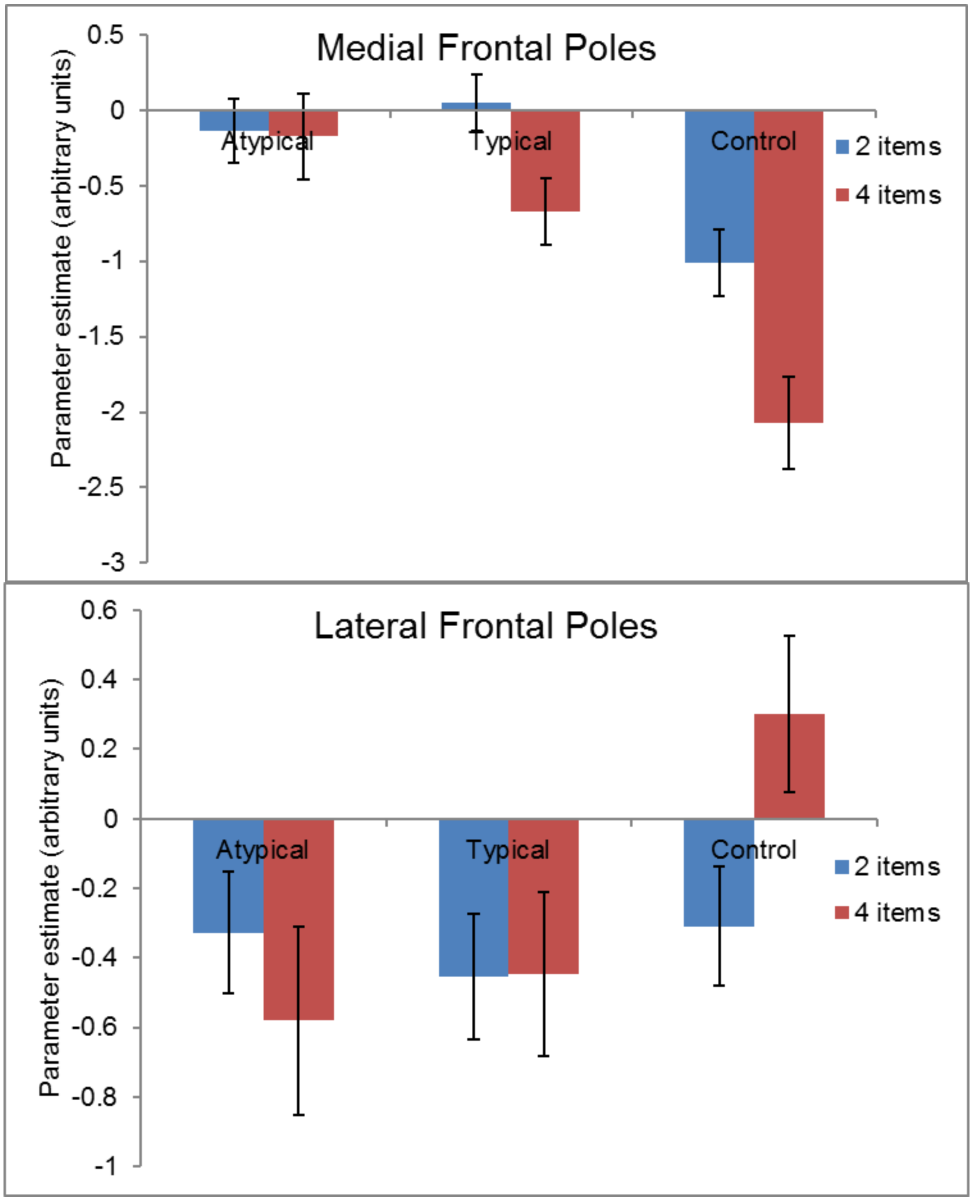

Figure 6.7. Mean level activity from the bilateral medial and lateral frontal poles for all task conditions.

6.3.3 Subsequent Memory

To examine regions showing a subsequent memory effect, I compared trials where at least one item word was recalled to trials where no words were recalled, collapsing across typicality conditions. In terms of subsequent memory effects, no regions showed increased activity when correcting for multiple comparisons. At a threshold of $p < .005$, 10 voxels, significant activity was found in a small cluster in the left supplementary motor area. Similarly, the reverse contrast of forgotten – remembered trials yielded one cluster in the left middle frontal gyrus, at a similar statistical threshold. Neither the contrasts comparing typical and atypical remembered trials yielded any regions showing significant activity, even at a liberal threshold of $p < .01$, 10 voxels.

One reason for the lack of effects may have been the low number of trials per condition: on average, subjects successfully recalled 8 trials per condition, which was likely an insufficient number of trials to have the statistical power needed for fMRI. To further examine subsequent memory effects, I re-analyzed the data by collapsing across all conditions to create a model with only 2 regressors, remembered and forgotten trials. Comparing increased activity during remembered vs. forgotten trials, there were significant clusters in the left posterior hippocampus, left inferior temporal cortex, right middle temporal gyrus including the temporal pole, and right fusiform gyrus, at a threshold of $p < .001$, 20 voxels, (Table 6.5).

The reverse contrast comparing increased activity for forgotten trials vs. remembered trials yielded a significant cluster in the left DLPFC at a similar statistical threshold (Table 6.5).

Table 6.5. Regions of increased activation comparing subsequently remembered and forgotten IMAGINE conditions. Peak of activation are denoted in MNI coordinates

Remembered - Forgotten

Hemisphere	Brain Region	BA*	MNI coordinates	Cluster Size	Z Score
	<u>Temporal Lobe</u>		x, y, z		
R	Temporal Pole	21	62 -2 -24	14	3.53
R	Middle Temporal Gyrus	37	52 -66 12	31	3.41
R			46 -68 22	same cluster	2.72
R	Fusiform Gyrus	20	40 -28 -18	15	3.24
L	Hippocampus	20	-32 -30 -6	49	3.17
L			-26 -36 0	same cluster	2.93
R	Inferior temporal cortex	37	36 -34 -14	same cluster	2.91

Forgotten - Remembered

Hemisphere	Brain Region	BA*	MNI coordinates	Cluster Size	Z Score

	Frontal Lobe		x, y, z		
L	Middle Frontal Gyrus	46	-24 44 28	61	4.99

*Brodmann areas are approximate

6.3.4 Brain-Behaviour Correlations

To obtain a more complete view of the association between brain activity and different aspects of task performance, three separate Behavioural PLS analyses were conducted using mean relational coherence scores, ratings of typicality, and ratings of remindingness. These analyses extract latent variables that maximize the correlation between behavioural measures and brain activity, thus revealing a network of brain regions that are coactive (i.e. functionally connected) as a function of task performance. Brain regions were considered reliably active if they had a cluster size of 10 contiguous voxels with a bootstrap ratio (BSR) of +/- 3.5, corresponding to a probability of $p < .0005$.

Relational Coherence

The analysis yielded one latent variable that accounted for 48% of the variation in brain activity and task performance, across subjects. Put differently, the latent variable represented brain networks associated with variation in task performance, regardless of whether subjects imagined atypical or typical events, using 2 or 4 item words (Appendix 5).

Brain regions positively associated with relational coherence are shown in blue, whereas regions negatively associated are shown in yellow. Notably, bilateral anterior hippocampal activity during early phases of the task (4 – 8s post stimulus onset) were associated with increased task performance across subjects, suggesting that subjects who made more inter-item relations activated the anterior hippocampi to a larger extent than subjects whose performance was poorer (Figure 6.8). Other regions positively correlated with the number of relations include the bilateral VLPFC, DLPFC, dorsomedial prefrontal cortex, and posterior cingulate cortex/precuneus (see Appendix 6 for whole brain activation and Appendix 7 for a list of peak activations over time).

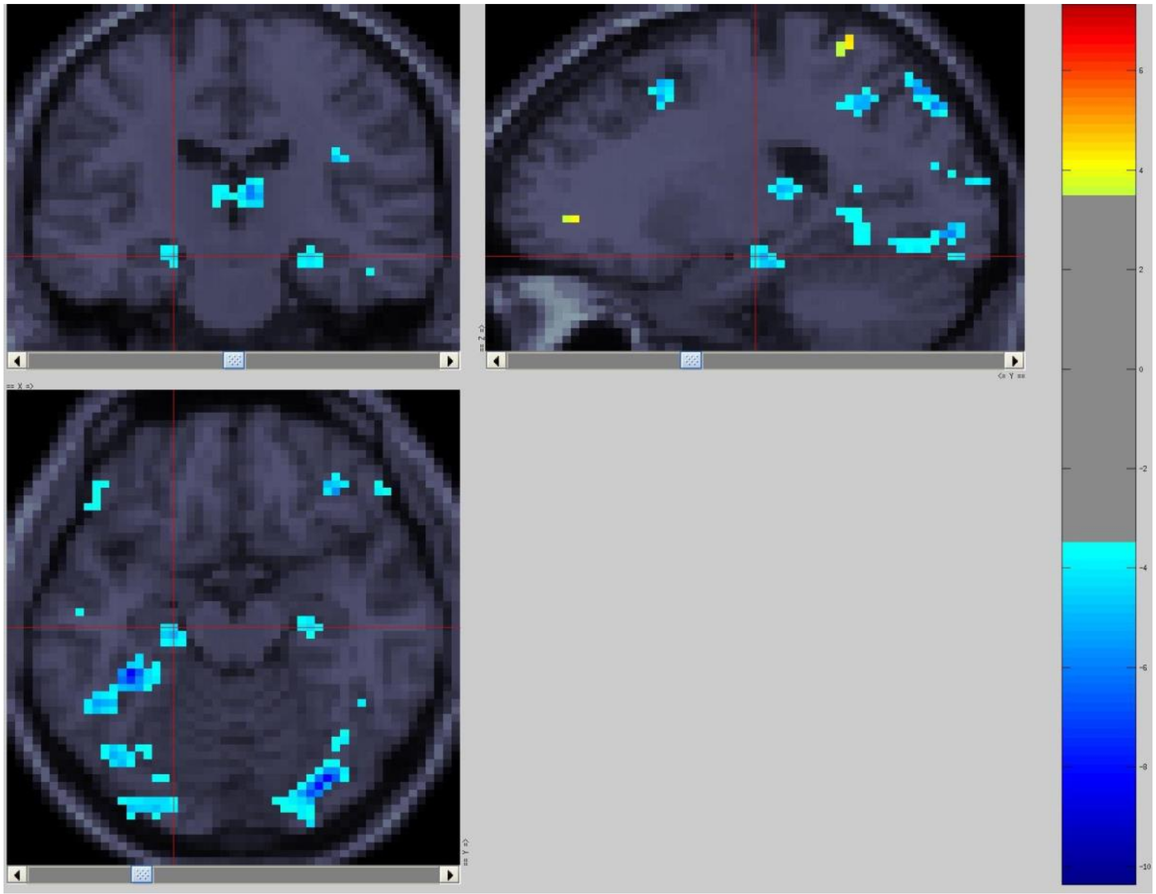

Figure 6.8. Increased bilateral hippocampal activity at TR 2 (4 – 6 s post-stimulus onset) positively associated with individual differences in the number of relations formed/trial across all conditions. Brain regions positively associated with task performance are shown in blue, whereas regions negatively associated with performance are shown in yellow

Regions associated with poorer task performance appeared later in the trial (8 – 12 s), and included the ventromedial prefrontal cortex, precuneus, and left parahippocampal gyrus. Activity in these regions was most robust during the last 2 seconds of the task (Figure 6.9).

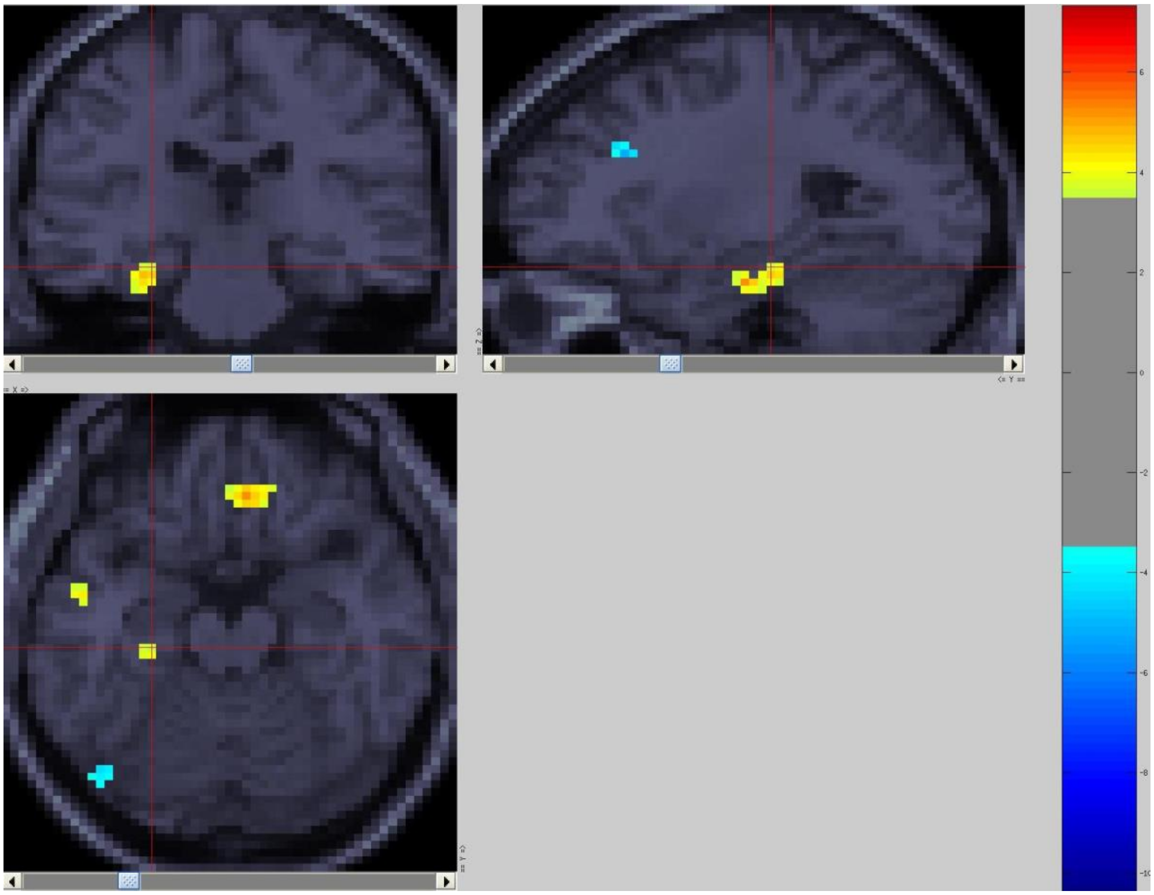

Figure 6.9. Brain regions at TR 5 (10 – 12 s post-stimulus onset) negatively associated with individual differences in the number of relations formed/trial across all conditions. Brain regions positively associated with task performance are shown in blue, whereas regions negatively associated with performance are shown in yellow

Ancillary analysis: posterior hippocampus and relational coherence

The previous behavioural PLS analysis showed only anterior hippocampal involvement with coherence scores across subjects. To determine whether the posterior hippocampus is functionally coactive with the anterior hippocampus and other brain regions during event construction, an additional behavioural PLS was run using relational coherence scores and brain activity from a seed in the left posterior hippocampus (coordinates = -20 -18 4, from peak activation in the comparison of IMAGINE 4 vs. 2). This analysis reveals what brain regions are maximally associated with relational coherence and/or posterior hippocampus, across all IMAGINE conditions. The PLS extracted 2 significant LVs, accounting for 53% and 14% of the variance, respectively. The first LV showed a correlation between a large cluster of the hippocampus, bilateral lateral prefrontal cortex, and medial and superior parietal cortices (Figure 6.11). However, this network was not correlated with relational coherence scores (Figure 6.10) (activation peaks in Appendix 8).

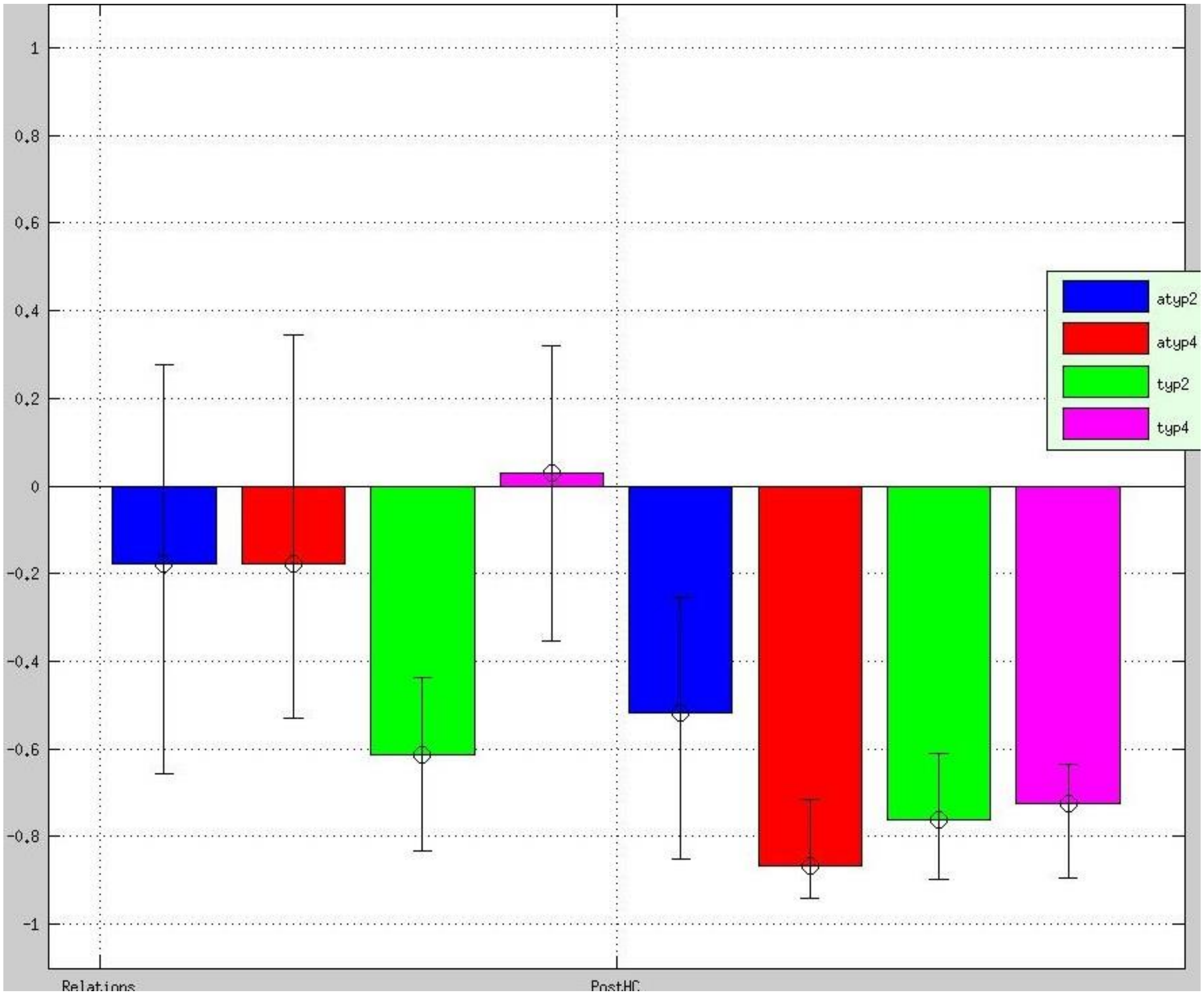

Figure 6.10. *Correlation plots showing the correlation between posterior hippocampal activity, relational coherence scores, and brain activity, for the first significant latent variable. Bars on the left half show correlations between relational coherence scores and brain activity, and bars on the right half show correlations between posterior hippocampal activity and brain activity. The functional network is strongly associated with posterior hippocampal activity in all*

IMAGINE conditions, whereas it is only associated with relational coherence scores in the typical 2 condition.

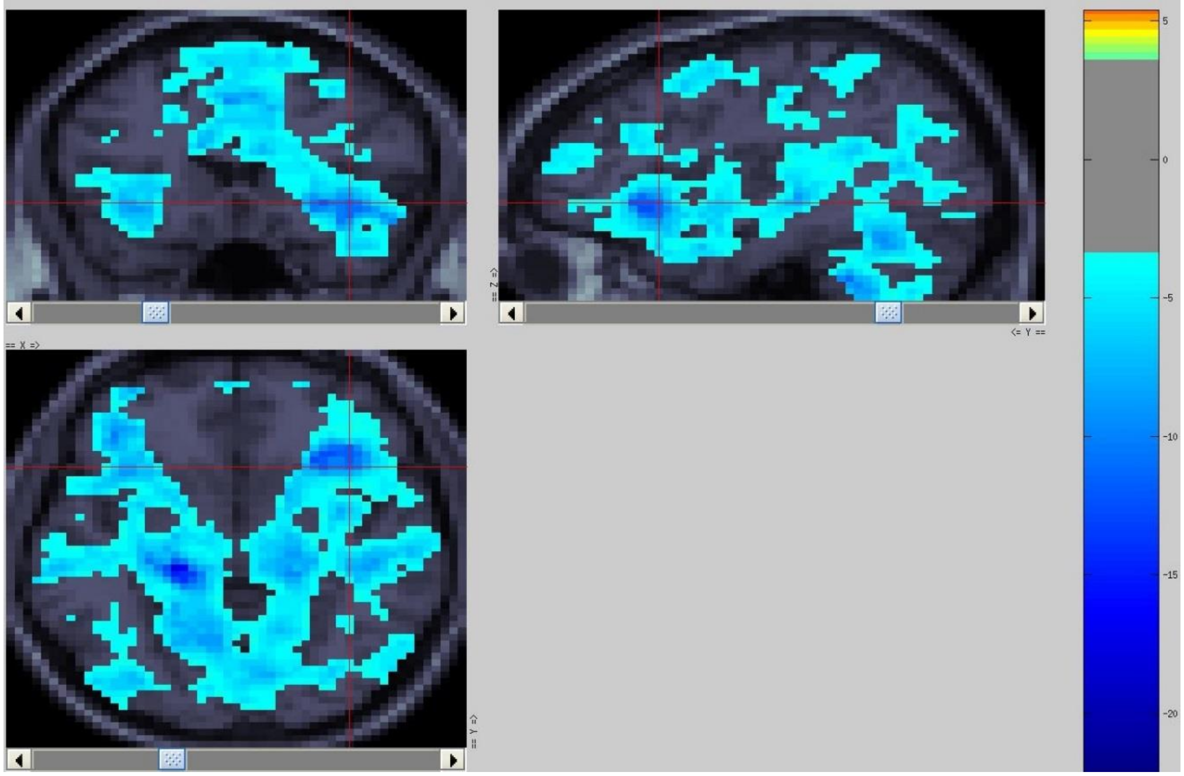

Figure 6.11. Brain regions at TR 3 (6 – 8s post stimulus) functionally connected with the posterior hippocampal seed across all IMAGINE task conditions. Regions co-active with the seed are shown in blue.

Conversely, the second LV extracted a network that was positively associated with relational coherence scores, but not with posterior hippocampal activity (Figure 6.12). This network was very similar to the network from the behavioural PLS on relational coherence scores, showing an association between task performance, anterior hippocampus, lateral temporal cortices, and precuneus (Figure 6.13).

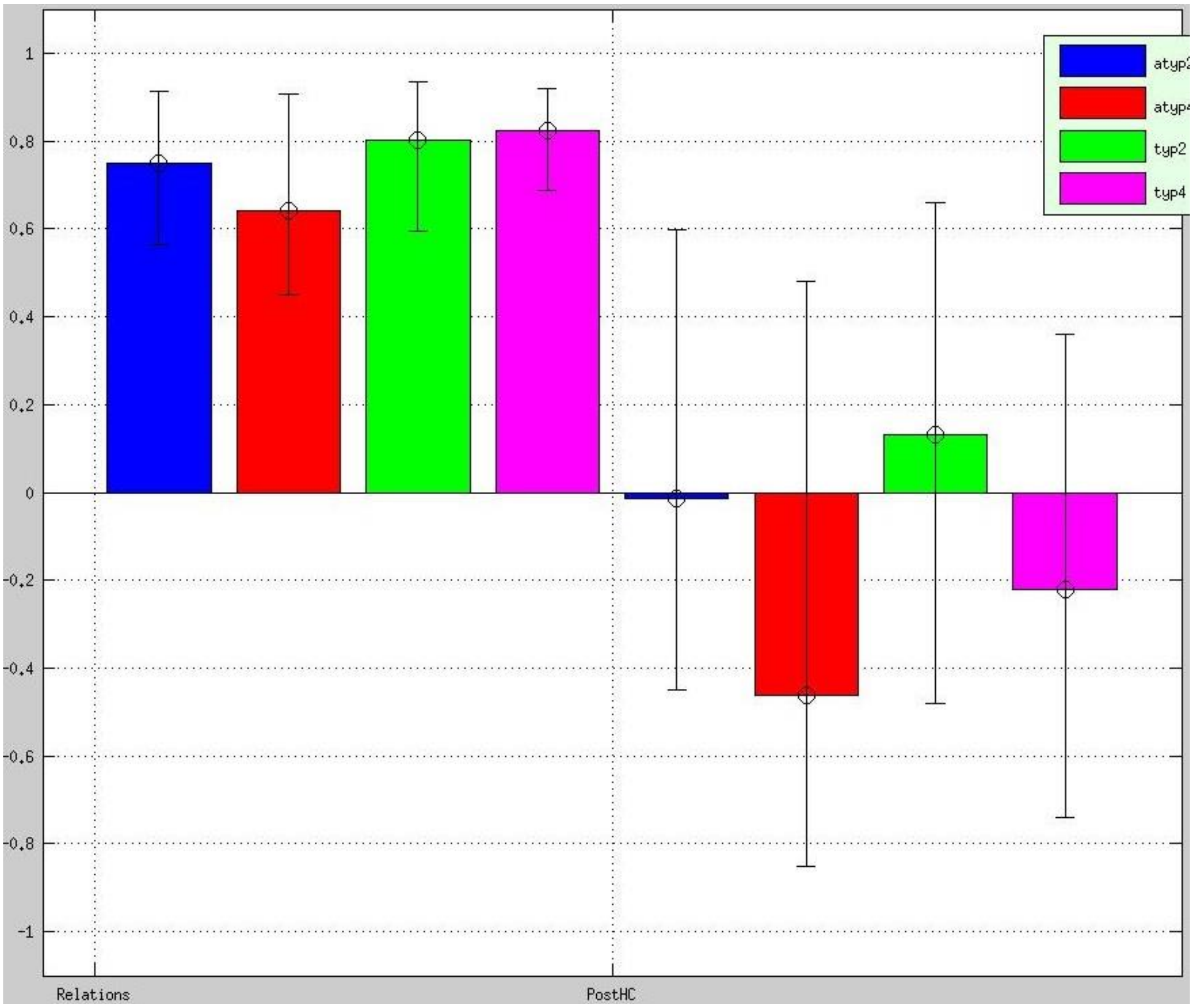

Figure 6.12. Correlation plots showing the correlation between posterior hippocampal activity, relational coherence scores, and brain activity, for the second significant latent variable. Bars on the left half show correlations between relational coherence scores and brain activity, and bars on the right half show correlations between posterior hippocampal activity and brain activity. This functional network is strongly associated with relational coherence scores in all conditions, but is not correlated with posterior hippocampal activity in any condition.

Thus, although the posterior hippocampus was associated with a functional network during IMAGINE trials, this network is not correlated with the anterior hippocampal network associated with coherence scores, suggesting it is associated with other aspects of the task.

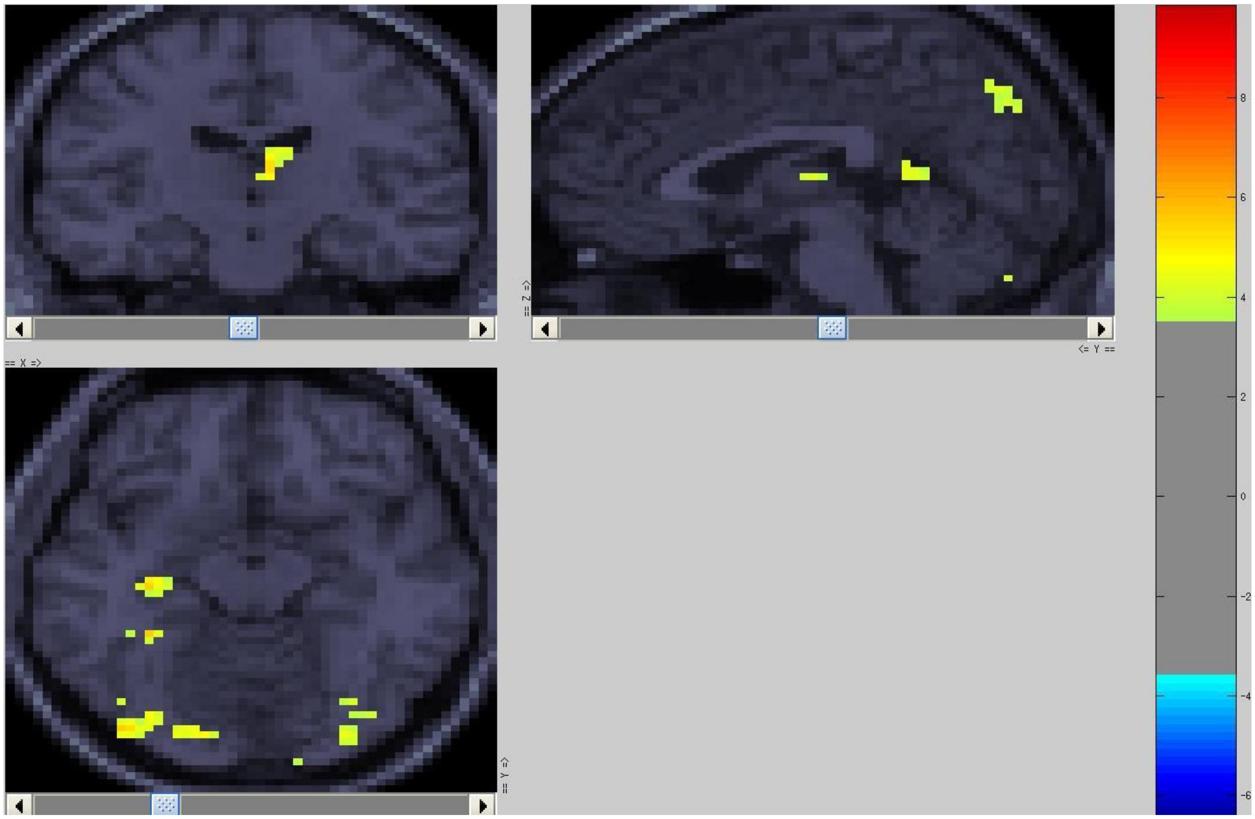

Figure 6.13. Increased left hippocampal activity at TR 1 (2 – 4 s post-stimulus onset) positively associated with relational coherence scores across all conditions. Brain regions positively associated with coherence scores are shown in yellow, whereas regions negatively associated with performance are shown in blue.

Typicality

Next, a behavioural PLS was conducted using typicality scores as the behavioural correlate of brain activity. One LV was significant, accounting for 48% of the variance across subjects, which was similar across conditions: thus, it represented the association between subjects' ratings of typicality and brain activity, irrespective of the typicality condition that was defined by the experimenter. Brain regions positively associated with typicality ratings are shown in blue, whereas regions negatively associated with ratings are shown in yellow. Activity associated with higher typicality scores was most prominent 2- 4 s post-stimulus and occurred in the right parahippocampal gyrus, as well as bilateral lateral temporal cortex, right medial frontal pole, bilateral VLPFC, and bilateral lateral frontopolar cortex, (Figure 6.14) (activation peaks in Appendix 9).

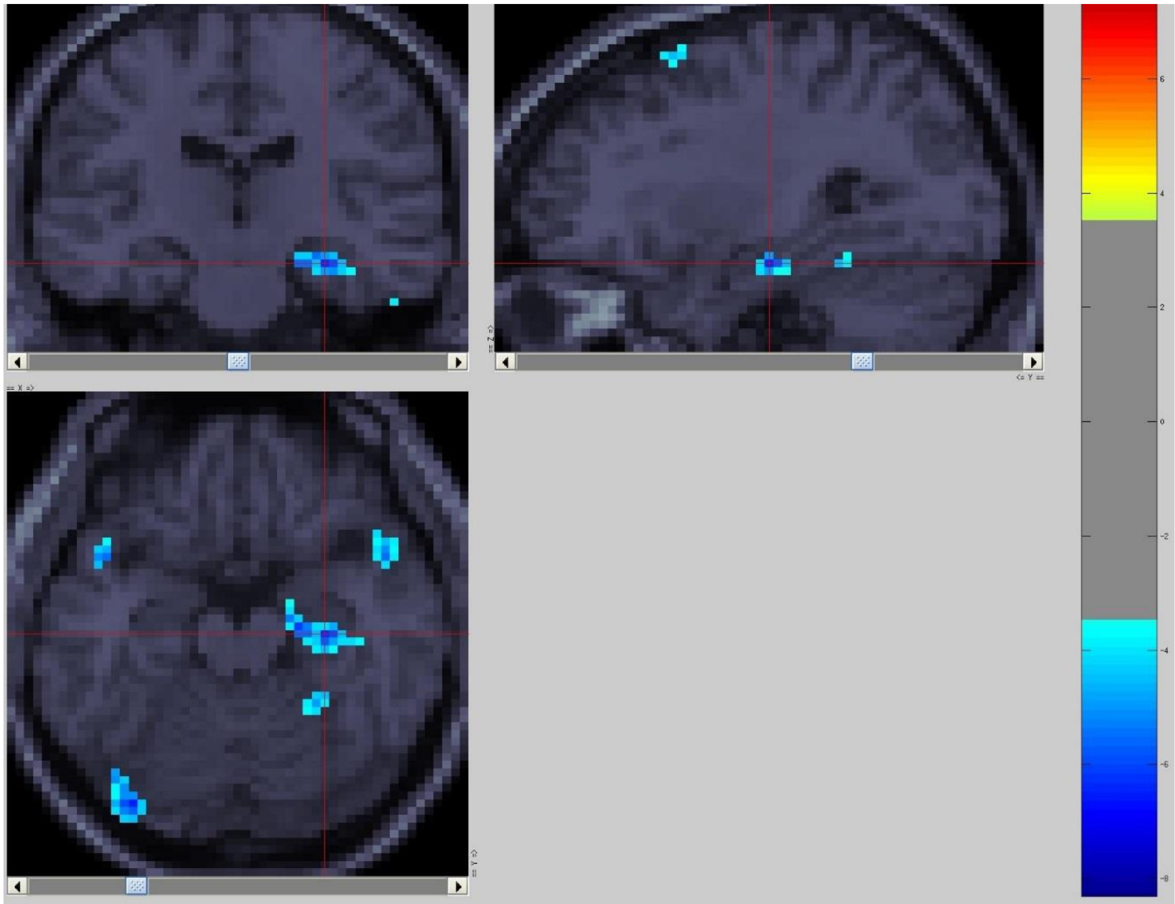

Figure 6.14. Brain regions at TR 1 (2 - 4 s post-stimulus onset) positively associated with individual differences in typicality scores across all conditions. Brain regions positively associated with typicality are shown in blue, whereas regions negatively associated with typicality are shown in yellow

Remindingness

The behavioural PLS using each subject’s mean remindingness ratings yielded one significant LV, accounting for 44% of the variance across subjects, which was similar across conditions: thus, it represented the association between how much an event reminded subjects of a previous memory and brain activity, regardless of typicality or set size. Unexpectedly, lower remindingness ratings were associated with early activity in the left posterior hippocampus, bilateral lateral prefrontal cortex, the left lateral frontopolar cortex, and bilateral inferior parietal lobules (Figure 6.15).

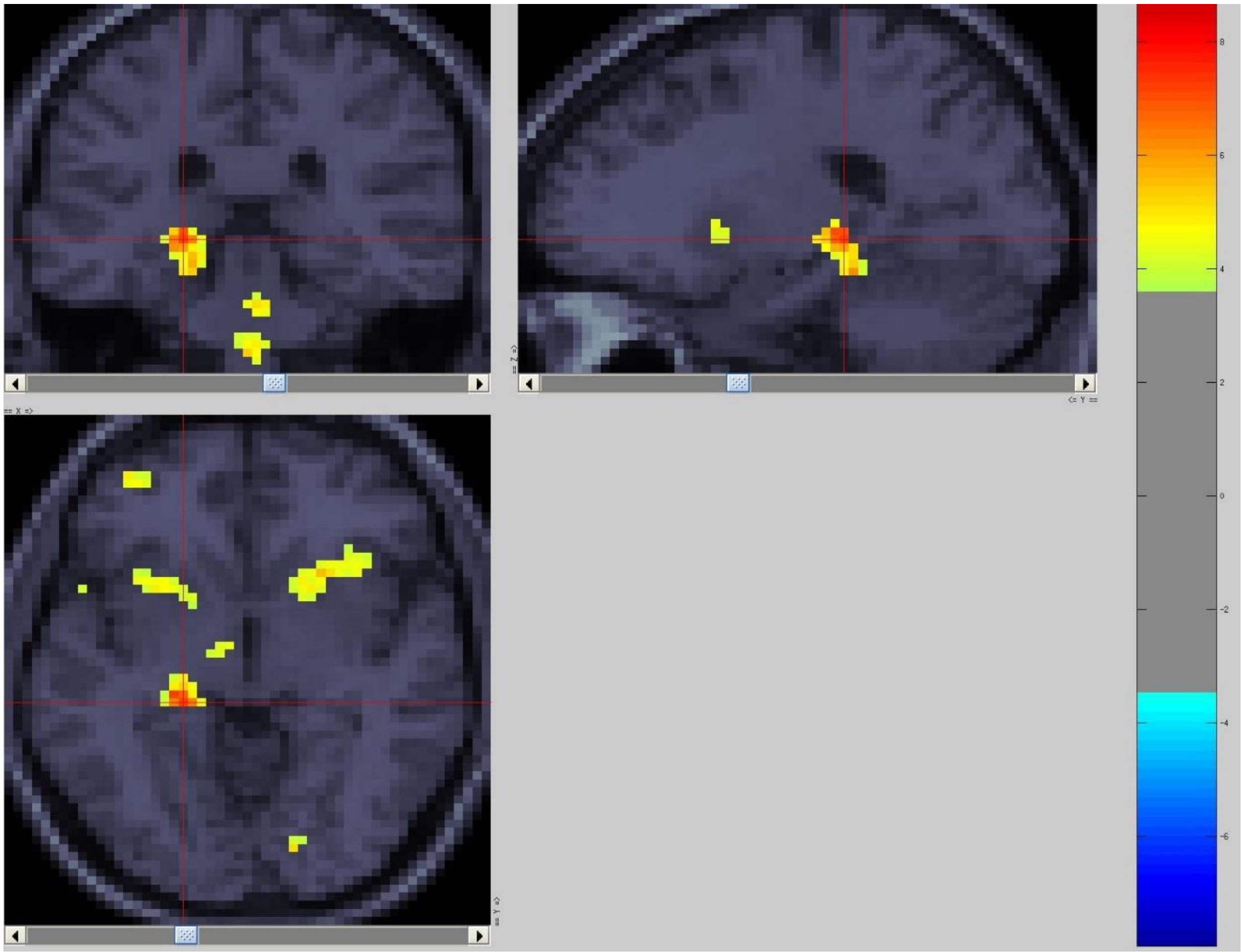

Figure 6.15. Brain regions at TR 2 (4 - 8 s post-stimulus onset) negatively associated with individual differences in remindingness scores across all conditions. Brain regions positively associated with remindingness are shown in yellow, whereas regions negatively associated with remindingness are shown in blue

6.4 Discussion

In the present experiment, engaging in event construction for non-personal novel events activated regions commonly associated with simulation of personal future events, including the anterior hippocampus, parahippocampal gyrus, posterior cingulate cortex, lateral parietal regions, and medial prefrontal cortex, including the medial frontal poles. However, there were also regions that displayed differential activity depending on task demands, providing new insight into the contributions of specific brain regions during imagining novel events.

Event Construction: Hippocampus

The current paradigm provided the items required for the initial construction, effectively decreasing retrieval demands: thus, activity during the task can be attributed largely to processes engaged during event construction (Addis et al., 2009; Martin et al., 2011). The results from both the whole brain analysis and the ROI analysis indicated the anterior hippocampi were responsive only to construction task demands, and not to mnemonic load or the semantic relatedness of the items, suggesting a role for event construction in general. Although all the precise functions of the anterior hippocampus have not been fully characterized, anterior hippocampal activity is also found when encountering novel information (Köhler, Danckert, Gati, & Menon, 2005; Poppenk et al., 2010; Poppenk and Moscovitch, 2010), encoding overlapping associative information (Shohamy & Wagner, 2008; Wimmer & Shohamy, 2012; Zeithamova, Schlichting, & Preston, 2012), and encoding the general gist of new information (Poppenk, Evensmoen, Moscovitch, & Nadel, 2013). With respect to imagining novel events, when stimuli are present in conscious awareness, either through perception or active retrieval from LTM, the resultant mental representation that is formed is a novel event with high associative memory demands, thus likely implicating the anterior hippocampus regardless of the nature of the stimuli.

Moreover, the behavioural PLS analyses provided complementary evidence to support the role of the anterior hippocampi in event construction. Crucially, activity in these regions was positively associated with task performance, implying they were directly associated with how well events are constructed. Thus, for event construction, the ability to bind items together in conscious awareness requires the hippocampus.

Event Construction: medial frontal poles

Some studies showed that activity in the medial frontal regions is most strongly associated with mentalizing tasks, which involves considering oneself or another, suggesting this region is implicated in some common aspect of event construction (Amodio & Frith, 2006; Andrews-Hanna, 2012; Burgess et al., 2006). However, in other paradigms, medial frontal pole activation increases when imagining oneself in a familiar vs. unfamiliar context (Szpunar et al., 2009), and increases with the semantic relatedness of the items (Green et al., 2010; Raposo et al., 2011), suggesting its role in event construction may be sensitive to typicality. Indeed, in our study, the behvaioural PLS analysis showed that higher ratings of typicality across subjects was associated with greater medial frontopolar activity early in the construction phase (i.e. 2 – 4 s post-stimulus onset).

There are several possible explanations for this effect: One possibility is that medial frontal pole activity is driven by self-related processing (Craik et al., 1999). However, whereas previous studies used self-relevant task instructions or stimuli, the present paradigm used common words, and instructed subjects to construct generic mental representations with imageable words, thus encouraging construction of less-personal events. Indeed, ratings of whether the events reminded subjects of a personal memory were at most 2.5 on a 4-point scale, suggesting the events were not particularly self-referential. Moreover, the behavioural PLS analysis on ratings of remindingness did not show any medial frontal pole activity that tracked with subjective ratings of remindingness. Thus, to the extent that subjects were actually constructing events with the stimuli, and their subjective ratings were accurate, these findings suggest the medial frontal poles are also involved in simulation of more personally-detached mental representations, in addition to highly self-referential simulations.

Another related possibility is that this region is involved in the representation or reflection upon mental states. This region has been implicated in constructing personal future events (A. D'Argembeau et al., 2010; Northoff et al., 2006), thinking about a close person (Mitchell, 2009), inferring the intentions of another (Amodio & Frith, 2006), or reasoning about a past autobiographical experience or social dilemma (A. D'Argembeau et al., 2013; Van Overwalle, 2009). Andrews-Hanna (2012) suggested a core 'mentalizing' network during future simulation, including the dorsomedial prefrontal cortex, lateral temporal cortex, and lateral parietal lobes, all regions active during the event construction conditions.

Specifically, the region of the medial frontopolar cortex that was active in this study may be important for simulating more general, schematic events. The behavioural PLS analysis on subjective typicality ratings showed greater activity associated with higher ratings of typicality, further suggesting a role in the simulation of more generic events. Indeed, in a recent meta-analysis, Denny, Kober, Wager, & Ochsner (2012) found that although medial prefrontal activity is prominent on tasks involving self- or other-related processing, a dorsal-ventral gradient exists for peaks of activation, with more ventral areas being preferentially implicated during self-related processing, and more dorsal regions being implicated with other-related processing. The medial frontopolar peak in the whole brain analysis was relatively dorsal, suggesting that activation in this region may reflect simulation of less self-referential mental representations.

Typicality Effects

In terms of the typicality of imagined events, typical events showed a performance advantage, as evidenced by faster completion times, and better subsequent memory. In addition, subjective ratings suggested that events in the typical condition were indeed more typical than the events in the atypical condition, replicating findings from Experiment 3b. However, the main effect of typicality was smaller, only trending towards significance, whereas in Experiment 3b the conditions were significant. Similarly, there was only a small difference between conditions in terms of the neural response: the only region showing increased activity in the atypical condition was the dorsal anterior cingulate (dACC), at a lower statistical threshold. There is a considerable literature suggesting the anterior cingulate cortex is implicated in cognitive control in general, particularly the dorsal portion (Carter & van Veen, 2007). Specifically, several processes have been associated with dACC activity, most notably conflict monitoring. In addition, anterior cingulate activity is also observed when comparing future simulation conditions to autobiographical recall, when comparing event construction to event elaboration, and when comparing imagining specific vs. general events (Addis et al., 2007; 2011).

Consequently, it is difficult to determine the precise contribution of the dACC in the present study. One may speculate that due to the nature of the task, increased dACC activity could represent conflict monitoring demands: that is, viewing a context being paired with unrelated items triggers activation of a conflict response, which serves to correct behavior on a trial-by-trial basis (Sheth et al., 2012). Such a process would result in decreased completion times, consistent with the behavioural findings. A related possibility is that such activity reflects the undetermined nature of the atypical condition: whereas typical trials are more easily constructed based on pre-existing knowledge, the construction of unrelated items is more open-ended. Anterior cingulate activity is also associated with more open-ended response conditions, such as verb generation (Thompson-Schill, D’Esposito, Aguirre, & Farah, 1997). Future studies will need to tease apart these potential factors to identify the contribution of dACC to future simulation.

It is worth noting that dACC activity was only apparent at a lower threshold, suggesting that imagining typical and atypical events have more similarities than differences in terms of the implicated brain regions. Indeed, both the behavioural and neural responses to the manipulation of typicality were not as large as the effects of set size. This may have been due to the nature of the event construction task, which required subjects always to construct new scenarios, using stimuli not taken directly from personal past episodes: consequently, nearly all of the imagined scenarios shared little with subjects' previous experiences, as evident by their subjective ratings.

Although this typicality contrast did not yield significant effects, typicality effects did emerge when using individual differences in typicality ratings, rather than pre-defined discrete conditions. Interestingly, the behavioural PLS analysis using typicality ratings painted a different picture: subjects who rated the stimuli as more typical showed increased early activity in the right parahippocampal cortex, bilateral lateral temporal cortex, and medial and lateral frontopolar cortex. Given the well-established role of the parahippocampal cortex in contextual processing (Aminoff, Kveraga, & Bar, 2013), and the established role of the lateral temporal cortex in semantic memory (Hodges & Patterson, 2007; Irish, Piguet, & Hodges, 2011), one plausible explanation is that these regions were implicated in the retrieval of prior semantic contexts. That is, those subjects who perceived the stimuli as fairly typical were more likely to retrieve a pre-existing contextual schema to aid in the construction task, compared to subjects who perceived the stimuli as atypical. Such an account is also consistent with the role of the parahippocampal cortex and medial frontal poles in future simulation of familiar events (Szpunar et al., 2008), and with the behavioural findings of facilitated performance for typical trials compared to atypical trials.

Set Size Effects

Increasing mnemonic load resulted in increased activity in several brain regions. Most relevant to the present study, activity in the posterior hippocampus was greater when constructing events with 4 items, as compared to 2 items. This was apparent both during the whole brain analysis, and during the ROI analysis. Previous reports of future simulation show that posterior hippocampus activity increases parametrically with the amount of detail of future events (Addis & Schacter, 2008). However, examination of the ROI effects revealed that the posterior hippocampus shows similar differential activity with set size in the control condition, which did not involve any imagining. Thus, it would appear that activity in this region was sensitive to the amount of information being manipulated or held in memory, regardless of the nature of the task.

Although not traditionally thought to be crucial for working memory, the posterior hippocampus is implicated for some working memory tasks, particularly those involving complex or novel stimuli (Ezzyat & Olson, 2008; Hannula et al., 2006; Olson et al., 2006). The most convincing evidence comes from intracerebral EEG recordings in the hippocampi of patients with epilepsy, while they completed a Sternberg short term memory task and a later subsequent memory test (Axmacher, Elger, & Fell, 2009; Axmacher, Schmitz, Weinreich, Elger, & Fell, 2008). Items that were later remembered during a long-term memory test showed increased hippocampal activity during the maintenance phase of the short-term memory task, whereas forgotten items did not. This suggests that the posterior hippocampus is implicated in processing information online, either through temporarily maintaining the information, or forming associations between items.

Also, the behavioural PLS analysis using posterior hippocampal activity and relational coherence scores yielded two different functional networks, one that was associated more with relational coherence scores and the anterior hippocampus, and the other correlating largely with posterior hippocampal activity. This further suggests that posterior hippocampal activity is implicated in another aspect of the task, but not in event construction per se.

Subsequent memory

Collapsing across conditions, subsequently remembered trials showed increased activity in posterior hippocampus, compared to forgotten trials. Although early fMRI studies of subsequent memory effects suggested successful encoding was associated with anterior hippocampal activity, the results have not always been consistent (Kim, 2011; Poppenk et al., 2013). For example Park & Rugg (2011) compared successful encoding related activity for within- and across-domain pairs, and found posterior hippocampal activity for remembered pairs, regardless of the stimulus modality. Poppenk et al. (2011) also found posterior hippocampal activity at encoding predicted subsequent memory. In terms of future simulation, Martin et al. (2011) found that subsequent memory of imagined events seems to depend on both the posterior and anterior hippocampal regions, whereas imagining future events implicates the anterior hippocampus only. This, along with the present findings, would suggest that the posterior hippocampal activity at encoding may be more important for subsequently remembering imagined events.

Remindingness

Low ratings of remindingness were associated with functional network including the left posterior hippocampus, bilateral lateral PFC, and bilateral inferior parietal lobules. The average ratings of remindingness were moderate, only reaching an average of 2.38 on a 4-point scale, suggesting the stimuli were skewed towards being more novel, in line with the purpose of the paradigm. Moreover, subjects were explicitly instructed to imagine a new event, not to base one on previous experience. Consequently, these ratings likely reflect a measure of novelty. Thus, the identified functional network may reflect incidental encoding of novel details, which would be consistent with the role during working memory for novel stimuli (Hannula & Ranganath, 2008; Rose et al., 2012).

These results, along with the set size and subsequent memory effects, suggest that during event construction, the posterior hippocampus may encode additional incidental details, which do not necessarily relate to task performance, but would increase the likelihood of remembering the event subsequently. Such details may include the product of the event construction, and/or any incidental, peripheral details that were not central to the task (i.e. additional contextual information, spontaneous thoughts).

Summary

Constructing a novel mental representation recruited a common network of regions, including medial prefrontal cortex, lateral prefrontal cortex, medial and lateral parietal regions, lateral temporal regions, and anterior hippocampus. Posterior hippocampus showed increased activity with increasing mnemonic load, but was not functionally connected to the functional network involved in event construction. Moreover, posterior hippocampal activity was associated with low remindingness scores, and with subsequent memory of the items, suggesting it may be implicated in task-irrelevant encoding of details. Individual differences in typicality ratings were positively associated with parahippocampal and lateral temporal cortices, as well as medial frontal poles. Thus, the results reflect a nuanced role for the hippocampus in the construction of novel events, a core set of regions implicated in simulating novel representations, and other functional networks corresponding to different aspects of the constructed events.

7 General Discussion

The purpose of the present study was to explore the mechanisms underlying the construction of imagined events, in terms of the factors that moderate event construction performance, and the associated neural correlates. Specifically, I sought to determine the extent to which changes in memory ability also affect event construction performance, whether mnemonic load and the semantic relatedness of items (i.e. typicality) affect task performance, and whether the hippocampus and frontal poles are sensitive to such manipulations. To this end, I used a novel paradigm wherein subjects were presented with a written context and several items, which were to be constructed into a novel event by relating the items as much as possible to the context and to each other. The number of explicitly-mentioned inter-item relations was taken as an objective metric of task performance.

In Experiment 1, younger and older adults were compared on the event construction task, while also manipulating set size (3 – 6 items). Older adults produced fewer relations than did younger adults, becoming significant at a set size of 5. Similarly, older adults were also more prone to omit item words from their descriptions, becoming apparent at a set size of 5. Interestingly, within older adults, individual differences in the number of relations formed was positively correlated with a classic measure of LTM (logical memory), but not with simple working memory span. Older adults also showed worse cued recall of the items, both in terms of the total number of recalled words, and in terms of the proportion of bound words that were recalled. Within both age groups, task performance was positively associated with cued recall. These findings suggested that LTM-related processes were implicated in event construction, and that one’s ability to construct an imagined event affects the memory for that event subsequently.

In Experiment 2, a similar paradigm was used with amnesic patients with MTL lesions, to test the necessity of the hippocampus to event construction performance. Compared to controls, patients produced fewer relations, even at a set size of 3, and were more prone to omit items at a set size of 4, suggesting that the hippocampus is necessary to construct a novel event containing as few as 3 items. Nonetheless, the deficit in event construction was much less severe than the corresponding memory deficit for the constructed event, suggesting that extra-hippocampal structures can contribute more to event construction than to long-term memory formation and retention.

In Experiment 3a, I varied the typicality of item-context pairings, and tested whether typicality and set size affect task performance, and to what extent event construction relies on relational processing abilities or verbal fluency. Typical events showed a performance advantage over atypical events, in terms of the number of relations formed, completion times, and subjective ratings of coherence, detail, and difficulty. Moreover, the ability to form associations during event construction was correlated with relational reasoning ability, but not verbal fluency. Experiment 3b replicated the typicality and set size effects on task performance, and also showed that typical events are better recalled than atypical events, likely because the typical context serves as a more instructive cue for the items at retrieval.

Finally, in Experiment 4, I investigated the neural correlates of event construction using fMRI, again with the typicality and set size manipulations, focusing on the hippocampus and frontal poles. The anterior hippocampus was involved in event construction across all set sizes and typicality conditions, and was positively associated with individual differences in relational coherence scores. The posterior hippocampus showed a general effect of set size across task conditions, as well as modulation by low remindingness, and subsequent memory effects at a lower statistical threshold. The medial frontal poles were more active across all imagining conditions compared to the control conditions, and were modulated by subjective ratings of typicality, but not by experimental manipulations of typicality or set size. By contrast, the lateral frontal poles were only active in the control condition at a set size of 4. Collectively, event construction yielded activity in regions previously associated with future simulation, including medial prefrontal cortex, medial and lateral parietal cortex, and the medial temporal lobes, even using a novel paradigm and non-personally relevant stimuli.

When one tries to simulate a novel event, there is an additional constructive element beyond retrieving the relevant facts: as imagined events are novel, they must be pieced together from components in memory, in order to form a coherent mental representation in line with task demands. In the present study, I examined how such a process takes place by providing both the context and the elements which were to be constructed into a novel scenario, thus reducing retrieval demands from LTM. Across four experiments, various manipulations affected event construction performance, each revealing a facet of what occurs when complex mental representations are constructed.

7.1 Number of Items in Novel Mental Representations

Previous studies of future simulation have measured the amount of detail or quality of the representations by using open-ended stimuli, and having subjects produce or embellish as much as possible. Consequently, many of the findings have measured the amount of episodic-like or semantic information that is provided, rather than measuring how well subjects can construct an imagined event when provided with a certain amount of information. In the present set of studies, a key issue is at what mnemonic load does certain deficits or manipulations exert their effects on event construction, and what do these findings imply about the nature of the mental representation?

In Experiment 1, older adults showed poorer performance at a set size of 5, both in terms of the number of relations formed and the propensity to omit items. Similar effects in Experiment 2 were found at a lower set size in MTL lesion patients. These patterns suggest that for event construction, an initial representation can be successfully formed, but constructing increasingly complex representations is hampered by poor binding mechanisms. Notably, in Experiments 3a, 3b, and 4, subjective ratings of coherence were higher for events with 2 items compared to 4 items, and differences in the number of relations occurred only at a set size of 4, further suggesting that an initial representation can be successfully formed at lower set sizes: thus, deficits in event construction may occur with as few as 3 items (Experiment 2), and may be more apparent with increasing mnemonic load or decreasing typicality.

A related issue is how the present findings fit with notions of WM and LTM. In Experiments 1 and 2, performance was measured across set sizes of 3 - 6 items, which would conceivably span the distinction between WM and LTM, even at the highest estimates of WM capacity (Cowan, 2001). The notion of event construction performance depending preferentially on certain memory stores is not a useful one for several reasons. One obvious one is that the involvement of WM and LTM will depend on task demands, such as if the items presented exceed WM capacity, or if the information is amenable to chunking (Cowan, 2001; Miller, 1956). Moreover, the definition of WM capacity is also variable: Cowan (2001) describes four chunks or units as the key limit, whereas McElree (2006) defines the limit as one item, in which case any imagination task involving more than simple visual imagery of an object would implicate LTM. Finally, whereas distinctions between short term memory and LTM were born out of the resilience of the recency effect to experimental manipulation (Watkins, 1974), the same cannot be said for event construction: effects of typicality and memory impairment exerted effects across set sizes that fall within and outside estimates of WM capacity. Thus, without independent signatures of whether an item resides in WM or LTM, these issues will not likely be resolved.

7.2 Semantic Relatedness of Items in Novel Mental Representations

Although a useful distinction, it was always assumed that semantic and episodic memories were not completely independent, and may interact based on task demands (Greenberg

& Verfaellie, 2010; Tulving, 1972). Autobiographical memories are nested within varying semantic themes, corresponding to different periods of time in one's life (Conway & Pleydell-Pearce, 2000). Similarly, simulating novel events must also vary along a semantic continuum, particularly since imagined events are less constrained in that they have not occurred. Given that prior knowledge often benefits cognitive processing, it is possible that a similar effect would be found in event construction. Indeed, Experiments 3a, 3b, and 4 showed that behaviourally, constructing atypical events takes more time, is slightly more difficult, and results in fewer associations between items.

Data from Experiment 4 showed that subjects who rated the stimuli as more typical recruited regions consistent with retrieval of semantic context, namely, parahippocampal cortex, lateral temporal cortex, and medial frontal poles. Furthermore, the time course of the activation in these regions occurred in the very early period of the trial (2 - 4 s post stimulus), whereas hippocampal activity correlated with relational coherence became prominent shortly after (4 – 8 s post stimulus). These data are consistent with the notion of early retrieval of schematic information acting as a scaffold to construct a novel event.

The null effect when typical and atypical conditions were compared in Experiment 4 may reflect the variability in the characteristics of the stimuli. Although the stimuli were based on normative data from Experiment 3a, such data reflect how any set of stimuli is perceived on average, and there may be considerable individual variability in the reactions certain stimuli evoke. Consequentially, both the nature of the mental representation during imagining, and any observed functional networks may depend on stimulus characteristics/task demands to a greater extent than previously thought, which has implications for how to conceptualize mental simulations in general (see General Discussion: Simulation, Construction, and Beyond).

7.3 Memory for Simulated Events

The present study yielded interesting encoding and retrieval effects related to event construction. In terms of encoding, in Experiment 1 the ability to form more inter-item associations was positively correlated with memory for the items at cued recall. This is consistent with the effects of elaborative processing and visual imagery on subsequent memory (Bower, 1970; Craik & Tulving, 1975), and shows that an additional consequence for having well-constructed events is that they are more likely to be recalled at a later point in time.

A more interesting retrieval effect was found for imagined events: both Experiments 3b and 4 showed that memory for typical imagined events was greater than atypical events. In these studies, given that the context words were used as cues, one could argue that cued recall is likely the most ecologically-valid form by which imagined events would be recollected. That is, in real life one would not freely recall past simulations, but rather think back to such imagined events given a situational demand or environmental cue. If this were the case, manipulations of context should affect memory for previously experienced or imagined events. Indeed, Delaney, Sahakyan, Kelley, & Zimmerman, (2010) showed that delayed recall for a word list was poorer if during the delay, subjects daydreamed about a faraway context vs. a context physically closer to the testing location. Moreover, there was a positive correlation between distance and forgetting, suggesting that contexts are a crucial factor in memory for simulated scenarios.

Because of this retrieval advantage for typical imagined events, there is the potential for a recursive strengthening of a simulation based on familiar ideas: although we may imagine several scenarios related to an event and subsequently encode those simulations, the one that most matches existing semantic knowledge may be the most accessible. The implication is that although the flexibility of memory allows for simulation, the inter-relation between episodic and semantic memory affects the accessibility of previous events. This limits the accessibility of the more esoteric simulations, placing a boundary condition on the overall utility of imagining.

An interesting parallel exists in the evaluation of "novel" ideas, or in creative thinking: that is, given the task of generating a novel mental simulation, the ability to think of novel examples may be constrained based on prior knowledge biasing retrieval to congruent information (i.e. a mental rut). Notions of an inability to release from a certain mindset date back to the Gestalt Psychologists, noting people who read a certain vignette could not discover the alternate uses of the items in the story to solve the dilemma (i.e. functional fixedness; Dunker & Lees, 1945). Similarly, if we imagine an event going a certain way, and are more likely to be reminded of that imagined event, then the accuracy of our predictions may become quite poor, and are defined not by our ability to imagine the event well, but by the accessibility of those simulations. Indeed, our simulations of the emotional responses to a future event are biased, and subject to gross distortion due to essentialized information (Gilbert & Wilson, 2007). In sum, the utility of future simulation relies both on the ability to simulate in general, and the accessibility of those simulations.

7.4 The Hippocampus and Event Construction

In line with previous findings of the centrality of the hippocampus for future simulation and autobiographical recall, I also found the hippocampus to be necessary for event construction, even for non-personal, novel events. In Experiment 2, patients with damage to the MTL showed poorer event construction performance, measured in terms of the number of inter-item relations formed, and with the propensity to omit items despite their constant presence in the environment. Moreover, although patients showed impaired performance, they showed some ability to increase the number of relations with additional items, but they could not keep pace with the age-matched controls. Similarly, patients showed an increased omission rate at a set size of 4, which increased significantly at higher set sizes. These patterns of impairment suggest that patients could initially form some mental representation of an event, but had difficulty forming additional associations as information load increased, sometimes neglecting to include the added information at all. These data are consistent with the role of the hippocampus in relational processes at encoding, whereby the ability to bind items together consciously is impaired following hippocampal lesions (Diana, Yonelinas, & Ranganath, 2007; Henke, 2010).

In addition, the fMRI findings from Experiment 4 suggest the hippocampus is important for event construction. Specifically, the anterior hippocampus is particularly involved in event construction. Recent evidence suggests that the hippocampus is not a monolithic entity: aside from subfields, it can also be divided by anterior and posterior regions, which are implicated differently across a myriad of paradigms. Poppenk et al. (2013) reviewed potential functional differences between anterior and posterior hippocampal regions in terms of gist/schema-based information vs. more detailed information, and in terms of memory encoding and retrieval. Specifically, there is evidence to suggest the anterior hippocampus is more implicated in processing general schematics of a new memory (i.e. the gist), whereas the posterior regions are more implicated in encoding and retrieval of specific details of a memory. Consequently, this distinction between gist-like and more detailed imagined events may result in a preferential involvement of anterior vs. posterior hippocampus in event construction, depending on the nature of the events to be imagined (Gaesser, Spreng, McLelland, Addis, & Schacter, 2013).

In line with this notion, results from Experiment 4 showed that anterior hippocampal regions were active during event construction. As the nature of the task was only the initial construction of general, non-personal events, the most parsimonious explanation is that the anterior hippocampus is implicated in forming the inter-item associations. The behavioural PLS analysis confirmed that activity in the anterior hippocampus increases with increasing task performance across subjects, bolstering the notion of its involvement in the construction process. Interestingly, this involvement seems to be invariant to the number of items or how semantically-related items are, suggesting it is more the nature of the process, rather than a strict episodic/semantic memory distinction or mnemonic load, which engages the anterior hippocampus in event construction. Similarly, Race et al. (2013) found that hippocampal amnesia patients had difficulty constructing detailed future simulations of semantic events, failing to provide specific details concerning general facts. Such a task bears similarities to the task from Experiments 3a, 3b, and 4, in that the tasks focus on creating an initial event from existing knowledge, rather than creating events from past experience and embellishing upon those details. In sum, under conditions requiring the creation of novel associations across multiple elements, the anterior hippocampus seems to be crucial.

Regions that were also modulated by relational coherence scores (i.e. functionally related to the anterior hippocampus) included a cluster in the dorsomedial prefrontal cortex, precuneus, and bilateral inferior parietal lobules, which have all been previously implicated in future simulation (Andrews-Hanna, 2012; Spreng et al., 2010). However, other regions also emerged, which have not typically been associated with future imagination, including bilateral VLPFC, and lateral temporal cortices. Given that Experiment 4 used words and not information from subjects' personal past, it is conceivable these regions capture additional aspects of task performance that are present in this study but not in previous investigations.

Indeed, parahippocampal, lateral temporal, and medial frontopolar cortices showed early activity on each trial that was sensitive to how typical imagined events were perceived. This suggests that these regions may contribute to the initial construction by retrieving contextual and semantic information, providing an initial mental representation upon which a novel event may be constructed upon (Irish & Piguet, 2013). Taken together, it may be that event construction proceeds in a serial or cascading fashion, wherein a stimulus elicits rapid retrieval of previously stored contextual and semantic information, which may then be associated and bound with additional information by the anterior hippocampus.

Posterior hippocampal activity was modulated by the amount of information present (i.e. set size), individual differences in remindingness, and to a lesser extent, subsequent memory. Moreover, the posterior hippocampus was associated with a widespread functional network that included bilateral lateral prefrontal cortex and bilateral medial and superior parietal regions. However, this network was not correlated strongly with the functional network associated with coherence scores. Thus, the posterior hippocampus was not sensitive to construction performance, but some other aspects of event construction. Given the subsequent memory effects, modulation by lower remindingness (i.e. novelty) scores, and sensitivity to mnemonic load, the posterior hippocampus may incidentally encode aspects of task performance, such as the product of the construction task or peripheral details, which would be more likely under conditions of large mnemonic load or with novel stimuli.

7.5 Frontal Poles and Event Construction

Based on the involvement of the medial prefrontal cortex in future simulation in general, and the fact that semantic relatedness sometimes modulates activity in the medial prefrontal cortex during both imagining tasks and other paradigms, one prediction was that the typicality of imagined events would also modulate activity in the medial frontal poles.

Mean level activity in the medial prefrontal cortex, including the medial frontal poles, was higher for event construction compared to the control condition. Although the medial frontal poles were not sensitive to a general manipulation of typicality, subjective ratings of typicality were positively correlated with medial frontal pole activity, suggesting it is more responsive to familiar/prototypical imagined events. Regions functionally connected with the medial frontal poles as a function of typicality scores included lateral temporal cortices, right parahippocampal cortex, and VLPFC, which have been associated with retrieval of contextual information and semantic memory (Binder & Desai, 2011; Hannula, Libby, Yonelinas, & Ranganath, in press). As event construction tasks evoke activity in a widespread functional network, several sub-networks may exist that make different contributions. In this case, the medial frontal poles co-activating with lateral temporal and parahippocampal cortices may serve to provide an initial semantic representation to base any constructed events. Specifically, lateral temporal and dorsomedial prefrontal regions have been conceptualized as convergence zones for multimodal information, perhaps storing amodal, abstract representations of objects, locations, or situations, which may be deployed as task parameters requires (Binder & Desai, 2011; Denny, Kober, Wager, & Ochsner, 2012; Wood & Grafman, 2003). Such an account would be consistent with Andrews-Hanna's classification of a dorsomedial PFC "mentalizing" network within the default mode network, and further characterizes this sub-component with the representation of a schematic context, which would be necessary for imagining novel events, regardless of whether they are personally-relevant (in the case of imagining personal future events) or not (i.e. ToM).

7.6 Simulation, Construction, and Beyond

The present work used a novel paradigm, involving controlled amounts of information and relatively non-personal stimuli, to examine how relational coherence varies according to changes in memory ability and task demands. The findings presented here were largely consistent with the extant literature, despite using a more constrained paradigm, with less-personal stimuli, extending our knowledge of future simulation effects to more abstracted mental representations.

However, other aspects of event construction require further exploration. For example, an inherent assumption in event construction research is the nature of the underlying mental representation: we assume that when recalling previous events or imagining new ones, the subjective experience and associated neural codes are similar to those elicited by to perceptual input. Yet, the exact nature of these representations is not known: parallel debates arose previously regarding whether visual imagery involved actual images, or proposition-type representations (Moulton & Kosslyn, 2009). Whether imagined events have a common representation to memories and/or perceptions requires further examination. One approach would be to test whether imagined representations show similar behavioural effects to recently presented perceptual stimuli, such as perceptual priming effects. Parallel effects in terms of neural activity would also be predicted, such as repetition suppression effects in domain-specific cortical regions when perceiving stimuli that were recently imagined, or vice versa. Other approaches may involve probing different items within the representation during imagination, to get a sense of their accessibility, although such methods are limited by the possibility of interference from other items or the cue itself (Watkins, 1974).

Another relatively unexplored facet is the extent to which simulations actually influence subsequent behaviour. If the purpose of future simulation is to provide possible outcomes to guide future decisions or actions, then the factors that govern the potency or likelihood of simulations for decision making should be refined. For example, given an actual prior experience vs. an imagined outcome, it is not known which would influence subsequent behaviour to a greater extent should a related situation arise. Work in social psychology has already shown that the content and nature of what is imagined influences the likelihood of behavioural change. Specifically, when setting goals, imagining the specific processes and intermediary steps to achieving those goals results in better success rates, compared to imagining the end result (Pham

& Taylor, 1999). However, simulating process vs. outcome can also hamper decision-making for purchases, suggesting the impact of simulation is closely linked to context (Thompson, Hamilton, & Petrova, 2009).

Much of the future simulation research has focused on the functional utility of imagining: that is, the ability for us to go beyond the present perceptual environment to consider other information in memory. However, this is only one form of simulation: humans have the ability to experience simulation under other conditions, which seem to share many properties. Arguably, perceptual hallucinations, very elaborate delusions, confabulations and ruminative thoughts are also mental simulations, but are considered signatures of psychopathology. Moreover, they are also imbued with similar properties of episodic future simulations: they may be very detailed, based on ‘semantic’ facts (i.e. unrealistic beliefs), can be highly emotional, and also influence subsequent behaviour. Similarly, certain types of narrative prose seem to evoke a sense of experiencing akin to autonoetic consciousness, and also tend to evoke spontaneous recollection related autobiographical events, suggesting these facets of the human mental experience are associated in some way (Mar & Oatley, 2008). Whether all these types of simulations should be regarded as separate classes of ‘imaginations’, or whether they differ by degree rather than kind, is an important theoretical issue for subsequent research on imagining.

8 Conclusion

Overall, the results from this thesis extend our understanding of how simulations of novel events are constructed, and how distinct brain regions and stimulus properties may contribute to such a process. This work lays the foundation for subsequent investigation on how episodic and semantic memories are retrieved, re-configured, and subsequently used, to serve some goal-directed behaviour. Theoretically, these studies further define the processes underlying imagining novel events. Pragmatically, this work elucidates how information is recycled in our stream of consciousness, which may underlie a host of distinctly human abilities, such as creativity, storytelling, or mentalizing.

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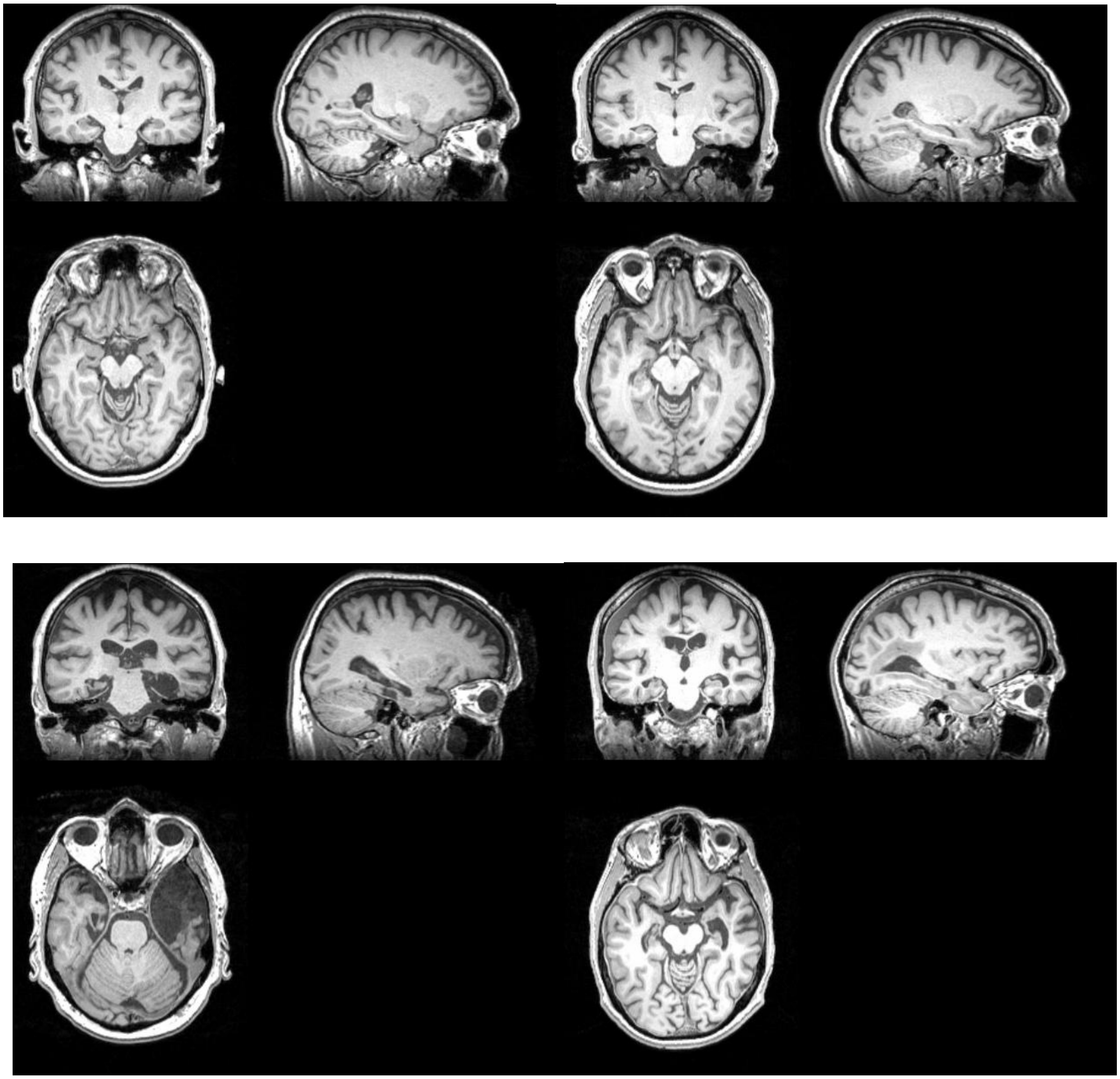
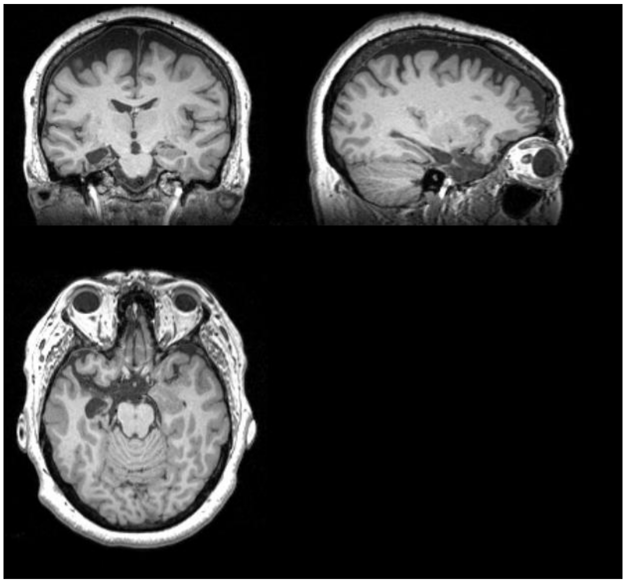
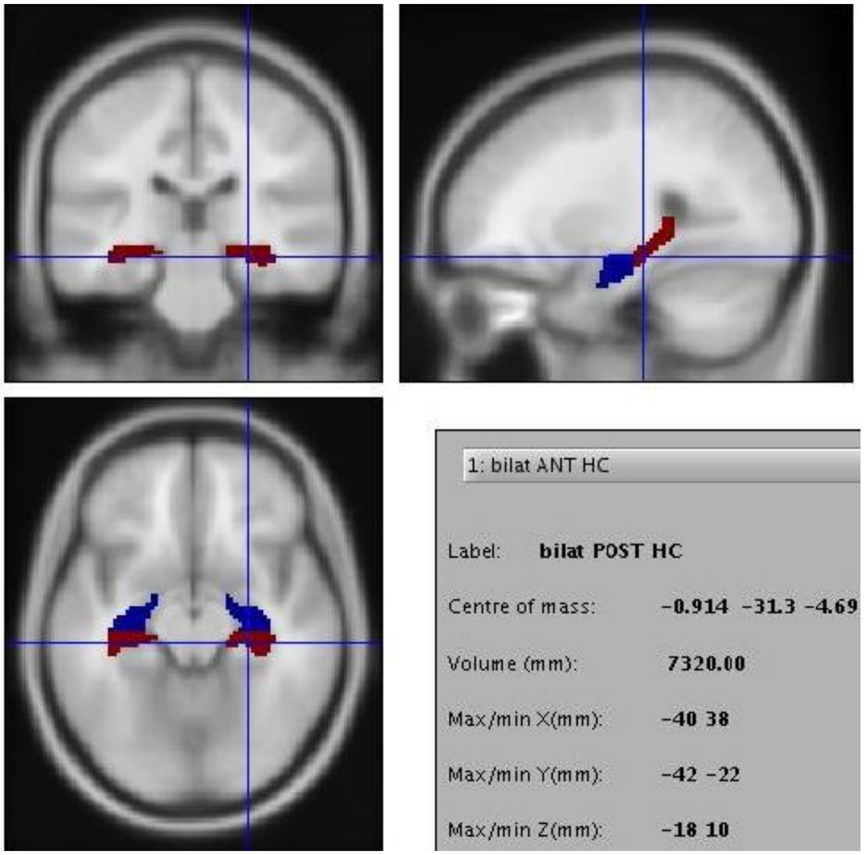
Appendices

Appendix 1: Representative structural magnetic resonance images of patients with medial temporal lesions in Experiment 2





Appendix 2: Structural region of interest definition of the bilateral anterior and posterior hippocampus for Experiment 4



1: bilat ANT HC

Label: **bilat POST HC**

Centre of mass: **-0.914 -31.3 -4.69**

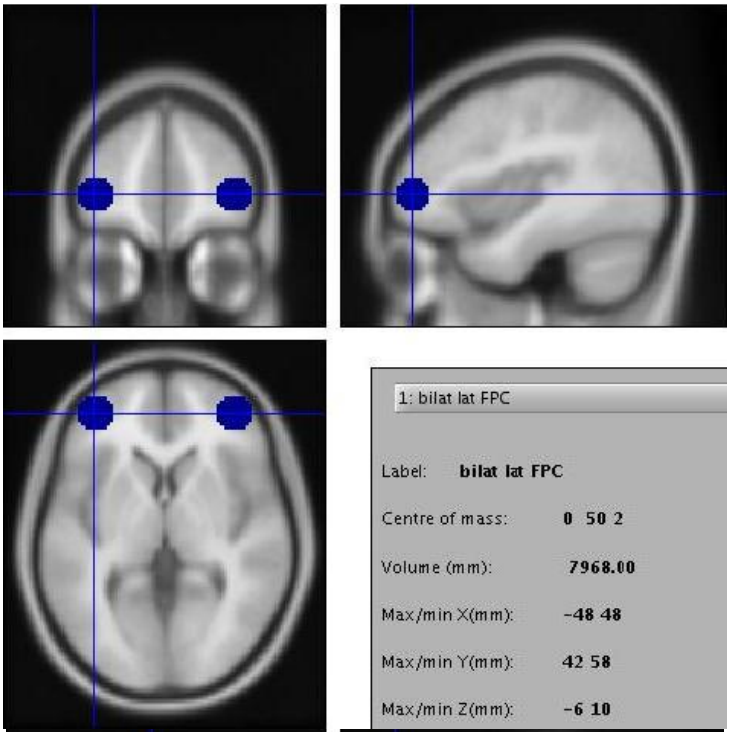
Volume (mm): **7320.00**

Max/min X(mm): **-40 38**

Max/min Y(mm): **-42 -22**

Max/min Z(mm): **-18 10**

Appendix 3: Functional region of interest sphere of the bilateral medial and lateral frontal poles for Experiment 4



1: bilat lat FPC

Label: **bilat lat FPC**

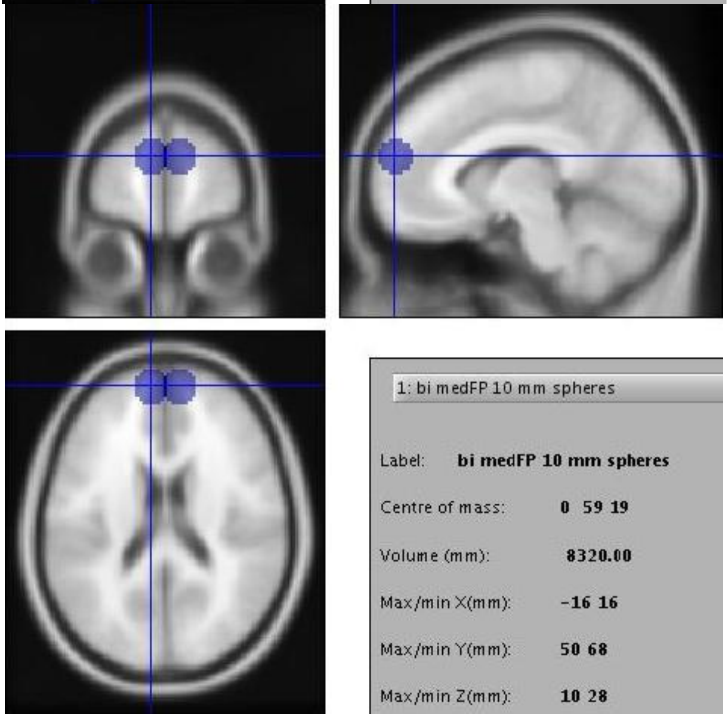
Centre of mass: **0 50 2**

Volume (mm): **7968.00**

Max/min X(mm): **-48 48**

Max/min Y(mm): **42 58**

Max/min Z(mm): **-6 10**



1: bi medFP 10 mm spheres

Label: **bi medFP 10 mm spheres**

Centre of mass: **0 59 19**

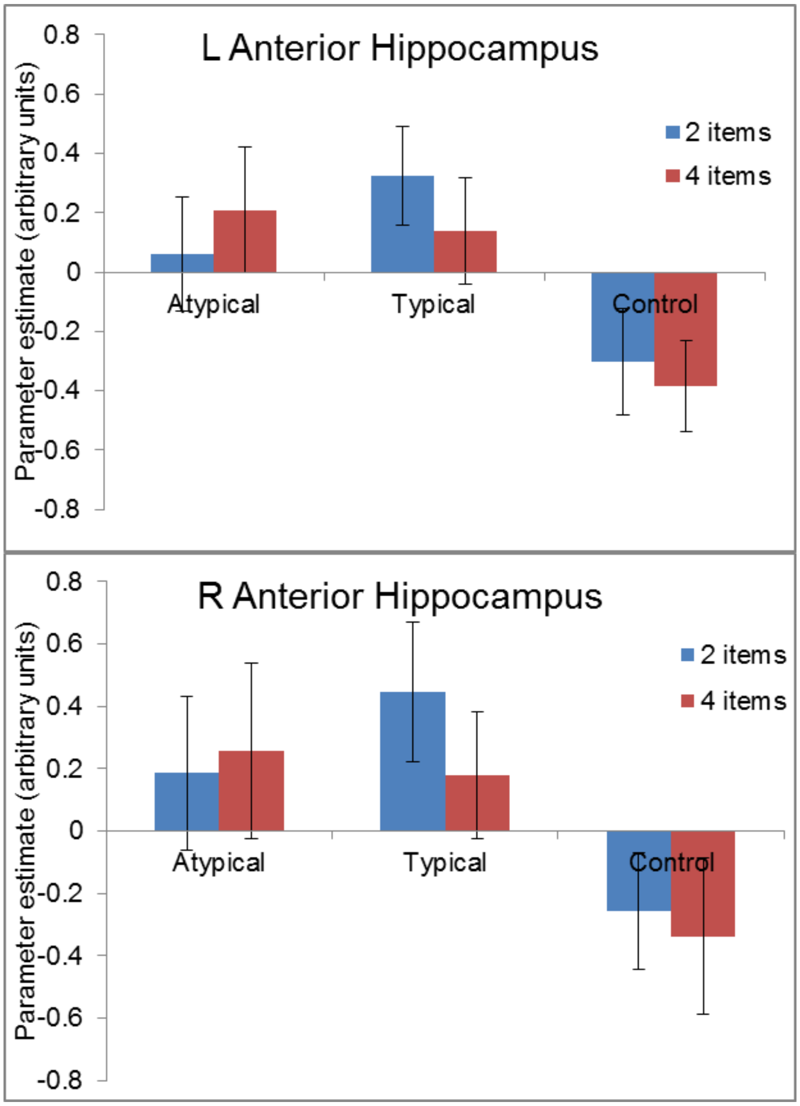
Volume (mm): **8320.00**

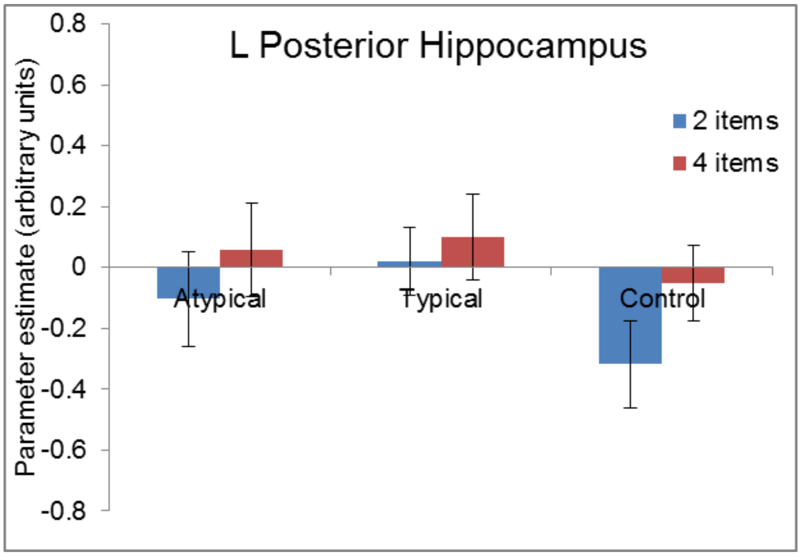
Max/min X(mm): **-16 16**

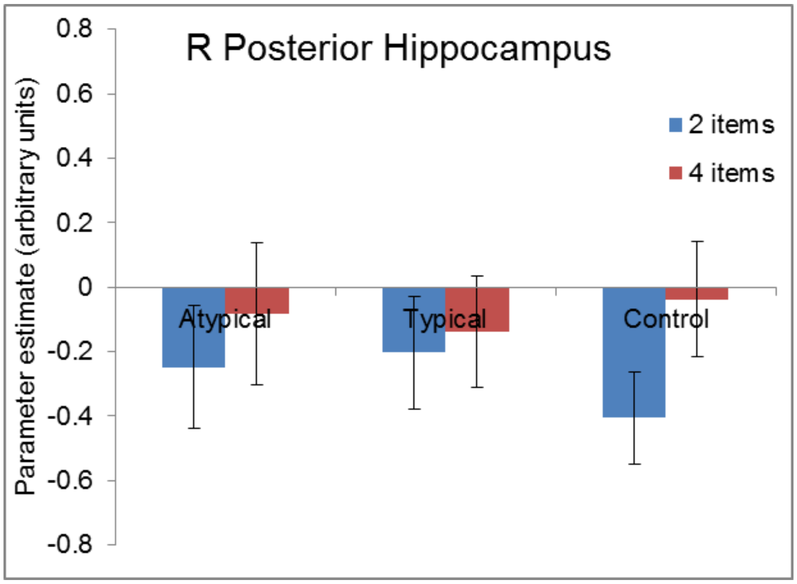
Max/min Y(mm): **50 68**

Max/min Z(mm): **10 28**

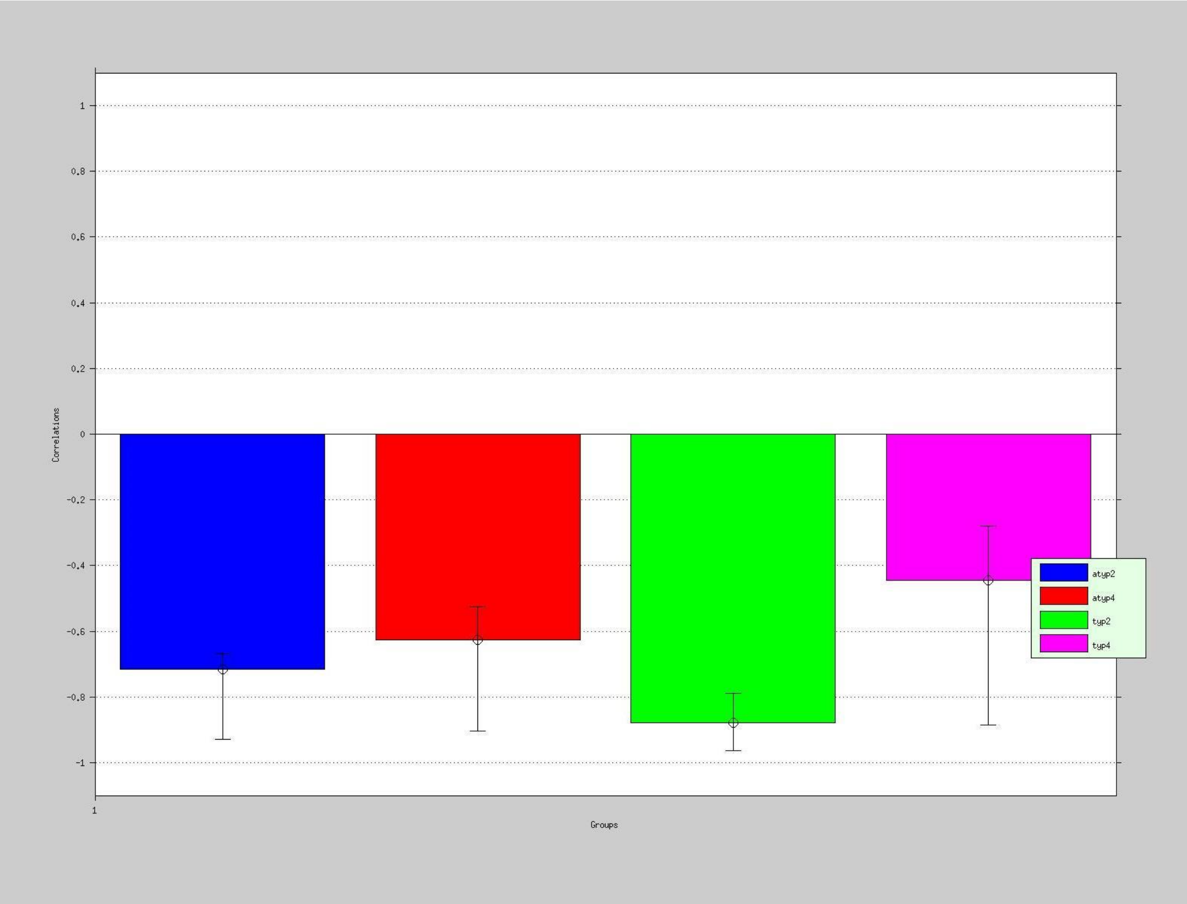
Appendix 4: Mean level neural activity for the left and right anterior and posterior hippocampus in Experiment 4



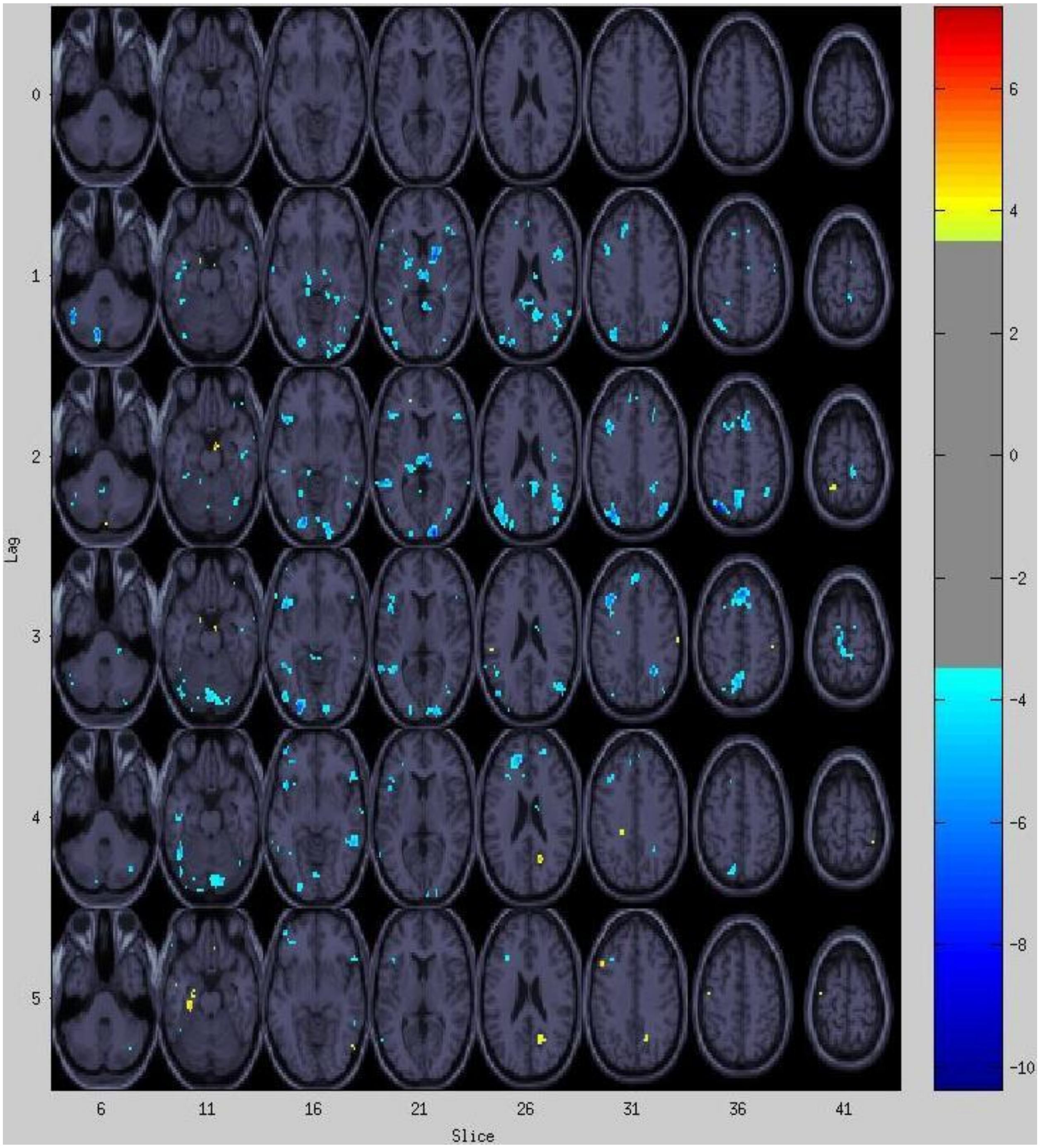

L Posterior Hippocampus
Parameter estimate (arbitrary units)
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
■ 2 items
■ 4 items
Atypical
Typical
Control


R Posterior Hippocampus
Parameter estimate (arbitrary units)
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
■ 2 items
■ 4 items
Atypical
Typical
Control

Appendix 5: The association between the latent variable explaining brain activity and task performance, and the different task conditions. The position of the bars above/below the x-axis indicates whether the latent variable affects task conditions similarly or differently. All conditions are on the same side of the origin, meaning the correlation between networks of brain activity and behaviour is similar across all task conditions. This latent variable explained 47.94% of the variance between brain activity and task performance, $p < .0005$



Appendix 6: Whole brain activation associated with individual differences in construction performance across task conditions. The x-axis going left to right shows axial slices of the brain from ventral to dorsal; the y-axis going from top to bottom shows task-related activity from 0 – 12 s in 2 s increments. Areas positively correlated with performance are shown in blue, and areas negatively associated with performance are shown in yellow.



Appendix 7: Peaks of activation associated with individual differences in event construction performance across task conditions. Peaks positively correlated with performance have a negative bootstrap ratio (BSR) value, and areas negatively associated with performance have a positive BSR value. Peaks are shown in MNI coordinates.

TR 1: 2 - 4 s post-stimulus onset						Cluster	
	Region	BA	x	y	z	size	BSR$_a$
	Frontal						
L	Cingulate Gyrus	32	-15	33	36	52	-8.02
R	Inferior Frontal Gyrus	47	48	27	-15	30	-5.97
R	Inferior Frontal Gyrus	45	45	27	12	20	-4.94
L	Middle Frontal Gyrus	9	-48	15	36	22	-5.04
R	Middle Frontal Gyrus	8	33	30	45	10	-5.85
R	Medial Frontal Gyrus	6	21	12	60	12	-4.98
	Temporal						
L	Parahippocampal Gyrus	37	-33	-42	-12	47	-6.88
L	Parahippocampal Gyrus	30	-15	-36	-6	11	-4.70
R	Parahippocampal Gyrus	36	30	-39	-9	24	-6.59
R	Parahippocampal Gyrus	30	18	-36	-3	12	-4.85
L	Middle Temporal Gyrus	21	-66	-12	-12	16	-6.02
L	Middle Temporal Gyrus	21	-48	-15	-18	15	-5.09
R	Middle Temporal Gyrus	39	39	-60	24	41	-5.98
L	Superior Temporal Gyrus	38	-57	6	-12	12	-4.17
R	Fusiform Gyrus	37	48	-48	-18	18	-5.11
	Parietal						
R	Posterior Cingulate	29	6	-48	9	78	-6.56
R	Posterior Cingulate	31	12	-57	27	43	-5.49
L	Precuneus	19	-33	-66	51	40	-5.25
R	Precuneus	39	45	-69	39	48	-5.21
R	Precuneus	7	33	-63	45	17	-4.84
R	Precuneus	7	33	-51	60	15	-4.75
L	Precentral Gyrus	6	-45	-3	48	10	-6.16
R	Precentral Gyrus	6	15	-12	78	35	-5.19
R	Precentral Gyrus	6	48	3	24	22	-4.50
L	Paracentral Lobule	5	3	-36	69	30	-4.88
	Occipital						
R	Inferior Occipital Gyrus	17	21	-99	-3	56	-7.11
L	Middle Occipital Gyrus	19	-51	-75	9	15	-6.63
L	Middle Occipital Gyrus	18	-39	-90	6	19	-6.60
L	Middle Occipital Gyrus	19	-27	-87	27	132	-6.43
R	Lingual Gyrus	19	36	-69	3	16	-5.16
	Other						

R	Caudate		18	9	12	196	-8.59
R	Caudate		42	-36	-3	10	-4.37
L	Caudate		-15	3	15	88	-6.37
R	Thalamus		15	-12	-3	11	-4.92
L	Substania Nigra		-9	-24	-9	19	-4.39
L	Cerebellum		-9	-78	-36	35	-7.99
L	Cerebellum		-48	-60	-33	41	-6.89
R	Cerebellum		33	-78	-15	40	-6.13

TR 2: 4 - 6 s post-stimulus onset						Cluster	
	Region	BA	x	y	z	size	BSR[a]
	Frontal						
R	Middle Frontal Gyrus	47	36	39	-18	19	-6.38
R	Middle Frontal Gyrus	8	27	24	36	39	-5.89
L	Middle Frontal Gyrus	47	-45	42	-18	14	-4.00
R	Superior Frontal Gyrus	6	9	18	51	109	-6.28
R	Inferior Frontal Gyrus	45	54	24	6	24	-6.18
L	Inferior Frontal Gyrus	47	-45	21	-6	93	-6.05
	Temporal						
R	Middle Temporal Gyrus	39	48	-75	30	247	-10.36
L	Middle Temporal Gyrus	21	-54	-45	9	31	-6.22
L	Middle Temporal Gyrus	21	-39	-9	-33	19	-5.39
L	Parahippocampal Gyrus	36	-36	-36	-15	80	-8.31
L	Hippocampus	35	-21	-21	-15	20	-5.14
R	Hippocampus		27	-18	-15	14	-4.39
R	Inferior Temporal Gyrus	20	51	-9	-27	24	-4.84
R	Fusiform Gyrus	37	51	-63	-12	10	-4.24
	Parietal						
L	Superior Parietal Lobule	7	-21	-51	72	10	4.49
L	Superior Parietal Lobule	7	-33	-69	54	326	-9.32
R	Superior Parietal Lobule	7	36	-51	60	61	-5.25
R	Precuneus	31	27	-48	42	40	-7.12
L	Precuneus	7	-6	-60	45	167	-6.22
R	Posterior Cingulate	23	9	-54	24	44	-5.25
L	Posterior Cingulate	30	-6	-54	12	14	-4.24
L	Precentral Gyrus	9	-36	15	39	38	-6.44
R	Paracentral Lobule	6	9	-27	72	35	-4.70
	Occipital						
L	Lingual Gyrus	18	-18	-84	-6	98	-6.37
L	Lingual Gyrus	19	-24	-51	0	22	-4.89
L	Lingual Gyrus	27	-12	-33	-3	20	-4.84
L	Middle Occipital Gyrus	19	-27	-84	18	44	-5.07
	Other						
L	Hypothalamus		9	-6	-21	10	5.89
R	Thalamus		6	-21	9	72	-7.18
L	Thalamus		-21	-27	12	29	-5.15
R	Caudate		18	6	15	79	-7.08
R	Cerebellum		33	-78	-15	184	-8.34

R	Cerebellum		15	-33	-51	57	-6.23
R	Cerebellum		39	-63	-18	16	-4.17
L	Cerebellum		-15	-36	-51	92	-6.12
L	Cerebellum		-27	-90	-15	29	-4.83
L	Cerebellum		-42	-54	-48	12	-4.64
L	Cerebellum		-3	-54	-33	23	-4.56

TR 3: 6 - 8 s post-stimulus onset						Cluster	
	Region	BA	x	y	z	size	BSR$_a$
	Frontal						
R	Gyrus Rectus	11	6	30	-15	17	3.98
L	Inferior Frontal Gyrus	13	-45	24	3	203	-8.88
R	Inferior Frontal Gyrus	45	54	24	6	11	-4.88
L	Middle Frontal Gyrus	8	-33	24	36	83	-7.33
L	Superior Frontal Gyrus	6	-6	24	57	235	-7.26
L	Cingulate Gyrus	32	-21	15	48	11	-4.44
	Temporal						
L	Fusiform Gyrus	37	-42	-54	-12	277	-8.19
L	Middle Temporal Gyrus	19	-45	-78	24	23	-5.38
L	Middle Temporal Gyrus	39	-45	-57	27	11	-4.95
	Parietal						
L	Precuneus	7	-3	-66	57	156	-7.51
L	Precentral Gyrus	6	-9	-15	69	38	-5.69
	Occipital						
L	Middle Occipital Gyrus	18	-24	-90	-3	144	-8.20
L	Middle Occipital Gyrus	18	-27	-87	15	37	-5.86
R	Middle Occipital Gyrus	19	39	-78	12	18	-3.98
R	Lingual Gyrus	17	15	-93	0	291	-8.02
R	Superior Occipital Gyrus	19	42	-75	30	96	-6.90
	Other						
R	Thalamus		9	-12	18	79	-5.67
L	Thalamus		-18	-30	12	18	-4.64
L	Cerebellum		-39	-51	-51	10	-5.46
L	Cerebellum		-45	-45	-30	15	-5.28
L	Cerebellum		0	-57	-15	18	-5.21
L	Cerebellum		-9	-39	-3	17	-4.90
L	Cerebellum		-12	-42	-51	10	-4.83
L	Cerebellum		-18	-78	-18	11	-4.41

TR 4: 8 - 10 s post-stimulus onset						Cluster	
	Region	BA	x	y	z	size	BSR$_a$
	Frontal						
R	Gyrus Rectus	11	6	33	-18	15	4.11
L	Superior Frontal Gyrus	9	-15	45	24	74	-6.65
L	Superior Frontal Gyrus	6	-9	3	75	23	-5.27
L	Middle Frontal Gyrus	8	-36	24	45	65	-5.97
R	Inferior Frontal Gyrus	47	54	24	-12	41	-4.97

	<u>Temporal</u>						
L	Fusiform Gyrus	37	-42	-66	-12	193	-6.33
R	Middle Temporal Gyrus	37	57	-42	-6	46	-5.47
L	Middle Temporal Gyrus	21	-63	-51	0	46	-4.82
L	Inferior Temporal Gyrus	20	-51	-18	-27	35	-4.97
L	Fusiform Gyrus	19	-27	-87	-9	16	-4.32
R	Fusiform Gyrus	20	36	-33	-27	10	-4.07
	<u>Parietal</u>						
R	Precuneus	31	18	-60	24	18	5.16
L	Precentral Gyrus	44	-54	15	3	128	-8.49
L	Superior Parietal Lobule	7	-3	-63	63	58	-7.95
R	Superior Parietal Lobule	7	12	-66	60	10	-4.72
	<u>Occipital</u>						
R	Lingual Gyrus	17	9	-99	6	45	-4.75
	<u>Other</u>						
R	Thalamus		12	-12	21	61	-6.14
L	Thalamus		0	-24	12	13	-4.48
L	Caudate		-15	-21	18	11	-4.02
L	Cerebellum		-3	-75	-9	131	-5.13
L	Cerebellum		-12	-93	-21	10	-4.12
R	Cerebellum		42	-69	-36	17	-4.82

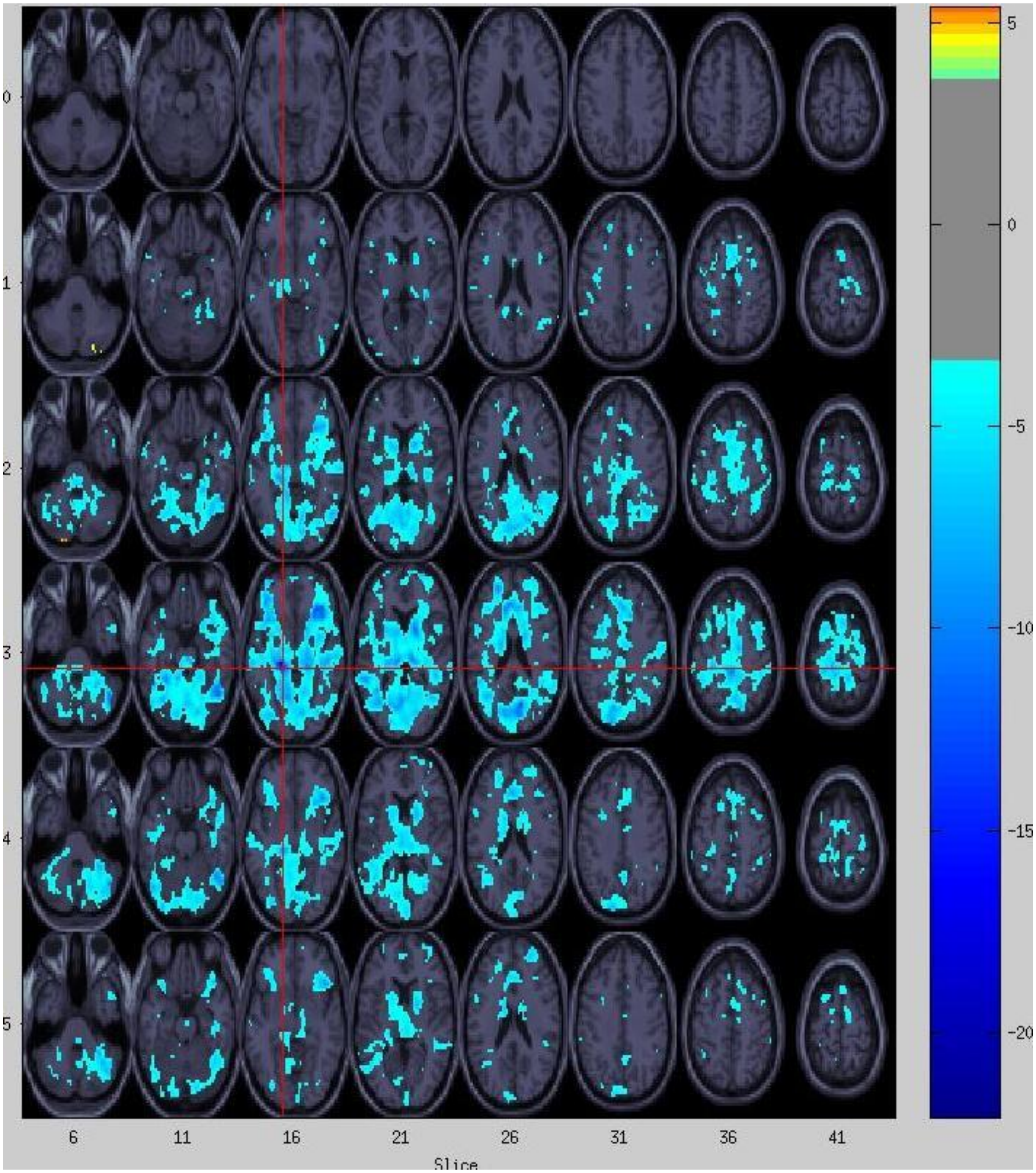
TR 5: 10 - 12 s post-stimulus onset						Cluster	
	Region	BA	x	y	z	size	BSR[a]
	<u>Frontal</u>						
R	Gyrus Rectus	11	6	36	-18	51	5.31
L	Middle Frontal Gyrus	9	-27	27	27	20	-5.13
	<u>Temporal</u>						
L	Parahippocampal Gyrus	28	-24	-15	-24	46	5.32
L	Superior Temporal Gyrus	38	-54	-3	-15	16	4.83
	<u>Parietal</u>						
R	Precuneus	31	18	-57	36	52	4.67
L	Postcentral Gyrus	3	-48	-15	57	11	4.17
	<u>Other</u>						
L	Cerebellum		-45	-72	-15	23	-4.80

BA = Brodmann Area, approximate; BSR = Bootstrap ratio

[a]: Bootstrap ratio is the parameter estimate over its standard error and is proportional to a z-score. Negative BSR values indicate a positive correlation with task performance, positive BSR values indicate a negative correlation with task performance.

All estimates survived a threshold of BSR = +/- 3.5, equivalent to $p < .0005$

Appendix 8: Functional network of latent variable 1, associated with individual differences in posterior hippocampal activity across task conditions. The x-axis from left to right shows axial slices of the brain from ventral to dorsal; the y-axis from top to bottom shows task-related activity from 0 – 12 s in 2 s increments. Areas positively correlated with hippocampal activity are shown in blue



Appendix 9: Peaks of activity associated with posterior hippocampal activity across task conditions. Peaks positively correlated with the posterior hippocampus have a negative bootstrap ratio (BSR) value, and areas negatively associated with posterior hippocampus have a positive BSR value

TR 1: 2 - 4 s post-stimulus onset		BA	x	y	z	Cluster size	BSR[a]
	Frontal						
L	Medial Frontal Gyrus	6	-3	0	60	357	-6.835
R	Superior Frontal Gyrus	6	24	9	63	48	-4.594
R	Middle Frontal Gyrus	46	42	15	18	41	-6.320
L	Middle Frontal Gyrus	10	-39	51	-6	18	-5.595
L		6	-27	3	57	58	-4.894
L	Superior Frontal Gyrus	8	-18	39	39	14	-5.481
L	Inferior Frontal Gyrus	9	-39	6	27	36	-5.213
R	Inferior Frontal Gyrus	47	39	30	-12	28	-5.276
R	Cingulate Gyrus	31	12	-9	45	147	-8.094
L	Cingulate Gyrus	31	-15	-48	24	30	-4.813
	Temporal						
L	Superior Temporal Gyrus	38	-51	12	-18	24	-4.561
R	Superior Temporal Gyrus	41	36	-30	12	34	-8.191
R		39	48	-54	27	110	-5.407
R	Middle Temporal Gyrus	21	54	9	-33	48	-5.230
L	Fusiform Gyrus	20	-33	-42	-15	214	-6.620
	Parietal						
L	Inferior Parietal Lobule	7	-21	-48	54	55	-5.884
L	Supramarginal Gyrus	40	-51	-45	36	40	-4.900
R	Superior Parietal Lobule	7	30	-51	60	14	-4.278
R	Posterior Cingulate	29	6	-42	18	12	-4.723
L	Precentral Gyrus	6	-42	-9	48	220	-7.486
R	Postcentral Gyrus	2	45	-24	33	41	-5.181
R	Paracentral Lobule	5	15	-36	51	56	-5.260
	Occipital						
R	Fusiform Gyrus	19	27	-84	-12	92	-5.561
L	Lingual Gyrus	18	-9	-63	3	14	-4.894
L	Middle Occipital Gyrus	18	-30	-90	0	17	-4.762
R	Cuneus	18	15	-99	6	25	-4.480
	Other						
R	Cerebellum		6	-27	-27	27	-4.982
R			27	-87	-33	11	5.407
L	Cerebellum		-18	-84	-30	18	4.726
L			-39	-69	-15	73	-6.369
R	Putamen		18	9	9	113	-5.681

L	Putamen		-21	12	15	58	-5.556
R	Thalamus		9	-12	0	28	-5.176
L	Insula	13	-48	12	3	11	-4.410

TR 2: 4 - 6 s post-stimulus onset	Region	BA	x	y	z	Cluster size	BSR_a
	<u>Frontal</u>						
R	Superior Frontal Gyrus	10	30	60	15	29	-6.316
L	Superior Frontal Gyrus	9	-18	42	39	46	-5.807
L	Middle Frontal Gyrus	10	-39	57	6	22	-5.362
L		6	-42	-3	51	12	-4.383
R	Middle Frontal Gyrus	11	48	51	-15	28	-4.859
R		10	45	48	21	10	-4.806
R		6	42	3	57	79	-7.155
R	Inferior Frontal Gyrus	47	30	24	-9	14772	-11.493
	<u>Temporal</u>						
L	Superior Temporal Gyrus	38	-39	21	-27	10	-4.423
L	Middle Temporal Gyrus	22	-60	-30	3	69	-6.063
R	Middle Temporal Gyrus	21	54	9	-33	53	-5.644
L	Inferior Temporal Gyrus	20	-45	-15	-21	11	-4.488
	<u>Parietal</u>						
L	Precentral Gyrus	6	-18	-15	69	90	-8.747
L	Postcentral Gyrus	2	-54	-24	48	67	-5.297
	<u>Other</u>						
L	Insula	13	-42	6	15	46	-6.051
L		13	-42	-27	21	128	-5.110

TR 3: 6 - 8 s post-stimulus onset	Region	BA	x	y	z	Cluster size	BSR_a
	<u>Frontal</u>						
R	Medial Orbital Gyrus	10	0	60	0	127	-7.971
L	Superior Frontal Gyrus	10	-27	66	12	28	-5.165
R	Middle Frontal Gyrus	8	27	36	45	21	-4.688
	<u>Temporal</u>						

L	Parahippocampal Gyrus	27	-21	-30	-3	25738	-22.111
	<u>Parietal</u>						
L	Inferior Parietal Lobule	40	-57	-33	48	85	-7.454

TR 4: 8 - 10 s post-stimulus onset	Region	BA	x	y	z	Cluster size	BSR$_a$
	<u>Frontal</u>						
L	Superior Frontal Gyrus	10	-21	45	24	101	-6.350
R	Superior Frontal Gyrus	10	21	51	24	169	-5.807
R	Middle Frontal Gyrus	6	36	12	48	36	-6.198
L	Inferior Frontal Gyrus	9	-54	9	27	43	-5.378
L	Middle Frontal Gyrus	6	-36	12	45	65	-5.299
L		9	-39	27	27	16	-4.475
L	Inferior Frontal Gyrus	44	-51	15	6	23	-4.819
L		47	-30	21	-12	64	-7.765
No Gray Matter found	Supplementary Motor Area	6	9	-9	75	594	-6.107
L	Cingulate Gyrus	31	-9	-27	45	104	-4.816
	<u>Temporal</u>						
R	Middle Temporal Gyrus	22	69	-45	3	27	-4.623
	<u>Parietal</u>						
R	Precentral Gyrus	4	33	-24	69	38	-5.047
R		6	51	3	27	26	-5.370
L	Postcentral Gyrus	7	-9	-51	66	19	-4.429
L		40	-57	-27	51	40	-5.906
R	Postcentral Gyrus	2	60	-27	45	28	-4.657
R	Supramarginal Gyrus	40	51	-48	33	15	-4.645
R	Angular Gyrus	39	30	-63	36	22	-4.472
	<u>Other</u>						
R	Cerebellum		51	-63	-27	5531	-12.830
L	Caudate		-12	6	18	5312	-10.918

TR 5: 10 - 12 s post-stimulus onset	Region	BA	x	y	z	Cluster size	BSR$_a$
	<u>Frontal</u>						
L	Medial Frontal Gyrus	10	-6	54	6	21	-4.172
R	Medial Frontal Gyrus	10	12	60	-3	16	-5.332

L	Superior Frontal Gyrus	6	-21	12	72	48	-4.452
L		9	-24	51	30	41	-4.959
L	Middle Frontal Gyrus	47	-39	36	-3	172	-6.015
L		6	-36	12	51	25	-4.686
L		9	-30	30	27	11	-4.131
R	Middle Frontal Gyrus	6	39	9	45	26	-4.211
R		46	30	57	21	162	-7.337
R		9	45	27	30	14	-4.729
R	Inferior Frontal Gyrus	47	45	24	-9	406	-12.314
L	Inferior Frontal Gyrus	9	-51	9	27	23	-5.030
L	Anterior Cingulate	24	-3	30	21	148	-6.886
L	Supplementary Motor Area	6	-9	-15	75	36	-5.752
R	Supplementary Motor Area	6	9	-6	75	461	-8.034
	Temporal						
L	Parahippocampal Gyrus	36	-39	-30	-12	32	-5.216
R	Fusiform Gyrus	20	45	-21	-24	54	-6.823
R	Superior Temporal Gyrus	41	42	-33	3	148	-6.274
R	Middle Temporal Gyrus	21	51	9	-39	64	-5.922
	Parietal						
L	Precuneus	7	-3	-60	66	20	-5.538
R	Precuneus	7	3	-57	36	48	-5.265
R	Precentral Gyrus	6	45	0	27	27	-5.102
R	Postcentral Gyrus	2	63	-27	45	20	-4.246
	Occipital						
L	Cuneus	19	-9	-87	39	228	-6.131
L	Inferior Occipital Gyrus	18	-33	-81	-6	29	-5.260
L	Inferior Parietal Lobule	40	-36	-48	45	41	-5.572
L		40	-60	-36	45	37	-4.850
	Other						
L	Cerebellum		-9	-36	-24	85	-4.787

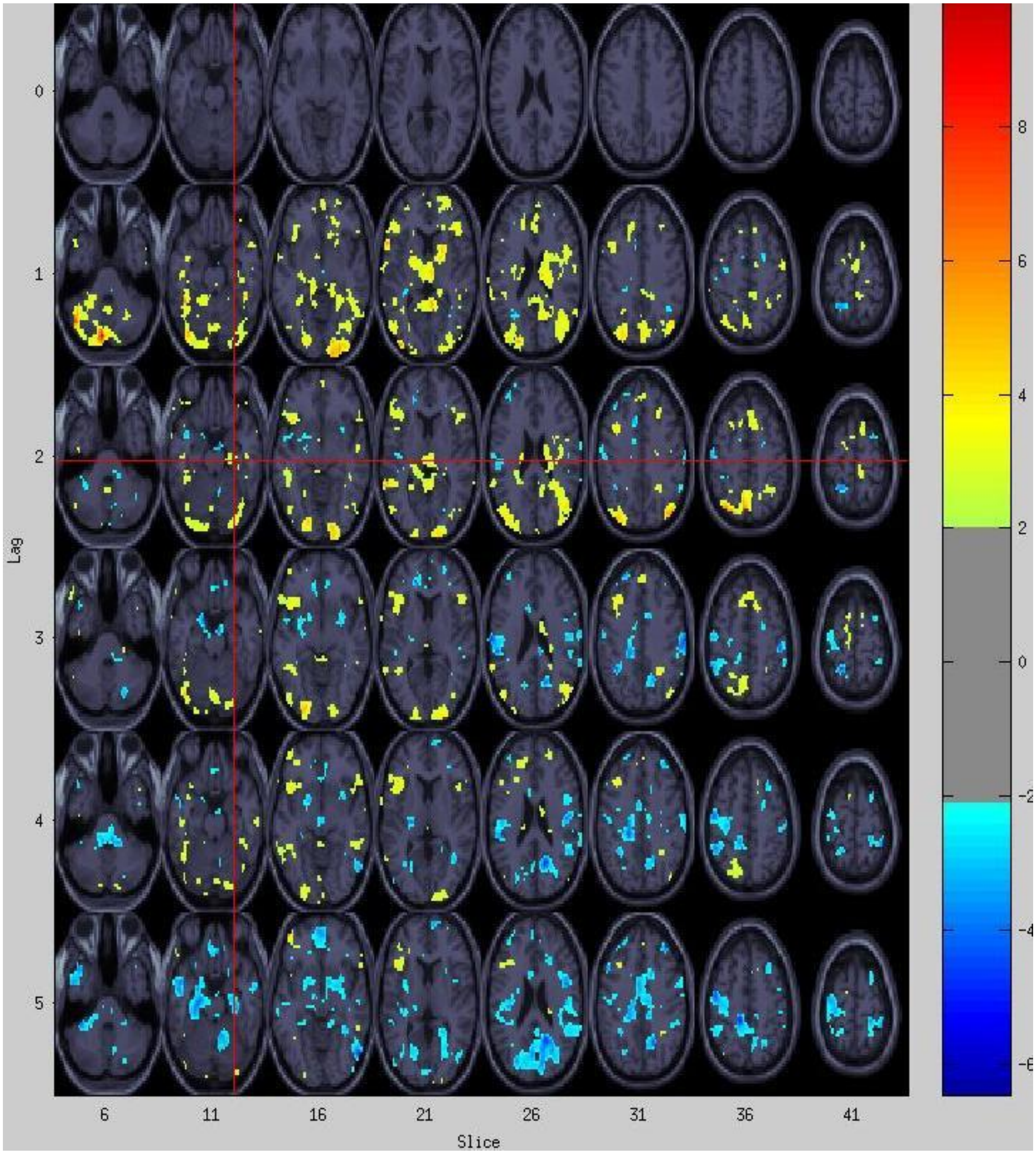
L		-45	-66	-27	234	-5.791
L		-21	-84	-24	124	-5.614
R	Cerebellum	39	-54	-39	1204	-12.729
R	Putamen	21	6	12	234	-7.864
L	Caudate	-12	0	21	1677	-7.751

BA = Brodmann Area, approximate; BSR = Bootstrap ratio

[a]: Bootstrap ratio is the parameter estimate over its standard error and
is proportional to a z-score. Negative BSR values indicate
a positive correlation with posterior hippocampal activity, positive BSR values indicate
a negative correlation with posterior hippocampal activity.

All estimates survived a threshold of BSR = +/- 3.5, equivalent to *p* < .0005

Appendix 10: Functional network of latent variable 2, associated with individual differences in relational coherence scores across task conditions. The x-axis from left to right shows axial slices of the brain from ventral to dorsal; the y-axis from top to bottom shows task-related activity from 0 – 12 s in 2 s increments. Areas positively correlated with performance are shown in yellow, and areas negatively correlated with performance are shown in blue.



Appendix 11: Peaks of activity associated with relational coherence scores across task conditions. Peaks positively correlated with coherence scores have a positive bootstrap ratio (BSR) value, and areas negatively associated with performance have a negative BSR value

TR 1: 2 - 4 s post-stimulus onset		BA	x	y	z	Cluster size	BSR[a]
	Frontal						
L	Superior Frontal Gyrus	8	-15	33	36	19	5.8490
L	Inferior Frontal Gyrus	44	-60	15	9	10	5.2847
	Temporal						
L	Hippocampus		-33	-21	-12	18	5.2274
R	Superior Temporal Gyrus	41	42	-36	3	21	5.8625
	Parietal						
L	Precuneus	7	0	-72	51	20	4.1973
R	Precuneus	29	6	-48	9	20	5.7263
	Occipital						
L	Inferior Occipital Gyrus	18	-39	-87	-15	100	6.9610
L	Middle Occipital Gyrus	19	-39	-90	6	14	6.8363
R	Lingual Gyrus	18	21	-99	-3	123	6.5146
R	Middle Occipital Gyrus	19	36	-69	3	10	5.7144
L	Cuneus	19	-27	-81	33	83	5.6933
	Other						
L	Cerebellum		-42	-45	-21	36	5.6974
L			-9	-81	-36	69	9.8599
L			-48	-66	-36	77	7.1743
R	Caudate		18	12	15	69	6.4873
R	Thalamus		6	-18	12	41	5.1979

TR 2: 4 - 6 s post-stimulus onset	Region	BA	x	y	z	Cluster size	BSR[a]
	Frontal						
L	Inferior Frontal Gyrus	47	-42	24	-3	13	4.8975
	Temporal						
L	Fusiform Gyrus	20	-36	-36	-15	11	6.1151
R	Superior Temporal Gyrus	22	36	-51	18	12	5.1392
L	Middle Temporal Gyrus	21	-63	-48	9	10	5.0613
L		39	-48	-78	27	21	4.6087
L	Fusiform Gyrus	37	-45	-48	-15	12	4.2297
	Parietal						
L	Precuneus	7	-6	-72	54	39	7.7583
L		7	-21	-78	51	75	5.9027

R	Superior Parietal Lobule	7	27	-51	42	14	5.0844
	<u>Occipital</u>						
R	Superior Occipital Gyrus	19	45	-78	30	100	7.7637
R	Lingual Gyrus	17	15	-93	-3	53	5.3114
	<u>Other</u>						
R	Cerebellum		30	-84	-15	32	7.0857
L	Cerebellum		-42	-69	-15	16	4.8208
L	Pulvinar		-15	-33	15	11	4.8782

TR 3: 6 - 8 s post-stimulus onset

	Region	BA	x	y	z	Cluster size	BSR_a
	<u>Frontal</u>						
L	Inferior Frontal Gyrus	47	-42	24	0	32	6.0389
R	Superior Frontal Gyrus	8	3	48	45	22	5.7517
	<u>Temporal</u>						
L	Superior Temporal Gyrus	22	-63	15	0	12	5.3520
R	Middle Temporal Gyrus	39	48	-75	30	25	4.8714
	<u>Parietal</u>						
R	Superior Parietal Lobule	7	30	-51	45	18	5.3804
L	Postcentral Gyrus	1	-63	-18	24	10	-4.5804
R	Postcentral Gyrus	2	63	-21	48	51	-6.4603
R		2	48	-27	57	10	-4.4833
	<u>Occipital</u>						
L	Inferior Occipital Gyrus	18	-24	-90	-3	25	5.0925
R	Middle Occipital Gyrus	18	21	-99	6	36	4.7075
	<u>Other</u>						
L	Cerebellum		-42	-75	-18	40	5.0859
R	Cerebellum		30	-81	-18	14	4.5647
R	Caudate		9	-6	21	11	4.4616

TR 4: 8 - 10 s post-stimulus onset

	Region	BA	x	y	z	Cluster size	BSR_a
	<u>Frontal</u>						
L	Inferior Frontal Gyrus	45	-54	15	3	61	5.1222
L	Cingulate Gyrus	31	-18	-30	39	16	-4.2775
	<u>Parietal</u>						
R	Postcentral Gyrus	2	45	-33	66	19	-4.6917
	<u>Occipital</u>						
L	Fusiform Gyrus	19	-42	-66	-12	10	4.2688
R	Precuneus	31	15	-63	24	30	-4.6333

TR 5: 10 - 12 s post-stimulus onset

	Region	BA	x	y	z	Cluster size	BSR_a
	<u>Frontal</u>						
R	Medial Frontal Gyrus	11	6	36	-18	14	-4.0653
R	Inferior Frontal Gyrus	47	18	12	-18	11	-4.3357

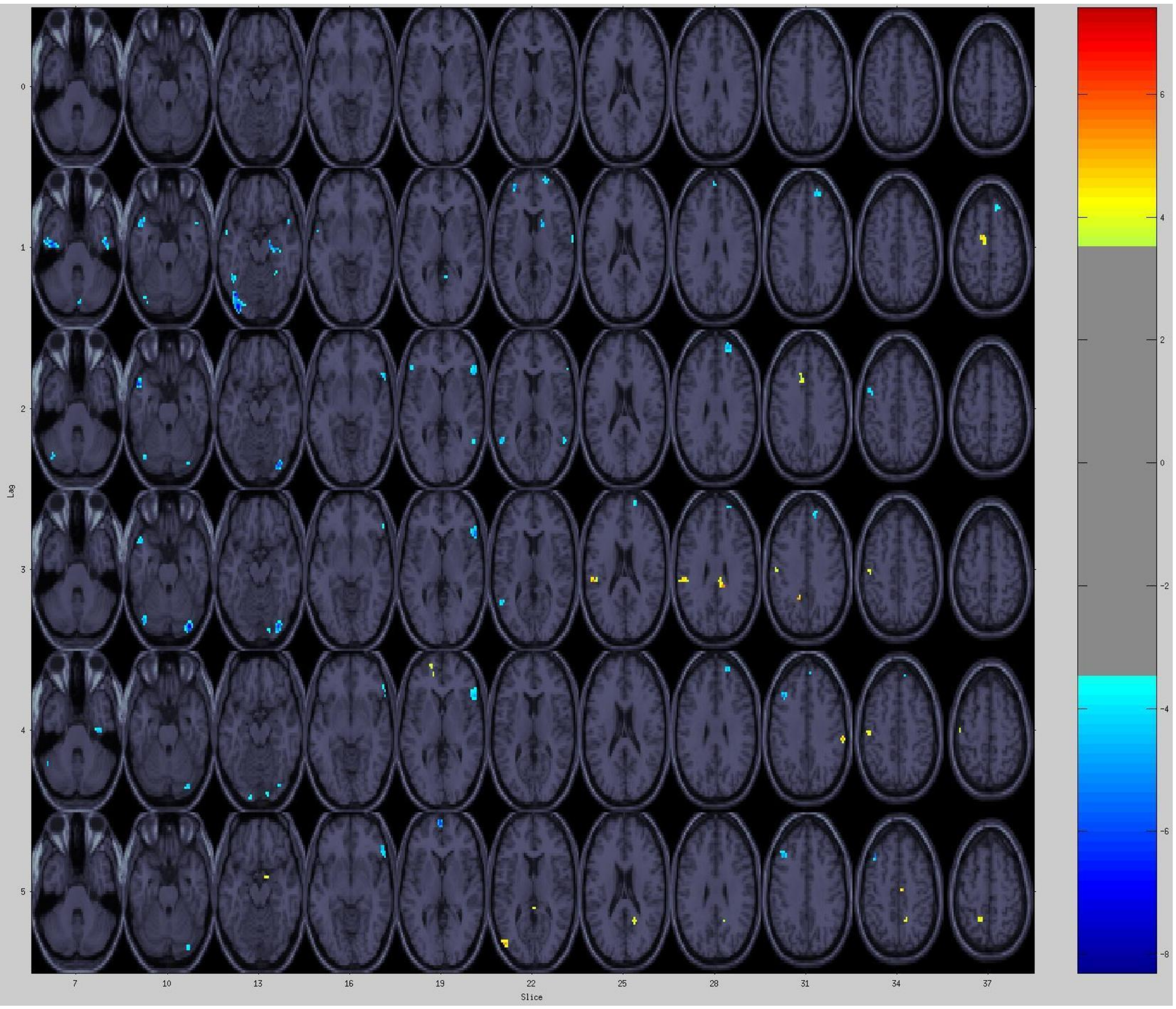
R	Cingulate Gyrus	31	15	-54	27	96	-4.8445
	<u>Temporal</u>						
L	Parahippocampal Gyrus	36	-24	-18	-24	27	-4.7255
L	Middle Temporal Gyrus	21	-54	0	-15	32	-4.7843
	<u>Parietal</u>						
R	Precuneus	7	21	-60	48	16	-4.6586
L	Precentral Gyrus	6	-48	-9	54	13	-3.9641
L	Paracentral Lobule	5	-15	-33	51	47	-5.1433
	<u>Occipital</u>						
R	Middle Occipital Gyrus	19	57	-69	-6	12	-4.5419

BA = Brodmann Area, approximate; BSR = Bootstrap ratio

[a]: Bootstrap ratio is the parameter estimate over its standard error and is proportional to a z-score. Positive BSR values indicate a positive correlation with task performance, negative BSR values indicate a negative correlation with task performance.

All estimates survived a threshold of BSR = +/- 3.5, equivalent to *p* < .0005

Appendix 12: Functional network associated with individual differences in typicality ratings across task conditions. The x-axis from left to right shows axial slices of the brain from ventral to dorsal; the y-axis from top to bottom shows task-related activity from 0 – 12 s in 2 s increments. Areas positively correlated with ratings are shown in blue, and areas negatively correlated with ratings are shown in yellow.



Appendix 13: Peaks of activity associated with typicality ratings across task conditions. Peaks positively correlated with the typicality have a negative bootstrap ratio (BSR) value, and areas negatively associated with performance have a positive BSR value

TR 1: 2 - 4 s post-stimulus onset		BA	x	y	z	Cluster size	BSR$_a$
	Frontal						
L	Medial Frontal Gyrus	6	-12	-3	57	28	5.365
L	Medial Frontal Gyrus	9	0	57	30	10	-4.0432
L	Superior Frontal Gyrus	10	-30	54	12	19	-5.2152
R	Superior Frontal Gyrus	8	21	48	42	23	-4.8805
R	Superior Frontal Gyrus	10	21	63	9	19	-4.6473
R	Superior Frontal Gyrus	6	15	30	60	27	-4.5113
R	Middle Frontal Gyrus	6	30	15	63	13	-4.5953
	Temporal						
R	Parahippocampal Gyrus		30	-18	-18	50	-6.3286
L	Superior Temporal Gyrus	38	-48	12	-21	29	-8.3055
R	Superior Temporal Gyrus	38	51	12	-18	25	-5.6022
L	Middle Temporal Gyrus	21	-57	0	-12	20	-5.1342
R	Superior Temporal Gyrus	22	66	-6	9	14	-4.9366
L	Inferior Temporal Gyrus	20	-45	-12	-33	26	-6.9868
R	Inferior Temporal Gyrus	20	51	-9	-33	12	-5.7986
L	Fusiform Gyrus	37	-45	-51	-12	17	-5.3801
	Occipital						
R	Lingual Gyrus	30	9	-51	6	10	-4.5867
L	Inferior Occipital Gyrus	18	-36	-87	-15	90	-7.478
	Other						
L	Cerebellum		-48	-60	-39	15	-5.8774
L	Cerebellum		-27	-39	-39	12	-5.8656
R	Cerebellum		27	-45	-18	11	-4.8488
R	Cerebellum		6	-75	-39	26	-4.9724
R	Caudate		15	12	12	13	-5.2065

TR 2: 4 - 6 s post-stimulus onset	Region	BA	x	y	z	Cluster size	BSR$_a$
	Frontal						
R	Superior Frontal Gyrus	9	21	54	30	26	-4.9465
L	Inferior Frontal Gyrus	44	-54	33	0	12	-4.3351
L	Inferior Frontal Gyrus	9	-36	12	36	12	-5.3858
R	Inferior Frontal Gyrus	47	60	21	-6	68	-4.9116
L	Middle Frontal Gyrus	6	-45	6	45	16	-4.5833

L	Cingulate Gyrus	32	-6	15	39	10	4.2175
	Temporal						
L	Superior Temporal Gyrus	38	-51	12	-24	22	-6.6322
L	Superior Temporal Gyrus	39	-54	-54	15	17	-4.8568
R	Superior Temporal Gyrus	39	54	-54	9	26	-5.4001
	Parietal						
L	Postcentral Gyrus	5	0	-42	72	62	-4.5608
	Other						
R	Cerebellum		33	-84	-18	40	-6.2164
L	Cerebellum		-39	-72	-36	28	-4.9774

TR 3: 6 - 8 s post-stimulus onset

	Region	BA	x	y	z	Cluster size	BSR[a]
	Frontal						
R	Inferior Frontal Gyrus	45	57	24	3	51	-5.8437
R	Superior Frontal Gyrus	8	12	48	42	23	-4.9914
R	Superior Frontal Gyrus	10	21	60	21	18	-4.3026
	Temporal						
L	Superior Temporal Gyrus	38	-45	15	-24	13	-4.6701
L	Superior Temporal Gyrus	39	-54	-54	12	11	-4.424
	Parietal						
L	Inferior Parietal Lobule	40	-54	-30	21	40	5.4969
L	Precuneus	7	-15	-51	39	10	5.0951
L	Postcentral Gyrus	4	-54	-15	42	13	4.4739
	Other						
R	Cerebellum		36	-84	-21	83	-7.5354
L	Cerebellum		-42	-75	-24	26	-4.945
R	Cerebellum		18	-87	-18	10	-4.1917

TR 4: 8 - 10 s post-stimulus onset

	Region	BA	x	y	z	Cluster size	BSR[a]
	Frontal						
L	Superior Frontal Gyrus	10	-18	60	6	14	4.3399
L	Middle Frontal Gyrus	8	-39	24	39	25	-5.7626
R	Inferior Frontal Gyrus	47	60	24	-3	59	-4.9202
R	Superior Frontal Gyrus	9	21	54	30	17	-4.5932
R	Superior Frontal Gyrus	8	9	48	45	12	-4.2793
	Temporal						
R	Inferior Temporal Gyrus	20	39	-18	-33	17	-4.7804
R	Inferior Parietal Lobule	40	60	-27	36	12	5.6733
	Parietal						
L	Postcentral Gyrus	1	-51	-18	51	23	4.6123
	Occipital						

L	Lingual Gyrus	17	-15	-93	-18	11	-4.3562
	<u>Other</u>						
R	Cerebellum		33	-81	-21	25	-5.5491
L	Cerebellum		-51	-57	-36	12	-4.386
R	Cerebellum		18	-87	-18	11	-4.0132

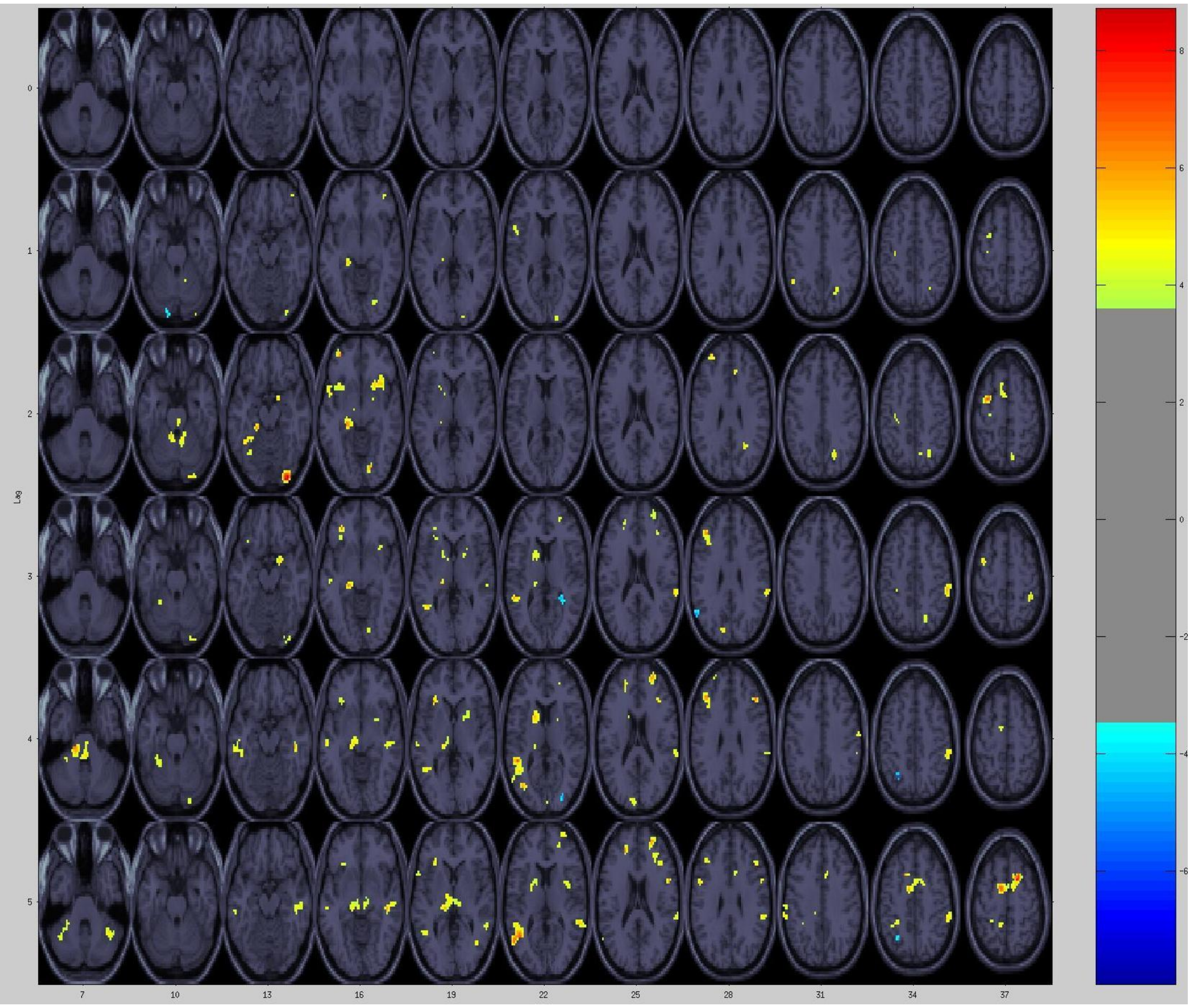
TR 5: 10 - 12 s post-stimulus onset						Cluster	
	Region	BA	x	y	z	size	BSR$_a$
	<u>Frontal</u>						
R	Cingulate Gyrus	31	6	-15	45	16	4.99
L	Middle Frontal Gyrus	8	-39	24	45	33	-6.7386
L	Medial Frontal Gyrus	10	-3	63	3	19	-6.3367
R	Inferior Frontal Gyrus	47	60	27	-6	25	-4.7596
	<u>Parietal</u>						
R	Posterior Cingulate	29	6	-36	15	17	4.9446
R	Precuneus	31	18	-51	27	16	4.8039
R	Precuneus	7	12	-51	51	10	4.4318
L	Superior Parietal Lobule	7	-15	-48	57	14	4.5276
	<u>Occipital</u>						
L	Middle Occipital Gyrus	19	-48	-78	12	27	5.2192
	<u>Other</u>						
R	Cerebellum		36	-81	-21	10	-4.1841
R	Cerebellum		9	3	-9	21	7.419

BA = Brodmann Area, approximate; BSR = Bootstrap ratio

$_a$: Bootstrap ratio is the parameter estimate over its standard error and is proportional to a z-score. Negative BSR values indicate a positive correlation with task performance, positive BSR values indicate a negative correlation with task performance.

All estimates survived a threshold of BSR = +/- 3.5, equivalent to *p* < .0005

Appendix 14: Functional network associated with individual differences in remindingness ratings across task conditions. The x-axis from left to right shows axial slices of the brain from ventral to dorsal; the y-axis from top to bottom shows task-related activity from 0 – 12 s in 2 s increments. Areas positively correlated with ratings are shown in yellow, and areas negatively correlated with performance are shown in blue.



Appendix 15: Peaks of activity associated with remindingness ratings across task conditions. Peaks positively correlated with the remindingness have a positive bootstrap ratio (BSR) value, and areas negatively associated with performance have a negative BSR value

TR 1: 2 - 4 s post-stimulus onset						Cluster	
		BA	x	y	z	size	BSR$_a$
	<u>Frontal</u>						
R	Middle Frontal Gyrus	11	39	48	-9	17	6.5465
L	Middle Frontal Gyrus	6	-30	3	60	11	4.894
L	Inferior Frontal Gyrus	44	-51	12	15	15	4.6227
	<u>Temporal</u>						
L	Hippocampus		-21	-30	-3	25	5.2398
	<u>Parietal</u>						
L	Inferior Parietal Lobule	40	-51	-51	39	17	4.7731
R	Superior Parietal Lobule	7	24	-60	45	21	4.6875
L	Precentral Gyrus	4	-33	-18	54	13	5.1708
	<u>Occipital</u>						
R	Cuneus	18	18	-96	9	18	4.747
R	Lingual Gyrus	18	30	-87	-18	13	4.4976
R		18	24	-78	-3	10	4.4222
	<u>Other</u>						
R	Cerebellum		12	-51	-21	14	5.4868

TR 2: 4 - 6 s post-stimulus onset						Cluster	
	Region	BA	x	y	z	size	BSR$_a$
L	Middle Frontal Gyrus	10	-36	51	-6	21	5.8943
R	Inferior Frontal Gyrus	47	33	18	-9	77	6.3203
R	Medial Frontal Gyrus	9	9	30	33	10	5.1178
L	Superior Frontal Gyrus	9	-33	51	30	13	5.0647
	<u>Temporal</u>						
L	Hippocampus		-21	-30	-3	61	7.0035
L	Fusiform Gyrus	37	-42	-48	-15	18	4.8191
L	Superior Temporal Gyrus	38	-54	15	-6	13	4.683
	<u>Parietal</u>						
R	Precuneus	7	9	-63	51	21	4.3884
L	Inferior Parietal Lobule	40	-51	-51	36	15	4.2594
L	Precentral Gyrus	4	-30	-18	54	20	4.5689
L		6	-33	0	57	32	6.5214
L		6	-3	6	54	22	4.8825
	<u>Occipital</u>						
R	Inferior Occipital Gyrus	18	33	-90	-15	85	8.7259
R	Lingual Gyrus	18	15	-78	-9	19	5.6551

	Other						
L	Cerebellum		-33	-60	-12	13	5.1951
L			-9	-36	-27	20	5.4324
R	Cerebellum		9	-48	-21	31	5.053
R			3	-30	-27	25	4.739
L	Putamen		-24	15	0	45	5.3303
L	Thalamus		-9	-12	0	13	5.0228

TR 3: 6 - 8 s post-stimulus onset						Cluster	
	Region	BA	x	y	z	size	BSR[a]
	Frontal						
L	Middle Frontal Gyrus	47	-33	39	-6	48	6.4782
L		9	-39	33	30	43	5.79
L		6	-39	0	57	13	4.9578
R	Middle Frontal Gyrus	46	24	51	15	46	5.2351
R		9	33	30	24	14	5.0269
L	Superior Frontal Gyrus	10	-21	48	24	18	4.9002
R	Inferior Frontal Gyrus	47	36	18	-3	18	4.5453
	Temporal						
R	amygdala	34	18	0	-12	26	5.7496
L	Middle Temporal Gyrus	37	-45	-51	0	15	6.603
L		21	-51	-21	-9	12	4.7565
L	Superior Temporal Gyrus	22	-54	-42	12	21	5.3944
L		39	-60	-60	30	13	-5.0793
R	Superior Temporal Gyrus	22	57	-27	0	13	4.8782
	Parietal						
R	Inferior Parietal Lobule	40	63	-36	24	37	7.8724
R		40	60	-30	45	41	6.3104
R		40	42	-42	57	14	5.1664
L	Postcentral Gyrus	1	-45	-27	63	16	5.9139
L	Postcentral Gyrus	3	-30	-36	45	11	4.0938
L	Precuneus	7	-6	-48	66	32	4.9132
R	Superior Parietal Lobule	7	18	-66	51	12	4.504
	Occipital						
L	Cuneus	18	-12	-81	27	22	5.0625
R	Lingual Gyrus	18	18	-81	-3	10	4.2738
	Other						
L	Cerebellum		-27	-45	-21	12	4.9891
R	Cerebellum		24	-87	-21	50	4.7794
L	Putamen		-15	6	9	60	5.5907
R	Putamen		21	9	0	35	4.7125
R	Caudate		30	-42	9	13	-4.5993

TR 4: 8 - 10 s post-stimulus onset						Cluster	
	Region	BA	x	y	z	size	BSR$_a$
	<u>Frontal</u>						
L	Superior Frontal Gyrus	10	-21	51	24	27	4.7337
R	Middle Frontal Gyrus	10	24	51	18	52	7.3099
R		9	42	30	27	28	6.4584
L	Middle Frontal Gyrus	9	-39	30	27	45	6.2196
L	Inferior Frontal Gyrus	47	-33	27	3	44	6.4982
	<u>Temporal</u>						
L	Middle Temporal Gyrus	22	-48	-42	12	110	6.7528
L		39	-39	-72	12	18	5.5267
L		21	-54	-27	-12	68	5.3938
R	Fusiform Gyrus	20	45	-27	-12	41	5.9725
	<u>Parietal</u>						
R	Precentral Gyrus	6	63	-12	36	14	4.8672
L	Postcentral Gyrus	4	-6	-39	66	97	7.1045
R	Inferior Parietal Lobule	40	57	-36	51	28	4.8931
R	Inferior Parietal Lobule	40	69	-36	24	26	5.4431
L	Superior Parietal Lobule	7	-27	-60	51	13	-6.4026
	<u>Occipital</u>						
L	Cuneus	18	-12	-87	21	23	4.3903
R	Cuneus	18	3	-90	9	10	4.3145
R	Middle Occipital Gyrus	19	30	-84	12	15	-4.7919
	<u>Other</u>						
L	Cerebellum		-30	-45	-21	24	4.4709
L			-33	-39	-39	15	5.6106
R	Cerebellum		21	-90	-21	24	5.0701
R	Putamen		24	9	0	49	5.7438
L	Putamen		-21	12	9	50	5.2259

TR 5: 10 - 12 s post-stimulus onset						Cluster	
	Region	BA	x	y	z	size	BSR$_a$
	<u>Frontal</u>						
L	Superior Frontal Gyrus	10	-21	42	21	15	6.0308
R	Superior Frontal Gyrus	6	18	9	57	143	7.7617
L	Middle Frontal Gyrus	9	-39	30	27	18	6.4271
R	Middle Frontal Gyrus	10	24	51	18	75	8.0207
R		9	45	27	27	52	5.0693
L	Medial Frontal Gyrus	6	-9	0	57	155	6.3321
R	Inferior Frontal Gyrus	44	54	9	21	27	5.7201
L	Inferior Frontal Gyrus	47	-33	30	0	26	5.5336
L		9	-51	6	30	14	4.8739
L		45	-63	15	3	10	4.3563

L	Cingulate Gyrus	31	-12	-30	42	14	4.3966
	<u>Temporal</u>						
L	Middle Temporal Gyrus	39	-42	-54	9	129	6.7273
L		21	-60	-24	-9	18	4.7382
R	Superior Temporal Gyrus	22	45	-24	-6	67	5.5986
R		22	60	-42	9	94	5.4572
	<u>Parietal</u>						
L	Postcentral Gyrus	5	-9	-45	63	77	5.1382
L		1	-66	-21	36	10	4.4276
L		3	-27	-39	54	32	4.3153
L	Inferior Parietal Lobule	40	-63	-33	36	20	4.96
R	Inferior Parietal Lobule	40	57	-36	54	32	5.8358
L	Superior Parietal Lobule	7	-27	-60	51	10	-4.8435
	<u>Occipital</u>						
R	Middle Temporal Gyrus	37	42	-63	6	10	4.9293
	<u>Other</u>						
R	Cerebellum		42	-51	-33	30	5.0087
L	Cerebellum		-42	-57	-30	17	4.5062
L			-30	-42	-33	17	4.3404
L	Thalamus		-15	-24	0	157	5.6953
R	Insula	13	36	3	15	17	4.5963
L	Putamen		-24	0	12	21	4.5295

BA = Brodmann Area, approximate; BSR = Bootstrap ratio

[a]: Bootstrap ratio is the parameter estimate over its standard error and is proportional to a z-score. Positive BSR values indicate a positive correlation with task performance, negative BSR values indicate a negative correlation with task performance.

All estimates survived a threshold of BSR = +/- 3.5, equivalent to *p* < .0005

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