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# **Memory for the Future:**

### The Encoding and Phenomenology of Episodic Simulations

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#### **Abstract**

Neuroimaging and neuropsychological research has established that our capacity to imagine future events is dependent on our capacity to remember the past. Both tasks engage a common core network of brain regions including the medial prefrontal, medial parietal, and medial temporal cortices, which suggests that they share similar underlying neural and cognitive processes. The hippocampus, a medial temporal lobe structure known to be critical for episodic memory, has a controversial role in imagining the future. The hippocampus might serve to encode and store imagined future events in memory, just as it does for real-life events. However, the encoding and retention of imagined future events has yet to be systematically investigated.

The studies in this thesis use both fMRI and novel behavioural methods to provide insight into how imagined future events are encoded. *Study 1* reveals that the hippocampus contributes to the encoding of imagined events, as both its anterior and posterior extents are more active while participants are imagining events that they will later remember than while imagining events that they will later forget. *Study 2* clarifies that the interaction of the hippocampus with a wider whole-brain network is important for the imagination of future events, and that this connectivity is modulated by encoding success. *Study 3* demonstrates that recall rates are higher for imagined events rated by participants as being more detailed and more plausible, and for those rated as involving more familiar people and places. Finally, as subjective participant ratings are widely used in studies of episodic future thinking, including *Studies 1* and *3*, the validity of participant ratings for their imagined future events was explored in *Study 4*. Specifically, the study shows that subjective participant ratings predict objective measures of the episodic content of participants' imagined future events, as quantified in an adapted version of the Autobiographical Interview. Broadly, these findings expand our knowledge of the role of the hippocampus in the encoding of episodic

representations, including future simulations. They also highlight the contributions of the episodic system to our ability to make, encode and execute plans for the future.

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### **Chapter 1: General Introduction**

#### 1.1 Introduction

The knowledge of some other part of the stream, past or future, near or remote, is always mixed in with our knowledge of the present thing. (James, 1890, p. 606).

Most of our daily thoughts involve consideration of things we have experienced and what we plan to do in the future. We constantly ruminate over the events in our lives, replaying them in our minds, analysing their consequences, imagining new endings, and predicting what will happen in the future. The extent to which this happens tells us how important it is to our survival; it emphasizes that a primary function of the brain is to allow for the consideration of what has happened before and to use this information to determine future behaviour. In this sense, remembering the past and imagining the future are functionally linked.

Research over the past several years has given insight into the relation between remembering and imagining. *Episodic memory*, or memory of events for which the specific time and context are recalled (Tulving, 1972), has been studied in great depth, particularly over the course of the last fifty years. However, it is only in the last few decades that the similarities between remembering and imagining have been explored in depth. Initial evidence for this link came from studies of patients with damage to brain regions such as the medial temporal lobe and prefrontal cortex (Hassabis, Kumaran, Vann, & Maguire, 2007; Tulving, 1985b; Wheeler, Stuss, & Tulving, 1997). These patients suffered from amnesia and could not remember events from their past, but more surprising was the difficulty they had when asked to imagine their future. These findings suggested that memory and imagination

both rely on the ability to mentally project oneself into representations of scenarios outside the present. Neuroimaging research has confirmed this idea, demonstrating that both remembering and imagining activate a common core network that had previously been associated with autobiographical memory retrieval, including the prefrontal cortex, medial temporal lobe, and posterior parietal cortex (Addis, Wong, & Schacter, 2007; Okuda et al., 2003; Schacter, Addis, & Buckner, 2007, 2008; Szpunar, Watson, & McDermott, 2007). This network, which is now thought to comprise part of the 'default network' due to its activation during rest, is involved in numerous forms of self-projection, including autobiographical memory, imagining the future, and imagining the perspectives of other people (Andrews-Hanna, 2011; Buckner, Andrews-Hanna, & Schacter, 2008).

Although the overlap in active brain regions is significant, some regions of this common network are more active for imagining the future than remembering the past. The hippocampus, a medial temporal lobe structure often implicated in memory tasks, is one such region; the right hippocampus is more responsive to the construction of imagined future events than remembered past ones (Addis, Wong, et al., 2007). The role of the hippocampus in memory is well-established (Eichenbaum, 2001; Eichenbaum, Sauvage, Fortin, Komorowski, & Lipton, 2011), but the reason for its increased involvement in imagination is not clear. One possibility is that the hippocampus is encoding these newly constructed scenarios into memory for later use, as hippocampal activity is known to predict subsequent memory for a variety of stimuli, in particular those of a visuospatial nature (Kim, 2011). It seems critical that imagined events are successfully stored into long-term memory so that they can be recalled when the imagined situation arises, as from an evolutionary perspective, the ability to imagine future events is only adaptive if it allows for greater preparation for when such events actually occur at some later date.

The aim of this thesis is expand our understanding of how imagined future events are stored and retained in memory. *Study 1* uses functional magnetic resonance imaging (fMRI) to examine whether the hippocampus is more active for imagined events that are later remembered in a post-scan test than those that are later forgotten. *Study 2* investigates the functional connectivity of the hippocampus with other brain regions for later-remembered and later-forgotten imagined future events. *Study 3* aims to identify the characteristics of an imagined event that predict whether or not it will be remembered later, and *Study 4* examines the validity of using participant ratings as measures of such event characteristics.

### 1.2 Episodic Memory

Memories of personal experiences have been studied at least since the beginnings of psychology as a discipline (James, 1890, p. 644). While the study of introspection became unpopular for much of the 20<sup>th</sup> century, with focus turning instead to the study of observable and measurable external behaviour (Danziger, 1980), interest in inner thought processes resumed in the '60s and '70s. In this context, the concept of episodic memory was first described by Endel Tulving (1972). He noted that classification of various memory 'types' can be theoretically useful; these classifications often take the form of dichotomies where one type of memory is defined not only by its own characteristics, but also by it not being some other type of memory. He first outlined the idea of semantic memory, described at the time in research literature as a collection of abstracted knowledge, particularly about words and the meanings of various symbols. The definition of semantic memory has evolved somewhat, now referring to each person's collection of general conceptual knowledge, not only about language and the meanings of words, but also for facts about the world that are not tied to any specific context (Tulving, 1985a). Tulving argued that semantic memory exists in contrast with another class of memory: recollection of specific events with identifiable spatial and temporal contexts. It is this sort of memory that is involved when people remember what it

was like to experience things that have happened in their past, such as attending a graduation or wedding, and it is also thought of as being the type required when participants are exposed to various stimuli (e.g. lists of words) and then asked to recall them (though see Gilboa (2004) and McDermott, Szpunar, and Christ (2009) for a discussion of the neural distinctions between these two types of events). What is common to both of these cases is that during recall, the original episode is to some extent mentally reinstated along with features of its setting. Tulving termed this *episodic memory*, and while he acknowledged that episodic and semantic memory work together, he believed that they could also function independently to a degree that made the distinction one worth considering.

In Tulving's (1972) foundational chapter, he posits that episodic information is taken in via perceptual systems while a person is experiencing an event. This information is then stored in temporal relation to other events that have happened previously. In other words, these events are stored on a sort of mental 'timeline', and the rough position of any given new event on this timeline is determined by its temporal association to other events that have been stored there. This idea is supported by the known tendency for participants to rely on temporal associations between stimuli to improve episodic recall (Kahana, 1996), and further by the fact that participants who rely heavily on temporal associations when recalling items tend to show better episodic recall performance than participants who rely less on these associations (Sederberg, Miller, Howard, & Kahana, 2010). The spatially- and temporally-based organisation of episodic memory is one of its unique features; with semantic memory, associations between items are more abstract and conceptual.

Furthermore, Tulving (1972) argues that the very process of retrieving episodic memories can form another type of 'input' into this system, and these memories are therefore particularly vulnerable to change and distortion at each time of retrieval. This idea has since

been supported by evidence for 'reconsolidation', a process by which retrieval of well-established episodic memories renders them temporarily vulnerable to the incorporation of additional relevant information, perhaps as a mechanism for maintaining memories as relevant and up-to-date (Forcato, Rodriguez, Pedreira, & Maldonado, 2010; Lee, 2009; Squire, 2007; Tse et al., 2007).

Tulving (1985b) later expanded on his ideas about the distinction between memory types, and proposed that each type was accompanied by its own form of 'consciousness'. His three varieties of consciousness included anoetic (non-knowing), noetic (knowing), and autonoetic (self-knowing). Anoetic consciousness was described as an awareness that is confined only to the current situation being experienced, requiring no knowledge of anything that exists outside of it. In contrast, his idea of noetic consciousness does allow understanding of items and concepts not currently present, including symbolic representation, and he suggests that this type of consciousness accompanies semantic memory encoding and retrieval. At the highest level, however, is autonoetic consciousness. This form of consciousness allows a person to have knowledge of the timeline of his or her own life, and the understanding that each event that has been experienced is tied to a 'self' whose existence is constant across time. Autonoetic consciousness is therefore necessary for projecting oneself back into specific moments in the past, and therefore for the remembrance of an episode.

Of course, it was later pointed out that distinguishing between episodic and semantic memories is not always straightforward, with some arguing that the distinction was not empirically justified (McKoon, Ratcliff, & Dell, 1986) or theoretically useful (Eyesenck, 1988). Specific episodes often spring to mind as examples when we are trying to recall certain facts, and some memories cannot easily be classified as either episodic or semantic

(e.g. events that happen so regularly that it is difficult to think of one particular instance, like eating breakfast each day) (Greenberg & Verfaellie, 2010; Neisser, 1986). Moreover, specific moments in time are embedded within a conceptual framework of one's life (Conway & Pleydell-Pearce, 2000), and thus representations of an episodic event inherently contain some semantic elements (Levine, Svoboda, Hay, Winocur, & Moscovitch, 2002). It is therefore most likely that the two memory systems are interdependent.

There are a number of theories about how episodic and semantic memory interact, one being that semantic memory consists of the abstracted regularities that occur over the course of many repeated episodic events. For example, because all of the cats we have seen generally have a similar appearance (pointed ears, a long tail, fur and four legs, etc.) we eventually develop a canonical idea of a cat that does not depend on recall of any specific situation involving one, and this representation of a cat can be held in the mind without an accompanying spatial or temporal context. In support of this theory, an intact episodic memory appears to assist in the formation of semantic memories. For example, while patients suffering from episodic memory deficits can learn new conceptual information, it is much more difficult for them to acquire semantic knowledge as compared with healthy controls who are able to embed new information within their relevant memories of past experiences (Greenberg & Verfaellie, 2010). Others have argued that semantic memories are not inherently different from episodic memories. It has been suggested that semantic memories are simply mnemonic representations for which the spatiotemporal context is not a salient feature, and that repeated retrieval of these representations without the corresponding contextual information results in the gradual loss of the memory source (i.e., the context in which the information was learned) (McClelland, McNaughton, & O'Reilly, 1995). There are, however, some patients who have been amnesic for episodic events since birth but have nonetheless acquired semantic memories (Vargha-Khadem et al., 1997), suggesting that the

above explanations may be too simplistic (but see Squire & Zola, 1998 for a discussion of the fact that their episodic memory may not have been entirely impaired).

Amnesic patient H.M., who suffered profound loss of recent episodic memories after bilateral temporal lobectomy (Scoville & Milner, 1957) was for the most part unable to easily acquire new semantic information, particularly in the form of learning new words that entered the English language after his lobectomy (Gabrieli, Cohen, & Corkin, 1988). Many amnesic patients with complete damage to the medial temporal lobes cannot learn new semantic information at all (Bayley & Squire, 2005), and when amnesic patients can learn new semantic material, it generally requires extensive repetition and the memories do not show the same rapid flexibility as that of normal control participants (Kensinger & Giovanello, 2005). However, H.M. was unimpaired on a wide variety of tests assessing general world knowledge that he had learned prior to his operation (Kensinger, Ullman, & Corkin, 2001). These findings suggest that while intact episodic memory certainly facilitates the formation of new semantic memories, it is not required for retrieval of semantic information once it has already been acquired (Kensinger & Giovanello, 2005). Therefore, episodic and semantic memory may not initially be distinguishable, though with time memories of each type seem to become increasingly distinct in a neurophysiological sense.

Both episodic and semantic memories can be *autobiographical*. Autobiographical memory (AM) is not another separate and distinct classification, but more an indication of the self-related content that some memories possess, regardless of whether they are episodic or semantic. A number of theories define what constitutes an episodic autobiographical memory. Conway (1990) notes that autobiographical memories are complex, concern the self (Brewer, 1986), contain a variety of information from each of the sensory, perceptual, and internally reflective domains (Johnson, 1983), consist of visual imagery (Conway & Pleydell-

Pearce, 2000), and include a personal interpretation of what is happening. The association with the self and the corresponding first-person perspective seem to be particularly significant, and this point was remarked upon even by William James (James, 1890, p. 652) when he wrote that "the sense of a peculiar active relation in it to *ourselves* is what gives to an object the characteristic quality of reality, and a merely imagined past event differs from a recollected one only in the absence of this peculiar feeling".

Tulving (1972) described episodic memory as constituting both autobiographical events from one's personal past and also laboratory-based 'events' like the learning of word and picture lists. However, these two types of events have been shown to have important differences. The developmental trajectories of episodic and autobiographical memory differ, such that children perform at adult levels on autobiographical memory tasks earlier than they do on episodic memory tasks that do not involve self-relevant stimuli (Pathman, Samson, Dugas, Cabeza, & Bauer, 2011). The two forms of event memory seem to have different underlying neural representations as well. Self-referential autobiographical memories tend to involve ventromedial prefrontal cortex, while laboratory-based episodic tasks (e.g. learning word and picture lists) recruit dorsolateral prefrontal cortex as well, possibly due to the increased uncertainty that is associated with remembering events that are not personally-relevant (Gilboa, 2004). Therefore, while most naturally-occurring episodic memories are autobiographical, it does not necessarily follow that all episodic memories can be described as such.

Episodic memories can be inaccurate or distorted, which is to say that they tend not to be exact renditions of how the events actually occurred at the time. They may be more like summaries of events that capture the general idea of what happened, often with very vivid perceptual details but with no guarantee of their accuracy. Some have proposed that memory

distortions result from the *reconstructive* nature of episodic memory: when we recall an episodic memory, we piece back together the fragments of the scenario and recombine them to form the event (Neisser, 1986; Schacter, Norman, & Koutstaal, 1998). This constructive form of recall is required because when an event is experienced, its various elements and features (e.g. visuospatial, perceptual, and emotional) are processed in topographically separate brain regions and therefore create a pattern of activity that is distributed across the entire brain. During recall, it is therefore necessary to at least partially restore this pattern, often via the encounter of a cue or fragment of the memory that allows the brain to 'complete' the rest of the pattern (Schacter et al., 1998).

Bartlett (1932) was one of the earliest to theorize about the constructive nature of memory. In his series of experiments, he noticed that his subjects very rarely recalled experimental stimuli in a literal way. Bartlett's participants seemed to take in a general impression of a scenario, and then when later asked to recall the finer details, they would 'construct' these details based on what was likely or justified given the overall gist of the stimulus, even though some of these details were quite inaccurate. He concluded that the constantly dynamic nature of our surroundings renders exact recall unnecessary. To store each experience exactly in the way it unfolded is not economical, because not every aspect of what happened will be useful to recall in the future. It also does not allow for any flexibility, and Bartlett believed that memory must afford us some "adaptability, fluidity, and variety of response" (p. 218).

Neisser (1986) agreed that recalling episodic memories is constructive because it is not possible to remember every aspect of an event's context, and as a result, we often simply remember the most salient or relevant main components. The less central details are therefore often omitted from our memories, or else we fabricate them, and Neisser believes that the

extent to which details are 'made up' depends heavily on the recall situation; when recalling in a social context, the incentive to construct missing aspects of the memory might be higher than when recalling just to oneself. Barclay (1986) argues further that the reconstructive nature of episodic memory can be partly attributed to memory details being adjusted to fit the stories or *schemata* that we have built up about ourselves based on past experiences (Barclay, 1986; Bartlett, 1932), which is one example of the mutual influence of episodic and semantic memory.

The fact that we are able to change perspective while recalling an episodic memory also supports the idea of memory being reconstructive. When an episodic memory is recalled and the scenario is recreated in a person's mind, there are two perspectives that can be taken. When recalling from a *field* perspective, the mental images are generated as if they are being viewed by the person's own eyes, and they correspond roughly to the way the scene would have actually looked at the time to the person. When recalling from an *observer* perspective, the person can 'see' him- or herself in the scenario, as if watching from a bird's eye view (Nigro & Neisser, 1983). It is possible to switch from one perspective to the other (Robinson & Swanson, 1993), and the perspective taken when recalling seems to vary depending on the age and emotional content of the memory. More recent memories tend to be recalled from the field point of view, and more emotional memories from the observer point of view (Nigro & Neisser, 1983). Memories that conflict with a person's current self-concept or self-assessment tend to be remembered from a distant observer perspective, suggesting that semantic selfknowledge influences the way autobiographical memories are recalled (Libby & Eibach, 2002). The very fact that it is possible to recall from an observer perspective suggests that such a memory is being reconstructed to some degree, because at no point during the actual event would a person have seen his or her own body from the perspective of another person. Events recalled from a third-person perspective therefore necessarily involve the fabrication

of at least details about the person's own physical appearance. Older memories and ones that are emotional (and thus have probably been recalled many times) have had more opportunities for 'reconstruction' and may become more semanticised (Winocur & Moscovitch, 2011), which may explain the increased likelihood of being remembered from the observer perspective.

Conway (2009) recently proposed a hierarchical model of episodic memories. He suggests that the most basic components of episodic memories are the brief perceptual flashes, often in the form of visual images, which depict with some degree of accuracy what was actually experienced at the time of the original event. A number of these *episodic* elements, when they occur contiguously and with an organisational 'framework' of knowledge interpreting the meaning of the perceptual information, can make up what Conway calls a *simple episodic memory*. The frame behind the episodic elements can be thought of as a summarised conceptual understanding of the event, and while its accuracy can be distorted by the knowledge, goals, and motivational state of the person, it has adaptive correspondence in that it reflects reality sufficiently to confer some benefit. Meanwhile, the episodic elements retain some of the specificity of the event details, though these may be lost over time, leaving only the general conceptual knowledge accessible to memory. Conway suggests that the perceptual episodic elements are mediated by posterior parietal regions of the brain, while the conceptual frame involves more anterior structures, meaning that the physical presence of an episodic memory in the brain is dispersed through a number of distinct cortical areas.

### 1.3 The Neuroanatomy of Episodic Memory

The increased availability of neuroimaging methods, such as positron emission tomography (PET) and fMRI, has allowed the accumulation of evidence for the neural

correlates of autobiographical episodic memory. Neural representations of episodic memories are complex and widespread throughout the brain, illustrating the multifaceted nature of vivid recollection and its diverse sensory, perceptual, spatiotemporal, and emotional components. The overall network of brain regions supporting episodic memory retrieval includes ventromedial and ventrolateral prefrontal cortex, posterior cingulate and retrosplenial cortex, and medial and lateral temporal cortex, in particular the hippocampal formation (Maguire, 2001; Svoboda, McKinnon, & Levine, 2006). These regions comprise what we now refer to as the *default mode network* (Buckner et al., 2008), a term derived from the fact that this broad network is notably active when the brain is in its resting or default mode, and deactivated when participants are engaging in some external stimulus-driven task (Raichle et al., 2001).

The discovery of this network as a default mode of brain function was an inadvertent result of the use of rest or 'fixation' states as control conditions in neuroimaging experiments. During such rest blocks, participants are asked to passively view a fixation cross, and this is used as a baseline for comparison with other blocks in which participants are actively engaging in some cognitive task. It was noticed that a core network of regions was more active during the baseline blocks than the task blocks, and it was therefore thought that this pattern of activation might reflect a 'default mode' of passive brain function. However, it was also shown that these regions that were active during rest (i.e. while participants were allowed to engage in unconstrained thought) overlapped with those active during a focused episodic memory retrieval task (Andreasen et al., 1995). Furthermore, when participants are interviewed about the sorts of thoughts they have during rest blocks, they tend to report frequent thoughts about past and future episodic experiences (Andreasen et al., 1995; Andrews-Hanna, Reidler, Huang, & Buckner, 2010; Stawarczyk, Majerus, Maj, Van der Linden, & D'Argembeau, 2011).

Therefore, while the 'rest' blocks are designed to induce a passive or inactive mental state, participants are just as mentally active as during the task blocks, the only difference being that their cognitive processes are more internally-focussed than when attending to external stimuli in the task blocks. Based on these and other similar findings, the 'default network' was redefined as one supporting mental simulation of scenarios that differ from the present one, including mental self-projection into the past and future (Buckner & Carroll, 2007; Spreng, 2012). It was further argued that this network, or at least part of it, is what allows us to imagine the perspectives of other people, based on activation during tasks requiring theory of mind (Buckner et al., 2008).

Meta-analyses have now enabled the parcellation of the default network into a collection of subsystems (Andrews-Hanna, 2011; Buckner et al., 2008; Kim, 2012): 1) the medial temporal lobe subsystem, supporting memory-related processes including the recall/simulation of episodic events, and consisting of the hippocampus, parahippocampal gyrus, retrosplenial cortex, and ventromedial prefrontal cortex (PFC), as well as 2) the dorsal medial prefrontal cortex subsystem, supporting inferences about the mental states of the self and others, and consisting of the dorsal medial PFC, temporoparietal junction, lateral temporal cortex, and temporal pole (Andrews-Hanna, 2011; though see Irish, Piguet, & Hodges, 2012 for a discussion of the validity of the functional attributions of these subsystems). The subsystems both converge on the posterior cingulate cortex and the anterior mPFC; these two regions serve as hubs linking the subsystems together. The following sections contain a discussion of the structures in these subsystems known to be critical for episodic memory.

#### 1.4 Default Network Structures Important for Episodic Memory

### 1.4.1 The Hippocampus and Medial Temporal Lobe

Within the default network's medial temporal lobe subsystem, the hippocampi – a pair of curved cortical regions in the medial temporal lobes that loosely resemble the shape of ram's horns – are some of the most fundamental structures for episodic memory. The importance of the hippocampus and the medial temporal lobe to memory became apparent in the 1950s, after a number of patients underwent a medial temporal lobectomy as a treatment for their intractable temporal lobe epilepsy; most of these patients (most notably, one referred to as H.M.) developed an immediate and profound amnesia for recent episodic events that had occurred prior to their surgery, and were also unable to store new memories for experiences that happened afterwards (Penfield & Milner, 1958; Scoville & Milner, 1957). Their general knowledge or semantic memory was largely intact, suggesting that the medial temporal lobe was only necessary for the reinstatement of an event's specific spatiotemporal context.

After many decades of research with both human and rodent subjects, the role of the medial temporal lobe in memory is now even clearer. The structures comprising the medial temporal lobe include the hippocampus proper, the entorhinal and perirhinal cortices, and the parahippocampal cortex. The hippocampus receives its input via the entorhinal cortex, which runs parallel to and below the more anterior extent of the hippocampus. The entorhinal cortex in turn receives much of its information from the laterally adjacent perirhinal cortex and also from the parahippocampal gyrus, which runs parallel to and below the more posterior aspect of the hippocampus and adjoins the perirhinal cortex (Lavenex & Amaral, 2000; Squire, Stark, & Clark, 2004). All of these structures have been shown to be vital for episodic memory and show wide-ranging connectivity with regions in the frontal, temporal, and parietal lobes. Regions in the ventral occipito-temporal cortex that project to these

components of the medial temporal lobe have been shown to be involved in the perception and representation of very specific items such as faces (fusiform face area), bodies and body parts (extrastriate and fusiform body areas) and places (parahippocampal place area) (Grill-Spector, 2003; Reddy & Kanwisher, 2006). More generally, input to the perirhinal cortex comes from object-related visual regions in the ventral stream, while input to the parahippocampal gyrus originates in dorsal stream parietal regions known for their involvement in spatial processing. The perirhinal and parahippocampal cortex both integrate information from higher-level cortical areas, and given that the hippocampus receives simultaneous input from both of these, this structure is anatomically well-placed to integrate visuospatial information even further (Lavenex & Amaral, 2000; Squire et al., 2004).

Despite the differential connectivity of the perirhinal and parahippocampal cortices, studies investigating their unique functions have not always yielded consistent results, other than to illustrate that complete damage to all parts of the medial temporal lobe produces more severe memory deficits than only partial damage (Squire et al., 2004). It has been shown that activity in perirhinal cortex predicts later source memory for individual objects, while activity in parahippocampal cortex predicts later source memory for scenes (Staresina, Duncan, & Davachi, 2011). The parahippocampal gyrus often seems to respond selectively to scenes and spatial stimuli (Epstein, 2008; Epstein, Harris, Stanley, & Kanwisher, 1999; Zeidman, Mullally, Schwarzkopf, & Maguire, 2012). Parahippocampal activity during encoding also predicts later recall of scenes (Staresina et al., 2011), and greater connectivity between the hippocampus and parahippocampal gyrus has been found during the encoding of scene-face than object-face combinations (Tambini, Ketz, & Davachi, 2010), suggesting that the structure has a role in storing spatial representations in memory. Bar et al. have argued, however, that the general function of the parahippocampal gyrus is to process rich contextual associations, and that the representation of scenes is just one example of this function (Bar,

Aminoff, & Schacter, 2008), though this issue is currently debated (e.g. Kravitz, Peng, & Baker, 2011). Others have shown that even though perirhinal and parahippocampal cortices are found to be maximally responsive to faces and scenes, respectively, when using univariate methods of analysis, representational similarity analyses reveal that specific face and scene representations are distributed throughout the medial temporal lobe (Liang, Wagner, & Preston, 2012). The specific functions of the perirhinal and parahippocampal cortices, therefore, are still controversial.

More generally, the broad connectivity of the hippocampus is thought to allow it to capture and index overall whole-brain patterns of activation that are elicited by the perception or mental representation of an event (Lavenex & Amaral, 2000). Reciprocal connections between the hippocampus and widespread neocortical regions are thought to allow a 'compressed' representation of the event to be stored in the hippocampus in the form of rapid synaptic changes (McClelland et al., 1995). It has been suggested that what we think of as memory recall involves a recapitulation or reactivation of these previously-experienced patterns of activity, resulting in the reinstatement of an earlier mental state. The way in which this occurs may be as a type of pattern completion; if part of the previously-elicited pattern of activity is re-encountered, activation may then spread within and from the hippocampus to the remaining components, resulting in the mental recreation of a previous episode (McClelland et al., 1995). An illustration of the mechanism of episodic recall comes from in vivo single-neuron recording in the medial temporal lobes of epilepsy patients, which shows that when participants view a stimulus for the second time, neuronal ensembles appear to 'jump' back in time and recreate the state they were in just prior to the first presentation of the stimulus (Howard, Viskontas, Shankar, & Fried, 2012).

The involvement of the hippocampus in memory retrieval may be time-limited in terms of the age of the memory, although this idea is heavily debated. Damage to the hippocampus often produces a graded amnesia, with patients suffering a complete loss of recent memories but with relative sparing of remote ones (Rempel-Clower, Zola, Squire, & Amaral, 1996; Scoville & Milner, 1957). Evidence from animal studies shows that damage to the hippocampus only impairs memory for learned associations when the damage occurs shortly after the memories are formed. For example, hippocampal lesions in monkeys result in impaired performance on an object discrimination task when the lesions are inflicted two or four weeks after learning has taken place, but not when inflicted after eight, twelve, or sixteen weeks (Zola-Morgan & Squire, 1990). These findings indicate that while the hippocampus may be necessary for initial storage and retrieval of episodic memories, after a certain period of time (possibly in the order of decades for humans), memory traces appear to be transferred elsewhere. This process is referred to as 'consolidation'. It is thought that while initial learning involves synaptic changes in the hippocampus that link to an overall pattern of representation in the neocortex, eventually, after the pattern has been reinstated enough times, there are incremental synaptic changes in the neocortex itself, such that the pattern can be restored without the assistance of the hippocampal index (McClelland et al., 1995).

There are, however, a number of amnesic patients whose deficits do not fit with this standard theory of consolidation, and who do not show a temporally graded amnesia. To explain such findings, others have argued in favour of *multiple trace theory* (Nadel, Samsonovich, Ryan, & Moscovitch, 2000), and more recently for the *transformation hypothesis* (Winocur & Moscovitch, 2011). They propose that the decline in hippocampal involvement in recall over time simply reflects a modification in the nature of the memory involved, such that some episodic memories become more semanticised and lose contextual detail after years of repeated retrieval. However, they argue that vivid recall of an event's

spatiotemporal context is always dependent on the hippocampus, regardless of the memory's age (Winocur & Moscovitch, 2011). It therefore follows that patients who are amnesic following hippocampal damage but who can nonetheless recall remote autobiographical events are relying on more semanticised forms of the memories. This idea of semanticisation of memories over time is supported by recent research showing that the various components of episodic memories decay at different rates, with memory for spatial configural details deteriorating more quickly than memory for the objects featured in the memories (Talamini & Gorree, 2012).

There has been a strong focus on the role of the hippocampus (particularly its posterior extent) in representing spatial information. This role in spatial processing may explain the specific involvement of the hippocampus for episodic memory as opposed to semantic or procedural memory, given that a defining characteristic of episodic memory is the successful reinstatement of an event's initial spatiotemporal context. Awareness of the importance of the hippocampus for representing spatial information began with the discovery of 'place cells' in the hippocampus that code for spatial distance by firing maximally in specific spatial locations (O'Keefe & Dostrovsky, 1971). The idea is further supported by the fact that damage to the hippocampus impairs spatial navigation (Chan et al., 2009), and posterior hippocampal volume increases over time with constant visuospatial retrieval, as in the case of London taxi drivers (Maguire et al., 2000; Woollett & Maguire, 2011). Other medial temporal lobe structures outside the hippocampus proper may also contribute to spatial processing, as it was recently reported that cells in the entorhinal cortex (termed 'path cells') code for whether participants are moving in either a clockwise or counter-clockwise direction in a virtual environment (Jacobs, Kahana, Ekstrom, Mollison, & Fried, 2010). The hippocampus itself may act as a sort of cognitive map, storing allocentric representations of space (i.e., in a map-based fashion, regardless of the specific position or perspective of the

observer) (O'Keefe & Nadel, 1978), though others believe that hippocampal involvement in spatial processing is simply one instance of this structure's general function in forming cross-modal associations or arbitrary associations between item or event features (Eichenbaum, 2007). Again, the involvement of the hippocampus in spatial navigation may be time-limited, as the right hippocampus is active when mentally navigating through a relatively new environment, but not when navigating through the same environment once it had become familiar one year later (Hirshhorn, Grady, Rosenbaum, Winocur, & Moscovitch, 2012).

In support of the idea that the hippocampus serves a broad range of functions, there is now increasing focus on the fact that the hippocampus may be involved in the representation not only of space, but also of time. It was recently found that there are some hippocampal neurons that represent the temporal organisation of events, referred to as 'time cells' (MacDonald, Lepage, Eden, & Eichenbaum, 2011). Furthermore, the hippocampus has also been shown to be active when separately retrieving both spatial and temporal information after having navigated through a virtual city (Ekstrom, Copara, Isham, Wang, & Yonelinas, 2011). Critically, in this study the two types of information were purposefully not associated with each other (unlike in typical real-life episodic events, when proximal locations are usually visited at points in time that are close together) and retrieval of spatial details could not facilitate retrieval of temporal details.

Hippocampal function is somewhat lateralised, with activation in the left hippocampus more often associated with episodic and autobiographical memory tasks (Svoboda et al., 2006), and activation in the right hippocampus associated with the processing of spatial locations from an allocentric perspective (Burgess, Maguire, & O'Keefe, 2002). For example, the most significant distinguishing feature of right as distinct from left temporal lobe atrophy (including the hippocampus) is a tendency to get lost (Chan et al., 2009), and

right hippocampal volume is associated with impairments in allocentric spatial navigation in patients with mild cognitive impairment or Alzheimer's disease (Nedelska et al., 2012). However, patients with right-sided damage also experience episodic memory impairments, suggesting that memory and spatial functions are closely integrated. Episodic events take place within a spatial context, and the right hippocampus has been shown to represent visuospatial information in the context of episodic memories. Right hippocampal activity is significantly greater when participants retrieve either personal autobiographical memories or memories of video clips (both of which contain vivid visual and spatial detail), as compared to when they retrieve memories of narrative stories (for which vivid detail was rated as significantly lower than in AMs and clips; St-Laurent, Moscovitch, & McAndrews, 2010). While both hippocampi are important for episodic memory, the relative contributions of the right and left hippocampus to the retrieval of autobiographical memories may change according to the temporal distance of the memories. It appears that the right hippocampus becomes less important for the retrieval of more remote events, likely because some of the visuospatial detail is lost as memories age (Maguire & Frith, 2003).

In addition to the differences in hippocampal lateralisation, there is evidence to suggest there are functional differences across the longitudinal axis of the hippocampus. The anterior hippocampus responds to novel stimuli that belong to a wide variety of categorical domains (e.g. faces, scenes, words, etc.; Liang et al., 2012). It has also been shown that activity in the left anterior hippocampus is significantly correlated with the presentation of novel relative to familiar words, and that activation in this area is highest when participants are highly confident that the stimulus has not been seen before (Daselaar, Fleck, & Cabeza, 2006). For this reason, some have characterised the anterior hippocampus as a 'novelty detector'.

Novel stimuli are by nature yet-to-be encoded, and thus it is difficult to distinguish between the processes of novelty detection and encoding when participants are exposed to new items. The very act of encoding may be better understood as the detection and subsequent retention of a novel condition that contradicts what is expected or predicted (Henson & Gagnepain, 2010). Indeed, there is a significant amount of evidence suggesting that the anterior hippocampus is important for encoding, particularly the encoding of associations between arbitrary items or features (Giovanello, Schnyer, & Verfaellie, 2009). Bilateral activity in the anterior hippocampus is highly correlated with successful encoding of the face-name associations, as opposed to the encoding of faces alone (Chua, Schacter, Rand-Giovannetti, & Sperling, 2007; Sperling et al., 2003). It has also been shown that anterior hippocampal activity is higher during the process of encoding associations than when retrieving them, and that this effect is particularly strong for cross-domain perceptual associations as opposed to semantic ones (Prince, Daselaar, & Cabeza, 2005). More recently, Spaniol et al. (2009) conducted an activation likelihood estimation (ALE) meta-analysis of 26 studies of encoding success and 30 studies of retrieval success, contrasting ALE maps for each process. This analysis confirmed that the anterior hippocampus was more reliably activated during successful encoding than during successful retrieval.

In contrast, activation within the posterior hippocampus is associated more with retrieval than encoding (Prince et al., 2005). An encoding-retrieval distinction along the long axis of the hippocampus, with anterior regions supporting encoding and posterior regions supporting retrieval, was proposed over a decade ago (Lepage, Habib, & Tulving, 1998; Schacter & Wagner, 1999). Further evidence for this anterior-posterior distinction comes from research on London taxi drivers. Their profession requires constant retrieval of visuospatial associations but less often the formation of new ones. Interestingly, they exhibit a loss of volume in the anterior hippocampus, but a relative increase in posterior hippocampal

volume in comparison to age-matched controls (Woollett & Maguire, 2009). They also show relative impairments on memory tasks that require encoding of new visuospatial locations. Taken together, these findings support the idea of an encoding-retrieval gradient in the hippocampus, although they may also be explained by the proposition that the anterior hippocampus responds to domain-general novel stimuli, while the posterior hippocampus is specialised for spatial processing (Liang et al., 2012). Others have found that posterior, but not anterior, hippocampal volumes significantly predict performance on a variety of tests of recollective episodic memory, not just those involving spatial stimuli (Poppenk & Moscovitch, 2011).

Specialisation along the longitudinal axis of the hippocampus may be explained by differential connectivity along the hippocampus with other medial temporal lobe regions: the perirhinal cortex (associated with visual recognition of objects) displays intrinsic functional connectivity with the anterior hippocampus, while the parahippocampal cortex (associated with spatial processing) shows connectivity with the posterior hippocampus; specialisation within the hippocampus may therefore reflect the nature of the input to that region (Kahn, Andrews-Hanna, Vincent, Snyder, & Buckner, 2008; Libby, Ekstrom, Ragland, & Ranganath, 2012). However, as findings have not always been consistent, the functional specialisation of the anterior and posterior hippocampus is still under investigation.

### 1.4.2 The Lateral and Anterior Temporal Lobes

The lateral and anterior temporal lobes are involved in semantic memory, but are often active during retrieval of autobiographical episodic memories as well, further reflecting the interdependence of semantic and episodic information. Patients with semantic dementia, who typically suffer bilateral anterior temporal atrophy, show a corresponding loss of semantic memory, particularly in word-finding due to the frequent left-lateralisation of

atrophy (Hodges, Patterson, Oxbury, & Funnell, 1992). Although patient evidence strongly implicates these regions in semantic memory, anterior temporal activation is not always found in fMRI studies of semantic memory; this may reflect the fact that these areas are particularly susceptible to signal dropout and distortions (Visser, Jefferies, & Lambon, 2010). When these issues are minimised, reliable activation can be found in lateral and anterior temporal lobes during semantic tasks such as verbal semantic categorisation (Visser, Embleton, Jefferies, Parker, & Ralph, 2010). The specific function of the anterior temporal lobes is still not perfectly clear; regions within this area (including temporal poles as well as anterior entorhinal and perirhinal cortex, anterior fusiform, and temporal gyri) may serve as conceptual hubs that link together semantic representations, or simply may store unique representations of specific entities (e.g. people, landmarks), conceptual social information (Simmons & Martin, 2009), or conceptual autobiographical information such as generic or repeated events (Addis, McIntosh, Moscovitch, Crawley, & McAndrews, 2004; Graham, Lee, Brett, & Patterson, 2003). The anterior and lateral temporal lobes have been characterised as integrating converging multi-modal conceptual information that has been abstracted from original perceptual experiences, e.g. knowledge about an item's visual appearance and knowledge of its function (Binder & Desai, 2011).

### 1.4.3 The Ventromedial Prefrontal Cortex

The prefrontal cortex (PFC), particularly the ventral aspect of the medial PFC, plays an organisational and evaluative role in episodic autobiographical memory retrieval. In order to retrieve a specific episodic memory, it is often necessary to engage in iterative and effortful searching that involves a number of steps (Cabeza & St Jacques, 2007).

Ventrolateral regions of the PFC play a role in the initial searching for and locating of specific episodic memories, and particularly in the process of specifying appropriate search cues that point to relevant memories (Conway & Pleydell-Pearce, 2000; Moscovitch, 1992).

Ventromedial PFC then evaluates the suitability of the recovered memory trace, determining whether or not the memory is accurate and fits the search criteria (Conway, Pleydell-Pearce, Whitecross, & Sharpe, 2003; Holland, Addis, & Kensinger, 2011, Moscovitch & Winocur, 2002). Activation in these regions tends to be lateralised to the left hemisphere, perhaps reflecting the verbal or semantic information used in the search process (Svoboda et al., 2006). More medial components of the PFC are also recruited by tasks that are self-referential in nature, and so are particularly active during autobiographical memory retrieval and the evaluation of the self-relevance of retrieved memories (e.g., viewing photos that were taken either by the self or by someone else; Cabeza et al., 2004; Martinelli, Sperduti, & Piolino, 2012). The ventromedial prefrontal cortex may play an integrative role, facilitated by its strong reciprocal connectivity with limbic regions such as the hippocampus, ventral striatum, and amygdala, therefore incorporating information about an event's spatiotemporal context with reward contingencies and emotional valence to create an overall sense of motivational salience (Nieuwenhuis & Takashima, 2011).

### 1.4.5 The Posterior Medial Parietal Cortex

Regions of the posterior medial parietal cortex, including the posterior cingulate cortex (PCC), the retrosplenial cortex, and the precuneus<sup>1</sup>, support mental imagery and both imagined and physical navigation from an egocentric perspective, as opposed to the allocentric spatial representations mediated by the hippocampus. In other words, these posterior parietal regions underpin the ability to remember and imagine what a scenario might look like from a first-person perspective, as if looking out from one's own eyes.

The posterior cingulate gyrus and retrosplenial cortex both show strong connectivity with the hippocampus, especially with its posterior aspect and the parahippocampal cortex

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<sup>&</sup>lt;sup>1</sup> The precuneus is not universally accepted as being part of the default network because of its minimal connectivity with the medial temporal lobe (Buckner et al., 2008).

(Sugar, Witter, van Strien, & Cappaert, 2011; Vogt, Hof, & Vogt, 2004), and the retrosplenial cortex in particular may serve to translate and update movements in space (both actual physical movements as well as imagined ones) such that the image seen from a first-person egocentric perspective properly corresponds to the topographical layout of the spatial location as represented in the hippocampus (Lambrey, Doeller, Berthoz, & Burgess, 2012; Vann, Aggleton, & Maguire, 2009). The precuneus, with major connections to the retrosplenial and posterior cingulate cortex, mediates these first-person perspective-dependent mental images, and is active in a wide range of tasks requiring mental imagery, including motor imagery (e.g. imagining moving through space) but also mental rotation and mental navigation (Cavanna & Trimble, 2006).

The posterior cingulate cortex has broad visuospatial functions, such as in the assessment of large visual scenes (Vogt et al., 2004), but this heterogeneous region has been associated with a variety of domains and therefore has no single unified function (Pearson, Heilbronner, Barack, Hayden, & Platt, 2011). For example, while the more caudal aspect of the PCC has been implicated in studies of episodic memory, the more rostral portion may be important for the perception of pain (Nielsen, Balslev, & Hansen, 2004). The PCC has been identified as a cortical hub with expansive connectivity (Hagmann et al., 2008), which means that it likely serves to functionally integrate a range of processes, including emotional, reward, and long-term memory processes. One hypothesis about the PCC's more comprehensive and overarching role is that it serves to detect changes in the environment and direct the accompanying necessary changes in behaviour (Pearson et al., 2011).

# 1.5 Memory and Imagination

William James (1890, p. 643) had the insight to notice that our representations of the past and future are linked, and he wrote about "...conceived time, past and future, into one

and form a systematic order of them by giving to each a date." When the concept of episodic memory was first developed, its focus was on the domain of remembering past experiences (Tulving, 1972). But it has now become apparent that our ability to remember the past is intimately related to our capacity for imagining the future. Bartlett (1932, p. 219) noticed early on that our ability to form brief mental images allows us flexible use of our memories; "By the aid of the image ...a man can take out of its setting something that happened a year ago, reinstate it with much if not all of its individuality unimpaired, combine it with something that happened yesterday, and use them both to help him solve a problem with which he is confronted today." This link between remembering and imagining was cemented further by neuropsychological observations of amnesic patients who showed parallel deficits in both abilities, and neuroimaging evidence that the two processes have shared neural substrates (Schacter et al., 2008). Consequently, the episodic system has now been reconceptualised as a broader mechanism for simulation of events, with which we can voluntarily re- or pre-experience events in rich detail and in both the past and future.

The amnesic patient K.C. is one of the early cases that contributed to this idea (Tulving, 1985b). After suffering a head injury in a motorcycle accident, he could not recall a single specific event from his past, and more interestingly described experiencing mental 'blankness' when trying to imagine what he might be doing in the future. Despite these deficits, K.C.'s personal semantic memory and general knowledge of the world was intact (Rosenbaum et al., 2005). Observations of this patient prompted Tulving to suggest that the ability to remember episodes from the past is vital for imagining the future. A decade later, it was noted that patients with memory loss following damage to the prefrontal cortex also exhibited a lack of self-concern, limited plans and ambitions for the future, and a reduced desire to daydream and self-reflect (Wheeler et al., 1997). Since these patients also typically

retained their semantic knowledge, this finding offered even more support for the idea that in the absence of recollective episodic memory, the ability to mentally travel forward in time is impaired.

Amnesic patient D.B. was reported to show a similar pattern of parallel deficits following cardiac arrest and hypoxic brain damage (Klein, Loftus, & Kihlstrom, 2002). D.B. showed profound impairment on episodic memory tasks, but his semantic knowledge was mostly spared. Interestingly, on specific measures of temporal awareness, he was unable to provide details about events in his own personal past or future, but he possessed adequate semantic knowledge of both past and future events in the public domain. In concordance with Wheeler, Stuss, and Tulving's (1997) arguments, this suggests that self-referential, episodic mental time travel can be dissociated from semantic awareness of general temporal knowledge. Moreover, it suggests that *episodic* memory plays a particularly important role in imagining future *episodes*, but that semantic memory is sufficient to support semantic forms of future thinking (Atance & O'Neill, 2001).

New findings from patients with semantic dementia illustrate, however, that episodic future thinking requires the contribution of both episodic and semantic elements. Semantic dementia patients, as mentioned previously, have anterior temporal lobe damage and corresponding semantic memory deficits, but intact episodic memory (Hodges et al., 1992). Such patients have sometimes been shown to recall events from their past in as much detail as controls, but are specifically impaired at imagining detailed future events (Irish, Addis, Hodges, & Piguet, 2012). This evidence would suggest that while access to memories of past events is necessary for episodic future thinking, it is also necessary to draw upon conceptual knowledge when constructing and imagining a new future event, perhaps using this information as an organisational framework in which to place the episodic details.

Other evidence from amnesic patients has specifically implicated the medial temporal lobes in the ability to imagine the future (Hassabis, Kumaran, Vann, et al., 2007). Five patients with damage restricted to the bilateral hippocampus were asked to imagine future scenarios in response to a verbal cue. Compared to controls, the patient group's descriptions of the imagined events were lacking in richness and spatial coherence. Specifically, the details that they did manage to provide seemed fragmented and incompletely bound together. It was thus argued that the hippocampus also has a significant role in imagining the future, particularly in binding details together and integrating them into a spatial context.

A variety of other studies have illustrated the close relationship between past and future thought. The developmental trajectory of episodic memory and future thinking are similar, with both abilities emerging gradually at approximately four years of age (Atance & O'Neill, 2005; Suddendorf & Corballis, 1997). This emergence corresponds with the ability of children to imagine themselves taking different perspectives (Russell, Alexis, & Clayton, 2010). When children are asked to imagine future scenarios and select one of three items that will help them in those scenarios, it is only by five years of age that children are not distracted by items that are semantically related to the scenario but in fact unhelpful to them (Atance & Meltzoff, 2005). The ability to accurately describe plans for the next day increases significantly between the ages of three and five years (Busby & Suddendorf, 2005), and when children are asked what they did yesterday and what they will do tomorrow, the ability to answer the former question predicts the ability to answer the latter (Suddendorf, 2010). Such a link between the development of memory and imagination further supports the idea of similar underlying processes.

At the other end of the lifespan, parallel changes are observed for both abilities. Older adults tend to produce significantly fewer episodic details than younger adults both when

remembering past events and imagining future ones, and the number of details generated for past events is significantly correlated with the number of details generated for future ones. (Addis, Musicaro, Pan, & Schacter, 2010; Addis, Wong, & Schacter, 2008). Such parallel declines in past and future are evident when older adults are cued with words, and also when they are asked to imagine events using pictorial cues (Gaesser, Sacchetti, Addis, & Schacter, 2011). Instead of being able to describe vivid visuospatial aspects of the scenes they imagine, older adults are instead more likely to provide semantic or conceptual information that may or may not be relevant to their imagined events. Furthermore, the number of details generated by older adults is highly associated with their scores on a test of relational memory, which, given the role of the hippocampus in relational memory (Konkel & Cohen, 2009), again points to the importance of the medial temporal lobes for imagining the future (Addis et al., 2008). When constructing imagined future events, older adults do not show the same level of activity as younger adults in regions known to be important for vivid episodic detail, such as the hippocampus, parahippocampal gyrus, and the precuneus, (Addis, Roberts, & Schacter, 2011). Furthermore, while elaborating on their imagined events, older adults show greater activation than young adults in lateral temporal areas associated with semantic processing (Addis, Roberts, et al., 2011). When participants rate how much detail they have generated in their imagined events, the detail ratings of young adults are linearly associated with hippocampal activity, while in older adults the ratings correlate with activity in the lateral temporal lobes (Addis, Roberts, et al., 2011). The tendency for older adults to focus on semantic information instead of episodic detail is therefore not only a behavioural phenomenon, but is also reflected in the neural activity underlying older adults' imagined events.

Electrophysiological and neuroimaging studies have investigated the neural networks involved in both remembering the past and imagining the future, and the finding of a

common neural network underlying both processes supported the earlier data from patients suggesting a relation between them. Electroencephalography (EEG) evidence shows similar significant left frontal activation for the construction of both remembered and imagined events (Conway et al., 2003). PET and fMRI studies have indicated that both remembering and imagining tend to produce similar activation in a core network of regions, including medial prefrontal, medial temporal, and posterior parietal cortices (Addis, Wong, et al., 2007; Hassabis, Kumaran, & Maguire, 2007; Okuda et al., 2003). This common network activation points to a similar underlying cognitive process, potentially that mental images acquired in the past and stored in posterior areas are then reactivated during both remembering and imagining via direction from prefrontal regions (Szpunar et al., 2007).

As a result of the converging evidence linking remembering and imagining, Schacter and Addis formulated their *constructive episodic simulation* hypothesis, which suggests that in order to simulate hypothetical situations, details are extracted from episodic memories of past experiences and recombined in a coherent way (Addis & Schacter, 2012; Schacter & Addis, 2007). This theory fits well with the idea of episodic memory for the past being highly constructive in nature (Bartlett, 1932; Neisser, 1986), with events encoded in a piecemeal fashion instead of as a fixed 'instant-replay' style recording. As mentioned previously, a constructive system is an economical one, as specific details need not be represented in the brain as many times as the person experiences them. The ability to draw on these details in a novel way to imagine future experiences may be simply an adaptive extension of the inherent system design, such that the outcomes of past experiences can flexibly inform choices made about upcoming events.

An alternative hypothesis for the commonality underlying remembering and imagining was proposed by Hassabis and Maguire (2007). They argue that both of these

abilities involve the construction of three-dimensional spatial scenes, requiring the mental representation of a location's spatial layout and the insertion of various event elements at various places within it. This *scene construction* hypothesis was based on the known role of the hippocampus in spatial navigation (Maguire et al., 2000), as well as on their findings that patients with hippocampal damage imagine events that are significantly less spatially-coherent than the events of normal controls (Hassabis, Kumaran, Vann, et al., 2007). This evidence suggested that the role of the hippocampus in imagining the future is in spatially binding the elements of the event into the scene.

The scene construction hypothesis does not necessarily conflict with the constructive episodic simulation hypothesis, as they both propose that some form of construction is required in both remembering and imagining. It is likely that both theories are correct and complementary, in that episodic details (e.g. people, locations, and objects) are extracted from previous experiences and then rebound (and in the case of future events, rearranged) into new three-dimensional scenes. Spatial and contextual information therefore provides a vital platform upon which to build these scenarios. It has been found that the familiarity of a simulated event's location determines how vividly and clearly it will be imagined (Arnold, McDermott, & Szpunar, 2011a; Szpunar & McDermott, 2008), which is consistent with the idea of the context as a fundamental base for episodic simulation. Furthermore, remembering and imagining events that take place in familiar locations both similarly engage posterior parietal regions (e.g. posterior cingulate cortex and parahippocampal gyrus) significantly more than remembering and imagining events in unfamiliar locations (Szpunar, Chan, & McDermott, 2009). This finding suggests that the similar engagement of posterior parietal regions during remembering and imagining may reflect the fact that both tasks typically require the retrieval of familiar locations. The hippocampus, known for spatial processing (Kumaran & Maguire, 2005; O'Keefe & Nadel, 1978), is particularly important for the

generation of specific imagined future events as opposed to general or routine imagined future events that might happen repeatedly, perhaps also reflecting the precise spatiotemporal context characterising events that are highly specific (Addis, Cheng, Roberts, & Schacter, 2011). All of this evidence supports the idea that clear contextual information serves as a foundation for episodic processes.

## 1.6 Functions of Imagining the Future

According to the constructive episodic simulation hypothesis and related perspectives, the ability to draw on episodic details in a novel way to imagine future experiences is a design feature of episodic memory (Schacter & Addis, 2007; Suddendorf & Corballis, 2007). As noted by Schacter (in press), such a feature must be sufficiently beneficial to the organism that it is worth the associated cost in memory errors that can result from occasionally mistakenly combining those elements. Simulating future events therefore ought to serve important functions for an organism, and several lines of research indicate that this is so.

Conway (2009) suggests that the relationship between remembering and imagining reflects their common purpose: to allow us to maintain goals that refer to time periods extending beyond our immediate circumstances. This idea is based on his experiment in which participants describe as many of their own specific memories as possible for each day prior, up to the point of five days before the present, and then imagine specific upcoming future events in the same manner but in the forward direction in time (Conway, 2009). The number of specific events listed by participants decreases steadily as time progresses either into the past or future, and Conway interprets the range of days on which participants could list multiple specific events to reflect a stable *remembering-imagining window*. This window allows a person to have simultaneous awareness of both recent and approaching events, and it

supports the idea that the function of our ability to remember and imagine is to keep a constant and current mental representation of our more immediate goals.

Others have also found that the numbers of remembered and imagined events that had taken or would take place near the present is relatively high, and then decreases linearly with time in both the past and future directions (Spreng & Levine, 2006). In addition, temporally close events are more specific, detailed, and vivid than distant ones (Trope & Liberman, 2003), regardless of whether they are remembered in the past or imagined in the future (D'Argembeau & Van der Linden, 2004), although this may be due to difficulty in imagining a clear location in which to set temporally distant future events (Arnold et al., 2011a). Imagining specific personal goals and the steps required to achieve them engages the same default network regions seen when people imagine future events in general (Gerlach, Spreng, Gilmore, & Schacter, 2011; Spreng, Stevens, Chamberlain, Gilmore, & Schacter, 2010). Furthermore, imagined future events that are relevant to participants' personal goals engage medial prefrontal and parietal regions of the default mode network more than imagined events that do not relate to their personal goals (D'Argembeau et al., 2010). When asked to imagine and describe the detailed steps required to solve open-ended real-world problems, patients with temporal lobe epilepsy (and the corresponding episodic memory deficits that accompany medial temporal lobe damage) describe fewer relevant steps than controls (Sheldon, McAndrews, & Moscovitch, 2011), suggesting an association between episodic processes and goal-directed problem solving. These findings converge on the idea that the processes of remembering and imagining serve as a way to inform present behaviour while maintaining immediate personal aims.

Mental simulation of the future has other adaptive functions in addition to maintaining personal goals. Imagining specific future events reduces temporal discounting, which is the

general tendency to assign relatively less value to a large reward in the distant future than to a smaller reward that could be acquired immediately (Benoit, Gilbert, & Burgess, 2011). In other words, imagining the specific act of receiving the large reward in the distant future reduces the tendency to devalue it. Therefore, imagining future events allows a person to make decisions that he or she may not have otherwise made after simply considering the immediate situation, and these decisions are generally found to be ultimately more beneficial. People often have difficulty following through with their good intentions for the future, frequently because their plans are too vague or they are disproportionately influenced by more immediate goals. Planning in advance the exact actions one will take when faced with a specific situation removes the influence of distracting immediate factors on decision-making. Deciding to engage in behaviour X when in situation Y, or forming an 'implementation intention' (Gollwitzer, 1999) creates a mental representation of the goal behaviour for which recall is triggered by encountering the situation itself. This ease of recall allows the goaldirected behaviour to become almost automated and therefore less influenced by distraction. Consequently, the ability to imagine events that might happen in the future allows people to make more advantageous decisions.

A higher-level cognitive role of episodic memory is in maintaining a stable and healthy sense of self, and this function has now been demonstrated to extend to episodic simulation of the future. The ability to remember past autobiographical events, particularly from early adulthood, seems to be vital for preserving a strong identity (Addis & Tippett, 2004). Highly significant memories that are personally meaningful and described as 'self-defining' may be particularly important for maintaining identity and for the development of self-worth (Sutin & Robins, 2005). It has now been shown that people have corresponding self-defining imagined future events as well as remembered past events (e.g. 'when I get married', or 'when I graduate from university'), and these self-defining future events carry

significant personal meaning, create a sense of self-continuity, and contribute to self-esteem (D'Argembeau, Lardi, & Van der Linden, 2012). When people imagine episodic events that will happen in their future, these events tend to cluster around time periods in which participants expected to acquire certain future self-images or self-definitions (e.g. 'I will be a parent'), suggesting that these episodic future events are tied to semantic representations of the future self (Rathbone, Conway, & Moulin, 2011). Furthermore, manipulating participants' perceived self-efficacy alters the way in which they imagine future episodic events; those prompted to identify themselves as having high self-efficacy imagine events that are more specific and that contain more positive words (Brown, Dorfman, Marmar, & Bryant, 2012), further illustrating the mutual influence of episodic future thinking and self-related constructs.

Emotional valence significantly affects episodic processes, including the simulation of future events. For example, most people have an *optimism bias*, or a general tendency to expect that positive things will happen to them in the future, as well as a corresponding inclination to underestimate the likelihood of negative events happening to them personally (Sharot, 2011). When participants imagine future events that have either positive or negative emotional connotations (e.g. 'winning an award', or 'the end of a romantic relationship'), positive events are perceived as being closer in time to the present than negative ones, and are also rated as eliciting a stronger sense of actually experiencing the event (Sharot, Riccardi, Raio, & Phelps, 2007). Imagined events that have positive emotional connotations are more likely to be remembered across long delays when participants are asked about them later than are imagined events with negative connotations (Szpunar, Addis, & Schacter, 2012). These tendencies have been shown to be important for maintaining mental health, as the strength of a person's optimism bias is associated with their overall well-being (Schweizer, Beck-Seyffer, & Schneider, 1999). Optimism bias is also negatively correlated with depressive

symptoms, such that people who are more optimistic are less likely to experience symptoms of depression (Strunk, Lopez, & DeRubeis, 2006). The ability to imagine an optimistic future is therefore beneficial to the individual.

Despite the broad importance of this ability, there are individual differences in the ability to mentally project oneself into the future. It would be expected that individuals who spend a great deal of time considering hypothetical future scenarios in the course of their daily lives would eventually become 'expert' at episodic simulation. In support of this idea, those who score highly on the 'Future' category of the Zimbardo Time Perspective Inventory (Zimbardo & Boyd, 1999), indicating that their mind is often turned towards the future, tend to show correspondingly higher scores on measures of visual details and vividness when they imagine future events (D'Argembeau, Ortoleva, Jumentier, & Van der Linden, 2010) and report feeling a strong sense of pre-experiencing their imagined events (Arnold, McDermott, & Szpunar, 2011b). Furthermore, those who score highly on measures of visual imagery tend to imagine future events that contain more visual, sensory, and emotional details, and are set in a clearer spatiotemporal context (D'Argembeau & Van der Linden, 2006). There are also hints of cultural and gender differences in episodic simulation. For instance, females have been found to provide more specific episodic details in their imagined events than males, and Western European participants provide more specific details than Chinese participants (Wang, Hou, Tang, & Wiprovnick, 2011).

## 1.7 Differences Between Remembering and Imagining

Remembering and imagining are, of course, not identical processes. We must have some way of distinguishing between experienced and hypothetical events so that we can accurately guide our behaviour based on the realities of our environment. In support of this idea, it has been shown that some of the phenomenal characteristics known to accompany the

process of remembering the past are slightly different for simulated future events. For example, memories of actual past experiences tend to have significantly more detailed sensory and perceptual features than imagined future events (D'Argembeau & Van der Linden, 2004; Gamboz, Brandimonte, & de Vito, 2010; Johnson & Raye, 1981) and therefore engage visual regions to a greater degree (Addis, Pan, Vu, Laiser, & Schacter, 2009; Conway et al., 2003; Weiler, Suchan, & Daum, 2010). Real memories also contain more detailed spatial and temporal contextual information, while imagined events are more schematic (Johnson & Raye, 1981). Moreover, the clarity and sensory detail of memories for imagined events also dissipates much more rapidly over time as compared to memories of real events (Suengas & Johnson, 1988).

When participants are asked to imagine future events in laboratory-based settings, they are often instructed to generate a highly specific scenario, and in these cases, the imagined future events generally take place in precise spatial and temporal contexts (Addis, Cheng, et al., 2011). However, when spontaneous future thoughts are examined instead (i.e. naturally occurring thoughts of the future that were not prompted by some experimental task), they tend to be less specific and more semantic in nature than spontaneous thoughts of the past (Anderson & Dewhurst, 2009). Therefore, naturalistic future thinking seems to be generally more conceptual and less likely to involve specific and detailed episodic scenarios than both laboratory future tasks and thinking about real past experiences. However, it is also noted that repeated rehearsal of apperceptive aspects of both remembered and imagined events (i.e. dwelling on the thoughts and feelings that one would or did have during the event) results in the two types of events being more easily confused (Suengas & Johnson, 1988). More specifically, with this sort of rehearsal that emphasizes emotional components, the sensory and perceptual detail of real memories becomes more difficult to access, while the emotional and cognitive content of the events increases. Consequently, the characteristics

that typically distinguish between real and imagined events become less clear. So while remembering and imagining are distinct in many ways, this distinction can be affected by factors such as rehearsal.

Some key differences between remembering and imagining appear to emerge when the event is first being formulated. Both processes involve two phases: 1) the initial construction of an event and 2) the process of mentally elaborating upon it once constructed (Conway et al., 2003). When recalling a memory of a past experience, participants engage in a search process to locate a memory that fits with the provided cue or search criteria, after which the previously-experienced representation can be reactivated. In contrast, when imagining a new future event, depending on the task and cue involved, disparate episodic details from multiple memories must be located and then incorporated into the new scenario. Therefore, imagined future events have elements of generation, recombination, and construction that are more intensive than for remembered past events. In an fMRI study, Addis, Wong, and Schacter (2007b) had participants indicate with a button-press once a past or future event had been generated, after which they elaborated on the constructed event in as much detail as possible. During initial construction of these events, there was significant differentiation in active regions between past and future. The ventrolateral prefrontal and right frontopolar cortices were more active during construction of future than past events. Furthermore, while the left hippocampus was recruited for construction in both temporal directions, the right hippocampus showed selective engagement for the construction of future events (Addis, Wong, et al., 2007). In contrast, during elaboration, these differences were no longer present and a common core network of activation was again observed for both remembering the past and imagining the future, including left medial prefrontal cortex and medial posterior regions.

When the results of the above study were re-analysed with respect to the amount of vivid detail generated for each event, the roles of several brain regions in imagining the future were even more clearly delineated (Addis & Schacter, 2008). It was found that during elaboration of future events, activity in the right frontal pole and anterior hippocampus was directly related to the amount of detail in each event, as rated by the participant. Given that frontopolar activation has previously been found to correlate with the degree of intentional thought comprising an imagined event (Okuda et al., 2003), the frontal pole activity in this study may reflect the increased intentional information that accompanies thinking about detailed future plans. The anterior hippocampal activity may come from the creation of multiple new associations between the details that are incorporated and encoded into a coherent event (Giovanello et al., 2009).

# 1.8 The Hippocampus and Episodic Simulation of the Future

The patient and neuroimaging evidence discussed above indicates that the hippocampus may play an important role in imagining the future (Addis & Schacter, 2012; Schacter & Addis, 2009), over and above its already well-established role in remembering the past. This is unsurprising, given that a core function of the hippocampus is to bind together disparate features of stimuli and form new associations (Eichenbaum, 2001; Eichenbaum et al., 2011), and these processes are fundamental to the representation of new, multifaceted representations. The amount of recombination and binding required to imagine an event depends largely on how similar it is to previous experiences, such that imagined events that are unlikely to occur in real life engage the right anterior hippocampus to a greater extent than more probable events (Weiler, Suchan, & Daum, 2009). The importance of this structure for imagining the future also supports Addis and Schacter's *constructive episodic simulation* hypothesis and Hassabis and Maguire's *scene construction* hypothesis, since an integral part

of these ideas is that simulation depends on the binding together of details from previouslyexperienced events into new representations of spatial scenes.

Nonetheless, the role of the hippocampus in imagining the future is currently controversial, due to conflicting evidence for and against the ability of hippocampal amnesic patients to imagine future events. Building on the previously discussed findings reported by Hassabis and colleagues (2007) demonstrating scene construction deficits in hippocampal amnesics, some recent findings have illustrated further that amnesic patients are impaired at episodic simulation of the future (Andelman, Hoofien, Goldberg, Aizenstein, & Neufeld, 2010; Kwan, Carson, Addis, & Rosenbaum, 2010; Race, Keane, & Verfaellie, 2011; Zeman, Beschin, Dewar, & Della Salla, 2012), and that this deficit is in the act of constructing specific episodic scenarios, rather than in simply considering outcomes that might happen in the future (Kwan et al., 2011). In contrast, others report that amnesic patients perform as well as controls on episodic simulation tasks (Hurley, Maguire, & Vargha-Khadem, 2011, though note that this was a developmental amnesic patient; Squire et al., 2010).

It has been proposed that the timing of hippocampal damage may affect the extent of the patient's deficit in episodic simulation, such that patients who sustained damage in infancy or early childhood may be less impaired as adults than those whose damage was acquired in adulthood. This idea is based on two lines of evidence. First, developmental amnesic patient Jon, who suffered 50% bilateral loss of his hippocampal tissue perinatally, can imagine future events that are as coherent and detailed as those of control participants (Maguire, Vargha-Khadem, & Hassabis, 2010). Jon's ability to imagine future events is attributed to his residual hippocampal tissue, which is active during autobiographical memory retrieval (Maguire, Vargha-Khadem, & Mishkin, 2001), and scene construction (Mullally, Hassabis, & Maguire, 2012). Second, a group of amnesic children with hippocampal damage

resulting from neonatal hypoxia and ischemia were also shown to be unimpaired at imagining fictitious experiences (Cooper, Vargha-Khadem, Gadian, & Maguire, 2011), although their later recall of these imagined experiences was significantly worse than that of control children. These two sets of findings have been explained either by potentially active residual hippocampal tissue (as confirmed in Patient Jon) or by the reliance on a store of accumulated semantic knowledge which may be able to support scene construction (Addis & Schacter, 2012). This theory of the timing of damage does not explain the finding that patient H.C., a developmental amnesic patient, shows deficits in imagining the future (Kwan et al., 2010), although this result is disputed (Hurley et al., 2011).

There are several other factors that may explain the conflicting findings with amnesic patients, including the way in which simulation ability is measured. The various experiments investigating this issue have used a variety of different tasks. For instance, in the adapted Autobiographical Interview (Addis et al., 2008; based on Levine et al., 2002) a single generic cue word is provided and the participant has three minutes to describe as much detail about an imagined event as possible. This task has been used to assess the number of episodic and non-episodic details comprising amnesic patients' future events (Squire et al., 2010). In contrast, the scene construction task (Hassabis, Kumaran, Vann, et al., 2007) involves provision of the general scenario and the participant is required to build upon the preconstructed scene, at times receiving specific prompts about visuospatial information (Berryhill, Picasso, Arnold, Drowos, & Olson, 2010; Hurley et al., 2011; Mullally et al., 2012). The memory and temporal experience questionnaire (Klein et al., 2002) has participants answer questions about their known (semantic) and lived (episodic) past and future (Andelman et al., 2010). The importance of the choice of task is made particularly obvious by the conflicting results found in a single patient: H.C. is unimpaired on the scene

construction task (Hurley et al., 2011), but significantly impaired on the adapted Autobiographical Interview (Kwan et al., 2010).

The choice of task also interacts with patient factors, such as the specific aetiology and nature of the brain damage suffered. Squire et al. (2010) argue that many of the patients who have been found to have deficits in imagining the future also have damage to a number of extra-hippocampal regions that could explain their impairment. In support of this claim, damage to regions outside the hippocampus has been shown to affect episodic simulation ability. Patients with damage localised to the posterior parietal cortex or to the prefrontal cortex, and with intact hippocampi, imagine fictitious scenarios in much less detail than controls (Berryhill et al., 2010). Furthermore, it has been shown that semantic dementia patients with atrophy of the anterior temporal lobes, who show deficits in semantic memory but with a relative preservation of episodic memory, are selectively impaired when imagining the future and not when remembering the past (Irish, Addis, et al., 2012). This same pattern of results was also found in two patients with thalamic lesions (Weiler, Suchan, Koch, Schwarz, & Daum, 2011).

Alternatively, deficits in episodic simulation may be explained by broader deficiencies; some amnesic patients, even those with otherwise normal cognitive abilities, may have a general impairment in their capacity to describe their surroundings, even when no mental projection is required and they are simply asked to describe their present situation (Zeman et al., 2012), though others have not found this to be the case (Race et al., 2011). It has been argued that amnesic patients who are unimpaired at imagining the future are those who do not suffer from complete amnesia; with their relatively preserved remote episodic memory, such patients are able to draw upon a residual store of episodic details and therefore can construct scenarios in the same way as controls (Addis & Schacter, 2012). However,

other patients with intact remote episodic memory still show deficits in future thinking (Andelman et al., 2010). It is clear that much further work remains to be done in order to understand the role of the hippocampus in imagining future events.

# 1.9 Current Objectives

Given the current controversy over the role of the hippocampus in episodic simulation of the future, one goal of this thesis is to explore one of its potential contributions to future thinking that has yet to be examined. It is universally accepted that the formation of new episodic memories relies on the hippocampus. The ability to imagine future events would confer no cognitive advantage if the events were not retained in memory; if they are to influence later behaviour to ensure positive outcomes, traces of these hypothetical events must be stored for later use (Ingvar, 1985). It is therefore possible that the involvement of the hippocampus in future simulation may reflect encoding-related processes. The studies that comprise this thesis serve to investigate how imagined events are stored into memory, and to clarify whether the role of the hippocampus in the episodic simulation of future events is in encoding the event representations. Study 1 uses fMRI to examine whether the hippocampus is more active for imagined events that are later remembered in a post-scan test than those that are later forgotten, which would suggest that the hippocampus plays a role in encoding events into memory. The contribution of the hippocampus to the generation of episodic detail is also examined in this experiment. Study 2 investigates the functional connectivity of the hippocampus with other brain regions for later-remembered and later-forgotten imagined future events, examining whether this connectivity changes depending on encoding success. Study 3 aims to identify the phenomenological characteristics of an imagined event that predict whether or not it will be remembered later. Finally, Study 4 examines the validity of phenomenological ratings as have been applied to imagined future events.

# Chapter 2: Study 1 – Hippocampal Contributions to the Construction and Encoding of Imagined Future Events

## 2.1 Introduction

Remembering past experiences and imagining future events both rely on a common network of brain regions, including medial prefrontal, medial and lateral parietal, and medial and lateral temporal regions (Addis, Wong, et al., 2007; Nyberg, Kim, Habib, Levine, & Tulving, 2010; Okuda et al., 2003; Szpunar et al., 2007). However, despite this overlap, some regions within this network, particularly the right anterior hippocampus, are preferentially engaged by imagining future events relative to remembering past events (Addis, Cheng, et al., 2011; Addis, Wong, et al., 2007; Weiler et al., 2009). Furthermore, some patients with hippocampal damage, in addition to showing impaired episodic memory, also have difficulty imagining detailed and coherent future events (Andelman et al., 2010; Hassabis, Kumaran, Vann, et al., 2007; Kwan et al., 2010; Race et al., 2011). These findings suggest that the hippocampus is important for imagining the future. Recently, however, adult developmental amnesic patients (Hurley et al., 2011; Maguire et al., 2010), a group of developmental amnesic school-aged children (Cooper et al., 2011), as well as a group of patients with bilateral hippocampal damage but spared remote episodic memory (Squire et al., 2010), were all shown to be unimpaired at imagining detailed future events, implying that a fully intact hippocampus may not be required for episodic simulation. The role of the hippocampus in imagining the future, which has emerged recently as a critical issue in the cognitive neuroscience of memory, future thinking, and imagination (Buckner, 2010; Schacter & Addis, 2009), is, therefore, currently controversial (Maguire & Hassabis, 2011; Squire et al., 2010).

An inherent characteristic of newly-imagined future events is that they have not occurred (or been imagined) and as such, they are yet to be encoded. If a simulation is to

serve a functional role in future behaviour, it must be retained in memory so that it can be referred to if and when the imagined event is occurring. This issue was recognised by Ingvar (1985), who suggested that the process of encoding and retaining a simulation of future behaviour constituted a "memory for the future". Encoding and retrieval are critical aspects of the adaptive significance of episodic simulations, and virtually nothing is known about the processes that support these functions. The hippocampus has a well-established role in memory encoding; the anterior aspect in particular has been shown to be important for the formation and storage of new associations between stimuli or item features (e.g. Jackson & Schacter, 2004; Kirwan & Stark, 2004; Prince et al., 2005; Sperling et al., 2003). Therefore, it is possible that the increased anterior hippocampal activity seen for imagined future events reflects the events being encoded and stored in memory.

If a major function of the hippocampus during simulation is to encode the imagined scenarios, hippocampal damage would not necessarily prevent the events from being constructed initially, which may explain some of the conflicting results found in amnesic patients. Indeed, when children with hippocampal damage are asked to imagine future events, they can do so as well as controls. But when asked to recall these imagined events the next day, they are less accurate than controls at describing the original details (Cooper et al., 2011). The location of damage within the hippocampus may be critical as to whether the construction of simulations is affected. Based on the literature implicating the anterior hippocampus in associative encoding, and on the fact that some patients with hippocampal damage can still imagine the future but not recall their simulations, we hypothesised that the anterior hippocampus would play a role in encoding imagined events, thereby providing empirical evidence directly relevant to Ingvar's (1985) early claim.

Other regions of the hippocampus may be involved in additional aspects of episodic simulation. Another major component process of imagining the future is detail

recombination, or the rearrangement of disparate episodic details taken from past experiences into novel scenarios. Participant ratings of the amount of detail contained in their imagined future events offer some insight into the amount of detail recombination that has occurred, and anterior hippocampal activity increases linearly with such detail ratings (Addis & Schacter, 2008). The anterior hippocampus has also been implicated in the spatiotemporal integration of disparate details (Staresina & Davachi, 2009). It is not clear whether the contribution of the anterior hippocampus to imagining the future is in encoding, detail recombination, or both of these processes.

To this end, we used a novel approach incorporating both the experimental recombination (Addis et al., 2009) and subsequent memory (Wagner et al., 1998) paradigms. In an fMRI session, participants were presented with random recombinations of person, location, and object details extracted from their own memories, and for each, imagined a novel future event and rated it for the amount of detail generated. Participants completed an unexpected post-scan cued-recall test, in which memory for each imagined event was probed by testing recall of the person, location, and object details. We examined hippocampal activity related to successful encoding of future simulations by contrasting simulation-related activity for events that were later recalled versus those that were later forgotten. We expected anterior hippocampal activity to be higher for events that were successfully encoded and later-remembered relative to events for which the key details were later forgotten. We also examined hippocampal activity related to detail recombination by locating regions in which signal was linearly related to increases in detail ratings.

## 2.2 Methods

## 2.2.1 Participants

Twenty-nine young adults (12 males, aged 18-35) were recruited in compliance with the principles of The University of Auckland Human Participants Ethics Committee; all were right-handed, fluent in English and did not meet exclusionary criteria (neurological/psychiatric conditions, ferromagnetic implants, psychotropic medication use). Four participants (one male) were excluded: two due to neurological abnormalities, one due to excessive movement, and one due to task non-compliance; data from 25 participants were analysed.

### 2.2.2 Procedure

We employed an adapted version of the episodic recombination (Addis et al., 2009) and subsequent memory (Wagner et al., 1998) paradigms (see Figure 1) consisting of three phases: a pre-scan session in which the memory details were collected, a scan session in which participants imagined future events, and a post-scan cued-recall test for the future event details.

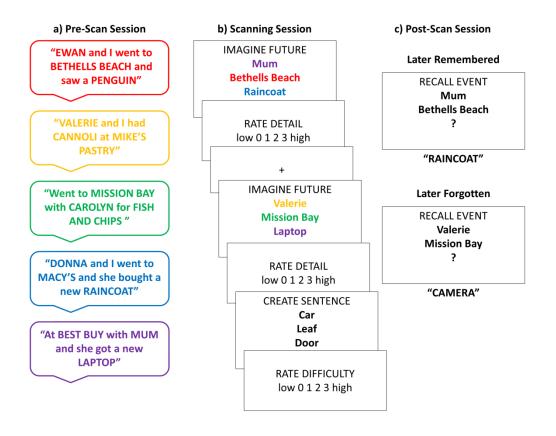


Figure 1. Future simulation paradigm.

A schematic diagram of example details collected during the pre-scan session (a), recombined details presented during the scan to elicit future simulations (b), and the post-scan cued-recall memory test (c).

#### 2.2.3 Pre-scan Session

Participants described 110 personal episodic events that they had experienced in the past 10 years. In order to facilitate retrieval of these episodes, participants were allowed to refer to a list of events commonly experienced by young adults (see Appendix A). This list was adapted from a previous study (Addis et al., 2009) so as to be more applicable for participants residing in New Zealand. For each event, participants identified three main details: a person and tangible object that featured in the event and the specific location of the event. To ensure each detail was distinct, participants could not duplicate details across different events, i.e. if they used 'Jane' as the person in event X, they could not list 'Jane' again as the person for event Y. During initial piloting, participants struggled to generate 110 unique details when referring to events experienced in the last five years; consequently, the time period was extended to the preceding 10 years, and further piloting with 13 participants confirmed that they were now able to generate the required details. The memory details were then randomly rearranged into new combinations. This recombination resulted in 110 rearranged detail sets that each contained a person, location, and object, and each person, location, and object was taken from a different memory. These recombined sets of details were used as cues for the imagined future events during the scan session.

## 2.2.4 Scan Session

Approximately one week later (M = 10.72 days, SD = 2.43), participants returned for the scan session. During this session, participants were randomly presented with four types of trials: *future, control, fixation,* and *re-imagine*. During each of the 90 future trials, participants were shown the recombined sets of memory details for 8 s (the average time needed to construct a future event; Addis, Wong, et al., 2007). Prior to scanning, they were instructed to imagine (from a first-person field perspective, as opposed to viewing themselves from a third person's observer perspective; Nigro & Neisser, 1983) specific future events that

might occur in the next five years, and that integrated all three detail cues into the scenario (see Appendix B for detailed instructions). Each event was followed by a four-point detail rating scale shown for 4 s (0 = low detail; 3 = vivid detail), and participants pressed the corresponding key on a button box to rate how much detail they had incorporated into their event.

On each of the 45 trials of the control task (Addis et al., 2009), participants were presented with three nouns taken from Clark and Paivio's (2004) extended norms, and were given 8 s in which to incorporate them into a sentence of the form "X is bigger than Y is bigger than Z", making relative size judgements about the nouns in the process. The objects used were high in imageability (M = 5.67), familiarity (M = 5.42), and concreteness (M = 6.91) on seven-point scales as described by Clark and Paivio (2004). After constructing the sentence, participants then rated how much difficulty they had doing so on a four-point scale (0 = 100) and difficulty; 0 = 1000 extreme difficulty).

There were also 45 re-imagine trials which were not analysed as part of the present study as they were unrelated to the aims of the current chapter. These trials consisted of imagined future events constructed from generic cues during the pre-scan session. In the scanning session, participants were shown these cues and spent the 8 s trials imagining each already-constructed future event, followed by the same 4 s rating scale for detail.

One fifth of scan time was composed of jittered null (fixation-cross) trials, ranging in duration from 4 to 16 s. Optseq2 (Dale, 1999) was used to determine the optimal duration of each null trial, as well as to establish the sequence of trials from all four conditions, that together would allow for the best estimation of the hemodynamic response function.

#### 2.2.5 Post-Scan Session

Ten minutes after scanning, participants completed an unexpected cued-recall task. This task followed the format of Jones's (1976) procedure for testing memory of events with multiple components, where he established that presenting partial combinations of different types of event components as cues in most cases resulted in equivalent levels of recall for the remaining cue. In our experiment, participants were presented with two of the details from each future trial event imagined in the scanner and asked to recall the missing detail. As participants were instructed to integrate all three details into an event, memory for the three integrated details gives an indication of the extent to which the details were bound and encoded into a coherent scenario. The particular detail tested (person, location, or object) was random and counterbalanced, such that on one third of the trials participants recalled the person, on another third of the trials they recalled the object, and on the remaining third they recalled the location. This subsequent memory task yielded approximately equal numbers of remembered and forgotten trials (51.7% remembered trials), which is ideal for a subsequent memory fMRI analysis. Based on cued-recall accuracy, that is, whether the missing detail was recalled or not, each future trial from the scan session was classified as either successfully or unsuccessfully encoded.

## 2.2.6 MRI Acquisition, Pre-Processing, and GLM Analysis

MRI data were collected on a Siemens Avanto 1.5 Tesla MRI scanner. For the anatomical scan, a magnetisation-prepared rapidly-acquired gradient echo (MP-RAGE) sequence was used (Brant-Zawadzki, Gillan, Nitz, 1992), which is a standard structural sequence that allows for high image quality and contrast. The functional scans were collected with a T2\*-weighted echo planar imaging (EPI; Stehling, Turner, & Mansfield, 1991) sequence, which is a sequence that allows for the very rapid acquisition of images spanning the whole brain within a very short period of time (TR = 2000ms, TE = 23ms, matrix size =

64 x 64, FOV = 200mm, flip angle = 90°). Twenty-five coronal oblique slices (5 mm thick) were acquired in an interleaved fashion, perpendicular to the long axis of the hippocampus and covering the whole brain. This specific slice orientation allows for optimal imaging of the medial temporal lobe, particularly the hippocampus, which is our *a priori* region of interest. Five functional runs were acquired for each subject, with 270 time points (summing to nine minutes) per run. During the functional scans, the task stimuli were projected onto a screen in the scanner room and reflected into a mirror within the head coil. All participant responses were collected using an MRI-compatible four-button response box.

In order to allow the longitudinal magnetisation to reach equilibrium, the initial four images from each run were discarded; these images appear brighter than those following them and therefore are generally automatically discarded by the scanner immediately after acquisition. MRI data were pre-processed in SPM8 (Wellcome Trust Centre for Neuroimaging, London, UK) using a standard protocol. This included slice timing correction to adjust for the fact that the scanner cannot acquire all slices within a volume simultaneously, realignment and unwarping to correct for participant movement and inhomogeneities in the main magnetic field, spatial normalisation to the Montreal Neurological Institute's (MNI) template brain (resampled at 2x2x2 mm voxels), spatial smoothing to improve the signal to noise ratio and to make the distribution of error more normal (8 mm Gaussian kernel), high-pass filtering to remove low-frequency drifts and physiological noise (128 s cut-off), and an AR(1) model was used in order to correct for serial correlations between proximal time points. One participant's data contained significant movement artefacts, which were repaired (via interpolation of data taken from surrounding time points) using ArtRepair Software (Mazaika, Whitfield-Gabrieli, & Reiss, 2007). Artefacts found in specific slices in the raw functional images were repaired before any preprocessing, and whole-volume artefacts were repaired after realignment but before estimation.

Each event was modelled by a stick function convolved with SPM8's canonical hemodynamic response function, applied at stimulus onset. Each fixed-effects model comprised (1) five regressors of interest: later-remembered future events, later-forgotten future events, parametric modulation regressors for each of these conditions (detail ratings, modelled linearly), and *control trials*; and (2) two regressors of no interest (*re-imagine* condition; rating task). Importantly, with the inclusion of the detail regressors in the model, the contrast images for the later-remembered and later-forgotten conditions quantify the effect of these conditions while controlling for any linear effects of detail. From each participant's fixed effects model, contrast images for each regressor of interest (relative to implicit baseline) were entered into a random-effects flexible factorial model with two factors, condition and subject. Two contrasts were then computed. To replicate previous findings of core network activity during future simulation, all imagine future trials were contrasted with control trials. A subsequent-memory contrast (later-remembered > laterforgotten future events) was computed to identify encoding-related activity, independent of any effects of detail. Investigating the effect of detail, while also controlling for encoding success, involved testing the parametric effect of detail in only later-remembered events. Thus, contrast images of this detail regressor were created in every participant and entered into a random-effects one-sample *t*-test.

Univariate fMRI analyses necessarily involve a very large number of statistical tests, as they are conducted for each of the approximately 150,000 brain voxels. As a result of these 'multiple comparisons', the likelihood of encountering a false positive result is dramatically increased relative to when analysing behavioural experiments. Therefore, it is generally considered essential to correct for this possibility (e.g. Bennett, Baird, Miller, & Wolford,

2010). In *Study 1*, for whole brain analyses, a combined voxel-wise threshold of p = .005 and a spatial extent threshold of 145 voxels (k) was employed to achieve an  $\alpha$  of .05, corrected for multiple comparisons. The minimum cluster size required for corrected significance was determined using a Monte Carlo simulation (10,000 iterations) implemented using AFNI's 3dClustSim program to estimate the overall probability of false positives within the 3D whole brain search volume (178,888 2x2x2mm voxels). We also computed the required cluster size for the correction of multiple comparisons within our *a priori* region of interest - the bilateral hippocampus (Yassa & Stark, 2008). Using an anatomical mask of the bilateral hippocampus (generated using MARINA; Walter et al., 2003) with a search volume of 1,878 2x2x2 mm voxels, the Monte Carlo simulation (10,000 iterations) indicated that a voxel-wise threshold of p = .005 combined with a spatial extent threshold of 26 voxels was required to correct for multiple comparisons within the hippocampus at p < .05.

MNI coordinates of peak voxels were converted to Talairach space for the purposes of localisation, and regions of activation were localised in reference to a standard stereotaxic atlas (Talairach & Tournoux, 1988). All coordinates in this thesis are reported in MNI space. For all figures, thresholded activation maps from SPM8 were overlaid on a standard anatomical template image (ch2better.nii) in MRIcron (Rorden, Karnath, & Bonilha, 2007). For those figures depicting activity from analyses focused on hippocampal activity, thresholded whole-brain maps were masked to show only voxels falling within the hippocampus (using an anatomical mask of the hippocampus from MARINA; Walter et al., 2003) and then overlaid on a standard anatomical template.

Per cent of signal change data, which serve as quantifiable measures of effect size, were extracted from clusters of activation using the REX toolbox (Whitfield-Gabrieli, 2009) for SPM8. From each subject's first-level model,  $\beta$ -values (which reflect the effect size of each individual condition, averaged across all active voxels within a 3 mm sphere) were

extracted from each condition of interest in each run. These data were then converted to per cent of signal change by dividing by the value of the constant of that same run and multiplying by 100. Once rescaled, the per cent of signal change values for each condition from each run in that subject were averaged to create one value per condition per subject.

These values were used to compute the mean per cent of signal change (and standard error of the mean) for each condition of interest.

Note that as the option to plot group level parametric modulation effects is not available in SPM8, in order to obtain estimates of mean blood-oxygen-level-dependent (BOLD) signal for high and low detail trials, it was necessary to compute a new fixed effects model for each participant. In this model, later-remembered trials were divided into two conditions: low detail (ratings 0-1) and high detail (ratings 2-3); per cent signal change data were extracted from these beta images using the REX toolbox as described above.

## 2.3 Results

## 2.3.1 Behavioural Results

The number of trials in the control (M = 45, SE = 0), later-remembered (M = 46.52, SE = 2.16), and later-forgotten (M = 43.48, SE = 2.16) future conditions were not significantly different, F(2,48) = 0.49, p = .613, suggesting that contrasts between these conditions should be unbiased. Later-remembered future events were rated as significantly more detailed (M = 2.16, SE = 0.07, p < .001) than later-forgotten ones (M = 1.67, SE = 0.09) on a four-point scale (0 = 1) low detail, 3 = 1 high detail). The type of missing detail in the cuedrecall test affected rates of recall, F(2,48) = 8.17, p = .001. Pairwise comparisons revealed that the mean proportion of successfully-recalled events was significantly lower when participants were required to recall the object detail than when they were asked to recall the person (p = .005) or location (p = .03) details. Recall proportions did not differ significantly

for the person and location details (p = .49, see Figure 2). The average temporal distance of future events was one year into the future (SE = 0.28).

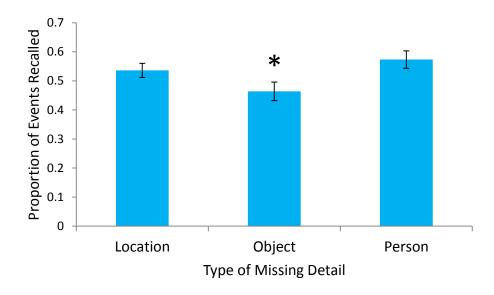


Figure 2. Mean rates of recall according to type of detail missing in cued-recall test. When participants were required to recall the object detail, they recalled significantly fewer events than when required to recall the person or location details. Error bars reflect SEM, \* = p < .05.

# 2.3.2 Regions Engaged by Imagining Future Events

To examine whether future simulation activated the common core network as evident in previous studies (Addis et al., 2009; Addis, Wong, et al., 2007; Botzung, Denkova, & Manning, 2008; Hassabis, Kumaran, & Maguire, 2007; Nyberg et al., 2010; Okuda et al., 2003; Szpunar et al., 2007), we performed a random-effects contrast of all future simulation trials (irrespective of encoding success) with all control trials. This contrast revealed a large bilateral network comprised of the medial prefrontal and parietal cortex, medial temporal lobes (including bilateral hippocampus), bilateral angular gyrus and lateral temporal cortex, and right inferior frontal gyrus (p < .005, k > 145 voxels, see Figure 3 and Table 1).

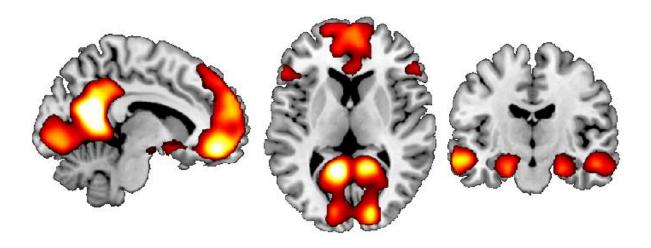


Figure 3. Regions engaged by imagining future events.

The contrast of future events (collapsed across encoding success) relative to control trials revealed activation of the core network, including bilateral medial parietal and prefrontal cortices (left and middle), and bilateral medial temporal lobes and lateral temporal cortex (right). Activations are overlaid on the ch2bet template in MRIcron (Rorden et al., 2007), and shown at a voxel-wise threshold of p < .005 uncorrected and an extent threshold of 145 voxels, providing correction for multiple comparisons at p < .05.

Table 1. Regions activated by imagining future events relative to the control condition.

Cluster	Brain Region	MNI coordinates			z-score	<i>p</i> -value**
size*		Х	у	z		
27,892 <sup>†</sup>	L Retrosplenial cortex (BA 31)	-8	-56	20	13.63	<.001
	R Lingual gyrus (BA 17)	16	-88	2	9.48	<.001
	L Inferior temporal gyrus (BA 21)	-58	-6	-18	9.14	<.001
	R Middle temporal gyrus (BA 21)	58	-6	-20	8.70	<.001
	L Lingual gyrus (BA 17)	-14	-88	0	8.16	<.001
	L Medial frontal gyrus (BA 10/11)	-8	46	-12	9.89	<.001
	L Medial frontal gyrus (BA 8)	-22	24	42	8.28	<.001
	L Medial frontal gyrus (BA 9)	-6	56	22	8.07	<.001
	R Parahippocampal gyrus (BA 35/36)	28	-28	-18	6.47	<.001
	R Parahippocampal gyrus (BA 28)	-22	-14	-22	6.31	<.001
	L Temporal pole (BA 38)	-46	12	-34	6.13	<.001
	L Inferior frontal gyrus (BA 47)	-32	30	-16	6.05	<.001
	L Parahippocampal gyrus (BA 36)	-24	-36	-14	5.98	<.001
	R Hippocampus	26	-18	-20	5.93	<.001
	R Temporal pole (BA 38)	48	14	-32	5.51	<.001
	R Superior frontal gyrus (BA 9)	12	52	40	4.82	<.001
1,589	L Angular gyrus (BA 39)	-46	-70	32	10.04	<.001
1,228	R Inferior frontal gyrus (BA 47)	36	32	-14	5.01	<.001
	R Inferior frontal gyrus (BA 46/45)	52	28	16	4.98	<.001
795	R Angular gyrus (BA 39)	50	-62	26	6.62	<.001

*Note:* All clusters are significant at p < .05, corrected for multiple comparisons. Where z-scores were reported as infinite in SPM, t-scores were converted to non-infinite z-scores using a method developed by Jenkinson and Woolrich (2002). \*Cluster size (k) indicates the number of voxels comprising the cluster; only clusters with a minimum extent of 145 voxels are reported. \*\*Voxel-level p value is provided. †Cluster extends bilaterally. BA = Brodmann area; L = left; R = right.

## 2.3.3 Encoding-Related Hippocampal Activity

Hippocampal activity related to successful encoding was examined using a random-effects contrast of later-remembered versus later-forgotten future events. With the inclusion of detail as a parametric modulation regressor in the fixed-effects model, the contrast images for later-remembered and later-forgotten events entered into the random-effects analysis reflect the effect of these conditions while controlling for any effects of detail, which is important given that hippocampal activity during future simulation has also been linked to increasing detail (Addis & Schacter, 2008) and detail ratings were significantly higher for later-remembered events than later-forgotten ones. At a whole-brain corrected threshold of p

< .05, this encoding contrast resulted in activity in some regions of the core network, including bilateral precuneus, parahippocampal gyrus and cerebellum, left inferior frontal gyrus and right posterior hippocampus (see Table 2).

Table 2. Regions activated by the successful encoding of future events.

Cluster size*	Brain Region	MNI coordinates			z-score	<i>p</i> -value**
		$\boldsymbol{\mathcal{X}}$	у	z		
706	R Precuneus (BA 31)	22	-58	20	3.91	<.001
	R Retrosplenial cortex (BA 30)	10	-50	18	3.24	.001
694	L Parahippocampal gyrus (BA 30)	-18	-48	-2	3.71	<.001
	L Parahippocampal gyrus (BA 36)	-26	-44	-8	3.22	<.001
	R Parahippocampal gyrus (BA 36)	36	-34	-14	3.27	.001
	R Fusiform gyrus (BA 37)	28	-44	-16	2.84	.002
$375^{\dagger}$	L Inferior frontal gyrus (BA 47)	-20	32	-12	3.97	<.001
	L Anterior cingulate cortex (BA 32)	-12	34	-10	3.71	<.001
214	L Precuneus (BA 31)	-16	-58	16	3.48	<.001
189	R Hippocampus	34	-26	-8	3.36	<.001
173	L Cerebellum	-24	-48	-30	3.98	<.001
149 <sup>†</sup>	R Cerebellum	6	-48	-32	3.09	.001

*Note:* All clusters are significant at p < .05, corrected for multiple comparisons. \*Cluster size (k) indicates the number of voxels comprising the cluster; only clusters with a minimum extent of 145 voxels are reported. \*\*Voxel-level p value is provided. †Cluster extends bilaterally. BA = Brodmann area; L = left; R = right.

Because the hippocampus was an *a priori* region of interest, we also examined activity in the hippocampus by employing a corrected threshold on the basis of the volume of the bilateral hippocampus (p < .005, k > 26 voxels). This regional analysis revealed activity in the right posterior hippocampus, as expected given the identification of this cluster in the whole brain analysis; 54 voxels of the cluster identified in the whole brain analysis were located within the hippocampus itself (x y z = 34 -26 -8, voxel-level p < .001, z = 3.36, k (within HC) = 54 voxels<sup>2</sup>). Additionally, this regional analysis revealed another more anterior cluster of encoding-related activation in the right hippocampus (x y z = 20 -12 -16, voxel-level p < .001, z = 3.34, k = 49 voxels; see Figure 4a). The opposite contrast of later-forgotten

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<sup>&</sup>lt;sup>2</sup> Note that here, k (number of voxels comprising a cluster) for the hippocampal regional analysis is adjusted to provide only the number of voxels in the cluster that fall within the bilateral hippocampal mask.

versus later-remembered future events yielded no significant clusters, in either in the whole brain analysis, or the regional analysis.

Mean per cent signal change was extracted from the two hippocampal clusters identified in the encoding analysis; these data for later-remembered and later-forgotten trials are displayed in Figure 4b for descriptive purposes. Note that these data quantify the effect of the encoding conditions while controlling for any linear effects of detail (due to the inclusion of the parametric regressors in the model).

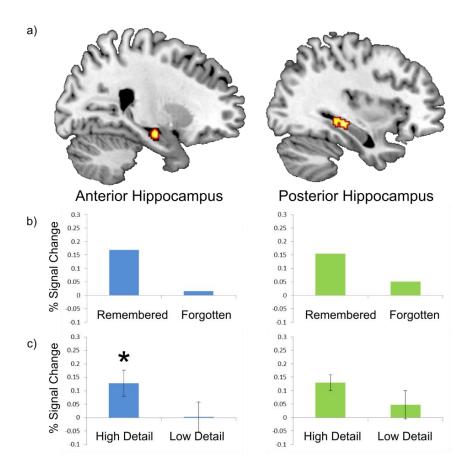


Figure 4. Regions engaged by successful encoding of imagined future events.

(a) A subsequent memory analysis revealed clusters in anterior right hippocampus (left panel, x y z = 20 -12 -16) and posterior right hippocampus (right panel, 34 -26 -8). Activations are corrected for multiple comparisons (p < .05), and are overlaid on the ch2bet MRIcron template at a voxel-wise threshold of p < .005 uncorrected (masked to only show voxels within the bilateral hippocampus). (b) For illustrative purposes, per cent signal change is shown for later-remembered and later-forgotten trials (note that error bars are not included as this effect is not independent of voxel selection). (c) Per cent signal change is broken down according to the level of detail of the simulations (high vs. low). Error bars show SEM. \*p < .05.

## 2.3.4 Detail-Related Hippocampal Activity

We were interested in whether signal from the clusters identified in the encoding analysis would also exhibit an effect of detail<sup>3</sup>. We extracted signal from these clusters during trials rated high in detail (i.e., ratings of 2 and 3) and trials rated low in detail (i.e., ratings of 0 and 1). Pairwise comparisons revealed that while a numerical difference between high and low detail was evident in both clusters (see Figure 4c), this effect was significant in the anterior (t(24) = 2.42, p = .02) but not the posterior (t(24) = 1.68, p = .11) cluster.

Furthermore, we investigated whether any regions throughout the entire brain showed a parametric response to detail ratings, such that activation increased linearly with unit increases in detail ratings. In this analysis, only imagined events that were later remembered in the recall test were included, so as to not introduce encoding success as a confounding variable. Unfortunately, with only half of the trials being used in this analysis (i.e., later-remembered trials only) and thus reduced power to detect an effect, no activation survived the whole brain or the regional (bilateral hippocampus) corrected thresholds. However, hippocampal responses to detail ratings were evident at an uncorrected threshold of  $p \le .001$ , in line with other studies reporting parametric modulation analyses (Addis, Moscovitch, Crawley, & McAndrews, 2004; Addis & Schacter, 2008; Rombouts et al., 1999). Within the hippocampus, a right anterior cluster laterally adjacent to the cluster from the encoding analysis was revealed (x y z = 30 -14 -16, uncorrected p = .001; see Figure 5 and Table 3).

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<sup>&</sup>lt;sup>3</sup> Because these clusters were selected on the basis of an encoding analysis, and moreover that analysis controlled for the effect of detail (achieved by including detail as a parametric modulation regressor), the contrast of interest (the effect of detail) is independent of voxel selection.

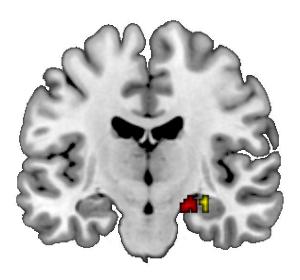


Figure 5. Hippocampal responses to encoding and detail.

A subsequent memory analysis that controlled for the amount of detail of future events revealed a cluster (red) in medial anterior right hippocampus (x y z = 20 - 12 - 16); the parametric modulation analysis for detail ratings in later-remembered events revealed a more lateral cluster (yellow) in anterior hippocampus (x y z = 30 - 14 - 16) in which activity linearly increased with detail ratings. All activations survive an uncorrected threshold of  $p \le .001$ , and are overlaid on MRIcron's ch2bet template at uncorrected p < .005, masked to only show voxels within the bilateral hippocampus.

Table 3. Regions exhibiting a parametric effect response to level of detail (for successfully encoded future events only).

Cluster	Brain Region	MNI Coordinates		z-score	
size*		х	у	Z	_
26	L Anterior cingulate cortex (BA 24/32)	-12	14	36	3.84
47	R Middle temporal gyrus (BA 20)	44	8	-36	3.69
15	L Middle temporal gyrus (BA 21)	-44	6	-32	3.62
15	R Inferior frontal gyrus	48	8	12	3.26
9	L Cerebellum	-14	-40	-46	3.21
9	R Anterior hippocampus	30	-14	-16	3.06

*Note*: All activations evident in this parametric modulation analysis survived an uncorrected threshold of  $p \le .001$ . \*Cluster size (k) indicates the number of voxels comprising the cluster; for brevity, only clusters exceeding a cluster extent threshold of  $k \ge 5$  are reported. BA = Brodmann area; L = left; R = right.

#### 2.4 Discussion

The major aim of this study was to establish whether hippocampal activity evident during episodic simulation of the future reflects the events being encoding into memory. Because prior models suggest that the anterior hippocampus is particularly important for the encoding of novel associative combinations (Chua et al., 2007; Prince et al., 2005), we hypothesised that the anterior aspect of the hippocampus would be particularly important for the encoding of imagined events. However, our findings suggest that both the anterior and posterior regions of the right hippocampus contribute to the encoding of imagined future events.

The finding that the right anterior hippocampus is responsive to successful encoding fits with the idea of an encoding-retrieval distinction along the long axis of the hippocampus (Lepage et al., 1998; Schacter & Wagner, 1999). More recently, Spaniol et al. (2009) conducted a meta-analysis of 26 studies of encoding success and 30 studies of retrieval success, and confirmed that the anterior hippocampus was more reliably activated during successful encoding than during successful retrieval. Moreover, the anterior hippocampus appears to be particularly responsive to the encoding of associative (Kirwan & Stark, 2004) and novel (Kohler, Danckert, Gati, & Menon, 2005) information, both of which characterize imagined future events.

The posterior hippocampus was also responsive to encoding success. Given that the posterior hippocampus has been shown to be particularly important for the processing of spatial relations (Hassabis et al., 2009; Maguire et al., 2000; Ryan, 2009; Woollett & Maguire, 2009), the importance of this area for episodic simulation may be in the domain of creating a spatiotemporal context in which to ground the event. Imagining future events requires recall or generation of spatial locations in which to set them, and may also include simulated navigation through these contexts, both of which may be supported by the

hippocampus (Byrne, Becker, & Burgess, 2007). It would be interesting to examine in future research whether encoding-related hippocampal activity in this paradigm is driven primarily by recall of the imagined events' location (as opposed to recall of the person and object details); unfortunately, in the present study there are an insufficient number of trials to complete such an analysis.

The posterior hippocampus has also been implicated previously in the successful encoding of future-related representations using a different paradigm that focuses on the scenes in which the events take place. Poppenk et al. (2010) had participants view scenes in the scanner and either generate future intentions or present actions associated with the scenes. Post-scan, participants viewed scene cues and recalled whether they were seen in the scanner and if so, under what task conditions (i.e., generating an intention or a present action). Results revealed a right posterior hippocampal cluster in which activity covaried with overall subsequent memory performance, and since encoding success depended on participants successfully integrating action or intention details into a spatial context, the results of this study further support the idea of a role for the posterior hippocampus in contextual processing.

The fact that highly-detailed imagined events were more likely to be encoded suggests that detail can influence the process of encoding. The amount of detail generated for the imagined event may be related to some extent to the amount of detail associated with the event components, which is a question examined directly in *Chapter 4*. More specifically, constructing a memorable imagined event will depend to some degree on how well the event details could be retrieved from memory. Since the cues for the imagined future events consisted of familiar people, places, and objects, retrieval of these familiar items was necessary before event construction. The posterior hippocampus has been associated with retrieval (Prince et al., 2005; Schacter & Wagner, 1999) and the reinstatement of previous

conditions (Giovanello et al., 2009; Preston, Shrager, Dudukovic, & Gabrieli, 2004).

Moreover, according to the constructive episodic simulation hypothesis (Schacter & Addis, 2007), episodic details need to be retrieved from memory to build a coherent scenario, and the posterior hippocampus has been found to respond to the amount of episodic detail comprising both past and future events (Addis & Schacter, 2008). Indeed, our behavioural results demonstrate that more detailed events were more likely to be successfully encoded. Activity in regions supporting retrieval of contextual and visuospatial information, such as the parahippocampal gyrus (Bar & Aminoff, 2003; Szpunar et al., 2009) and the precuneus (Cavanna & Trimble, 2006), also exhibited an encoding effect. It is, however, a challenge to tease apart neural activity related to the retrieval of details from episodic memory and the integration of these details into a coherent imagined scenario. Developing paradigms that can disambiguate these component processes is an important focus for future research (Addis & Schacter, 2012).

Activation in the anterior hippocampal encoding cluster was significantly higher for events rated as having high detail than for events rated as having low detail. This result suggests that the contribution of the anterior hippocampus to encoding success might depend, at least in part, on the ability to construct a detailed and memorable simulation. A right anterior hippocampal response to the amount of detail comprising future events is consistent with other findings (Staresina & Davachi, 2009) showing that that a right anterior hippocampal cluster was more responsive when participants had to integrate spatiotemporally-separated details than when details were presented in a combined form. Their participants were scanned while presented with objects and colours, and asked first to imagine the item in that colour and then rate how plausible that item/colour combination would be in real life. In order to manipulate the discontiguity of details in space or time, objects were either depicted directly in the specified colour, with the colour presented as a

frame around the greyscale object (and therefore spatially separated), or with the greyscale object presented 500 ms after the coloured frame (separated in both spatial and temporal domains). A right anterior hippocampal cluster was found to be more responsive to trials in which the details were presented separately during encoding than when they were presented in a combined form. The interpretation of this finding was that this region of the hippocampus serves to bind together spatially- or temporally-separated details. A key component of our study is the integration of event details taken from disparate times and locations into a coherent future simulation, and its similar findings bolster the idea that a lateral anterior area of the right hippocampus is involved in detail integration.

Furthermore, the parametric modulation analysis revealed a second anterior hippocampal cluster in which activation was linearly related to detail ratings. It is notable that the anterior hippocampal cluster showing a linear relation with detail ratings was laterally adjacent to the cluster associated with successful encoding. The spatial proximity of these two clusters is such that they may simply be two different peaks within the same larger area of anterior hippocampal activation, and thus reflect a single underlying cognitive process. Given that the cluster identified in the encoding analysis also showed a significant effect of detail, it is likely that detail integration and encoding are closely related. However, this finding is still important to consider because it suggests that successful encoding and detail recombination may be distinguishable at a neural level. In particular, it is possible that these component processes of simulation are mediated by specific hippocampal subfields. The hippocampal formation is a circuit comprised of several anatomically-distinct subregions, including the dentate gyrus, three cornu ammonis  $(CA_{1/2/3})$  areas, and the subiculum. The resolution of functional images collected in the current study is not sufficient to localise activity to hippocampal subfields. High-resolution fMRI has, however, identified subregions that are important for encoding. For instance, the perirhinal cortex and dentate gyrus and

CA<sub>2/3</sub> subfields of the hippocampus are involved in the encoding of information that remains in memory for at least a week, while parahippocampal cortex may be important for more transient encoding (Carr, Viskontas, Engel, & Knowlton, 2010). The future use of high-resolution fMRI could advance our understanding of the relative contributions of different hippocampal subfields to the component processes of future simulation.

Our results have important implications for the debate on whether hippocampal damage disrupts the ability to imagine the future (Andelman et al., 2010; Cooper et al., 2011; Hassabis, Kumaran, Vann, et al., 2007; Kwan et al., 2010; Maguire & Hassabis, 2011; Maguire et al., 2010; Race et al., 2011; Squire et al., 2010). It is possible that in a damaged hippocampus, the ability to construct detailed scenarios may remain intact while encoding of these representations is disrupted. This appears to be the case both for the children with hippocampal damage who were less accurate in later recalling their imagined events (Cooper et al., 2011), and for the patients with hippocampal damage whose imagined events were described as repetitive, as if they could not recall the portions of the event that they had already constructed (Squire et al., 2010). Depending on the location of hippocampal damage, whether anterior or posterior, differential impairments may be seen in tasks that require the generation of imagined episodic details, the encoding of imagined events, or both.

This study generates specific predictions for further research on the role of the hippocampus in future simulation, as the location of damage within the hippocampus could affect the type of impairment seen in amnesic patients. Further behavioural testing of amnesic patients with well-characterised damage to the hippocampus is required; testing subsequent memory for imagined future events will be critical to establish whether episodic detail generation and recombination can occur independently of successful encoding.

In summary, this study provides a more comprehensive understanding of hippocampal contributions to two related component processes of future simulation: encoding and detail

recombination. We have localised two regions of the right hippocampus involved in encoding, one anterior and one posterior. Furthermore, activity in the right anterior hippocampus was modulated by event detail, suggesting that the generation of episodic details and their storage into memory may be related processes. Future thinking confers an adaptive benefit: simulating solutions to potential obstacles increases chances for success and survival (Suddendorf & Corballis, 2007). Thus, generating detailed simulations and encoding these for later use are important aspects of this ability. Further research examining the ways in which the hippocampus interacts with other structures across the brain during encoding of imagined events will further expand our knowledge of the neural underpinnings of episodic simulation.

# Chapter 3: Study 2 – Hippocampal Connectivity During Encoding of Imagined Events

### 3.1 Introduction

In Study 1, two regions of the hippocampus were found to be important for the encoding of imagined future events, one anterior and one posterior. Interpretation of the specific contributions of these regions to episodic simulation is complex, since while a general function of the hippocampus with respect to memory is to integrate distinct representations of objects and people with contextual information into coherent scenarios (Eichenbaum, Yonelinas, & Ranganath, 2007), the anterior and posterior aspects of the hippocampus may differ in terms of their contributions to this process (Giovanello et al., 2009; Kirwan & Stark, 2004; Woollett & Maguire, 2009). Some current models propose that the posterior hippocampus is important for reinstatement of an episode in its original form, whereas the anterior hippocampus is involved in more 'flexible' domain-general encoding of associative information (Chua et al., 2007; Preston et al., 2004; Prince et al., 2005). The involvement of the posterior hippocampus in episodic reinstatement may also be reflecting the processing of familiar spatial contexts and storage of cognitive maps for the purpose of navigation (Burgess et al., 2002; Maguire et al., 2000). Based on this evidence, it seems possible that different regions of the hippocampus may play different but complementary roles in the process of simulation.

With respect to episodic memory and simulation, both remembered past experiences and imagined future events are situated within a spatial framework. Without such a platform upon which to build the scenario, the events would lack a vital sense of coherence (Hassabis, Kumaran, Vann, et al., 2007), suggesting that the posterior hippocampus should be critical for episodic processing in general. This idea is supported by the finding that activity in the posterior hippocampus is modulated by participant ratings of detail, including spatial and

contextual details, for *both* remembered past and imagined future events (Addis & Schacter, 2008). However, the anterior aspect of the hippocampus is differentially activated by future events relative to past events (Addis, Cheng, et al., 2011; Addis, Wong, et al., 2007; Weiler et al., 2009). The aforementioned hippocampal models would predict that such anterior hippocampal activity reflects the binding together of episodic details into novel and flexible arrangements and/or the encoding of these representations, and consistent with this prediction, anterior hippocampal activity has been shown to correlate with the amount of detail comprising future but not past events (Addis & Schacter, 2008). Moreover, the disparateness of the details being integrated can modulate engagement of this region. For instance, Weiler, Suchan, & Daum (2009) found that right anterior hippocampal activity was associated with simulating unlikely future events for which the degree of 'flexible processing' may be particularly amplified.

The evidence for functional specialisation of the anterior and posterior hippocampus suggests that the two hippocampal clusters resulting from the encoding analysis in *Study 1* may be making independent contributions to episodic simulation. Further insight into the nature of these contributions can be gained by examining the network of regions with which the anterior and posterior hippocampus interacts, and the measurement of functional connectivity is one method of acquiring such information. This technique involves the identification of regions throughout the brain in which changes in activation are occurring at the same time and at a similar magnitude to the changes in activation in specific regions of interest. Any areas exhibiting such a correlation are broadly thought to be functionally interacting with the 'seed' regions in some way (Friston, 2011; Rogers, Morgan, Newton, & Gore, 2007).

It has already been established that there are differences in the resting state functional connectivity of the anterior and posterior hippocampus. Functional correlations between

regions during resting states are thought to reflect intrinsic anatomical connections. The anterior hippocampus exhibits intrinsic functional connectivity with lateral temporal cortex and temporal poles, while the posterior hippocampus displays connectivity with posterior regions such as lateral parietal cortex, posterior cingulate cortex, and retrosplenial cortex (Kahn et al., 2008; Poppenk & Moscovitch, 2011) and these findings are consistent with current knowledge about the anatomical connectivity of the hippocampus (Duvernoy, 2005). Manns and Eichenbaum (2006) propose that this differential pattern of hippocampal connectivity reflects the simultaneous input and convergence of spatial and non-spatial information into the hippocampus. More specifically, input to the anterior hippocampus via the perirhinal cortex comes from regions in the ventral visual stream involved in the identification of individual objects, while input to the posterior hippocampus via the parahippocampal gyrus comes from the dorsal visual stream and conveys spatial and contextual information. Differential contributions of the anterior and posterior hippocampus to episodic future simulation may also therefore stem from this diversity in connectivity.

To investigate this possibility further, in *Study 2* we examined the functional connectivity of the two seed regions identified in the encoding analysis of *Study 1*. *Study 2* extends previous findings by examining how the established intrinsic functional connectivity of the anterior and posterior hippocampus persists during an episodic simulation task and whether the connectivity changes depending on encoding success. Because anterior and posterior hippocampal regions were shown to be important for encoding events into memory in *Study 1*, and hippocampal-cortical connectivity has been shown to be predictive of subsequent memory (Gagnepain et al., 2011), we examined whether task-related patterns of functional connectivity would change depending on whether the events were later remembered in the post-scan cued-recall test or later forgotten. We hypothesised that while the two seeds may be strongly connected with each other, functional connectivity with other

regions in the brain would likely differ between anterior and posterior seeds given their known anatomical and intrinsic connectivity. Moreover, we expected that these patterns of connectivity would be related to task performance to some extent, such that connectivity would be enhanced during successful encoding. To this end, we conducted a partial least squares (PLS) analysis of functional connectivity on the two hippocampal seeds yielded by *Study 1*.

#### 3.2 Methods

# 3.2.1 Participants and Data Collection

The participants and data used in *Study 2* are the same as those used in *Study 1*.

Descriptions of participant characteristics and methods of data acquisition can be found in the Methods section of *Study 1*.

# 3.2.2 Partial Least Squares Analyses

Two significant clusters within the right hippocampus had emerged in the encoding analyses of  $Study\ 1$  as being more active for later-remembered imagined future events than later-forgotten ones: one was in the anterior extent of the hippocampus ( $x\ y\ z=20\ -12\ -16$ ) and the other in the posterior extent (34 -26 -8). We were interested in whether these regions exhibited similar patterns of task-related functional connectivity, both with each other and with the rest of the core network, and whether functional connectivity differed according to encoding success.

We used spatiotemporal PLS (McIntosh, Bookstein, Haxby, & Grady, 1996) to assess functional connectivity over an 18 s temporal window. PLS is a covariance-based multivariate technique that enables examination of connectivity between regions of interest ('seeds') and activity across the whole brain over time and whether there are similarities or differences in connectivity across experimental conditions (McIntosh et al., 1996; McIntosh, Chau, & Protzner, 2004; McIntosh & Lobaugh, 2004). For this analysis, mean per cent of

signal change was extracted (using REX as described in *Study 1*) from two seed regions within the right hippocampus (x y z = 20 –12 –16; 34 –26 –8). These data were entered as seeds in the PLS analysis. First, correlations were computed between the signal in each seed region and all other voxels for each condition across subjects. The resulting correlation maps were stacked and analysed with singular value decomposition, producing a set of orthogonal latent variables (LVs), each containing three matrices: (i) a singular value indicating the amount of covariance for which the LV accounts; (ii) a linear contrast between the seeds and the conditions that codes the effect depicted by voxels; and (iii) the singular image of voxel weights or 'saliences' (akin to a component loadings in principle components analysis) that are proportional to the covariance of activity with the linear contrast. Each extracted latent variable successively accounted for a smaller portion of the covariance (as indicated by the singular value) and are thus determined by the strength of effects in the dataset.

The statistical significance of each LV was assessed by use of a permutation test. This procedure involved randomly reassigning each subject's data to experimental conditions, rerunning the PLS analysis, and determining the new singular value for each reordering; this was done 500 times. Thus, significance reflects the probability on the basis of the number of times the singular value from the permuted data exceeds the original singular value (McIntosh et al., 1996). A threshold of p < 0.05 was used. Note that unlike in univariate analyses, the significance of whole-brain patterns of activity are determined in one single analytic step, therefore obviating the need to correct for multiple comparisons.

The reliability of the voxel saliences was computed using bootstrap estimation of the standard error. This procedure involves randomly resampling subjects with replacement, rerunning the PLS analysis, and determining new saliences for each sampling. After carrying this procedure out 300 times, the *SE* of the saliences was computed (McIntosh et al., 1996).

Clusters of five or more voxels in which bootstrap ratios were greater than  $\pm 4.5$  (roughly equal to a z score, or a p value of < 0.0001), were considered to represent reliable voxels.

### 3.3 Results

This analysis identified a significant latent variable (LV), (p = .006), explaining 57.35% of the covariance, that indicated that functional connectivity for these hippocampal regions was modulated by encoding success. When constructing a simulation that was later remembered, both seeds were strongly functionally connected with each other, as well as with the same distributed pattern of activity (see Figure 6). The pattern of functional connectivity peaked at TR 3 (6 to 8 s after task onset), and results from this TR are reported here (see Table 4). The whole-brain pattern of activity included regions such as the bilateral parahippocampal gyrus, medial parietal/cingulate cortex, medial prefrontal cortex, left inferior frontal gyrus and left inferior parietal lobule (see Figure 7a). This strong connectivity during successful encoding reflects positive correlations between activity in both seed regions and the whole brain network identified by the LV (anterior seed, r = .58; posterior seed, r = .58) .85; Figure 7b). However, when constructing a simulation that was later forgotten, the posterior hippocampal seed region was no longer functionally connected with the anterior hippocampal seed or with the wider network of regions, illustrated by an absence of correlation between posterior hippocampal activity and the whole brain pattern (r = -.10; Figure 7c). The connectivity for the anterior hippocampal seed and the wider network was evident irrespective of encoding success (r = .50; Figure 7c).

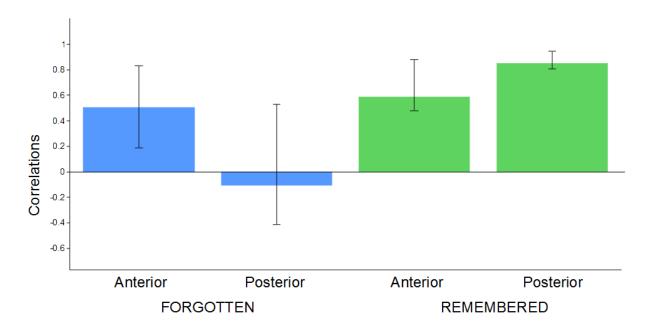


Figure 6. Correlations of anterior and posterior seeds with whole-brain network. When imagined events were later remembered, signal in both anterior and posterior hippocampal seeds showed a strong correlation with activity in the associated whole-brain network. However, when imagined events were later forgotten, only the anterior seed showed this pattern, while the correlation of the posterior seed was not significantly different from zero. Error bars reflect 95% confidence intervals.

Table 4. Regions showing significant functional connectivity with the hippocampal seed regions.

Cluster size*	Brain Region	х	у	Z	BSR
8044	L Medial parietal/cingulate cortex (BA 29) †	-12	-50	10	15.62
	<u>.</u>				
753	R Inferior occipital gyrus (BA 19)	50	-76	-6	14.75
290	L Precentral gyrus (BA 6)	-38	-2	26	11.89
221	L Superior temporal gyrus (BA 22)	-48	-12	-12	14.19
137	R Inferior temporal gyrus (BA 20)	46	-14	-24	9.12
126	L Medial frontal gyrus <sup>†</sup> (BA 10)	-4	66	-2	10.13
123	R Thalamus <sup>†</sup>	0	-10	6	7.45
119	L Cerebellum	-32	-34	-32	8.14
104	L Middle frontal gyrus (BA 8)	-40	16	58	8.96
93	R Parahippocampal/inferior temporal gyrus (BA 20/36)	36	-14	-26	6.16
82	R Fusiform gyrus (BA 20)	48	-34	-22	6.84
78	L Middle frontal gyrus (BA 8)	-28	16	42	9.39
72	L Thalamus	-12	-30	6	8.90
71	L Inferior frontal gyrus (BA 47)	-38	30	-14	9.62
68	R Middle frontal gyrus (BA 10)	38	54	30	8.43
42	L Inferior parietal lobule (BA 40)	-42	-38	32	9.06
40	L Cerebellum <sup>†</sup>	-6	-40	-22	5.95
37	L Precentral gyrus (BA 4)	-54	-10	56	6.16
33	L Parahippocampal gyrus (BA 36)	-22	0	-38	7.85
24	R Cerebellum	16	-56	-34	6.10
23	R Hippocampus	30	-30	-8	5.60

*Note:* Only clusters evident during the peak timepoint (TR 3) with a bootstrap ratio of greater than  $\pm$  4.5 (roughly equivalent to a p-value of p < .0001) are reported. \*Cluster size (k) indicates the number of voxels comprising the cluster; only clusters with a minimum extent of 20 voxels are reported. BA = Brodmann area; BSR = Bootstrap ratio; L = left; R = right. †Cluster extends bilaterally.

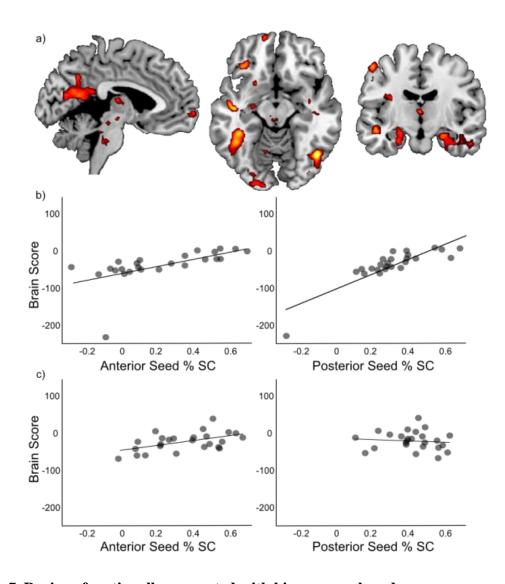


Figure 7. Regions functionally connected with hippocampal seeds.

(a) A Seed PLS analysis showed that two hippocampal seed regions (see Methods for coordinates) exhibited functional connectivity with each other and with a distributed pattern of brain regions at TR 3. Warm colours indicate regions significantly correlated with the seeds and the whole brain pattern, and represent the relative strength of this correlation (thresholded at p < .0001). (b) Both seeds exhibited connectivity during successful encoding, as indicated by strong positive correlations between seed activity and brain scores (a weighted average of activation across regions exhibiting significant functional connectivity). (c) During unsuccessful encoding, the anterior seed continued to show this connectivity pattern but the posterior seed did not. % SC = per cent signal change.

#### 3.4 Discussion

In this study, we sought to examine the functional connectivity of the right anterior and posterior hippocampus in the context of episodic simulation. We expected that while the anterior and posterior hippocampus may work together to some extent when participants imagine future events, they would also show differential connectivity. This hypothesis was based on other evidence showing that the anterior and posterior extents of the hippocampus exhibit differential functional connectivity during resting states (Kahn et al., 2008; Poppenk & Moscovitch, 2011). Our findings indicated no overall anterior-posterior hippocampal distinction in functional connectivity, although this result was modulated by encoding success. When participants were imagining events that they would later recall in a post-scan cued-recall test, both the anterior and posterior right hippocampus showed similar connectivity both with each other and with a distributed group of default network regions, including medial prefrontal, posterior cingulate, and parahippocampal cortex. When participants imagined future events that would later be forgotten in the post-scan test, the anterior hippocampus still showed this same pattern of connectivity with the distributed network, but the posterior hippocampus did not. Our PLS analysis therefore suggests that the connectivity of the right posterior hippocampus to the anterior hippocampus and other core autobiographical regions might be critical to successful encoding. This result is in contrast to previous findings suggesting that the anterior hippocampus seems to have a more important role in encoding than the posterior hippocampus (e.g. Spaniol et al., 2009). This discrepancy might be explained by the paradigm used in the present study; the use of participants' own familiar details as event cues meant that a greater degree of episodic retrieval (and therefore involvement of the posterior hippocampus) was required in order for event construction and successful encoding to occur.

In general, however, the finding that hippocampal connectivity was modulated by encoding success is consistent with previous research. It has been shown that there is increased functional connectivity between the hippocampus and a broad network of cortical regions (including perirhinal, orbitofrontal, retrosplenial, and posterior cingulate cortices) during the successful encoding of line drawings of complex objects, relative to when encoding is unsuccessful (Ranganath, Heller, Cohen, Brozinsky, & Rissman, 2005).

Similarly, during the encoding of word-sound associations, heightened connectivity between the hippocampus and superior temporal gyrus is predictive of successful later recollection (Gagnepain et al., 2011), and functional connectivity between the posterior hippocampus and the inferior frontal gyrus is associated with subsequent memory for repeated objects (Manelis, Paynter, Wheeler, & Reder, 2012). The interaction of the hippocampus with wholebrain networks mediating the details comprising the to-be-encoded representations appears to be crucial for the formation of new memories.

The whole-brain network found in the current study to be functionally connected with both the anterior and posterior hippocampus was fairly consistent with networks of regions whose intrinsic connectivity with the hippocampus has already been established. Kahn et al. (2008) illustrated that the body of the hippocampus and posterior parahippocampal cortex shows resting-state connectivity with lateral parietal cortex, posterior cingulate, retrosplenial cortex, and ventromedial prefrontal cortex, while the anterior hippocampus and the perirhinal/entorhinal cortices showed connectivity with the lateral temporal cortex and temporal pole. Regions found to be functionally connected during future simulation in the current study included many of those identified by Kahn et al. (2008), such as the posterior cingulate/retrosplenial cortex, lateral temporal regions, lateral parietal cortex, and the medial prefrontal cortex. There were a number of additional regions included in the network found in the current study that were not observed by Kahn et al. (2008) such as the cerebellum,

thalamus, and precentral gyrus; any such discrepancies likely result from the task-dependent nature of the current study relative to Kahn et al.'s resting state design.

Our results indicated that when imagined events were successfully encoded, no anterior/posterior distinction in hippocampal functional connectivity was evident. This was somewhat unexpected, given that as mentioned earlier, the anterior and posterior hippocampus each displays intrinsic connectivity with separate networks (Kahn et al., 2008). However, it is possible that the act of imagining future events recruits both networks simultaneously and to an equivalent degree. Since episodic simulation is such a multifaceted cognitive task, with numerous component processes (such as visual imagery, drawing upon episodic and semantic memory, detail recombination, encoding, and goal-related processing), it is not surprising that it would recruit both extents of the hippocampus as well as their corresponding functional networks.

The current findings provide more insight into the potential relative contributions of anterior and posterior hippocampus to episodic simulation. The anterior hippocampus appears to be serving some role that is important for imagination in general, regardless of whether the event is stored in memory or not. Its involvement is necessary, but not sufficient, for imagining future events that are later recalled. The role of the anterior hippocampus in episodic simulation might therefore be in the realm of constructing or generating the new scenario. In contrast, the integration of the posterior hippocampus with other components of the autobiographical network is needed if the event is to be remembered after a short delay. Therefore, the posterior hippocampus likely performs some process over and above construction per se that is particularly important to successful encoding.

Evidence supports the idea that the anterior hippocampus might be particularly involved in event construction, and thus exhibits connectivity with other simulation-related regions even if the encoding of that simulation is ultimately unsuccessful. As suggested by

the results of *Study 1*, the anterior hippocampus was particularly responsive to the amount of detail comprising a simulation irrespective of encoding success, consistent with its purported role in the formation of novel stimulus associations and combinations across space and time (Staresina & Davachi, 2009). Furthermore, the intrinsic connectivity of the anterior hippocampus with lateral and anterior temporal cortex (Kahn et al., 2008) may support the construction of future simulations by mediating an interaction between semantic and episodic information. Evidence from patients with anterior temporal lobe damage who show intact episodic memory but an impaired ability to imagine future events illustrates that semantic memory is necessary for the generation of hypothetical episodic events, perhaps serving as a sort of cognitive scaffold with which to guide their construction (Irish, Addis, et al., 2012).

The particular importance of the posterior hippocampus to the successful encoding of future simulations is not fully understood. The posterior hippocampus has a strong functional relationship with other posterior regions such as the parahippocampal gyrus and parts of the posterior parietal cortex (Kahn et al., 2008), all of which are known to support related functions such as spatial processing (Epstein et al., 1999; Kumaran & Maguire, 2005; Staresina et al., 2011; Tambini et al., 2010; Zeidman et al., 2012) and mental imagery (Burgess, Becker, King, & O'Keefe, 2001; Cavanna & Trimble, 2006; Vann et al., 2009). Such connectivity between these regions suggests that creating an image of the contextual layout and mentally navigating through the imagined location may enhance encoding success. Indeed, imagined events set in familiar locations engage posterior cortical regions such as the posterior cingulate cortex and parahippocampal gyrus more than events set in unfamiliar locations (Szpunar et al., 2009), and these regions exhibit strong functional connectivity with the posterior hippocampus (Kahn et al., 2008).

It is conceivable that when participants imagine future events that are rich in imagery and have a detailed spatial context, these events may be more easily remembered later on, and this could explain the importance of the posterior hippocampus in encoding episodic simulations. Source memory is also improved when participants use an imagery strategy to associate an item with a context (Kuhlmann, 2012), which is a task that is similar in many ways to our future simulation trials. However, more direct evidence linking spatial detail with posterior hippocampal activity during simulation and with successful encoding is needed to confirm this hypothesis. Activation is observed in similar posterior parietal regions during retrieval of familiar people (Maddock, Garrett, & Buonocore, 2001; Shah et al., 2001), indicating that the contribution of these regions to simulation may not restricted to scene-related processing. Moreover, the formation of non-spatial mental images may be sufficient to enhance encoding of simulations. For instance, creating mental images of paired associations during encoding improves later memory performance relative to rote rehearsal (Richardson, 1998), and posterior parahippocampal gyrus activation is associated with the act of forming such mental images (Leshikar, Duarte, & Hertzog, 2012). Future research examining whether imagined events situated in more familiar or more detailed contexts are more likely to be encoded will help to clarify this issue.

Alternatively, it has been suggested that the contribution of the posterior hippocampus to successful recollection may be in post-encoding processes (Poppenk & Moscovitch, 2011). This hypothesis is based on evidence that increased covariance between signal in the posterior hippocampus and in its associated network during post-encoding rest periods significantly explained the relationship between posterior hippocampal volumes and recollective memory performance found in the study. Others have also shown that post-encoding hippocampal-cortical interactions are associated with later subsequent memory (Tambini et al., 2010), which may reflect the act of consolidation, or the transfer of information from the hippocampus to neocortical areas (McClelland et al., 1995).

Unfortunately, it was not possible to assess post-encoding connectivity with the present data

because the trial sequences generated by Optseq (Dale, 1999) did not always include a rest block after each future trial. However, it would be interesting to examine in future work whether the pattern of hippocampal-cortical connectivity during encoding persists into postencoding blocks, as has previously been found to be the case for the encoding of movie clips (van Kesteren, Fernandez, Norris, & Hermans, 2010).

A more detailed understanding of how hippocampal connectivity contributes to the successful encoding of future events requires knowledge of what constitutes a memorable imagined event. While we know from *Study 1* that later-remembered events are typically rated as having significantly more detail, it is not clear why some simulations are more detailed than others. On the basis of the current results, it might be that the familiarity of certain components of the simulation, such as the location, may be an important predictor of whether the simulation is detailed and/or successfully encoded. Moreover, if the components already fit well together and are similar to person/place/object combinations encountered in previous experiences, this might influence the plausibility and memorability of the scenario. Further investigation of the impact of these phenomenological variables on event encoding will clarify the potential role of the hippocampus in encoding imagined future events.

### Chapter 4: Study 3 – The Phenomenology of Later-Remembered Future Events

#### 4.1 Introduction

A distinctive attribute of humankind is a capacity to imagine how things might be in the future and to make plans to achieve these imagined future states. We are able to conceive of ideas that are drastically removed from our present situation and formulate the complex steps required to accomplish them. Nevertheless, a capacity for imagination is not sufficient to ensure that plans for the future are carried out. In order for imagined events to serve some adaptive purpose, it is critical that they are maintained in memory. More specifically, if a person imagines the way in which he or she will go about facing an upcoming problem, the simulation will only be helpful if it can be recalled when the person actually encounters the problem later on. Such remembered simulations have been characterised as 'memories of the future' (Ingvar, 1985) and comprise a person's expectations and plans. Bar (2009) suggests that they exist as a collection of 'scripts' that form our predictions for future events, and that these scripts are based both on the outcomes of experiences that we have had previously, as well as on events that we have only imagined. However, very little is known about how these imagined events are stored in memory or the characteristics of those simulations that are encoded.

We do know that the hippocampus, a structure important for encoding and storing real-life episodic memories (Eichenbaum, 2004), is more active when participants imagine future events that they will later recall, relative to when they imagine events that they will later forget (Study 1; Martin, Schacter, Corballis, & Addis, 2011). Moreover, the functional connectivity of the posterior right hippocampus to a wider autobiographical network appears to be particularly important for the successful encoding of episodic simulations (Study 2; Martin et al., 2011). Others have also found that posterior hippocampal activity predicts

source memory for imagined actions or intentions that take place within scenes (Poppenk, Moscovitch, et al., 2010). It is likely that the hippocampus serves to encode and store imagined events in much the same way as it encodes episodic events that have actually occurred. It was also evident in *Study 1* that the anterior hippocampus was responsive to the amount of detail comprising a simulation (see also, Addis et al., 2008), and more detailed future events were more likely to be encoded (Martin et al., 2011). Therefore, it may be that the vividness of a simulation may play an important role in whether it is ultimately encoded or not.

In order to hypothesize about the specific roles played by the anterior and posterior hippocampus in the encoding of imagined future events, it is necessary to understand what features of later-remembered events make them more likely to be recalled. For instance, particular types of detail may be more likely to enhance encoding success. Given that the posterior hippocampus is associated with the processing of scenes and spatial stimuli (Kumaran & Maguire, 2005; Maguire et al., 2000) and novel spatial arrangements of familiar stimuli (Pihlajamaki et al., 2004), it is conceivable that a greater degree of spatial and contextual processing may be particularly effective at increasing encoding success. It is notable that imagined future events that are set in familiar locations are rated as easier to imagine (Arnold et al., 2011a), evoke a stronger subjective experience, and contain more sensorial detail (de Vito, Gamboz, & Brandimonte, 2012; Szpunar & McDermott, 2008). Therefore, simulated events placed within a rich and familiar spatial context may be more memorable than those for which the context is less vivid. Accordingly, the familiarity of the location may be one factor influencing the recall of imagined future events.

The recombination paradigm used in Martin et al. (2011) was such that imagined event details, including the locations in which the events were set, varied in familiarity<sup>4</sup>. The paradigm required participants to generate their own personal cues in a pre-scan session. These cues consisted of people, places, and objects that had featured in episodic memories experienced by the participant over the preceding 10 years. During the scanning session, participants then imagined future events that incorporated a person, place, and object, each taken from a different real episodic memory. A consequence of this method of obtaining cues is that participants inevitably included details with which they have varying degrees of familiarity. It follows then that during some trials, participants imagined events taking place in locations they visited each day and involving their closest friends and favourite objects. In these cases, each event component was likely to have many other associated rich episodic details that could then be incorporated into the imagined event. In contrast, there would have been other trials in which participants imagined events involving people, places, and objects with which they had only had cursory experiences. Imagined events consisting of these unfamiliar components may have been less detailed, as there would be fewer accompanying episodic associations available to integrate into the scenario. It therefore seems possible that event encoding was affected by how well participants knew the details that were to make up the imagined event.

Familiarity with the overall scenario has already been shown to influence the encoding of imagined future events (Klein, Robertson, Delton, & Lax, 2012). When participants are asked to make judgements about the relevance of items in a list to a planned imagined future event, and then are later given an unexpected recall test for those items, recall performance is significantly higher when the judgements are made in the context of a

<sup>&</sup>lt;sup>4</sup> The term 'familiarity' is used here to describe the extent to which participants knew and could easily imagine the episodic details that comprised their imagined events. This definition is not to be confused with another concept of familiarity often used in the context of memory research, denoting a feeling of knowing without vivid recollection of contextual details (Yonelinas, 2002).

familiar versus an unfamiliar imagined future event. Specifically, when participants decide whether an item is needed for an imagined event that is similar to those they have experienced before (e.g. a dinner party or a picnic), they are more likely to recall the item later than if they make the decision in the context of a more foreign or novel scenario (e.g. a trip to Antarctica or making a meal for zoo animals). Klein et al. argued that when planning for the more familiar imagined scenarios, participants had more previous personal episodic memories of similar occasions upon which to base their simulations, and evaluated each item with respect to these episodic memories. In contrast, when planning for unfamiliar scenarios, participants relied primarily on their semantic representations of such novel events. This interpretation is supported by findings that when participants imagine implausible events with which they have little experience, they tend to incorporate details not from their own memories, but from external sources such as media and friends' experiences (Anderson, 2012).

The familiarity of event *components* has also been shown to affect the vividness of imagined future events. D'Argembeau and Van der Linden (2012) showed participants single word cues and asked the participants to imagine future events in response to the cues. After imagining each event, participants rated a number of its phenomenological characteristics including the familiarity of the location and featured people and objects. When entered as predictors into a hierarchical linear model (HLM; Wright, 1998), the familiarity ratings of the event components significantly predicted future event vividness. The familiarity of the event components thus determines how well the simulation can be pictured and imagined; whether or not this also affects encoding of simulations is yet to be investigated.

It may be that the importance of the familiarity of the event components changes depending on how encoding success is measured. For instance, it is possible that familiarity with event details could influence performance on the cued-recalled test utilized in *Study 1* 

Martin et al. (2011). In that study, details were randomly arranged, such that each imagined future event likely contained a combination of more and less familiar elements. However, the cued-recall procedure (in which two of the person/place/object details were presented from each trial and participants were required to recall the third detail), depended heavily on the missing detail being successfully integrated into the event. If the single missing detail was not well incorporated into the scenario, which may have been the case if that particular detail was not one the participant knew very well, the event might have been more likely to be classified as forgotten (i.e. not sufficiently encoded to have bound all three key details together). In the present study, this issue is addressed via the examination of whether the familiarity of the event components predicts later recall of the event.

Other phenomenological characteristics of event components in addition to familiarity, such as emotionality and personal significance, could also affect the nature of the simulation and whether or not it is encoded. Emotionality can in some situations enhance episodic memory, possibly via interactions between the amygdala and hippocampus (Phelps, 2004), and information relating to the self is remembered better than self-irrelevant information (Symons & Johnson, 1997). Moreover, the likelihood of an imagined future event happening in real life has also been shown to influence the phenomenology of imagined events. For instance, when emotional imagined future events are repeatedly simulated, participants rate the events as being more plausible than when they are simulated only once (Szpunar & Schacter, 2012). Crucially, such increases in plausibility are also accompanied by corresponding increases in participant ratings of detail, ease of simulation, and arousal, and/or may affect encoding success directly. Accordingly, it appears that both the familiarity of the event components and the plausibility of the imagined event in general increase the amount of detail incorporated into the event.

The present study investigates whether the familiarity, emotionality, and personal significance of event components, as well as the detail and plausibility of the events, influence how well the events are encoded into memory. The experimental design, like that used in Study 1 (Martin et al., 2011), incorporates the episodic recombination (Addis et al., 2009) and subsequent memory (Wagner et al., 1998) paradigms, but participants were in this case required to make additional ratings about the familiarity, emotionality, and personal significance of each event component, and ratings of detail and plausibility for the events overall. We then used HLM (Wright, 1998) to assess whether these ratings could significantly predict the likelihood of the imagined future event being successfully recalled in an unexpected cued-recall test. It was hypothesized that imagined events involving more familiar, emotional, and personally-significant components would be more likely to be remembered later than events involving components with low ratings on each of these measures. Furthermore, so as to investigate whether the cued-recall procedure (in which two details from each event were presented and the remaining detail recalled) was a valid measure assessing the encoding of the simulation in general, and not just the familiarity of the missing detail, we calculated whether the likelihood of recalling each individual detail type (person, place, or object) was predicted only by the familiarity of that particular detail, or also by the familiarity of the other details. Accordingly, it was anticipated that recall of each component type would be predicted by familiarity ratings of all three of the imagined event's components.

The use of a multilevel statistical approach such as HLM is arguably the most appropriate method for memory research when particular memories or simulations are nested within individuals (Wright, 1998). Despite this fact, HLM has rarely been used in the field of episodic memory until recently (Boritz, Angus, Monette, & Hollis-Walker, 2008; D'Argembeau & Van der Linden, 2012; Song & Wang, 2012; Petrican, Gopie, Leach, Chow,

Richards, & Moscovitch, 2010). Its application to memory for imagined future events is therefore a relatively novel approach. Rather than losing rich trial-by-trial information by aggregating data into participant means, the multilevel analyses used here allow us to directly test whether the phenomenology of a particular individual simulation can predict the mnemonic fate of that simulation, that is, whether or not it is successfully encoded and maintained in memory.

#### 4.2 Methods

# 4.2.1 Participants

Twenty-three young adults (7 males, aged 18-35) were recruited in compliance with the principles of The University of Auckland Human Participants Ethics Committee; all were right-handed, fluent in English and did not meet exclusionary criteria (neurological/psychiatric conditions or psychotropic medication use). Two participants (both female) were excluded: one due to misunderstanding the task in the second session, and the other declined to participate in the second session; data from 21 participants were analysed.

#### 4.2.2 Procedure

As in *Study 1* (Martin et al., 2011), an adapted version of the episodic recombination (Addis et al., 2009) and subsequent memory (Wagner et al., 1998) paradigms were employed, consisting of the same three phases: *Session 1*, in which the memory details were collected, *Session 2*, in which participants imagined future events, and *Session 3*, a cued-recall test for the future event details. Unique to the present study was the inclusion of additional ratings of the person/place/object event components collected in *Session 1* (see Figure 8). The data analysed in this experiment were the behavioural data acquired during an fMRI study. As such, the data from *Session 2* were collected during an fMRI scanning session, though the fMRI analyses were unrelated to the current objectives and thus will not be discussed here.

#### **4.2.3 Session 1: Interview**

Participants described 110 personal episodic events that they had experienced in the past 10 years. For each event, participants identified three main details: a person and tangible object that featured in the event and the specific location of the event. To ensure each detail was distinct, participants could not duplicate details across different events. For each of the three main details isolated from every past episodic event, participants made three ratings on a four-point scale ranging from 0 to 3: *familiarity* (0 = very unfamiliar, 3 = extremely familiar), *emotionality* (0 = no emotional connotations for that particular detail, 3 = strong emotional connotations), and *personal significance* (0 = no significant role in the participant's life, 3 = an important and meaningful role in the participant's life).

The memory details were then randomly rearranged into new combinations to use as cues for the future events that would be imagined in *Session 2*. This rearrangement resulted in 110 recombined detail sets that each contained a person, location, and object, with each person, location, and object having been taken from a different memory.

### **4.2.4 Session 2: Imagined Future Events**

During the second session, participants completed 90 future simulation trials in which they were shown the recombined sets of memory details for 8 s each. They were instructed to imagine (from a first-person field perspective, as opposed to viewing themselves from a third person's observer perspective; Nigro & Neisser, 1983) specific future events that might occur in the next five years, and that integrated themselves and all three detail cues into the scenario. Each event was followed by two four-point rating scales each shown for 4 s: detail (0 = low detail; 3 = vivid detail) and plausibility (0 = very unlikely to happen in real life, 3 = could very easily happen in real life), and participants pressed the corresponding key on a button box to make their ratings.

To provide appropriate baselines for the fMRI component of this study, participants also completed trials of a control task and a baseline task, interspersed randomly throughout the experiment; the data from these tasks are not considered in the results of the present study but the tasks are described here for completeness. On each of the 45 trials of the control task (Addis et al., 2009), participants were presented with three nouns taken from Clark and Paivio's (2004) extended norms, and were given 8 s in which to incorporate them into a sentence of the form "X is bigger than Y is bigger than Z", making relative size judgements about the nouns in the process. After constructing the sentence, participants then rated how much difficulty they had doing so on a four-point scale (0 = no difficulty; 3 = extreme difficulty) and how related all of the objects were to each other (0 = completely unrelated, 3 = highly related). The baseline task was an odd/even judgement task; on each 2 s trial, participants were shown a digit from 1 to 9 and asked to press a button indicating whether the digit was odd or even (left button = odd, right button = even).

### 4.2.5 Session 3: Cued-recall Test

Ten minutes after *Session 2*, participants completed an unexpected cued-recall test. Participants were presented with two of the details from each *future* trial event imagined during the second session and asked to recall the missing detail. The particular detail tested (person, location, or object) was randomly-ordered and counterbalanced, such that on one third of the trials they recalled the person, on another third of the trials they recalled the object, and on the remaining third they recalled the location. Based on this test, each future trial from the second session was classified as either successfully or unsuccessfully encoded depending on whether the missing detail was recalled or not.

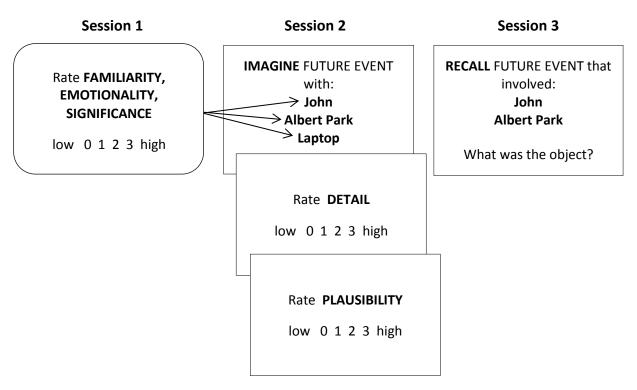


Figure 8. Future simulation paradigm with additional ratings.

The paradigm used in Study 3 is an adapted version of that used in Studies 1 and 2. Unique to this study was the requirement for participants to make ratings of familiarity, emotionality, and significance for each person, place, and object retrieved in Session 1, and to rate the plausibility of the simulation generated in Session 2.

# 4.2.6 Hierarchical Linear Modelling

Multi-level hierarchical linear modelling (Garson, 2012; Raudenbush & Bryk, 1992; Wright, 1998) was used so as to take into account the inherent nested quality of autobiographical memory data (i.e. that multiple events are nested within multiple participants). The use of multilevel modelling corrects for biases in parameter estimates and the underestimation of standard errors that results from the grouped and therefore potentially correlated nature of the data (Guo & Zhao, 2000). Using HLM 7 software (Raudenbush, Bryk, & Congdon, 2011), two-level random coefficient models were created in which each imagined future event was modelled at the lower within-subjects level, and each participant at

the higher between-subjects level, resulting in 1828 records at level one<sup>5</sup> and 21 records at level two. For every imagined event, 15 variables were considered: ratings of familiarity, emotionality, and significance for each of the person, place, and object details, mean ratings of familiarity, emotionality, and significance across all components within each event, as well as recall success (a binary measure where 0 = forgotten, 1 = remembered) and ratings of detail and plausibility. When entered as level-one predictors, both the slopes and intercepts of all variables were allowed to vary across participants. With recall success as the outcome variable, its binary values by definition did not fit a normal distribution. It was therefore necessary to refer to a Bernoulli distribution and use a logistic link function to restrict predicted values to fall between 0 and 1 (i.e. to conduct a multi-level logistic regression) (Guo & Zhao, 2000). The unit-specific models were then estimated using a high-order Laplace approximation of maximum likelihood with 20 iterations (Raudenbush, Yang, & Yosef, 2000). All ratings were mean centred, such that the mean of each rating for each participant was calculated across all of their events, and the individual rating from each event was then subtracted from its respective mean. This resulted in the centred ratings representing the deviation from that participant's average response, thus removing the variation among participant means from the model (Kreft, de Leeuw, & Aiken, 1995).

### 4.3 Results

### **4.3.1 Ratings**

In the cued-recall test, participants successfully recalled an average of 55% (SD = .16, SE = .04) of their imagined future events. A repeated-measures ANOVA illustrated that the type of missing detail significantly influenced rates of recall (F(2,40) = 14.62, p < .001, see Figure 9), providing a replication of *Study 1* (Martin et al., 2011). Pairwise comparisons

<sup>&</sup>lt;sup>5</sup> Although each participant imagined 90 future events, some participants did not successfully make all ratings for each of their 90 events. Events with missed ratings (an average of 3 per participant) were not included in the analysis.

showed that when asked to recall the object detail, participants recalled a significantly lower proportion of imagined events than when asked to recall the person (p < .001) or location (p = .02) details. When participants were asked to recall the person detail, they recalled a significantly larger proportion of imagined events than when asked to recall the location (p = .04) or object (p < .001) details. In other words, the person detail was the easiest type of detail to recall, while the object detail was the most difficult of the three to remember.

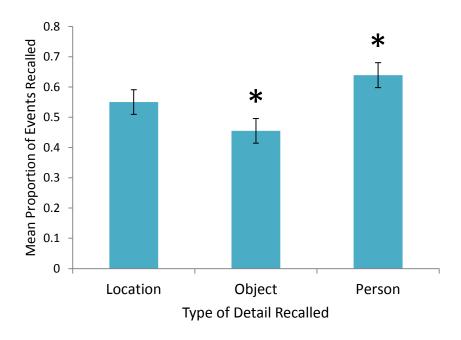


Figure 9. Mean proportions of events recalled according to the type of detail missing at cued-recall.

When asked to recall the object, participants performed significantly worse than when asked to recall the location or person. When asked to recall the person, participants performed significantly better than when recalling the location or object. Error bars represent standard error of the mean. \*=p<.05.

Descriptive statistics for all ratings are shown in Table 5 and illustrated in Figure 10. Mean ratings suggest that future events were fairly detailed, but an average plausibility score of less than 1 on a scale ranging from 0 to 3 suggests that they were not particularly plausible. A repeated-measures ANOVA with factors of detail type (person, place, and object) and rating type (emotionality, familiarity, and significance) was applied to examine the way in which these factors interact. The assumption of sphericity was significantly violated for the factor of rating type (Mauchly's W(2) = 0.414, p < .001) and for the detail by rating type interaction (W(9) = 0.141, p < .001). Consequently, a Greenhouse-Geisser correction was applied. There was a significant main effect of both detail type (F(2,40) = 28.78, p < .001)and rating type (F(1.26,25.22) = 17.94, p < .001), while the detail type by rating type interaction was not significant, F(2.21,44.14) = 1.85, p = .166. Bonferroni-corrected pairwise comparisons indicated that the main effect of detail type reflected the person detail (M = 1.63, SE = 0.06) being rated significantly higher across all dimensions (emotionality, familiarity, and significance) than both the location (M = 1.35, SE = 0.09, p < .001) and object (M = 1.16, p < .001)SE = 0.10, p < .001) details. Additionally, the location detail tended to be rated significantly higher for all ratings than the object detail (p = .011). The main effect of rating type was related to significantly higher scores for familiarity ratings (M = 1.77, SE = 0.09) than emotionality ratings (M = 1.20, SE = 0.11, p = .001) and significance ratings (M = 1.17, SE = .12, p < .001). Mean emotionality and significance ratings were not significantly different from each other (p = 1.0).

Table 5. Descriptive statistics for participant mean ratings of their imagined events.

	Rating Type	Mean	SD	Minimum	Maximum
Event Components					
Person	Emotionality	1.502	0.485	0.079	2.556
	Familiarity	1.958	0.378	1.411	2.843
	Significance	1.425	0.470	0.382	2.478
Location	Emotionality	1.158	0.586	0.034	2.467
	Familiarity	1.769	0.412	1.011	2.753
	Significance	1.128	0.598	0.186	2.367
Object	Emotionality	0.939	0.583	0.146	2.489
	Familiarity	1.587	0.505	0.811	2.584
	Significance	0.960	0.622	0.174	2.456
All Details	Mean Emotionality	1.200	0.514	0.086	2.504
	Mean Familiarity	1.771	0.392	1.122	2.727
	Mean Significance	1.171	0.528	0.360	2.433
Imagined Events					
	Detail	1.814	0.373	1.186	2.831
	Plausibility	0.863	0.339	0.299	1.494

*Note*. Ratings are on a four-point scale ranging from 0 (low) to 3 (high), SD = standard deviation.

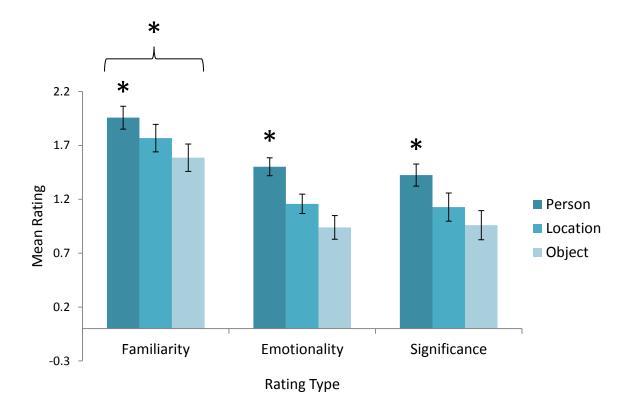


Figure 10. Mean participant ratings for each event component.

Ratings of familiarity were significantly higher than ratings of emotionality and significance. Ratings made for the person detail were also significantly higher than ratings of the location and object details, and the location detail was rated significantly higher than the object detail. Error bars reflect standard error of the mean, \* = p < .05.

#### 4.3.2 Predictors of Later Recall for a Future Simulation

When conducting the hierarchical linear modelling portion of the analysis, we first specified an intercept-only or 'empty' model, which included recall success as the Bernoulli-distributed outcome variable but no additional predictors. This model tested whether a significant portion of the variance in recall success was due to between-participant variation; if this were true, it would indicate that the use of a multi-level model that clustered scores within individuals would therefore be more suitable than a single-level model. In this case, the variance component for the intercept was significant ( $\tau(20) = 0.456$ , p < .001) and the intra-class correlation (ICC = 0.122) indicated that 12.2% of the variance in the data was between participants (Snijders & Bosker, 1999, p. 224), suggesting that the application of a multi-level model was appropriate for this particular data set.

Given that ratings of the components comprising a future simulation have been shown to influence the phenomenology of those simulated future events (D'Argembeau & Van der Linden, 2012), we next examined whether the model fit was improved relative to the initial empty model when ratings for familiarity, emotionality, and significance, averaged across all three imagined event components, were included as level-1 predictors of later simulation recall. This new model resulted in a significant reduction in the deviance statistic (a value reflecting the lack of fit between the model and the data) relative to the empty model, as shown with the likelihood-ratio test ( $\chi^2(12) = 60.91$ , p < .001). Only one of the three variables was a significant predictor of recall success. The mean familiarity rating significantly predicted whether the event would be later remembered or later forgotten (t(20) = 3.73, p = .001, odds ratio (OR) = 1.58), indicating that future events involving more familiar components were more likely to be later recalled 6. Mean emotionality (t(20) = .23, p = .821,

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<sup>&</sup>lt;sup>6</sup> An additional analysis also established that mean familiarity ratings significantly predicted the amount of detail in the event; as this was a direct replication of the findings of a previous study (D'Argembeau & Van der Linden, 2012) these results are not reported for brevity.

OR = 1.05) and mean significance (t(20) = 1.51, p = .148, OR = 1.41) did not significantly predict later recall.

With mean familiarity rating across all three event components as a significant predictor of recall, we next investigated how the individual familiarity ratings of each event component contributed to this predictive ability. Familiarity ratings for each of the person, location, or object details were entered as level-1 predictors of recall success. This new model revealed that while familiarity ratings of the person (t(20) = 5.60, p < .001, OR = 1.58) and location (t(20) = 3.03, p = .007, OR = 1.20) both significantly predicted event recall, familiarity ratings of the object (t(20) = 1.47, p = .157, OR = 1.09) did not.

Although overall mean ratings of emotionality and personal significance did not predict event recall when entered into the model with familiarity, we examined whether the individual emotionality and significance ratings of the person, location, and object held any explanatory power. Specifically, we were interested in whether it would again be the case that the ratings of the person and location (and not the object) predicted later memory for the imagined events. This was indeed true in both new models. When all three ratings of emotionality were entered as predictors of recall, ratings for the person (t(20) = 4.63, p < .001, OR = 1.40) and location (t(20) = 2.36, p = .029, OR = 1.22) were significant predictors, while ratings for the object were not (t(20) = .48, p = .636, OR = 1.04). The same pattern emerged for significance ratings; ratings for the person (t(20) = 4.78, p < .001, OR = 1.40) and location (t(20) = 2.68, p = .014, OR = 1.22) were significant predictors of later memory, while ratings for the object were not (t(20) = 1.10, t = 0.285, t = 0.08).

We then examined whether the phenomenology of the simulation at the time of construction could predict later recall of that simulation. Both detail (t(20) = 8.07, p < .001, OR = 2.23) and plausibility (t(20) = 4.27, p < .001, OR = 1.38) were significant predictors

when entered together into the model, indicating that more detailed and more plausible future events were more likely to be remembered later. Adding the previously-significant person familiarity as a third predictor improved the fit of the model by reducing the deviance statistic  $(\chi^2(5) = 21.65, p < .001)$ , while adding location familiarity  $(\chi^2(6) = 8.46, p = .205)$ , person significance  $(\chi^2(6) = 4.89, p > .5)$ , location significance  $(\chi^2(6) = 9.30, p = .156)$ , person emotionality  $(\chi^2(6) = 2.64, p > .5)$ , or location emotionality  $(\chi^2(6) = 7.48, p = .278)$  as a fourth predictor did not improve the fit further. Therefore, the most parsimonious model examining the outcome of recall success included person familiarity, detail, and plausibility as level-1 predictors. When all of these variables were entered simultaneously in the model, they remained as significant predictors of event recall and the fit of the model was significantly better than one containing only detail and plausibility. See Table 6 for the coefficients and statistics of this model.

Table 6. Coefficients and statistics for multilevel model of imagined event recall.

					- 0		
Fixed Effect	Standardized	SE	t-ratio	d.f.	p	O.R.	C.I.
	Coefficient						
Intercept	-	0.179	1.281	20	.215	1.257	(0.866, 1.825)
Detail	0.57	0.097	7.808	20	<.001	2.136	(1.744, 2.616)
Plausibility	0.203	0.076	3.934	20	<.001	1.347	(1.150, 1.578)
Person Familiarity	0.226	0.076	3.898	20	<.001	1.347	(1.148, 1.579)

*Note.* SE = standard error, d.f. = degrees of freedom, O.R. = odds ratio, C.I. = confidence interval

## 4.3.3 Predictors of Later Recall for Specific Event Components

The measure of successful performance on the cued-recall paradigm used in *Study 1* (Martin et al., 2011) depended on the single missing component having been well-integrated into the event at the time of simulation. It is possible that the recall test was not truly a measure of event encoding, but simply a reflection of some characteristic of the missing component. To investigate this issue, we next used hierarchical linear modelling to identify significant predictors of whether participants could later recall the person, location, or object components of the simulation.

Given the number of ratings made in this experiment, and the fact that familiarity ratings had been shown in the previous section to be the most influential on later recall, we restricted this analysis to whether familiarity ratings of the person, location, and object predicted memory for trials requiring recall either of the person, location, or object. More specifically, we were interested to see whether the familiarity ratings for the components provided as cues in the recall test would predict memory for the missing component. If this were the case, it would indicate that the cued-recall paradigm was measuring something about the associations created during the imagined event and not simply how well participants could recall the single missing component.

Three new multilevel models were created for this analysis, with one model for each type of missing component (i.e. one for trials in which the person was to be recalled, one for the location, and one for the object). The number of level-1 records (i.e. the total number of trials across all participants) in each model was therefore one-third of the number in the original models in the previous section, though the number of level-2 records (i.e. the total number of participants) remained the same. Familiarity ratings for the person, location, and object were entered as level-1 predictors into each of the three models. When evaluating predictors of memory for the object component, familiarity of the person (t(20) = 2.20, p = 0.00)

.040) and location (t(20) = 2.55, p = .020) were significant predictors, while familiarity of the object was not a significant predictor of object recall (t(20) = .685, p = .501). In the model of recall for the location component, person familiarity (t(20) = 3.88, p < .001) was a significant predictor, while familiarity of the location (t(20) = 1.72, p = .101) and object (t(20) = .072, p = .943) were not. When participants were asked to recall the person component, the familiarity of the person (t(20) = 5.15, p < .001) and object (t(20) = 2.30, p = .033) were significant predictors of recall success, and the familiarity of the location (t(20) = .072, p = .943) was not.

#### 4.4 Discussion

The aim of this study was to examine whether characteristics of imagined future events and their components influenced the likelihood of the event being retained in memory. It was hypothesised that imagined events involving more familiar, significant, and emotionally-associated people, places, and objects, and more detailed and more plausible events, would be more likely to be recalled in a later cued-recall test. Results indicate that out of the three ratings made for the imagined event components (familiarity, emotionality, and significance), familiarity was the strongest predictor of event recall success relative to ratings of emotionality and significance. Specifically, future events involving components that were on average rated as highly familiar were more likely to be remembered later. Examining the ratings made for each individual event component revealed that ratings made for the person and location components were predictive of later recall of the imagined event, while ratings made for the object component did not significantly predict later memory for the imagined event or the majority of its components. Of the ratings made about the imagined events, both detail and plausibility were strong predictors of later event recall, such that more detailed and more plausible simulations were more likely to be remembered later.

Familiarity ratings for the components comprising the future events were significant predictors of later recall. This finding is in line with previous research showing that familiarity improves episodic source memory (Poppenk, Kohler, & Moscovitch, 2010; Poppenk, McIntosh, Craik, & Moscovitch, 2010), and especially that increased familiarity of imagined scenarios enhances recall for the event details (Klein et al., 2012). The mechanism behind the enhancing influence of familiarity on event recall is unknown. It might be related to the finding that the familiarity of event components predicts how vividly the event will be imagined (D'Argembeau & Van der Linden, 2012), a finding replicated herein, which may then in turn predict whether the imagined event will be later recalled. However, even though detail ratings predicted later recall, it is notable that familiarity ratings (at least for the person component) could predict later recall over and above what is predicted by the amount of detail in the simulation.

Another explanation might be that familiar people, places, and objects are more heavily tied to past experiences, and that increased associations between a new simulated event and other previous experiences may aid recollection. Bar (2009) has suggested that memory encoding occurs when scenarios deviate from the expectations we have accumulated over the course of experiencing many past events. Participants would have more expectations for familiar than unfamiliar event components, and the random arrangement of these familiar components into new combinations would result in scenarios that are very different from the contexts in which participants have encountered them before. Therefore, the violations of expectations that result from randomly recombining familiar components may enhance encoding. Indeed, it has been shown that when participants are tested on their ability to recall a series of past autobiographical events, those events involving behaviours that were atypical or unusual for the person in the event are better recalled than events involving behaviours that were typical of the person or neutral (Skowronski, Betz, Thompson, & Shannon, 1991).

Our findings also demonstrate that recall of each individual component type on the cued-recall test was not solely predicted by familiarity ratings of just the missing component, but also by ratings of the other components as well. Recall of the object was predicted by familiarity ratings for the person and location, and recall of the location showed this same pattern. Recall of the person was significantly predicted by familiarity ratings of the person and object. The finding that the recall of each component type was influenced by the familiarity of other types of components in the event suggests that this cued-recall paradigm does in fact measure something about the simulation and the associations formed between the cues, as opposed to the test simply being a measure of how well participants could recall that particular component. In fact, it appears that the inclusion of either a familiar person or location in the event tended to enhance recall regardless of which component was being tested.

The familiarity of the person featured in the event was a strong determinant of whether the event would be remembered or not. Familiarity ratings for the person significantly predicted the likelihood of recall not only for the person, but also the location and object components of the simulation, as well as the likelihood of recall in general. It would appear, therefore, that the person detail was particularly salient or central to the imagined events in this experiment. Indeed, the person was also the most likely of the three event components to be later recalled. This importance of the person detail to imagined events is in contrast to previous studies that have focused on the importance of the familiarity of an event's location on its phenomenological characteristics (Arnold et al., 2011a; Szpunar et al., 2009). The apparent importance of the quality of the location supports the scene construction hypothesis (Hassabis, Kumaran, Vann, et al., 2007), which posits that the commonality between remembering and imagining is that they both require the mental representation of three-dimensional scenes. Although the familiarity of the location was a

significant predictor of event recall in the present study, location familiarity did not explain any variance in recall performance over and above that already explained by the familiarity of the person and the detail and plausibility of the simulation.

While there may indeed be something special about the contribution of the featured person to the memorability of imagined future events, there are other factors that may explain these findings. The person details were rated by participants as significantly more familiar, more emotional, and more significant than the locations and objects. Therefore, out of the three components comprising the imagined event, participants generally had a richer representation of the person than they did the other components. It may be the case that having any highly familiar detail in the scenario results in the event and all its components being more likely to be recalled, and the fact that the person detail just happened to be the most familiar is inconsequential. It is also possible, however, that aspects of the experimental design may have contributed to the current results. First, in the stimuli-collection interview, it was required that the three components identified in each memory be unique and not repeated across memories. It is conceivable, therefore, that participants could think of a larger number of familiar people than familiar locations or objects. Consequently, if the simulation is built around the most familiar component, this would most often be the person. Second, when the simulation cues were presented to the participants, the details were always presented in the same order (person, location, and then object). The consistent ordering of event components might have influenced participants to construct their scenarios around the person detail and then subsequently incorporate the remaining two components. The consistent lack of influence displayed by the object detail may therefore be explained both by the fact that the objects were less familiar to the participants and also that they were the last cue to be read during the trial. Future research could clarify this issue, by determining whether explicitly

manipulating the order in which the cues are presented affects later recall of each component type.

The results of this study have implications for the use of this style of cued-recall paradigm for assessing the recall of imagined future events. Testing recall of the event by requiring participants to remember the object does not appear to be equivalent to testing for the person or location. Not only were the objects rated as significantly lower in familiarity, emotionality, and personal significance than the other details, but also the recall rates for the object were significantly lower than for the other details, and object familiarity only contributed to recall for one of the simulation details. Consequently, the object appears to be contributing relatively little to the encoding of the scenario. In future studies making use of a similar paradigm, it may therefore be more meaningful to limit the cued-recall test to only the person and location details, or to replace the object cue with a possibly more meaningful event component such as an action.

In addition to the familiarity of the event components, the detail of a future simulation was another significant predictor of its later recall. This finding fits well with previous neuroimaging and behavioural findings showing a relationship between encoding and detail generation: regions of the hippocampus that are more active for later-remembered imagined future events than later-forgotten ones are also more active for highly-detailed than less-detailed events (Martin et al., 2011), activity in both anterior and posterior hippocampus is linearly related to ratings of detail for imagined future events (Addis & Schacter, 2008), and later-remembered events are rated as having more detail than later-forgotten ones (Martin et al., 2011). The nature of the interaction between detail generation and encoding is not entirely clear. Others have observed very high correlations between the two constructs in autobiographical memory, such that very detailed memories are the easiest to recall, though the fact that this association was modulated by variables such as the age, rehearsal frequency,

and emotional content of the memories suggests that detail and encoding are, to some extent, separable processes (Ritchie, Skowronski, Walker, & Wood, 2006). In the context of imagining future events, the constructive episodic simulation hypothesis (Schacter & Addis, 2007) would suggest that incorporating more episodic details extracted from previous experiences into the simulated event, along with the three provided event components, results in the event being correspondingly more integrated with existing episodic knowledge and thus easier to access during the cued-recall test.

Plausibility ratings also predicted the successful recall of a simulation, over and above the predictive power already ascribed to detail and familiarity ratings. In the present study, the effect of perceived plausibility on later recall was somewhat surprising given that overall mean plausibility ratings were very low. However, the use of multi-level modelling allowed for the examination of trial-by-trial variation that revealed a significant influence of plausibility ratings on recall success. The plausibility ratings made in the current study are based to some degree on participants' own past experiences, as in order to judge the reasonableness of the combination of details, it is necessary to compare the combination to events that have happened before and to what is known to be possible. Imagined events rated as being highly plausible are likely to be those that are relatively more similar to previous experiences, and thus given the use of random recombinations of memory details in the current study, it is not surprising that mean plausibility was low.

Previous research on the plausibility of imagined future events has focused on its effects on the phenomenology of the simulations (e.g. Anderson, 2012; Szpunar & Schacter, 2012). The concept of plausibility has different connotations in different studies; in the current study, the rating reflected the degree to which the combination of familiar event components was logical or reasonable, whereas in other studies it can reflect the unfamiliarity of the situation as well as its elements. For example, when imagining an implausible trip into

outer space (Anderson, 2012), the scenario and its components are unfamiliar, but the arrangement of the components is generally one that makes sense. Differences in the functional definition of plausibility may explain some of the varied findings in the literature. In Anderson's (2012) study, which did not involve familiar stimuli, event plausibility did not affect ease of simulation, whereas Szpunar and Schacter (2012), using a similar paradigm to the present study, found that increases in plausibility were accompanied by increases in detail and ease of simulation. The findings from the current study expand on those of Szpunar and Schacter (2012) by showing that the influence of plausibility on the phenomenology of imagined future events also extends to their encoding. This effect of plausibility on encoding may operate *via* its proven influence on phenomenology, although the fact that plausibility was a significant predictor over and above detail suggests that it exerts some independent influence.

In summary, imagined future events that are more detailed, more plausible, and that are comprised of more familiar elements have a higher likelihood of being recalled later in a cued-recall test. In the current paradigm, the familiarity of the person featured in the event was a more important predictor of simulation recall than the familiarity of the location and object, but this finding can be at least partially explained by the fact that the person detail was consistently rated as more familiar than the other details. A commonality between all three significant predictors (component familiarity, simulation detail, and simulation plausibility) is that simulations that are rated more highly on all of these characteristics can be thought of as having stronger associations to past episodic experiences. Imagined future events involving more familiar people, places, and objects also likely incorporate the greater number of associations that these elements have with other past events. Events that are highly detailed involve the incorporation of a larger number of episodic details extracted from past events, while highly plausible events are ones that have been classified as relatively likely to happen

in real life, presumably after comparison with previous experiences. The episodic encoding of stimuli and imagined events that are more highly-related to past experiences may be subject to a sort of 'scaffolding' (Poppenk & Norman, 2012) by the already-existing episodic knowledge, resulting in enhanced recall performance.

# Chapter 5: Study 4 – Do Subjective Ratings Correspond to the Content of Imagined Future Events?

## 5.1 Introduction

The majority of studies examining episodic simulation of future events (including Studies 1 and 3) incorporate at least one subjective participant rating, with the intention of capturing information about the quality of each imagined event. Common measures include Likert-type scale ratings of phenomenological characteristics such as detail (Addis & Schacter, 2008; Addis, Wong, et al., 2007; D'Argembeau, Xue, Lu, Van der Linden, & Bechara, 2008), plausibility (Szpunar & Schacter, 2012), vividness and spatial coherence (Hassabis, Kumaran, & Maguire, 2007; Mullally et al., 2012), sense of experiencing (D'Argembeau & Van der Linden, 2006), emotionality (D'Argembeau et al., 2008), and numerous others. Detail ratings in particular have been shown to be predictive of other aspects of imagined events, as they are associated with the magnitude of hippocampal activity during an imagined event (Addis & Schacter, 2008; Martin et al., 2011), and they predict the likelihood of the imagined event being remembered in a later cued-recall test (*Study 3*).

The construct validity of these ratings has not yet been systematically investigated. Although participant ratings are a typical component of fMRI studies of future thinking, it is generally not possible within the context of these paradigms to assess whether ratings are actually reflecting the concepts that they are supposed to measure. This is because contact with participants is limited while they are imagining events in the scanner, and post-scan interviewing about each imagined event can only occur after a delay of up to an hour. However, assessment of rating validity is important if these ratings are to be accurately interpreted or used as predictive variables in models of imagined event characteristics. There are a number of factors that may affect the validity of these subjective ratings, including the degree to which participants understand the rating they are making. Although the instructions

for making detail ratings in *Studies 1* and *3* included a mention of vividness as a factor defining highly-detailed imagined events (see Appendix B), the rating is otherwise somewhat open to interpretation. The concept of 'detail' is one that could be construed in a variety of ways, and may include elements such as the amount of visual detail comprising the imagined event, the number of things occurring in the event, or the degree to which the participant felt as if they were actually experiencing it. A group of imagined events that are all rated as high in detail may therefore not all share the same phenomenological characteristics. Assessment of rating validity therefore requires that the constructs being measured are clearly outlined.

The usefulness of asking participants to report the characteristics of their inner states has always been controversial, and many have argued that participants have limited access to their own mental processes (Wilson, 2003). The ability to meaningfully introspect about cognitive processes seems to depend heavily upon the task being completed (Kellogg, 1982), and participants' subjective judgements about their memory performance has often been found to be weakly related to more objective measures (Schmidt, Berg, & Deelman, 2001). With respect to episodic future thinking, the relation between detail ratings for imagined future events and activity in the hippocampus while the events are being imagined suggests that subjective detail ratings are consistently reflecting something about the episodic qualities of the simulations. Other studies have also provided evidence that participants can successfully evaluate the vividness of their own mental imagery. For example, participants' subjective ratings of stimulus vividness are associated with a perceptual bias towards that particular stimulus in a binocular rivalry paradigm (Pearson, Rademaker, & Tong, 2011), and self-reported visual imagery ability is associated with higher activation in early visual cortical regions while participants imagine dynamic scenes (Cui, Jeter, Yang, Montague, & Eagleman, 2007).

Despite these findings, it is possible that the validity of detail ratings for imagined future events are vulnerable to a form of social desirability bias (Nederhof, 1985). The relevance of this bias to studies of episodic simulation stems from the fact that participants are required to report the extent to which they did what was asked of them. Having been instructed to imagine specific future events in as much detail as possible, participants may be inclined to report having imagined a highly detailed event so as to give the impression that they performed the task as requested. There are also potential issues with the use of Likerttype scales that require participants to choose one of a group of ordered values. When completing such scales, participants frequently avoid choosing values at either extreme, perhaps because of uncertainty that some other item may exist that exhibits the measured characteristic to a greater or lesser degree. This tendency may limit the variation in responses and consequently hinder their predictive ability. Furthermore, the number of options in a Likert-type scale can influence participants' responding; five- or seven-item scales have a midpoint value and can encourage participants to favour a neutral response, while four- or six-item scales may force participants to choose one or the other side when they truly have no preference (Clark & Watson, 1995).

Study 4 explores the validity of ratings made about imagined future events, making use of an adapted version (Addis et al., 2008) of the Autobiographical Interview (Levine et al., 2002), combined with hierarchical linear modelling (Wright, 1998). Participants imagined their future events out loud in response to cue words, and their descriptions were transcribed and coded by trained raters to assess the content of the events. We then examined the association between subjective ratings the participants made about the episodic specificity of their imagined events and objective measures of the episodic content of the imagined events.

More specifically, we determined whether participant ratings about the imagined events' vivid detail, as well as the spatial and temporal clarity of the events, could together significantly predict the overall number of episodic details (but not the number of external or non-episodic details) in verbal descriptions of each imagined event as determined by the independent raters. If this is the case, it would suggest that imagined events perceived by participants as vividly detailed and spatiotemporally specific are more likely to contain a larger number of episodic details of all types, and that the ratings together reflect the degree to which the imagined events can be considered episodic.

Subsequently, we conducted more specific analyses assessing whether the individual participant ratings of vivid detail, clarity of location, and clarity of temporal context each predicted the number of details coded by the independent raters to contain visual information, location-related information, and temporal information, respectively. It was expected that if the subjective participant ratings have convergent validity, then they would accurately reflect the type of information contained in the imagined events. In other words, the events rated by participants as high in vivid detail or having clear spatial or temporal contexts would contain more of each of those types of detail as classified by the independent raters. Furthermore, it was anticipated that the predictive ability of participant ratings would be restricted to only related types of details, confirming the divergent validity of these ratings. In other words, the number of visual details would be predicted only by the rating of vivid detail and not by the other two ratings, while the number of temporal details would be predicted only by the rating of temporal clarity, and the number of spatial details would be predicted only by the rating of location clarity.

#### **5.2 Methods**

## 5.2.1 Participants

Twenty-one young adults (8 males, aged 18-35) were recruited via on-campus advertisements in compliance with the principles of The University of Auckland Human Participants Ethics Committee; all had English as a first or very early language and did not meet exclusionary criteria (neurological/psychiatric conditions or psychotropic medication use).

# **5.2.2.** Adapted Autobiographical Interview

Participants imagined their future events in the context of the Adapted Autobiographical Interview (AI) (Addis et al., 2008). The AI paradigm was initially designed to objectively measure proportions of episodic and semantic details comprising autobiographical memories (Levine et al., 2002) without having to rely on self-report (Levine, 2004). In the present study, the Adapted AI consisted of one practice trial followed by 12 test trials. On each trial, participants were shown a single cue word on a computer screen (see Table 7 for the list and characteristics of cue words used) as well as a time period in which the event should be situated (either 'next few weeks', 'next few years', or 'next 20 years'). The cue words were presented in a random order for each participant, and the combinations of cue words and time periods were also random. Participants were asked to imagine a plausible and specific event that might happen to them during the specified time period in response to the cue word. It was not necessary that the event directly involve the cue word, as long as the event was specific in time and place and had not been experienced before. The events were imagined out loud, and participants were given three minutes in which to describe as much detail about the imagined event as possible. The cue word and time period remained on the screen throughout the duration of the trial. Input from the experimenter was minimal, and was limited to general probes such as 'can you tell me any

more about that?' used only when necessary and as described in the administration instructions in Appendix C. The limitations on examiner input were intended to prevent participants from being influenced to include any particular types of details in their imagined events. The experimenter recorded the descriptions on an audio recorder for later transcription. At the end of the three minutes, a timer sounded, indicating that the participant should end their description.

Table 7. List of cue words used in the Adapted Autobiographical Interview.

Cue Word	Imageability	Concreteness	Thorndike-Lorge
			Frequency
OVEN	5.97	6.96	1.477
HORSE	6.1	6.94	2.004
CAR	5.97	7	2.004
TREE	6.39	7	2.004
LETTER	5.42	6.94	2.004
STAIN	5.23	6.25	1.462
PIANO	5.81	6.85	1.431
BABY	6.26	6.9	2.004
PHOTOGRAPH	6.06	6.56	1.556
SHOES	5.52	7	2.004
DRESS	5.84	6.93	2.004
NEWSPAPER	5.84	6.56	2.004

*Note.* Ratings of imageability and concreteness are on seven-point scales from 1 (low) to 7 (high), words were chosen to be high on these two ratings (Clark & Paivio, 2004). Thorndike-Lorge Frequency values are taken from Thorndike & Lorge (1944).

After imagining each event, participants were asked to make a number of ratings about what they had just imagined. First, they indicated the time period in which they had imagined the event occurring (to ensure the time period matched that in the instructions).

Next, they made ratings on seven-point Likert-type scales about the amount of vivid detail (1 = no vivid detail, 7 = extremely vivid and detailed), the clarity of the imagined event's location (1 = no clear idea about the location, 7 = precise knowledge about the location), and the clarity of the temporal context (1 = no specific time for the event, 7 = the event was imagined to be happening at an exact time). After making these ratings, the experiment proceeded to the next trial as soon as the participant was ready. Seven-point scales were used

in this study instead of the four-point scales used in *Studies 1-3* so as to expand the possible range of values and to allow for a middle or neutral response (Clark & Watson, 1995).

## **5.2.3 Scoring**

The audio-recordings of each participant's imagined events were transcribed by a research assistant, and each event was coded by one of two independent raters. To ensure impartiality, the data from participants' subjective ratings were stored separately from the transcripts and were not examined until the imagined events from the AI had already been segmented and coded. The method of coding was adapted from Addis et al. (2008), which itself was an adapted version of the scoring system described by Levine et al. (2002). Coding involved segmenting each transcription into small pieces of information that each conveyed a unique idea, and then classifying each piece of information as belonging to one of several categories. The adaptation consisted of the categorisation of more specific subcategories of episodic details. The broadest categories were *internal* (details that were specific to the main episodic event being described) and *external* (details that conveyed semantic information or that related to other episodic events besides the main one being described). If participants described more than one episodic event, the rater would score the specific event that was described in most detail as the main episodic event and the others as external episodic events.

Within the internal category, details relating to the episodic event could fall into one of eight sub-categories (full instructions for scoring can be found in Appendix D). Of relevance to this study were *visual* details (details about the appearance of the event that were non-spatial), *place* details (describing where the event is located), *spatial orientation* details (information about distances and positions in allocentric or egocentric space), *time* details (noting when the event is occurring), and *duration/temporal sequence* details (descriptions of how long things lasted or the order in which they were occurring).

Inter-rater reliability was established by first having both raters code data from 20 remembered past and imagined future events collected in a previous study. An intra-class correlation analysis indicated that inter-rater reliability was high for internal (Cronbach's  $\alpha$  = 0.96), external ( $\alpha$  = 0.86), visual ( $\alpha$  = 0.87), place, ( $\alpha$  = 0.87), spatial orientation ( $\alpha$  = 0.86), time ( $\alpha$  = 0.73), and duration ( $\alpha$  = 0.84) details.

#### 5.2.4 Hierarchical Linear Modelling

As in *Study 3*, the imagined events in this study had an inherently nested structure, such that imagined events were nested within participants. In order to take this structure into account, we again employed hierarchical linear modelling (Wright, 1998). Using HLM 7 software (Raudenbush et al., 2011), two-level random coefficient models were created in which each imagined future event was modelled at the lower within-subjects level, and each participant at the higher between-subjects level, resulting in 250 records at level one<sup>7</sup> and 21 records at level two.

For every imagined event, a number of variables were considered: level-one predictor variables included participant ratings of the amount of *vivid detail*, the *clarity of the location*, and the *clarity of the time* at which the event occurred; level-one outcome variables included an *AI - total internal* variable in which all the internal detail classifications were summed, an *AI - total external* variable in which the external detail types were similarly combined, the number of *AI - visual details*, an *AI - overall spatial* variable for which place and spatial details were summed, and an *AI - overall temporal* variable for which time and duration details were summed. All ratings were mean centred, such that the mean of each rating for each participant was calculated across all of their events, and the individual rating from each event was then subtracted from its respective mean. This resulted in the centred ratings representing the deviation from that participant's average response (Kreft et al., 1995). All

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<sup>&</sup>lt;sup>7</sup> Although each participant imagined 12 future events, two participants did not successfully make all ratings for 1 of their 12 events. These two events with missed ratings were not included in the analysis.

predictor variables were modelled such that both intercepts and slopes were allowed to vary across participants. The models were then estimated using a restricted maximum likelihood method with a maximum number of 100 micro-iterations.

#### **5.3 Results**

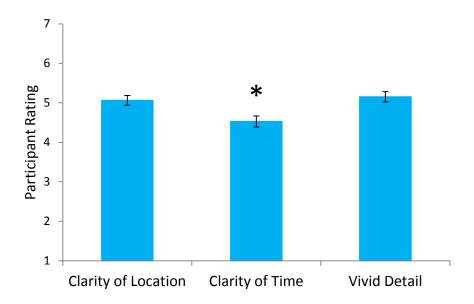
## **5.3.1 Ratings**

Participants generally rated their imagined future events as high in vivid detail, location clarity, and temporal clarity. See Table 8 for descriptive statistics of these three ratings. A repeated-measures ANOVA revealed that there was a significant effect of rating type, F(2,40) = 7.93, p < .001. Pairwise comparisons showed that both vivid detail ratings (p = .009) and location clarity ratings (p = .016) were significantly higher than time clarity ratings. Ratings of location clarity and vivid detail were not significantly different (p = 1.0).

Table 8. Descriptive statistics for participant ratings of their imagined future events.

Participant Rating	Mean	SD	SE
Clarity of Location	5.06	0.57	0.12
Clarity of Time	4.53	0.64	0.14
Vivid Detail	5.15	0.60	0.13

*Note*. Ratings were made on a seven-point (1 = low, 7 = high) scale. SD = standard deviation, SE = standard error of the mean.



*Figure 11.* Mean participant ratings for their imagined future events. Error bars reflect standard error of the mean, \* = p < .05.

#### **5.3.2** Event Details

The imagined events were generally found to be specific and episodic in nature by the raters, as indicated by the mean proportions of each detail type coded in the transcriptions (see Table 9 for descriptive statistics for all detail types). The imagined events were composed primarily of event, visual, and semantic details, with the remaining detail types each comprising a relatively smaller proportion.

As has previously shown to be the case in young adults (Addis et al., 2008), participants generated significantly more internal details (pertaining to the main episodic event being described) than external details (referring to other events or to semantic information) for their imagined future events, t(20) = 6.67, p < .001, see Figure 12. This again indicates that participants were describing specific aspects of the events being imagined, as opposed to external events or related semantic information.

Table 9. Descriptive statistics for each type of event detail as measured by independent raters.

Detail Type	Mean	SD	SE	
Internal Details				
Internal Details				
Event	27.51	9.45	2.06	
Place	1.94	0.66	0.14	
Time	1.77	0.99	0.22	
Perceptual	2.15	1.56	0.34	
Visual	8.13	6.96	1.52	
Duration	1.66	1.32	0.29	
Spatial Orientation	1.69	1.25	0.27	
Emotion/Thought	4.87	3.63	0.79	
Total Internal	49.72	12.77	2.79	
External Details				
Semantic	8.88	7.04	1.54	
Repetitions	2.27	1.51	0.33	
External Episodic	2.25	2.03	0.44	
Routines	0.81	0.82	0.18	
Other	6.59	4.67	1.02	
Total External	20.80	12.86	2.81	

*Note.* SD = standard deviation, SE = standard error of the mean.

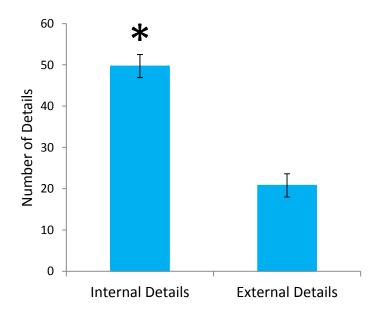


Figure 12. Mean numbers of internal and external details generated by participants in the Adapted Autobiographical Interview.

Error bars reflect standard error of the mean, \* = p < .05.

## 5.3.3 Associations Between Participant Ratings and Internal/External Details

Two empty (intercept-only) multilevel models were created initially, with AI – total internal and AI - total external details as the two normally-distributed continuous outcome variables. The purpose of these models was to test the suitability of hierarchical linear modelling for this particular data set. The empty model of AI - total internal revealed that a significant proportion of the variance in the number of internal details was due to variation between participants (ICC = 0.45,  $\chi^2(20) = 210.99$ , p < .001) indicating that the use of a multi-level model was appropriate. This was also the case for the model of AI - total external (ICC = 0.65,  $\chi^2(20) = 456.49$ , p < .001).

Following this, we investigated whether the participant ratings together predicted the overall numbers of internal and external details in the imagined events. Two 2-level models with normal and continuous outcome variables were created, one with AI - total internal as the outcome, and the other with AI - total external as the outcome. Each model contained the participant ratings of vivid detail, location clarity, and time clarity as the level-1 predictors. The first model revealed that for the total number of internal details, vivid detail ratings (t(20) = 2.71, p = .013) and time clarity ratings (t(20) = 2.47, p = .022) were significant predictors, and location clarity ratings approached significance (t(20) = 1.80, p = .087). In contrast, the second model indicated that none of the three ratings significantly predicted the total number of external details (vivid detail, t(20) = -0.62, p = .544; time clarity t(20) = -1.23, p = .232; location clarity, t(20) = -0.68, p = .502). Together, these findings establish the divergent validity of the participant ratings, as they indicate that imagined events rated highly on all three dimensions were more likely to contain specific episodic information, but were not any more likely to contain external, non-episodic information. See Table 10 for the coefficients and statistics for each of these two models.

Table 10. Statistics and coefficients for models of total internal and external details in the Adapted Autobiographical Interview (AI) as predicted by subjective participant ratings.

Fixed Effect	Standardized	SE	<i>t</i> -ratio	d.f.	<i>p</i> -value
	Coefficient				
Total Internal Details in AI					
Intercept	-	2.79	17.87	20	<.001
Clarity of Location Rating	0.05	0.60	1.80	20	.087
Clarity of Time Rating	0.08	0.60	2.47	20	.022
Vivid Detail Rating	0.12	0.97	2.71	20	.013
Total External Details in AI					
Intercept	- -	2.81	7.45	20	<.001
Clarity of Location Rating	-0.02	0.62	-0.68	20	.502
Clarity of Time Rating	-0.03	0.42	-1.23	20	.232
Vivid Detail Rating	-0.03	1.19	-0.62	20	.544

*Note.* SE = standard error of the mean, d.f. = degrees of freedom.

# 5.3.4 Associations Between Participant Ratings and Corresponding Detail Types

Next, we examined the relationship between each individual participant rating and its corresponding detail type in the Adapted AI. First, we assessed whether participant ratings of the amount of vivid detail in each imagined event significantly predicted the number of details that would later be classified by the independent raters as containing visual information. We initially created an empty two-level model in which AI - visual details was the continuous outcome variable; this model showed that a significant proportion of the variance in the number of visual details was due to variation between participants (ICC = 0.49,  $\chi^2(20) = 241.87$ , p < .001). Following this, we added the participants' vivid detail rating as a single predictor. Results illustrated that the rating of vivid detail was indeed a significant predictor of the number of visual details, t(20) = 3.84, p = .001. Figure 13a illustrates that while differences between participants are larger for imagined events rated as more highly detailed, a consistently positive association is observed across the entire sample.

This model, while illustrating that ratings of vivid detail predicted the total number of visual details, did not establish that the predictive ability was specific to only this subjective

rating. To investigate this further, we therefore added in the other two ratings of time clarity and location to the model of AI - visual details. With all three ratings entered simultaneously, the rating of vivid detail was the only one to significantly predict the number of visual details, t(20) = 3.32, p = .003. Ratings of location clarity (t(20) = -1.54, p = .140) and time clarity (t(20) = 1.31, t(20) = 1

We then examined whether participant ratings of the clarity of the event's location predicted the number of details that would be coded by the independent raters as mentioning spatial information. An empty model was created with AI - overall spatial as the normally-distributed outcome variable; this model showed that a significant proportion of the variance in the number of overall spatial details was due to variation between participants (ICC = 0.27,  $\chi^2(20) = 105.62$ , p < .001). Following this, location clarity rating was added as the single predictor. Contrary to expectations, participant ratings of the clarity of the location did not significantly predict the number of overall spatial details, t(20) = 0.19,  $p = .852^8$ . Figure 13b illustrates that participants tended to mention the same amount of spatial information across all of their imagined events, regardless of how clear the location was to them.

Entering all three ratings together as predictors into a model of AI - overall spatial revealed that while ratings of location clarity (t(20) = -0.69, p = .498) and time clarity (t(20) = -0.22, p = .828) did not predict the number of spatial details, ratings of vivid detail did so significantly (t(20) = 2.48, p = .022). Participant perception of the amount of vivid detail in an imagined event was therefore a better predictor of the number of spatial details than participant perception of the clarity of the event's location.

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<sup>&</sup>lt;sup>8</sup> This same analysis was conducted with two additional models, one with only AI – place details as the outcome variable and the other with only AI – spatial details as the outcome, and the location clarity rating similarly did not significantly predict either of these. These analyses were done so as to ensure that the aggregation of these two measures into the AI – overall spatial variable was not limiting the predictive ability of the location clarity rating.

Finally, we assessed the association between participant ratings of the clarity of the time at which the event was taking place and the number of temporal details in their imagined future events. An empty model was created in which AI -  $overall\ temporal$  was the normal and continuous outcome variable; this model showed that a significant proportion of the variance in the number of overall temporal details was due to variation between participants  $(ICC = 0.35, \chi^2(20) = 147.01, p < .001)$ . Adding participant ratings of time clarity as a single level-one predictor revealed that this rating significantly predicted the overall number of temporal details, t(20) = 2.30, p = .032. Figure 13c illustrates that the majority of participants exhibited a positive association between subjective ratings of time clarity and the number of temporal details in the AI.

Again, to examine the specificity of this predictive ability, all three participant ratings were then added simultaneously as predictors in a model of AI - overall temporal details. In this case, the rating of temporal clarity still approached significance as a predictor (t(20) = 1.74, p = .097) with the other predictors in the model, while ratings of location clarity (t(20) = 1.56, p = .136) and vivid detail (t(20) = 0.47, p = .646) did not significantly predict the number of temporal details.

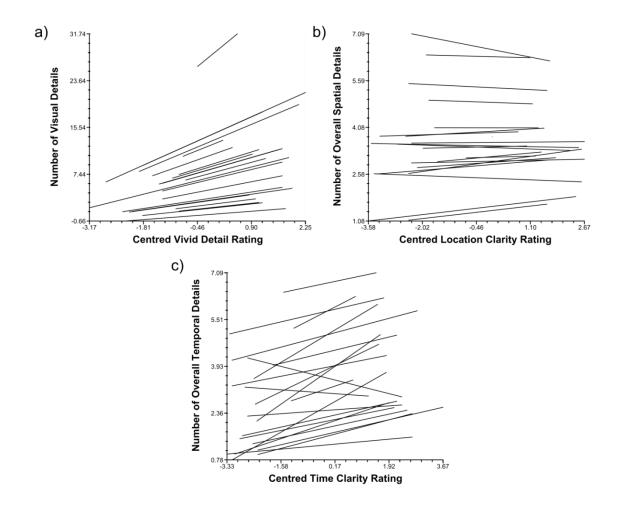


Figure 13. Associations between subjective participant ratings and objective measures of imagined event content.

Regression lines for each individual participant illustrate the relationship between subjective ratings of vivid detail, location clarity, and time clarity with objective measures of corresponding detail types in their imagined future events described in the Adapted Autobiographical Interview.

## **5.3.5** Associations Between Subjective Ratings

Lastly, we examined the associations among the three subjective participant ratings. An empty model of participants' vivid detail ratings showed that a significant proportion of the variance was due to difference between participants, (ICC = 0.21,  $\chi^2(20) = 83.95$ , p < .001). Adding the other ratings of location and time clarity as level-one predictors revealed that events rated highly on both location (t(20) = 4.50, p < .001) and time (t(20) = 3.44, p = .003) clarity were more likely to be rated highly in vivid detail.

An empty model of participants' location clarity ratings showed that the proportion of variance due to participant differences approached significance (ICC = 0.04,  $\chi^2(20) = 30.94$ , p = .056), suggesting that between-participant differences on this rating were smaller than for the other variables in this study. Entering the other two ratings as level-one predictors showed that while ratings of vivid detail predicted ratings of location clarity (t(20) = 5.16, p < .001), ratings of time clarity did not (t(20) = 0.75, p = .462).

Finally, the intercept-only model of time clarity ratings indicated a significant proportion of variance resulting from between-participant differences (ICC = 0.08,  $\chi^2(20) = 39.47$ , p = .006). The addition of the other two ratings as level-one predictors indicated that again, ratings of vivid detail predicted ratings of time clarity (t(20) = 3.85, p = .001), but ratings of location clarity did not (t(20) = 1.03, p = .317)

## 5.4 Discussion

The objective of this study was to investigate the degree to which participant ratings of their imagined future events truly reflect the corresponding content of the imagined events, at least in the sense that an imagined event is truly represented in a verbal description. This question was investigated by examining the association between participant ratings of vivid detail, the clarity of the imagined event's location, and the clarity of the time at which it was

taking place with the quantities of certain detail types mentioned by the participants in the Adapted AI (as measured by independent raters). As these ratings were designed to capture aspects of the imagined events' episodic specificity, it was hypothesised that all of the participant ratings together would predict the total number of internal or episodic details of all types, while there would be no relation between the ratings and the number of external or non-episodic details. This pattern was generally observed: ratings of vivid detail and temporal clarity significantly predicted the number of internal details in the AI (and ratings of location clarity approached significance as a predictor), but none of the three ratings predicted the number of external details.

It was further anticipated that events rated highly in vivid detail would contain more details in the AI classified as containing visual information, events rated as having a clear location would contain more details describing spatial information, and events rated as having a clear temporal context would contain more details describing temporal information. Two of these three hypotheses were confirmed, such that ratings of vivid detail and ratings of temporal clarity did predict the numbers of relevant details in the imagined events described in the AI. However, ratings of location clarity did not predict the number of spatial details. Additional analyses illustrated the specificity of these effects: the number of AI visual details was predicted only by the rating of vivid detail, and not by the other two ratings, and the number of AI temporal details was only predicted (albeit at a trend level when all ratings were entered simultaneously) by the rating of temporal clarity, and not by the other two ratings. Interestingly, the number of spatial details in the AI was also predicted by ratings of vivid detail, and not by ratings of location or time clarity.

Overall, these findings demonstrate the validity of participant ratings for capturing the contents of imagined future events. Particularly relevant is the observation that imagined events perceived by participants as being higher in vivid detail and temporal clarity also

included a higher number of details containing visual and temporal information in the AI, and that the predictive ability of these ratings was specific to episodic details related to the constructs being rated. These results suggest that participants' understanding of what constitutes a vivid and temporally-specific event corresponds to that of the experimenters as measured by the AI. The results also imply that when participants are asked to assess the visual and temporal quality of their imagined events, they can do so accurately. Furthermore, the fact that ratings of vivid detail significantly predicted and were predicted by ratings of location and time clarity indicate that imagined events rated highly in one measure of specificity tend to be rated highly in other measures as well.

The finding that subjective ratings of location clarity did not correspond to the number of spatial details in the AI was unexpected. This lack of association does not appear to result from any unusual qualities of the means or distributions of either the subjective location clarity ratings or the total number of spatial details. It is therefore not clear why ratings for the location are relatively weaker predictors of event characteristics. One possible explanation is that participants generally imagined their events taking place in very clear locations (as shown by the high mean ratings of location clarity), but tended not to describe aloud this aspect of their events to a corresponding degree, choosing instead to focus on other features such as visual details. This explanation is supported by the fact that while ratings of location clarity were significantly higher than ratings of time clarity, the numbers of overall spatial and overall temporal details included in the Adapted AI were not significantly different (t(20) = 0.453, p = .655).

It is possible that a participant rating about the clarity of an imagined event's location is not particularly strongly linked to other event qualities. The fact that the rating of location clarity was also the only rating of the three to not significantly predict the total number of internal event details supports this idea. More specifically, the episodic nature of the

imagined events was tied less to the clarity of the event's location than it was to the amount of vivid detail and the clarity of its temporal context. This lack of association between location clarity and episodic detail is surprising, given that previous studies have shown that the clarity and familiarity of an imagined event's location significantly influences a number of other event characteristics. For example, Szpunar and McDermott (2008) and de Vito et al (2012) established that imagined events set in clear and familiar locations are rated by participants as more vivid than those set in unfamiliar locations. Arnold et al. (2011a) found that differences in vividness between events imagined in the near and far future are driven by the clarity of the imagined locations, and again that events imagined to take place in familiar locations are more vivid than those imagined in unfamiliar locations. Study 3 illustrated that the familiarity of an imagined event's location predicts later memory for the imagined event. A factor that differentiates these studies from the present one is that they involve explicit manipulation of the clarity of the locations (with the exception of *Study 3*), and they all provide locations known to the participants as cues. The Adapted AI does not involve any overt mention of imagined event locations, as the cues consist only of single generic nouns, and participants' events are not required to be situated anywhere specific. The validity of participants' location clarity ratings may therefore be reduced when locations are not obviously specified.

Another possibility is that participants struggled to differentiate between the concepts of vivid detail and location clarity. Because events with clear locations are likely to contain a large amount of vivid detail, and highly-vivid events probably tend to have clear spatial contexts, participants may have experienced confusion when required to rate two very similar or related event characteristics. This explanation is reinforced by the finding that participant ratings of vivid detail significantly predicted the number of details coded by the raters as mentioning location and spatial information, while the ostensibly more theoretically-related

rating of location clarity did not. In future research examining the validity of subjective participant ratings, it will therefore be helpful to ensure that each rating measures a distinct and non-overlapping construct.

Despite the limited association between subjective and objective measures of imagined event location details, the participant ratings together did generally correspond to objective measures of imagined event specificity, as measured by the number of internal details in the events. Furthermore, the absence of a link between the three participant ratings and the number of external details establishes that the ratings are capturing information primarily about the episodic nature of the event, and not simply the amount of detail described overall. The correspondence between subjective and objective measures found in the current study fits with some of the findings of a recent study in which similar results were found for both participant and experimenter measures of imagined event characteristics (de Vito et al., 2012). In the first of two experiments, the authors showed that imagined events situated in familiar settings were rated by participants as containing more sensorial detail, being more clearly represented, and evoking a stronger sense of experience than events set in unfamiliar settings. Critically, these events also contained more internal details as measured with the AI scoring system. However, in their second experiment they found that selfrelevant imagined future events, while containing more internal details than self-irrelevant imagined future events, did not differ significantly in ratings of sensorial details or the clarity of the location. Therefore, while it appears that participant ratings for imagined future events frequently correspond with objective measures of event specificity, this may not be the case when there are changes in certain subcategories of internal details that are unrelated to the subjective ratings being made. For example, it is conceivable that self-relevant imagined events might contain more emotion- or thought-related internal details in the Adapted AI than self-irrelevant imagined events, which would boost the total number of internal details, but

the two types of events would not differ in the number of sensorial or location-related details mentioned, hence the similar subjective ratings of such characteristics.

There is an important limitation of using the correspondence between participant ratings and numbers of imagined event details in the Adapted AI as an indication of rating validity. When participants imagine future events without having to verbalize what they have imagined (e.g., within the MRI environment), the ratings made afterwards are based solely on the participant's mental representations of their events. However, in the context of the Adapted AI, participants make such ratings after having just verbally relayed specific aspects of the imagined events to the experimenter. This verbalisation may create an inclination for the participants to make their ratings based on the particular details they chose to describe aloud, rather than on the basis of the entire mental representation. It is conceivable that what is described in the Adapted AI does not necessarily encompass all aspects of what was imagined. Therefore, the conclusions about participant ratings made in the present study may not be entirely generalizable to studies in which participants are not required to describe their imagined events out loud.

To summarize, this study is the first to systematically examine and provide evidence for the construct validity of participant ratings for imagined future events. Participant ratings of vivid detail and temporal clarity predicted objective measures for the amounts of associated details in their imagined events. Specifically, events rated by participants as being high in vivid detail were more likely to be coded by independent raters as containing a larger number of visual details, and similarly, events rated as having a clear temporal context were more likely to be coded as having a larger number of temporal details. Moreover, ratings of vivid detail and temporal clarity together predicted the number of internal, or episodic details in the imagined events, but not the number of external or non-episodic details. Unexpectedly, participant ratings for the clarity of the imagined events' locations did not predict the number

of details coded as containing spatial information, although this rating approached significance as a predictor of internal details. However, participant ratings of vivid detail did in fact predict the number of spatial details, suggesting that the participant ratings of location clarity and vivid detail were conceptually overlapping. In general, it appears that participants are indeed able to provide accurate ratings about their imagined future events that do in fact reflect specific qualities of the simulations. Therefore, it seems that such subjective ratings can be used meaningfully as predictors of other aspects of imagined future events.

## **Chapter 6: General Discussion**

# **6.1 Summary**

In 2007, four studies clearly demonstrated a link between remembering past events and imagining future ones (Addis, Wong, et al., 2007; Hassabis, Kumaran, & Maguire, 2007; Hassabis, Kumaran, Vann, et al., 2007; Szpunar et al., 2007). Since then, there has been a rapid expansion in our knowledge about the mental simulation of episodic events and the processes that are common to both remembering and imagining. An aspect of episodic simulation that has received relatively little attention is the way in which imagined events are stored and retained in long-term memory. Some have noted that memories for imagined future events are what make up our expectations and plans (Bar, 2009; Ingvar, 1985), but the neural and cognitive bases of successfully encoding imagined events have not been fully investigated. The neuroimaging and behavioural studies comprising this thesis provide novel insight into how and when this encoding occurs.

Studies 1 and 2 illustrate that the hippocampus plays a central role in the encoding of imagined future events. In Study 1, it was shown that when participants imagine future events, both the anterior and posterior extents of the right hippocampus are more active during the simulation of events that will be later remembered in a cued-recall test than those that will be later forgotten. In Study 2, the functional connectivity of the hippocampus was demonstrated to be modulated by encoding success. Taken together, the findings from these two studies suggest that the hippocampus serves to encode internally generated episodic stimuli.

Study 2 employed functional connectivity analyses to highlight that it is not the hippocampus alone that works to store imagined events into memory. A critical aspect of successful encoding appears to be the functional integration of the hippocampus with a

broader whole-brain network, and the connectivity of the posterior extent of the hippocampus with such a network was found to be particularly important for the encoding of imagined future events. This finding fits well with previous research showing that hippocampal functional connectivity is predictive of subsequent memory for a variety of other types of stimuli (Gagnepain et al., 2011; Ranganath et al., 2005). Our finding that this connectivity differed for the anterior and posterior extents of the hippocampus illustrates that distinct hippocampal sub-regions may be making different contributions to episodic simulation.

An understanding of how imagined events are stored into memory requires knowledge about what makes a simulation more or less likely to be later recalled. In *Study 3*, it was established that imagined events rated by participants as being more detailed, more plausible, and involving familiar people and locations were more likely to be remembered later than events with low ratings on these characteristics. This finding converges with that of *Study 1* where imagined events that were later remembered were rated as being more detailed than events that were later forgotten, and suggests a close association between detail generation and encoding. One interpretation of these findings is that imagined events with stronger links to past episodic experiences are more easily encoded, perhaps due to the already-existing episodic knowledge forming cognitive scaffold that aids in the incorporation of new simulations (Poppenk & Norman, 2012).

Finally, as subjective participant ratings had been used in *Studies 1* and *3* (as well as in other studies, e.g. D'Argembeau & Van der Linden, 2012) to predict characteristics of imagined future events, we investigated the validity of these ratings. *Study 4* illustrated that participants' perceptions of the features of their imagined future events corresponded well with experimenters' classifications of relevant content in verbal descriptions of the imagined events. Specifically, participant ratings about the temporal clarity and the amount of vivid detail in their simulations predicted the number of details in the imagined event descriptions

that would be coded by the experimenters to include temporal and visual information, as well as the amount of episodic content overall. While participant ratings of location clarity did not predict the number of spatial details in the imagined event descriptions as coded by the experimenters, participant ratings of vivid detail did so significantly, suggesting that the constructs of location clarity and vivid detail are conceptually overlapping. Together, these results confirm that participants can make accurate ratings about the content and characteristics of their imagined future events.

# **6.2 Encoding of Imagined Future Events**

The results of *Studies 1*, *2*, and *3* expand our knowledge of how imagined events are encoded into memory. Our finding from *Study 1* that the hippocampus was more active for later-recalled imagined future events than later-forgotten ones suggests that the hippocampus works to store imagined events into memory, just as it does for episodic events experienced in real life. Previous research has shown a hippocampal response to subsequent memory for a wide range of other stimuli, including face-name associations (Westerberg, Voss, Reber, & Paller, 2012), the temporal contexts of episodic events (Jenkins & Ranganath, 2010), pairs of words, pairs of pictures, and word-picture pairs (Park & Rugg, 2011), and associations between items as well as associations between items and their context (Park, Shannon, Biggan, & Spann, 2012). As described in the *General Introduction*, the hippocampus is thought to integrate and capture whole-brain patterns of activity that occur while an event in the external world is being experienced, creating a sort of index that can be used to recreate the same pattern later on during memory retrieval (McClelland et al., 1995). It follows from our neuroimaging findings that this process likely also extends to the capture of patterns of activation that are internally-generated.

If the role of the hippocampus is to capture and encode whole-brain patterns of activity reflecting on-going experience (McClelland et al., 1995), it is unsurprising that the

connectivity of the hippocampus with other brain regions is required for successful storage of imagined events into memory, as demonstrated in Study 2. Our finding that increased connectivity of the posterior hippocampus with several regions of the default network was associated with successful encoding of imagined events illustrates that it is the interaction of the hippocampus with wider networks that is crucial. However, a recent study found that hippocampal functional connectivity with default network regions, while enhanced during retrieval of imagined events, was diminished during their encoding (Huijbers, Pennartz, Cabeza, & Daselaar, 2011). This apparent discrepancy can, however, be explained by the type of internally-generated events being encoded. In Study 2, the encoding task required participants to imagine autobiographical episodic events, which is a task that is known to strongly recruit many aspects of the default network (Addis, Wong, et al., 2007). In contrast, Huijbers et al. (2011) had participants encode imagined isolated sounds or images, a task that would arguably recruit these default regions to a lesser degree. Indeed, Huijbers et. al (2011) noted that during their encoding task, default network activity associated with task-irrelevant internal cognition (such as imagining personal events) was likely disruptive to successful encoding. Therefore, the enhanced interaction between the hippocampus and regions of the default network should only be expected to improve encoding when the encoding task itself strongly recruits the default network, as was the case in *Study 2*.

Studies 1 and 3 provide evidence that the more vivid and detailed an imagined event is, the more likely it is to be retained in memory. Prior to the recent focus on the similarities between remembering and imagining, others had examined the encoding of internally-generated events and found that imagery influenced later memory for such representations. This type of memory for imagined events had most often been investigated in the context of reality monitoring (Johnson & Raye, 1981) and in the formation of false memories when participants mistakenly report having experienced an imagined event in real life. A consistent

finding is that imagined events which are erroneously perceived as being real are typically higher in perceptual details (Johnson, Foley, Suengas, & Raye, 1988) and accompanied by activation in posterior regions associated with visual imagery (Gonsalves & Paller, 2000; Gonsalves et al., 2004). Vividly imagining a hypothetical event therefore makes it more likely to be endorsed by the participant as having actually happened, although in this context, the effect of vividness can perhaps be more accurately described as impairing the accuracy of source memory. Broadly speaking however, imagined events that are high in vividness and detail are perceived by participants as being particularly realistic, salient, and memorable.

Finally, Study 3 illustrates that the degree to which an imagined event is related to previous experiences affects how well it is stored in memory. Imagined events that are more likely to happen in real life and that involve familiar people, places, and objects are more easily remembered later. Results from Studies 1 and 2 implicate the hippocampus as the structure underlying this improvement in rates of recall. A possible mechanism for this facilitative effect follows again from the broader role of the hippocampus in episodic encoding. If the hippocampus has already created enduring links to a pattern of activation that corresponds to a particular previously-experienced event, and the participant imagines a new scenario that differs only in some minor details from this original event, it is possible that a memory trace for the new imagined event is more easily created than one involving a completely new pattern of activation that has never been experienced before. A more specific hypothesis is proposed by Shohamy and Wagner (2008), who argue that encountering an experience that overlaps significantly with a past event prompts retrieval of that past event, and any discrepancies between the two can be characterised as deviations from our expectations and predictions. When predictions are violated, interaction between the hippocampus and the ventral tegmental area is increased and storage into long-term memory is enhanced (Lisman & Grace, 2005).

## **6.3 Trial-by Trial Analysis**

Studies 3 and 4 make use of hierarchical or multilevel modelling (Raudenbush & Bryk, 1992), a method that is relatively uncommon in episodic memory research despite being particularly appropriate (Wright, 1998). More often, analyses are conducted on aggregated participant means, resulting in the loss of rich trial-by-trial information. This conventional type of analysis limits the types of conclusions that can be made. For example, if examining the association between detail ratings and rates of recall for imagined events, one could conclude only that participants who rated their imagined events as more detailed tended to later recall more of these events than participants who rated their imagined events as less detailed. In contrast, multilevel techniques allow researchers to track the fate of individual representations or trials, such that it is possible to conclude (as in *Study 3*) that a specific individual imagined event rated as being high in detail was significantly more likely to be recalled later. This type of trial-by-trial analysis was also critical in order to meaningfully examine the relationship between participant ratings of their imagined events and the corresponding content of those events in *Study 4*.

Multilevel techniques also allow for more accurate estimation of models in which the observations are correlated or not independent of each other, as is the case in numerous research contexts. This method is particularly applicable to the study of episodic memory (Wright, 1998), as there are significant differences between participants in the quality and characteristics of their episodic memories and simulations, which might lead to between-subject variance obscuring effects of interest. While hierarchical linear modelling has been used frequently in social and personality psychology, especially in the study of naturalistic events or social interactions that are nested within multiple participants (Nezlek, 2001), it has been under-utilised in the field of episodic memory thus far. *Studies 3* and *4*, along with two

other recent studies (D'Argembeau & Van der Linden, 2012; Hennessey Ford, Addis, & Giovanello, 2012), are therefore novel in using this informative approach.

The parametric modulation analyses conducted in *Study 1* also operated on a trial-by-trial basis, and this method allowed us to identify regions of the brain in which activation was changing in a manner that corresponded to the changes in detail ratings for each event trial within an individual. Such additional information would not have been available with more typical fMRI analyses in which activation is averaged across broad categories of events or stimuli. Trial-by-trial analyses are becoming increasingly common in neuroimaging research, and have been applied in a variety of domains such as identifying regions associated with variability in participant reaction times (Yarkoni, Barch, Gray, Conturo, & Braver, 2009) as well as in the use of multivariate pattern analysis (Visser, Scholte, & Kindt, 2011)

# **6.4 Applications and Future Directions**

The conclusions from the studies contained in this thesis have several implications for future research. *Studies 1* and *3* emphasize that the concepts of successful encoding and detail generation are linked, although the neuroimaging findings from *Study 1* illustrate that different regions within the hippocampus may be involved in these two processes to different degrees. The resolution of the structural and functional images collected in *Study 1* did not allow for the localisation of encoding- and detail-related activation to individual hippocampal subfields. However, we are currently collecting data for another study using high-resolution fMRI that will allow us to investigate this question further. This new study makes use of the same paradigm as that in *Studies 1* and *3*, in which participants imagine future events and then recall them in a post-scan cued-recall test. During the scanning session of this new study, we acquire a high-resolution T2-weighted turbo spin echo (TSE) structural sequence in addition to the standard T1-weighted MP-RAGE sequence; the activation found with the high-resolution functional EPI sequences can therefore be overlaid on this TSE image for

localisation to specific subfields of the hippocampus. We anticipate that if encoding and detail generation are not two concepts reflecting the same underlying process, that activation in the hippocampus corresponding to each will be associated with different hippocampal subfields. The subregions of the hippocampus are hypothesized to make different contributions to memory (Norman & O'Reilly, 2003). Specifically, the hippocampus creates distinct and non-overlapping representations of individual events in the dentate gyrus/CA3 subfields (a process referred to as pattern separation). In contrast, the CA1 subfield is associated with pattern completion, or the process of reconstructing a previously-encountered event when presented with a partial cue. Based on these hypotheses and the locations of the encoding and detail clusters found in *Study 1*, we expect that encoding-related activity will be localised to the dentate gyrus/CA3, while detail generation (which can be likened to pattern completion) will be localised to CA1. High-resolution fMRI has already revealed subfield specialisation in episodic encoding; for example, activation in the CA1 hippocampal subfield is associated with match/mismatch detection in an associative encoding task (Duncan, Ketz, Inati, & Davachi, 2012), and encoding processes in the dentate gyrus and CA2/3 are enhanced under conditions of reward (Wolosin, Zeithamova, & Preston, 2012).

It would also be beneficial to examine whether the conclusions from the studies in this thesis extend to patient populations. As discussed in the *General Introduction*, the evidence for amnesic patients' ability to imagine future events has been mixed. Some amnesic patients with damage to the hippocampus cannot imagine future events in as much detail as controls (Andelman et al., 2010; Hassabis, Kumaran, Vann, et al., 2007; Kwan et al., 2010; Race et al., 2011), while others show no such deficit (Cooper et al., 2011; Hurley et al., 2011; Squire et al., 2010). Amnesic patients who show impairments in imagining hypothetical events also show poorer subsequent memory for their imagined events than controls (Romero & Moscovitch, 2012), but with the exception of one study with developmental amnesic children

(Cooper et al., 2011), no one has yet assessed whether those amnesic patients who *are* capable of imagining future events are similarly able to recall those imagined events after a delay. It would therefore be interesting to apply the encoding paradigm used throughout this thesis to a population of amnesic patients who are able to imagine the future. Cooper et al. (2011) found that children with developmental amnesia, who were unimpaired at imagining detailed future events, performed significantly worse than control children when asked to accurately recall events that they had previously imagined. It is therefore conceivable that other amnesic patients with hippocampal damage showing similarly unimpaired abilities to imagine future events would also show deficits in encoding. If this was the case, it could indicate that different regions of the hippocampus are responsible for different aspects of episodic simulation, with some contributing more to construction and other regions contributing to the encoding of imagined future events. Findings from *Study 2* indicate that if hippocampal damage affected the posterior aspect of the structure in particular, this would disrupt the connectivity of the posterior hippocampus with other default network regions that is essential to the encoding of imagined future events.

It is also unclear whether the findings from *Studies 3* and 4 would extend to patients with hippocampal damage. Even though it could be expected that rates of recall for imagined events would be lower in amnesic patients, it is possible that subjective ratings of detail, plausibility, and familiarity would still predict patients' later memory for the simulations. Similarly, although such patients might describe less internal detail than controls when imagining future events in an Autobiographical Interview (Kwan et al., 2010), their ratings may still be predictive of the changes in amount of internal detail across trials. However, previous findings cast doubt on these possibilities, as it has already been shown that the accuracy of subjective ratings made by patients with left temporal lobe epilepsy (LTLE) about their autobiographical memories is questionable (Addis, Moscovitch, & McAndrews,

2007). Specifically, LTLE patients and controls made ratings of detail and personal significance after recalling autobiographical memories during a scanning session. In controls, these ratings were positively correlated with objective measures of internal detail described in the Autobiographical Interview, while in LTLE patients the two measures were negatively correlated. In other words, patients whose descriptions in the AI contained less internal detail tended to rate their recalled autobiographical memories as more detailed and more personally significant. Therefore, it appears that patients with hippocampal damage are often unaware of the extent of their own memory deficits. Consequently, it seems unlikely that subjective patient ratings of the detail, plausibility of their imagined events and of the familiarity of event components would be predictive of later recall for their simulations.

Older adults have also been shown to imagine future events in less detail than young adults (Addis, Roberts, et al., 2011; Addis et al., 2008; Gaesser et al., 2011), and older adults' subsequent memory for their imagined events is associated with the degree to which they are able to imagine coherent scenarios (Romero & Moscovitch, 2012). Successful encoding in older adults is associated with activation in the same regions seen in young adults, including the hippocampus (Morcom, Good, Frackowiak, & Rugg, 2003), suggesting that the hippocampus would likely still be implicated in the encoding of imagined future events in this population. Others have found that in addition to exhibiting poorer source memory performance, older adults show a reduction in hippocampal activity associated with successful source memory encoding relative to young adults, and that older adults' hippocampal connectivity during source memory encoding shifts from the posterior regions seen in younger adults to more anterior regions (Dennis et al., 2008). Older adults may therefore not show the same magnitude of hippocampal activation when encoding imagined future events, and age-related changes in hippocampal functional connectivity could negatively impact their ability to encode episodic simulations.

The accuracy and predictive ability of older adults' subjective ratings for imagined future events is not known. In many situations, it seems that while older adults show a decline in episodic memory performance, they are often aware of this change (Castel, McGillivray, & Friedman, 2012) and can make accurate estimates of their own forgetting (Halamish, McGillivray, & Castel, 2011), though others have found weak relations between subjective memory ratings and measures of memory performance in older adults (Schmidt et al., 2001). Even though older adults imagine future events in less detail than young adults (Addis et al., 2008), it seems possible that older adults may still be able to accurately rate the phenomenological characteristics of their imagined events, and that these ratings would predict objective measures of the events' content. However, there is evidence that even though older adults generate fewer internal or episodic details than young adults when both remembering and imagining episodic events, their ratings of detail, emotionality, and personal significance made for their past and future events are not any lower than those made by young adults, and are even in some cases significantly higher (Addis et al., 2010). Considering that older adults appear to substitute semantic detail for episodic detail when they generate past or future events (Addis et al., 2008), it is possible that older adults are making their ratings based on the semantic content of their events, and therefore are still making subjectively accurate ratings. If this is the case, it suggests that the correspondence between participant ratings and episodic imagined event content found in Study 4 may not persist in older adults. Alternatively, it may imply that older adults' ratings would predict the amount of external, non-episodic detail. In either case, older adults' ratings of detail, plausibility, and familiarity may not show the same predictive power for later imagined event recall.

#### **6.5 Limitations**

There are some limitations to the studies in this thesis. The experimental recombination and cued-recall paradigms used in *Studies 1*, 2, and 3 have a number of features which could be improved. As noted in *Study 3*, the requirement for participants to recall 110 people, places, and objects in the pre-scan interview may have affected the characteristics of the event components recalled. Specifically, it might have been easier to come up with a larger number of highly-familiar people than it was to recall highly-familiar places or objects. This difference resulted in the person component generally being rated as more familiar, emotional, and personally-significant than the location and object details, which in turn may have caused the uneven rates of recall depending on which event component was missing in the cued-recall test. Moreover, these discrepancies may have biased the predictive ability of the ratings made about each person, place, and object event component, given that ratings made about the person component were more predictive of later memory for the imagined events than ratings made about the location and object components.

The differential influence of each imagined event component on later recall may also have been affected by the order in which participants saw the cues. When participants were imagining their future events *in Studies 1*, 2, and 3, the order of the person, place, and object cues was not counterbalanced. In other words, the person was always presented at the top of the list, followed by the location and then the object. As noted in *Study 3*, this unchanging order may have encouraged participants to create each imagined event around the relevant person, incorporating the other two details incrementally. This design is problematic if the last component was not well-integrated into the imagined event due to time constraints; if this was the case, and it happened to occur on a trial in which the object would be the missing component in the cued-recall test, the imagined event might have been erroneously classified

as forgotten. Therefore, in future research making use of this paradigm, it will be important to counterbalance the order in which the cues are presented.

The cued-recall task itself may not have been an ideal way of testing memory for the imagined events. The aim of this test was to objectively measure the associations formed between the three event components as a result of imagining them together in a specific future event. Because participants generated events silently in the MRI scanner, the only known features of each simulation for which memory could be tested were the three cues. However, participants' demonstrated ability to recall one of the imagined event components does not necessarily guarantee that they were able to recollect the event that they had imagined. The possibility remains that participants were merely recalling the three cues in the recall test and not the imagined event. However, the unexpected nature of the cued-recall test prevented participants from simply rehearsing the person/location/object combinations, rendering this explanation less likely. Furthermore, our finding that activation in posterior medial temporal regions predicted subsequent memory for imagined events corresponds to the findings of Poppenk et al. (2010) who used an entirely different source memory paradigm to test participants' memory for their imagined actions and intentions. This correspondence between findings indicates that our results are unlikely to simply be artefacts of the cuedrecall paradigm.

There are also limitations with the use of the Adapted Autobiographical Interview. Transcription and scoring of participants' imagined event descriptions is very labour-intensive, which limits both the number of participants that can be collected and the number of trials administered to each participant. A further limitation, as described in *Chapter 5*, is the fact that participants' descriptions might not capture every aspect of what they imagine. Verbal descriptions may not be adequate at conveying certain features of mental representations. Moreover, participants may believe that the experimenters are particularly

interested in certain aspects of their imagined events and will accordingly describe these features in more detail than some other aspects which have been deemed as less important. It is therefore vital to ensure that instructions given to each participant are consistent and purposefully neutral so as to minimize this type of influence as much as possible.

## **6.6 General Conclusion**

The studies described in this thesis examine the interactions of a number of the component processes of episodic simulation. They provide novel information about the neural and phenomenological mechanisms underlying the encoding of imagined events. They reveal that the encoding of internally-generated autobiographical events depends critically upon the hippocampus and its interactions with other regions of the default network, and also that such encoding is modulated by various features of the imagined events, including detail, plausibility, and the familiarity of the event components. These findings expand our knowledge of the general function of the hippocampus and its broader role in the episodic system, and also give insight into the adaptive nature of future thinking. They provide compelling evidence that a function of the episodic memory system is to allow us to draw upon what has happened to us in the past so as to generate and store plans for the future. This recent reconceptualization of the episodic system as a mechanism for 'mental time travel' is a significant and influential step in the study of episodic memory, and much future research is needed to fully understand the processes involved.

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#### **Appendices**

# Appendix A: List of cues provided to participants in order to facilitate retrieval of episodic events.

- Birthday party
- Family celebration
- Attending a funeral
- Attending a wedding
- Baby shower
- A good or bad babysitting experience
- A heated argument
- Particularly bad weather
- Experiencing an earthquake
- Going to a concert
- Going to a play/opera/ballet
- Visiting a museum
- Visiting a gallery
- Visiting the zoo
- Visiting an aquarium
- Going to a party
- Giving/receiving a gift
- Going to a good/bad restaurant
- Flying in a plane
- Buying something large
- Taking a driving test
- Buying a car
- Getting into or seeing a car accident
- Getting a parking ticket
- Getting a speeding ticket
- A bad experience at the dentist
- Losing/winning money at a casino
- · Going on a date
- Having a first kiss
- A good or bad Valentine's Day
- A good or bad New Year's Eve
- A school reunion
- Moving to a new house
- Taking a trip overseas
- Packing for a trip overseas
- Staying in a hostel/hotel
- Goodbye party
- Getting a pet
- Losing a pet
- Meeting a new friend
- Meeting a celebrity
- Giving a presentation
- Performing in a play or concert
- Taking an exam
- Losing your wallet
- Finding something valuable
- Doing something embarrassing
- Being late for something
- Hurting someone's feelings

- Telling a lie
- You or someone you know being ill
- Getting food poisoning
- Having an operation
- Getting a good or bad haircut
- Participating in a sport
- Winning an award
- Bungee jumping
- Surfing
- White water rafting
- Going up the Sky Tower
- Trying something for the first time
- Tramping/camping
- Staying at a bach
- Going on a ferry trip
- Watching a sports game
- Going to the beach
- Whale watching
- Job interview
- First day on a job
- A bad day at work
- Leaving a job
- First day of high school
- Going to a high school dance
- Winning a prize
- High school graduation
- School trip
- Visiting universities
- Acceptance to university
- First day of university
- Moving into residence
- Moving into a flat
- Meeting room/flatmates
- A conflict with flatmates
- Painting a room/house
- Buying textbooks
- Inappropriate cell phone ring times
- Walking into the wrong classroom
- Forgetting/confusing someone's name in conversation
- Cheating on a test
- Receiving a care package
- Participating in an experiment
- Voting for the first time
- Tutoring
- Volunteering

#### **Appendix B: Scanning Session: Instructions**

In this study we are interested in how we remember the past and how we imagine events in our future.

Today, you will be doing three types of tasks on the computer.

One of them will be to **imagine a future event which might occur** sometime in the **next 5 years**, just like you did in the first session. Only this time, instead of generic people, locations, and objects, you will see the people, places, and objects that you provided for us in your own memories last time. These details have been randomly rearranged, and you need to imagine a future event involving the ones you see on the screen. Note that these details will **come from three different memories**. Again, these should be plausible events that haven't actually happened.

When creating your imagined event, try to have the specified person and object **physically present** in the location. Also, the events you imagine need to be **specific time and place**. So if you're thinking of a vacation, focus in on one event that might happen in that vacation (e.g., visiting the Eiffel tower). Again, it doesn't matter **how important or how trivial** the event is, as long as it is an event which is specific in time and place.

For all events, imagine as much **detail** as you can about the event. At the end of each trial, it will ask you to rate how much detail you imagined on a scale of 0 to 3. Rate the event 0 if you were not able to generate much detail at all, and up to 3 if the event was highly vivid and detailed. Also, try and imagine these event through **your own eyes**, as you would experience it if you were there, rather than from an external vantage point where you see yourself in the event.

The second task you'll have to do is to **reimagine the events that you imagined in session**1. You will see the same combinations of people, locations, and objects that you saw last time, and you just need to again imagine them in as much detail as possible. Just like before, you will be asked to rate the amount of detail you imagined after each trial.

Finally, there will be a **sentence task.** For this one, you will see 3 objects and you need to fit them into a sentence. The sentence is "**X** is **bigger than Y** is **bigger than Z**" – say this sentence in your head, fitting the three objects in the place of X, Y, and Z. So if you saw the three objects DOG, HOUSE, SHOE, you would say "HOUSE is bigger than DOG is bigger than SHOE". This task will also have you do a rating, only this time you need to rate how difficult it was to make the sentence.

The three types of tasks that I just described will be presented randomly on the computer screen, so be prepared to switch between them. Again, the three tasks are to 1) **imagine a** future event using the details provided, 2) re-imagine the events you imagined last time, and 3) construct the sentence using the nouns provided.

#### **IMAGINING FUTURE EVENTS**

**IMAGINE FUTURE** event that could IMAGINE FUTURE EVENT that involves: happen in the **NEXT 5 years** but hasn't yet This event needs to include the person, Sarah from work location and object specified Memory titles are provided to remind you Piha Beach where these details came from Pink Socks **CONTINUE** to imagine as much detail as you can about the event until next screen appears **RATE** how **DETAILED** your imagining was: 0 = vague with no/few details 3 = vivid and highly detailed rate DETAIL low 0 1 2 3 high **REST** – relax; focus on the crosshair

**Example:** I imagine that 5 years from now I am at Piha Beach and I run into Sarah from work – she is wearing bright pink socks!

#### **RE-IMAGINING FUTURE EVENTS**

**Example:** I imagine that 5 years from now I go to the post office with my friend John, as we go in we notice someone's wallet on the floor and pick it up.

### SENTENCE TASK

• **CREATE SENTENCE** that takes the CREATE SENTENCE, start with LARGEST: form: "XXX is bigger than YYY is bigger than ZZZ" BULB i.e., order the objects by physical SIZE **NEEDLE** TREE RATE how DIFFICULT it was to come up with a sentence and define each rate TASK DIFFICULTY of the words: 0 = easylow 0 1 2 3 high 3 = hard**REST** – relax; focus on the crosshair

Example Sentence: TREE is bigger than BULB is bigger than NEEDLE

Do you have any questions before we begin?

#### **Appendix C: Adapted Autobiographical Interview Administration Manual**

Version: May 2010

**Adapted from:** Addis, DR, Wong, AT, Schacter, DL (2008). Age-related changes in the episodic simulation of future events. *Psychological Science*, *19*, 33–41.

Levine, B, Svoboda, E, Hay, J, Winocur, G, Moscovitch, M. (2002). Aging and autobiographical memory: dissociating episodic from semantic retrieval. *Psychology and Aging, 17*, 677-689.

This adapted version of the Autobiographical Interview involves showing subjects cue words (nouns) in order to elicit the generation of imagined events which may occur in the subject's future. Subjects are given 3 minutes (from when the cue is first shown) to generate and describe the event in as much detail as possible. The events are required to have episodic specificity. In other words, the event should be one that is a few hours in duration, specific in time and place, and not one that was experienced or could be experienced many times (e.g., routine events). These requirements are explained to subjects in the detailed instructions below.

#### **General Administration Instructions**

#### The following instructions are read to subjects prior to commencing practice events:

I want to begin by telling you a bit about this study – we are looking at how people imagine events that might happen in the future. To help with scoring, we will be audiotaping your responses, but as with all studies, your responses will be kept completely confidential and your tape will be assigned a subject number and stored in a secure place.

Over the course of the experiment, you will be seeing a number of cue words on the screen. For each cue word, you will be asked to **imagine** an event that may occur in your **future**. The event does not have to specifically involve the cue word – it is just there to prompt you and to help you begin your search.

For each event, you will be given a **time-period**. For instance, you will be asked to imagine events that might happen to you in the "next few weeks" (within the coming month or so) or "the next few years" (up to about 5 years from now) or "the next 20 years" (when you're about 40).

For each future event, I want you to think about a single event that might happen at a **specific time and place** in the future, and you want to create or imagine or invent a scenario that hasn't happened to you before. It has to be something that lasted less than one full day. When creating these future scenarios, you can be creative, but you cannot be totally unrealistic, so you can't tell me about going to the moon, for example. So you want to think about scenarios which are plausible given your plans and thoughts about the future. For that reason, you shouldn't imagine yourself doing something like cooking in a restaurant in the next few years if you don't have any plans to work as a chef.

For all these events, you will be given a **three minutes** to tell me as much **detail** as you can about them. So remember, you can tell me everything you can imagine about the event. We

are not so much interested in which events you choose to describe, but how much detail you can imagine when you describe them. So it doesn't matter whether the event is important or trivial, as long as it is an event which is specific in time and place, and was one that you were personally involved in (so not something someone else told you about). I will be guiding you to help make sure you come up with a specific event, so I may be interrupting you at some points. And when you hear the bell, we will have to move onto the next section.

After each event you tell me, I will ask you some questions about the event that you described (provide sheet of rating scales). Firstly, I will ask you to tell me when the event might happen. Then I will ask you to rate how many vivid details you were able to come up with, rated on a scale from 1 to 7. If you couldn't really see anything in your mind's eye, give it 1, or up to a 7 if it was vivid and detailed and plays out like a movie in your mind. Then I will ask you to rate how clear it was that you were in a specific location in your imagined event. Give it a 1 if you didn't have a good idea of where it was located, up to a 7 if you had a very clear sense of where the event took place with relation to the surrounding area. Next, I will ask you to rate how clear the time of day of the event was. Give it a 1 if it was not at any particular time, up to a 7 if you had an idea of the exact time at which the event took place.

So in overview, you will be seeing a cue word and a time period on the screen. Using those guides, you will have to tell me a future scenario you have made up. Try and see the situation in your mind's eye, and you will have a couple of minutes to tell me as much detail about the event as possible, so things like when and where it was, all the different sensory information like sights, sounds, smells, and feelings, and what things happened during the event. Then we will go through the questions to get a bit more information about the event.

#### Free Recall & General Probing

Once a cue is shown, subjects are encouraged to freely recall or imagine as much as they can about an event this cue makes them think of. Throughout, general probes are used. The purpose of general probes is to help the subject focus in on a single event if they have given non-specific information, or if they have misunderstood some other aspect of the instructions. Thus, the interviewer can use any of the probes, listed overleaf, to guide the subject and keep them on track. If the subject describes a specific event (i.e., a few hours in duration, specific in time and place, and not an event that was repeated several times) that is rich in detail, general probing is not necessary. If in doubt, though, it is better to probe. The overall goal of General Probe is to remind the subject that we are looking for an event that is specific time and place and to encourage generation of as much detail as possible. Do not provide any other guidance such as telling the subject which event to focus on, or suggesting ideas for events they could describe. You can, however, reiterate the instructions.

#### **General Probing: Scenarios**

The following are scenarios that often arise during interviewing, and general probes which can be used.

#### 1. The subject provides a detailed account of an event specific to time and place.

Response: If the subject finishes before the 3 minutes is up, use one of the following probes to ensure there is nothing else they wish to add:

- Is there anything else you can tell me?
- Are there any other details that come to mind?

#### 2. Some subjects provide a vague description of a specific event.

Response: Use the following probes for eliciting more details and encourage a full description of the event:

- *Is there anything else you can tell me?*
- *Tell me more about it.*
- Tell me more details about ....
- What do you remember / imagine about ...?
- Is that everything you can say about it? I want to know all the details that come to mind.
- Are there any more details about what you were doing, thinking or feeling?

If the subject reiterates what was said or begins recalling another incident in response to the probe, this may indicate that most of the available information has been produced.

## 3. Some subjects may have trouble distinguishing specific from general events (i.e., they only give semantic information or describe a very routine event)

Response: If it is not clear that the event being described is specific, say:

- Is this something that happened to you more than once? (if yes, say)
- Can you tell me about a specific instance of....?
- Tell me about one particular time ... that you ...
- That's not quite what I was looking for. I need a single event or instance that happened to you.
- Can you tell me about an incident that happened at a particular time and place?

### 4. The subject recalls/generates more than one event or an event that is extended over time (e.g. a vacation)

Response: Provide guidance by asking them to focus on one of those episodes. However, be careful to let the subject select the event, rather than asking them leading questions.

• You mentioned a number of events. I'd like you to pick just one of them to focus on and tell me as much as you can about that event.

# 5. The subject generates a future event but it is not clear if this is an event they have already experienced.

Response: Determine whether this is a novel event or if they are just remembering as past event.

- *Has this happened to you before?*
- How is this future event different?

### Adapted Autobiographical Interview Paradigm

Next Few Weeks	(shown for 3 minutes; bell sounds when time is up)
When might this event happen?	(no time-limit; participants type response into E-Prime program)
rate VIVID DETAIL low 1 2 3 4 5 6 7 high	(no time-limit; response keyed in to be recorded by E-Prime)
rate CLARITY OF LOCATION low 1 2 3 4 5 6 7 high	(no time-limit; response keyed in to be recorded by E-Prime)
rate CLARITY OF TIME low 1 2 3 4 5 6 7 high	(no time-limit; response keyed in to be recorded by E-Prime by the experimenter)
+	(Fixation cross shown until subject ready for next trial)

#### Appendix D: Adapted Autobiographical Interview Scoring Manual

Version: May 2010

**Adapted from:** Addis, DR, Wong, AT, Schacter, DL (2008). Age-related changes in the episodic simulation of future events. *Psychological Science*, 19, 33–41.

Levine, B, Svoboda, E, Hay, J, Winocur, G, Moscovitch, M. (2002). Aging and autobiographical memory: dissociating episodic from semantic retrieval. *Psychology and Aging, 17*, 677-689.

#### Overview

The Adapted Autobiographical Interview quantifies elements of descriptions of specific events which may occur in the subject's personal future (i.e., simulations). In each trial, a cue word (e.g., "DOG") and a time period (e.g., "Next Few Weeks"; "Next Few Years") is shown. The subject must think of a specific event in the time period that the cue makes them think of, and describe as much detail as possible within 3 minutes. The events must be specific to a particular time and place. When describing events, general probes may be used by the interviewer to focus the subject on a specific event and to encourage full description (e.g., "Can you tell me more about that? Can you describe a specific incident relating to that event?")

The interview is recorded digitally and transcribed. For each event, the scorer isolates or defines the main event, then divides the entire response (including information external to the main event) into small segments (details). These details are categorised as either 'internal' or 'external' to the main event. This will be explained in more detail below.

#### **Isolating and defining the event**

Although the test instructions request specific events, many subjects give more than one event or events that are difficult to define (i.e., non-specific events). It is therefore necessary to be clear what the event is before any scoring takes place. This will come into play when categorizing segments, as segments that are not part of the event (external details) are tallied separately from those that are part of the event (internal details).

Subjects are instructed to provide an event in which they were personally involved and that is singular (not repeated) and specific to a time and place. The event should be restricted in time, no more than a few hours in duration. If an event extends over days or weeks (e.g., a vacation), the scorer must restrict scoring to the best time-restricted event available. If more than one exists, choose the time-restricted event which is described in most detail. In such cases, the examiner will have tried to focus the subject on a single event in the probing conditions.

One of the most difficult scoring situation is when the event is very impoverished or non-existent (e.g., only factual information is given, or an event that was repeated). In such cases, it may be possible to select some details as *probably* specific to an event and to score them accordingly, but qualitative ratings cannot be assigned.

#### Text segmentation and categorisation

A segment, or detail, is an information bit; it is a unique occurrence, observation, fact, statement, or thought. This will usually be a grammatical clause -- a sentence or part of a sentence that independently conveys information (i.e., a subject and a predicate), although a single clause may contain more than one detail. For each clause, consider whether its constituent parts convey additional information. If so, the parts can be separated and scored as separate segments. For example, the statement "he had an old, brown fedora" would be segmented into three details: a "fedora" is different from a "brown fedora", which in turn is different from an "old brown fedora". Each of these details adds information that significantly alters the meaning of "fedora", which on its own would receive one detail.

The main categorical distinction for details is internal or external to the event. To be categorised as **Internal**, a detail must pertain directly to the main event, isolated as defined above. Internal details can include the following:

- 1) **Event details**. Overall, event details describe the unfolding of the story. They are usually happenings (e.g., "I fell down"), but also include who was there (1 point per name/person up to a maximum of 5), reactions/emotions in others, the weather, one's clothing if it is part of the action, physical occurrences and actions of others. If an item qualifies to be in another category (e.g., perceptual richness), then priority is given to that more specific category. An item cannot be scored as an event detail if it is in another category. e.g., He jumped out of the chair; It was sunny; My sister Sue was with me; She was jealous/angry/happy; We went to the hotel; It was my birthday.
- 2) **Place details.** Any information that involves localisation in space, including countries, bodies of water, provinces, cities, streets, buildings, rooms, and locations within a room.
- 3) **Time details.** Life epoch ("My twenties"), year, season, month, date, day of week, time of day, or clock time. It has been argued that one cannot directly encode or retrieve temporal information (i.e., when an event occurred), but only infer it from other information. That is, it is not possible to re-experience a given point in time without reference to some related episodic thought, feeling, or other detail. Therefore, when scoring time information, people should not be penalised for making inferences (which are usually scored as 'other' details), because this is the normal way to figure out when something occurred.
- 4) **Perceptual details.** Perceptual details include auditory, olfactory, tactile/pain, taste, excluding visual details as they are a separate category.
- 5) **Visual details** (but non-spatial). Object details, colours, clothes. In the case of objects, it can be difficult to distinguish between a perceptual and an event detail. Objects that are directly involved in the unfolding of an event are considered event details ("We lit the candles") whereas objects that are part of the visual landscape are considered visual details ("There were lit candles everywhere").
- 6) **Duration and temporal sequence details.** Duration information ("We were there for 20 minutes") or information about the sequence of events ("Mary came later than Sam", where "Mary came" is an event detail, and "later than Sam" is a duration/temporal sequence detail).
- 7) **Spatial orientation details.** Details about positions, distances, and orientations in allocentric/egocentric space, e.g. one's own orientation in space ("I was to the right of Edgar").

8) **Emotion/Thought details**. Any detail that pertains to the mental state of the subject at the time of the event. These include feeling states, thoughts, opinions, expectations, or beliefs. Thoughts expressed in retrospect (either at the time of the interview or at any time after the event occurred - "I found out later I was wrong") are tallied as external. Beliefs or opinions that are long-standing (not specific to the event - "I never believed in ghosts") are also external and are scored as semantic details. Inferences about other people's mental state ("She was sad") are considered event details, unless these inferences reflect the subjects' own mental state at the time ("I thought he was angry with me"), in which case they are internal thought details.

**External details** are events that are not part of the main event or factual (semantic) information that is not specific to the main event. These can include the following:

- 1) Semantic details. Semantic details involve general knowledge or facts. They can represent general knowledge ("Paris is the capital of France") or be specific to the person ("I always hated yams." "I worked as an engineer"). The distinction between semantic and other kinds of details can depend on the context. For example, "Paris fell to the Germans" would be semantic if it is described as a historical fact ("We couldn't go to Paris because it was in German hands") or an event detail ("We watched in disbelief as Paris fell to the Germans."). In general, details that reflect a long-standing state of being or without a clear beginning or end are considered semantic. Semantic information can be "brought in" to episodic recollection (and scored as an internal detail) if it becomes an integral aspect of the episode: "Arizona is hot" is semantic, but "Arizona was hot when we went there" is episodic. Note that the richness of the description is independent from the episodic/semantic distinction; very richly described factual information is still semantic, and impoverished, minimal details can still be episodic.
- 2) Repetitions. A detail is a repetition if it is an unsolicited repetition of a prior information-containing detail. It does not have to be a verbatim repetition, but it should not add any new information to the prior detail ("I hoped for the best. I kept my fingers crossed" -- second sentence is a repetition). Score all repetitions, even if they are part of normal discourse, except for repetitions that are clearly prompted by the examiner, which may occur if the examiner queries a detail that was given earlier. Repetitions must convey information (as opposed to just words that are repeated). In the example below, "... and stuff" is repeated, but there is no information in this utterance, so it is not considered a repetition. As well, only score repetitions when they convey the same information as in an earlier detail. In the example below, "They really really liked me" is not a repetition of "They were happy with my work." Similarly, "I was a carpenter's helper", "I helped them", and "They could depend on me" are all different. "They liked what I did" however is the same as "They liked my work." Then he repeats this repetition straight away.
- 3) Other details. This category is for details that do not reflect recollection and do not fit into other categories. It includes meta-cognitive statements ("Let me see if I can remember that"), editorializing ("That doesn't matter." "That's amazing."), inferences ("I must have been wearing a coat because it was winter"), or other statements that convey verbosity but are not related to the main event. Replies to a query that are clauses (E: "Do you remember any more about that day? S: No, right now I don't. I don't remember anymore") are also scored as 'other', although simple reflexive replies such as "No" are not scored. Do not score an 'other' detail for any utterance only those that contain information. Generally an 'other' detail will be a clause of some sort. Fragments such as "um" are not scored.

- 4) **External episodic details.** Episodic events that are secondary to the main episodic event, e.g. if the person is imagining the birth of their first child (as the main event), but also talks about going to the pharmacy to buy prenatal vitamins a few months before.
- 5) **External generic events/routines.** Semantic details that refer to events (and not general knowledge), but events that are repeated or routine, e.g. "I always go to the dairy down the road."

The **sums of internal and external details** are important measures of a subject's performance. With experience, a scorer will be able to simultaneously segment and categorize a response.

In some cases it can be difficult to distinguish internal from external details. The rule of thumb in these cases (the "benefit of the doubt" rule) is that if a detail could reasonably be internal, it is scored as such. This rule, however, should not be applied to all details that could possibly be internal; only those that could reasonably be internal.

### **Scoring example**

EXT1 EXT2 EXT3 EXT4

It was a company / out of New Bedford / that was building / & did the shelves and

EXT5 EXT6 EXT7 EXT8

that,/ the rough /carpenter work /& then there was another company/ that came in/

EXT9 EXT10 EXT11

and did the finish work /but they were all happy /with my work and stuff /and

EXT12 EXT13 EXT14

saw that I listened and stuff/and I was a carpenter's helper / and I helped /

EXT15 EXT16

when they needed something /and they could depend on me /and the company really

EXT17 EXT18 REP (of EXT18)

really liked me / what I did /and the work I did and stuff./

**Categorisation:** All details are classed as external as there is no specific, time-limited event described. The subject is describing the company he worked for and his role. However, this is somewhat open to interpretation. Another scorer might decide that the description of another company coming in (i.e., "another company came in and did the finish work but they were all happy with my work and saw I listened") is a single episode rather than a matter of due course on every job. This is an example of a judgement call. Many scoring decisions are judgement calls. Scorers will be somewhat influenced by their own knowledge and experience with the subject matter. Score according to your knowledge. If two people could

reasonably score a detail more than one way, simply score it the way that seems best rather than agonize over it.

**Segmentation:** The clause "It was a company out of New Bedford that was building" contains three details, a company, from New Bedford, that does building. Thus, "company" can stand alone (i.e., he works for a company, and not, for instance, himself) but the subject tells us something about what type of company it is (i.e., they do building). The second detail is a place detail, telling us that the company was based in New Bedford. This clause illustrates that one cannot always find the dividing line between details. The dividing of segments can be somewhat arbitrary. Where one places the dividing lines is not as important as the number of information bits one scores.

The "shelves ... and rough carpenter work" can be segmented into three details: "doing shelves" (a type of building), "carpenter work" (another description of the type of work), and then further refining the carpenter work (as "rough"). Next, another company comes in. This instance of "company" is not a repetition of the first, as it is a different company. The "coming in" was scored as a separate detail because it implies a happening, something this other company did. Their being happy is a state of being/emotion; the cause of the happiness (i.e., the subject's work) is a further detail. Likewise, the subject imparts a number of details about his role: a "carpenter's helper"; the task was to help; but not just whenever, but "when something was needed"; he was dependable ("they could depend on me"); the company liked him; and they also liked the work he did ("what I did" and repeated in "the work I did")

We have come up with some other **segmentation rules**, given scoring dilemmas which have arisen:

- **Time details:** The location of the event in time (e.g., "next few weeks", "in a couple years", "yesterday") should not be segmented as this usually reflects the time period given as part of the cue; SCORE=1
- **Relationship details:** The relationship of the subject to someone else (e.g., "boyfriend", "last boyfriend", "uncle", "great uncle", "friend", "best friend", "Donna's friend") should be SCORE=1 if this is used as a pronoun. Often, as the subject doesn't know the examiner, they will just consistently refer to someone as "my best friend". However, if they have used the name and are using the phrase to describe the relationship, then it can be segmented accordingly (e.g., "she was my best friend" is SCORE=2 as she's not just a friend, but a best friend.)
- Activities: "I was sitting on the couch"; "I was driving to the market" are SCORE=2 phrases, as "I was sitting" and "I was driving" are activities in of themselves. The subject doesn't need to provide the location of sitting ("couch") or the destination of driving ("market") for it to make sense. However, "I went to the market" is a SCORE=1 phrase, as "went" is not a stand-alone activity.
- **Senses:** "I saw the tower", "I heard a noise" are all SCORE=1 phrases as the sense description is part of the experience of the content (i.e., you can't see a noise or hear a tower). Also, the sense verbs cannot stand alone (e.g., "I saw.")
- **Dialogue:** Whether the dialogue is external (speech) or internal (thoughts), each statement/thought represents one detail (i.e., it is one happening) and so it is not segmented (e.g., "I thought, blah blah blah" or "She said, 'blah blah blah" are both SCORE=1 phrases). If there are masses of dialogue, then divide it up reasonably, by phrases.
- **Emotions:** If a feeling is followed by the cause or target of the feeling (e.g., "I was happy that he came over"), then it is a SCORE=2 phrase. This is because "I was happy" can stand alone, and more information is provided by describing the reason.

• **Metacognitive:** "I remember", "let me see if I remember", "I can envisage" are all SCORE=1 (External)

### Other segmenting and scoring tips

- 'Negative' events, or the absence or failure of something to occur ("Bob wasn't there") are still scorable, as they reflect the subject's recollection.
- External details include both external episodes and semantic details. In cases where the two are difficult to distinguish, apply the benefit of the doubt rule.
- Do not give credit for information that is not there. "We went to a place where we could swim with the dolphins" contains one descriptive event detail, but the actual location is not mentioned, so it is not scored under place details. The place is implied, but is not scored until it is mentioned.
- Scoring of fragmented sentences should allow for natural speech patterns even when they do not appear fluent in the transcription. The scorer should attempt to interpret fragmented sentences in a way that would be transparent to others.

Remember: Segmentation of details should be consistent regardless of whether the details are internal or external.