Episodic Cognition: What is it, Where is it, and When does it Develop?

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Summary

Episodic Cognition (or "Mental Time Travel") is the ability to mentally re-experience events from our personal past and imagine potential events from our personal future. This capacity is fundamental to our lives and has been argued to be uniquely human. The aim of this thesis is to use behavioural tasks developed in comparative cognition to integrate both the literature on different research subjects (animals, children, adults, patients) but also from different theoretical perspectives, with the hope of facilitating communication and comparison between these fields.

The backbone of the thesis is the behavioural tasks themselves, along with their origins in theory. Specifically, the "What-Where-When", "Unexpected Question" and "Free Recall" episodic memory tasks and the "Bischof-Köhler" test of episodic foresight. Each of these tasks stems from different theoretical approaches to defining episodic cognition. Whilst extensively studied, these four tasks have never been undertaken by the same subjects and have never been directly compared. It is thus unclear whether these different theoretical perspectives converge on a single "episodic cognition" system, or a variety of overlapping processes. This thesis explores these issues by presenting these tasks to previously untested animal (the Eurasian Jay), developing children (aged 3-6), and a sample of human adults (Cambridge Undergraduates). Finally, these findings are applied in the assessment of episodic cognition in a population that is thought to have mild hippocampal damage – the overweight and obese.

It was predicted that if all these putative tests of episodic cognition were tapping into the same underlying ability, then they should be passed by the same animal species, develop at the same time in children, correlate in human adults and be impaired in those with damage to the relevant brain areas. These predictions were, to some degree, confirmed. While the novel animal model could not be tested on all paradigms, the jays performed well on Bischof-Köhler future planning test. However, the results of the What-Where-When memory test were equivocal. There was a relatively low degree of correlation between performance on all the tasks in human children, along with a suggestion that each had a distinct developmental trajectory. The study of human adults revealed that while performance on all the tasks were related to one another, this relationship was often nonlinear, suggesting the contribution of several different psychological processes. Finally, it was found that both memory and performance on the Bischof-Köhler future planning task were altered in individuals who are overweight. A potentially surprising theme throughout the results is that performance on the Bischof-Köhler tasks is in fact *negatively* related to performance on memory tests, and *improves* in patients thought to have mild hippocampal damage.

It is concluded that there may be a significant degree of overlap in the processes tapped by different putative tests of episodic memory, but that they can not be considered to be equivalent. Furthermore, it is suggested that episodic cognition is a fundamentally ineffective system with which to predict future motivational states, because it is biased by current feelings.

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Publications

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Cheke LG, Loissel E & Clayton NS (2012) How do Children Learn Aesop's Fable? *PLoS ONE* 7(7): e40574

Ostojic Lj, Shaw RC, Cheke LG & Clayton NS (*in revision*) Attribution of desires to partners governs food sharing behaviour by Eurasian jays. *Proc. Natl. Acad. Sci.*

Declaration

No part of this dissertation has been previously submitted for a qualification.

This dissertation is the result of my own work and includes nothing which is the outcome of work done in collaboration except where specifically indicated below, and in the text

For chapter 4, data collection was carried out by Mathilda Hay and Stephanie Bailey as part of their undergraduate project, under my supervision. The study was designed by me and the analysis and interpretation of the data are my own.

In chapter 5, data collection for experiment 1 was carried out by Sophie Catt and Jasmine Sawyer as part of their undergraduate project, under my supervision. The study was designed by me and the analysis and interpretation of the data are my own. Experiment 2 was carried out in conjunction with GSK as part of a broader study on the effects of GSK1521498 on obesity. This work included input from a number of people: Ziauddeen H, Chamberlain SR, Nathan PJ, Koch A, Napolitano A, Bush M, Tao WX, Miller S, Dodds CM, Maltby K, Skeggs AL, Brooke AC, Richards DB, Fletcher P, Bullmore ET. The data collection was carried out by on-site staff in Addenbrookes hospital. Hisham Ziaudeen and I designed the study reported in this thesis, and supervised data collection. The data analyses and interpretation contained within the thesis are entirely my own.

Contents

Chapter 1

On the Difficulties in Introducing Episodic Cognition

Articles about a particular subject, by tradition, begin with a sentence defining that subject and why it is important. In the case of episodic cognition such a sentence is not easy to produce; episodic cognition and its component elements have many different names (e.g. mental time travel, episodic memory, source memory, autobiographical memory, episodic foresight, episodic prospection, episodic future thinking, future-planning…) and an equally diverse array of definitions. To compound issues, various literatures may use the same name for two potentially different processes, or different names for what may be a single process. On top of this, psychological tests are sometimes labelled for the way they assess memory (e.g. free recall, cued recall) and sometimes for the memory that they putatively test (episodic memory test, semantic memory test), though different researchers disagree on which of the former correspond to which of the latter. Furthermore, different literatures are interested in establishing different things about episodic cognition - whether it exists in animals, when it develops in children, what brain regions it is dependant upon, which disorders in which it is impaired - with only partial consensus as to what it *is*. All these fractionations make the body of research pertaining to episodic cognition tricky to traverse and almost impossible to distil down into a single coherent literature.

The various "working definitions" of episodic memory overlap on a central core feature, namely that episodic memory refers to the memory for events from the personal past. Most theorists now agree that episodic memory forms part of a broader

process (variously labelled Mental Time Travel [Suddendorf and Corballis, 1997] or Episodic cognition [Clayton *et al*., 2009]) that allows mental "re-experience" of events from the personal past and "pre-experience" of events from the personal future. However they differ on many other key features. Box 1 demonstrates the variety of different "facts" that have been stated about episodic cognition by various researchers, many of which are contradictory. Part of the confusion is historical. As with any new field, definitions have been adapted over time to the evidence that has been accumulated. Tulving first suggested, forty years ago, the distinction between episodic memory for spatiotemporal events in the personal past and semantic memory for timeless facts (Tulving *et al*., 1972). However he has since included the concept of "autonoetic" (self-knowing) consciousness (e.g. 1985b) which accompanies episodic memory and gives the rememberer the knowledge that what it being experienced is a *re*-experience of an event from one's *own* past. Finally, Tulving added "chronesthesia" (2002); the sense of autobiographical subjective time that allows "mental time travel" into the personal past and future. Thus research that was thought to investigate episodic cognition in 1975 was not assessing episodic cognition as it was defined in 1985, and research from 1985 has only partial relevance to episodic cognition as it was defined in 2005. Evolution of the goal posts of the definition over time is not the only factor, however. Part of the confusion lies in the juxtaposition of "official" definitions and *working* definitions – that is, different people's interpretations of those definitions, and people's own intuitive ideas about what

Box 1. 1

Researchers on Episodic Memory Disagree Over…

Whether it is a storage mechanism, an encoding mechanism or a retrieval mechanism:

Episodic Memory….

*"…**receives and stores**…"* Tulving 1972, p.385

*"…is defined as the **recollection**…"* Hampton & Schwartz, 2004, p.192

*"…is the ability to **encode**…"* Babb & Crystal, 2006, 1317

*"…is designed to **store**…"* Swartz et al., 2005, p.1

*"…refers to our **repository**…"* Graham et al., 2000, p.313

Whether it is defined by content, experience or both:

Episodic Memory….

*"…retrieves and stores information **about temporally dated episodes or events, and temporal-spatial relations** among these events…"* Tulving 1972, p.385

*"…is defined by the **nature of conscious awareness** that accompanies retrieval.."* Wheeler 2000, p.597

*"…is the conjunction of three concepts – **self, autonoetic consciousness, and subjective time…"*** Tulving, 2005; p.9

*"…is the ability to **encode multiple features** about previous experiences, in particular, **its content (what), location in space (where) and occurrence in time (when)…"*** Babb & Crystal, 2006, p.1317

*"…is defined by the **integration of all the distinct features of experiences** that supports the **conscious recollection** of those events…"* DeVito & Eichenbaum, 2010, p.318

*"…is **perceptual** in nature…"* Plancher et al., 2010, p.379

*"…is concerned with **unique, concrete, personal experiences**…."* Tulving 1983, p.1

*"…is **accompanied by the experience of having been there personally**…"* Hampton & Schwartz, 2004, p.192

*"…is explicit or intentional – we process it **consciously and with reflection**…"* Markowitsch, 1995 p.118

*"…allows one… **through the medium of autonoetic awareness**, to remember one's own **previous "though-about" experiences**."* Tulving, 2005; p.9

Whether it is part of, or distinct from, Semantic Memory:

Episodic Memory…

*"…**and semantic memory [are] two parallel and partially overlapping** information systems…"* Tulving 1972, p.401

*"…**is a specialised subsystem of semantic memory**…"* Tulving 1985, p. 385

*"…**require, but go beyond, the semantic memory system**…"* Tulving 2005, p.9

*"…**is not solely reliant on the integrity of semantic knowledge**…"* Simons et al., 2001, p.102

Whether is it Voluntary:

Episodic Memory…

*"…is explicit or **intentional**…"* Markowitsch, 1995 p.118

*"…is frequently **involuntary**…"* Boyer, 2008, p.6

Whether it is Long-Term:

Episodic Memory….

*"…is designed to store relevant individual events from one's personally experienced past over **long stretches of time**."* Swartz et al., 2005, p.1

*"…**is typically associated with memory for an event that has taken place sometime before**….but **it is not clear in what sense a long delay between the event and the retrieval is necessary to conclude that the memory is episodic**."* Zentall et al., 2008, p.97

episodic cognition is *to them* – that create significant discrepancies in the literature. On top of this, there are a number of fields that exist parallel to the episodic cognition literature that have their own terminology that partially, but not completely, overlaps with those in the episodic memory literature (e.g. long-term memory, autobiographical memory, declarative memory, source memory, source monitoring, reality monitoring, delayed imitation, delayed matching to sample, childhood amnesia, prospective memory, planning, delay of gratification, temporal discounting).

Is that a Needle, or is it Hay?

> *"Mental time travel allows one, as an "owner" of episodic memory ("self"), through the medium of autonoetic awareness, to remember one's own previous "thought-about" experiences, as well as to "think about" one's possible future experiences. The operations of episodic memory require, but go beyond, the semantic memory system. Retrieving information from episodic memory ("remembering") requires the establishment and maintenance of a special mental set, dubbed episodic "retrieval mode". The neural components of episodic memory comprise a widely distributed network of cortical and subcortical brain regions that overlap with and extend beyond the network subserving other memory systems. The essence of episodic memory lies in the conjunction of three concepts – self, autonoetic consciousness, and subjective time."* (Tulving, 2005, p.9)

From this example it is possible to see how Tulving's *theory* of episodic memory is built into his *definition(s)* of episodic memory, creating a problem of circularity in the literature. For example, Tulving states that "the operations of episodic memory require, but go beyond, the semantic memory system" (Tulving, 2005, p.9). However, it has been recently demonstrated that patients suffering with semantic dementia (who have severe semantic memory impairments) are able to remember episodically (e.g. Graham *et al*., 1997, Graham *et al*., 2000, Simons *et al*., 2001, Graham and Hodges, 1997, Hodges *et al*., 1992, Snowden *et al*., 1996, Simons *et al*., 1999). While some might argue that this proves this aspect of Tulving's theory of episodic cognition wrong, Tulving might argue that *because* the memory tests used by these researchers were performed successfully by patients with semantic dementia, they cannot, by definition, have been testing episodic memory (since episodic memory is *defined* by the fact that it requires but goes beyond semantic memory). The situation is similar when it comes to the demonstration of episodic cognition in animals. Immediately before the definition quoted above, Tulving stresses that "before we can undertake the task of evaluating the presence of episodic memory in nonhuman animals, the concept needs to be sharpened…We need to be clear about the kind of memory that I am denying to our feathered and furry friends" (Tulving, 2005, p.9). Yet the definition of episodic memory that immediately follows from this statement declares that episodic memory is "recently evolved…and probably unique to humans" (p.9). Given this, it is *by definition* impossible for episodic cognition, as it is defined by Tulving, to exist in animals.

Thus a discrepancy has been created between what has been empirically demonstrated about the nature of cognition in humans and animals, and how these are related to

Tulving's *definition* of episodic cognition. Because episodic cognition is defined as "late developing" (e.g. Tulving, 2002, 2005), it cannot, by definition, be present at birth. Therefore any empirical demonstration of memory in newborns cannot be evidence for episodic memory. However, the concept of episodic memory is an intuitive one that we all recognise from our own mental lives: "we know what mental time travel is because we can introspectively observe ourselves doing it and because people spend so much time talking about their recollections and anticipations" (Suddendorf and Corballis, 2007, p.301). Thus individuals' ideas of what episodic cognition *is* exist independently of Tulving's definition(s) of it. Because of this, if there is evidence of a given memory ability in an infant or an animal that meets an individual's personal conceptualisation of episodic cognition, it is declared as such, regardless of what limitations Tulving has built into his definitions. A situation therefore currently exists in which evidence for episodic cognition exists for a number of nonhuman species (e.g. Zentall, 2005) or no nonhuman animals at all (e.g. Suddendorf and Corballis, 2007), in 16-month old babies (e.g. Bauer and Dow, 1994) or in no children younger than 4 (e.g. Suddendorf *et al*., 2011) depending on which papers you read.

One might say that the field of episodic cognition is looking for a needle in a haystack, but that no-one can agree on what constitutes a needle and what constitutes hay. Given the difficulty in establishing what episodic cognition *is,* how then, is episodic cognition actually *assessed?*

Interviews

Adult humans are able to verbally report both the content of their memory and their subjective experience of remembering. As such, many researchers have investigated episodic cognition using interview. These interviews have taken many forms. Autobiographical memories can investigated using cue-words (such as "river") to elicit related memories that must be described, located and dated (The Crovitz Technique: e.g. Crovitz and Schiffma.H, 1974). Periods of the lifetime (e.g. "childhood") can also be used as cues for recall (The Autobiographical Interview: Kopelman *et al*., 1989). More controlled testing conditions can be created by eliciting recall of naturalistic events originating in the laboratory (e.g. Hashtroudi *et al*., 1990). Furthermore, individuals can be asked to imagine themselves in a future scenario (Buckner and Carroll, 2007), or mentally construct a novel/future scene or event (Schacter and Addis, 2007a, Hassabis and Maguire, 2007). While there is little controversy that measurement of accuracy and vividness of mental experience through interview can effectively tap episodic processes, (Addis and Schacter, 2008, Maguire and Mummery, 1999, Hokkanen *et al*., 1995, Barr *et al*., 1990, Kapur *et al*., 1997, Tanaka *et al*., 1999, Buckner and Carroll, 2007, Hassabis *et al*., 2007) these tests are heavily reliant on verbal competence and therefore not always appropriate for patient groups (for example, where language may be impaired) or young children (where it is difficult to disentangle elements of verbal and cognitive development; see Chapter 3). Thus there is a need to develop and validate tests of episodic cognition that are less reliant on verbal capabilities.

"Laboratory" tests of a cognitive process essentially define a behavioural criterion[1]: if a subject demonstrates behaviour X, then they can be said to be using mental process Y. However, consensus on a *true* behavioural criterion for episodic cognition has proved difficult. In the first instance, the different definitions of episodic cognition highlight different "defining features". As such, the behavioural criteria born out of these definitions emphasize different features. A related problem is that there is little agreement (yet little explicit *debate*) over which behavioural criteria can be said to test episodic cognition, and which test related, yet distinct, processes such as semantic memory, rule-learning or familiarity. Even within an individual publication opinions on such matters are riddled with what seem like inconsistencies. For example, Tulving (1984), in describing the work of McKoon & Ratcliff (1979), refers to word-stem completion as a semantic memory test and recognition as an episodic memory test. Yet only a few lines later, describing the work of Schacter and colleagues (1982), he suggests that while episodic amnesics have great difficulty remembering events from their lives, they have no difficulty in recognising faces, suggesting that their semantic memory is intact. Similarly, Wheeler and colleagues (1997) describe Tulving's (1985a) finding that while free recall is correlated with a report of "remembering" rather than "knowing", cued recall and recognition paradigms are supported to a larger extent by semantic memory processes. However, a little later in the same article they discuss evidence for frontal lobe involvement in episodic memory that consists entirely of studies that used cued recall as their episodic memory test (Buckner *et al*., 1995, Squire *et al*., 1992, Shallice *et al*., 1994). Such apparent lack of consistency even *within* an individual argument (let alone between them) suggests that an explicit debate is needed within the field as to what empirical tests can be considered to assess

[1] For the purposes of this thesis, the term "Behavioural" refers to a subject's behaviour (verbal or nonverbal) rather than any other indices (such as activation of a particular brain area). The term "nonverbal" will be used when referring to tasks which do not require language.

episodic cognition. The following section explores different behavioural criteria that have been argued as necessary for the demonstration of episodic cognition.

Episodic Memory Must … Represent Spatiotemporal Relations

Clayton and Dickinson (1998) argue that if episodic cognition is to be investigated in nonverbal subjects, then the assessment cannot require demonstration of subjective phenomenology. These authors suggest that a behavioural criterion for episodic memory could be derived from Tulving's original definition of episodic memory as a system that "receives and stores information about temporally dated episodes or events, and temporal-spatial relations among these events" (Tulving *et al*., 1972, p.385): In other words, as memory for *what* happened, *where* and *when* (Clayton and Dickinson, 1998). In later writings, Clayton and colleagues emphasize that for a what-where-when paradigm to be considered to be testing something resembling episodic memory, the memory demonstrated must be integrated (i.e. the what, where and when elements must form a *single* representation) and should be able to be used flexibly to guide behaviour (i.e. the subject should represent the event, not a fixed response rule or intention based on the event; Clayton *et al*., 2003).

Clayton and Dickinson (1998) label memory demonstrated using the what-where-when paradigm as episodic-*like* because nonverbal paradigms cannot demonstrate any of the subjective phenomenology associated with later definitions of episodic memory (such as the feeling of "re-experiencing" and Tulving's concepts of "autonoetic consciousness" and "chronesthesia"). Suddendorf and Busby (2003a) admit that to insist that evidence of episodic memory in animals must include a demonstration of

autonoetic consciousness renders the hypothesis that episodic cognition is limited to humans unfalsifiable. They argue, however, that this does not make it parsimonious to accept that animals possess episodic memory, but rather that they form *what-where-when* (WWW) memories which *may* be episodic, but that a more parsimonious account would be that they involve cognitive processes that make no reference to the past at all, but instead involve rule-learning or response algorithm. Suddendorf and Busby (2003a) furthermore argue that it is possible to create a double dissociation between being able to remember the what, where and when of an event and involvement of episodic memory:

> *"One can know what happened where and when without being able to remember the event (e.g. your birth) and, conversely, one can travel back in time without access to accurate when and where information. I (TS) can vividly re-experience meeting a fascinating character once in the Philippines (or was that Indonesia?) sometime in the early nineties (or was that the late eighties?)"* (Suddendorf and Busby, 2003a, p.6).

However such examples are flawed because they emphasize semantic knowledge about location and time that has been received verbally (no one remembers, semantically or otherwise, the time and place of their birth from *experiencing* it) and inappropriately impersonal and specific definitions of time and place to emphasize the inaccuracy of spatiotemporal information in episodic memory (both "Indonesia" and the "Philippines" are "far away" [or even more specifically, "far away south-east from here"] and both "the early nineties" and "the late eighties" are "long ago" [or even more specifically, "about 20 years ago" or "when I was about 5 years old"]). Note that

while “the Philippines” and “the late eighties” are *impersonal* features of an event, “south-east of here” and “when I was 5” are *personal* features of an event. Because this quote was written by *Thomas Suddendorf* in *New Zealand* in *2003*, and *I* am discussing it in *England* in *2012*, all of the impersonal features (“Philippines”, “late eighties”) are identical, but the personal features (“south-east of here”, “when I was 5”) are changed. Given that episodic memory is memory for *personal* events, it is surely more likely that the what, where and when elements would be recorded from a *personal* perspective. No one argues that episodic memory allows an individual to locate precisely on a man-made map or calendar when an event occurred. It is widely argued, however, that episodic memory differs from semantic memory in that it involves the representation of spatial and temporal information about an event as well as what the focal event itself was.

The inclusion of the temporal element in the “what-where-when” criterion has been controversial. Researchers have disagreed as to the type of encoded “when” information (i.e. distance based [how long ago]; location based [when exactly] or order based [before/after judgments]) that constitutes evidence for episodic (-like) memory (see Friedman, 1993). Roberts (2008) argues that only location-based temporal judgements are episodic while distance based temporal judgements do not require memory (but merely “keeping track of how much time has elapsed”: p.113). However, Friedman (1993) reviews evidence suggesting that location-based temporal judgements are reliant on *logical inference* of time based on contextual details and knowledge about time-courses: e.g. *“it must have been in 2001 because I was doing my GCSEs, which means I was 16, which means it was 16 years after 1985 which is when I was born”*. Thus Friedman argues that location-based temporal judgements are

largely dependant on semantic knowledge *about* the contextual details contained in episodic memory. Furthermore, Friedman's model of memory for time (1993) includes the judgement of temporal distance as the first process in the series of temporal judgments in human memory. As such, it is not clear on what basis Roberts (2008) and others argue that memory for "when exactly" something occurred is somehow more episodic than memory for "how long ago" it occurred.

Eacott and colleagues (2005) argue that the "when" component of episodic-like memory serves only as an "occasion setter" with which to distinguish multiple similar experiences (Eacott and Norman, 2004), and consequently that a "what-where-which" criterion – where the "which" demarcates the experience as a unique episode - could equally be used to define this kind of memory (Eacott and Norman, 2004, Eacott and Gaffan, 2005). Cheke & Clayton (2010) agree that replacing "when" with "which" brings the what-where-when criteria more into line with other memory tests that emphasis memory for *context* (discussed below). However, they argue that the reason that the "what", "where" and "when" elements are *all* important is that they can be varied independently: In terms of a behavioural criterion "which" cannot avoid being confounded by elements of "what" and "where" *unless* it is temporally defined – i.e. unless it is *when*. Consider the following example: two games of tennis (what) at the park (where) could be differentiated by which partner you played, which top you were wearing, which court you played on, which tennis racquet you used... but each of these could be confounded with "what" (tennis-with-John vs. tennis-with-Jane) or where (court in school vs. court in the park). Thus while it is certainly arguable that episodic-like memory of an event need not entail recollection of "when" it occurred, this element is necessary to behaviourally confirm that the memory is for a *specific*

episode rather than for timeless facts about the spaces or objects involved in that episode.

While the What-Where-When behavioural criterion stipulates the content, integration and flexibility of demonstrated memory, other behavioural criteria emphasize aspects of the encoding or retrieval situation.

Episodic Memory Must … Be Internally Cued

> *"All retrieval is cued: Retrieval does not occur in situations in which appropriate retrieval cues are absent….An important research problem lies in the identification of the nature of "invisible" cues… in situations in which no cues appear to be present."* (Tulving, 1984, p.229)

Memory retrieval can occur in response to external cues that trigger the retrieval of a memory (cued recall) or uncued/in response to an internally generated cue (free recall). Tulving (1985b) argued that the contribution of episodic cognition (or rather, the self-knowing "autonoetic" consciousness that he argues accompanies episodic cognition) to memory for items on a list can be assessed by asking subjects if they *remembered* an item's occurrence on the list, or whether they simply *knew* "on some other basis" (p.8) that the item was on the list. He found that subjects were more likely to report "remembering" items from a word-list during a free recall task than during a cued recall task (although this difference was small: 88% compared with 75%). Thus he concluded that if the memory was *internally cued* by some cognitive process then it was more likely to be remembered episodically then if it was

externally cued by some information in the environment (such as the first letter of the to-be-remembered word).

The remember/know procedure has been mostly adopted by researchers studying recognition memory to differentiate between recollection and familiarity, and has been shown to successfully identify the involvement of the hippocampus in memory retrieval (e.g. Eldridge *et al*., 2000). However this literature has thus far failed to identify different recognition *tests* that can be used to tap episodic retrieval rather than semantic retrieval or familiarity judgements. The remember/know paradigm has instead been used to identify which particular items in a given recognition task are episodically remembered. Tulving's findings of a difference in remember judgements between free and cued recall have, however, led to the conclusion by some theorists (e.g. Perner and Ruffman, 1995) that free recall tasks tap episodic cognition to a greater extent than cued recall tasks.

Tulving's findings were specific to a free recall task using a word-list. However there are a number of types of free recall tests. Some are purely verbal, in which a list of words (or a section of prose) is read by or read to subjects which then, after some delay, has to be repeated back. Some are partially verbal in that the studied item is not a word but an object or picture, but the recall is verbal, in that subjects must report the items they have seen. There is considerable evidence that all these types of free recall test draw upon hippocampal regions (e.g. Fernandez *et al*., 1998, Baxendale, 1998, Frisk and Milner, 1990, Baxendale *et al*., 1998). But it appears that free recall of different types of stimuli rely differently on the dominant (usually left) and subdominant (usually right) hippocampus, with recall of verbal and narrative stimuli

tending being more associated with the former (e.g. Frisk and Milner, 1990, Baxendale, 1998, Baxendale *et al*., 1998) and recall of images and objects being more associated with the latter (Baxendale *et al*., 1998). Thus it may be that different types of free recall task tap episodic memory differently, or to different extents.

Subjects that are required to recall words from a list often use deliberate encoding and retrieval strategies to aid this task. Recalling a list of words seems intuitively not to lend itself to the use of episodic memory. The list has no spatial context, no "scene" and no coherent narrative. It is interesting to note, therefore, that many of the strategies people use to aid their memory for such stimuli have the effect of *adding* context and narrative and linking the words into a spatio-temporal scene. Possibly the most "episodic" technique is the "method of loci" in which subjects mentally place list-items at various points in a well-known journey, such as the journey through their own house. This allows the subject to recall not only the identity of the items, but their order with impressive accuracy (e.g. Roediger, 1980). It is notable that with this method a word-list is in essence converted into a what-where-when test: the subject remembers what word was presented, where in the house/room and at which stage of the journey. It is possible that such methodologies are so effective in part because by utilising both verbal and visual information, they enable contribution from *both* hippocampal formations to facilitate memory (rather than just the left or the right hippocampus). Indeed it has been shown that people who are highly skilled at the method of loci show increased activation in the right hippocampus when encoding relative to those untrained in the technique (Maguire *et al*., 2003). On the other hand, many mnemonic techniques have the effect of essentially turning a free recall test into a cued recall test: for example, the process of categorising words. Thus it is important

when considering performance on a free recall test, not only to record accuracy, but also encoding/retrieval *techniques* that may alter the contribution of episodic cognition to performance.

In the majority of tests putatively assessing episodic memory, there are focal elements (e.g. words on a word list) that must be remembered and the subjects are explicitly informed of the impending memory test. These features set the majority of memory tests apart from the scenarios in which episodic memories are encoded and retrieved in everyday life. In reality, memories are often encoded without the encoder's knowledge that they are later to be tested, and memories must often be retrieved about events that were not explicitly attended to at the time they occurred. Some schools of thought suggest that these features of episodic memory can be considered defining. That is, episodic memory is *unique* in its catch-all recording of *entire* events, whether or not they are deliberately memorized or even explicitly attended to (e.g Morris and Frey, 1997).

This "automatic encoding" feature of episodic memory has been investigated in two ways. Some researchers have sought to explore the difference between the encoding of target items that have been deliberately or non-deliberately memorized. Here, the to-be-remembered item is the centre of attention at the time of encoding, but the subject does not deliberately encode it into memory. Others have investigated memories for contextual details of a learning event, rather than the "target" item. Here, the to-be-remembered detail is incidental at the time of encoding.

Episodic Memory Must … Be Memory for Unattended Context

> *"It is useful to distinguish between the setting and the focal element (or elements) of an event*" (Hollingworth, 1913, p.532-33)

The importance of memory for contexts rather than focal items was highlighted in Tulving's early writings on episodic memory: "As the remembering of settings has not yet been studied, it can be argued that research on episodic memory has not yet begun." (Tulving, 1984, p.229). However, it has never appeared as part of any of Tulving's *definitions* of episodic memory (though one might argue that it is implied).

Fact memory for focal elements and source memory for contexts have been established as independent (e.g. Shimamura and Squire, 1987, Johnson and Raye, 1981) suggesting that they represent differential memory systems and may be equivalent to semantic and episodic memory respectively. Some patients with amnesia have demonstrated relatively preserved memory for facts learned during an experimental session, but severely impaired memory for *how and when* those facts were learned (e.g. Shimamura and Squire, 1987, Schacter *et al*., 1984). This inability to remember the *source* of a semantic memory is known as source amnesia. Schacter and colleagues (1984) demonstrated that source memory impairment was correlated with measures of frontal lobe pathology, suggesting that memory for the source of knowledge may be related to the function of frontal lobe structures whereas general anterograde amnesia is related to medial temporal lobe function. In fact it seems that it is the *retrieval* of source information that may rely on frontal lobe structures, while the *encoding* of this information may depend on more temporal regions. Recent

investigations using fMRI have suggested that the anterior prefrontal cortex (PFC) is particularly important for source memory retrieval performance. Furthermore, different regions of the anterior PFC may be differentially engaged depending on whether the "source" being retrieved is internally (i.e. what task were you performing when you saw this word?) or externally generated (i.e. what position on the screen was this word in when you saw it?). Lateral regions, it is suggested, are activated by either source memory task, while medial regions are recruited specifically when subjects must recall their own cognitive processes (Simons *et al*., 2005, 2008a). In contrast, Davachi and colleagues (2003) found that activation in the hippocampus and posterior parrahippocampal cortex during encoding predicted later source memory but not item recognition, while perirhinal cortex activation predicted later item recognition, but not source memory.

It could be argued that the difference in memory for focal and contextual features of an event may be due to the deliberateness of encoding. Focal items in a memory test may be encoded differently to contextual details because they are deliberately memorized while contextual features are incidentally encoded.

Episodic Memory Must … Not Be Deliberately Encoded

Zentall and colleagues (2001, 2008) argue that deliberate encoding of stimuli may lead them to be stored as semantic memories rather than episodic memories: "The critical aspect of the question is that at the time of encoding, there should be no expectation that one would be asked to retrieve the information" (Zentall *et al*., 2008, p.97). However, while there is evidence that deliberate encoding of information may

improve recall performance (e.g. Craik and Lockhart, 1972, Greene, 1986, Neill *et al*., 1990, Bower and Reitman, 1972, Carlson *et al*., 1976, Paivio, 1971) there is little evidence to suggest that deliberate encoding reduces the contribution of episodic memory to recall performance. Shimamura and colleagues (1987) demonstrated that amnesic patients had comparable deficits in fact and source memory regardless of whether the fact learning and testing situations were explicit (i.e. subjects were taught a fact and then tested for the fact and when they had learned it) or incidental. This finding suggests that knowledge of the impending memory tests did not reduce the impairment of the amnesic patients on either fact or source memory, nor did it increase the relative performance of the controls. Furthermore, Holland and Smulders (2011) and Plancher and colleagues (2010) found that deliberateness of encoding did not change episodic markers of What-Where-When memory.

Evidence from cognitive neuroscience suggests that *both* deliberately and automatically encoded memories are episodic, but that they rely on different yet overlapping components of the fronto-temporal neural network that underlies episodic cognition (Simons and Spiers, 2003, Moscovitch, 1992, Moscovitch, 2008). Morris and Frey (1997) argue that an explicit distinction must be drawn between automatic and effortful encoding, but that both are "episodic". The former, they suggest, involve "online" catch-all information capture in which events are temporarily encoded in association with the contexts in which they occur. Such processes are dependant on hippocampal long-term potentiation (e.g. Treisman, 1996, Zimmer *et al*., 2006). Deliberate encoding, in contrast, incorporates intentions, goals and task demands and may be dependant on a broader fronto-temporal network (Squire and Zola-Morgan, 1991, Shallice *et al*., 1994, Kapur *et al*., 1994, Tulving *et al*., 1996, Hayes *et al*.,

2004, Isingrini and Taconnat, 2008, Moscovitch and Winocur, 1995, Piolino *et al*., 2010, Tulving, 2002, Simons and Spiers, 2003, Dobbins *et al*., 2002, Fletcher *et al*., 1998a, Fletcher *et al*., 1998b, Henson *et al*., 1999, Wagner *et al*., 1998).

There seem to be distinctions between memory for items that have been deliberately or incidentally encoded and between memory for focal or contextual elements of an event. The suggestion is that while contextual details are remembered episodically, memory for focal items does not differ in its engagement of episodic cognition depending on whether it is deliberately or incidentally encoded. One can combine these approaches into a single task which assesses memory for the *context* of a learning episode with *unexpected* questions. Thus the memory tapped is both contextual *and* incidentally learned.

Episodic Foresight?

The behavioural criteria explored thus far have been designed to test only the retrospective aspect of episodic cognition. However, as mentioned earlier, there is growing consensus that the same system subserves both episodic memory for the past and episodic foresight, that is, the ability to imagine (or "pre-experience") potential future scenarios. It has, moreover, been theorised that the adaptive advantage of episodic memory lies not in its recording of the past *per se* but in its potential for increasing fitness in the future (Suddendorf & Corballis, 2007, Schacter & Addis, 2007b). While it is not obvious how the ability to re-experience a past event may increase the fitness of an individual, if this ability facilitates the generation of potential future scenarios, this would allow an organism to act in the present to

prepare for future need, giving that organism an obvious advantage over others without this capacity.

The study of episodic foresight is a "younger" science than the investigation of memory, and as such there are fewer concepts of what would constitute behavioural criteria. There is not, for example, and equivalent of the "remember/know" paradigm for future thought. However, of the few specific paradigms and criteria proposed, there is a common consensus that evidence for episodic foresight requires an individual to act in the present to secure fulfilment of a future need.

Episodic Foresight Must … Act for a Future Need

Tulving (2005) suggests that an example of a behaviour that demonstrates episodic foresight lies in an Estonian children's story. In this tale, a young girl dreams of a party where the guests are served a delicious pudding, but she cannot eat because she doesn't have a spoon. The following night, anticipating that she may return to the party in her dreams, she takes a spoon to bed with her. Tulving suggests that the "spoon test" requires an individual to "act analogously to carrying their own spoon to a feast that is likely to come in another place and time….they can do so, the argument is, if and only if they possess the ability to mentally travel into (or foresee, pre-experience, anticipate) the future." (p.44).

One major criticism of the spoon test paradigm is that it is not clear whether it requires a concept of a *future* need or simply the association between a given tool (e.g. a spoon) and a reward (e.g. chocolate pudding; Cheke and Clayton, 2010).

Suddendorf and Corballis (1997, 2007) suggest that a demonstration of episodic foresight can be obtained only if the need or motivational state that is to be addressed is *different* to that currently experienced. Thus saving a spoon can be seen as an action to fulfil a *current* desire for chocolate cake. If access to the chocolate cake happens to be in the future, then all this means is that the ongoing task of "obtaining chocolate cake" commences with spoon acquisition and ends with cake achievement and just happens to have a long frustrating period in the middle in which cake is not available. If however the girl were to have eaten her fill of chocolate cake (and in fact become quite sick of it) but *still* save the spoon this would indicate her understanding that while she is *currently* sick of chocolate cake, in the future she will not be and she will want a spoon with which to eat it[2].

Following the work of Köhler (1926), Bischof (1985), and Bischof-Köhler (1985) which argued that the actions of animals are always performed in pursuit of current goals, Suddendorf and Corballis's "Bischof-Köhler" hypothesis (1997) suggests that episodic foresight is necessary for an individual to plan for the fulfilment of a need or motivational state *that they are not currently experiencing*. It furthermore suggests that this ability is unique to humans. This claim will be addressed in Chapter 2. The Bischof-Köhler criterion is useful as a conservative test for future thought, but may not be useful in differentiating between semantic and episodic cognition. Situations involving episodic foresight often involve the use of a current motivation to make plans for the future: I might plan a relaxing holiday in the sun (involving researching hotels, booking flights and much time imagining myself on a beach) because I am *currently* feeling cold, wet and overworked. On the other hand, an

[2] Note that such a criterion does not explicitly address the issue of the associative explanation. This is explored in chapter 2.

individual can logically infer a future motivational state (that is different from that currently being experienced) from factual regularities without the need to "pre-experience" that motivational state (People who haven't eaten for a while are hungry. Therefore if tomorrow I haven't eaten for a while, I will be hungry). Arguably pre-experience of a drive state is in fact a *less* intuitive way of allowing an individual to plan for a future need than is inference from semantic knowledge; one cannot easily re-experience thirst or hunger from memory while currently quenched or sated (Osvath and Osvath, 2008, Loewenstein, 2000). The crux of the matter is that acting for a future motivational state over a present one does not prove episodic future thought any more than acting for a present motivational state rules it out.

Behavioural Criteria: Helpful?

Having reviewed the behavioural paradigms that have been argued to assess episodic cognition, are we any nearer in differentiating the needle from the haystack? Arguably not. Each of these paradigms has its supporters and its critics, its advantages and its caveats. Most importantly, each of these paradigms is being used by different researchers in different fields and quite often on different *species*. Thus we cannot be sure that any of these paradigms assess *the same cognitive ability as each other* let alone hope to identify *what that ability is.*

This thesis represents an attempt to address the first of these issues. The different behavioural paradigms reviewed above are distilled into four (putative) tests of episodic cognition:

1. What-Where-When (WWW). A test of memory for *what* item was hidden *where*, *when.*
2. Unexpected Question (UEQ). A test of memory for aspects of the context that was not focal at the time of encoding.
3. Free Recall (FR). A test for memory for items presented on a list that is not cued by environmental features.
4. Bischof-Köhler (BK). A test of planning for a future time in which the individual's motivational state will be different from what it currently is.

These different tests are presented to the same subjects, and the relationship between performances on each is assessed. In terms of surface features at least, these tasks are very different. As such, one would not expect 100% overlap in the cognitive challenges that they represent. The investigation undertaken in this thesis is thus not one of *whether* they are different tests of the same ability, but *to what extent* these different tasks assess the same underlying cognitive process. The overarching prediction is that, to the extent to which these tasks *do* assess the same cognitive ability, one would expect them to:

1. Be phylogenetically consistent (i.e. if given species passes one test they should be more likely to pass another).
2. Be related in development (i.e. performance should improve at the same rate and in the same pattern in children).
3. Be related in maturity (i.e. adult humans who perform better at one should also perform better at the others).

4. Be affected in the same way in the same patients (factors that cause deficits in one should cause deficits in the others).

These four predictions are addressed in the four empirical chapters. Chapter 2 explores the evidence for episodic cognition in animals. The biggest challenge in the comparative cognition literature is often not in deciding upon a behavioural criterion for a given cognitive process, but in demonstrating that the specific experimental design did not allow the animal to solve the task through some simpler means such as associative learning (see Chapter 2). Despite this, the literature suggests that those species that have been found to pass some tests of episodic cognition also perform well on the others. Two experiments are presented in a previously untested species - the Eurasian jay. This species is an intensive food-caching corvid which caches both perishable and non-perishable food throughout the year (e.g. Clayton *et al*., 1996). It was thus argued to be a good candidate for a species whose ecological pressures might have selected for the development of episodic cognition (e.g. Grodzinski and Clayton, 2010). In the first experiment, the jays are shown to significantly adapt their caching behaviour to provide for their future needs. Moreover, they demonstrate an ability to account for two distinct future motivational states and provide for each appropriately. The second experiment failed to demonstrate convincing evidence that jays remember what food they cached, where and when. However, with the very small sample size this result is difficult to interpret. In the context of wider literature, these findings provide (very) tentative support for the first prediction of the thesis: that performance on different tests of episodic cognition are phylogenetically consistent.

Chapter 3 explores the literature on memory and planning development in human children. Much of the developmental psychology literature on episodic cognition is concerned with conceptualist notions of what it *means* to be a "owner" of episodic memory (Tulving, 2005, p.9). Chapter 3 reviews conceptualist and minimalist theories of episodic cognition and suggests potential hypotheses arising from the two. An experiment is then presented in which the same sample of 3-6-year-old children are tested on three putative tests of episodic memory (What-Where-When, Unexpected Question and Free Recall); one test that is thought to assess both episodic and semantic memory (Cued Recall) and one putative test of episodic foresight (Bischof-Köhler). It is found that performance on all these tests increased gradually between the ages of 3- and 6-years. There was considerable inter-correlation between performance on all the memory tests, but much of this was lost when age was partialled out. This finding suggests that, beyond general cognitive development, there is little relationship between performance on these different tests in children. There was furthermore little to no relationship between performance on the memory tests and performance on the Bischof-Köhler test, beyond a trend towards a *negative* relationship with Unexpected Question performance.

This result provides some *refutation* of the second prediction of the thesis: that performance on different tests of episodic cognition should be related in development. However, given that this age range (3-6) is a period of great development generally, it may be that immaturity of non-mnemonic factors (such as language and executive functions) may differentially affect performance on different tests. Thus to interpret these results it was necessary to conduct the same experiment with human adults.

Chapter 4 presents an experiment in which the three putative tests of episodic memory (what-where-when, unexpected question and free recall) and one putative test of episodic foresight (Bischof-Köhler) were presented to the same sample of healthy young adults. It is found that performance on all these tests is interconnected, but not always in a linear fashion. This finding suggested that multiple processes contribute to performance, and that all these processes may not always be shared by different tasks. Following from the finding of a negative relationship between Unexpected Question and Bischof-Köhler performance in the developmental data, it is found that memory performance is *inversely* related with performance on the Bischof-Köhler test. Thus those subjects that had better memories for non-focal elements of the experiment were *more* biased by their current motivational state when making decisions for the future than those subjects with poorer memory performance. Thus while these results support the third prediction of the thesis: that performance on the different tests should be related in maturity, the full picture is manifestly more complex, with evidence for contributions from other, non-shared, processes.

Finally, Chapter 5 explores factors that may impair episodic cognition and asks whether performance on different (putative) tests of episodic cognition is affected by the same factors. Evidence is explored for an association between excess body weight (obesity) and high levels of dietary fat and sugar, and poor hippocampal function. Given the evidence that patient groups with damage to the hippocampus show deficits in episodic cognition (Scoville and Milner, 1957, Addis *et al*., 2007, Squire, 1992, Isaacs *et al*., 2000, Golomb *et al*., 1993) it is predicted that episodic cognition deficits would also be evident in overweight individuals and those with high levels of dietary fat and sugar.

This prediction is assessed in two experiments. Experiment one compares the performance of individuals with varying body mass indices (BMIs) and diet content on an unexpected free recall test and a Bischof-Köhler bias test. The results revealed that BMI and diet differentially affect performance on these tests. There is a suggestion of a negative relationship between BMI and performance on an episodic memory test in women. In contrast, men (but not women) with high levels of dietary fat and sugar are *less* biased by their current motivational state in the Bischof-Köhler test relative to individuals with healthy diets. In the second experiment, free recall and Bischof-Köhler performance is assessed in a sample of obese binge-eating subjects. In the Bischof-Köhler test, current state is manipulated by reduction of hedonic experience (μ-opioid antagonism) rather than satiety (as was used in the previous experiments and chapters). It is found that obese binge-eating subjects are significantly impaired on the free recall task, and are completely unbiased by their current motivational state when choosing food for future consumption. Taken together, these findings suggest that performance on these different episodic cognition tasks is differentially affected by harmful lifestyle factors (e.g. poor diet and obesity), providing refutation for the fourth prediction of the thesis: That performance on all the tests should be affected in the same way in the same patients.

The evidence from the four empirical chapters therefore suggest that the degree to which different (putative) tests of episodic cognition can be said to be assessing the same underlying psychological process is limited. This idea is expanded in Chapter 6. Two of the four central predictions of the thesis (that performance on all the tests should be related in development and affected in the same way in the same patients)

are actively refuted, while the other two predictions (that performance on all the tests should be phylogenetically consistent and related in maturity) are, at best, only tentatively supported. This suggests that behavioural tests born out of different theoretical conceptions of episodic cognition may not, to any significant degree, test the same cognitive process. Such evidence may indicate that different theories of episodic cognition may not be theorizing about the *same thing.* These findings emphasize the need for greater coherence and communication in the field of episodic cognition in order to establish agreed criteria and definitions of the remarkable phenomena that allows us to travel mentally in time.

Chapter 2
Episodic Cognition in Animals

Fifteen years since Suddendorf and Corballis first claimed that episodic cognition was unique to humans, the ensuing debate remains unresolved. The chief difficulty in resolving this question has been how to translate theories of episodic cognition into meaningful behavioural tests. This chapter reviews the behavioural paradigms that have been used to assess episodic cognition in animals. It is suggested that greater coherence is needed within the field to establish the extent to which all – or any – of these behavioural tests are measuring the same ability, and to begin to establish what that ability might be. Two experiments are presented investigating performance on two putative tests of episodic cognition in a previously untested species: the Eurasian jay. It is found that jays are able to cache a food that they will want in the future, rather than that which they currently desire. There is also tentative evidence that Eurasian jays are able to keep track of what they cached, where and when. It is proposed that testing multiple paradigms in the same subjects will aid our understanding of the psychological processes underpinning performance on these tests.

2.1 Introduction

The idea that humans and animals differ fundamentally in their mental capacities is an ancient and established one. Many modern theories, including those involving episodic cognition (Tulving, 1983), still draw their inspiration and essence from "intuitive" and philosophical notions of the human and animal mind (e.g. Descartes, 1637, Jaynes and Woodward, 1974). More recently it has been possible to investigate such implicit assumptions using empirical enquiry. However, the success with which we have been able to truly divorce our interpretations of these data from intuitive and philosophical attitudes is perhaps questionable. One theory that has dominated the recent literature on animal cognition is Suddendorf and Corballis's "Mental Time Travel" hypothesis (1997). This theory states that the processes by which we mentally re-experience our personal past are the same as those with which we mentally *pre*-experience our personal future, and that this "mental time travel" is unique to humans. In their initial paper and many subsequent publications (e.g. Suddendorf and Busby, 2005) the authors argue that non-human animals lack many of the necessary cognitive processes to support mental time travel (episodic cognition).

The idea that episodic cognition represents a discontinuity between humans and animals continues to be the subject of much controversy and has been vigorously challenged experimentally (e.g. Clayton *et al*., 2003c, 2003a, Clayton *et al*., 2003b, Suddendorf and Corballis, 2008, 1997, 2007, Clayton and Dickinson, 1998, Griffiths *et al*., 1999, Roberts, 2002, Zentall *et al*., 2001, 2005, 2006, 2008, Clayton *et al*., 2008). The purpose of this chapter is not to explore the evidence for the existence of episodic cognition in nonhuman animals, as this has been done extensively elsewhere (e.g. Suddendorf and Corballis, 1997, 2007, Suddendorf and Busby, 2003b, Roberts,

2002, Raby and Clayton, 2009, Cheke and Clayton, 2010, Zentall, 2005) . The purpose of this chapter is to investigate how the animal cognition literature can address the main question of this thesis: Do tests born of different theories of episodic cognition test the same thing? That is, is there a single underlying psychological process that is targeted by tests that have arisen out of the different conceptualisations of episodic cognition?

The literature on episodic cognition in nonhuman animals is now extensive. As discussed in Chapter 1, different experimental paradigms have arisen from varying conceptions of episodic cognition and, in particular, what various researchers and theorists consider to be the defining feature(s) of episodic cognition that can or should be empirically evaluated. The use of many different experimental paradigms limits the extent to which the findings of this literature can be interpreted. The following section shall briefly review the evidence that has accrued for episodic cognition in nonhuman animals using these paradigms.

What-Where-When

The first empirical test of the hypothesis that episodic cognition was unique to humans came from Clayton and Dickinson (1998). In their seminal experiment, Western scrub-jays (*Aphelocoma californica*) learned that wax worms would degrade after a long period (124 hours) but not a short period (4 hours). These delays were chosen such that cache retrieval always occurred at the same time of day, to prevent the use of circadian cues. During training, the jays were given the opportunity to cache wax worms and peanuts in trial-unique trays. They were then permitted to retrieve their caches after 4 or 124 hours. In a final extinction test, in which no food

was present at retrieval (to make sure that memory was being used, rather than visual or olfactory cues) the birds returned to their caches after either 4 or 124 hours. When returning after the shorter interval, the birds searched in the location where they had cached wax worms. However, when returning after the longer retention interval, the birds seemingly understood that the wax worms would be degraded and searched in the location in which they had cached the peanuts. Controls and follow-up studies showed that this result was not due to familiarity cues, because the jays could identify how long ago they cached a given food even when both foods were cached in the same tray, or when the tray was experienced between caching and recovery (Clayton *et al*., 2001a). It was also shown that the precise identity and decay rate of each cached food was encoded by the jays (Clayton *et al*., 2001a), and that the "what", "where" and "when" elements formed an integrated representation (Clayton *et al*., 2001a). Furthermore the memory was highly flexible; the birds continued to respond appropriately when, between caching and retrieval, new information was acquired about the decay rate (Clayton *et al*., 2003c) or value (Clayton and Dickinson, 1999b) of the food, or when the food "ripened" rather than degraded (de Kort *et al*., 2005).

More recently, successful performance on a what-where-when (WWW) memory test has been demonstrated by another corvid using a slightly different experimental paradigm (Zinkivskay *et al*., 2009). Here, Magpies (*Pica pica*) cached egg pellets of two different colours in an open area. In training, birds returning to their caches later that day found that pellets of one colour had been replaced with wooden beads, while the other remained edible. A day later, however, the opposite would be true. When tested in extinction the magpies searched preferentially in locations where caches would be edible.

A very similar experimental design was used by Gould and colleagues (2012) to investigate WWW memory in a third corvid, the Clark's Nutcracker (*Nucifraga columbiana*). They found that while the birds were able to differentiate between food that would or would not be edible after a long retention interval, they were unable to identify and retrieve food that would only be edible after a short retention interval (although both types of food were retrieved accurately, suggesting that it was not that they *forgot* the location of the beads after the long retention interval). Given that the exact same methodology was used, it is perhaps surprising that the Clark's Nutcrackers failed this task when the Magpies passed (especially when nutcrackers have been shown to remember the locations of phenomenal numbers of cached items over long periods). The authors suggest that the explanation may lie in their diet. While Magpies and Western scrub-jays cache a wide variety of different foods, all with different decay-rates, Clark's Nutcrackers "appear to cache only pine seeds, which remain palatable for many months" (Gould *et al*., 2012, p.38). Therefore they may be under less selective pressure to remember information about the contents of the cache (such as its decay rate). It is also possible that the Nutcrackers struggled to understand that something could be inedible after a short period but edible after a long period, as this is not a common natural phenomenon. Nonetheless, the results suggest that while Magpies and scrub-jays appear to demonstrate memory for what-where and when, Nutcrackers may be able to form only what-where memories

The ability to remember *what* and *where*, but not *when* has been found in other genera, including rats (*Rattus norvegicus*) and Rhesus monkeys (*Macaca mulatta)* (Bird *et al*., 2003, Griffiths and Clayton, 2001, Hampton *et al*., 2005). Others have

demonstrated memory for all three components, but have had assessed them separately (e.g. (Hoffman *et al*., 2009) or have failed to demonstrate integrated representations (Skov-Rackette *et al*., 2006, Ergorul and Eichenbaum, 2004) . Some studies show potential for demonstrating integrated WWW memory, but success may have been achieved through extra-target strategies such as circadian cues (Ferkin *et al*., 2008) or familiarity judgements (Babb and Crystal, 2006, see Cheke and Clayton, 2010 for a detailed critique).

Clayton and colleagues (1998) refer to WWW memory as episodic-*like* because a behavioural test cannot demonstrate the phenomenology of re-experiencing a past episode. However, there are other features of episodic cognition that can be investigated in nonverbal subjects. Martin-Ordas and colleagues (2010) showed that apes (chimpanzees (*Pan troglodytes)*, bonobos (*Pan paniscus*) and orang-utans (*Pongo Pongo*)) were able to keep track of which iced juice had been hidden and how long ago (and therefore how likely to be melted) when observing two events consecutively, suggesting that they were demonstrating integrated WWW memory. Interestingly, the authors also showed that performance on the WWW task, but not on a spatial memory task, demonstrated an inverse U-shaped developmental trajectory, with the youngest and oldest subjects performing worse than the young adults (Martin-Ordas *et al*., 2010). This is significant for two reasons. First, it matches the inverse U-shaped developmental trajectory seen in episodic, but not semantic, memory in humans (e.g. Tulving and Craik, 2000, Craik and Salthouse, 2000, Bialystok *et al*., 2006, Craik and Bialystok, 2006b, Craik and Bialystok, 2006a). Second, it is similar to the developmental trajectory reported for mirror self-recognition in chimpanzees (Povinelli *et al*., 1993; see Chaper 3 for an in-depth

discussion of the potential relationships between self-awareness and episodic cognition).

Thus there is evidence from a number of species (scrub-jays, magpies, chimpanzees, orang-utans) that some non-human animals may be able to pass WWW memory tests. What the literature highlights however, is how extra-target strategies or challenges may affect performance. As has been argued elsewhere (Cheke and Clayton, 2010), many studies claiming to demonstrate WWW memory fail to control for simpler strategies (including associative learning, familiarity or circadian cues), while others may limit the performance of the subject animal by imposing heavy cognitive loads beyond that of the memory performance (e.g. Dekleva *et al*., 2011). The What-Where-When paradigm was inspired by the natural challenges experienced by food-caching birds. However, the ecology of many animals may not have provided the evolutionary pressure to pay attention to the relevant stimuli involved in a WWW memory test, either because of the manner in which it is carried out (for example, with certain foods "disappearing" after a given interval (Dekleva *et al*., 2011) or having a set replenish rate (Babb and Crystal, 2006)) or because their natural behaviour in a given context does not need to take account of certain features (e.g. "when": Clark's nutcrackers cache only non-perishable foods (Gould *et al*., 2012), or "where": rats are larder hoarders and never need to remember the location of several caches (Vander Wall, 1990, Bird *et al*., 2003)). Thus it may be that the WWW paradigm is not appropriate for assessing episodic cognition in all species.

The Unexpected Question

Many theories (e.g. Morris and Frey, 1997, Zentall *et al*., 2001, 2008, Tulving, 1984) suggest that the defining feature of episodic cognition is that it is the memory for the unattended *context* of an experience, rather than its focal element. Zentall (2001) distilled this theoretical stance into a behavioural paradigm for testing episodic memory in animal subjects in which the subject of the memory test is incidental at the time of encoding: The Unexpected Question (UEQ). Zentall and colleagues (2001, 2008) presented a proof of concept experiment with pigeons. They demonstrated that pigeons taught two separate response rules (e.g. "peck green if you've just pecked left" and "peck horizontal stripes if you've just seen blue") can report on their previous actions correctly if the rules are combined such that first question unexpectedly follows the second. Thus, the authors suggest, this test assesses memory for something that was incidental at the time of encoding (i.e. where they pecked) and therefore requires episodic memory to retrieve. Zentall and colleagues (Zentall *et al*., 2008) argue that their paradigm is better than the WWW procedure because there is no training for the test phase – it is an unexpected question about something that was incidental at the time of encoding. However, Cheke and Clayton (2010) argue that given the very short retention interval (2 seconds) and the repeated testing, Zentall's study cannot be considered a test of *memory* let alone of anything "unexpected".

In a recent attempt to assess UEQ performance in rats, Zhou and colleagues (2012) trained rats to use whether or not they had just received food as a discriminative stimulus in a T-maze. They found that the rats could perform this task correctly when unexpectedly asked to do so after receiving (or not receiving) food as part of an

unrelated spatial memory task. They furthermore demonstrated that this performance was dependant on hippocampal function while an "expected question" (essentially another T-maze training trial) was not. However, the rats may well have used a physiological response to eating (such a feeling of fullness or a residual taste in the mouth) as a discriminative stimulus for passing the T-maze probe. Given that use of such physiological responses as a discriminative cue is dependant on the hippocampus (Davidson and Jarrard, 1993, Hock and Bunsey, 1998), Zhou and colleagues' (2012) findings may not have been evidence for memory at all, let alone episodic memory.

These studies are the only example to date of research using the UEQ paradigm in animals. This may speak to the practical difficulties inherent in asking animals *unexpected* questions while at the same time being sure that they understand *what* question is being asked and how to answer it. Thus it may be that, while conceptually sound, the UEQ test does not represent a realistic behavioural paradigm with which to assess episodic cognition in nonhuman animals. Moreover, as discussed in Chapter 1, it may be that deliberateness of encoding does not affect the contribution of episodic memory to performance, but rather it is whether the to-be-remembered item is focal or contextual at the time of encoding that determines whether episodic memory is necessary for successful retrieval.

Episodic Foresight and the Bischof-Köhler Test

Some theorists have argued that the adaptive function of episodic cognition lies in the capacity for episodic *foresight* rather than episodic memory, and thus that the most promising paradigms for assessing episodic cognition in nonhuman animals

may be tests of episodic foresight (e.g. Suddendorf and Corballis, 2007). The ability to act in the present in preparation for future events is fundamental to the survival of a number of species. However, the extent to which such action can be considered to be controlled by cognitive processes, and in particular, whether any qualify as examples of episodic foresight remains unclear. Suddendorf and Corballis, following Köhler (1926), have argued extensively (e.g. Suddendorf and Corballis, 1997, 2007) that while animals may perform actions that are functionally prospective, they are not able to perform any action that is not driven by a currently experienced motivational state:

> "*…the selective advantage of mental time travel is the increased flexibility in acting in the present to secure future needs. First, therefore, one has to be capable of conceiving having different future needs, such as imagining being thirsty when currently quenched*." (Suddendorf and Corballis, 2007, p.305).

Thus, in their "Bischof-Köhler" hypothesis, Suddendorf and Corballis argue that only humans are able to disengage from their present motivational state to plan for a future need (Suddendorf and Corballis, 1997).

Suddendorf and Busby (2003b) suggest that the ability to save a currently useless item for a future time in which it would be needed would constitute evidence for episodic foresight. One candidate for future-orientated cognition is the tool transportation exhibited by many primate species (e.g. Goodall, 1986, Jalles-Filho *et al*., 2001, Cleveland *et al*., 2004, Boesch and Boesch, 1984). Mulcahy and Call investigated whether tool transportation by great apes (orang-utans and bonobos*)* meets the

Bishof-Köhler criterion for future planning (Mulcahy and Call, 2006). The authors demonstrated that bonobos and orang-utans chose an appropriate tool that would be useful to access a reward an hour in the future. However, the results of their control for associative learning suggest that the apes may simply have associated that tool with reward rather than representing their future needs (Suddendorf *et al*., 2009, Cheke and Clayton, 2010).

In an attempt to answer such criticisms, Osvath and Osvath (2008) showed that apes chose a tool that would be useful in the future *above* a favoured fruit that could be consumed immediately, suggesting that they could overcome a present drive state to achieve a future goal. In an elegant control, the authors also found that, when offered the same options twice in a row, subjects would only chose the functional tool on the first choice, and the fruit on the second, indicating that the tool had not become a secondary reinforcer. In a final experiment, the apes chose a novel functional tool over novel non-functional but visually similar tools. The authors argued that this indicates subjects' ability to mentally pre-experience their future encounter with the apparatus to rehearse the potential functionality of the novel tools. While it is not clear that this performance necessitates pre-experience of a future scenario (rather than an understanding that the apparatus requires a long hollow tool), these results show impressive flexibility in planning for an explicitly *future* need (but see Suddendorf *et al*., 2009 for a critique).

One study described by Shettleworth (2007a) as the first that unambiguously meets the requirements for future planning (and is similar in design to the "Rooms Task" suggested by Suddendorf and Busby (2003b) to satisfy the Bischof-Köhler (BK)

criterion) is that conducted by Raby and colleagues (2007). Western scrub-jays were given experience of two compartments on alternate mornings. In one compartment they were given food (the "breakfast" compartment) and in the other they were not (the "no breakfast" compartment). At test, the birds were unexpectedly given food to cache and eat in the evening. The authors argued that if the jays were capable of episodic future thinking, they should have cached more food in the "no breakfast" compartment than in the "breakfast" compartment, which they did. In a second experiment, when given one food type in one compartment and another food type in the other, subjects cached the food they would not receive in that compartment the next morning. This study shows remarkable flexibility in planning for a future need. However, it has been argued (Cheke and Clayton, 2010) that it is possible to explain these results with an associative account. Acquisition of associations between a location and food has been shown in rats, who ate more of a given food type when in a location associated with that food (Petrovich *et al*., 2007). That scrub-jays responded with the opposite behaviour means that a purely associative account is insufficient. However, it is plausible that scatter-hoarders would possess a heuristic leading them to avoid caching a food type in a place where it is plentiful. Thus entering the room associated with food A could activate a representation of "plenty of food A" and lead jays *not* to cache that food in that location. A similar criticism has been levelled by Suddendorf and Corballis (2008).

Other studies have attempted to address such issues by manipulating the current and future motivational states of animals such that the choice of the correct option *requires* them not to be acting for their current desires. I have dubbed this paradigm the "Bischof-Köhler Test". In the first of these, Squirrel monkeys (*Saimiri sciureus*)

were taught that choosing a small quantity of food would lead to a short period of water deprivation, while choosing a large quantity would lead to a long period of water deprivation. Subjects learned to choose the small number of items despite showing a robust preference for the larger amount at the beginning of the study (Naqshbandi and Roberts, 2006). Follow-up experiments revealed that this pattern of choices was not shown with rats, and was not due to thirst experienced at the time of, or immediately after, the choice. Although it has been argued that the gradual learning of this behaviour implies associative processes (Shettleworth, 2007b, Suddendorf and Corballis, 2008). Cheke and colleagues (2011b) argue that it is not clear why *speed* of learning should be used as evidence for *type* of learning; associative learning can occur within a single trial or take hundreds of trials to appear. By standard operant learning criteria, the action and reinforcer in this study (food choice and return of water) were not sufficiently temporally contiguous to allow associative learning, nor were conditions met for "long delay" associative learning (Lett, 1975). However, the results of this study must nonetheless be treated with caution since they present the behaviour of only two subjects.

In what is perhaps a more convincing experiment, Correia and colleagues (2007) fed scrub-jays to satiety on one food type, then allowed them to eat and cache this and an alternative food type. Later that day, subjects were fed to satiety on the other food type and then allowed to retrieve their caches. Thus at the time of caching they experienced a significantly different motivational state from that which they felt at the time of cache retrieval. After only one trial, the birds cached more of the food that would be desired at the time of retrieval, rather than the food more desired during caching.

In their critique of this study, Suddendorf and Corballis (2008) suggest that the birds could have learned a "simple rule" that they should stop caching items that turn out to be plentiful at recovery. This type of learning has been demonstrated in scrub-jays that cease caching an item that has been regularly degraded at recovery (Clayton *et al*., 2005). However, since Correia and colleagues' birds were pre-fed *both* foods at some point during the day, an incentive learning account (Balleine *et al*., 1994, Balleine and Dickinson, 1998) would predict decreased caching of *both* foods, because a food's incentive value is insensitive to *when* it had a low value (see Clayton *et al*., 2008 for an in-depth discussion of this). At the very least, then, the difference in the proportions of the two food types cached must have reflected some cognitive representation of a situation in which the value of these food types would be different. Recent work by Correia and colleagues (unpublished data) addresses this criticism by demonstrating that scrub-jays can not only overcome a current motivational state to cache what they will desire at the time of cache retrieval, but can distribute caches across two locations that they will have the opportunity to return to in two different motivational states. This within-subjects version of the original study indicates that the birds could not have been forming a simple rule about a given food item ("not good to cache").

Summary

The debate as to the existence of episodic cognition in nonhuman animals continues. With little coherence in methodology and less agreement over precise definitions as to what kind of data *would* constitute *bona fide* evidence for episodic cognition, the path

ahead does not seem to be any clearer. The considerable influence of extra-target factors (such as executive function demands and associative learning) muddies the water still further. Some species (e.g. scrub-jays, chimpanzees) have been tested on multiple experimental paradigms and the data are consistently positive, potentially suggesting that the different tests of episodic cognition *are* phylogenetically consistent – that is, that if a given species passes one, they are more likely to pass the others. However, because of the tendency not to publish negative results – and the considerable differences in experimental effort put into testing different species – even this finding is difficult to interpret. What is needed is a focus on testing multiple paradigms on the same species and for the negative results to be considered alongside the positive. In this way it may be possible to form a coherent picture of the phylogenetic consistency of different tests of episodic cognition.

This chapter presents the first explorations into episodic cognitive abilities in a previously untested species: the Eurasian jay. Eurasian jays share many ecological traits with previously tested corvid species. Like magpies and Western scrub-jays, Eurasian jays cache a wide variety of foods with different decay rates (Goodwin, 1951, Clayton *et al*., 1996) and rely on these caches over long periods. Eurasian jays, like Clark's nutcrackers, are classed as "intense" cachers. This differentiates them from Western scrub-jays and magpies, which are classed as "moderate" cachers. As such, Eurasian jays represent a prime candidate for an animal model that has had the ecological pressure to develop long-term, flexible memory and foresight.

To investigate the phylogenetic consistency of different tests of episodic cognition, the jays were tested on two different behavioural paradigms. Experiment 1 was a

putative test of episodic foresight (based on the within-subjects design of Correia and colleagues [unpublished data] and named the "Bischof-Köhler" test, in deference to the Bischof-Köhler hypothesis (Suddendorf and Corballis, 1997)). Experiment 2 was a putative test of episodic memory (a variant of the WWW test (Clayton and Dickinson, 1998)). It was predicted that if the birds passed one of the tests they would also pass the other.

In Experiment 1, the birds were fed to satiety on one of two foods. They were then given the opportunity to cache these two foods in two trays. One of these trays was later returned to the birds at a time when they had just been pre-fed the same food as at caching (the "Same" tray) and one was returned when they had been pre-fed the other food (the "Different" tray). The hypothesis is that, if the birds are able to make decisions for the benefit of their future selves, and not based on current feelings, they should cache food in the two trays differentially depending on the state they will experience on receiving those trays.

2.2. Experiment 1

2.2.1. Methods

Subjects

The subjects were five 2-year-old Eurasian jays (two females: Hunter and Wiggins; three males: Ainsley, Hoy and Romero). Romero was subsequently excluded for failing to consistently cache both foods, leaving N=4. The jays were pair-housed in 4x1x1 m cages that could be divided into two test areas by insertion of opaque dividers. Birds were maintained at 21±1 ºC on a 12:12-hour light-dark cycle. Birds

received a maintenance diet (MD) of kibble, vegetables, fruit and seeds. Water was always available. Subjects cached in Tupperware boxes (17x24 cm) filled with wood chips and individuated by coloured blocks. Work adhered to Home Office licence PPL 80/1975.

Specific satiety

To use the specific satiety procedure in the Bischof-Köhler (BK) test, it was necessary to first establish specific satiety in Eurasian Jays. Subjects were food-deprived and isolated in half of their home cage for 2 hours before testing. They were then given 15 minutes' access to a powdered/liquidized version of one of the test foods (Food A: peanuts; Food B: suet pellets or raisins, depending on each bird's preference). This processed food was not cacheable. Subjects were then given a caching tray, 40 items of Food A and 40 items of Food B, and were allowed to eat and cache for 15 minutes before trays were removed and the cages cleaned. Trays were inspected for caches out of sight of the birds. The number of food items eaten was calculated as the items missing when the bowls, cage and trays had been searched. Trays were then returned to allow cache retrieval. Finally, birds were reunited with their cage-mate and MD was returned. This procedure was then repeated on a different day such that each bird was pre-fed both foods once.

Bischof-Köhler Test

Each bird received three trials of a three-stage procedure (Figure 2.1). Subjects were food-deprived and isolated for 1 hour before each stage. On the first trial ("Baseline")

subjects were pre-fed MD before the caching phase such that they would cache according to their general preference. On the two subsequent trials they were pre-fed one of the test foods (powdered/liquidized), such that a preference for the non-pre-fed food was established before the caching period. Pre-feeding order across all stages was counterbalanced between birds (Fig. 1b).

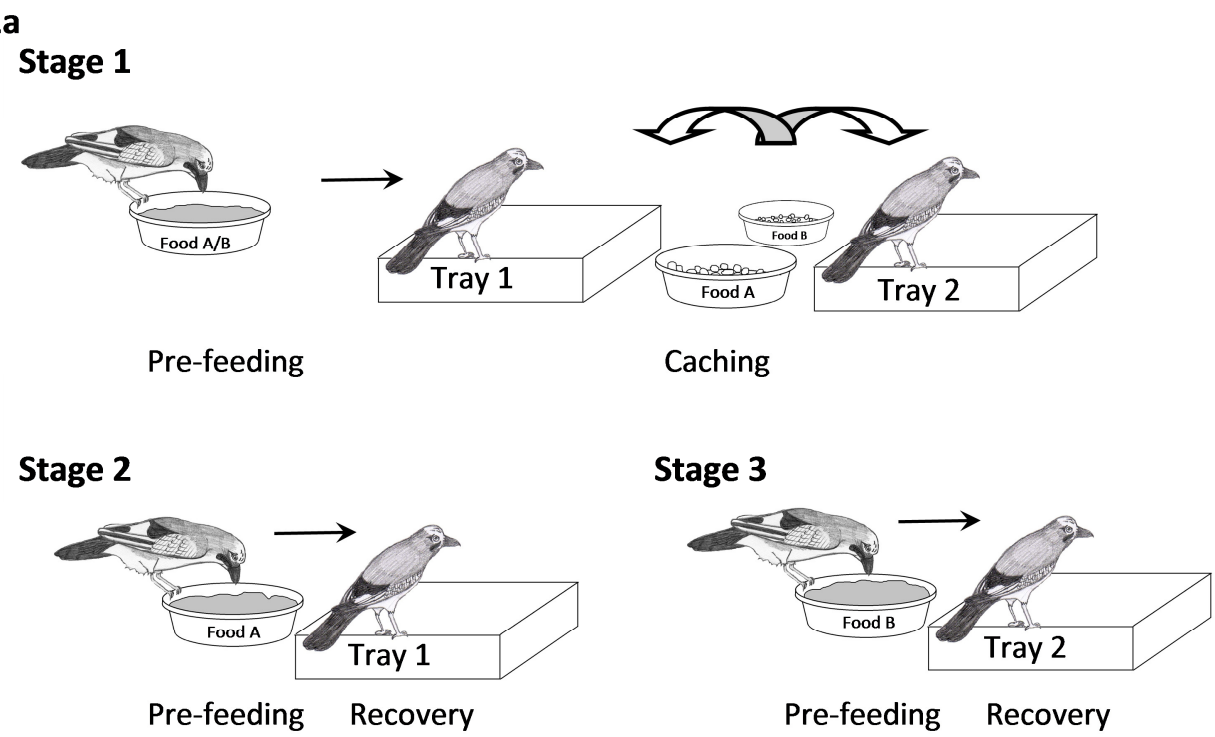
Stage 1 – Caching: Subjects were pre-fed for 15 minutes before being given access to two caching trays (Trays 1 and 2) placed equidistantly from two bowls each containing 40 food items (Foods A and B) and allowed to cache and eat for 15 minutes. Bowls and trays were then removed, birds reunited and MD returned. Trays were checked for caches out of sight of the birds.

Stage 2 – Retrieval 1: Food-deprivation for Stage 2 began 3 hours after the end of Stage 1. Subjects were pre-fed one of the test foods (powdered/liquidized) for 15 minutes before caching trays were returned. Retrieval lasted for 15 minutes, during which time Tray 2 was blocked by a transparent cover and Tray 1 was accessible. Birds were then reunited and MD returned.

Stage 3 – Retrieval 2: Stage 3 occurred the following day, at the same time of day as Stage 2. Stage 3 was the same as Stage 2, except that the birds were pre-fed the other test food, and Tray 1 was blocked while Tray 2 was accessible.

Thus one of the trays was accessible when the birds were in the same motivational state as at caching (the "Same" tray) and one was accessible when birds were in a different motivational state (the "Different" tray).

1a



1b

Trial 1 (Baseline)				Trial 2			Trial 3		
	Stage 1	Stage 2	Stage 3	Stage 1	Stage 2	Stage 3	Stage 1	Stage 2	Stage 3
	Caching	Recovery (Tray 1 available)	Recovery (Tray 2 available)	Caching	Recovery (Tray 1 available)	Recovery (Tray 2 available)	Caching	Recovery (Tray 1 available)	Recovery (Tray 2 available)
Hoy	Pre-fed maint	Pre-fed suet	Pre-fed Peanuts	Pre-fed peanuts	Pre-fed suet	Pre-fed Peanuts	Pre-fed peanuts	Pre-fed suet	Pre-fed Peanuts
Hunter	Pre-fed maint	Pre-fed peanuts	Pre-fed suet	Pre-fed peanuts	Pre-fed peanuts	Pre-fed suet	Pre-fed peanuts	Pre-fed peanuts	Pre-fed suet
Wiggins	Pre-fed maint	Pre-fed peanuts	Pre-fed raisins	Pre-fed raisins	Pre-fed peanuts	Pre-fed raisins	Pre-fed raisins	Pre-fed peanuts	Pre-fed raisins
Ainsley	Pre-fed maint	Pre-fed peanuts	Pre-fed raisins	Pre-fed peanuts	Pre-fed peanuts	Pre-fed raisins	Pre-fed peanuts	Pre-fed peanuts	Pre-fed raisins

"Same" Motivational state as at caching "Different" Motivational state than at caching

Figure 2.1. a. *Experimental Procedure. In Stage 1, birds are pre-fed, then cache foods A and B in Trays 1 and 2. In Stage 2 birds are pre-fed one food then allowed to retrieve from one of the two trays. In Stage 3 birds are pre-fed the other food and allowed to retrieve from the other tray. b. Experimental timetable, pre-feeding orders and counterbalancing. Reproduced from Cheke & Clayton 2011.*

Analysis

Data were analysed using two-tailed repeated-measures ANOVAs with number of eaten/cached items as the dependant variable. Alpha was set at 0.05.

2.2.2. Results

Specific satiety

Birds showed specific satiety by eating and caching less of the pre-fed food than the non-pre-fed food (Figure 2.2a). There was a significant effect of the pre-fed food type on the birds' subsequent food preferences (repeated-measures ANOVA: *Pre-fed:* $F_{1,3}$=12.4, p=0.039), and a trend suggesting that the birds cached more food than they ate ($F_{1,3}$ =6.593, p=0.083). The effect did not differ between eating and caching, suggesting that both behaviours responded similarly to pre-feeding (*Action x Pre-fed*: $F_{1,3}$=0.97, p=0.400).

Bischof-Köhler Test

Birds cached both foods in equal amounts in both trays on Trial 1, but then developed a differential preference between the trays, preferentially caching in each tray the food they would desire when retrieving from it (Figure 2.2b). There was no general preference for one food (repeated-measures ANOVA; *Food*: $F_{1,3}$=0.66, p=0.480) or tray (*Tray*: $F_{1,3}$=5.55, p=0.100), and birds did not reduce caching overall during the experiment (*Trial*: $F_{2,2}$=0.26, p=0.800). Crucially, there was a significant interaction between trial, tray and food (*Trial x Tray x Food*: $F_{2,2}$=24.95, p=0.039), suggesting that birds altered their caching behaviour according to what they would desire at retrieval. Note that there was no difference between what was cached in the two trays on Trial 1 (Repeated Measures ANOVA; *Tray x Food*: $F_{1,3}$=3.0, p=0.180), but there was by Trial 2 (Repeated Measures ANOVA; *Tray x Food*: $F_{1,3}$=14.24, p=0.030). On Trial 3 this interaction was lost (*Tray x Food*: $F_{1,3}$=2.258, p=0.230), but while behaviour on Trials 1 and 2 was consistent across birds, the loss of significance on

Trial 3 may be due to the behaviour of a single bird (Hunter) whose preference disappeared on Trial 3 (Figure 2.2c). When the data were analysed without her, the effect approached significance (*Tray x Food*: $F_{1, 3}$=15.429, p=0.059).

The birds' consumption of Foods A and B in Stage 1 (caching) of Trials 2 and 3 showed a specific satiety effect that approached significance and was similar to that shown in the specific satiety experiment (*Pre-fed*:$F_{1,3}$=9.64, p=0.053). Importantly, in contrast to the specific satiety experiment, the birds' caching behaviour differed from their eating behaviour (*Action x Pre-fed:* $F_{1,3}$=19.99, p=0.021). The birds were thus responding to their current specific satiety in their eating, but not in their caching behaviour.

2.2.3. Discussion

The results indicate that Eurasian jays, like scrub-jays (Correia *et al*., unpublished data), distribute their caches according to their future, rather than current, desires. This within-subjects design addresses many of the criticisms of the original scrub-jay study (Correia *et al*., 2007). Not only are these birds capable of planning for a future desire, but of planning for two temporally distinct future desires.

Three out of four birds showed a reliable pattern across Trials 2 and 3 of choosing where to cache each food type according to what they would desire when retrieving caches from those locations. One bird, Hunter, lost this preference on the third trial.

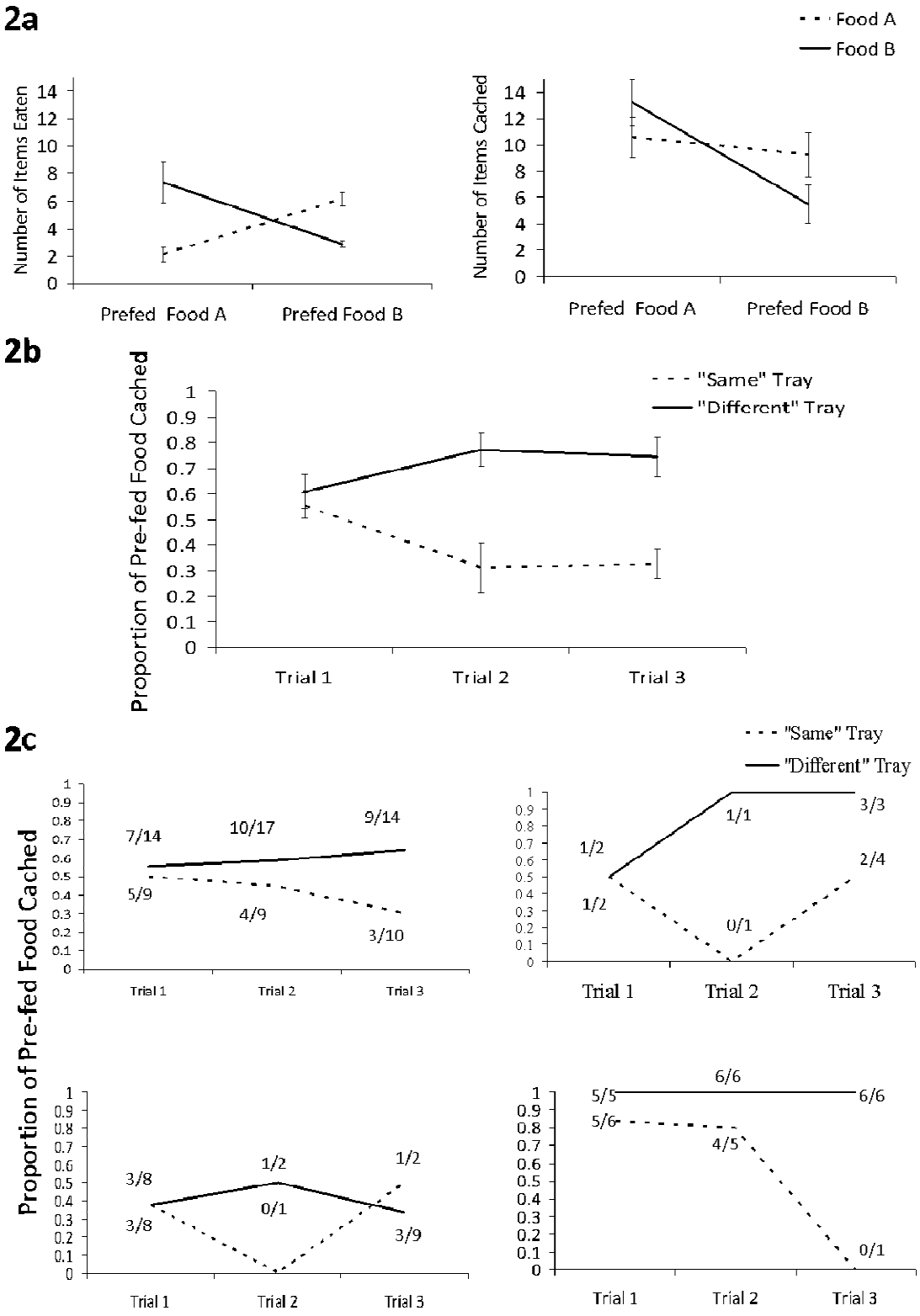


Figure 2.2. ***a)*** *Performance in Specific Satiety Experiment.* ***b)****. BK test. Proportion of total food cached that was pre-fed food in "same" and "different" tray.* ***c)*** *Proportions cached in BK test by individual birds. Reproduced from Cheke & Clayton 2011.*

It is possible that this bird used a different strategy. Instead of adapting her caching to account for food consumed immediately before cache retrieval, she may have decided *not to eat* before cache-retrieval. This would be a valid strategy, particularly if she preferred whole to powdered peanuts. Such a strategy cannot be fully investigated here as we lacked sufficiently sensitive weighing equipment to confirm if powdered food had been consumed, but visual observations (of bill-probes, food spillage) indicated that while the other birds had eaten the pre-feeding powder on trial 3, Hunter had not. This warrants investigation in future studies.

The major critique of the previous work on scrub-jays (Correia *et al*., 2007) was that the jays could have "learned not to cache items that turned out to be of little value" (Suddendorf and Corballis, 2008). However, it is not clear by which learning mechanism this could occur (Raby and Clayton, 2009), or how such a criticism could be extended to the work presented here. In the current study, while it is possible to form an association between motivational states and cache locations, this association would need to have a sufficiently powerful impact on the bird's current motivational state to overcome its current desires. We have argued elsewhere (Cheke *et al*., 2011a, Cheke and Clayton, 2012) that there is limited value in attempted to contrast "simple" associative processes with higher cognitive abilities. Associative processes can be highly complex, flexible and adaptive and they mediate much of our behaviour (e.g. Shettleworth, 2010; Epstein, 1984; Dickinson, 2011). Our aim should not be to "rule them out" but to explore the ways in which apparently high-level cognition may interact with associative processes so as to employ simple, "cost-effective" learning processes for complex tasks.

Episodic cognition may be uniquely useful in providing a means by which associative learning processes can be recruited in contexts in which they wouldn't normally be effective: to provide, through re- or pre-experience, the outcome of an action *at the time of the action itself*. Boyer (2008b) argues that a crucial part of episodic cognition is the re- or pre-experience of *emotions* and that often these emotional experiences clash with current goals. Boyer argues that this clash may represent the function of episodic cognition: to give an action's (temporally distant) consequences emotional salience in the present and act as a counter-motivation against current desires. This process would be entirely outside of cognitive control, as it would be triggered without deliberate construction. Given that caching birds have been shown to have semi-independent motivational systems for eating and caching (Clayton and Dickinson, 1999a),they would be ideally placed to exploit such a mechanism. Couching this theory in associative learning terms, episodic cognition may provide a means for temporal contiguity of action and outcome to be artificially increased to allow learning of its consequences. A similar account, the "Mnemonic Associative Theory" (MAT; de Kort *et al*., 2007, Dickinson, 2011), suggests that, rather than previous outcomes being re-experienced at the time of action, previous actions are re-experienced at the time of the outcome. This, it is argued, leads to the formation of an association between action and outcome that drives future behaviour in similar contexts. Thus "future-oriented" action is performed in response to previously formed associations rather than direct response to a retrieved memory. These two theories share many commonalities (for instance the necessity for episodic memory). Fundamentally, both accounts suggest the possibility that when an episodic memory of an event is retrieved at the time of another event, an association can be formed

between the two, and that this may be a mechanism for long-delay associative learning.

This mechanism may have allowed humans to be long-term planners despite our overarching tendency to make decisions based on our present feelings (Read and van Leeuwen, 1998). Indeed, there is evidence that use of episodic cognition can reduce impulsive behaviour (Benoit *et al*., 2011, Peters and Buchel, 2010, Boyer, 2008b). There is no controversy in the statement that human episodic cognition is extremely flexible and domain-general, and that it is this that makes it so powerful in guiding our behaviour. It allows us to simulate complex scenarios in great detail and combine features of innumerable past events into novel scenes. However, there are some puzzling elements of episodic cognition; it is often "involuntary, goal incongruent, emotion laden and uncontrollable" (Boyer, 2008b, p.6). These elements may suggest that full-scale human episodic cognition may have its roots in a less-sophisticated mechanism of automatic involuntary re-/pre-experience of *emotions or motivational states.* Such a system would not involve many of the features that some believe to be the "hallmarks" of human episodic cognition, such as self-awareness and sense of subjective time (Tulving, 2002, Suddendorf and Corballis, 2007), but would be a functional means of bringing future motivational states *into the present* and thus encouraging prospective behaviour.

Whether jays "pre-experience" the future remains an open question, but these results provide strong evidence that they can act for a future motivational state that is different from their current one, and do so flexibly (i.e. based on learned contingencies rather than "instincts"). This evidence directly challenges the Bischof-

Köhler Hypothesis. However, if Boyer is correct and episodic cognition allows future motivational states to be experienced in the present, then episodic cognition may have developed in some animals *precisely because* the Bischof-Köhler Hypothesis is correct. If an individual can act only on a current motivational state, then the only way for them to be prospective is by *changing* that motivational state, rather than disengaging from it.

If the birds in this study *were* utilising episodic cognition to solve this task (i.e. if the BK test genuinely taps episodic cognition in jays), one might expect the same birds to do well on a completely different test of episodic cognition. Thus the same cohort of birds were tested on a variant of the WWW procedure, based on test used by Clayton and colleagues (2001b) and Zinkivskay and colleagues (2009). The birds were trained that the peanuts would become inedible (turn into baking beads) after a 28 hour delay and that suet would become inedible (turn into a short length of dowel) after a 52 hour delay, but that both would be fresh after a 4 hour delay. In the final extinction test, the birds had two caching sessions and one retrieval session. In the first caching session they cached suet pellets *and* peanuts in one tray, with another tray present but closed off. At the second caching session the birds cached suet pellets and peanuts in the second tray, with the original tray present but closed off. At retrieval, the birds were allowed to access both caching trays at a time that was 52 hours after the first caching session and 28 hours after the second. This meant that only the *more recently cached* suet would still be edible. Birds that remembered what the caches where, and from how long ago, should therefore search in the location that they cached suet during the *second* caching period. The test was carried out in extinction (with no food actually in

the trays) such that visual or olfactory cues could not be used by the birds to locate their caches.

It was predicted that, since the birds had performed well on the BK experiment, they should also perform well on the WWW experiment. Furthermore, the individual differences in performance in the BK experiment should be mirrored by the individual differences in performance in the WWW experiment, reflecting the episodic cognitive ability of individual birds.

2.3. Experiment 2

2.3.1. Methods

Subjects

The subjects were six 3.5-year-old Eurasian jays (three female: Hunter, Wiggins and Webb; three male: Ainsley, Hoy and Romero). Webb and Ainsley were subsequently excluded for failing to produce a minimum number of valid trials, leaving N=4. The jays were pair-housed in 4x1x1 m cages that could be divided into two 2x1x1 m test areas by insertion of opaque dividers. Birds were maintained at 21±1 ºC on a 12:12-hour light-dark cycle. Birds received MD, and water was always available. Subjects cached in caching trays formed from seed trays consisting of 15 (three rows of five) 5.5 cm diameter x 6 cm depth plant pots ("cells") in a 20x30 cm tray. These pots were filled with wood chips, and each of the trays was a different colour to allow the use of "trial-unique" trays. Work adhered to Home Office licence PPL 80/1975.

Training

Caching: Birds were food-deprived for 1.5 hours before caching sessions. They were then given two trial-unique trays, one covered and one uncovered (available to cache in), and given the opportunity to cache peanuts and suet pellets. A single "caching session" consisted of two consecutive 15-minute intervals, such that one of the foods was available to cache for the first 15 minutes, and the other was available for the second 15 minutes. The order in which the two foods were available to cache was counterbalanced between birds and across trials.

The quantities of the two foods varied relative to the birds' tendency to eat and cache them, with the aim of having relatively even numbers of each food cached in the trays. As such, 10 peanuts (which are readily cached but not eaten in great numbers in short periods) and 20 suet pellets (which are also readily cached but eaten in larger quantities) were available. Greater numbers of suet pellets were provided because of the birds' tendency to eat (rather than cache) a higher proportion of these, which are also slightly smaller than the peanuts.

The trays were then removed, the cages were cleaned and checked for out-of-tray caches, MD returned and the birds reunited with their cage-mates. The trays were checked for caches out of sight of the birds. The quantity and location of each food type was recorded. Trials were considered valid if birds cached at least one item of each food.

Retrieval: Birds were food-deprived for 1.75 hours before retrieval sessions to ensure that they were motivated to recover the caches they had made. Retrieval sessions occurred 4 hours, 28 hours or 52 hours after caching (the order of these delays was counterbalanced between birds and across trials; see figure 2.4). During the 15-minute retrieval sessions, the birds were given the same two trays they had at caching, with the same one covered and the same one open. The caches they had made in the open tray were still present, but varied in condition according to the delay. Both foods were edible after 4 hours. After 28 hours peanuts were inedible (i.e. replaced with baking beads) but suet was still edible. After 52 hours both foods were inedible (peanuts were replaced with baking beads, suet pellets were replaced with short lengths of dowel).

After 15 minutes, the trays were removed, the cages were cleaned and checked for out-of-tray caches, MD returned and the birds reunited with their cage mates. The trays were checked for remaining caches and re-caches out of sight of the birds. The delay between caching and retrieval was varied between trials such that the birds could not, at caching, predict the delay until recovery (see Figure 2.4).

To assess the accuracy with which caches were recovered, a "retrieval quotient" (RQ) was calculated for both food types. This measure followed the procedure used by Smulders and colleagues (2000) to determine cache-retrieval accuracy relative to number of items cached. RQ was calculated using the following formula:

$$RQ = \frac{r(n) - c(n)}{n - c(n)}$$

In which n is the total number of items cached, $r(n)$ is the number of cells containing that item searched after the bird has searched n unique locations (revisits not counted)

and *c(n)* is the number of items that would be expected to be retrieved after the bird has searched n unique locations if searching at random (i.e. chance). C(n) is calculated

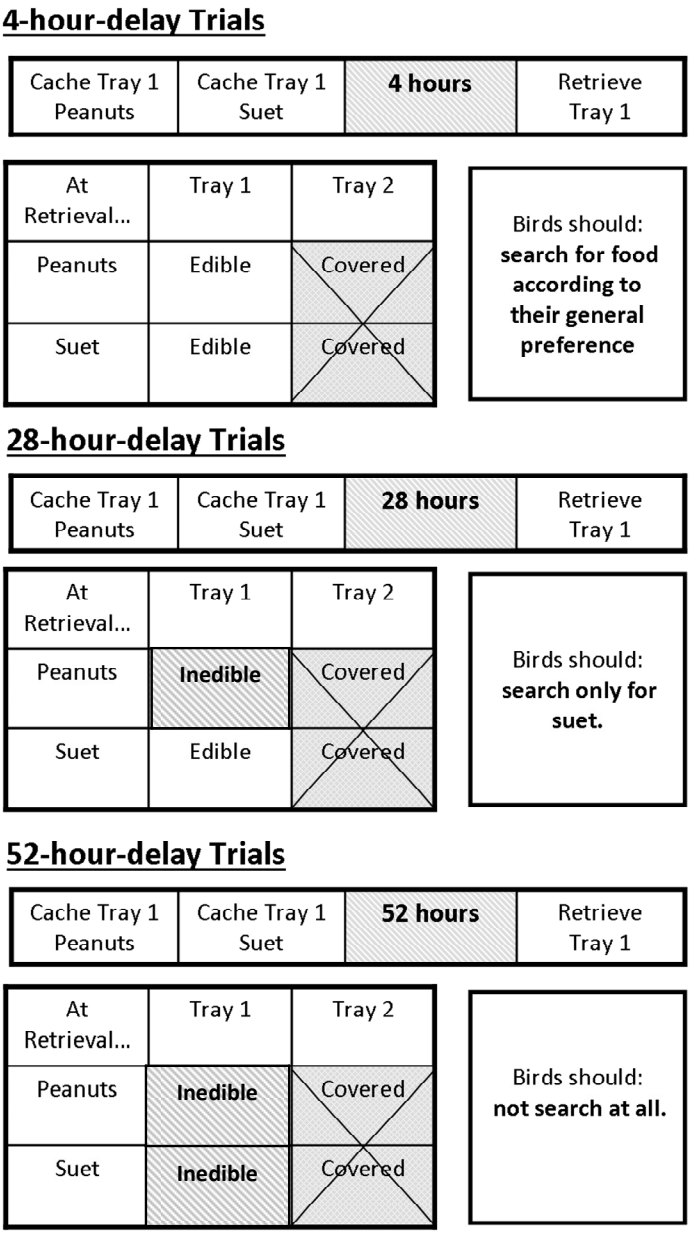


Figure 2.3. *Schematic of training*

by dividing the total number of items by the total number of storage sites and multiplying by *n*. As such, an RQ of 1 would indicate perfect performance, while an RQ of 0 would indicate chance performance.

Extinction Test

The extinction test occurred after the birds had experienced at least five valid trials of each delay. Some birds received more than five trials for some delays to make sure they did not go for a long period without experiencing one of the delays (see Figure 2.4). In particular, 4-hour-delay trials were given regularly to maintain the jays' willingness to cache (as food was always edible on these trials). Both caching and retrieval sessions were identical in form to those in the training trials.

The extinction test consisted of a three-stage procedure. The birds were given two caching sessions 24 hours apart followed by a single retrieval session that was 52 hours after the first caching session and 28 hours after the second caching session. In

Hoy	4	52	4	52	28	4	4	28	28	28	52	4	4	52	4	52	28	
Hunter	4	4	52	4	52	4	52	28	28	4	52	4	52	28	28	52	28	
Romero	28	52	28	4	4	52	28	28	4	28	52	4	4	52	4	52	28	
Wiggins	4	52	28	4	4	52	52	28	4	28	52	4	4	52	4	52	28	28

Figure 2.4. *Timeline of valid trials undertaken by each bird. The numbers represent the hours of delay between caching and retrieval each bird experienced in each trial.*

each of the caching sessions the same two trays were used, but in the first caching session Tray 1 was available and Tray 2 was covered, and on the second caching session Tray 2 was available and Tray 1 was covered. As such, the birds first had the opportunity to cache both foods in Tray 1 and then 24 hours later had the opportunity to cache both foods in Tray 2. Both trays were then available during the retrieval period, which was 52 hours after the first caching session and 28 hours after the second caching session (Figure 2.5). Thus, according to the decay rule the birds

learned in the training, the only food that was edible at retrieval was the suet cached in Tray 2.

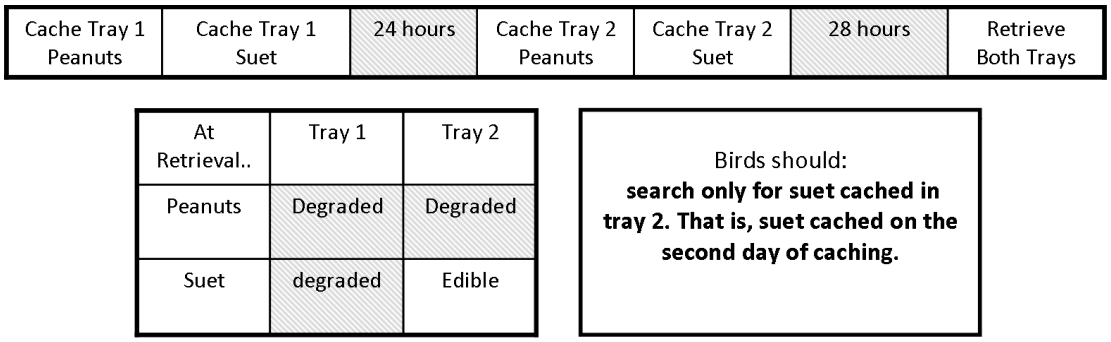


Figure 2.5. *Schematic of extinction test.*

To be considered "successful" in the extinction trials, the birds had to integrate their knowledge of the decay rates of the two foods (peanuts = 28 hours, suet = 52 hours) and their memory for how long it had been since they had cached both these two foods in the two trays (tray 1 = 52 hours, tray 2 = 28 hours), to conclude that only the suet from the tray 2 would still be edible. The birds could make different kinds of errors in integrating these rules. They could search for the wrong food (a "what" error), they could search for food cached at the wrong time (a "when" error) or they could search in cells in which they had not, in fact, cached (a "where" error). They

Table 2-1. *Details of six "types" of cell in which the birds could probe in the extinction test. These 6 "types" represent the different types of what-where-when success/error combinations available for the birds to make. The grey column represents the correct combination.*

	Tray 1 (i.e. cells that were available in first caching period)			**Tray 2 (i.e. cells that were available in the second caching period)**		
	In which cached suet	In which cached peanuts	In which did not cache	In which cached suet	In which cached peanuts	In which did not cache
What	Correct	Incorrect	Incorrect	Correct	Incorrect	Incorrect
Where	Correct	Correct	Incorrect	Correct	Correct	Incorrect
When	Incorrect	Incorrect	Incorrect	Correct	Correct	Correct
Name:	S1	P1	E1	S2	P2	E2

could also make combinations of these errors. Table 2-1 demonstrates the 6 different cell types available. These are cells in which suet is cached from the first and second caching periods (S1 and S2), cells in which peanuts were cached from the first and second caching period (P1 and P2) and cells which were available, but not cached in, during the first and second caching periods (E1 and E2). The "target" cell is thus S2.

Analysis

Data were analysed using two-tailed repeated measures ANOVAs with alpha set at 0.05.

2.3.2. Results

Training

Figure 2.6 shows the RQ for peanuts and suet across the training trials in the different delay conditions, averaged across birds. From this figure it is clear that the jays were not more accurate in locating suet than peanuts in the 28-hour condition (when peanuts would be inedible but suet edible). It is possible that differential motivation to

retrieve suet may have been revealed in search effort rather than retrieval accuracy.

Error! Reference source not found. shows the change in proportions of total probes that were made in cells containing suet and peanuts over the course of the training trials. No bird showed a pattern of increased preference for probing in the suet cells after the 28 hour delay compared with peanuts, or compared with suet in the other delay conditions.

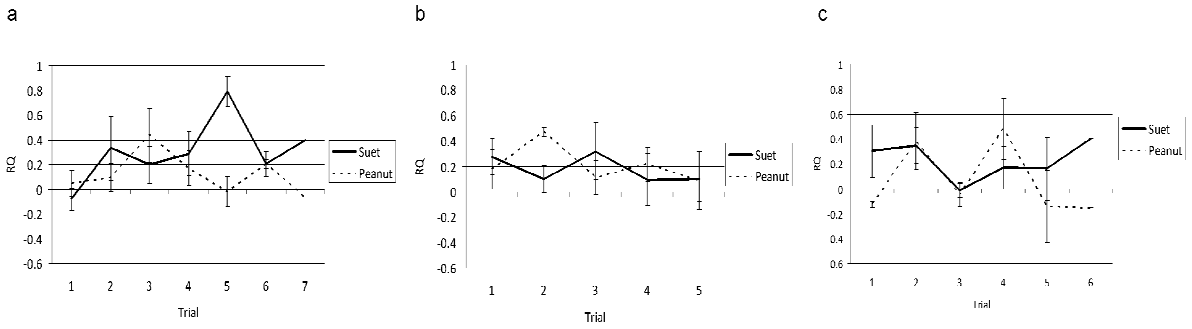


Figure 2.6. Retrieval Quotient of peanuts suet for 4-, 28- and 52-hour delay conditions, averaged across birds.

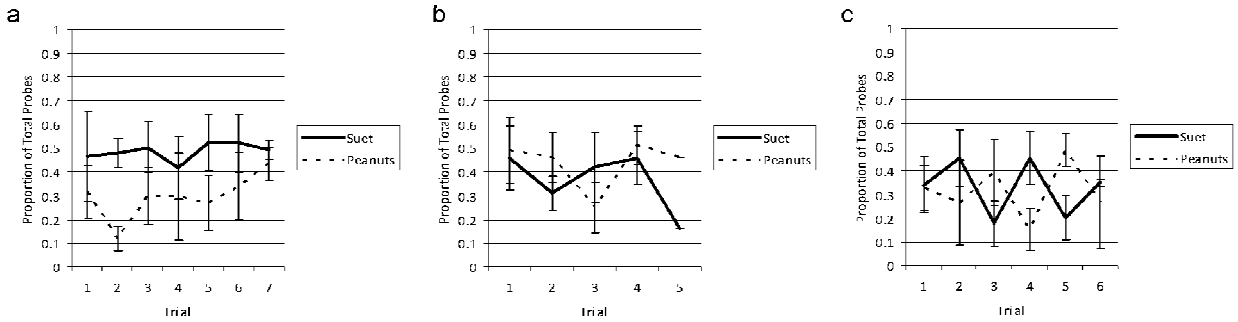


Figure 2.7. *Proportion of total probes made in cells containing suet and peanuts across the training trials, averaged across birds.*

It is, however, inappropriate to draw conclusions from training data alone. As the birds received feedback for their probing (i.e. they found the items) it is difficult to know what their behaviour indicates: the jays could have responded to finding a baking bead in place of a peanut by reducing searching in the other peanut cells

(deciding that all were now inedible). On the other hand, finding an unexpected item (e.g. a baking bead) in a cell where they were expecting food (e.g. a peanut) may cause a bird to probe more in that location to try to find the missing peanut. It is furthermore likely that a proportion of time was spent eating during trials in which actual food was available (e.g. 4-hour delay and 28-hour delay), which would reduce both probing rates and retrieval numbers.

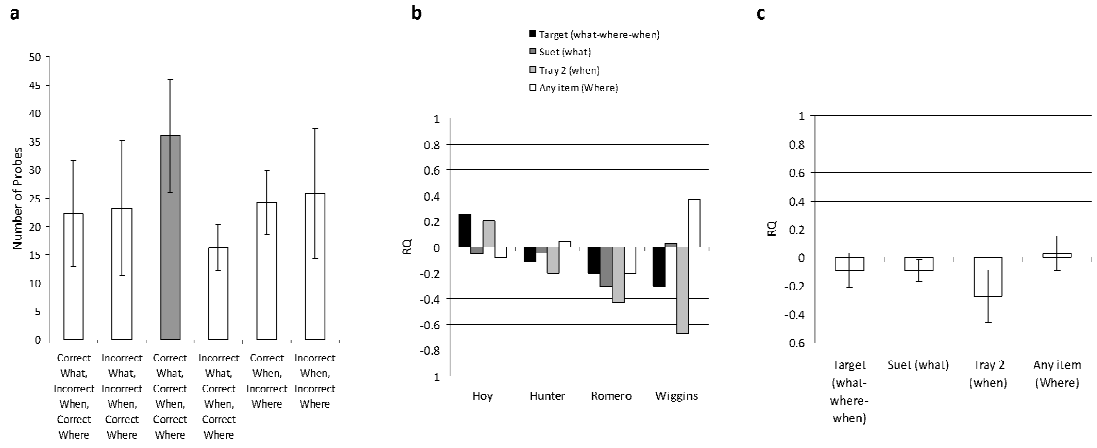


Figure 2.8. a) Number of probes in each cell type. b) RQ of each bird for target item (correct what-where-when), suet (correct what), Tray 2 (correct when) or any item (correct where). c) RQ of each type averaged across birds.

Extinction trials

There were six "types" of cell in which birds could probe: S1, S2, P1, P2, E1 and E2 – of which S2 was correct (see Table 2-1). Table 2.2 shows the number of probes made in each different cell type in the extinction trials. It can be seen from this that, numerically, the birds searched more in S2 cells than in any other type of cell (see figure 2.8a). However, this result was not statistically significant. Birds probed more in S cells than P cells (repeated measures ANOVA, *food*: $F_{1,3}$=32.767, p=0.011) but they did not probe more in Tray 2 cells than Tray 1 cells (*when:* $F_{1,3}$=0.219, p=0.671). There was, crucially, no significant difference between number of probes in S2

(correct) cells and other cached-in cells (*food* x *when*: $F_{1,3}$=2.335, p=0.224). These results suggest that while birds searched preferentially in areas in which they had cached suet, they did not take account of whether that suet would be inedible. They also did not probe more times *in each individual cell* in which they had cached suet than in each individual cell in which they had cached peanuts. However, this may be because more suet was cached than peanuts (see Table 2-2). As such, RQ was calculated for target item (correct what-where-when), suet (correct what), Tray 2 (correct when) or any item (correct where). Figure 2.8b and c show that birds were not accurate in any of these areas (with the possible exception of Hoy, who's accuracy, while very low, was higher than that of the others).

Table 2-2. *Distribution of Caches.*

	S1	**S2**	**P1**	**P2**	**E1**	**E2**
Mean Cells of	4	4.75	3.25	3.25	7.5	6.75
This Type (sd)	(2.2)	(1.2)	(1.7)	(1.0)	(3.4)	(2.5)

Relationship Between Individual Performance on Experiments 1 and 2

Three birds (Hoy, Wiggins and Hunter) took part in Experiment 1 (BK) and Experiment 2 (WWW). An overall "score" was calculated for these experiments. The BK scores were calculated using the following formula:

$$BK = \frac{(CC_1 - CI_1) + (CC_2 - CI_2)}{2}$$

In which *CI* is caching rates in those food-tray combinations that should have reduced over time (i.e. suet cached in the tray where suet would be devalued), *CC* is caching

rates in those food-tray combinations that should have increased over time (i.e. suet cached in the tray where peanuts would be devalued) and *1* and *2* indicate the first and second trials. The WWW score was the RQ for the target item. The birds were then ranked relative to one another (1=high, 3=low) on these two scores. Table 2-3 indicates that, with such a small sample at least, there is little evidence to indicate a relationship between performances on the two tasks.

Table 2-3. . *Ranking of relative performance of Hoy, Hunter and Wiggins on the BK and WWW tests.*

	Bischof-Köhler		**What-Where-When**	
	Score	Rank	Score	Rank
Hoy	5	1	0.25	1
Hunter	-1	3	-0.11	2
Wiggins	2.5	2	-0.3	3

2.3.3. Discussion

Four adult Eurasian jays took part in the What-Where-When experiment. It was found that the birds probed in cells in which they had cached the correct food more often than cells in which they had cached the incorrect food (*what*), but that there was no significant preference for probing in the cells that should contain *edible* food (*what x when interaction*). It is possible that the failure to find a positive result in this experiment may be due to the very small sample size. Figure 2.8**Error! Reference source not found.** indicates that, numerically, the target cell-type (S2) was the most probed. However, the retrieval accuracy (RQ) was very low.

There are some factors that may have limited the birds' performance. Firstly, unlike the scrub-jay studies (Clayton and Dickinson, 1998, Clayton *et al*., 2003c), the "degrading" process used in this study was artificial – the foods did not in fact degrade but turned into inedible objects. This may have been difficult for the birds to understand and they may, while searching, have dismissed the presence of these objects as irrelevant and continued to look for the food, thus considering the food "missing" rather than "degraded". It may be that jays find it more difficult to associate food going missing with a particular timeline, compared with food degrading, which is more naturally associated with a timeline. Indeed, the "pilfer" group in Clayton and Dickinson's original study showed a reduced effect, suggesting that Western scrub-jays found this rule harder to learn (Clayton and Dickinson, 1998). This may have been why the Clarks Nutcrackers (Gould *et al*., 2012) also struggled with the "when" element. Such an account requires an explanation, however, for how magpies managed to learn on a task in which egg pellets became wooden beads after a given amount of time (Zinkivskay *et al*., 2009). Furthermore, the replacement items very closely resembled the foods (see Figure 2.9). It is possible that the jays' previous experience with caching and retrieving these foods over long time periods (see Experiment 1) may mean that they found it difficult to relearn the decay rates. It is also possible that the close proximity of the cache sites may have decreased accuracy both because of the very fine level of spatial resolution required (a "correct" cell would be only 5cm from an "incorrect" cell) and because of the low cost in non-accurate searching. Indeed, Feeney and colleagues (2009) found that black-capped chickadees were able to remember what, where and when if tested in a large foraging site, but not when tested using small boards. Finally, this experiment represents a

Figure 2.9. *Top left: baking beads, top right: peanuts, bottom left: Dowel, bottom right: suet pellets*

much more challenging version of the WWW test than has previously been conducted. In the extinction test, the birds needed to simultaneously keep track of two degrade rates (peanuts = 28 hours and suet = 52 hours), two delays (52 hours since the first caching session and 28 hours since the second) and 30 potential object locations. It is possible that the sheer executive challenge imposed by this task reduced performance levels irrespective of memory ability

2.4. General Discussion

Eurasian Jays were shown to adapt their caching to provide for their future needs on the BK test of episodic foresight. There was, however, little evidence to suggest that they were able to take account of what they cached where and when on the WWW test of episodic memory. The data presented in this chapter thus provide little support for the idea that good performance in one putative episodic cognition test predicts

good performance on another. Direct relationships between individual performances on the two tests are, however, difficult to interpret with such a small sample.

Different intuitive, theoretical and philosophical stances have culminated in a plethora of different behavioural tests of episodic cognition in animals. Each of these emphasizes different factors. Of those explored here, the WWW paradigm, originating in Tulving's original definition of episodic memory (1972), emphasizes its integrated spatiotemporal nature, while the BK test emphasizes the ability to disengage from current feelings to consider noncurrent needs. These two tests, like the others explored in the Introduction, are designed to assess a single ability, but stem from different conceptions *of* that ability, and emphasize different criteria for an animal to be considered capable of demonstrating it. Intuitively, one might say that *all* of these factors are central to episodic cognition, insofar as humans understand our own experience of it. However, the capacity of these tests to inform about the potential for episodic cognition of nonhuman animals is severely limited by the fact that they have rarely been conducted in the same *species* let alone the same subjects. There is thus no way of knowing what, if any, relationship exists between the psychological capacities required to pass each test.

The experiments presented in this chapter represent a modest attempt to address this problem. Of course, species differences on a number of factors apart from episodic cognition may contribute to successful or unsuccessful performance on a number of putative episodic cognition tests. One solution to this difficulty is to assess individual differences *within* a given species. If multiple behavioural tests *do* tap the same psychological process, then one would expect a high level of correlation in

individuals' performance on these tests. This is obviously difficult to achieve in animal studies such as this one, which often contain very small sample sizes. As such, the assessment of related performance in animals on a number of episodic cognition tasks need to be accompanied by other arms of investigation. The next chapter assesses a number of these tests in young children. The prediction is that if these tasks assess the same underlying psychological process, they should show the same developmental trajectory and be correlated in children.

Chapter 3
Episodic Cognition in Children

A sample of 106 children aged between 3- and 6-years were tested on three different putative episodic memory tests (What-Where-When, Unexpected Question and Free Recall), one test thought to tap both episodic and semantic memory (Cued Recall) and one putative test of episodic foresight (Bischof-Köhler). It was predicted that performance on the memory tests would be positively correlated with one another. It was furthermore predicted that children who passed the Bischof-Köhler test would perform better on the memory tests than those who failed. Children were found to perform well on all the memory tests, but no age group passed the Bischof-Köhler test. Performance improved gradually with age. It was found that while performances on all the tests were related, few relationships survived when age was partialled out. Furthermore, performance on the Bischof-Köhler test was negatively related to age and performance on the Unexpected Question test. It is suggested that episodic cognition may, at least in development, be a multifactorial process in which different component processes develop at different rates.

3.1 Introduction

Chapter 2 explored the evidence for episodic cognition in nonhuman animals. It was concluded that the different theoretical perspectives from which the different tests of episodic memory were developed may limit the ability to interpret the literature. At present, evidence concerning episodic cognition can originate from studies testing essentially different skills (such as remembering what happened where and when, and the ability to plan for a non-current need state) that have been hypothesised to tap the same psychological process. A previously untested species (the Eurasian jay) was tested on two different behavioural tests of episodic cognition, and was found to adapt its behaviour appropriately to provide for its future needs (the Bischof-Köhler test), but showed little evidence of an ability to remember the spatiotemporal aspects of a past event (the What-Where-When test). These results suggest that the same animal model can perform well on very different tests of episodic cognition, perhaps indicating that they do indeed test the same underlying ability. Were this the case, one would expect performance on these tests to be developmentally, as well as phylogenetically, consistent. In other words, tests that assess the same psychological process should show similar developmental trajectories. This chapter explores performance on different putative tests of episodic cognition in children.

The development of memory in children has been a subject of scientific investigation for almost a century. The literature, as with that on animal memory, is plagued by contrasting and often contradictory definitions, theoretical perspectives and assumptions. In contrast, the study of prospective thought in children is a relatively recent development (Suddendorf and Moore, 2011). To date, there is little agreement on what children of different stages of development experience when they remember

or think about the future, and at what point this cognition can be referred to as "episodic".

There is evidence that some form of long-term memory exists in humans even before we have left the womb: children as young as a few days are able to recognise stimuli that were presented to them prenatally (DeCasper and Spence, 1986). From birth, the speed of encoding, longevity and, most importantly, flexibility of memory continues to develop at a considerable rate. Hayne and colleagues (2000) argued that it is this increase in flexibility of the long-term memory system, allowing the retrieval of memories outside of the context in which they were encoded, that is the crucial development in infant memory. As infants' brains develop, memories can be encoded with sufficient flexibility to be retrieved in increasingly divergent contexts. This may also explain the longevity of the memories, given that the passage of time can be considered as a change in temporal context. Eventually, these memories are of sufficient flexibility to be able to be recalled by adults, who, by definition are in an utterly different internal and external context to their infant selves.

This gradual development may explain why most adults cannot recall events that occurred before the age of about 2 years (e.g. Usher and Neisser, 1993). Between the ages of 6 and 18 months, while an action can be remembered and memory demonstrated in the same way (as shown in deferred imitation paradigms), there is significant development in the extent to which children need to be cued by contextual cues that were present in the encoding episode. It is significant to note that children of 16-20 months generalize to new objects, but do not forget the specifics of the original event (Bauer and Dow, 1994). Thus there is a gradually increasing ability to engage in

"free recall" (i.e. recall of events without cues that were present at encoding). Indeed, at 18 months, children begin to verbally report past events, though these tend to refer to the immediate past or familiar routines. At about 20-24 months children make more extended verbal references to events that occurred in the more distant past (Nelson and Ross, 1980).

This continuing increase in memory longevity and flexibility continues during the pre-school years, and is reflected in the development of prospective thought. Sachs (1983) and Nelson (1989) both report on references to the past and future made in spontaneous speech by 2-year-old children, which refer to specific events involving the self. This type of "displaced speech" increases significantly between the ages of 1.5 and 4.5 (e.g. Adamson and Bakeman, 2006). Using a questionnaire for parents, Benson (1994) found that children from 12 to 36 months show increasing levels of behavioural expectation of the future. Much of the debate in the developmental literature concerns the point at which we can consider children's memories and prospections to be "episodic".

Clayton and Russell (2009) formalised the theoretical positions in developmental psychology into two camps: the conceptualists and the minimalists. This is a useful perspective from which to consider the episodic cognition literature, which is so rich in theory that it can often be difficult to differentiate empirical findings from theoretical inferences. The following section shall briefly review these theoretical approaches.

Conceptualist theories posit that for episodic cognition to be defined as such, it must be accompanied by a conceptual grasp of what is being experienced. There is, however, no absolute agreement about the *specific* concept that needs to be grasped. Many theorists (e.g. Howe and Courage, 1993, Fivush and Nelson, 2004, Levine, 2004, Povinelli *et al*., 1996, 1999, McCormack and Hoerl, 1999, Hoerl and McCormack, 2001, Tulving, 2002) have suggested that maturation of the sense of self is fundamental in the development of episodic cognition. They argue that, while the memory traces exist before this time, the emergent concept of self allows the encoded traces to become organised around a "me" who experienced them. This consciousness of memories as events previously experienced by the self is referred to elsewhere as "autonoetic consciousness" (Tulving, 2002, Wheeler *et al*., 1997). Thus before development of the sense of self, memory exists, but it only becomes *episodic* memory when one is capable of self-knowledge (autonoesis*)*. This has been expanded (e.g. Fivush and Nelson, 2004, Levine, 2004) to suggest that the concept of the "temporally extended self" (Povinelli *et al*., 1996, 1999, 2001) is required; that is, a self-identity that extends into the personal past and personal future: "It is only the self with a specific past that is endowed with the unique capacity to re-experience the past" (Nelson, 2001, p.21). These theorists authors cite Povinelli's work (1996, 1999) showing that when children were filmed having a sticker surreptitiously placed on their head and subsequently shown the video, 75% of 4-year-olds reached up to remove the sticker, while no 2-year-olds and very few (25%) 3-year-olds did so. Furthermore, while 4-and 5-year-olds tended to refer to an image of themselves as "me", children of 3 years and younger tended to refer to the image in the third person, with a proper name. This evidence for the emergence of a concept of "self in time" at

4 years has been taken by many (e.g. Levine, 2004, Suddendorf and Busby, 2005) as evidence that episodic memory cannot exist before the age of 4 years.

Arguing along similar lines as the self-awareness theorists, Perner and colleagues (Perner, 1991, Perner, 2000, Perner, 1990, following Tulving, 1985b) argued that for episodic memory to exist, children must be capable not only of experiencing a memory trace, but of also recognising that trace as a *representation* of an event previously experienced by a *past self*. This, it is argued, requires not only the ability to understand that the past self had a mental life different from that which the child currently experiences, but also the understanding that the trace currently being experienced is not direct experience or imagination but a memory (that is, a representation) of a past experience. Perner thus theorised that episodic memory development depends on the development of representational theory of mind (that is, the ability to understand that one's own and other's minds contain representations of the world which may or may not be accurate), which is thought to develop around the age of 4 years (e.g. Flavell *et al*., 1983, Gopnik and Astington, 1988, Moore *et al*., 1990, Perner *et al*., 1987, Wimmer and Perner, 1983, Flavell *et al*., 1993).

There is some empirical support for the idea that the development of episodic cognition is related to development of self-awareness and theory of mind. Early in development, autobiographical memory skills are related to mirror self-recognition (Reese, 2002), and there is a relationship between performance on the delayed self-recognition test (Povinelli *et al*., 1996, 1999) and ability to tell a detailed personal narrative (Lemmon and Moore, 2001). Lemmon and Moore (2001) demonstrated that 4-year-olds' delayed self-recognition performance was significantly related to

memory for order and context, and that these memory scores were furthermore associated with ability on a delay-of-gratification test. These relationships were not seen in 3-year-olds, although the performance of these younger children was not convincingly different from that of 4-year-olds. However, Zelazo and colleagues (1999) and Suddendorf (1999) both showed that 3-year-olds' apparent inability to recognize delayed video images of themselves may stem from an inability to understand external representations rather than an undeveloped sense of self. Furthermore, Naito and Suzuki (2011) demonstrated that, when age and verbal ability were controlled for, delayed-self recognition was not related to source memory, delayed gratification or performance on a test assessing sequencing of future events.

In terms of the relationship between episodic memory and representational theory of mind, Perner and Ruffman (1995) showed that, in 3- to 6-year-old children, understanding the relationship between sensory experience and information acquisition was related to free recall performance (when cued recall and verbal intelligence were controlled for). Similarly, Perner and colleagues (2007) found that theory of mind performance related to memory accuracy on a "directly experienced" paradigm (thought to allow/require re-experience of an event) but not on an "indirectly experienced" paradigm (thought not to allow re-experience). However, Naito (2003) found that free recall was not related to either the "Sally-Anne"/Unseen Displacement test or Deceptive Appearance False Belief test. They found that the Deceptive Appearance test correlated with source monitoring (that is, knowing *how* you know something) only in 6-year-olds (see Templeton and Wilcox, 2000 for similar findings). This suggests that, rather than one ability preceding and underlying the other, memory and theory of mind may develop separately and come together later

in childhood (although see Karmilof-Smith (e.g. , 1994, 1997) for an argument favouring increasing modularity with age).

It is interesting to note that proponents of both self-awareness and metarepresentation theories allow the existence of *memory traces* in early childhood, but suggest that they become *episodic* only with the development of the necessary conceptual ability. Such an account raises the question: what were they before? What seems not to be discussed in this literature is that this difference between self-conscious and non-self-conscious re-experiencing *is not the same as* the difference between semantic and episodic memory. Semantic memory is knowledge that does not involve re-experiencing. If we accept Tulving's (1985b) definition of episodic memory as requiring autonoetic consciousness, what then do we call a memory that involves re-experiencing but does not occur in the presence of autonoetic consciousness?[3] Surely the distinction between a *self-conscious re-experience* and a *conscious re-experience in the absence of self-awareness* is not necessarily one of the nature of the memory (i.e. mere knowledge versus re-experience), but of the same self-consciousness that can be applied to any aspect of mental life. It is true that episodic cognition as we experience it as human adults involves an understanding of the temporally extended self,[4] but only in the same degree required by every other mental experience of the human adult . In contrast, I argue that the underlying cognitive phenomenon is capable of existing independently of an organism's conscious awareness of it, and this

[3] Note that in Tulving's work with patient NN (1985) he did not report seeing pictures in his mind that he can't identify - he reports *blankness*. Is this, then, failure of autonoetic consciousness or lack of re-experiencing?

[4] Although see Tulving's (2005, p.27) report of the episodic amnesic KC, in which he states that it "is not unreasonable to imagine that giving KC a Gallup mirror test, or even Povinelli's delayed video test in order to check his self-awareness would be equivalent to giving a Columbia university professor a test of the alphabet."

argument is not purely theoretical. Conceptualist theorists argue that, because the temporally extended self concept (Povinelli *et al*., 1996, 1999) or representational theory of mind (Perner, 1990, 1991, 2000) do not develop until the age of around 4 years, episodic cognition cannot develop until this age. It is manifestly true that if one *defines* episodic memory as incorporating self-awareness or metarepresentation, and then proves that these capacities do not develop until 4 years, then by definition episodic memory *cannot* develop until 4-years. However, one might ask if this is a useful line of argument. If a cognitive ability is defined by its most sophisticated manifestation, then by definition it cannot exist in any other form. Furthermore, self-awareness and metarepresentation are general cognitive capacities that enrich and alter *all* forms of experience. One might just as well say that drinking water cannot be defined as such if it is not accompanied by the *self-conscious awareness* of drinking water, the *understanding* that the need to drink is in response to thirst and the *flexibility* to drink when one is not thirsty (such as to avoid a hangover the next day). Were drinking water defined in this way, we would be arguing that infants and animals do not drink.

Against such conceptualist theories, Russell and colleagues have proposed a "minimalist" approach (Clayton and Russell, 2009, Russell *et al*., 2010, Russell *et al*., 2011) [5]. These authors suggested that there currently exist two forms of minimalism: "Episodic-like" minimalism, which emphasizes the binding of spatiotemporal features (and makes no assumptions or claims pertaining to phenomenology (Clayton and Dickinson, 1998), and "Kantian" minimalism, which emphasizes that memory must take the first-person perspective. Russell and colleagues (2011) cite Kant's (1992)

[5] This paper (Russell, Cheke, Clayton & Melzoff, 2011) includes research carried out by myself when I was a research assistant and Part II undergraduate student in the Experimental Psychology department.

statement that "[H]e who sees his first tree does not know what he sees" and argue that "children lacking adults' sophisticated conceptual apparatus might still exhibit some legitimate form of episodic memory and foresight" (Russell *et al*., 2011, p.2). That is, that children do not need to *understand* what is going on in their heads for it to *be* going on their heads.[6]

Thus it seems that conceptualist and minimalist theories agree that some form of memory trace exists before such time as children are able to conceptualise the nature and content of that trace, but disagree on whether the memory can be considered "episodic" before this time. If there were there a distinct change in memory and prospective processing with the development of self-awareness and metarepresentation (around the age of 4 years), then one might expect such an abrupt change to be evident in performance on tests assessing episodic cognition at around that age. Furthermore, if various methodological paradigms are differently able to tap episodic cognition, then this change should be evident in studies using some paradigms but not others. The following section will explore the extent to which there is evidence for such a developmental discontinuity.

The Developmental Trajectory of Episodic Cognition

A number of different paradigms have been employed to investigate cognition in developing children, but very few authors make explicit claims to tap *episodic*

[6] One point requires clarification and that is the difference between *imagination* and a re-experience in the absence of self-aware knowledge that what is being experienced is a memory. Imagination differs from memory in the way it is produced (purely constructive vs. retrieved) and its novelty (imagined scenes are novel (if built from familiar components); memories are familiar as a whole). One can experience familiarity in the absence of understanding of why one is feeling it (e.g. *deja vu*). I suggest that memories differ from imagination insofar as they are *familiar* or *recognised* experiences rather than necessarily being *understood* experiences.

memory. In the following section of this chapter I shall explore the findings from paradigms that do make this claim, or are potential candidates for episodic cognition research.

Free and Cued Recall

As has been discussed in detail in Chapters 1 and 2, the free recall (FR) paradigm involves the subject learning a series of items (usually words or pictures) and then being asked to recall these at a later time without the aid of any external cues. In contrast, cued recall (CR) paradigms provide subjects with external cues (such as category words) to aid their recollection. Tulving (1985) found that people were much more likely to report "remembering", rather than "knowing", the words in a free recall test than in a CR test. As such, the FR paradigm is thought to preferentially tap episodic memory, while the CR paradigm is thought to assess both episodic *and* semantic memory. If there was a developmental discontinuity in episodic, but not semantic memory, one might expect to see an abrupt change in performance in FR, but not CR, tests at around the age of 4 years.

Perner and Ruffman (1995) found a significant improvement in both FR and CR performance between the ages of 3 and 4 years. However, this development appears to be part of a gradual increase in performance in both these abilities between the ages of 3 and 8 years (Naito, 2003, Sluzenski *et al*., 2004). This suggests that the increase in performance is not specific to free recall, and is not "abrupt".

Free recall can also take the form of autobiographical report. This type of technique has been used to investigate children's episodic cognition both into the past (episodic memory) and future (episodic foresight). Suddendorf and Busby (2005) and Suddendorf (2010) asked children to report what they did yesterday and what they would do tomorrow (questions that amnesic patients are unable to answer (Klein *et al*., 2002, Tulving, 1985b)). Around 30% of 3-year-olds, 50-60% of 4-year-olds and 60-75% of 5-year-olds were able to successfully report a past event and a planned future event. The authors thus suggested that the ability to envisage future scenarios develops at the age of 4 years. However, given that 30% of 3-year-olds were successful, one might more accurately say that this ability *improves* between the ages of 3 and 4 years. Similarly, Hudson and colleagues (1995) found that specific plans for a future event (episodic) increased significantly across the ages of 3-5 years, while general descriptions of similar events (semantic) were relatively consistent across this age range. Hayne and colleagues (2011) conducted a similar experiment in which children were asked to describe events in the past and future. The authors found that 5-year-olds reported significantly more information about their personal past and future than did 3-year-olds, but interestingly that there was no age difference in the proportion of first-person references or future-oriented talk.

The difficulty with these purely verbal tests is that, in the period in question (0-7 years of age), both language in general and temporal language specifically develop dramatically (Veneziano and Sinclair, 1995, Friedman and Kemp, 1998, Friedman, 2000, Friedman, 2002, Harner, 1976, Harner, 1980, Harner, 1982, Trosborg, 1982, Weist, 1991, Busby-Grant and Suddendorf, 2011). Thus, reliance on verbal measures puts researchers at risk of assuming an absence of memory because of a lack of ability

to communicate it, and of assuming the existence of memory because of sophisticated, yet misleading, language use (e.g. Lyon and Flavell, 1994). There is also the risk of assuming gradual increases in mnemonic abilities from gradual increases in verbal abilities. As Suddendorf and Busby (2005) themselves allow, "children can hardly be expected to answer a question about yesterday if they don't know what the word means." (Suddendorf and Busby, 2005, p.7). It is because of these language difficulties that many researchers have adopted more behavioural tests for assessing episodic cognition.

Tool Choice/Transportation (the "Spoon Test")

In a similar way to autobiographical report tests, the "tool-transportation" (Mulcahy and Call, 2006) or "Spoon-Test" (Tulving, 2005) paradigm has been used to investigate episodic cognition into the past and future. This test is based on an Estonian folk story in which a child dreams of attending a party in which she is unable to eat her favourite cake because she hasn't got a spoon. The following night, fearing that she will again dream of the party, she takes a spoon to bed with her (Tulving, 2004). Thus this test assesses the ability of subjects faced with tools that are not currently useful to save them for a time or transport them to a place in which they will become useful.

Atance and colleagues (2001, 2005) examined children's ability to choose tools for hypothetical future trips. They found that 4- and 5-year-old children chose the correct items significantly more often than 3-year-olds and that 3-year-olds were more likely to be misled by incorrect but semantically related items. In addition, 4- and 5-year-

olds made more references to the future in their reasoning than younger 3-year-olds and were better at predicting their future actions. While these results indicate an improvement from 3 to 4 years of age, in both instances the performance of the 3-year-olds was still reasonable, suggesting that they were able to demonstrate prospective thought. Given this, it seems premature to conclude that these tests indicate any particular discontinuity between 3-, 4- and 5-year-olds on future-planning tests. Indeed, the only studies that seem to demonstrate a developmental discontinuity in future-oriented decision making are those employing pass/fail tests. For example, Suddendorf and Busby (2005) showed that, while 4- and 5-year-olds were able to appropriately choose an item that would be useful in the future significantly more often than a control group, 3-year-olds were not. Similarly, Suddendorf and colleagues (2011) showed that 4-year-olds were able to use the memory of a problem previously experienced – but never directly solved – to choose the appropriate tool for its future solution. However, 3-year-olds' performance did not differ from chance. With these tests it is difficult to determine whether it is the presence or absence of a cognitive ability that is being demonstrated, or merely a relatively arbitrary threshold imposed by the test demands on what would be a gradually improving performance if tested differently. Such a conclusion may be supported by the finding of Scarf and colleagues (2011) that 3-year-olds' ability to use a memory of a past problem to choose an appropriate tool for future use decreased gradually with increasing time since exposure to the original problem, while the 4-year-olds' performance remained relatively stable for up to a week. Thus it may be that, in younger children, the memory trace is successfully formed and they are able to use it, but it is more vulnerable to decay and disruption (see also Atance and Meltzoff, 2005).

One major criticism of tool-transportation/spoon-test paradigms is that they may be solved on the basis of the functional features of the tool/apparatus/situation rather than the concept of a future need. Russell and colleagues propose that the subject will be required to "take the perspective" of their future self only if they are not required to envisage themselves acting from a particular spatial position. Russell and colleagues (2010) adapted this paradigm such that children were required to predict what they would need to play a game of "blow-football" from a novel spatial perspective. Children were asked either to predict which tools they themselves would need to play in the future, or which tools another child would need. The authors argued that in the latter condition children would be more likely to use semantic functional reasoning (i.e. what does the game need) rather than imagining playing from a particular spatial position. While 3-year-olds were unable to pass either condition (though able to pass control conditions in which they were choosing for "right now") and 5-year-olds passed both conditions, 4-year-olds were successful only when choosing for another child, and not when choosing for themselves. Russell and colleagues suggest that this represents a transitional phase in which episodic cognition is present but cannot be used flexibly.

The What-Where-When Paradigm

The What-Where-When (WWW) paradigm has only recently been used to investigate episodic cognition in children. This test requires subjects to take account of the time and location of a particular event when making a decision. It has been argued (Clayton & Dickinson, 1998) that this requires an integrated spatiotemporal

representation of the event, which corresponds to Tulving's (1972) original definition of episodic memory.

Hayne and Imuta (2011) used a hide-and-seek WWW paradigm to reveal that while 3-year-olds performed significantly worse than 4-year-olds, they still remembered a good proportion of what toys they had hidden where, particularly on the non-verbal test. We (Russell *et al*., 2011) previously used a WWW paradigm to investigate episodic foresight. In this test children were presented with two locations (a hot box and a cold box) and two foods (preferred chocolate and non-preferred-but-acceptable biscuit). The children received training that the chocolate would melt if left in the hot box for a long time, but not a short time, and that the biscuit would stay fresh in both boxes. There were then two conditions. In the "Future-Self" condition, children were asked to place the chocolate in the hot box and the biscuit in the cold box. They were then asked to predict which box they would open if they came back after a short or long delay. In the "Self-Caching" condition, children were provided with only the hot box, informed that they were going to go away for a short or long time, and asked which food they would like to place in it. We hypothesised that the former condition would require children to imagine their own future actions, while the latter condition could be solved though functional/semantic reasoning. We found that 3-year-olds did not perform above chance on either test. The 4- and 5-year olds performed above chance in the self-caching condition but not the future-self condition, although there was no significant difference between performance in the two conditions. The performance of the 4-year-olds was replicated in a follow-up study in which food ripened (cake-mix became cake) rather than degraded. Based on these data, we concluded that children of 4- and 5-years struggle to overcome their current

preference for the presently preferable/edible food to predict their future actions or needs at a time when the world will be different. Thus this study suggests that children struggle with tests in which the state of the world changes between the present and the future. While we (Russell *et al*., 2011) tested this with a change in state of the external world, the Bischof-Köhler test investigates the ability of children to plan for a change in internal state.

The Bischof-Köhler Paradigm

The 'Bischof-Köhler' (BK) paradigm involves manipulation of a subject's current or future motivational state to assess whether they are able to plan for a time at which their motivational state will be manifestly different. Suddendorf and Corballis (1997, 2007) suggest that one of the central functions of episodic cognition is to allow an organism to disengage from their current needs to provide for the needs of their future selves. To date there is only one exploration of performance on the BK test in children. Atance and Meltzoff (2006) conducted a test in which children were made thirsty by eating a bowl of pretzels. After this they were asked if they would like water or pretzels tomorrow. *All* 3- 4- and 5-year-olds reliably chose water for tomorrow, despite the 4- and 5-year-olds passing comprehension tests about the word "tomorrow". This result is particularly interesting as it suggests that the BK test is passed *later* in development than other tests aiming to assess episodic foresight.

The Unexpected Questions Paradigm

Zentall (2001, 2008) argued that when an organism experiences an event *in the knowledge that what they learn will be important later*, they are more likely to encode target features of the event semantically than if they were passively experiencing it. It is suggested that only through asking 'unexpected questions' (UEQ) can the memory for the unattended *context* be tested.

There is little direct literature assessing the impact of "unexpectedness" on memory tests in developing children. There is, however, literature on the development of effortful encoding strategies, which may speak to the development of a difference between "expected" and "unexpected" questions in the extent to which children are capable of preparing for a memory test. Children have been shown not to start spontaneously rehearsing to-be-remembered items until around the age of 7 years (Flavell *et al*., 1966) and are only adept at this strategy at around 10-11 years (Cuvo, 1975, Ornstein *et al*., 1975, 1977) . Similarly, only children of 10-years and older spontaneously categorise to-be-remembered items to facilitate encoding (Moely *et al*., 1969). These data suggest that it is only relatively late in childhood that the "expectedness" of a memory test would alter the nature of the encoding process.

Source memory tests, it has been argued (Wheeler *et al*., 1997), test memory for the context of an event rather than its focal targets. Here, subjects are required to report not only what was learned, but (unexpectedly) also *how* or *when* they learned it. Studies have reliably indicated very poor performance on source memory in children under the age of 5 years (O'Neill and Gopnik, 1991, Gopnik and Graff, 1988,

Wimmer *et al*., 1988, Whitcombe and Robinson, 2000, Taylor *et al*., 1994, Drummey and Newcombe, 2002) However, models of source memory suggest that that qualitative differences in the experience of remembering information acquired from different sources are used to differentiate between these memories and determine their source (Johnson *et al*., 1993, Lindsay and Johnson, 1987). Thus this monitoring requires not only the re-experience of the event(s), but also the ability to distinguish between multiple representations. It is therefore difficult to determine whether the difficulty young children experience lies in the ability to mentally re-experience the learning event, or to use elements of it (such as, for example, its vividness) as discriminative stimuli in decision making. Indeed, Sluzenski and colleagues (2004) argue that it is possible that young children (in the case of their own study, 4-year-olds) may struggle with source/reality monitoring because "their memories are often relatively impoverished and that, in such a circumstance, it is hard to distinguish between real and imagined events using the richness of memories as a criterion for the decision" (p. 16). An alternative possibility may be that "4-year-olds do not consistently appreciate that the richness of memories can be used to judge reality status" (p. 16).

Both strategic remembering and source monitoring are known to rely on the frontal lobes ("Effortful encoding strategies"*:* (Moscovitch, 1992, Gershberg and Shimamura, 1995, Hirst and Volpe, 1988), "Source monitoring": (Janowsky *et al*., 1989, Squire and Knowlton, 1995, Knowlton and Squire, 1995, Schacter *et al*., 1984, Shimamura and Squire, 1987, Shimamura and Squire, 1991, Senkfor and Van Petten, 1998). It is thus possible that the same gradual development of frontal function over the first decade of life (e.g. Huttenlocher, 1979, Bourgeois, 2001) is responsible for

the reduced ability to use encoding strategies *and* for poor source monitoring in young children (Schacter *et al*., 1995, Leichtman *et al*., 2000, Ruffman *et al*., 2001). These data produce inconsistent predictions for young children's performance on an unexpected memory test. On the one hand, children may not be able to employ the strategies through which one might expect episodic traces to be recoded into semantic knowledge until around the age of 7 years. On the other hand, they also seem unable to answer unexpected questions about the source of their knowledge until around the same age, while being perfectly capable of acquiring and retaining that knowledge. One possible explanation is that both the use of deliberate encoding strategies and the capacity to understand the source of one's own knowledge require a level of reflexive self-awareness and/or theory of mind. That is, they must understand that their own knowledge state is a result both of their *external experiences* and *internal strategies*. This understanding may be cognitively demanding above and beyond the memory tests themselves.

In summary, there is mixed evidence for a developmental discontinuity in performance on episodic cognition tests. While most studies show a distinct improvement between the ages of 3 and 5 years, few show total failure in the under-4s or asymptotic performance in the over 5s. The widespread use of binary pass/fail paradigms means that there often appears to be a discrepancy between 3- and 4-year-olds' performances, when this may in fact result from a gradual improvement.

What is required is a thorough investigation of the relationship between different putative tests of episodic cognition across a wider age range. This would allow us to reconcile the existing evidence that uses different paradigms, as well as assess the

extent to which development can be considered abrupt or gradual. There is one current example of such a study. Atance and Jackson (2009) conducted a correlational study to relate the performance on several different tests of prospection on the same sample of children. Children between 3 and 5 years were tested on Delay of Gratification, Planning (Tower of Hanoi & Truck-loading tests), Prospective Memory and Episodic Foresight. The delay of gratification task used the Mischel procedure (Mischel *et al*., 1989) in which children must resist an immediate reward to receive two rewards after a delay. The planning tests included an adapted version of the Tower of Hanoi test in which children must move a series of discs from peg to peg to create a structure that matches a target arrangement (e.g. Carlson *et al*., 2004) and a truck loading test (e.g. Carlson *et al*., 2004) in which children must plan the shortest possible route through a series of destinations while taking into account a growing number of rules). The prospective memory assessment used a test developed by Kvavilashvili and colleagues (2001), in which children must sort through a pack of cards while remembering to put the card in a basket if it contains a picture of an animal, and a test developed by Guajardo and Best (2000), in which children were told to remind the experimenter about something after they'd finished playing a game. Finally, the episodic foresight assessment included a test identical to that used by Atance and Meltzoff (2005), in which appropriate items must be chosen that will be useful for a hypothetical future trip, and a test similar to that used by Busby and Suddendorf (2005) to assess children's ability to report what is likely to happen tomorrow. Atance and Jackson (2009) found significant improvement with age on all the tests, and performance on all tests were correlated with each other except for Busby and Suddendorf's test, which correlated only with Atance and Meltzoff's test and one prospective memory test. This relationship between the two episodic

foresight tests was one of the only correlations to remain once age and receptive vocabulary were partialled out. The authors suggest that this is "notable, given that both were independently designed to assess children's [episodic foresight]." (p.9). However, while showing a correlation between two tests suggests that they may assess the same ability, it cannot indicate what that ability is. Thus while Atance and Jackson (2009) have provided evidence that these two tests assess similar processes – although the correlation coefficient was only 0.38 – they do not provide evidence that the process in question is episodic foresight. I suggest therefore that the authors are not justified in their statement that "these two tests appear to be a good means of assessing [episodic foresight] developmentally" (p.9). It should, for example, be noted that while many of the other tests were behavioural, both episodic foresight tests were distinctly verbal, and that while the authors controlled for *receptive* vocabulary, they did not control for *productive* vocabulary, which is heavily required for both episodic foresight tests. The authors conclude that "in addition to some form of future orientation, these tests differentially require abilities such as theory of mind, working memory, and inhibitory control". Despite caveats of interpretation, this methodology of assessing intercorrelation between multiple tests putatively testing the same or overlapping psychological processes has the potential of offering new and vital insights into the mechanism and development of those processes.

In the experiment presented in this chapter, three different putative tests of episodic memory (WWW, UEQ and FR), one putative test of both episodic and semantic memory (CR) and one putative test of episodic foresight (BK) are presented to the same group of children aged 3 to 6 years. Autobiographical report and spoon tests were not conducted. The former because it is heavily reliant on both receptive and

productive verbal ability, the latter because it is heavily confounded with both functional reasoning (Russell *et al*., 2010) and instrumental learning (Cheke and Clayton, 2010, Suddendorf *et al*., 2009) and thus requires control groups to be interpretable. All the memory tests are designed to produce continuous data (i.e. they are not binary pass/fail tests). This enables us to investigate three central questions:

1. Is there a developmental discontinuity in episodic cognition performance?
2. Does children's' performance on the different tests of episodic cognition correlate?
3. Do different tests of episodic cognition produce different developmental trajectories?

3.2. Methods

Subjects

106 children aged between 3 and 6 years (3-year-olds, N=27; 4-year-olds, N=18; 5-year-olds, N=27; 6-year-olds, N=34) were recruited form schools and nurseries in the Cambridge area. The sample consisted of 49 girls and 57 boys (3-year-olds: 15 girls, 12 boys; 4-year-olds: 6 girls, 12 boys; 5-year-olds: 15 girls, 12 boys; 6-year-olds: 13 boys, 21 girls).

The study was approved by the Cambridge University Psychological Research Ethics Committee. Informed written consent was received from parents before any child took part.

Tests

Free Recall

Children were shown eight images and were asked to name each one in turn. They were then told to look at the images and try to remember what was in them. After a delay of around 5 minutes, children were asked to tell the experimenter what pictures had been on the cards. This methodology followed that of Perner & Ruffman (1995).

Cued Recall

Children were shown eight images, half of which were of animals and half of which were of toys, and were asked to name each one in turn (the category of each item was highlighted by the experimenter prompting the children for the name with "what *animal*/*toy* is this?"). They were then told to look at the images and try to remember what was in them. After a delay of around 5 minutes, children were asked to tell the experimenter what pictures of *animals* had been on the cards and what pictures of *toys* had been on the cards. This methodology followed that of Perner & Ruffman (1995).

What-Where-When

Fewer children took part in this experiment because children were split between this and another experiment (not reported). As such, 68 children took part in this experiment.

Children were told to pretend that they were a pirate with some treasure to bury. They were given three pieces of "gold treasure" (plastic £1 coins) and three pieces of "silver treasure" (plastic 20p coins). Children were shown two location-trays in which they could hide the treasure: the "forest" and the "town" (see Figure 3.1). These consisted of two upside-down 15-pot (3 x 5) seed trays, one painted green and one painted red, each of which contained five distinct land-marks. They were first asked to choose one tray to bury treasure in, and the other was then removed. They were then free to hide all six coins in any order under pots in their chosen location. Every time a coin was picked up the experimenter highlighted its identity by saying "Where are you going to hide that *gold/silver* treasure?". After a delay (approx 5-10 minutes), children were told that they were going to bury some more treasure and were given three more "gold treasure" coins and three more "silver treasure" coins, as well as the location-tray they had not previously used. Again they were free to hide them in any order and each coin identity was highlighted by the experimenter as it was hidden. After another delay (approx 5-10 minutes), Children were shown a toy crow ("Mr Crow") and informed that he was a "cunning thief" and had been watching them bury the treasure. The children were told that Mr Crow had stolen all of the treasure from one hiding-period (counter-balanced between subjects) and all of one type of treasure (counter-balanced between subjects) from the other hiding-period. Children were then asked to say which treasure was left. If they were unable to, they were told which treasure was left. All elements of the treasure that was left (particularly the "when" element) was described to them in a number of ways (e.g. "before"/"earlier"/"first"/ "longer ago") to increase their chances of understanding what was being asked. Children were then asked to identify the pots in which there should be treasure remaining by pointing to them. After they had done so, the trays were lifted and it was

revealed that Mr Crow had not in fact stolen any coins and that they could swap the coins for a sticker.

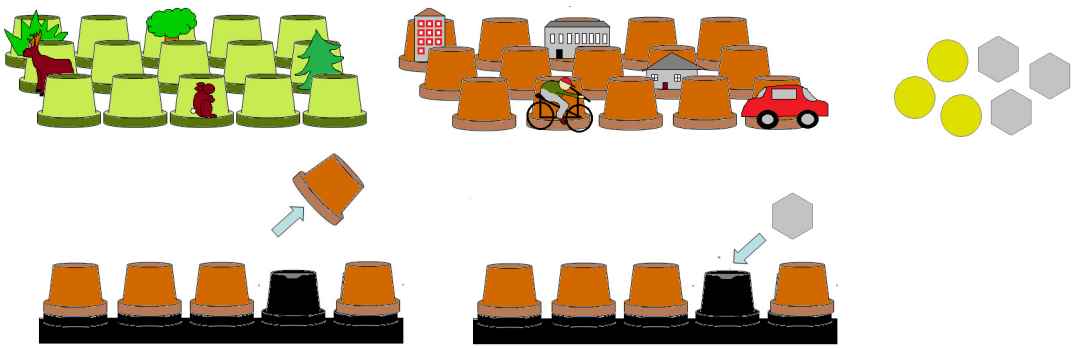


Figure 3.1. *Illustration of the What-Where-When Test. The two locations were the "forest" (left) and the "town" (right), and the items were "Gold" and "Silver". Items could be hidden under the pots as illustrated at the bottom of the figure.*

Unexpected Question (UEQ)

One week after the end of the experiment, the children were unexpectedly asked about elements of the "games" that had been played. Both open ended (e.g. "What animal stole the treasure in the pirate game?") and cued-choice (e.g. when we looked at picture of animals and toys, were they on cards or on the computer?) questions were asked. Some questions referred to games they had played that day, others referred to games they had played the previous week (see Table 3-1).

Table 3-1. *Unexpected Questions*[7]

Question	Answer(s)	Score
What Animal Stole the Treasure in the Pirate Game?	Crow/ Mr Crow (accepted: any bird)	1
Which video had a skeleton in it?	The Jungle Video (can answer by pointing)	1
When we looked at pictures of animals and toys, were they on cards or on the computer?	Cards	1
What was the prize in the shapes game?	Stickers	1
What were the two places we hid treasure	Town (accepted: city, village, street, road)	1
	Forest (accepted: jungle, wood, countryside)	1
Which video had a teddy bear in it?	Spotty Video (can answer by pointing)	1
Which drinks did I show you on a card?	Water	1
	Orange Juice (accepted: Juice, squash)	1
What kind of treasure did you hide?	Gold and Silver (accepted: money, gold or silver, £1 and 20p, coins)	1

Bischof-Köhler (BK)

There were two versions of this test that were conducted simultaneously. BKA was inspired by Klossek and colleagues' (2011) study in which "boredom" satiation was induced by multiple exposures to a short video clip. BKB was a replication of Atance and Meltzof's (2006) study in which "thirst" satiation was induced by ingestion of large numbers of salty biscuits. Children were shown two short (30s) video clips, one of which was pre-selected as "interesting" and one as "dull", and were asked which they preferred. Once they had chosen they were told they could "have something" while they were watching and were given the choice between Ritz biscuits or a glass of water. Most children were expected to choose the "interesting" video and the Ritz

[7] The items that appear in these questions were elements of other tasks. The teddy bear and skeleton videos as well as pictures of drink appeared in the BK experiment, the treasure and treasure-hiding areas appeared in the WWW experiment, the shapes game was an unreported experiment.

biscuits. These children were given a bowl of Ritz biscuits and shown a video that contained 16 repetitions of the interesting video interspersed with other similar clips. To keep them focussed, children were asked to watch out for particular items or events. If at any time they stopped eating the Ritz biscuits they were prompted that they could have as many as they wanted. After finishing the video the children were told that next week[8] the experimenter would come and play with them again, and that at that time they could watch a video and "have something" while they watched it. They were shown stills from both video clips and asked to indicate which video they would like to watch next week, and then shown pictures of Ritz biscuits and water and asked to choose which they would like to have while watching the video next week. After these choices had been made, children were asked the same question for *right now*. This was to ensure the efficacy of the satiation procedure: If children did not choose the dull video and the water for *right now* their data were excluded from the analysis. The following week, the experimenter returned and asked the children once again to choose a video and food for next week. This was to ensure that the satiating effects of the Ritz biscuits and video had not been so strong as to still be in effect the following week.

Procedure

The study had a nested design in which elements of each test formed the retention intervals for the other tests (see Figure 3.2). Children first undertook the encoding phase of the free/cued recall picture test (counterbalanced between subjects). They then played the first session of the pirate WWW game before the free/cued recall

[8] The term "next week" was supplemented with other descriptions such as "after 7 days" and "between now and then you will go to bed and get up many times" to try to ensure understanding of a significant time gap.

phase. Children then undertook the encoding phase of the recall (free/cued) test they had not previously done, followed by the second pirate WWW session, then the recall phase of the picture test. This was followed by the future-planning test and finally the recall phase of the pirate WWW game. The following week (7 days later) children returned and played some games (experiments not reported here) involving shapes and stickers. They then completed the second phase of the future planning test, and were finally asked the unexpected questions.

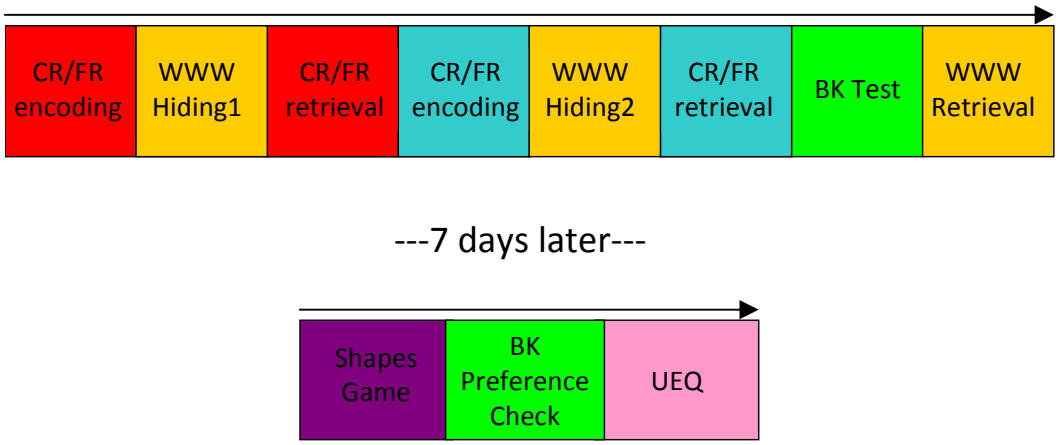


Figure 3.2. *Schematic of experiment order.*

Analysis

Where assumptions of normality were met, data were analysed using t-tests, one-way ANOVAs, Pearson's correlations and partial correlations. Where assumptions were violated, nonparametric equivalents (Mann-Witney U test, Wilcoxon signed-rank test, Kruskal-Wallis test, Friedman's ANOVA, Kendell's Tau correlation) were used. The developmental trajectory of different tests was assessed using a general estimating equations (GEE) analysis. Alpha was set at 0.05. Where multiple comparisons were conducted, a Šidák correction was used.

3.3. Results

Boys and girls did not differ in their performance on any test (see Table 3-2).

Table 3-2. Difference in performance between boys and girls in the memory tests

	FR	CR	WWW	UEQ
3-year-olds	t(25)=0.13, p(corr)=0.999	t(25)=1.05, p=(corr)0.738	t(25)=0.93, p(corr)=0.831	t(16)=2.41, p(corr)=0.185
4-Year-olds	t(16)=-0.004, p(corr)=0.999	t(16)=-1.340, p(corr)=0.998	t(16)= 0.732, p(corr)=0.999	t(16)= 0.343, p(corr)=0.999
5-Year-olds	t(25)= 0.066, p(corr)=0.999	t(25)=-0.00, p(corr)=0.999	t(25)=0.891, p(corr)=0.853	t(25)=-1.482, p(corr)=0.492
6-Year-olds	t(31)=-0.427, p(corr)=0.988	t(31)= 0.222, p(corr)=0.633	t(31)=0.422, p(corr)=0.988	t(31)=-1.454, p(corr)=0.497

Free Recall

Figure 3.3 indicates that performance on the FR test was normally distributed, with most children remembering 50% of the pictures.

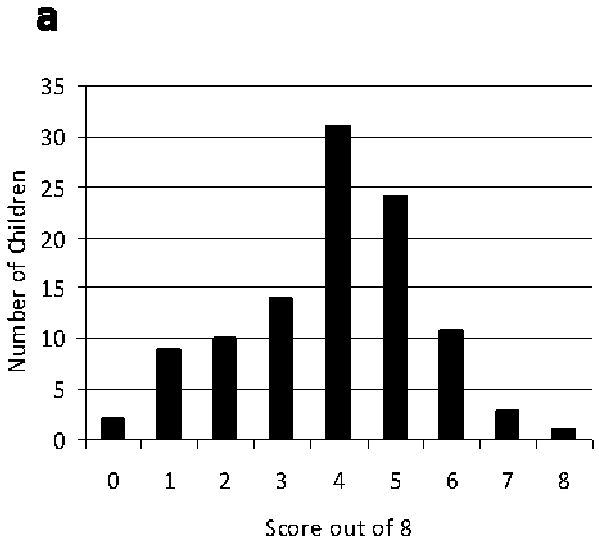


Figure 3.3**.** *Number of children who recalled 0-8* out of 8 *words in the free recall test*

Figure 3.5 shows a gradual increase in performance on the free recall test with age. Children of different age groups differed in their performance on the test (one-way ANOVA: $F_{3,101}=14.721$, $p<0.001$) with children of each age performing worse than children two years their senior, (simple effects test: 3/4, p[corr]=0.243; 3/5, p[corr]<0.001; 3/6, p[corr]<0.001; 4/5, p[corr]=0.644; 4/6, p[corr]=0.004; 5/6, p[corr]=0.227).

Cued Recall

Figure 3.4 shows that performance on the CR test was normally distributed, with most children remembering 4 to 6 out of 8 items.

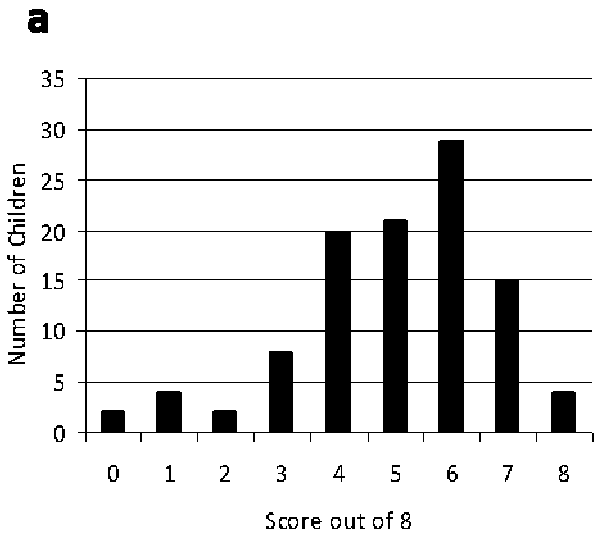


Figure 3.4. *Number of children who recalled 0-8/8 words in the cued recall test*

Figure 3.5 shows a sharp transition from the performance of 3-year-old children to that of 4-, 5-, and 6-year-old children in the CR test. There was a significant difference between age groups (one-way ANOVA: $F_{3,101}=26.082$, $p<0.001$). Post hoc

investigations revealed that 3-year-olds differed significantly from all other age groups, while none of the other age groups differed significantly from one another; (3/4, p[corr]<0.001; 3/5, p[corr]<0.001; 3/6, p[corr]<0.001; 4/5, p[corr]=1.0; 4/6, p[corr]=0.059, 5/6, p[corr]=0.086)

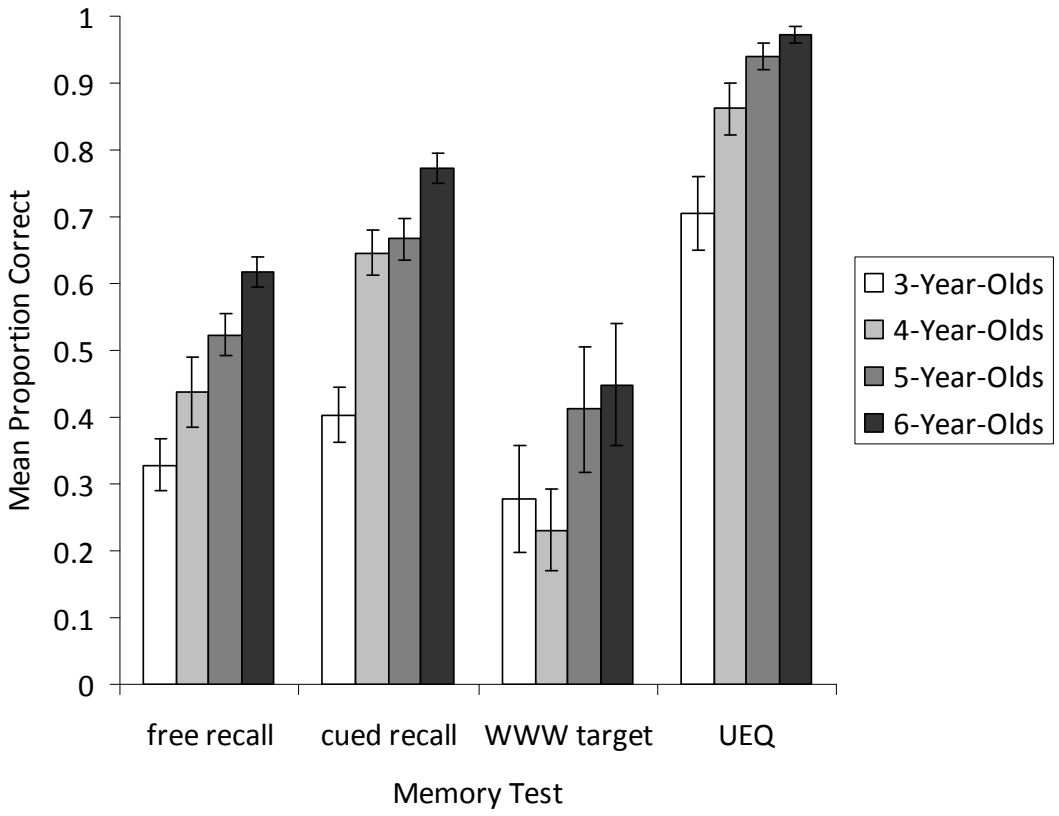


Figure 3.5. *Mean proportion of items correctly remembered by children of different age groups on different tests. Comparison of developmental progression from 3-6-years in different episodic memory tests. Error bars represent standard error.*

Comparisons of Free and Cued Recall

Overall, children were significantly better at CR than at FR (paired samples t-test: t[104]=7.182, p<0.001). A difference was present for every age group (4 years: t [17]=4.208, p=0.001; 5-years: t[26]=3.882, p=0.001; 6-years: t[32]=4.570, p<0.001)

although it was only a trend for the 3-year-olds (t[26]=1.925, p=0.065; see Figure 3.6).

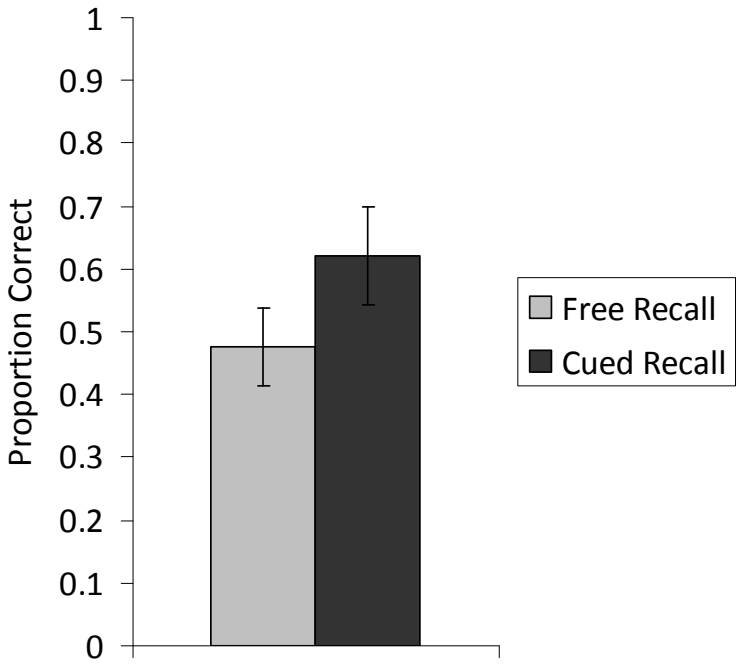


Figure 3.6. *Mean performance on FR and CR. Error bars represent standard error.*

What-Where-When

Overall, the proportion of children who identified correct coins was higher than would have been if children were choosing at random (chi square test: chose at least one coin correctly: $\chi^2[1]=96.2$, $p>0.001$; chose at least two coins correctly $\chi^2[1]=465.3$, $p>0.001$; chose all three coins correctly: $\chi^2[1]=644.7$, $p<0.001$). All age-groups identified at least one coin more often than would be expected by chance (3-year-olds: $\chi^2[1]=4.8613$, $p>0.05$; 4-year-olds: $\chi^2[1]=12.913$, $p<0.01$; 5-year-olds: $\chi^2[1]=29.393$, $p<0.01$; 6-year-olds: $\chi^2[1]=49.009$, $p<0.01$). All age-groups identified at least 2 of the 3 coins more often than would be expected by chance (3-year-olds: $\chi^2[1]=5.628$, $p>0.05$; 4-year-olds: $\chi^2[1]=10.60285$, $p<0.01$; 5-year-olds: $\chi^2[1]=125.113$, $p<0.01$; 6-

year-olds: $\chi^2[1]=411.4243$, $p<0.01$). None of the 3- or 4- year-olds identified all three coins correctly, while the 5- and 6-year-olds performed about chance (3-year-olds: $\chi^2[1]=639.114$, $p<0.01$; 6-year-olds: $\chi^2[1]=433.3255$, $p<0.01$) (see Figure 3.7).

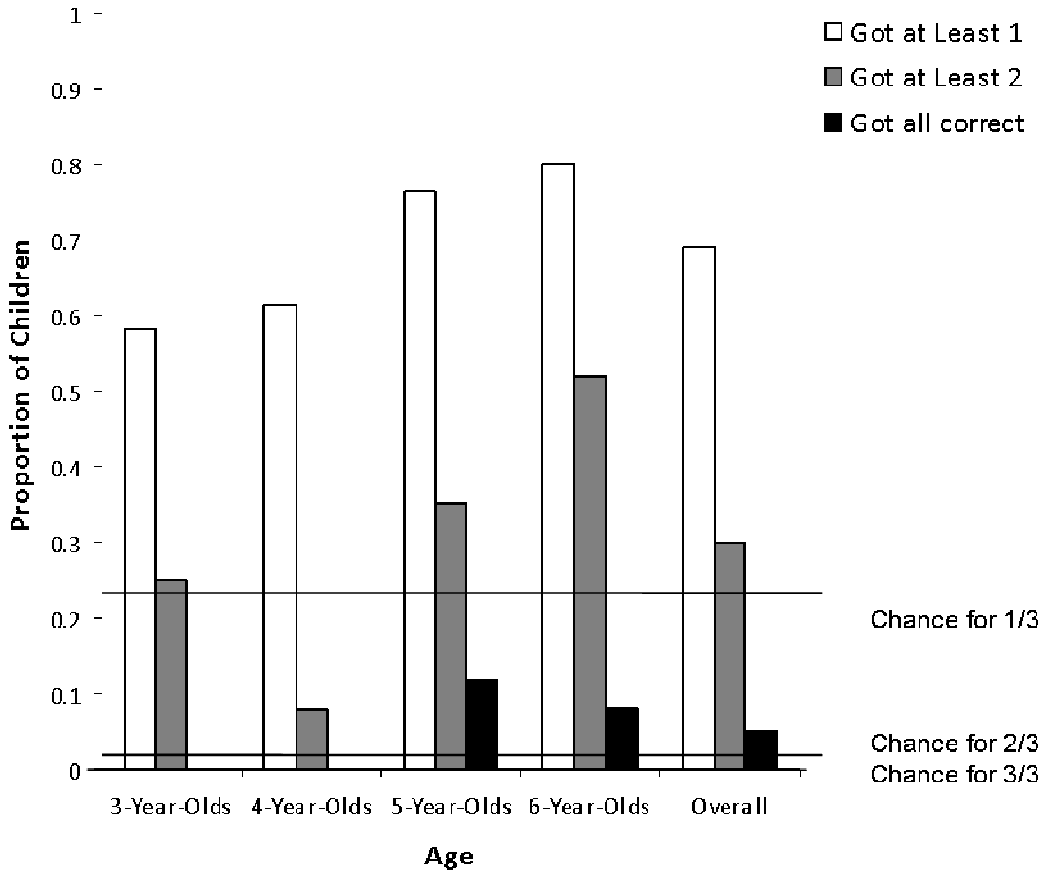


Figure 3.7. *Proportion of children of each age group that identified at least 1, at least,2 or all 3 coins in the What-Where-When test. Chance was calculated by the probability of pointing to a cup containing the correct coins given the number of available pots. Chance was therefore set at 0.22 for at least 1/3 coins, 0.0157 for at least 2/3 coins and 0.000366 for all 3 coins.*

Figure 3.5 shows what appears to be a developmental jump between the performance of 3/4-year-olds and the performance of 5/6-year-olds on the WWW test. There is a trend for an effect of age groups on performance (one-way ANOVA: $F_{4,67}=2.454$, $p=0.071$) but no age group differed significantly from any other (3/4: p[corr]>0.999;

3/5: p[corr]>0.999; 3/6: p[corr]=0.407; 4/5: p[corr]=0.567; 4/6: p[corr]=0.121; 5/6: p[corr]>0.999). Because fewer children took part in this test, this result may be due to reduced sample size. When 3/4-year-olds and 5/6-year-olds were grouped into two age groups (<5 and >5), the older children performed better than the younger children (t[67]=2.644, p=0.01).

Unexpected Question

Performance on the UEQ test was not normally distributed (Skewness: -1.938, SE=0.271; Kurtosis: 4.176, SE=0.535; see Figure 3.8). The data were transformed with an arcsin transformation. The transformed data were normally distributed (Skewness: -0.764, SE=0.271; Kurtosis: -0.507, SE=0.535). As such, parametric analysis could be used.

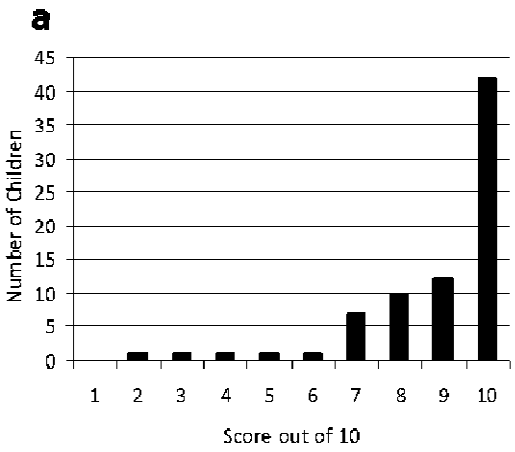


Figure 3.8. a) *Number of children who recalled 0-10/10 items in the Unexpected Question test*

Figure 3.5 shows a gradual improvement in performance in UEQ in increasing age groups (F_3=14.569, p<0.001). As with the FR test, post hoc investigations revealed that while children did not differ in performance with those only a single year older, they differed significantly in performance from children two years their senior, no matter what their age (simple effects test: 3/4:p[corr]=0.069; 3/5: p[corr]<0.001; 3/6: p[corr]<0.001; 4/5: p[corr]=0.399; 4/6: p[corr]=0.028; 5/6: p[corr]=0.809).

Relationship between Memory Tests

Performance on all memory tests improved significantly with age in months (FR: r=0.539, p<0.001; CR: r=0.632, p<0.001; WWW: r=0.268, p=0.029; UEQ: r=0.617, p<0.001; See Table 3-3). Performance on many of the memory tests were related (see Table 3-3). However, many of these relationships were dependant on age, and thus the correlations were lost when age was partialled out (see Table 3-4).

Table 3-3. *Correlations between memory tests, and between memory tests and age. Numbers represent Pearsons' R.*

	Free Recall	**Cued Recall**	**Unexpected Question**	**What-Where-When**
Age	0.539***	0.632***	0.617***	0.268*
Free Recall	-	0.544***	0.396***	0.172
Cued Recall	-	-	0.422***	0.323**
Unexpected Question	-	-	-	0.085

*p<0.05
**p<0.01
***p<0.001

Specifically, children who performed well on the CR test also showed high scores in the FR test, independent of age. Similarly, children who perfomed well on the WWW

test showed high scores in the CR test regardless of age. Children who performed well on the UEQ test, also performed well on the FR and CR tests, but this relationship was dependent on age. No other relationships between the memory tests were found.

Table 3-4. *Correlations between memory tests with age partialled out. Numbers represent Pearsons' R.*

	Cued Recall	**Unexpected Question**	**What-Where-When**
Free Recall	0.312***	0.105	0.048
Cued Recall	-	0.066	0.205†
Unexpected Question	-	-	0.001

†p<0.1
*p<0.05
**p<0.01
***p<0.001

Table 3-4 indicates that very few memory tests were correlated with each other independently of age. However, given the strong relationship of each test with age, it may be that an analysis partialling out age masks underlying relationships between performance on tests that have exactly matching developmental trajectories. For this reason, the data from all of the memory tests were entered in a GEE model assessing differences in developmental trajectory (i.e. change in performance over age in months) between the tests. The GEE had a linear response and an identity link function. Score was the dependent variable and the independent factors were age (years) and test. A generalized score chi-square was used as well as a model based estimator. The results suggested that performance on the different memory tests improved at different rates. There was a trend suggesting that the tests differed in the developmental trajectory (GEE: Test of model fit [Quasi-likelihood under Independence Model Criterion [QICC] =44.444 χ^2 = 16.149, p=0.064; see Figure 3.9).

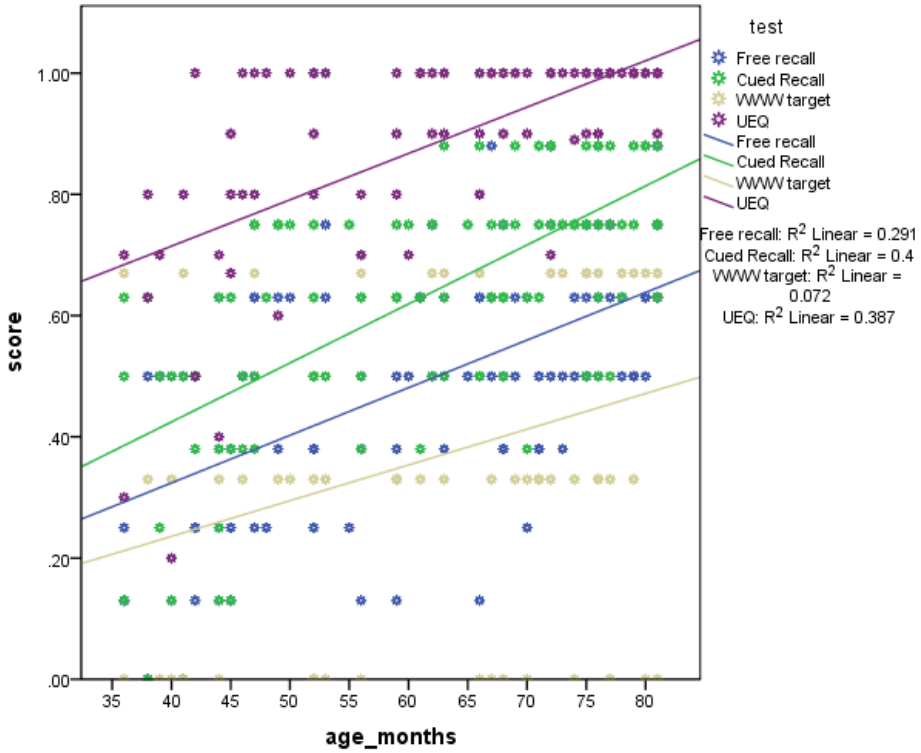


Figure 3.9. *Developmental trajectory of the different memory tests, with fit lines and R^2 values.*

Bischof-Köhler Test

There were two variants of the BK test. Both required children to predict their future desires while in a current state of satiety. BKA used satiety for entertainment (or boredom) (inspired by Klossek *et al*., 2011), and BKB used satiety for salty food (or thirst (equivalent to Atance and Meltzoff, 2006).

Bischof-Köhler A: Boredom

The satiety procedure had a significant effect on children's choices for future consumption. Children chose a dull video over an interesting video for their future

selves significantly more often when they had just watched the interesting video on repeat than when they had not (Related sample McNemar test: $\chi^2[1]=18.89$, $p<0.001$).

Overall, there was a trend suggesting that children were worse than chance at choosing an appropriate video for their future selves (one- sample binomial: p=0.093), in that they chose the dull (but new) video more than they chose the interesting (but old) video. All age groups performed at chance, except 6-year-olds, who performed significantly worse than chance (3-year-olds: p=1; 4-year-olds: p=1; 5-year-olds: p=1; 6-year-olds: p=0.021). Performance on this test did not improve with age: there was no significant difference between age groups ($\chi^2[3]=4.827$, p=0.185; see Figure 3.10). Interestingly, children who passed the test (picked the interesting but old video) were significantly *younger* than those who failed (t[21]=2.168, p=0.042).

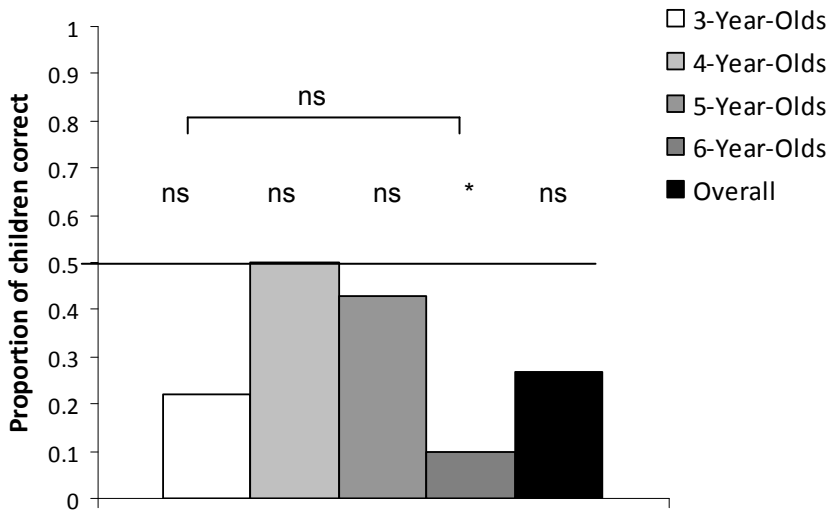


Figure 3.10. *Performance on the video future-planning test. No age group performed above chance and there was no difference between age groups.*

Bischof-Köhler B: Thirst

The satiety procedure had a significant effect on children's choices for future consumption. Children chose water (over Ritz biscuits) for their future selves significantly more often when they had just eaten Ritz biscuits than when they had not (Related sample McNemar test: $\chi^2[1]=10.316$, $p<0.001$).

Overall children did not perform above chance when choosing a snack for their future selves (one-sample binomial test, $p>0.999$). In fact, they chose the Ritz biscuits and water exactly as often as each other. No age group performed above chance (one sample binomial test: 3 years: $p=0.424$; 4 years: $p=0.607$; 5 years: $p=0.503$; 6 years: $p=0.824$; see Figure 3.11). There was no difference in age between children who passed and children who failed ($t[22]=0.477$, $p=0.638$).

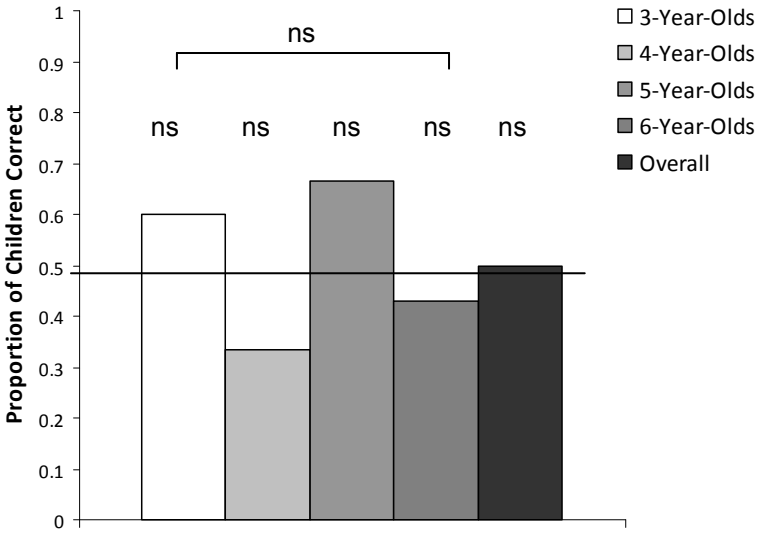


Figure 3.11. *Performance on the food future-planning test. No age group performed above chance and there was no difference between age groups.*

Relationships between Bischof-Köhler and Memory tests

Children who passed the BKA test showed a tendency to perform worse on the UEQ test than those who failed ($t[21]=1.904$, $p=0.071$). There were no other significant differences between children who passed or failed BKA in terms of memory test performance (FR: $t[21]=0$, $p=1$; CR, $t[21]=0.762$, $p=0.455$; WWW: $t[15]=0.633$, $p=0.536$). There was no difference between children who passed or failed BKB in performance on any of the memory tests (FR: $t[22]=-0.842$, $p=0.409$; CR: $t[22]=-0.482$, $p=0.635$; UEQ: $t[22]=0.475$, $p=0.640$; WWW: $t[14]=-1.293$, $p=0.217$).

3.4. Discussion

The aim of this experiment was to investigate the developmental trajectory and coherence of a number of different tests putatively assessing the same underlying psychological process: episodic cognition. Children between the ages of 3 and 6 years were shown to perform well on WWW, UEQ, FR and CR memory tests. Performance on all memory tests improved across age groups. For the most part, this improvement was gradual: there was no abrupt development from poor performance in younger children to good performance in older children. Such a developmental discontinuity might be predicted by conceptualist accounts positing that episodic cognition is not possible before the development of various other abilities (e.g. self awareness, representational theory of mind). The possible exception to this pattern of gradual development was in the CR test, in which 3-year-olds performed significantly worse than all other age groups, but no other age group differed from the others. This particular result is unexpected because CR is the only test in this battery for which an argument has been made that it is heavily affected by both semantic and episodic

cognition. In other words, CR is the one memory test in which conceptualist theorists would *not* predict an abrupt developmental advance.

There was a significant relationship between performance on FR and CR, and between both of these and UEQ. There was no relationship between WWW and UEQ or FR, but there was a relationship between WWW and CR. Of these, the relationship between FR and CR, and the relationships between CR and WWW persisted when age was controlled for (see Figure 3.12).

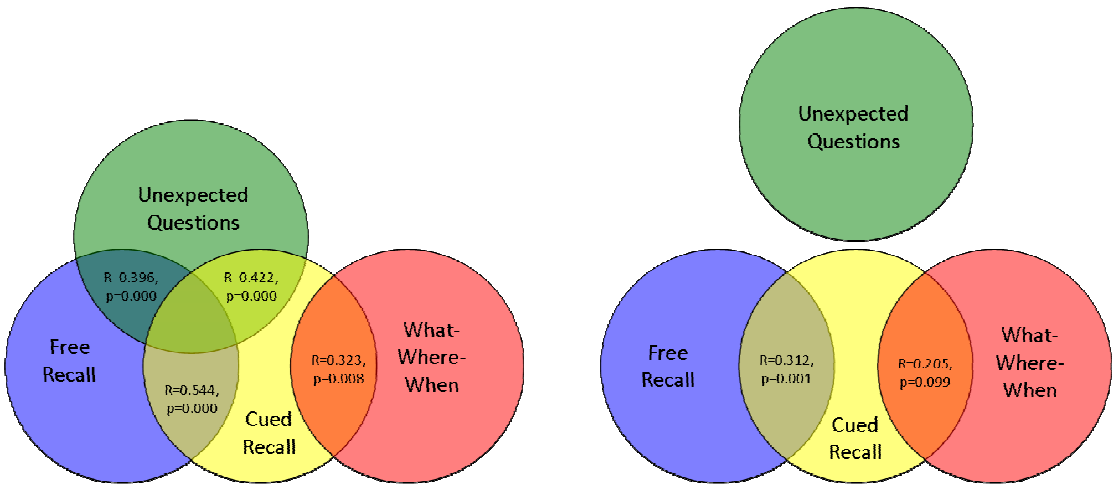


Figure 3.12. *Interrelationships between memory tests when age is (right) and is not (left) partialled out.*

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Children were not able to dissociate from their current motivational state (boredom or thirst) to choose the appropriate food/drink or entertainment for their future self. No age group performed above chance on this test and there was no development across age groups (if anything, children got worse as they got older). There was no relationship between performance on the BK tests and performance on any of the memory tests, except for a suggestion that children who passed BKA (the video test)

performed worse on the UEQ test than children who failed. This trend is difficult to interpret given the relationship of each with age.

Overall, these results show some interrelationships between the different memory tests (see Figure 3.12), and perhaps a negative relationship between UEQ and BK performance. However, while performance on all these tests improves with age, a non-significant trend towards different developmental trajectories means that we can't say with any confidence that they improve at the same rate. These findings suggest two things. First, that there is apparently no age at which episodic cognition "emerges". That is, performance on episodic memory tests does not abruptly improve and then plateau (or, at least, it does not plateau in children under 7 years). Instead, it appears that, no matter how you test for it, episodic memory improves gradually with age. Second, these different memory tests appear to tap somewhat different underlying processes in children; while there is some overlap, this is by no means overwhelming (no correlation statistic was higher than 0.55), there was also a trend that suggesting that they have slightly different developmental trajectories.

The finding that performance on all tests improved gradually with age is in contrast to the common assertion that episodic cognition "emerges" at the age of 4 years (e.g. Suddendorf and Corballis, 1997, Suddendorf and Busby, 2005, Suddendorf *et al*., 2011, Levine, 2004, Nelson and Fivush, 2004). The results presented here suggest that the only memory test for which children showed a sudden developmental jump between 3 and 4 years was CR, which has often been suggested as more reliant on semantic memory processes than other tasks (e.g. Tulving, 1985b, Perner and Ruffman, 1995). One possible account for this jump may lie in the increased semantic

knowledge that comes from the transition from nursery into school: increased semantic competency has been shown to greatly impact performance on episodic memory tests that have a semantic component - such as recognition memory tests (Robertson and Köhler, 2007).

There are, of course, many cognitive and non-cognitive abilities that develop across this age range. While partially behavioural, all the memory tests involved a linguistic element, and thus improvement of linguistic ability may be responsible for some of the developments in performance on all of the tests – and may differentially affect performance of some tests over others depending on the extent to which they offer a linguistic challenge. Similarly, children's willingness to talk to the experimenter (a strange adult) would differentially affect different tests. For example, in the WWW test, children's response was in the form of pointing, while in all the other tests the response was verbal. This may have contributed to the closer interrelationships between CR, FR and UEQ than between these and WWW. There were also differences between retention interval for different memory tests, as the CR, FR and WWW tests all had retention intervals of between 10 and 30 minutes, while some elements of the UEQ test assessed memory for events that had occurred one week previously; memory, especially in younger children, has been shown to decay dramatically over such a timeline (e.g. Scarf *et al*., 2011). Finally, given that the UEQ test was conducted on a different day to the other tests, it is possible that day-to-day variation may have reduced inter-task correlation.

In discussing this point, a distinction proposed by Carlson and Moses (2001) and highlighted by Atance and Jackson (2009) may be of relevance. Carlson and Moses

emphasized a difference between "emergence" and "expression" in terms of the role of, in their specific argument, executive function in theory of mind development. The authors argued that in an "emergence" account one might argue that it would be impossible for children to *conceive* of mental states (or future events) without a certain level of functioning in some other psychological process (e.g. executive functions/self-awareness/meta-representation). In contrast, an "expression" account suggests that children may *possess* the psychological ability (e.g. theory of mind/ episodic cognition) but be unable to translate "their knowledge into performance" (Carlson and Moses, 2001, p.1048) in the context of psychological tests with certain additional test demands.

I would like to extend this account and combine it with Clayton and Russell's (2009) minimalist approach to defining episodic cognition. I would argue that there are a number of features that come together to form adult human episodic cognition, and that the difficulty in defining what that cognition *is* stems from different theorists' relative emphasis on different contributing processes. Wheeler and colleagues (1997) suggest that "the development of episodic memory parallels the gradual growth of autonoetic consciousness and that both mature slowly over time" (p. 15). I would argue that, in the extent to which episodic cognition is defined in its most complex form (i.e. that enjoyed by adult humans); this argument is true of a number of capacities in addition to self-awareness/autonoetic consciousness. Moreover, depending on the level of development, these contributing processes may enable *both* emergence and expression at different times. Thus, depending on which contributing factor is emphasized by the theorist, and which target and extra-target processes are challenged by the experimental paradigm, the development and maturation of

completely different psychological processes may lead to successful or unsuccessful test performance. This account thus argues for a model of episodic cognition as a multifactorial process whose elements begin developing at or before birth, and whose peak performance is present to report for a relatively brief period in adulthood (before cognition begins to decline: e.g. Addis *et al*., 2008). Neurological evidence can support such a view. Carver and Bauer (2001) and Bauer (2007) argued that components of the temporal-cortical circuit essential for episodic cognition are present very early, but that the *network* begins to function as such only around the time of the child's first birthday (e.g. Gao *et al*., 2009). Furthermore they do not *finish* developing until adulthood. While much of the hippocampus is formed prenatally (Seress *et al*., 2001, Angevine, 1975, Rakic and Nowakowski, 1981, Arnold and Trojanowski, 1996),the dentate gyrus of the hippocampus and prefrontal cortex have a much more protracted development. Specifically, the dentate gyrus is not adult-like in structure until around 12-15 postnatal months (e.g. Seress and Mrzljak, 1992, Eckenhoff and Rakic, 1988) and, at least in animal models, neurogenesis continues throughout childhood and into adulthood (e.g. Altman and Das, 1965). The Prefrontal cortex similarly continues to develop for at least the first decade of life (Huttenlocher, 1979, Huttenlocher, 1990, Bourgeois, 2001). Following Goldman-Rakic (1987), Baur (2007) argues that this evidence suggests that the temporal-cortical network probably only reaches *functional* maturity during the second year of life, and that it then continues to develop and improve gradually for years afterwards.

No Relationship between Tests of Episodic Memory and Foresight: a Challenge for the Mental Time Travel Hypothesis?

Children who passed the BK tests were the same age (BKB) or younger (BKA) than children who failed them. There was no significant relationship between performance on either of the BK tests and any of the memory tests. There was, however, a trend suggesting that children who passed the BKA (the "boredom" test) were *worse* at the UEQ test than children who failed. There are several possible explanations for a lack of relationship or even a negative relationship between BK and memory tests. It is possible (even likely) that the BK test draws much more heavily on executive processes of self-inhibition than the other episodic cognition tests used in this experiment. As has been discussed above, this extra-target task-demand may have prevented the children from "translating their knowledge into performance" (Carlson and Moses, 2001, p.1048). However, this explanation does not account for the *decline* in performance with age and UEQ performance. An alternative explanation is that the abilities underlying the BK test may be *negatively related* to episodic cognition ability. This idea is discussed in detail in the following chapter.

If the different putative tests of episodic cognition used in this experiment differ in the extent to which extra-target test demands limit children's performance, then we should expect to see a very different pattern of relationships between performance in these tests in an adult sample, whose theory of mind, autonoetic consciousness and linguistic abilities are all, presumably, fully developed. However, if these tests tap fundamentally different memory processes, then we might expect the pattern of

relationships in a sample of human adults to appear more or less the same as at least the 5- and 6-year olds in this sample. This question is explored in Chapter 4.

Chapter 4
Episodic Cognition in Human Adults

A sample of undergraduates were tested on three different episodic memory tests (What-Where-When, Unexpected Question and Free Recall) and one test of episodic foresight (Projection Bias). It was predicted that performance on the memory tests would be positively correlated with one another. It was furthermore predicted that there would be a positive correlation between performance on the memory tests and the extent to which subjects were biased by their current motivational state in the Projection Bias test. It was found that performances on all the tests were related but that this relationship was not always linear. Instead, many of the tests showed a quadratic relationship, suggesting the contribution of multiple psychological processes.

4.1. Introduction

Chapter 3 explored the relationships between performance on different putative tests of episodic cognition in human development. It was found that while there were some relationships between the tasks, these were dependant on age, and did not remain when age was partialled out. There are a number of possible interpretations for this finding. The first is that these tests (What-Where-When [WWW]; Unexpected

Question [UEQ], Free Recall [FR] and Bischof-Köhler [BK]) all assess different psychological processes in humans. The second is that these tests assess the same psychological mechanism in *adults* but that disparate elements do not come together to form that mechanism until later in development. The third possibility is that these tests do tap the same psychological process, and do so in children, but that age-independent relationships cannot be seen due to the significant development of general cognitive capability that occurs between the ages of 3 and 6 years. Finally, it is possible that the different tests tap the same psychological process but are differently affected by extra-target factors (such as executive functions) that also develop dramatically during this period.

The current Chapter aims to differentiate between some of these interpretations by assessing performance on the same tasks (WWW, UEQ, FR and BK) in healthy young adults. If it is found that performance on these tasks is highly related in adults, it would suggest that the lack of (age-independent) relationship in children may be due to developmental factors. If, however, it is found that a similar lack of relationship between performance on these tests exists in adults, it would suggest that different tests of episodic cognition may not tap the same psychological processes in humans.

Much of the evidence concerning tests of episodic cognition in human adults was explored in Chapter 1. As such, the following section shall explore the literature concerning the central investigation of this chapter: whether WWW, UEQ, FR and BK assess the same psychological process, and whether that process is episodic cognition.

Episodic Memory Tests

To date there have been relatively few attempts to investigate WWW memory in humans. This has probably been the result of the perceived lack of requirement for nonverbal behavioural tests in verbally competent humans, as well as the considerable separation between the fields of animal cognition (in which the WWW test was developed) and human psychology. There have, however, been some recent attempts to apply this paradigm to human subjects (Easton *et al*., 2012, Holland and Smulders, 2011, Plancher *et al*., 2008, 2010). In all cases, these experiments have attempted to relate performance on the WWW test to other indices and putative tests of episodic memory.

Plancher and colleagues (2010) used memories of a tour around a virtual town to assess WWW memory in young and elderly adults, and compared performance on this test to FR and self-reported memory complaints in everyday life (i.e. a tendency to lose keys, forget names, etc.). The authors found that younger subjects were significantly more able than older adults to bind what, where and when components together (i.e. more able to remember *integrated* representations rather than only individual elements). It was also found that levels of memory complaint in everyday life correlated significantly with this WWW binding ability, but not with individual elements (what/where/when) or with FR. This emphasis on the binding of components corresponds with Clayton and colleagues' (2003b) arguments that it is not the content but the *integration* of the what, where and when elements that makes the memory episodic. Furthermore, the discovery that it is the *binding* of contextual features that is impaired in older adults – and that this is the feature most correlated with experience

of memory problems in everyday life – corresponds with related research that the binding of what-where, what-when and where-when features is more affected by age than memory for individual what, where or when elements (Kessels *et al*., 2007). It is also consistent with the finding that episodic amnesics are impaired on object-location-, object-order- and object-person-binding memory, but not on object recognition (Burgess *et al*., 2002).

Holland and Smulders (2011) found that people's accuracy in remembering where they had hidden two different types of coin (what) on two consecutive days (when) was related to their ability to remember incidental features of the hiding episodes (i.e. a UEQ test). They also found that subjects were generally more likely to associate their WWW memories with the experience of "remembering" rather than the feeling of "knowing". This pattern was replicated by Easton and colleagues (2012), who found that subjects were significantly more likely to report "remembering" than "knowing" when they had previously seen a specific object-location combination.

Together, these studies suggest that there are some relationships between different putative tests of episodic memory in human adults. Furthermore, the relationship between WWW (but not FR) and memory complaints (Plancher *et al*., 2010) and tendency for items to be reported as "remembered" rather than "known" (Easton *et al*., 2012, Holland and Smulders, 2011) suggests that the WWW test may tap episodic memory.

One point explicitly investigated by both Plancher and colleagues (2010) and Holland and Smulders (2011) was the extent to which active encoding (that is, the active

intention to memorize) affected performance and the contribution of episodic processes to performance. Plancher and colleagues (2010) found that the intentionality of encoding did not affect the bound what-where-when memory, but did improve memory for the individual elements in young, but not older, subjects. Holland and Smulders (2011) found that while intention to encode improved performance, it did not affect the extent to which memories were reported as remembered (rather than known). This is in line with the finding that intentional encoding may improve memory for *aspects* of an episode, but does not improve binding (Lekeu *et al*., 2002). It also corresponds to the findings of the cognitive neuroscience literature that both deliberately and incidentally learned information can be episodic, but may draw upon different elements of the episodic neural network (e.g. Morris and Frey, 1997; see Chapter 1). It also suggests that intentional encoding may not alter the contribution of episodic cognition to performance. Such a finding would be contrary to Zentall's argument that an "unexpected question" is more likely to tap episodic memory than an "expected question".

However, it is possible that the effect of deliberate encoding on the contribution of episodic cognition to memory performance may depend on the type of memory test. For example, in a WWW test, a subject knowing that they are going to have to remember what they hid where and when might purposefully hide items in a way that reduces the future memory load (such as , for example, hiding acorns under oak tress and conkers under horse chestnut trees). Note that this is not only a deliberate encoding strategy, but also a manipulation of the *content* of the memory (in this example, purposefully confounding what with where). However, such an account would predict that subjects in Plancher and colleagues' (2010) WWW test would not

show an effect of deliberate encoding on the contribution of episodic cognition (because they had no control over the memory content) but those in Holland and Smulder's (2011) WWW test would (because they could choose where to hide the coins). However neither study found an effect.

Episodic Foresight and the "Bischof-Köhler" Test

As has been discussed in Chapter 1, there are few established behavioural measures for episodic future thinking, the most popular being tests of the Bischof-Köhler Hypothesis. These involve dissociating from currently felt motivational states to plan for a future time in which motivational state will be different (see Chapter 1 for a discussion). In the following section, evidence shall be discussed that suggests that this ability to dissociate from current needs to plan for the future is something even adult humans are very poor at. It is hypothesised that, far from being an indicator of episodic cognition, the ability to plan for a future motivational state may be *limited* by the use of an episodic strategy.

Episodic Construction is Vulnerable to Bias from Current Feelings

Episodic memory is widely accepted to be a reconstructive process (e.g. Bartlett, 1932, Neisser, 1967, Schacter and Addis, 2007b, Suddendorf and Corballis, 2007). Neisser (1967) poetically likens it to the work of a palaeontologist, who must build a dinosaur skeleton from only fragments of bone, but also from extensive knowledge of dinosaurs: "out of a few stored bone chips, we remember a dinosaur" (p.285). Thus

memories (much like the early constructed dinosaur skeletons) can often be more representative of misconceived knowledge than of fact.

Tulving (1983) argued that "recollective experience and measured aspects of recollective experience do not provide evidence about the properties of information stored about the event, but rather about the joint (synergistic) effects of both the stored information and the retrieval information…memory distortions, rememberers 'remembering' things that did not occur, could be attributed to the constructive role of retrieval information" (pp. 180-181). It has been argued that this tendency for episodic memory to be skewed by current facts and feelings is a by-product of the flexibility required to construct future events:

> "*…future events are not exact replicas of past events, and a memory system that simply stored rote records would not be well-suited to simulating future events. A system built according to constructive principles may be a better tool for the job… Such a system will occasionally produce memory errors, but it also provides considerable flexibility*" (Schacter *et al*., 2007, p.27)

Episodic cognition acts to create or recreate an experience (be that emotional, visceral, perceptual etc.). Because of this, there is likely to be "seepage" from our current experience into our episodic representations; one cannot easily maintain two distinct emotional/visceral states simultaneously (e.g. Loewenstein, 1998, Loewenstein *et al*., 2000). Semantic (or "non-episodic") representations of emotional/visceral states should, however, be less influenced by current state as they do not involve the creation of an internal state. They may, however, be more

influenced by semantic knowledge about types of situations that are *likely* to induce such states. For example, one may semantically *know* that newlyweds are happy, but after a messy divorce find it difficult to *remember* feeling happy after one's own wedding. As Levine and Safer (2002) put it, "Memory for emotions is partially reconstructed on the basis of current feelings about, and appraisals of, past emotion-eliciting events." (p.3). Thus, to return to Neisser's (1967) analogy, one might consider that if the fragments of dinosaur bone have been stored in the same deposit as fragments of elephant bone, it would be very difficult to construct the dinosaur skeleton without accidentally including some erroneous bits of elephant.

There is evidence that current state affects the content and availability of episodic memories. Memories may be easier to recall if they are congruent with current moods, or may be altered in content such that the experience of the former self is more in line with current experience (See Box 2). For example, Safer and colleagues (2002) found that the grade achieved by students in an exam affected how anxious they remembered feeling before the exam: those who were informed that they had done well were less likely to remember high levels of pre-exam anxiety than those that had not yet been informed of their grade. The impact of current state on episodic cognition may be even more apparent in episodic foresight than episodic memory, given that "even the most plausible recollections can come in conflict with physical evidence and with other, inconsistent, recollections" (Read and van Leeuwen, 1998, p.15),. Indeed, the same pattern of errors is shown for predicted future experiences as for memories of the past (see Box 2). For example, heroin addicts asked to choose between extra rations of the heroin replacement buprenorphine (BUP) or extra cash on their next visit (5 days later) differed substantially in their choices depending on

whether they made them immediately before or immediately after BUP administration. Indeed, those making the choice before BUP administration valued the future BUP by almost twice as much as those who made the choice immediately after BUP administration (Giordano *et al*., 2002).

Box 2

The Effect of Current State on the Remembered Past and Imagined Future

There is considerable evidence that current state can affect the availability and content of memories. Memories may be more easily retrieved if they contain references to states similar to those currently experienced, or the states contained within the memories may be *altered* in recollection to become more similar to the current state.

Pain

Patients experiencing intense pain at the time of recall tended to overestimate their past feelings of pain while patients experiencing mild pain at the time of recall tended to underestimate the intensity of past pain (*Eich et al., 1985*). Similarly, people who have not experienced a source of pain (immersion of their hand in ice cold water) greatly underestimated the amount of pain that it will cause (Read and Loewenstein, 1999. *see also:Bryant, 1993; Norvell et al., 1987; Smith & Safer, 1993)*

Mood

In diurnal depressives, increasing depression levels during the day are associated with an increased probability of retrieving negative autobiographical memories in response to a neutral cue word (*Clark & Teasdale 1982*). Similarly, People's concept of the liklihood of favourable future events is dependant on the mood they are experiencing at the time of making the prediction (*Nygren et al., 1996; Johnson & Tversky, 1983. See also: Macleod & Matthews, 1991; Mineka & Sutton, 1992; Blaney, 1986; Matt et al., 1992; Bradley & Matthews, 1988; Bullington, 1990; Parrott, 1991, for more reports of mood-congruent memory availability, and Gilovich & Medvec, 1995; Levine 1997; Levine & Safer, 2002; Safer et al., 2001; Safer et al., 2002 for reports on memory content.)*

Drive States (Hunger, Craving, Sexual arousal…)

People are more likely to spend more on food if shopping while hungry than if shopping while sated (*Nisbett & Kanouse, 1969)*
(See also: Read & Van Leeuwen, 1998; Gilbert et al., 2002; Read and Loewenstein, 1995; Badger et al., 2007; Loewenstein et al., 1997)

This model of a failure of episodic cognition to construct past or future states independently of the influence of current state is in line with the "projection bias" theory of Lowenstein and colleagues (2003). They present a formal model of projection bias: the tendency to exaggerate the degree to which future tastes will resemble current tastes. They argue that while people understand the direction and qualitative nature of their changes in tastes, they underestimate their magnitude because it is extremely difficult to imagine what it is like to be in a different state from the one currently experienced (Loewenstein, 1998).

In light of these arguments, I suggest that, contrary to the suggestions of Suddendorf and Corballis (1997), the ability to disengage from one's current motivational state to plan for future needs is *negatively* related to the contribution of episodic cognition. Furthermore, the more vivid one's episodic simulation of a future need state, the more vulnerable that simulation is to bias from current feelings. Consider, for example, an attempt to predict how much one will enjoy watching a newly released romantic comedy next month. A person may *know* (semantically/non-episodically) that they are a great fan of romantic comedies, and therefore will enjoy it. However, they may be attempting to predict their future enjoyment at a time when they have just sat through a romantic comedy marathon and feel rather tired of the format. If this person were to make a decision on the basis of general trends, or semantic knowledge, they may opt to buy a ticket to the movie next month, as this would match their standard behaviour and preferences. However, if they attempt to put themselves into the shoes of their future self and imagine how they will *feel* about that movie, there is likely to be an effect of their current feelings of boredom on the tone of the projected scenario. Thus this person would be more likely to reject the movie on the basis of current feelings

the more they were absorbed into the imagined future, and the less they were influenced by timeless intransient facts (see Kahneman and Snell, 1992).

This chapter will investigate the relationship between performance on three putative tests of episodic memory (WWW, UEQ and FR). To investigate the potential contribution of episodic memory to performance, the subjects were asked to report on what "strategies" they used in performing these memory tests. It is predicted that those individuals who perform best on one test will also perform best on the others, and that the extent of the relationship will be predicted by the subjects' use of "episodic" strategies. Performance on these memory tests was compared to a version of the BK test. To assess the proposal that the contribution of episodic cognition may *reduce* the ability to disengage from current feelings, it was necessary to adapt the BK test to produce continuous data. Rather than a pass/fail test for the ability to dissociate from current feelings to plan for the future (as was used in Chapters 2 and 3), this test assesses the *extent* to which subjects are biased by their current feelings. As such, in deference to Lowenstein and colleagues (2003), it shall be referred to as the "Projection Bias" (PB) test. It is predicted that subjects who report using episodic strategies in the memory tests should show a negative relationship between performance on this test and memory accuracy. That is, the better they perform at the (putative) episodic memory tests, the more biased they should be in the PB test. People who report using a semantic strategy in the memory tests should show no relationship between memory and planning (because there is currently no reason to believe that semantic memory ability should relate to the ability to logically infer future events).

4.2. Methods

The experiments took place in a room in the department of Experimental Psychology, Cambridge, in the spring of 2011.

Subjects

The sample consisted of 77 subjects, of whom 42 were male. Subjects were undergraduates at the University of Cambridge, aged between 18 and 23 years, recruited and tested as part of an undergraduate research project conducted by Mathilda Hay and Stephanie Bailey, under my supervision.

Tests

Three (putative) episodic memory tests (WWW, UEQ and FR) were conducted alongside one (putative) episodic foresight test (PB).

Memory Tests

What-Where-When

The WWW test was conducted in the form of a computer game. Participants took on the character of "Swashbuckle", a pirate who has run aground on a desert island and must hide all his treasure before his evil rival "Pinkbeard" arrives to steal it. To hide the treasure, subjects could navigate between three locations on a "treasure map": the

beach, the village and the mountain. Clicking on any of these locations took the subject to the appropriate "scene", where they could then hide the treasure. The treasure was presented in two virtual treasure chests, one containing gold coins and one containing silver coins, from which subjects could drag and drop individual coins into virtual scenes, where they would disappear (see Figure 4.1). Before beginning to hide the treasure, subjects were informed that Swashbuckle would have to find the treasure again, and thus to try to remember where it was hidden. After the subjects had hidden half of their treasure (5 gold and 5 silver coins) they were informed that the sun was going down and they would have to continue "in the morning". Subjects undertook the PB test and were then told that it was now morning and that they should finish hiding the treasure. When all the treasure was hidden, it was revealed that Swashbuckle's treasure was in fact stolen from a leprechaun, meaning that the gold coins would disappear if left outside overnight. The subjects were then asked to identify on each scene the locations ("where") gold coins ("what") had been hidden *before* Swashbuckle slept ("when") (i.e. the treasure that would have disappeared). They did so by clicking on the area of the map that they thought they had hidden it, thus producing an "X" to mark the spot. Subjects made five "X marks the spot" judgements in total.

The accuracy of subjects' coin location was measured in terms both of integrated WWW and individual what, where and when elements. The integrated WWW score was calculated by assessing whether there was a "target" coin (i.e. a gold coin from the first hiding period) within 60 pixels (two coin widths) of the subject's "X marks the spot". The individual "What" and "When" elements were coded in terms of the identity (what) and origin (when) of the *nearest coin* to the subject's "X marks the

spot". Thus if the nearest coin was gold, subjects were coded as correct for "what" and if the nearest coin was hidden during the first hiding session they were coded as correct for "when". The "Where" element was calculated in terms of absolute distance from *any* coin. If there was a coin within 60 pixels of the subject's "X marks the spot", they were coded as correct for "where". To prevent subjects from reporting the same coin multiple times, individual coins that had contributed to the score (either integrated or individual) on a previous "X marks the spot" judgement it was discounted from subsequent judgements and the next nearest coin was considered.

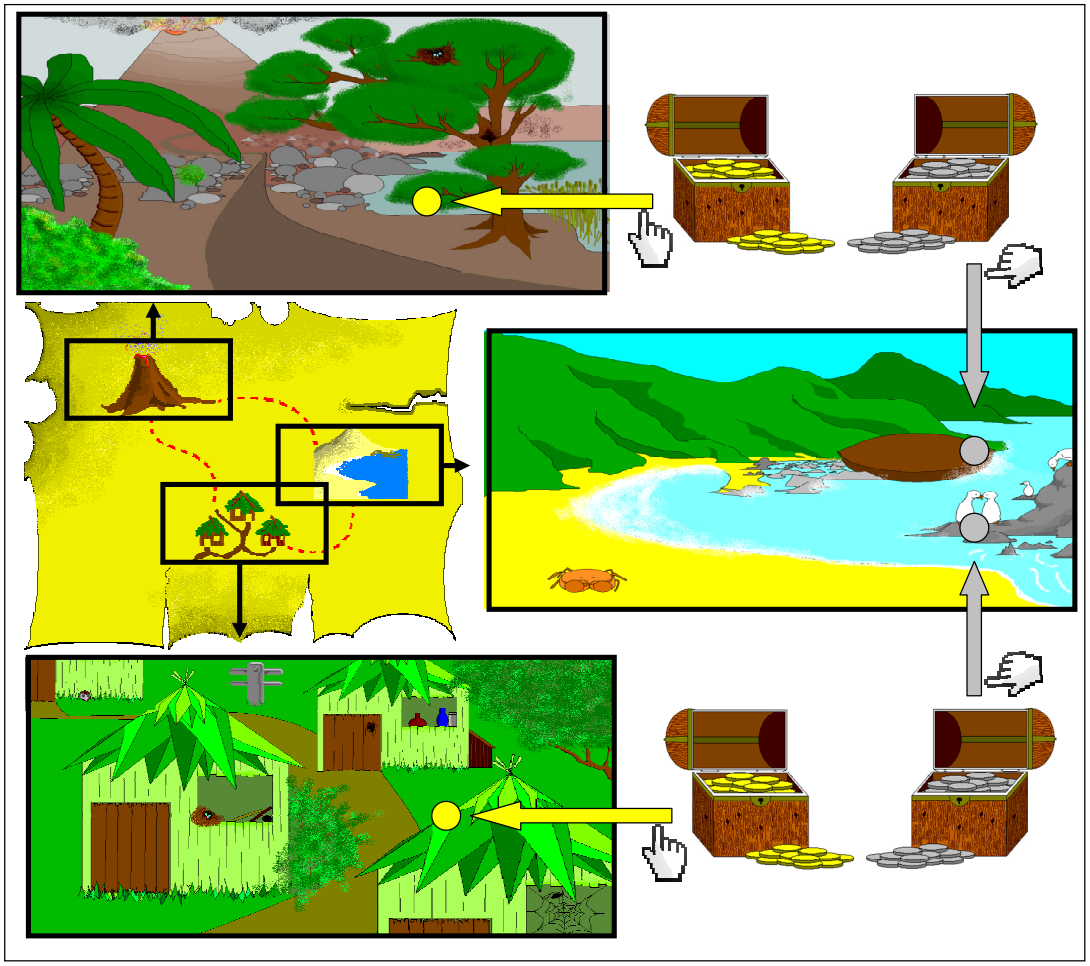

Figure 4.1. *Schematic of WWW pirate game hiding phase. Clicking on any of the symbols on the map takes the subject to one of the three scenes: mountain (top), beach (right) or village (bottom). At the bottom of each scene were two treasure chests from which subjects could drag and drop gold or silver coins into the scene to hide them.*

Unexpected Questions

Participants were unexpectedly asked 11 questions about aspects of the WWW test at the end of the computer session (see Table 4-1). Questions were relatively evenly distributed between asking identity related questions (e.g. "what animal was there in the village scene?"), spatial questions (e.g. "which of the pirate's shoulders was the parrot sitting on?") and number questions (e.g. "how many birds were there in the beach scene?"). This was designed such that the questions did not differ in content from the WWW questions, but simply differed in the fact that they a) were unexpected and b) did not explicitly require integration of memory for what, where and when. The questions were open-ended; subjects typed their answers into blank boxes. To make sure all subjects answered all questions, participants were not permitted to continue until they had typed an answer in every box.

Table 4-1 *"Unexpected" Questions asked at the end of the session*

Unexpected Questions
1. What colour was Swashbuckle's shirt?
2. Which of Pinkbeard's shoulders was his parrot sitting on?
3. Was the beach on the east or west of the island?
4. Of the three scenes, how many contained a bird's nest?
5. How many trees were there in the volcano scene?
6. Was the lake on the left or the right of the screen in the volcano scene?
7. Which animal was there in the village?
8. What colour were the roofs of the huts in the village?
9. How many birds were there in the beach scene?
10. What colour were the birds in the beach scene?
11. How many starfish were there in the beach scene?

Free Recall

A list of 28 words was selected from a list of 925 nouns that were rated for abstractness and imagery (Paivo *et al*., 1968) (see Table 4-2). 14 words were selected for scoring highly in "imagery" and "concreteness" while 14 words were selected for having low "imagery" and "concreteness" scores.

Table 4-2. *14 high-concreteness, (m=6.49) high-imagery words (m=6.39) and 14 low-concreteness, (m= 2.44), low-imagery words (m= 1.72) from Paivio et al., (1968)*

High-concreteness, high-imagery words	Low-concreteness, low-imagery words
Umbrella	Truth
Mountain	Tendency
Orchestra	Thought
Kettle	Misconception
Magazine	Intellect
Ink	Idea
Hotel	Gist
Forehead	Essence
Garden	Fate
Elbow	Ego
Engine	Criterion
Book	Disposition
Car	Concept
Clock	Attitude

Participants were read the word list and then immediately asked to recall it. They were then read the list in a different order and informed that they would be asked to recall the list again at the end of the experiment. The retention interval lasted approximately 30 minutes, in which subjects undertook the computerised tests (WWW, UEQ and PB).

Projection Bias Test

Participants were presented with eight menus, each containing six food items. Four of these menus were "distracter" menus containing savoury food and four were "test" menus which contained sweet food. In the test menus, the food was divided according to the extent to which it was considered "refreshing" by nine independent raters (see Appendix 1.). To control for specific taste effects, two items were chocolate-based, two items were citrus-based and two were neutral. Within these, one of each was highly refreshing (e.g. sorbet/milkshake) and one of each was highly thirst-inducing (e.g. chocolate fudge brownie/lemon drizzle cake). Pilot data (see Appendix 2.) indicated that pre-feeding had a robust effect on choice for refreshing foods, so this was the variable chosen for analysis. Subjects were told to pretend that tomorrow they would be visiting a restaurant with a group of friends, but that the restaurant had asked for menu choices in advance. Subjects were asked to rank the foods on the menu from 1 to 6 according to how much they would like to receive them *tomorrow* (see Figure 4.2).

After completing half of the menus (two distracter and two test) subjects underwent the pre-feeding procedure, which was presented to them as a "taste test". Subjects were split into two groups ("Chocolate" and "Citrus") and presented with 27 questions about specific features of six foods (see Appendix 3). The Chocolate group received and compared six chocolate-based foods and drinks (Frijj® Milkshake, Mars® Milkshake, Sainsbury's Basics® Chocolate Mousse, Cadbury's Buttons Chocolate Mousse®, Sainsbury's Basics® Milk Chocolate and Cadbury's Dairy Milk®), while the citrus group received and compared six citrus-based foods and

drinks (satsuma, clementine, and four squash drinks, the latter made up of differing proportions of Sainbury's Basics® Orange Squash and Robinson's® Lemon Squash, matched for strength). To encourage maximum consumption the participants were asked to retry the food and drink for every question.

After the pre-feeding period, subjects completed the final four menus, which contained non-identical but comparable foods. Again, they were asked to rank the foods from 1 to 6 based on how much they would like to receive it *tomorrow*. Thus choices made both before and after the pre-feeding session were made for the *future* (i.e. a time at which the satiating effect of the pre-feeding would no longer be felt).

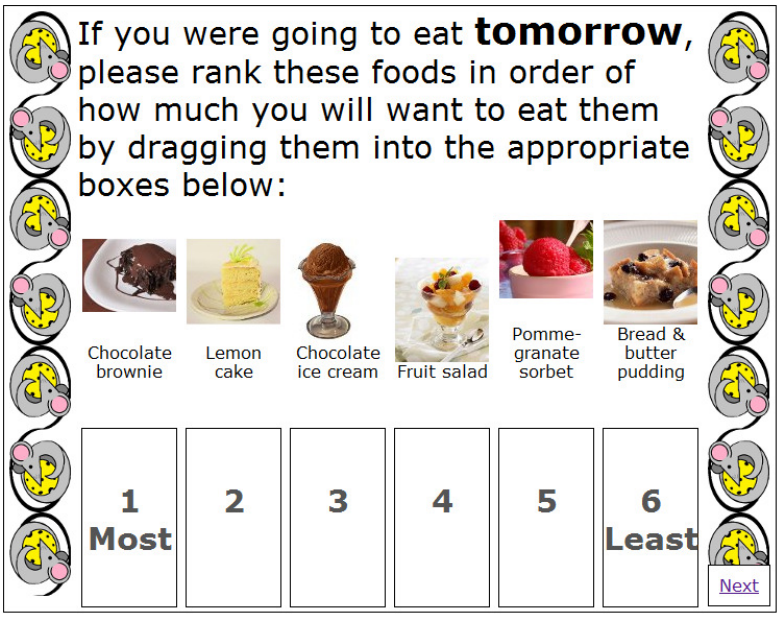

Figure 4.2. *Example of a test menu*

Subjects' "before" and "after" scores were calculated by multiplying the rank given to each food by its category-score (e.g. whether it was rated as highly "thirst-inducing" by the independent raters [1=thirst-inducing, 0=refreshing]). The resulting numbers were then summed for each set of menus. Thus, if highly thirst-inducing foods were

ranked 1st, 3rd and 6th in the first "before" menu and 2nd, 4th and 5th in the second "before" menu, the subject would receive a "before" score of 21. The difference between "before" and "after" scores (calculated by subtracting the "after" score from the "before" score) was used as the index of bias for each subject. The greater the distance from zero, the more the subject's preferences had altered between the two sets of menus.

Procedure

The subjects were asked to refrain from eating for at least an hour before taking part in the experiment. The WWW, UEQ and PB tests were computer based and in the form of video games. The FR test was administered orally by the experimenter.

The procedure was a nested design in which the phases of the different tests formed the retention interval for the other tests. The subjects underwent the learning phase of the FR test before starting the computer-based tests. They then undertook the first leaning phase of the WWW test, followed by the "before" section of the PB test. Subjects were then pre-fed (chocolate for the chocolate group, citrus for the citrus group) and undertook the "after" section of the PB test, followed by the second learning phase and then test phase of the WWW test. The final section of the computer game was the UEQ test. Finally, the subjects were asked to verbally recall the words that were read to them at the beginning of the session.

The subjects were then debriefed about the nature and purpose of the experiment, during which they were asked to give their consent for the use of their data and to

report on *how* they went about the different memory tests (see Table 4-3). Their answers were coded into categories that captured the essence of the report (Table 4-4). For FR and UEQ, these were then further coded into episodic and semantic strategies. For the WWW test, many of the different strategies could be interpreted as either episodic or semantic. Interestingly, many strategies offered by subjects involved methods both of encoding and retrieval, and often the encoding and retrieval

Table 4-3. *Self-report questions asked to subjects for each memory test.*

Test	Question
What-Where-When	"How do you think you went about identifying where you hid the coins in the pirate game?"
Unexpected Questions	"How do you think you went about answering the questions presented on the screen?"
Word Free Recall	"How do you think you recalled the words from the wordlist?"

elements of the strategies could not be separated. As such the strategies are not subdivided into encoding and retrieval strategies but coded as episodic or semantic on the basis of whether it added spatio-temporal information to the memory at encoding (such as creating a "narrative" from the hiding period [this included memory palaces and method of loci techniques] or used episodic strategies/phenomenology at retrieval [such as reporting "re-experiencing"]).

Analyses

To make them comparable, scores on all memory tests were re-calculated as a proportion, such that the maximum score was 1 and the minimum score was 0.

Table 4-4 *Categories of self-reported memory strategies. These were categorised by two coders with 91% agreement. Those presented in pale grey were coded as episodic strategies and those presented in darker grey were coded as semantic strategies, while those presented in white were coded as either/neither.*

Free Recall	Unexpected Question	What-Where-When
Heard (felt that they could hear experimenters voice in their head)	**Visualised** (felt that they could see the scene in their head)	**Order** (hid the coins in a specific order and used this rule to infer "what" and "when")
Visualised (felt that they could see the words in their head)	**Failed Visualisation** (*attempted* to see the scene in their head, but couldn't)	**Colour-Matching** (hid coins in areas of a similar colour and thus used colour as a retrieval cue for "what" and "where")
Categorise (Categorised words into different types)	**Guessed** (aware that answer was total guess)	**Landmark** (used salient landmarks when hiding and retrieving)
Linked (Linked words together)	**Semantics** (used logical inference to reach answer)	**Revisited** (mentally "went back" to the hiding event)
Knew ("just knew")	**Knew** ("just knew")	**Story/memory palace** (made the hiding event into a narrative)
Made a Story (Turned the word list into a narrative)		**Geometry** (used the geometry of the screen when hiding and retrieving)
Remembered own Thoughts (remembered what they were thinking at the time)		

Where assumptions of normality were met, data were analysed using paired and independent samples t-tests and Pearson's correlation. Where the data did not meet assumptions of normality, Friedman's ANOVA, related-sample Wilcoxon and Kendell's tau correlations were used. Nonlinear relationships between tests were assessed using a univariate general linear model (GLM).

4.3. Results

Performance for each of the tests (WWW, UEQ, FR and PB) is reported, followed by the relationships between performance on the different tests.

Gender Effects

Men and women did not differ in their performance on any of the tests (FR: t[75]=-1.061, p=0.292; UEQ: t[75]=1.441, p=0.154; WWW: t[65]=1.471, p=0.145; PB: t[75]=0.737, p=0.463). As such, all of the following analyses were conducted with data from men and women combined.

What-Where-When

Subjects had an average integrated WWW score of 0.73 (±0.242) - equivalent to correctly locating 3.6 of the 5 target coins. In terms of the individual what, where and when elements, subjects on average correctly identified gold coins ("what") with a score of 0.8 (±0.217), correctly identified coins from the first hiding episode ("when") with a score of 0.91 (±0.188) and correctly located coins ("where") with a score of 0.9 (±0.164). Thus subjects were generally very successful at the individual elements of the WWW test, but less successful at integrating this information. Subjects were differentially successful at the different elements of the test (Friedman's ANOVA: F_2=16.39, p<0.001). Planned contrasts (related samples Wilcoxon) revealed that subjects were significantly worse at identifying the type of coin ("what") than at identifying a coin from the correct hiding period ("when"; W=487, p=0.001) or

identifying coin location ("where"; W=486, p=0.015), but that these latter two elements did not differ from each other (W=245, p=0.322).

Subjects reported their strategies for remembering the location of the treasure, although it was often difficult to categorise these reports, given that many of them could be either semantic or episodic. Conservatively, only "re-experiencing" and "narrative" strategies were termed episodic; 30% of subjects reported using such methods. Overall, 48% of subjects reported hiding coins in a specific order and then using the order as a retrieval cue, 35% reported using landmarks, 26% reported "re-experiencing" the hiding event, 19% reported matching the colour of the background to the colour of the coin when hiding, and thus identifying location-identify combinations according to colour, 4% reported creating a story out of the locations and 4% reported using the geometry of the screen to identify locations. There was no significant difference in performance between those reporting "episodic" strategies (re-experiencing or story-creation) and those not (t[69]=0.887, p=0.378).

Unexpected Question

Subjects scored an average of 0.61 (±0.119) in the UEQ test, which is equivalent to 6.7 correct answers out of the 11 questions.

In the debrief, 87% of subjects reported using an episodic strategy in the UEQ test, while only 27% reported using a semantic strategy. Specifically, 80% of subjects reported visualising the context they were attempting to remember, 40% reported guessing, 19% "just knew" the answer, 10% reported using logical inference to infer

the answer and 6% reported attempting to visualise, but being unable to. Because only 4 people did not report at least one episodic strategy, it was not possible to compare performance of those reporting episodic strategies and those reporting only semantic strategies or guessing.

Free Recall

On average, the subjects achieved a score of 0.389 (±0.146) on the free recall test. This is equivalent to recalling approximately 11 words out of a possible 28. The words were divided into concrete "imaginable" words (e.g. magazine, elbow) and non-concrete, hard-to-visualise words (e.g. idea, gist). Subjects on average recalled 6.2 (±2.55) concrete words (out of a possible 14) and 4.8 (±2.3) non-concrete words (out of a possible 14). Subjects remembered significantly more concrete than non-concrete words (paired samples t-test, $t[70]=4.377$, $p<0.001$).

In the debrief, 53% of subjects reported using an episodic strategy while 48% reported using a semantic strategy (subjects could report as many strategies as they felt they used, so the same subjects contribute to multiple categories). Specifically, 40% reported visualising the words, 35% reported linking the words together, 20% of people reported mentally hearing the experimenter's voice, 14% reported that they "just knew" that the words had appeared on the list, 10% reported creating a narrative out of the words, 5% reported sorting the words into categories and using these as retrieval cues and 5% reported remembering their own thoughts in response to hearing the words. There was no significant difference in performance between people

reporting (any) episodic and those reporting (only) semantic strategies (t[38]=-0.230, p=0.819).

Memory tests overall

The subjects' scores on all three memory tests were averaged into a single "memory score", influenced equally by performance on all three tests. The subjects' self-reported strategies were grouped across the memory tests and scored according to the number of tests in which subjects reported using episodic strategies (1, 2 or 3). This was used as a metric of "tendency to use episodic cognition". There was no "0" score because only two subjects never reported using an episodic strategy in any of the tests. There was no effect of the tendency to use episodic strategies on the overall memory score (F_3=0.845, p=0.474). This suggests that those subjects reporting episodic strategies were neither more nor less successful overall in the memory tests.

The relationship between memory tests

Relationships between the memory tests were assessed using Pearson's correlations to assess linear relationships and using univariate GLMs to assess nonlinear relationships. There was a significant positive correlation between WWW and FR (R=0.233, p=0.041), which was driven by subjects who reported episodic strategies in the FR test (episodic: R=0.514, p=0.014; semantic: R=-0.344, p=0.163; see Figure 4.3). There was no correlation between UEQ and either FR or WWW (FR-UEQ: R=-0.124, p=0.281; WWW-UEQ: R=-0.024, p=0.833).

The lack of correlation between the performance in the WWW and UEQ tests may have been due to a nonlinear relationship. Univariate GLM revealed a quadratic relationship between WWW and UEQ scores (UEQ: $F_{1,74}$=3.733, p=0.057; UEQ²: $F_{1,74}$=4.343, p=0.041). This suggests that subjects who performed very well or very badly on the WWW test performed well on the UEQ test, while subjects who performed moderately on WWW performed badly on UEQ. There was no quadratic relationship between FR and UEQ (UEQ: $F_{1,74}$=0.660, p=0.419; UEQ²: $F_{1,74}$=0.713, p=0.401) overall, or when only subjects who reported episodic strategies in the FR test were included (UEQ: $F_{1,74}$=0.023, p=0.881; UEQ²: $F_{1,74}$=0.022, p=0.884).

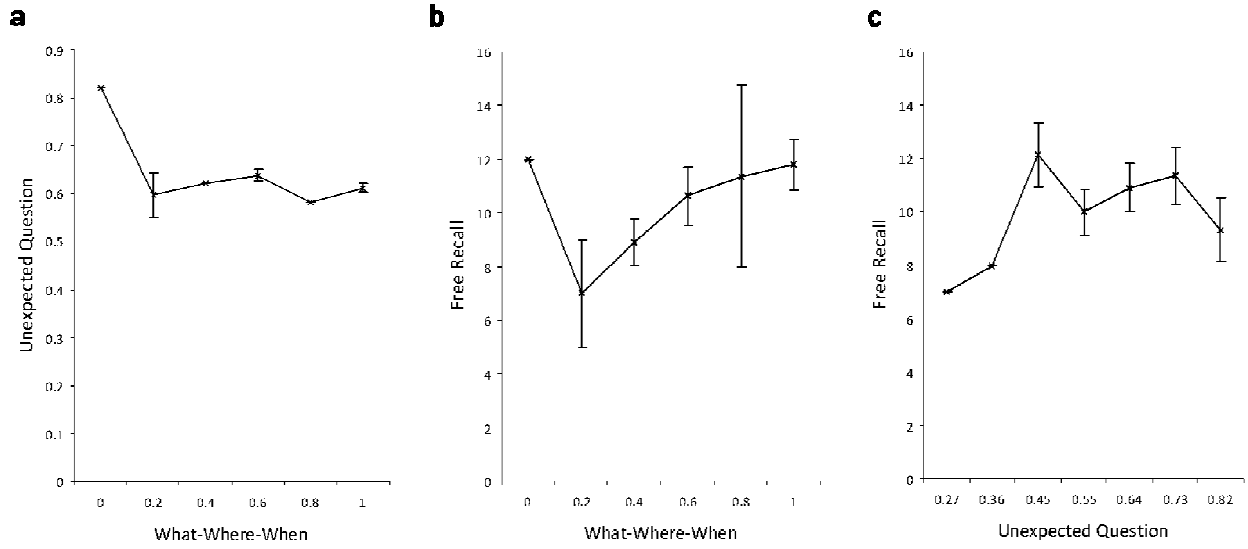

Figure 4.3. *Relationship between memory tests. a) Relationship between WWW and UEQ. B) Relationship between WWW and FR. C) Relationship between UEQ and FR. Error bars represent standard error.*

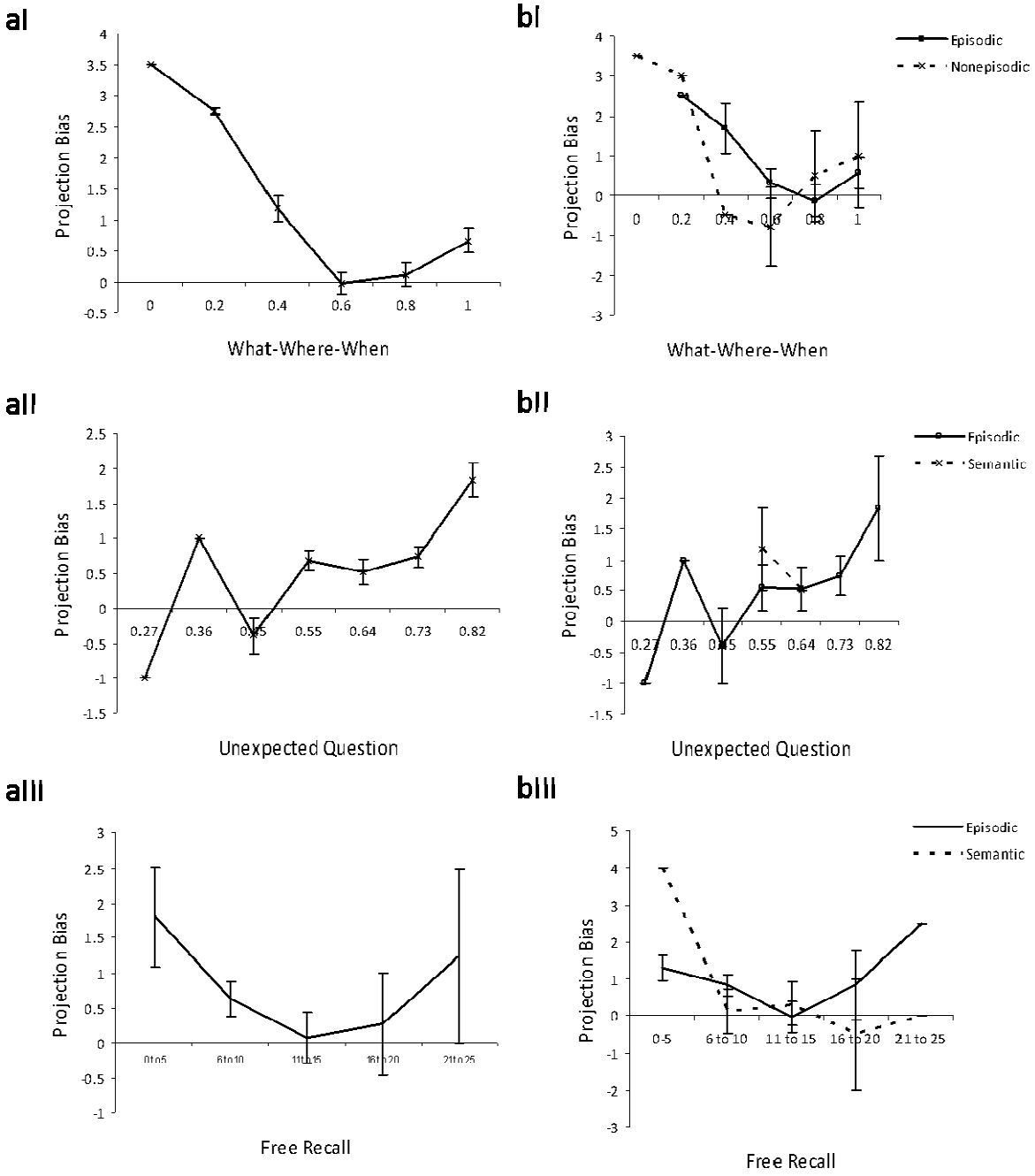

Figure 4.4. *Relationship between memory tests and PB. aI) Relationship between WWW and PB. aII) Relationship between UEQ and PB. aIII) Relationship between FR and PB bI-III) Relationships as divided by memory strategy. Error bars represent standard error.*

Relationships between sub-elements of the memory tests

There was no significant correlation between any of the what, where or when elements and UEQ, although there was a trend for "where" (Kendell's tau: what: R=-0.016, p=0.878; where: R=-0.177, p=0.096; when: R=0.057, p=0.596). There was also no significant correlation between any of the what, where or when elements and FR (Kendell's Tau: what: R=0.085, p=0.380; where: R=0.112, p=0.264; when: R=-0.08, p=0.434).

There was no significant correlation between UEQ and free recall of either concrete (R=0.016, p=0.893) or non-concrete (R=-0.048, p=0.690) words. There was, however, a significant correlation between WWW performance and free recall of non-concrete (R=0.253, p=0.033) but not concrete (R=0.193, p=0.107) words.

Projection Bias Test

It was predicted that subjects in the chocolate group would be more biased towards refreshing food than subjects in the citrus group (see appendix 2). Subjects were generally consistent in their choices: the menu choices made before pre-feeding were positively correlated with the menu choices made after pre-feeding (R=0.681, p<0.001). However, people were substantially biased by the pre-feeding. A difference score was calculated for each subject for menu choices made before and after pre-feeding. The chocolate group were significantly more biased towards choosing refreshing food for tomorrow than the citrus group (independent samples t-test t[75]=2.690, p=0.009). When the difference score for the two groups was combined

such that the pre-feeding effects went in the same direction (i.e. the scores of one group were multiplied by -1), this difference score was significantly different from zero (t[76]=2.672, p=0.009) suggesting that subject's choices for the future were significantly biased by their current motivational state, rather than changing in a group-independent manner over time.

Relationship between Memory Tests and Projection Bias

The relationship between PB and the memory tests was assessed using Pearson's correlation to test for linear relationships and univariate GLM to test for nonlinear relationships.

Free Recall

Subjects who performed very well or very badly on the FR test were more biased in the PB test than those that performed moderately. There was no linear relationship between FR and PB (R=-0.110, p=0.343). However, there was an effect of FR in the univariate GLM ($F_{1,74}$=4.327, p=0.041) as well as a trend towards a quadratic relationship ($F_{1,74}$=3.751, p=0.057; see Figure 4.4). There was no significant difference in magnitude of PB between subjects that reported episodic and those that reported semantic strategies in the FR test (t[38]=-0.201, p=0.841).

Subjects who reported episodic strategies but not semantic strategies (N=22) showed no linear relationship between FR and PB (R=-0.083, p=0.715). Figure 4.4 indicates, however, that there was a U-shaped curve in which people who performed badly at

FR and people who performed very well at FR were the most biased in PB, and people who performed moderately at FR were the least biased in PB (and, indeed, more likely to overcompensate[9]). This curve was associated with a trend in the GLM suggesting a main effect of FR on PB ($F_{1,74}$=4.265, p=0.054) as well as a quadratic relationship ($F_{1,74}$=3.991, p=0.061).

Subjects who reported semantic strategies but not episodic strategies (N=18) showed no relationship between FR and PB (Pearson's R=-0.261, p=0.295; univariate GLM, no effect of FR on PB: $F_{1,74}$=1.676, p=0.216; quadratic relationship: $F_{1,74}$=1.185, p=0.295).

Unexpected Question

Subjects that performed better on the UEQ tests were more biased in the PB test. There was a significant positive correlation between PB and UEQ (R=0.279, p=0.014; see Figure 4.4). There was neither a main effect of UEQ on PB ($F_{1,74}$=0.00, p=0.999) nor a quadratic relationship ($F_{1,74}$=0.109, p=0.743) in the univariate GLM.

Among subjects who used only episodic strategies (N=50), there was a significant positive correlation between UEQ performance and PB (Pearson's R=0.331, p=0.019), but no main effect of UEQ on PB ($F_{1,74}$=0.071, p=0.791) or quadratic relationship ($F_{1,74}$=0.251, p=0.619) in the GLM.

[9] Which is perhaps unsurprising given the finding that people tend to overestimate the satiating effects of consumption (e.g. Kahneman and Snell, 1992).

Only four subjects reported using solely semantic strategies in the UEQ test, thus the relationship between performance on the UEQ test and PB could not be assessed in this group.

What-Where-When

Subjects who were very accurate, or very inaccurate, at locating their treasure in the WWW test were more biased in the PB test than those who were moderately accurate (see Figure 4.4; univariate GLM effect of WWW on PB: $F_{1,74}$=9.612, p=0.003, quadratic relationship: $F_{1,74}$=8.206, p=0.005). This relationship was negatively skewed, suggesting that those who performed badly on WWW were more biased than those that performed well. There was, however, no linear relationship between integrated WWW score and PB (R=-0.160, p=0.168).

There was no significant difference in extent of bias in the PB test between people who reported episodic strategies and those who did not (t[69]=0.194, p=0.847). There was, however, a difference in the nature of the relationship between WWW and PB between subjects reporting different strategies. The quadratic (U-shaped) relationship between WWW and PB appears to have been driven by those *not* reporting episodic strategies. Among subjects who reported either re-experiencing or story-creation (the episodic strategies), there was no correlation between integrated WWW score and PB (R=-0.151, p=0.492). There was also no effect of WWW on PB ($F_{1,74}$=2.158, p=0.158) or quadratic relationship ($F_{1,74}$=1.872, p=0.187) in the GLM. Among subjects who *did not* report an episodic strategy there was no correlation between integrated WWW score and PB (R=-0.213, p=0.146). There was, however, a

significant main effect of WWW on PB ($F_{1,74}$=7.753, p=0.008) and a quadratic relationship ($F_{1,74}$=6.279, p=0.016).

Overall Memory Tests

There was no significant effect of the tendency to use episodic cognition (i.e. number of memory tests in which episodic strategies were used) and magnitude of bias in the PB test (univariate GLM: $F_{1,74}$=0.971, p=0.412).

Impact of Pre-feeding on Memory

In the design of this study, it was assumed that the pre-feeding (performed as part of the BK test) would not impact the other tests undertaken. However, there is a possibility that the pre-feeding may have affected the ability of subjects to remember episodically. There was a trend for an interaction between the tendency to use episodic cognition and pre-feeding condition to affect overall memory score ($F_{1,74}$=2.634, p=0.057). This analysis is post-hoc and exploratory, but raises the possibility that consumption of the chocolate pre-feeding foods between encoding and retrieval actually affected performance on the episodic memory tests. This is a possibility that is explored in the next chapter.

4.4. Discussion

A sample of undergraduates was tested on three putative episodic memory tests (WWW, UEQ and FR) as well as a putative test of episodic foresight (PB). There

were some relationships between performance on the memory tests, although these relationships were partial and relatively weak. Performance on the WWW test correlated positively with performance on the FR test. There was a possible quadratic relationship between WWW and UEQ, suggesting that those who performed very well or very badly on WWW were more accurate on UEQ than those who performed moderately. Degree of bias in the PB tests was related to performance on the memory tests in a similarly complex fashion. There was a positive correlation between PB and UEQ, suggesting that the better subjects performed on UEQ, the more biased they were by their current motivational state when making choices for the future. Both FR and WWW showed a U-shaped relationship to bias in the PB test, suggesting that those who performed very well or very badly on these tests were more biased by their current motivational state than those who performed moderately.

In general, the findings presented in this chapter roughly correspond to those found in Chapter 3. There was little linear relationship between different memory tests, and those subjects who were better at answering unexpected questions were *more* biased by their current state when making choices for the future. This suggests that the lack of relationship between memory tests found in Chapter 3 was not purely the result of developmental factors. There were not sufficient degrees of freedom to assess potential quadratic relationships between tests in the experiment presented in Chapter 3. However, an interesting focus of future research would be to assess the extent to which the nature of such a relationship may alter with age. For example, it would be interesting to discover if the relationship between UEQ and WWW is quadratic in all age groups, or whether it becomes so as children get older.

The finding that WWW did not correlate with UEQ is in contrast to previous findings that WWW performance correlated positively with UEQ (Holland and Smulders, 2011). However, there are a number of methodological differences between that study and the one presented here that may have resulted in this contrasting finding. In the first instance, the unexpected questions in Holland and Smulders' study were in a yes/no format, while in the present study they were open-ended. In a sense, this means that Holland and Smulders' study used a "cued recall" UEQ test, while the present study used a "free recall" UEQ test. Given the difference in the reported memory experience in free and cued recall paradigms (see Chapter 1), this may mean that the contribution of episodic cognition to UEQ performance might have been different in these two studies. Secondly, Holland and Smulders required participants to recite nursery rhymes during the hiding period to stop them verbally practicing the location of the coins, this was not done in the present study. This may mean that subjects in the present study had more opportunity to memorize the location of the coins using verbal rehearsal techniques. This may have altered the contribution of episodic cognition to WWW performance. Thirdly, the retention interval of Holland and Smulder's test was over the course of 3 days, while the retention interval for the current test was over the course of around 20-30 minutes. This may have meant that the memories retrieved in Holland and Smulder's study were differently consolidated compared with those in the present study. Finally, the retrieval scenario was different between the studies: while in Holland and Smulder's study subjects were asked to free recall the what, where and when for each coin, subjects in the current study behaviourally identified the location of a pre-specified what/when combination. This may have meant that subjects were differently motivated to get certain aspects (particularly the "what" aspect) correct. As Holland and Smulders discuss, the fact that both of their coin-

types (2p and 20p coins) had comparably little value may have meant that there was no significant motivation to identify the coin type correctly.

According to subjects' self-reports, they used an almost equal mix of episodic and semantic strategies in the free recall test. This is in contrast to UEQ where almost all subjects reported using an episodic strategy. These reports are difficult to compare to the self reports of subjects in the WWW test, in which it was difficult to code reports into episodic and semantic, but in which around a third of subjects reported "re-experiencing" or "making a story of" the hiding event. In none of the memory tests was there a significant effect of reporting using an episodic strategy on performance. This result is similar to that demonstrated by Easton and colleagues (2012), who found that when subjects were asked to recall *when* they had previously seen a particular object-location combination, their answers were significantly more like to be "remembered" than "known". However, whether subjects reported "remembering" or "knowing" the answer did not have any effect on their performance. The authors concluded that both episodic and semantic processes can be used to identify *when* a particular location-object pairing has been previously seen, but only episodic memory can be used to assess *in which context* it was seen. Interestingly, reports of "knowing" in the current study were relatively common in the FR and UEQ tests (14% and 19% respectively) but not in the WWW, in which "knowing" was not reported by any subject. This supports the findings of Holland and Smulders (2011) and Easton and colleagues (2012) that WWW tests are overwhelmingly reported as "remembered" rather than "known" (when given the option only between these two reports). However, this may also suggest that the type of memories tapped by WWW tests do

not lend themselves to being reported as "known" but do not necessarily involve episodic cognition.

Contributions of both semantic and episodic elements?

There was a significant linear relationship between UEQ and level of PB, suggesting that those subjects who were more successful on UEQ were the most biased in the PB test. Given that over 90% of subjects reported using an episodic strategy to solve the UEQ test, this raises the possibility that, contrary to the assumptions of the Bischof-Köhler hypothesis, episodic ability (insofar as it is assess by the UEQ test) may be *negatively related* to the ability to disengage from current state. This would be logical if one assumed that episodic cognition, due to its constructive nature, is more vulnerable to bias from current feelings than non-episodic/semantic cognition (see introduction of this chapter). This argument is potentially supported by the fact that those who reported only semantic strategies in the free recall test had no relationship between FR performance and level of PB, while those reporting episodic strategies showed a relationship between performance on the two tests. The fact that this relationship was quadratic rather than linear may be indicative of contributions from both episodic and non-episodic processes to FR performance, even if subjects report episodic experience. A similar quadratic relationship between performance on WWW and PB suggests again that this test also involved contributions from both episodic and non-episodic components.

Episodic constructions of both past and future are constrained and specified ("scaffolded") by known facts about the world. For example, someone might *know*

that it rains a lot in Glasgow, and thus when they imagine being in Glasgow, it is likely that the representation will contain rain. Similarly, if someone *knows* that there were 28 words on the wordlist, they are more likely to attempt to recall all 28 words – potentially resulting in recall of more words than if they were unaware of the number of words on the list. In both the WWW and FR tests (but not the UEQ test) subjects had the opportunity to use encoding strategies to aid their memories. The use of deliberate encoding strategies may have increased the contribution of such semantic "scaffolding". For example, subjects may have mentally categorised the words, leading them to *know* that there were two words relating to body parts and attempt to remember both.

There was differential opportunity for subjects to use semantic strategies in the different tests. Those engaged in answering an unexpected question on a single unusual event (hiding virtual treasure on a computer-generated island) have very little semantic scaffold (that is, few *facts*) to support their memory. Specifically, there is both no opportunity to deliberately *encode* semantic scaffolds (such as rules about where certain items are located) nor is there much of a knowledge base to rely upon (there is not, for example, a "usual" number of birds in a virtual beach scene). This lack of opportunity for semantic scaffolding was reflected in subjects' self reports: only four subjects reported using no episodic strategies in the UEQ test. This difference in opportunity for scaffolding, along with the evidence from the self-reports, may suggest that UEQ may represent a "purer" form of episodic memory test, with fewer contributions from non-episodic factors.

Where a semantic scaffold *is* available, one might expect the accuracy of a scaffolded memory to be modulated both by the vividness of the episodic contribution *and* the accuracy or applicability of the facts within the semantic scaffold. Thus people who constructed poor episodic details around a very accurate semantic scaffold may perform better (i.e. remember more accurately) than those who construct vivid episodic details around an inaccurate semantic scaffold. Those that have both an accurate semantic scaffold *and* vivid episodic details might be expected to perform the best. Thus the accuracy of the semantic scaffold would modulate the relationship between accuracy on a 'true' test of episodic memory and accuracy on a memory test that involved both semantic and episodic components; low-accuracy semantic scaffolds predicting a negative relationship and high-accuracy semantic scaffolds predicting a positive relationship. To give an example; suppose four people attend two different training courses; persons 1 and 2 (with a poor episodic memory and a vivid episodic memory respectively) attend a course that accurately teaches facts about anatomy. Persons 3 and 4 (with a poor episodic memory and a vivid episodic memory respectively) attend a course that teaches misinformation about anatomy. After these courses, all four watch an operation and are then quizzed about what they saw. When asked, for example, which organ was being operated upon, both the people with a very poor episodic memory may have to simply guess at the answer because they do not remember seeing the organ at all. Scaled up to the whole test, this would give them a chance level of performance (sometimes they will get the answer correct, sometimes they won't). Person 4 (with a very vivid episodic memory but completely inaccurate knowledge of anatomy) will get the answer wrong, because they confidently remember seeing the organ, they have labelled that organ incorrectly. Scaled up to the whole test, this would result in a below-chance performance. Finally,

person 2 (with both a vivid episodic memory and an accurate knowledge of anatomy) will consistently get the answers correct. At the level of the whole test these four people would demonstrate a quadratic relationship between performance on this "operation" memory test and performance on a theoretical "pure" episodic memory test (see figure 4.5). Among those that attended the misinformation course, there would be a negative relationship between episodic memory score and performance (in that the person with a vivid episodic memory would have performed worse) while in those that attended the genuine-information course would show a positive relationship between episodic memory score and performance (in that the person with a vivid episodic memory would have performed better).

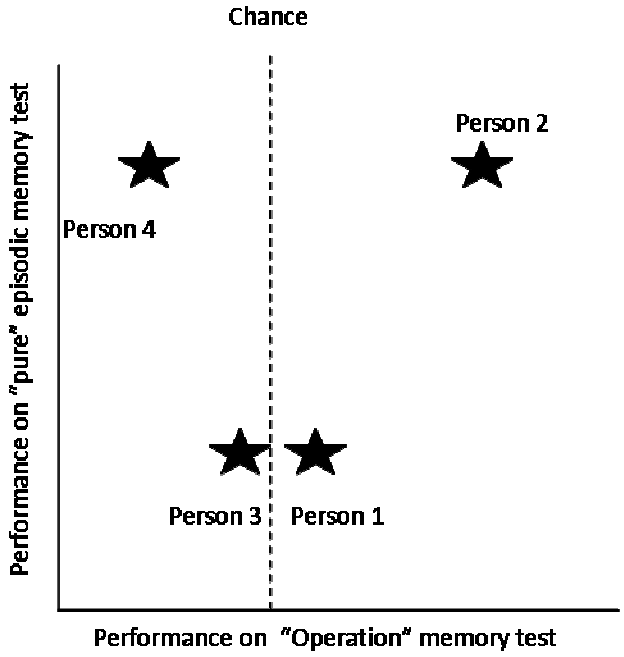

Figure 4.5. *Example of the relationship between performance on a "pure" episodic memory test and test that relies on both episodic memory and semantic knowledge where persons 1 and 2 have accurate semantic knowledge and persons 3 and 4 have inaccurate semantic knowledge.*

Such an explanation might neatly account for the findings of this experiment if it is assumed that UEQ and PB are relatively "pure" tests of episodic cognition while FR and WWW contain both episodic and semantic elements (such that the accuracy of the "scaffold" of the memory can modulate the relationship between episodic vividness and accuracy). Such an account could in theory be tested in future research with the inclusion of a semantic memory test to assess the accuracy/appropriateness of subjects' use of semantic information.

In conclusion, the findings presented in this chapter demonstrate a relationship between all three types of episodic memory test (WWW, UEQ and FR) as well as relationships between each and these and the PB test. Not all of these relationships were linear, and many were quadratic. Such quadratic relationships may be indicative of the contribution of multiple factors. Specifically, it was suggested that the quadratic relationships may have been the result of a modulation of episodic input by semantic scaffolding. Finally, it was briefly mentioned that the act of pre-feeding may have itself affected episodic memory performance. The impact of diet on hippocampal function and episodic cognition is explored in the next chapter.

Chapter 5
The Impact of Diet and Obesity on Episodic Cognition

There is considerable evidence to suggest that poor diet and obesity may lead to disrupted hippocampal function. Thus an investigation into the impact of these factors on episodic cognition is warranted. Two experiments were conducted to examine this issue. In the first, a population sample varying in body mass index (BMI), self-reported levels of dietary fat and sugar, and self reported levels of binge-eating was presented with a Projection Bias (PB) test and an Unexpected Free Recall (UFR) test. It was found that a high BMI predicted poor performance on the UFR test while a high fat diet predicted reduced bias in the PB test. In Experiment 2, a sample of obese binge-eating subjects underwent a PB test several times during 2-months' treatment with a μ-opioid antagonist. It was found that drug treatment made no difference to performance, suggesting that subjects were choosing according to semantic representations rather than being biased by their current state, as would be expected from an episodic strategy. It is concluded that obesity and diet do modulate episodic cognition, but affect different putative tests of episodic cognition differently.

5.1. Introduction

Chapter 4 used individual differences in performance on episodic memory tests in the adult human population to assess the relationship between different measures of episodic cognition. The present chapter explores the factors that may lead to such individual differences in performance. In particular, the overarching goal of this chapter is to explore the fourth prediction laid out in Chapter 1: that if different tests of episodic cognition assess the same underlying psychological process, performance on these tests should be impaired in the same way by the same factors.

It has been extensively demonstrated that patients with damage to hippocampal structures exhibit deficits in episodic cognition (e.g. Scoville and Milner, 1957, Tulving, 1985b, Mayes *et al*., 1988, Golomb *et al*., 1993, Sheline *et al*., 1996, 1999, Isaacs *et al*., 2000, Gadian *et al*., 2000, Allen *et al*., 2002, Levine *et al*., 2002, Piolino *et al*., 2002, Spreng and Levine, 2006, Addis *et al*., 2007, Piolino *et al*., 2010, Girard *et al*., 2010). . However these studies have been conducted in patient groups. The aim of this chapter is to explore factors that may lead to individual differences in hippocampal function in the non-clinical population and assess the impact of these factors on episodic cognition. There is accumulating evidence for an association between poor diet, obesity and damage to hippocampal functioning. However, the relationship between these factors and episodic cognition is yet to be explored.

This chapter contains two experiments. In the first, individuals who varied in body mass index (BMI), self-reported levels of dietary fat and sugar, and eating behaviour were tested on two forms of episodic cognition (namely unexpected Free Recall [FR]

memory and the Projection Bias [PB] test) in order to test the hypothesis that poor diet and obesity do result in poorer performance on such assessments. In the second experiment, a sample of obese, binge-eating individuals was tested on FR memory and was repeatedly tested on the PB menu choice test throughout treatment with a μ-opioid antagonist. μ-opioid antagonism is thought to reduce the hedonic experience of eating high-fat, high sugar food, and is thus being explored as a potential pharmacological treatment for obesity. This experiment investigated whether the same performance on the PB test would be seen in obese individuals if the modulation of current state was achieved through the reduction of hedonic experience (i.e. how much they *liked* eating the food) rather than through satiation. Such an investigation would test the possibility that abnormal behaviour in the PB test in the overweight may be due to unusual responses to satiation, rather than a differential use of episodic cognition.

Diet, Obesity and Hippocampal Functioning

Obesity is fast becoming an international health crisis. As of 2009, it was estimated that a billion people are overweight, and around 300 million are obese worldwide (World Health Organisation, 2009). In recent years, there has been an increased focus on the psychological and neurological correlates of obesity. Of relevance to this thesis, there has been increasing evidence that obesity, and risk factors associated with obesity (e.g. a high-fat, high-sugar diet and binge eating) are associated with damage to the hippocampus. This raises the question of whether such individuals would also show impaired performance on tests of episodic cognition, given the established role of the hippocampus in this process (e.g. Squire *et al*., 1992).

There are a number of angles from which the association between diet, obesity and hippocampal functioning can be investigated. Firstly, the impact of poor diet and obesity can be studied independently. Secondly, directionality should be explored: is obesity a symptom of disruption to hippocampal functioning, or is unusual hippocampal function a symptom of obesity? Finally, indirect associations can be investigated: are there factors implicated in memory performance that are affected by obesity and/or poor diet?

Hippocampal damage leads to obesity

Unusual ingestive behaviour has been reported in humans and animals with structural damage to the hippocampus. Patients with extensive bilateral damage to the hippocampal area (including the amygdala) are willing to eat a second (and even third) meal when presented only a few minutes after the first (Rozin *et al*., 1998, Hebben *et al*., 1985). It is difficult to determine whether this could result from simply failing to remember having consumed food (these subjects are densely amnesic) or an insensitivity to internal states (patient HM, for example, also showed aberrant reactions to temperature and pain: Hebben *et al*., 1985). However, this evidence does support the idea that the structural integrity of the hippocampus is important for normal meal-limitation. Rats with selective neurotoxic lesions to the hippocampus show increased motivation to work for food relative to controls (e.g. Schmelzeis and Mittleman, 1996, Clifton *et al*., 1998) and are less able to use cues of hunger, thirst or satiety as discriminative stimuli (Kennedy and Shapiro, 2004, Davidson and Jarrard, 1993, Hock and Bunsey, 1998). Furthermore, rats with lesions to the hippocampus

(but not the prefrontal cortex) gain more weight post-surgery and end up weighing more than control rats (Davidson and Swithers, 2004, Davidson *et al*., 2009). Davidson and colleagues argue that the incremental, modest weight gain of their rats (unlike the dramatic weight gain seen after hypothalamic lesions) is comparable to that seen in human obesity (e.g. Lewis *et al*., 2000).

Obesity leads to hippocampal damage and memory/episodic cognition impairment

There is some evidence to suggest that obesity may lead to hippocampal damage or unusual hippocampal function. The hippocampus is unusually activated after ingestion (or gastric stimulation designed to simulate ingestion) in obese or previously-obese individuals but not in healthy subjects (DelParigi *et al*., 2004, Gautier *et al*., 2001, Wang *et al*., 2006). Furthermore, obese subjects show atrophy in the frontal lobes and hippocampus compared to healthy controls (Raji *et al*., 2010, Gustafson *et al*., 2004b). Obesity and health problems that result from obesity (e.g. type 2 diabetes) are significant risk factors for cognitive decline and Alzheimer's disease in later life (Elias *et al*., 2005, Wolf *et al*., 2007, Irie *et al*., 2008, Leibson *et al*., 1997, Gustafson *et al*., 2004a) This may be a result of increased cerebral atrophy, although whether this is the result of Obesity, or lead to the obesity is as yet unclear.

There is also evidence that to suggest that memory may be impaired in obesity. Obese individuals have been shown to display deficits in both immediate and delayed FR and recognition (Elias *et al*., 2003, Gunstad *et al*., 2006, Gunstad *et al*., 2010), self-report more problems with memory (Trakas *et al*., 2001) and are impaired relative to

healthy controls on both digit-span retention and the Trail Making test (which can be considered a form of spatial/multi-stage planning test [Kilander *et al*., 1997]). This memory impairment may be mirrored by alterations to future-oriented decision making in obese individuals. Nisbett & Kanouse (1969) showed that, in a real-world variant of the PB test (as described in detail in Chapter 4) overweight individuals showed a substantially different pattern of behaviour to healthy-weight individuals. While healthy-weight individuals tended to buy more food the longer it had been since they had eaten, overweight people tended to buy *less* food the longer it had been since they had eaten.

Poor diet leads to hippocampal damage and poor memory

Research on rats suggests that a high-fat high-sugar diet causes changes in hippocampal function (Kanoski *et al*., 2007, Molteni *et al*., 2002, van der Borght *et al*., 2011) and impaired learning and memory (Molteni *et al*., 2002, Jurdak and Kanarek, 2009, Jurdak *et al*., 2008). Preliminary studies in humans also raise the possibility that individuals who consume high-fat high-sugar diets show impairments in the episodic memory (Francis and Stevenson, 2011).

Neurophysiological and neuroendocrine relationships between poor diet, obesity and hippocampal function and memory

Feeding is controlled and regulated by the complex interaction of a number of hormones and peptides (see Box 3). Some of the main hormones implicated in control of feeding behaviour are insulin, leptin, ghrelin, neuropeptide Y (NPY), brain-derived

neurotrophic factor (BDNF) and cholecystokinin (CCK). These hormones are dysregulated in obesity and by high levels of dietary fat and sugar (see Box 3). However, while the role of these hormones and peptides in energy regulation and feeding is well established, there is growing evidence that each of them both acts in the hippocampus and affects memory performance. In the following section, these shall be discussed in detail.

Cholecystokinin (CCK): CCK is a fast-acting, short-term satiety signal (see Box 3) that acts in the gut and brain. Plasma CCK and CCK secretion are increased in obese individuals. While to date there are no studies investigating the role of CCK on memory in humans, there is a possibility that the dysregulation of CCK in obesity (see Box 3) may be accompanied by a disruption of learning and memory. Much of the evidence for the role of CCK in obesity originates from research on the Otsuka Long-Evans Tokushima Fatty (OLETF) rats, which are known to become obese. These rats have also been shown to exhibit impaired hippocampal-dependent spatial learning, as measured by performance on the Morris water maze (Matsushita *et al*., 2003, Moran *et al*., 1998, Li *et al*., 2002a, Nomoto *et al*., 1999). There is also evidence for impaired long-term potentiation (LTP) expression in the dentate gyrus of the hippocampus in these animals (Nomoto *et al*,. 1999). However, some have argued (e.g. Biessels and Gispen, 2005) that the deficits seen in OLETF rats may be more attributable to their hyperinsulinemia than their lack of CCK receptors *per se*.

	Box 3		
	Neuropeptides/Neurotrophic Factors in Feeding, Obesity and Diet		
	Role in Feeding	**Dysregulated in Obesity**	**Dysregulated By High Fat High Sugar Diet**
Leptin	**Leptin acts to inhibit appetite (in part, by counteracting the effects of NPY). This effect is long-lasting, unlike the fast-acting satiating effects of CCK.** *Chin-Chance et al., 2000; Keim et al., 1998; Halford et al., 2000; Proulx et al., 2002; Forbes et al., 2001; Dhillion et al., 2001, Tschop et al., 1998; Blundell et al., 2001; Cohen, 2006; Shimizu et al., 2005; Joannic et al., 1998; Heini et al., 1998*	**Obesity is characterised by a period of leptin hypersensitivity followed by insensitivity. The absence of leptin (or its receptor) leads to uncontrolled food intake and resulting obesity** *Fleur et al., 2009; Farr et al., 2006; Montague et al., 1997; Maffei et al., 1995; Friedman & Halaas., 1998; Pelleymounter et al;., 1995; Clement et la., 1998; Considine et al., 1996; Enriori et al., 2007; Yildiz et al., 2004;* Takaya et al., 1996; Hassink et al., 1996	**High-fat, high-sugar diet increases plasma leptin concentrations, and low calorie diet reduced leptin levels** *Fleur et al., 2009; Farr et al., 2006; Weigle et al., 1997; Vasselli, 2008; Shapiro et al., 2008; Wang et al., 2001; Enriori et al., 2007; Heshka & Jones, 2001;* Melanson et al., 2007
Insulin	**Insulin is crucial in the removal of glucose from blood into cells. Insulin levels are used by the body as an indicator of energy need: An increase in the level of circulating insulin is associated with satiety.** *Rezek, 1976; Deetz & Wangsness, 1980; Chapman et al., 1998; Holt et al., 1995; Holt et al., 1992; Baura et al., 1993*	**Obesity is a major risk factor for developing type II diabetes, causing insufficient insulin production (Insulin resistance)** *Kissebah et al., 1982; Despres, 1993; Dowling et al., 1995; Albu et al., 1999; Lavau et al., 1975; Susini & Lavau, 1978*	**High Fat diet induces insulin resistance** *Storlien et al., 1986; 2006; Himsworth 1985; Anderson et al., 1973; Lavau et al., 1975; Susini & Lavau, 1978; Grundleger & Thenen, 1982;Hedeskov et al., 1992; Irani et al., 2007; Kaivala et al,. 2000; Boghossian et al., 2009; Clegg et al., 2004; Monteleone et al., 2003; Brøns et al., 2009 ; Wang et al., 2001;* Melanson et al., 2007
Ghrelin	**Ghrelin is a peptide found in the hypothalamus and stomach that stimulates food intake.** *Kojima et al., 1999; Tschop et al., 2000; van der Lely et al., 2004; Horvath et al,. 2003; Kojima et al., 2005; Tschop et al., 2001;* Schmid et al., 2005; Wren et al., 2001	**Ghrelin levels in the plasma of obese individuals are lower than those in leaner individuals** *English et al., 2002; Ariyasu et al,. 2002; Gottero et al., 2004; perreault et al., 2004; Yildiz et al., 2004; Cummings et al., 2002; Tschop et al., 2001; Shiiya et al., 2002; English et al., 2002*	**High fat diet reduces fasting plasma Ghrelin concentrations** *Beck et al., 2002; Lee et al., 2002; Shiiya et al., 2002; Robertson et al., 2004 ; English et al., 2002; Monteleone et al., 2003;* Melanson et al., 2007 *(but see Paul et al., 2005; little et al., 2008)*
Neuropeptide Y (NPY)	**NPY is a potent feeding stimulant.** *Danho et al., 1988; Flood et al., 1989; Jolicoeur et al., 1991; Kalra et al., 1990; McLaughlin et al., 1991; Magdalin et al., 1989; Clark et al., 1984; Levine et al., 1984; Morley et al., 1987b; Hanson & Dallman, 1995; White et al., 1994; King et al., 1999; Pomonis et al., 1997; Stanley 1993*	**Obesity is associated with an increase in NPY mRNA and NPY release. NPY can induce adipogenesis.** *Zarjevski et al., 1993; Kuo et al., 2008; Beck et al., 1992; McKibbin et al., 1991;* Williams et al., 1992; *Sanacora et al., 1990; Beck et al., 1993; Bchini-Hooft van Huijsduijnen et al., 1993; Sanacora et al., 1992; Kowalski et al., 1999; Mc Carthy et al., 1991; Widdowson, 1997; Stricker-Krongrad et al., 1994;* Hollopeter et al., 1998; Guan et al., 1998	**High fat high sugar diet stimulates the release of NPY** *Kuo et al., 2007; Wang et al., 2002; Warne & Dallman, 2007;* Maggio et al. 1988; Hollopeter et al., 1998
Cholecystokinin (CCK)	**CCK acts as a fast-acting, short-term satiety signal** *Gibbs et al,. 1973a; 1973b; 1976; Smith et al., 1974; Sturdevant & Goetz, 1976 ; Cupples, 2003; Liddle et al., 1984; Avery & Livosky, 1986; Le Sauter et al., 1988; Beglinger et al., 2001;* Antin et al., 1975; *Holt et al., 1992*	**Animals lacking CCK receptors are known to become obese. Plasma CCK is increased in Obese subjects and CCK secretion is high in Obese subjects (as compared to lean) following a high-fat meal.** *Matsushita et al., 2003; Moran et al., 1998, Li et al., 2002; Nomoto et al,. 1999; Kawano et al., 1992;* Oku et al., 1984; DeFanti et al., 1998; Cain et al., 1997; Wang et al., 1998; Miyasaka et al., 1994; Takiguchi et al., 1998; Funakoshi et al., 1995; Funakoshi et al., French et al., 1993; 2000; Baranowska et al., 2000 (but see Lieverse et al., 1994a; Lieverse et al., 1994b; Lieverse et al., 1995)	**Chronically elevated plasma CCK concentrations, induced by high fat diet mediate a reduced sensitivity to CCK** *Covasa & Ritter ,1998; Savastano & Covasa, 2005 ; Covasa & Ritter 2000; Covasa et al., 2000; Torregrossa & Smith, 2003; French et al., 1995; Spannagel et al., 1996.; but see Boyd et al., 2002 for evidence that high fat diet does not influence plasma CCK.*
Brain-Derived Neurotrophic Factor (BDNF)	**BDNF acts to reduce food intake** *Lebrum et al., 2006; Fox & Byerly 2004*	**Obese individuals have lower levels of serum BDNF (but this may be more associated with binge eating than obesity per se)** *El-Gharbawy et al., 2006; Nakazato et al., 2003,; Monteleone et al., 2004; Gray et al., 2006; Marlin et al., 1994; Yeo et al., 2004*	**High fat diet reduces BDNF in the hippocampus** *Kanoski et al., 2007; Molteni et al., 2002*

Leptin and Insulin: Leptin and insulin are peripheral hormones – released by fat cells and the pancreas respectively – that help to regulate consumption (see Box 3). High levels of dietary fat and sugar, as well as obesity, are associated with insensitivity to both leptin and insulin (see Box 3). There are dense populations of leptin and insulin receptors in the hippocampus (Lathe, 2001), suggesting that dysregulation of these hormones may affect hippocampal function. Evidence from rodent models suggests that this is the case.

Both administration of leptin and insulin have been shown to improve spatial memory and hippocampal LTP in rats (Farr *et al*., 2006, Zhao *et al*., 2004). Rodent models of diabetes are impaired on the Morris water maze of spatial memory, despite being relatively unimpaired on simple learned tests such as passive avoidance and, in the case of Zucker rats, in a frontal go-no go test; ; streptozotocin [STZ] induced diabetes: (Biessels *et al*., 1996, Popovic *et al*., 2001, Gispen and Biessels, 2000); BB/Wor rats: (Li *et al*., 2002b); Zucker Rats: (Li *et al*., 2002b, Winocur *et al*., 2005); diet-induced insulin resistance: (Stranahan *et al*., 2008)) These deficits are often accompanied by evidence of abnormal expression of LTP and decreased neuronal density in the hippocampus (STZ-induced diabetes: (Kamal *et al*., 2005, Gispen and Biessels, 2000); BB/Wor rats: (e.g. Li *et al*., 2002b); Non-Obese Diabetic (NOD) mice: (Valastro *et al*., 2002); Zucker rats; (e.g. Gerges *et al*., 2003); diet-induced insulin resistance: (Stranahan *et al*., 2008, Stranahan and Mattson, 2008)).

In humans, there is evidence for memory loss and impaired executive function in patients with type II diabetes (e.g. Ryan and Geckle, 2000) especially in older adults[10] (Awad *et al*., 2004, Convit *et al*., 2003). Higher fasting insulin levels have been associated with lower hippocampal and orbital frontal volume in older subjects, and type 2 diabetes is associated with atrophy of the frontal lobes and hippocampus (Raji *et al*., 2010, Bruehl *et al*., 2011); and unusual hippocampal blood flow (Wu *et al*., 2008). Higher fasting plasma insulin levels have also been associated with cognitive deficits in elderly subjects (Yaffe *et al*., 2004, Watson and Craft, 2003, Irie *et al*., 2008, Leibson *et al*., 1997). High circulating leptin levels, meanwhile, are associated with poorer performance on the Trail Making test (Gunstad *et al*., 2008).

Thus it appears that dysregulation of leptin and insulin, such as is seen in obesity and after high levels of dietary fat and sugar, is associated with deficits in hippocampal function and memory.

Ghrelin: Ghrelin is a peptide found in the stomach and brain that acts to stimulate food intake. High levels of dietary fat act to reduce circulating ghrelin levels, and ghrelin concentrations are reduced in obesity (see Box. 3).

Research in rodents has demonstrated that ghrelin binds to neurons of the hippocampal formation, where it promotes synapse formation and LPT. This neuronal action is accompanied by enhanced spatial learning and memory. Furthermore, disruption of the gene that encodes ghrelin resulted in fewer spine synapses and impaired memory. These effects were reversible by ghrelin administration (Diano *et*

[10] Although given that hippocampal atrophy and impaired memory are symptoms of normal aging, it is difficult to tell if this effect is additive or interactional

al., 2006, Chen *et al*., 2011). In rodents, ghrelin has been shown to improve spatial memory and memory retention (Carlini *et al*., 2002, Davis *et al*., 2011) as well as reducing memory impairments seen in rodent models of diabetes and Alzheimer's (e.g. Moon *et al*., 2011).

This evidence may suggest that lowered concentrations of ghrelin – as found in obesity and after a high-fat diet – may result in poorer hippocampal function and memory.

Neuropeptide Y (NPY): NPY is a neuropeptide that has roles in numerous areas of the brain. In particular, NPY is known as a potent appetite stimulant (see Box 3). Obesity is associated with increased NPY release and mRNA and a high fat diet can stimulate NYP release (see Box 3).

NPY receptors are distributed throughout the brain but are clustered in the hypothalamus and hippocampus (Dumont *et al*., 1992). In the rat hippocampus, large quantities of NPY-containing cells are found in the dentate gyrus, and the CA_1 CA_2 and CA_3 subfields (Chronwall *et al*., 1985, de Quidt and Emson, 1986b, 1986a, Köhler *et al*., 1986), a pattern that correlates closely with that seen in the human hippocampus (Chan-Palay *et al*., 1986a, 1986b). Intracerebroventricular (ICV) injections of NPY have been shown to enhance spatial memory (Morley and Flood, 1990, Flood *et al*., 1987, 1989, 1989) and reverse amnesia. However passive immunization with NPY antibodies, injected into the hippocampus, induces amnesia (Flood *et al*., 1987), an effect that is mediated by the rostral hippocampus and amygdala (Flood *et al*., 1989). NPY has also been shown to inhibit glutamate release

onto pyramidal cells in rat hippocampus (Colmers and Bleakman, 1994, Greber *et al*., 1994, Schwarzer and Sperk, 1998).

There has been no investigation as to what effect chronically increased NPY levels have on hippocampal function, so it is unclear whether it would have a positive or negative influence on memory. However, the evidence suggests that NPY modulation (as is seen in obesity) would have a potentially significant effect.

Brain-derived neurotrophic factor: BDNF is a protein that contributes to the survival, growth and maintenance of neurons (Alvarez-Borda *et al*., 2004, Allen and Dawbarn, 2006). BDNF concentrations have been shown to be reduced in obesity and by a high-fat, high-sugar diet (see Box 3).

BDNF is important for activity-dependent synaptic plasticity, LTP (particularly in the hippocampus: (Lu and Gottschalk, 2000)) and learning and memory (Lebrun *et al*., 2006, Rossi *et al*., 2006, Yamada and Nabeshima, 2003, Gartner and Staiger, 2002, Thoenen, 1995, Bramham and Messaoudi, 2005, Wibrand *et al*., 2006, Dalla *et al*., 2007, Kitabatake *et al*., 2007). In particular, it is thought that BDNF is important during the encoding phase of memory retention (Goldberg *et al*., 2008, Hariri *et al*., 2003).

In humans, it has been suggested that genetic polymorphisms modulating BDNF may contribute significantly to heterogeneity of episodic cognitive ability (e.g. Koppel and Goldberg, 2009). A common polymorphism of the human *BDNF* gene (val66met) which dramatically alters the intracellular trafficking and packaging of BDNF's

precursor peptide (pro-BDNF) has been shown to affect hippocampal volume (Szeszko *et al*., 2005, Bueller *et al*., 2006). The polymorphism also affects hippocampal function, producing deficits in episodic memory (Dempster *et al*., 2005, Egan *et al*., 2003, Miyajima *et al*., 2008, Cathomas *et al*., 2010, Dennis *et al*., 2011) and reduced hippocampal engagement during both encoding and retrieval (recognition) of complex novel scenes (Hariri *et al*., 2003). Finally, genetic haploinsufficiency for *BDNF*, and mutations of the BDNF receptor *TrkB* have been associated with obesity as well as severe learning and memory impairments (Gray *et al*., 2006, Yeo *et al*., 2004).

Thus BDNF is crucial for hippocampal LTP and also appears to modulate memory. This may suggest that the reduced concentrations of BDNF seen in obesity may have a substantial influence on hippocampal function and memory.

Summary of connection between poor diet, obesity and hippocampal function/ memory and planning

To date there is little direct evidence for a connection between poor diet, obesity and episodic cognition. Notable exceptions may include the works of Elias and colleagues (2003) and Gunstad and colleagues (2006, 2010) who demonstrated impairments in FR in obese subjects, and Francis and Stephenson (2011) study of poor FR in subjects who self-report high dietary fat and sugar. However, as has been demonstrated above, there is substantial evidence to suggest that there are associations between neurological and hormonal correlates of obesity and high-fat, high-sugar diet and those of hippocampal function and memory. This evidence suggests a clear

hypothesis: that high levels of dietary fat and sugar, leading to, or in combination with, obesity result in changes to hippocampal function. Based on this, there is a need for a dedicated investigation into the potential association between BMI, diet and episodic cognition.

To this end, I conducted an online study in which participants reported their height and weight (from which BMI was calculated) and the regularity with which they consumed certain foods (including high-fat foods, high-sugar foods and healthy distracters). Subjects also participated in two episodic cognition tests: first a PB test similar to that described in Chapter 4, in which the fat content of the foods, the presently experienced state of hunger or satiety, and the delay until receipt of the food were manipulated within-subject. Second, the UEQ test and FR test were combined into an Unexpected Free Recall (UFR) test, in which the to-be-remembered items were central to a subject's attention at the time of encoding, but subjects did not know that they needed to remember them. Subjects were unexpectedly asked to recall all the food items that had appeared on the menus. To ascertain food attitudes and eating style, subjects also completed the Eating Disorders Examination Questionnaire (Fairburn and Beglin, 2008). In particular, binge-eating score was recorded. This score is indicative of regularity of binge-eating episodes over the past 28 days. There are no explicit predictions for the effects of this measure, however the subjects in the Experiment 2 were pre-selected for high binge-eating scores (for reasons external to this investigation) and thus it was important to assess the contribution of this measure to performance in the population sample.

Given that episodic cognition is easily biased by current feelings and desires (see Chapter 1 and Chapter 4), one might expect *better* performance on the PB test (i.e. a smaller effect of current state) in subjects who are less able to recruit episodic processes in approaching the test. Thus, I hypothesise that there will be a smaller level of PB (i.e. effect of current state on menu-choices for future) meals in subjects with higher BMIs (as was suggested by Nisbett and Kanous's shopping test (1969)]) and/or higher levels of dietary fat and sugar (high "diet score"). In contrast, I predict that these subjects will perform worse on the UFR test.

5.2. Experiment 1

5.2.1. Methods

Pilot study

This study was piloted on a sample of 15 men (see Appendix 4).

Subjects

Participants were recruited via a range of social media websites, online forums and notice boards. 214 participants began the study, but there was a substantial dropout rate due to the requirement of successive website visits. A small number of subjects were also removed before analysis due to anomalous data or additional factors that influence BMI such as pregnancy or being 'very muscular' (as assessed by self-report). The remaining sample was 59 (29% male), aged 18-69 years, (mean age 36 years).

Ethical permission was obtained from the Cambridge Psychology Research Ethics Committee. Participants were asked a number of consent questions at the start of the

first questionnaire, and a final consent question at the end of the fourth questionnaire after the intentions of the study were revealed. As some of the questions involved weight and disordered eating behaviours, a list of support contacts was given at the end of the questionnaire, in case participants felt worried by any of the issues.

Procedure

Subjects were directed to a central web page, where they found links to the questionnaires. The survey was split into four questionnaires, to be completed at four different times over the course of two days. The times were "before lunch", "before dinner", "after lunch" and "after dinner". The aim of these timings was to make sure that subjects were fasted on some occasions (before meals) and fed on others (after meals). The order of these questionnaires was randomly counterbalanced between subjects. The subjects completed the questionnaires autonomously via an online survey website (www.freeonlinesurveys.com).

Figure 5.1. *Example Menu Choice*

In all four questionnaires, subjects were asked to confirm that they were completing the questionnaire at the appropriate time, either before or after their meal as

instructed, and to report on their hunger levels and how long (in hours) it had been since their last meal and since they had last eaten any food. They made three or four (depending on the questionnaire) forced choices between two similar foods that varied in fat-content and were to be eaten either immediately or in the future (see Figure 5.1). The fat content of the foods was not made explicit, but there were pictures and descriptions for each. After making their choices, subjects were asked if they disliked any of the foods mentioned. If so, the data from choices involving this food were excluded. A high-fat choice was scored 1 and a low-fat choice was scored 0.

Thus there were four conditions; fasted for now, fasted for future, fed for now and fed for future (see Table 5-1). Subjects were asked about each condition either twice or four times (controlling for future-state), with different foods each time (counterbalanced for order).

Table 5-1. *Four Within-Subjects Conditions of Projection Bias Test.*

	Now	**Future**
Fasted	Choosing when fasted for immediate consumption	Choosing when fasted for consumption later
Fed	Choosing when fed for immediate consumption	Choosing when fed for consumption later

At the end of the final questionnaire, subjects were asked for demographic details (including height, weight, age, gender) and for details about factors that may affect BMI (e.g. pregnancy or "muscliness"). To assess eating behaviour, subjects also completed sections from the Eating Disorders Examination Questionnaire (Fairburn and Beglin, 2008) and reported whether they had previously been diagnosed with an eating disorder, and if so which one.

Finally, at the end of the study subjects were unexpectedly asked to recall as many of the foods that had appeared on all the menus as they were able. These responses were scored for accuracy.

Analysis

Coding: Where subjects indicated a dislike of a particular food, data for choices involving those foods was removed. The subject's data was then calculated without this choice. This was an occurrence with just over 50% of subjects (31/59). To make sure that these omissions did not bias the data, the "now" and "later" choices were calculated by taking the average of the choices made when fasted and when fed and then taking an average of *these*. As such, if a given subject made more valid choices in either one of the "fasted" or "fed" conditions, this could not affect their "delay" scores. The "fasted" and "fed" score were calculated by averaging the choices made for now and later in a similar manner.

Statistics: Where assumptions of normality were met, data were analysed using repeated measures ANOVA, one-way ANOVA, Pearson's correlation and t-test. Where assumptions of normality were violated, nonparametric statistical tests (e.g. Freidman's ANOVA, Mann-Whitney U test, Wilcoxon signed-ranks test, Kendell's Tau) were used. Alpha was set at 0.05. Where *post hoc* investigations were carried out, a Šidák alpha correction was used.

5.2.2. Results

Pre-analysis results: BMI, binge-eating and diet data, memory and menu choices.

Most subjects were of a healthy weight, but subjects were distributed throughout all four weight categories (underweight, healthy weight, overweight and obese). The mean BMI, diet and binge-eating scores for each weight group are shown in Table 5-2. Before the analyses regarding the effect of BMI, diet and binge-eating on episodic cognition measures can be investigated, these demographic measures must be analysed independently.

Table 5-2. *Means and standard deviations of BMI (body mass index), diet score (indicative of level of high fat high sugar food in diet) and binge-eating score (indicative of regularity of binge-eating episodes, Fairburn & Beglin, 2008)*

	Underweight	Healthy Weight	Overweight	Obese	Overall
N	2	43	10	4	59
BMI	17.15 (±0.99)	21.9(±1.69)	26.95(±1.55)	40.51(±11.32)	23.80 (±5.88)
Diet score	2 (±0.1)	2.5 (±0.69)	2.66 (±0.52)	1.98 (±0.15)	2.45 (±0.65)
Binge-eating	1 (±1.41)	5.69(±8.19)	6.11(±11.37)	7.5 (±6.24)	5.7 (±8.4)

Relationship between BMI, diet and Binge-eating scores: There was no correlation between BMI and either of the eating behaviour measures (BMI/Diet: Kendell's Tau, N=58 R=-0.033, p=0.722; BMI/Binge-eating: Kendell's Tau, N=58, R=0.047, p=0.635). There was, however, a significant, yet small, negative correlation between the eating behaviour measures (Binge-eating/Diet: Kendell's Tau, N=58, R=-0.196,

p=0.05); those individuals who reported higher levels of binge-eating reported eating high-fat, high-sugar food less regularly.

Efficacy of the "Fasted" and "Fed" conditions: In order to access the efficacy of the "Fasted" and "Fed" conditions, the subjects' reported hungriness and time since last meal were compared between the conditions. It was found that subjects were significantly hungrier and had gone significantly longer since having last eaten in the "Fasted" condition than the "Fed" condition[11] (see Table 5-3).

Table 5-3. *Efficacy of "Fasted" and "Fed" conditions. Cells contain t-tests comparing hungriness, hours since food and hours since last meal in the Fasted and Fed conditions. Where N is too small for t-tests to be calculated, the mean and standard deviation are given.*

	Hungriness	Hours since food	Hours since meal
Overall	t(57)=-18.86, p<0.001	t(60)=6.27, p<0.001	t(60)=7.77, p<0.001
Men	t(16)=-7.63, p<0.001	t(16)=4.35, p<0.001	t(16)=5.22, p<0.001
Women	t(40)=-19.63, p<0.001	t(40)=4.81, p<0.001	t(40)=5.92, p<0.001
Underweight	N=2, Fasted: m=3, sd=0.7, Fed: m=4.2, sd=1.7	N=2, Fasted: m=4.5m sd=2.8 Fed: m=2.75, sd=2.47	N=2, Fasted: m=10.25, sd=4.5; Fed: m=10.75, sd=13.789
Healthy	t(42)=4.55, p<0.001	t(42)=4.552, p<0.001	t(42)=6.995, p<0.001
Overweight	t(8)=-4.464, p=0.002	t(8)=3.054, p=0.016	t(8)=3.323, p=0.01
Obese	N=4, Fasted: m:2.25, sd=0.28, fed: m=4.5, sd=0.7	N=4, fasted: m=4.2, sd=0.29, fed: m=1, sd=0.0	N=4, fasted: m=6.75, sd=3.8; fed: m=1, sd=0.0

Choice between high fat and low fat foods: There was a significant difference between weight groups in the percentage of occasions on which the high-fat food was chosen ($F_{3,54}$=2.985, p=0.039; see Table 5-4). There was a significant positive correlation between levels of dietary fat and sugar (diet score) and choice of high fat

[11] It should perhaps be noted that for the "underweight" group, the average time since their last meal in the "fed" condition was over 10 hours. This suggests that they either misunderstood the question and thought that it refered to the meal *before* that which they had just eaten, or that they had not, in fact, just eaten.

food in the menus (Pearson's N=59, R=0.485, p<0.001), but no correlation between levels of binge eating and choice of high-fat food in the menus (Kendell's Tau, N=59, R=0.052, p=0.604).

Table 5-4. Mean (±sd) *percentage of occasions in which high fat food was chosen*

	Mean percentage of occasions on which high-fat food was chosen (sd)
Overall	48.3% (±0.22).
Men	64.6% (±0.19)
Women	41.5% (±0.20)
Underweight	51% (±26)
Healthy	44% (±22)
Overweight	66% (±18)
Obese	49% (±14)

In the Fasted condition, there was no correlation between levels of reported hungriness and decisions for now (Kendell's Tau, N=58, R=-0.028, p=0.791) or the future (Kendell's Tau(58)=-0.093, p=0.388), while in the Fed condition those that were hungrier chose the high fat food on fewer occasions both for now (Kendell's Tau(58)=-0.366, p=0.001) and for the future (Kendell's Tau(58)=-0.221, p=0.033).

Sex Effects: There was a significant difference between men and women in BMI, diet score and proportion of occasions in which high fat food was chosen. Men on average had a higher BMI than women (Mann Whitney U, p<0.001) and reported eating high fat high sugar food more often (t[57]=2.095, p=0.041). Men also chose high fat high sugar food significantly more often than women on the test menus (t[56]=4.108, p<0.001). With a limited sample size, these strong and consistent sex differences risk confounding any main effects of the target factors (e.g. BMI, diet etc.) on episodic cognition with gender effects. For this reason, the main analysis was conducted separately on males and females.

Main analysis: Effects of BMI, diet and binge-eating on episodic measures

Main outcome measure 1: Effects of BMI, diet and binge-eating on memory

Men: In men, there was no relationship between any of the eating scores and memory performance (*BMI* $F_{1,12}$=0.043, p=0.838; *Diet* $F_{1,12}$=0.228, p=0.641; *Binge-eating* $F_{1,12}$=0.049, p=0.829).

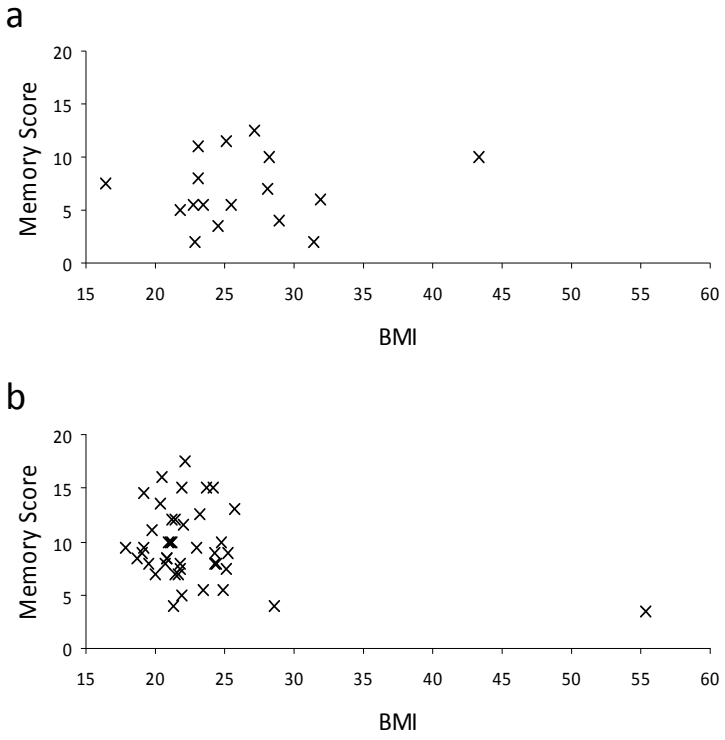

Figure 5.2. The effect of BMI on memory score in ***a)*** *men and* ***b)*** *women*

Women: Women with higher BMIs performed worse on the memory test, but there was no effect of diet or binge-eating (*BMI*: $F_{1,36}$=4.523, p=0.040; *Diet*: $F_{1,36}$=0.322, p=0.574; *Binge-eating*: $F_{1,36}$=0.426, p=0.518). However, this effect may have been driven by a single outlier (BMI=55). When the analysis was repeated without this

point, none of the effects was significant (*BMI*: $F_{1,36}$=0.590, p=0.45; *Diet*: $F_{1,36}$=0.24, p=0.63; *Binge-eating*: $F_{1,36}$=0.39, p=0.53).

Main Outcome Measure 2: Effects of BMI, diet and binge-eating on the influence of current state and delay on choices for high or low fat food.

The main analysis of interest was whether choices made for later were modulated by current state, and whether this modulation differed according to BMI, diet or binge-eating. However, this result is only relevant to the investigation of possible episodic cognition if the effect is specific to choices for the future (rather than for the present). Unfortunately, due to the small sample size (especially in men) the degrees of freedom are not sufficient to assess whether the two delays differ in the effect of dietary and weight factors on the modulation of choices by current state (a three-way interaction). Instead, two-way interactions are assessed in both delays.

Men: In choices made for "later", subjects chose more high-fat food when they were fasted than when they were fed (repeated-measures ANOVA: *Current state:* $F_{1,13}$=7.358, p=0.018). There was an impact on self reported levels of dietary fat and sugar on the effect of current state on choices of high- and low-fat food (*Current State x Diet*: $F_{1,13}$=5.872, p=0.031). The planned contrasts revealed a trend that those who reported rarely eating high-fat, high-sugar food chose more high-fat food when they were fasted than when they were fed (Wilcoxon signed rank test, p=0.051), while those who reported high levels of dietary fat and sugar showed no effect of current state on choices (Wilcoxon signed rank test, p=0.167; see Figure 5.3). There were no

other significant effects or interactions (*Current State x BMI*: $F_{1,13}$= 2.930, p=0.111; *Current State x Binge-eating*: $F_{1,13}$=0.803, p=0.387).

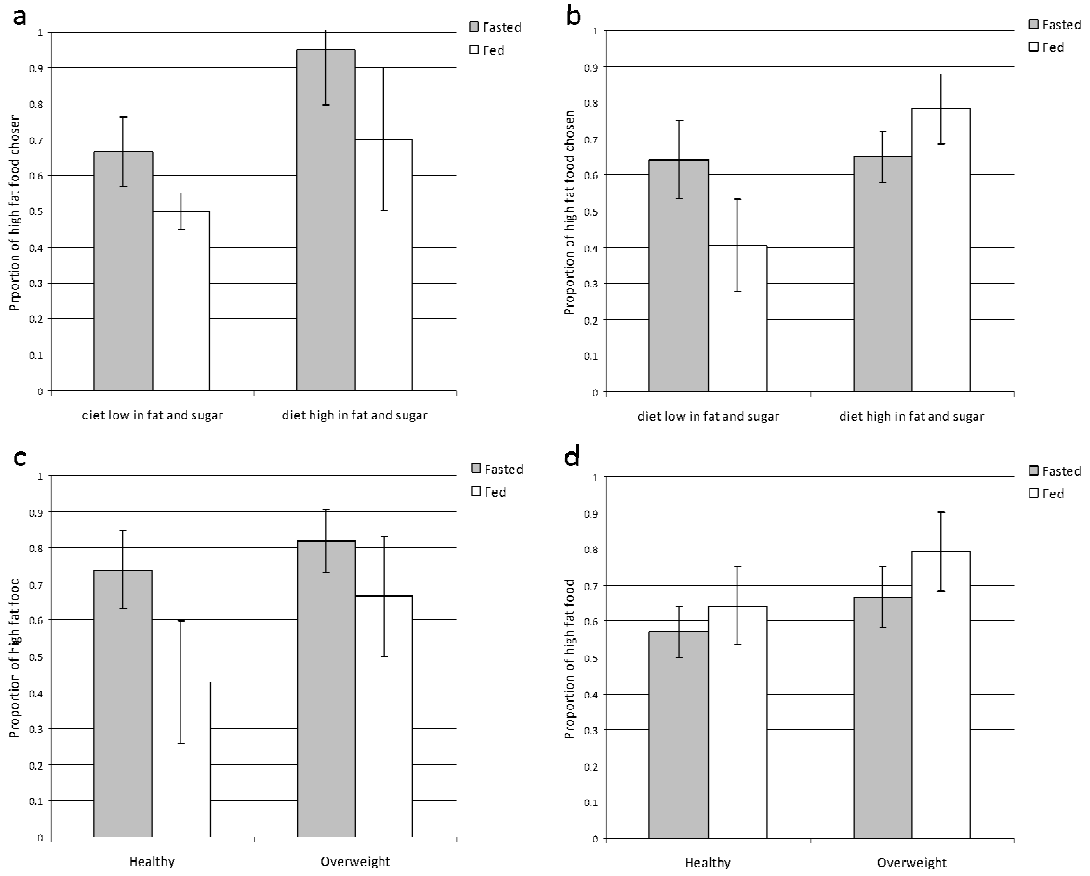

Figure 5.3. *Effect of Diet and BMI on the impact of current state on choices in men.* ***a)*** *Effect of Current State on choices of high fat food for now, divided according to dietary fat and sugar.* ***b)*** *Effect of Current State on choices of high fat food for later, divided according to dietary fat and sugar.* ***c)*** *Effect of Current State on choices of high fat food for now, divided according to BMI.* ***d)*** *Effect of Current State on choices of high fat food for later, divided according to BMI.*

In choices made for "now", subjects did not make different choices when they were fasted than when they were fed (repeated-measures ANOVA: *Current state:* $F_{1,13}$=1.665, p=0.219). Significantly, this was not modulated by dietary fat and sugar (*Current State x Diet*: $F_{1,13}$=0.184, p=0.675). There was, however, an impact of BMI on the effect of current state choices of high- and low-fat food (*Current State x BMI*: $F_{1,13}$=5.407, p=0.037). Planned contrasts revealed that subjects with a healthy BMI

chose higher-fat food when fasted than when fed (Wilcoxon signed rank test, p=0.04), while people who were overweight showed no effect of current state on their (Wilcoxon signed rank test, p=0.59; see figure 5.3). There was also a suggestion that number of self-reported binge-eating episodes had an impact on the effect of current state on choices of high and low fat food (*Current State x Binge-Eating*: $F_{1,13}$= 4.341, p=0.058; *Current State x Diet*: $F_{1,13}$=0.184, p=0.675).

Women: In choices made for "later", subjects did not make different choices when they were fasted than when they were fed (repeated-measures ANOVA: *Current state:* $F_{1,37}$=0.003, p=0.960). There was no impact of any of the weight or dietary variables (*Current State x Diet*: $F_{1,37}$=0.181, p=0.358; *Current State x BMI*: $F_{1,37}$= 0.243, p=0.625; *Current State x Binge-eating*: $F_{1,37}$=0.865, p=0.358).

In choices made for "now", subjects did not make different choices when they were fasted than when they were fed (repeated-measures ANOVA: *Current state:* $F_{1,37}$=0.028, p=0.869). There was no impact of any of the weight or dietary variables (*Current State x Diet*: $F_{1,37}$=0.474, p=0.496; *Current State x BMI*: $F_{1,37}$= 0.183, p=0.671; *Current State x Binge-eating*: $F_{1,37}$=0.225, p=0.638).

5.2.3. Discussion

Men and women differed significantly in BMI and diet and so the impact of BMI, diet and binge-eating on episodic measures was investigated in the sexes separately. In women, but not in men, it was found that subjects with higher BMIs performed worse

on the UFR memory test than subjects with lower BMIs, but that this effect was driven by a single outlier. In men, but not in women, there were effects of diet and BMI on PB, with a suggestion that BMI may have a general (delay independent) effect on the impact of current state on choices, while diet had a more specific impact on choices for the future. When choosing for immediate consumption, healthy subjects chose more high- fat food when they were fasted than when they were fed, while overweight subjects showed no effect of current state on their choices of high- and low-fat foods. When choosing for delayed consumption, subjects who reported low levels of dietary fat and sugar chose more high-fat food for their future selves when they were fasted then when they were fed. In subjects who reported high levels of dietary fat and sugar, however, there was no difference in choices for the future selves between when they were fasted and when they were fed. It is important to note that in neither of these instances was the lack of effect of current state due to a ceiling effect. In other words, this result did not stem from overweight individuals and those with high levels of dietary fat and sugar simply choosing the high fat food on all occasions.

These results do not replicate the findings that BMI is associated with poor FR performance (Elias *et al*., 2003, Gunstad *et al*., 2006, 2010). However, this difference may be the result of different sampling: the subjects in Elias and colleagues' experiment were hypertensive and obese, while those in the present study were mostly healthy with only a few overweight and obese subjects. Elias and colleagues also conducted their study on a sample of US citizens, while the present study was conducted with British subjects.

A relationship was also not found between UFR and levels of dietary fat and sugar. This is in contrast to the findings of Francis and Stephenson (2011). This difference may come from the manner in which FR was assessed. In the present study it was the unexpected recall of items that were presented both in text and images at various times across the past 2 days, while in Francis and Stephenson's study the verbal paired associates (VPA) and Logical Memory subtests of the Wechsler Memory Scale Revised (Wechsler and Stone, 1987) were used. These tests assess recall of aurally presented words and stories within a 30-minute time scale. Furthermore, the need to recall was expected, while in the present study it was unexpected. The difference in findings may also be due to the different ways in which diet was reported: Francis and Stephenson asked subjects to report regularity of consumption of certain foods over the course of the past year in terms of discrete quantities (e.g. "less than once a month"/ "more than 5 times a week.") while in the present study subjects merely reported a subjective estimate of the regularity of their consumption of certain foods (e.g. "rarely" / "often").

Overall, these data indicate that may indeed be a relationship between poor diet, obesity and episodic cognition. However the nature of this relationship remains difficult to define. It is not easy to assess, for example, the extent to which men and women differ in the relationship between BMI, diet and episodic cognition. While different results were found between the sexes, it is very difficult to establish whether this is a genuine sex effect or whether the differences in BMI and diet scores between the sexes mean that the male and female populations in this sample represent different eating profiles. The degrees of freedom (and large female bias) did not allow a direct investigation of this. One possibility is that the impact of BMI and diet on sex

hormones (e.g. Kirschner *et al*., 1990) may modulate the complex interaction of hormones and neuropeptides that are involved both in eating behaviour and hippocampal function (e.g. Lukanova *et al*., 2004, McTiernan *et al*., 2006, Hankinson *et al*., 1995, Boyapati *et al*., 2004, Bezemer *et al*., 2005); see 5.1. Introduction)

One reason that this relationship may be difficult to define is that these episodic tests have used food-related stimuli and motivational states. The performance of subjects on the episodic aspects of these tests may be modulated by the effects of diet and BMI on response to food stimuli and motivational state independent of episodic cognition. Furthermore, if the mechanism through which episodic cognition allows us to cater for future desires is by the establishment of mentally simulated hunger or satiation, then differences between overweight and healthy individuals in the way in which they respond to hunger-inducing and satiating situations may interact with episodic cognition.

Satiation reduces the wanting but not the liking of food

There is some evidence to suggest that overweight individuals have an unusual response to satiation. To explore this, it is first necessary to explore the nature of the cognitive response to satiation.

The evidence that overweight people respond differently to satiation is mixed. Overweight people do not differ from normal weight people in their self- reported satiety during and after a meal (Teghtsoonian *et al*., 1981). Some studies (Pliner, 1973, Schachter, 1968, Schachter *et al*., 1968, Tom and Rucker, 1975) find that while

healthy subjects reduce their eating after ingestion, obese subjects do not. Other studies, however, find no significant difference between obese and healthy subjects in the satiating effects of ingestion (Herman and Mack, 1975, Hibscher and Herman, 1977, Hill and McCutcheon, 1975, Nisbett, 1968b, Nisbett, 1968a, Price and Grinker, 1973, Rodin and Slochower, 1976, Ruderman and Wilson, 1979, Wooley, 1972). A review of this literature (Spitzer and Rodin, 1981) found no systematic differences between the studies that found significant or nonsignificant results in terms of hours of deprivation, time between pre-feeding and meal, dual-test performance, or level of deception.

It has been shown that food-induced satiety (Epstein *et al*., 2003) and imagination-induced satiety (Morewedge *et al*., 2010) reduce the reinforcement value (wanting) but not the hedonic value (liking) of food. Thus reinforcement value of food is transient and responsive to contextual information (e.g. whether or not you've just eaten), while hedonic value might be considered to be more of an *absolute* property of food. There are few studies investigating the willingness of overweight subjects to work for food after satiation. However, Nasser and colleagues (2008) found that after consumption of a liquid meal, there was a significant decrease in willingness to work for food in healthy-weight subjects, and that willingness to work was associated with ratings of hunger levels. In obese subjects with binge-eating disorder, however, there was no decrease in willingness to work, and there was no correlation between willingness to work and hunger ratings. Interestingly, when these subjects were compared to obese subjects *without* binge-eating-disorder, this difference still existed, suggesting that this maintained willingness to work following satiation may be a factor of binge-eating-disorder rather than obesity *per se*.

It is possible that overweight people (or people with high levels of binge-eating) represent food more in terms of its hedonic value than its reinforcement value and thus that their attitude towards it is less liable to change according to the context. While all subjects consume more food when it is palatable than when it is not, there is a substantially greater effect of palatability on amount eaten in overweight subjects compared to healthy-weight subjects (Grinker, 1975, Hill and McCutcheon, 1975, McKenna, 1972, Nisbett, 1968b, Nisbett, 1968a, Price and Grinker, 1973) (Rodin *et al*., 1976, Rodin and Slochower, 1976) . However it should be noted that overweight people do not seem to *like* palatable food more than healthy-weight people (de Graaf *et al*., 2005, Mela *et al*., 1992), but do seem to *want* it more. For example, overweight individuals are more willing to work for food rewards (Johnson, 1974, Saelens and Epstein, 1996, Epstein *et al*., 2008, Temple *et al*., 2008) than are healthy subjects.

One potentially interesting finding in Experiment 1 was that while subjects who reported rarely eating high fat high sugar food chose food for future consumption based on their current state of hunger, subjects who reported high levels of dietary fat and sugar did not respond to their current state when making decisions for the future. It may be that this finding is the result not of the reduced tendency to employ episodic cognition (i.e. a reduced tendency to be biased by current feelings but instead make decisions based on semantic facts), but instead be the product of a tendency to represent food rewards in terms of hedonic value (liking) rather than reinforcement value (wanting).

In simplistic terms, the reinforcement value ("wanting") of food and other rewards is thought to be mediated by the dopamine system (e.g. Berridge, 2007) while the hedonic value ("liking") of those rewards is thought to be mediated by the opioid system (e.g. Berridge, 2007, Pecina and Berridge, 2000, 2008, Barbano and Cador, 2007). In particular, opioids are thought to modulate the perceived palatability of food (Olszewski and Levine, 2007, Drewnowski *et al*., 1995, Levine *et al*., 1995, Thornhill *et al*., 1982, Dum and Herz, 1984). Binge-eating behaviour is considered to be hedonically driven consumption (Davis *et al*., 2009, 2010) because binging behaviour tends to occur almost entirely on highly palatable foods (e.g. Abraham and Beumont, 1982, Hetherington and Rolls, 1991). This type of feeding involves regulation by opioids (Levine and Billington, 2004); rodent models of binge-eating show similar patterns of excessive consumption of palatable food (Hagan *et al*., 2002a, 2002b, 2003). This behaviour has been successfully suppressed by opioid receptor antagonists, particular μ-opioid receptor antagonists (Morley *et al*., 1980, Giraudo *et al*., 1993, Bodnar *et al*., 1995, Hagan *et al*., 1997, Levine and Billington, 1997, Glass *et al*., 2001, e.g. Barbano and Cador, 2006, Hadjimarkou *et al*., 2004, Pecina and Berridge, 2000).

Recent pharmacological attempts to treat obesity have exploited the role of the opioid system in hedonic experience. There has been a general movement towards using opioid antagonism to reduce the tendency towards hedonic (rather than metabolic) intake in obese individuals (e.g. Mitchell *et al*., 1987, Nathan and Bullmore, 2009, see de Zwaan and Mitchell, 1992). This type of treatment can be harnessed to directly compare the two possible explanations for the effect of BMI on PB.

One can consider the *long-term representation* of a food's palatability (rather than the immediately perceived palatability upon tasting it) as a semantic fact about that food. ("Generally chocolate is nice, but I didn't like that piece of chocolate I just ate"). While treatment with a μ-opioid antagonist is likely to eventually reduce the long-term represented palatability of certain foods, extinction of responding for high-value rewards is generally slow, context-specific and easily reversed (e.g. Bouton and Peck, 1992). Thus once an individual has experienced a given food as highly palatable, it would take extensive (and multi-context) experience of that food being unpalatable for this revaluation to become part of the foods long-term mental representation. Thus short-term treatment with a μ-opioid antagonist should produce a transitory effect of unpalatableness that is insufficient to alter the long-term representation of the food, but is sufficient to reduce current liking of it (equivalent to feeling that you didn't like *this* chocolate, but you do like chocolate generally). These different hedonic representations shall herein be referred to as *experienced* palatability and *represented* palatability respectively.

In Experiment 2, a sample of obese individuals was treated with a μ-opioid antagonist for 28 days. During the study, subjects (unwittingly) repeatedly took part in a PB test. Subjects were required to choose which food they would like to receive for a meal later in the day. The foods in the menu varied in their fat content, and subjects were either fasted or fed at the time of making this decision. The two competing hypotheses (namely, that obese individuals represent food in terms of palatability rather than reinforcement value or that obese individuals represent food in terms of its semantic value rather than its current value) make different predictions as to the impact of μ-opioid treatment on performance on the PB test. If obese people represent food more

in terms of its hedonic value than its reinforcement value, then this transient change in palatability should have a similar effect on decisions for the future as satiation has in healthy weight subjects: it would reduce the value of food immediately after food has been consumed (after experience of the food having low *experienced palatability*) relative to when food has not been consumed for a long period (when this experience will be less salient/remembered). However, if obese individuals are unaffected by their current feelings, but instead make decisions according to semantic fact (i.e. represented palatability) then whether those are related to *liking* or *wanting* is irrelevant. Thus if they have recently been exposed to low *experienced* palatability, this should not affect their decisions as these will be based on *represented* palatability. There should in this case be a time-dependent effect of μ-opioid antagonism on performance on the PB test. In the early stages of treatment, one should see no change in decision-making, for despite reduced experienced palatability of the foods, this has not yet been translated into the long-term semantic represented palatability of the foods. However, after long-term treatment, this transfer into represented palatability should occur and overall choices for palatable food should decrease. There should not, however, be any change in the difference between fasted and fed conditions, as the drug does not affect hippocampal function. Thus the reduced impact of hippocampal-dependant episodic cognition on decisions making (and thus on the extent to which decisions for the future are affected by current state) should remain the same.

However, while decisions for the future should remain stable despite drug treatment, immediate *ad lib* consumption and palatability ratings should be reduced reflecting reduced experienced palatability of the food items.

The following experiment assessed the effects of 4 weeks of treatment with the μ-opioid receptor antagonist GSK1521498 on menu choices and consumption in binge-eating obese subjects. Furthermore, the relationship between BMI and memory is re-investigated in an entirely obese sample using a FR test.

5.3. Experiment 2

5.3.1. Methods

Subjects

Sixty-three volunteers (44% male) aged 18-60 years (mean age 41) with moderate to severe binge-eating symptoms (Binge Eating Scale scores ≥ 19; mean 26.4 ± 6.7) (Gormally *et al*., 1982; Gladis *et al*., 1998), and classified as obese (BMI ≥ 30 kg/m$^{2;}$ mean 37.3 ± 4.76 kg/m^2) took part in this study after meeting criteria and providing consent. The study (identification number EudraCT 2009-016663-11, ClinicalTrials.gov identifier NCT01195792) was conducted at Addenbrookes hospital and approved by Berkshire Research Ethics Committee, United Kingdom.

With the exception of binge-eating symptoms, subjects had no history of DSM-IV TR axis-I disorders (such as depression, anxiety or eating disorders). Subjects were excluded from the sample if they smoked, reported large average alcohol intake (>14 units/week), screened positive for illicit drugs on urine screen, or had taken any centrally active medications in the past 2 weeks.

Procedure

This study was conducted in collaboration with GlaxoSmithKline (GSK) as part of a multi-centre study investigating the general effects of GSK1521498 on physiology and feeding in obese subjects. The study utilized a double-blind placebo controlled parallel group design. After a 1-week single-blind placebo run-in, subjects received 4 weeks of treatment with either placebo (n=21), 2mg/day GSK1521498 (n=21), or 5mg/day GSK1521498 (n=21). Doses were chosen based on the findings of Nathan and colleagues (2011) of those that resulted in good drug-tolerance and high steady-state μ-opioid receptor occupancy.

Given that this study was multi-centre and had many endpoints, the procedures and methods reported hereafter refer only to the areas of the study relevant to this thesis and with which I was directly or indirectly involved. These were conducted alongside many other investigations involving physiological and neurological effects of GSK1521498 which are reported elsewhere and by others (e.g. Ziaudeen *et al*., *in press*). In addition, to maintain simplicity, only the results from the placebo and 5-mg drug groups were included in the following analyses.

Food palatability

The effect of GSK1521498 on the experienced palatability was examined using taste-testing of a number of dairy products that varied in fat and sugar content. At three timepoints during the study (Days -1, 14, and 28), subjects were asked to taste and

rate the palatability of these dairy products on a 9-point scale ranging from "dislike extremely" to "like extremely".

Consumption Levels

The effect of GSK1521498 on the *ad lib* consumption of food was examined with the use of natural meal consumption. Meals were provided to the patients in their beds by hospital staff. These meals were in the form of buffets in which subjects were presented with more food than they would be able to consume: this was assessed on days -1, 14, and 28 of the study. Subjects were given access to several portions of a wide variety of main course and pudding foods. Equicaloric portions of nine foods containing 20% fat, 40% fat or 60% fat were provided, six of which (two of each fat category) were savoury "main courses" and three of which (one of each fat category) were sweet "puddings". This gave subjects *ad libitum* access to food and allowed them to eat according to their preference and until they wanted to stop. Subjects were not informed of the fat category of their food, nor that their eating behaviour was being recorded. Subjects were instructed to leave all food that was not consumed on the plate on which they had received it. Thus the total calories consumed were approximated by weighing the plates before and after consumption[12].

Projection Bias test

The foods consumed in the buffet meals were also involved in the PB test. Subjects were divided into two groups: the "Fasted" group and the "Fed" group. Both groups

[12] Unfortunately homogenous foods could not be used for the study, so the weighing can only act as an approximation of calories consumed.

received a menu containing choices for that day's dinner; the Fasted group received these menus *before* eating a large quantity of snack foods (as part of an investigation not reported here; approximately 11am) and the Fed group received the menus *after* the snack-food consumption (approximately 2pm). Dinner was to be received at 6 pm. This procedure was repeated across 4 time-points (days -1, 1, 14 and 28).

The menus contained verbal descriptions of six main courses (two of each fat category) and three desserts (one of each fat category) that would be actually received later in the day. They were informed that for supply reasons they could not be guaranteed their first choice and that as such they should rank the foods in order of preference (1-6 for mains and 1-3 for desserts) and indicate how many portions (1-3 portions) they would wish to receive of each were they to be served it.

Subjects were not informed of the fat categories of the different foods, and always received all foods on the menu such that their choice never affected what they had the opportunity to learn about in terms of experienced palatability.

Free Recall Test

Subjects were presented with a delayed FR test as part of the Cognitive Drug Research (CDR) battery at the beginning of the study. A series of 15 words was presented at a rate of one every 2 seconds. The words consisted of a mix of one, two and three syllable words, matched for frequency, concreteness and imagery. The subjects were asked to immediately recall as many of the words as possible during a

period of 60 seconds ("immediate recall"). They were then asked to recall the words again several minutes later, also during a 60 second interval ("delayed recall").

Analysis

Where assumptions of normality were met, data were analysed using repeated measures ANOVA, one-way ANOVAs, Pearson's correlation and t-test. Where assumptions of normality were violated, nonparametric statistical tests (e.g. Friedman's ANOVA, Mann-Whitney U-test, Wilcoxon signed-ranks test, Kendell's Tau) were used. Alpha was set at 0.05. Where *post hoc* investigations were carried out, a Šidák alpha correction was used.

5.3.2. Results

Demographics

Men and women did not differ in BMI (men: 36.23 ±5.017; women: 37.97 ±4.47; $t[61]=-1.454$, $p=0.151$) or age (men: 40.16 ±7.43; women: 42.17 ±11.78; $t[65]=-0.818$, $p=0.417$). However, because the impact of BMI and diet on episodic cognition were analysed in the sexes separately in Experiment 1, the performance of men and women on the PB test are also assessed separately here, for the sake of continuity.

Taste-Testing

GSK1521498 successfully reduced the hedonic experience of high-fat food. There was a significant difference in the change in hedonic experience of high-fat and high-

sugar food between the drug group (5mg) and the placebo group at 28 days (fat: t[40]=2.279, p=0.028; sugar: t[40]=2.078, p=0.044). There was also a significant difference between the drug treatment groups in hedonic experience of sugar and a trend of fat at 14 days (fat: t[40]=1.801, p=0.079; sugar: t[40]=2.527, p=0.016).

Consumption

Consumption levels differed between foods that varied in fat content (One way ANOVA, $F_{2,54}$=23.817, p<0.001). Subjects consumed less of the 20% food than either the 40% or 60% food (20%/ 40%: t[66]=-7.668, p<0.001; 20%/ 60%: t[66]=-5.081, p<0.001; 40%/60%: t[66]=1.473, p=0.145).

Over the course of the study, the drug group reduced their consumption of high fat food compared with the placebo group. On day -1, the placebo and active drug groups consumed the same amount of food (t[35]=0.368, p=0.715). On days 14 and 28 however, there was a significant difference between the amount consumed by those in the placebo group and those in the active drug group (day 14: t[37]=2.225, p=0.032), day 28 (t[39]=2.330, p=0.025).

For the highest-fat food (60% fat) there was no difference between the drug and placebo groups on days -1 (t[35]=-0.073, p=0.942) or 14 (t[37]=0.230, p=0.819) but the placebo group consumed significantly more than the active drug group on day 28 (t[40]=2.368, p=0.023).

Episodic Cognition Measures

Free Recall

The subjects remembered an average of 6.25 (±1.96) words in the immediate recall test and 5.30 (±4.19) words in the delayed recall test. The figures for delayed recall cannot be considered to differ substantially from those found in the control groups of other studies using the same test (Wilkinson *et al*. 2002: M=5.2 [one sample t-test t(62)=0.187, p=0.8518]; Moss *et al*., 1998: M= 4.6 [one sample t-test t(62)=1.3241, p=0.1904]). However, the immediate recall score was different from that shown in these studies (Wilkinson *et al*. 2002: M= 6.9 [one sample t-test t(62)=-2.63, p=0.01]; Moss *et al*., 1998: M= 6.7 [one sample t-test t(62)=-1.8223, p=0.073]).

There was no relationship between BMI and FR (immediate: N=61, R=-0.17, p=0.166; delayed: N= 61, R=-0.104, p=0.416). Men and women did not differ in either immediate (t[61]=0.854, p=0.396) or delayed recall (t[61]=1.034, p=0.305).

Projection Bias

Rankings

Men: The drug had no impact on the effect of current state on average rankings of high-fat (60%) food. There was no difference between the drug groups in the effect of current state, and no change over time, or change over time in the effect of the drug (repeated-measures ANOVA: (*Day*: $F_{3,9}$=0.333, p=0.802; *Day x Drug*: $F_{3,9}$=0.980, p=0.444; *Current state x Drug x Day*: $F_{3,9}$=2.777, p=0.103). However there was a trend towards change over time in the effect of current state on the rankings of high fat food (*Day x Current state*: $F_{3,9}$=3.094, p=0.082).

Overall, there was no difference between the ranking of high-fat food of the Fasted and Fed groups (t[29]=-1.242, p=0.224). There was also no difference in the average ranking of high fat food between placebo and active drug group on day 1 (t[17]=-0.589, p=0.564) or on day 28 (t[18]=0.57, p=0.576).

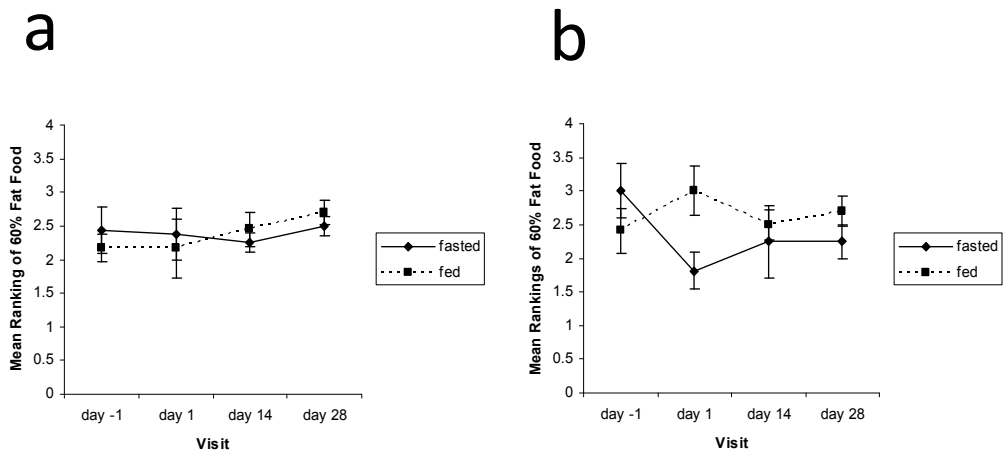

Figure 5.4. *A Comparison of the ranked preference for high-fat food in subjects who were fasted or fed in the **a)** placebo or **b)** drug group.*

There was no change in choices over the course of the study in either drug treatment group (repeated-measure ANOVA: placebo: *Day*: $F_{3,4}$=2.701, p=0.181; active drug: *Day*: $F_{3,3}$=2.026, p=0.288). There was no interaction between day of testing and current state in the drug group (*Day x Current State*: $F_{3,3}$=3.750, p=0.153) although there was a significant interaction between day and current state in the placebo group (*Day x Current State:* $F_{3,4}$=13.765, p=0.014). **Error! Reference source not found.** indicates that in drug and placebo groups there was a change from subjects in the Fasted group ranking 60% fat food higher than those in the Fed group, to subjects in the Fed group ranking 60% fat food higher than the Fasted group. However, in the placebo group this was a smooth gradual progression, while in the drug group the relationship consisted of a sudden large reversal on day 1 (t[7]=-2.574, p=0.037) which then reduced on subsequent visits.

Women: The drug had no effect on the impact of current state on rankings of high-fat food for future consumption (repeated-measures ANOVA: *Day*: $F_{3,10}$=1.008, p=0.429; *Day x Drug*: $F_{3,10}$=1.482, p=0.278; *Day x Current state*: $F_{3,10}$=0.212, p=0.886; *Current state x Drug x Day*: $F_{3,10}$=1.439, p=0.289).

Portions

Men: The drug had no impact on the effect of current state on number of portions of high-fat food requested. There was no difference between the drug and placebo groups in the number of portions of high-fat food requested by those who were fasted and those who were fed (*Day*: $F_{3,9}$=1.211, p=0.360; *Day x Drug*: $F_{3,9}$=2.278, p=0.138; *Day x Current state:* $F_{3,9}$=1.645, p=0.247; *Current state x Drug x Day* interaction: $F_{3,9}$=1.316, p=0.328).

Women: The drug had no impact on the effect of current state on the number of portions of high fat food requested. There was no effect of any of the variables on the number of portions of high fat food requested (repeated-measures ANOVA: *Day*: $F_{3,10}$=0.173, p=0.912; *Day x Drug:* $F_{3,10}$=0.745, p=0.549; *Day x Current state:* $F_{3,10}$=0.747, p=0.548; *Current state x Drug x Day*: $F_{3,10}$=1.404, p=0.298).

Relationship between Memory and impact of current state on choices for the future.

The FR test conducted at the beginning of the study was compared with the rankings and portions requested of high fat food. It was found that those subjects who requested more portions of high fat food tended to perform worse on the FR tests.

There was a negative correlation between number of portions of 60% fat food requested and immediate recall (N=42, R=-0.307, p=0.048) and a trend for delayed recall (N=42, R=-0.282, p=0.070). There was no correlation between ranking of 60% fat food and immediate (N=42, R=-0.001, p=0.994) or delayed recall (N=42, R=-0.003, p=0.986). Because the current state manipulation was between subjects (for reasons to do with GSK procedure) the relationship between memory performance and effect of current state on decisions for the future could not be investigated directly. However, it was found that in the fasted group, there was a trend towards a negative correlation between number of portions of 60% fat food requested for the future and delayed recall (N=18, R=-0.435, p=0.071) but not immediate recall (N=18, R=-0.302, p=0.224). Neither FR test correlated with portions requested in the Fed group (immediate: N=24, R=-0.325, p=0.121; delayed: N=24, R=-2, p=0.350). There was no correlation between recall and ranking of 60% fat food in either group (fasted delayed: N=18, R=-0.054, p=0.83; fasted immediate: N=18, R=0.05, p=0.842; fed delayed: N=24, R=129, p=0.548; fed immediate: N=24, R=-0.038, p=0.862).

5.3.3. Discussion

The results of Experiment 2 indicate that the μ-opioid antagonist was effective in reducing the hedonic experience of consuming high-fat and high-sugar food and was also effective in reducing levels of consumption of these types of food. However, it had little impact on the choices individuals made for the future.

The hypotheses laid out earlier suggest that were obese individuals choosing according to hedonics (liking) rather than motivational state (wanting) then treatment with an opioid antagonist would introduce a difference between choices made when

fasted and those made when fed. Specifically, those choosing when fasted should prefer higher-fat foods than those choosing when fed. If, however, subjects were choosing according to their long-term *represented palatability* of the food (semantic) rather than being biased by their currently *experienced palatability* of the food (episodic) then there should be no difference in the effect of current state between the drug groups. However, there should be a reduction in overall choice of high fat food after an extended treatment period during which subjects had increased experience of the new hedonic values of various foods. These may then be translated into a changed long-term represented palatability.

The results are somewhat mixed, and their ability to differentiate between these two hypotheses is limited. However, the overall suggestion is that there was no effect of the opioid-antagonist on the impact of satiation on choices for the future. Thus, it could be tentatively suggested that the results support the hypothesis that subjects were choosing according to semantic representations, rather than demonstrating projection bias (i.e. using episodic cognition). It is likely that 28 days was not a sufficiently long treatment period to give subjects enough exposure to different food types under the effects of the drug to change their long-term representation of high fat high sugar food. This is consistent with the finding that subjects did not lose any weight during the treatment period (Ziaudeen *et al*., *in press*). The amount of bias from current desires on future-oriented decision-making did not change with drug treatment. I suggest this is because the drug did not affect hippocampal function, but simply altered current feelings towards food.

An interesting finding was that subjects in this study differed significantly from other "normal" samples in immediate FR. This may suggest that, as found in Experiment 1 (and demonstrated by others: (e.g. Elias *et al*., 2003, Elias *et al*., 2005, Gunstad *et al*., 2010, Gunstad *et al*., 2006), there is a relationship between BMI and episodic memory impairment. There was also a correlation suggesting that the better subjects performed on the recall tests, the fewer portions they tended to request. This relationship is difficult to interpret because we cannot look directly at the impact of current state on portions requested.

There are some limitations of this study that may have reduced its power to differentiate between the hypotheses. In particular, counterbalancing issues[13] meant that the sample size for each of the groups was relatively small (placebo: fasted N=10; fed N=11; 5mg: fasted N=8; fed N=13), which reduced the power of the study.

5.4. General Discussion

In Experiment 1, a significant negative relationship was found between UFR Memory and BMI among women, but this was driven by a single outlier. No correlation was found in men. There was no relationships were found between UFR and levels of reported dietary fat and sugar or levels of reported binge eating (as calculated by the EDE-Q; (Fairburn and Beglin, 2008). In men, but not women, a significant relationship was found between the effect of current state on decisions for the future (projection bias) and levels of self-reported dietary fat and sugar. It was shown that

[13] This was caused by my not being informed of the introduction by GSK of a 2mg drug group, resulting in the drug groupings to be 3-way rather than dichotomous.

men who consumed low levels of fat and sugar showed a current-state-consistent bias in their decisions for the future (more high-fat food when fasted) while men who reported high levels of dietary fat and sugar showed a current-state-inconsistent bias in their decisions for the future (more high-fat food when fed). Thus the data do, very tentatively, support the idea that there is a relationship between obesity, diet and episodic cognition, but that this relationship is not a simple one.

In Experiment 2, it was found that there was no projection bias (i.e. current state had no impact on choices for the future) in an obese sample, and that μ-opioid antagonism had little-to-no effect on PB. While in men, but not women, there was an interaction between day, drug-group and current state, **Error! Reference source not found.** appears to suggest that this derives from increased volatility/variability in decision making in the drug group, rather than a trend in a particular direction. These data cautiously support the hypothesis that the lack of projection bias in overweight individuals is due to reliance on the semantic representation of foods palatability, rather than current experience of it.

In both Experiment 1 and 2, methodological issues may have contributed to the lack of clarity within the data. In Experiment 1, the reliance on an internet-based study using people's actual meal consumption to induce satiety may have meant that people were neither fully hungry nor fully satiated at the time of completing the test. Indeed, the data from the underweight subjects suggest that when instructed to complete the survey immediately after a meal, they still reported having been more than 10 hours since their last meal. In addition, the choice of some relatively unpopular foods meant data were lost. In Experiment 2, lack of control over testing led to problems with

counterbalancing. In both experiments, the distribution and sampling may have limited the efficacy of the investigation. In Experiment 1, the proportion of subjects that were overweight or obese was low such that much of the variation in BMI and diet were among the healthy population. This may have reduced the ability to detect the impact of *unhealthy* weight and diet on episodic cognition. Experiment 2 suffered from the opposite problem as it lacked a healthy control. This means that it was not possible to assess the impact of obesity itself on the variables, rather than the impact of the drug treatment on obese subjects.

The findings contained in this chapter appear to refute the final prediction laid out in Chapter 1: that different tests of episodic cognition should be affected in the same way in the same patients. It seems that factors that cause deficits in free recall do not also cause deficits projection bias, and vice versa. Specifically, diet appears to affect performance on the PB test and BMI appears to impair performance on UFR (although the issue with the outlier means that there may be no relationship). Does this suggest that these tests are subserved by different neural/psychological processes? The independence of these effects may be a product of the testing method. In the diet questionnaire (Experiment 1) participants were asked "how often" they eat certain foods, but this does not assess the *quantity* consumed on each occasion. It may be that the results presented here in fact indicate that *regular consumption* of high-fat high, high-sugar food has a different impact on episodic cognition as compared to regular consumption of *large quantities* of high-fat, high-sugar food. However, it is also possible that obesity and high fat high sugar diet impact different regions of the hippocampus, and that these are differentially recruited by different episodic cognition tests: It has been found that FR performance is heavily dependent on the

entorhinal cortex, but relatively independent of the function of the dentate gyrus (Brickman *et al*., 2011), while the dentate gyrus (but not the entorhinal cortex) which has an important role in pattern separation (Bakker *et al*., 2008). Pattern separation and may be integral to separating representations of different, yet similar, experiences (such as motivational states originating in imagined events and those currently experienced). Recent evidence suggests that blood glucose levels are associated with damage to the dentate gyrus, but not other areas of the hippocampus (Brickman *et al*., 2011, Wu *et al*., 2008), while high circulating insulin levels have been associated with damage to entorhinal cortex function (e.g. Wu *et al*., 2008). Thus it is possible that the entorhinal cortex function (and therefore FR) may be affected by obesity independently of diet, while high levels of dietary sugar (causing high blood-glucose levels) may, independently of BMI, selectively affect functioning of the dentate gyrus, causing problems with pattern separation (and therefore with the PB test). These ideas warrant further investigation.

Chapter 6
Discussion and Conclusions

At present there exist several distinct literatures on episodic cognition. The comparative cognition literature has chiefly been concerned with answering the question of *which* animals can be said to possess episodic cognition. The developmental literature has chiefly focussed on answering the question of *when* children develop episodic cognition. The cognitive neuroscience literature has been chiefly concerned with *where* in the brain episodic cognition is routed. Finally, the medical literature is concerned with *why* some individuals suffer deficits. Around and through each and all of these literatures can be found those concerned with theoretical, philosophical and intuitive notions of *what* episodic cognition *is*.

The aim of this thesis was to bring together not only disparate conceptions of episodic cognition (as represented by tests emphasising different features) but also literatures concerned with different experimental subjects. The results are reviewed in detail later in the chapter. Broadly speaking, they suggest considerable inconsistencies in the results obtained with different tests, suggesting that they may not be assessing the same underlying psychological process.

Unlike many phenomena (notable examples being language and tool-use) there are not multiple official definitions of episodic cognition proposed by different theorists. There is (arguably) a single original theorist of episodic cognition – Endel Tulving. However, there is not a single original *theory* of episodic cognition, because Tulving's concepts of it have evolved dramatically over time (e.g. Tulving *et al*., 1972, Tulving,

1983, Tulving, 2002). A central aspect of all manifestations of the theory concerns the phenomenology of episodic memory as a mental re-experience of a previous event. However the specifics of this defining phenomenology have evolved over time so as to allow for the continued inclusion of a second defining feature: that episodic cognition is late-developing and uniquely human (Tulving, 2005). While few researchers and theorists question the validity of the first defining feature, the second has divided opinions, in part because the statement is not based on evidence, but on intuition.

Everyone has their *own* experiences to draw upon when forming their beliefs, and will always interpret and apply theories in the light of these experiences. "we know what mental time travel is because we can introspectively observe ourselves doing it and because people spend so much time talking about their recollections and anticipations" (Suddendorf and Corballis, 2007, p.301). The difficulty with such a statement is that this personal "knowledge" of the phenomena informs, but also potentially clouds, our ability as humans to understand episodic cognition from any other perspective. Tulving's later (1983, 2002) definitions incorporate this introspective element as defining the form of consciousness necessary for episodic cognition. This recourse to personal experience and intuition when interpreting theory and evidence is useful in that it helps to keep psychological science grounded in "common sense". However, excess of this strategy leaves the field at risk of "surrendering to intuition" (Barr, 2007, p.315) rather than pursuing experimental investigation and, potentially, in the face of empirical evidence. What *evidence* is there that episodic cognition *requires* introspective self-awareness, other than that we as humans experience it in this context?

The different manifestations of Tulving's theory of episodic cognition (e.g. , 1972, 1983, 2002) as well as the different representations and interpretations that have been born out of them (e.g. Clayton and Dickinson, 1998, Zentall *et al*., 2001, Suddendorf and Corballis, 1997, Schacter *et al*., 1984, Levine, 2004) have led to the development of a wide range of tests that are considered to assess episodic cognition. Each of these tests emphasize different elements of episodic cognition (e.g. the spatiotemporal context of a unique past experience: (Clayton and Dickinson, 1998); automatic/non-deliberate encoding: (Zentall *et al*., 2001); awareness of self-in-time: (Suddendorf and Corballis, 1997, Levine, 2004); representational theory of mind: (Perner, 1990, Perner, 1991, Perner, 2000); disengaging from current feelings: (Suddendorf and Corballis, 1997). Furthermore, there is contradiction as to whether certain "classic" memory tests, such as cued recall, can be said to assess episodic cognition (e.g. Tulving, 1985, Fletcher *et al*., 1995b). Indeed, some theorists propose contradictory accounts of these tests *within a single publication* (e.g. Wheeler *et al*., 1997; see Chapter 1). Add to this the tasks and theories that have developed relatively independently of theories of episodic cognition but nonetheless overlap on several key elements (e.g. Long-term Memory, Declarative Memory, Delayed Imitation; as well as various literatures within social and consumer psychology and economics), and the resulting picture is not easy to interpret.

One might thus consider that there are two levels of fractionation in the episodic cognition literature. The first is theoretical - there exist many distinct yet overlapping concepts of episodic cognition. The second is empirical - there are many distinct, yet overlapping, fields of study depending on the experimental subject. This thesis represents an attempt to cohere elements of these two fractionations; to bring together

research using different techniques (born out of different theoretical conceptions) and different research subjects to ask the questions: *What* is Episodic Cognition, *Where* does it exist, *When* does it develop and *Why* does it fail?

The thesis concentrated on four putative tests of episodic cognition: What-Where-When, which assesses memory for spatiotemporal relations (Clayton and Dickinson, 1998, Tulving *et al*., 1972); The Unexpected Question Test, which assesses memory for unattended events (Zentall *et al*., 2001, Zentall *et al*., 2008, Morris and Frey, 1997); The Free Recall test of uncued memory for items on a list (Tulving, 1985b) and the Bischof-Köhler/Projection Bias test for the ability to disengage from current feelings in order to consider future needs (Suddendorf and Corballis, 1997, Suddendorf and Corballis, 2007).

The overarching prediction was that, to the extent to which these different tests assess the same underlying ability, one would expect them to:

1. Be phylogenetically consistent (i.e. if given species passes one test they should be more likely to pass another).
2. Be related in development (i.e. performance should improve at the same rate and in the same pattern in children).
3. Be related in maturity (i.e. adult humans who perform better at one should also perform better than the others).
4. Be affected in the same way in the same patients (factors that cause deficits in one should cause deficits in the others).

These four predictions were addressed in the four empirical chapters. Chapter 2 explored the evidence for episodic cognition in animals. There was a suggestion that those species that had been found to pass some tests of episodic cognition also perform well on the others. However, much of the research on animals is difficult to interpret due to the potentially major impact of extra-target factors (such as associative learning and executive demands) that may lead to "illegitimate" successes or failures. Two experiments were presented in a previously untested species - the Eurasian jay. This species is an intensive food-storing corvid which caches both perishable and non-perishable food throughout the year (e.g. Clayton *et al*., 1996). It was thus argued to be a good candidate for a species whose ecological pressures might have selected for the development of episodic cognition (e.g. Grodzinski and Clayton, 2010). Eurasian jays were shown to be capable of conceiving of a future motivational state different from that which they currently experienced (as assessed by the Bischof-Köhler test). The findings of the second experiment were equivocal, failing to provide convincing evidence that Eurasian jays are capable of remembering what they have cached, where and when (as assessed by the What-Where-When test). Considerable further investigation is required before the question of whether performance on different putative tests of episodic cognition is phylogenetically consistent.

Chapter 3 explored the literature on memory and planning development in children, concluding that there was little to no evidence for the asynchronous development of multiple memory systems, and in particular little evidence to suggest that episodic cognition "emerges" at a given point in development. However, as with the animal

cognition literature, a proliferation of different assessment techniques (and interpretation/classification of these techniques) limits the interpretability of the literature as a whole. An experiment was presented in which the same sample of 3-6-year-old children were tested on three putative tests of episodic memory (What-Where-When, Unexpected Question and Free Recall); one putative test of both semantic and episodic memory (Cued Recall) and one putative test of episodic foresight (Bischof-Köhler). It was found that performance on all these tests increased gradually between the ages of 3- and 6-years. There was considerable inter-correlation between performance on all the memory tests, but much of this was lost when age was partialled out. There are two possible interpretations to this finding; one is that, beyond general cognitive development, there was little relationship between performance on these different tests in children. The other is that the developmental trajectory of these different tests was so similar that the interrelationship between them is heavily intertwined with increasing age. To investigate this possibility, the similarity of the developmental trajectories was assessed. The analysis revealed a non-significant trend towards differences in the developmental trajectory of performance on the different tests, suggesting that the developmental trajectories may not have been sufficiently identical to mask age-independent correlations. Finally, there was little to no relationship between performance on the memory tests and performance on the Bischof-Köhler test, beyond the slight suggestion of a *negative* relationship with Unexpected Question performance.

Given the lack of internal consistency in the developmental cognition literature regarding the development of episodic cognition, the results of this study provide some *refutation* of the second prediction of the thesis: that performance on different

tests of episodic cognition should be related in development. However, because this age range (3-6) is a period of great development generally, it may be that immaturity of non-mnemonic factors (such as language and executive functions) may differentially affect performance on different tests. Thus to interpret these results it was necessary to conduct the same experiment with human adults.

There is extensive research on episodic cognition in human adults. However adult humans' ability to verbally report their memories has led to development of very different paradigms for assessment in this field as compared with the two literatures previously discussed (comparative and developmental psychology). This extensive use of highly verbal techniques to assess episodic cognition (e.g. Addis and Schacter, 2008, Addis *et al*., 2009, Hassabis and Maguire, 2007, Schacter *et al*., 2007) means that the more behavioural tasks have been less widely investigated. Chapter 4 reviewed research using the target paradigms (What-Where-When, Unexpected Question, Free Recall and Bischof-Köhler/Projection Bias) in healthy human adults. Preliminary studies (e.g. Holland and Smulders, 2011, Easton *et al*., 2012) suggest that there may be relationships between performance on some of these different memory tests.

An experiment was presented in which the three putative tests of episodic memory (What-Where-When, Unexpected Question and Free Recall) and one putative test of episodic foresight (Bischof-Köhler/Projection Bias) were presented to the same sample of healthy young adults. It was found that performance on all these tests was interconnected, but not always in a linear fashion. This finding suggested that multiple processes contribute to performance on these tasks, and that all these processes may

not always be shared by different tasks. Following from the finding of a possible negative relationship between Unexpected Question and Bischof-Köhler in the developmental data, it was found that memory performance (and particularly performance on the Unexpected Question test) was *inversely* related with performance on the Projection Bias test. Thus those subjects that had better memories for non-focal elements of the experiment were *more* biased by their current motivational state when making decisions for the future than those subjects with poorer memory performance. Thus while these results support the third prediction of the thesis (namely, that performance on the different tests should be related in maturity) the full picture is manifestly more complex, with evidence for contributions from other, non-shared, processes.

The final empirical chapter (Chapter 5) explored the possibility that obesity and high levels of dietary fat and sugar may lead to damage to episodic cognition. There is mounting evidence for an association between excess body weight, poor diet and impaired hippocampal function. This evidence is both from human subjects and animal models, and is both behavioural (e.g. spatial memory tests) and neurological (e.g. measurements of hippocampal LTP). Given that patient groups with damage to the hippocampus show deficits in episodic cognition (e.g. Scoville and Milner, 1957, Addis *et al*., 2007, Isaacs *et al*., 2000, Golomb *et al*., 1993) it was predicted that episodic cognition deficits would also be evident in overweight individuals and those with high levels of dietary fat and sugar. Furthermore, it was predicted that to the extent to which different putative tests of episodic cognition test the same underlying psychological process, they should be similarly affected by body mass index (BMI) and diet.

These predictions were assessed in two experiments. In the first experiment individuals from the normal population who varied in BMI and dietary fat and sugar were tested on an Unexpected Free Recall test and a Projection Bias test. It was found that BMI and diet differentially effected performance on these tests. There was a suggestion that, (only in women and when an outlier is included), subjects with higher BMIs performed worse on the memory test. There was also a suggestion (only in men) that subjects with higher levels of dietary fat and sugar were *less* biased by their current motivational state in the projection bias test. In the second experiment, Free Recall and Projection Bias were assessed in a sample of obese binge-eating subjects. In the Projection Bias test, current state was manipulated by reduction of hedonic experience (μ-opioid antagonism) rather than satiety (as was used in the previous experiments and chapters). It was found that obese binge-eating subjects were significantly impaired on the Free Recall test, and did not show a projection bias (i.e. were unbiased by their current motivational state when choosing food for future consumption). Taken together, these findings cautiously suggest that performance on these different episodic cognition tests is differentially affected by harmful lifestyle factors (e.g. poor diet and obesity). This provides some refutation for the fourth prediction of the thesis: That performance on all the tests should be affected in the same way in the same patients.

In summary, the evidence contained within this thesis suggests that, while there are *relationships* between different putative tests of episodic cognition, these are by no means robust or straightforward. Indeed, far from there being a one-to-one

relationship between performance on memory tests that have risen from different theoretical perspectives, there is often not even so much as a linear correlation.

Do Different Tests of Episodic Cognition Test the Same Psychological Process?

So what does this mean for the question as to what extent different tests of episodic cognition are assessing the same psychological process? I suggest that the answer lies in the question, or rather the assumption inherent within it. Episodic cognition is not *a* process, it's a *system*. There is not a single neural basis of episodic cognition; there is an extensive neural *network (*see Figure 6.1). The functioning of the network as a whole will thus be differently affected by injury, loss, underdevelopment or absence of different component parts. Similarly, tests born out of theories that differentially emphasize different parts of the system will likely measure individual differences in functioning of different brain regions.

Figure 6.1 depicts a simplified (and by no means exhaustive) representation of the neural substrates thought to be involved in episodic cognition. Consideration of the functional, evolutionary and developmental differences between various components of this extensive network emphasizes the problems inherent in investigating what defines episodic cognition, where and when it evolved and when it develops.

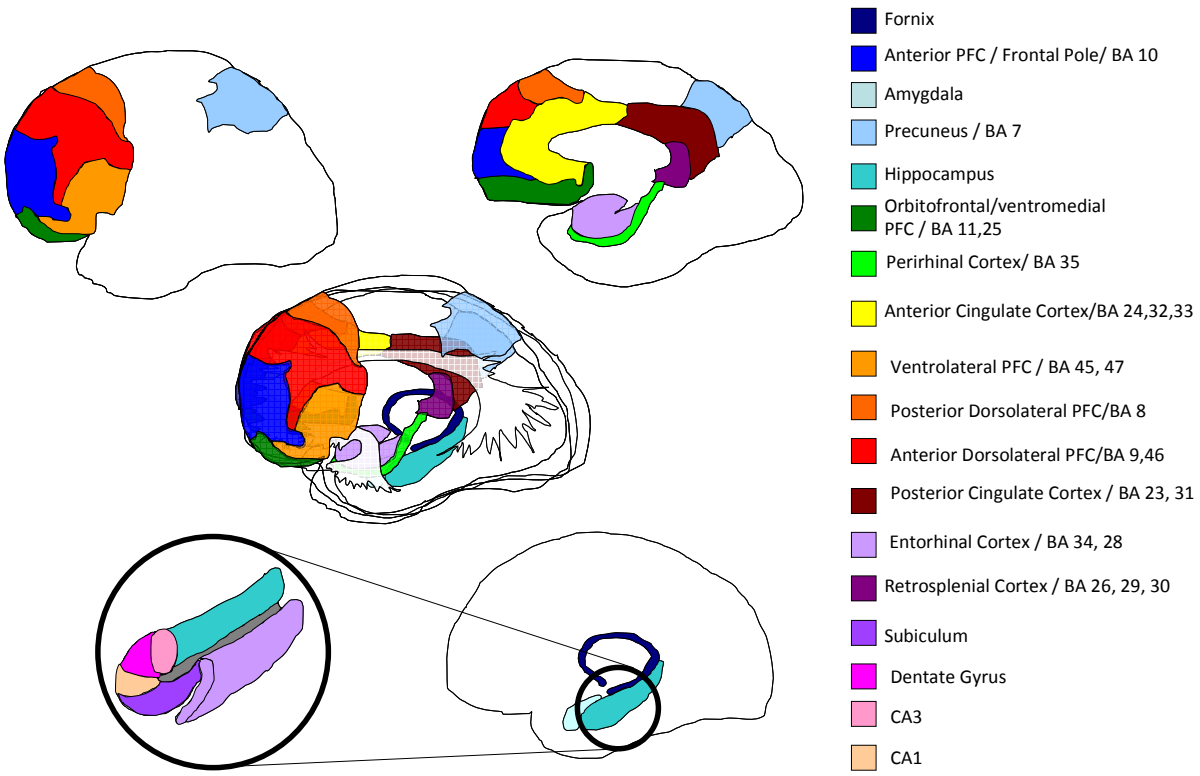

Figure 6.1. *A simplified representation of the brain regions shown to be involved in episodic cognition. The cross-sections show a lateral view of the cortex (top left), a medial view of the cortex (top right), a medial view of the striatum (bottom right) and a cross-section of the hippocampal formation (bottom left). The central picture combines these elements with an illustration of the connective white matter. Each "region" is identified by a different colour. Each of these regions has been suggested to have a distinct function in episodic memory and/or episodic foresight (Suzuki et al., 2002, 2003, Gaffan et al., 2000, 2004, Dolan et al., 2000, Murray and Mishkin, 1998, Squire and Zola, 1998, 1991, Zola-Morgan et al., 1983, Eichenbaum, 2000, 2007, Ennaceur et al., 1997, Sauvage et al., 2010, Fletcher et al., 1995a, Fletcher et al., 1995b, Fletcher et al., 1995c, Fletcher et al., 1997, Fletcher et al., 1998a, Fletcher et al., 1998b, Rugg et al., 1999, Shallice et al., 1994, Simons et al., 2008a, Simons et al., 2005, Simons et al., 2008b, Rugg et al., 2002, Henson et al., 1999, Graham and Hodges, 1997, Poldrack and Gabrieli, 1998, Smith and Jonides, 1999, Brickman et al., 2011, Bakker et al., 2008, Dobbins et al., 2002, Dobbins et al., 1998, Dobbins et al., 2003, Okuda et al., 2007, Cansino et al., 2002, Ranganath et al., 2003, Ranganath et al., 2000, Ranganath and Paller, 2000, Peters and Buchel, 2010, Squire et al., 1992, Levine et al., 1998, Markowitsch, 1995, Nyberg et al., 2003, Nyberg et al., 1996, Szpunar et al., 2007)*

Damage to various of the regions of the episodic network have been shown to result in episodic cognition deficits, suggesting that integrity of *many* different regions is crucial to "normal" episodic cognition in human adults (e.g. Incisa della Rocchetta, 1986, Smith and Milner, 1984, Wheeler *et al*., 1995, Schacter *et al*., 1984, Klein *et al*.,

2002, Tulving, 1985, Levine *et al*., 1998, Scoville and Milner, 1957). These different brain regions have changed differently over the course of evolution. Some central regions, such as the hippocampus, are evolutionarily ancient and can be considered to be shared by phylogenetically distant taxa such as birds and mammals (e.g. Szekely, 1999, Ariëns Kappers *et al*., 1936, Benowitz and Karten, 1976, Campbell and Hodos, 1970, Kuhlenbeck, 1938), while others are thought to have expanded dramatically in recent human evolution (e.g. the prefrontal cortex:Flinn *et al*., 2005, Deacon, 1997, Holloway, 1968, Holloway, 1996, Semendeferi and Damasio, 2000, Semendeferi *et al*., 2002, Rilling and Insel, 1999, Zilles *et al*., 1988, Preuss, 1999, Nimchinsky *et al*., 1999). However, even for these "recently evolved" brain areas, there are functional homologues in other taxa such as birds (e.g. Gunturkun, 2005a, Gunturkun, 2005b, Jarvis *et al*., 2005) that have been shown to be expanded in those species that show many examples of intelligent behaviour (e.g. Lefebvre *et al*., 1997, but see Rattenborg and Martinez-Gonzalez, 2011). Finally, these different brain regions develop at different rates in human infancy, with some, such as much of the hippocampus, being considered fully formed in the early stages of prenatal development (Seress *et al*., 2001, Angevine, 1975, Arnold and Trojanowski, 1996b, Arnold and Trojanowski, 1996a) and some taking many months or years of postnatal development (e.g. Dentate Gyrus: Seress and Mrzljak, 1992, Seress and Ribak, 1988, Eckenhoff and Rakic, 1988, Altman and Das, 1965; Prefrontal Cortex: Huttenlocher, 1979, Huttenlocher, 1990, Carver and Bauer, 2001).

In short, assessing which animals, and children of which particular age, "have" episodic cognition by focussing on a feature that may rely on a single region, or even a small cluster of regions, is much like defining the presence or absence of a skeleton

by focusing on a particular bone. Moreover, defining the presence of episodic cognition by the full-functioning presence of *all* regions may confine episodic cognition to a precious few individuals, even within our own species. As the evidence from Chapter 5 suggests, apparently simple aspects of an individual's every-day life such as diet can have measurable impact on episodic function. It may be that all of us are in different ways and degrees "amnesic", depending on our "poison of choice". Thus the literature may thus be better focused on understanding the different elements of episodic cognition rather than concentrating on all-or-nothing definitions.

Of course the concept of there being different "elements" of episodic cognition is not a new one. Indeed, "elements of episodic memory" was the title of Tulving's (1983) book, and the fact of an episodic *network* is central to much of the neurocognitive literature. However, this seems to be under-appreciated in the fields of developmental and comparative psychology. Episodic cognition is often discussed as a single entity that is either present or absent (but see Clayton and colleagues (2003b) for an acknowledgement of its multifaceted features). This may in part have developed as a response to the challenge of whether or not episodic cognition is uniquely human. Even where such all-or-none approaches are criticised, this is often in favour of a linear simple-to-complex continuum (e.g. Barr, 2007). It is clear that this narrowness is not due to ignorance of the many complex contributions of different processes, but to definitions of episodic cognition that deliberately and self-consciously include *only* episodic cognition *as it exists in healthy, young, human adults* (e.g. Tulving, 1983, 2002, Suddendorf and Corballis, 1997, 2007). However, even if one accepts this narrow (and, some might say, anthropocentric) definition, there is still little agreement as to what defines the healthy adult human experience of episodic cognition.

As it stands, there is a proliferation of behavioural tests that have arisen out of these different conceptions of episodic cognition. The evidence presented in this thesis suggests that each of these assess slightly different elements of episodic cognition. At present, this proliferation of semi-related tests could be considered to be a weakness/limitation of the field. However, if approached in the right way, it has the potential to be a great strength.

Brickman and colleagues (2011) recently assessed whether different standardised tests of memory/hippocampal function (e.g. the picture recognition component of the Benton visual retention test, and the delayed free recall component of the Selective Reminding test) drew on activation of the same areas of the hippocampus. They found that there was a double dissociation, with the delayed recall test relying heavily on the entorhinal cortex, and the picture recognition test drawing upon the dentate gyrus. Such findings allow clinicians to assess functionality of different brain regions without the need for scanning. Thus instead of maintaining several parallel investigations of episodic cognition using different, and somewhat non-comparable, methodologies the episodic cognition literature may be in a position to combine the data and expertise from currently different fields into a singularly useful tool. The ability to have a range of tasks that differentially assess different *aspects* of episodic cognition could, on the one hand, be usefully included into a battery that might be used to assess the episodic *system* as a whole (rather than narrowly defined elements of it). On the other hand, these tasks may also allow behavioural identification of *specific* functioning deficits within the brain. Such a battery could begin to address the

findings that standard neuropsychological tests of memory tend not to be related to the experience of memory complaints in everyday life (e.g. Plancher *et al*., 2010)..

Episodic Bias?

Perhaps the most surprising finding of the research contained within this thesis was the negative relationship between performance on the Bischof Köhler/Projection Bias tests and performance on tests of episodic memory (in particular the Unexpected Questions test). Specifically, it was found that those that performed better on the UEQ memory test tended to be more biased by their current state when choosing for the future. This finding is in contrast to the Bischof-Köhler hypothesis which suggests that episodic cognition is *necessary* for planning for motivational states different to those currently experienced (Suddendorf and Corballis, 1997). In Chapter 4 a possible account for this finding was discussed. It is possible that because of its constructive and experiential nature, episodic cognition is particularly vulnerable to bias from current feelings. As such, those individuals with a greater tendency to use episodic cognition to plan for future needs and/or have more "vivid" episodic experiences of their potential future, are more likely to mistakenly incorporate their current feelings into their representation of their future state. But how does this account cohere with the picture of episodic cognition presented in Chapter 2? Here it was discussed that episodic cognition may allow an action's temporally distant consequences to be "felt" in the present and thus act as a counter-motivation against current desires (Boyer, 2008a). This account suggests that the evolutionary function of episodic cognition may have been in bringing future motivational states *into the present* and thus encouraging prospective behaviour.

These two accounts are not necessarily contradictory. It may be that, from an evolutionary perspective, the development of episodic cognition allowed future needs to gain *some* motivational salience in the present, but this motivational change is limited. The "pre-experience" of a future state (if you take Boyer's account: 2008) or appropriate "re-experience" or a previous state (as might be suggested by Dickinson's MAT model: (2011)) does not result in the organism *replacing* their current feelings with those of their future self, but merely altering their current state to a point that lies somewhere between their current state and their future state (see Lowenstein and colleagues (2003) for a mathematical model of a similar idea). This would lead to behaviour that was future-oriented to a *degree*, but still substantially biased by current state. In contrast, logical inference about one's likely future state without recourse to "pre-experience" would not be so vulnerable to influence from current state (although may be influenced by current semantic beliefs). As such, it may be that the evolutionary development of episodic cognition allows an organism to act in the present in a way that secures *some* future benefit, but that in an organism possessing a *range* of prospective cognitive skills, episodic cognition may not be the most appropriate tool with which to predict and plan for future needs.

Conclusions

Taken together, the empirical results from chapters 2-5 showed that there is not a clear linear relationship between different putative tests of episodic cognition in jays, children, adults or patients. It was suggested that these tests may tap different components of the episodic system, and that they may be differentially influenced by

extra-target factors. Further research should concentrate on reducing the influence of extra-target factors by making the tasks entirely nonverbal and reducing the executive demands by making the scenarios simple and easy to understand and reducing the need for self-control. An episodic cognition 'battery' including these tasks could form a useful neuropsychological tool for assessing the episodic system as a whole and may be more effective at assessing deficits that are experienced in everyday life than current standardised tests. Development of such a battery would benefit greatly from fMRI investigation of the neural correlates of performance on each task, as well as investigation with patients with specific lesions. Finally, the results contained within this thesis pose a double refutation of the Bischof-Köhler hypothesis (Suddendorf and Corballis, 1997). Not only was a nonhuman animal shown to be capable of planning for future needs (Chapter 2), but there was a negative relationship Bischof-Köhler/Projection Bias task and episodic memory tests in human adults. This finding may suggest that episodic cognition is an inherently *ineffective* means by which to disengage from a current motivational state to provide for one's future self. Perhaps episodic cognition allows an organism without the capacity for detailed semantic/logical consideration of likely future cause-effect scenarios (e.g. "large meals lead to satiety") to *reduce*, if not eliminate, the impact of current desires on behaviour.

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Appendix 1.
Menu Creation

Nine subjects rated 68 pictures of chocolate-based, lemon-based or neutral puddings on three scales: how chocolatey and how citrusy, each on a 6-point scale ranging from "highly" to "not at all", and how thirst-inducing on a 6-point scale ranging from "would help quench my thirst" to "would help make me more thirsty" (see Figure 7.1). Items were chosen to appear in the same menu only if they differed substantially from the other menu items according to their category (e.g. the chosen chocolatey items were rated as significantly more chocolatey than the neutral or citrusy items). The items were then coded into "highly thirst-inducing"/"not at all thirst-inducing", "highly chocolatey"/"not at all chocolatey", "highly citrusy"/"not at all citrusy" and allocated 1/0 points in these categories respectively.

Fruit Salad

It would help quench my thirst					It would help make me more thirsty
1	2	3	4	5	6
Citrusy					Not at all citrusy
1	2	3	4	5	6
Chocolatey					Not at all Chocolatey
1	2	3	4	5	6

Figure 7.1. *Example ranking sheet*

The foods were divided into six categories: High Chocolatey/High Refreshing, High Chocolatey/Low Refreshing, High Citrusy/High Refreshing, High Citrusy/Low Refreshing, Low Chocolatey and Citrusy/High Refreshing, and Low Chocolatey and Citrusy/Low Refreshing. Items were selected to be included in the menus if they scored very high or very low on the appropriate scale. After the menus were constructed they were analysed using repeated measure ANOVA to make sure that the items of the different categories differed significant from each other in terms of how citrusy, how chocolatey and how thirst-inducing/refreshing (see Table 6-1).

Table 6-1. Within-menu differences between foods on the variables of "how chocolatey", "how citrusy" and "how thirst-inducing".

	Chocolatey	Citrusy	Refreshing/thirst inducing
Menu 1	$F=154$, $p<0.001$	$F=79.5$, $p<0.001$	$F=14.27$, $p<0.001$
Menu 2	$F=108.592$, $p<0.001$	$F=68.934$, $p<0.001$	$F=30.818$, $p<0.001$
Menu 3	$F=187.145$, $p<0.001$	$F=96.699$, $p<0.001$	$F=20.16$, $p<0.001$
Menu 4	$F=111.680$, $p<0.001$	$F=82.754$, $p<0.001$	$F=65.579$, $p<0.001$

Appendix 2.

Validation of Satiety Procedure

Methods

The pre-feeding procedure was piloted on thirteen subjects (six male, seven female). Participants were presented with eight menus, each containing six food items. Four of these menus were "distracter" menus containing savoury food and four were "test" menus which contained sweet food. In the test menus, the food was divided according to three categories: " Chocolatey", "Citrusy" and "Refreshing". Two items were chocolate-based, two items were citrus-based and two were neutral. Within these, one of each was highly refreshing (e.g. sorbet/milkshake) and one of each was highly thirst-inducing (e.g. chocolate fudge brownie/lemon drizzle cake). Subjects ranked the foods from 1 to 6 based on how much they would like to receive that food *right now* (see Figure 4.2)

After completing half the menus (four distracter and four test) subjects underwent the pre-feeding procedure, which was presented to them as a "taste test". Subjects were split into two groups (*Pre-fed*-chocolate and *Pre-fed*-citrus) and presented with 27 questions asking about specific features of six foods. The *Pre-fed*-chocolate group received and compared six chocolate-based foods and drinks (Frijj® Milkshake, Mars® Milkshake, Sainsbury's Basics® Chocolate Mousse, Cadbury's Button's Chocolate Mousse®, Sainsbury's Basics® Milk Chocolate and Cadbury's Dairy Milk®), while the *Pre-fed*-citrus group received and compared six citrus-based foods and drinks (Satsuma, Clementine, and four squash drinks, the latter made up of differing proportions of Sainbury's Basics® Orange Squash and Robinson's® Lemon

Squash, matched for strength). To encourage maximum consumption the participants were asked to re-try the food and drink for every question.

After the pre-feeding period, subjects completed the final four menus, which contained non-identical but comparable foods. Again, they were asked to rank the foods from 1 to 6 based on how much they would like to receive it *right now*.

Subjects' "before" and "after" scores were calculated by multiplying the category score of each food (e.g. whether it was highly thirst-inducing" etc.) by the rank, and then summing the resulting numbers for each set of menus (before/after). Thus, if highly thirst-inducing foods were ranked 1st, 3rd and 6^{th} in the first "before" menu and 2^{nd}, 4^{th} and 5^{th} in the second "before" menu, the subject would receive a "before" score of 21. A difference score between "before" and "after" menu choices were calculated by subtracting the after score from the before score.

Results

Figure 7.2 shows that the pre-feeding manipulation had an effect on subject's choices for food for *right now.* Repeated-measures ANOVA with the food categorisation (chocolatey, citrusy, refreshing) as within-subjects and pre-feeding type as between-subjects factor showed an interaction between the factors ($F=4.994$, $p=0.016$). Post hoc analyses indicated that there was a significant difference between the pre-feeding groups on refreshing/thirst-inducing foods ($p=0.008$), but not on citrusy/non-citrusy foods ($p=0.662$) or chocolatey/non-chocolatey foods ($p=0.043$) (Sidak correction, alpha=0.0169).

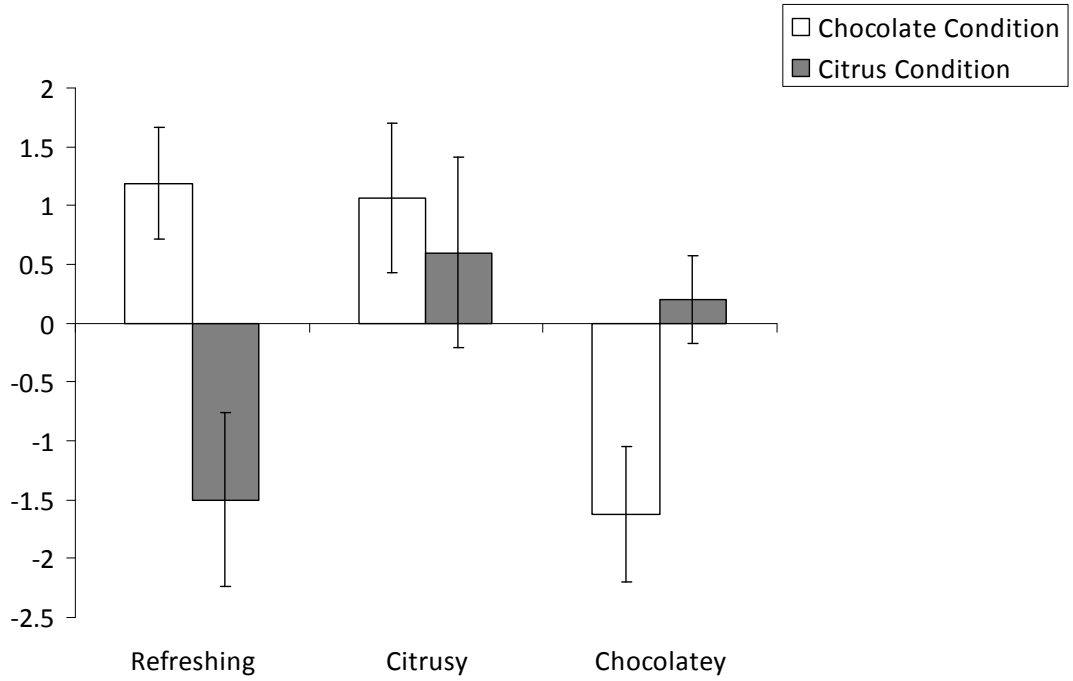

Figure 6.2. *Effect of Pre-feeding manipulation on subject's choices for right now. Bars show mean difference in choices between before and after pre-feeding.*

Conclusions

The pre-feeding test significantly affected choices for food for right now, suggesting that it is effective in causing specific satiety. Due to the more robust effect of pre-feeding on change in choices for refreshing items, only analysis into refreshing/thirst-inducing foods will be continued into the main study.

Appendix 3

Pre-feeding questions:

Citrus group

Which do you think is sweeter?	**Drink 1**	**Drink 2**
Which do you think is sweeter?	Drink 3	Drink 4
Which do you think is sweeter?	Fruit 1	Fruit 2
Which do you think is healthier?	Drink 1	Drink 2
Which do you think is healthier?	Drink 3	Drink 4
Which do you think is more flavoursome?	Fruit 1	Fruit 2
Which is more "citrusy"?	Drink 3	Drink 4
Which is more "citrusy"?	Drink 1	Drink2
Which is more "citrusy"?	Fruit 1	Fruit 2
Which do you prefer?	Drink 1	Drink 2
Which do you prefer?	Fruit 1	Fruit 2
Which do you prefer?	Drink 3	Drink 4
Which is more refreshing?	Fruit 1	Fruit 2
Which is more refreshing?	Drink 1	Drink 2
Which is more refreshing?	Drink 3	Drink 4
Which is more drinkable?	Drink 1	Drink 2
Which is more drinkable?	Drink 3	Drink 4
Which is more "more-ish"?	Fruit 1	Fruit 2
Which is more bitter?	Drink 3	Drink 4
Which is more bitter?	Drink 1	Drink 2
Which is more bitter?	Fruit 1	Fruit 2
Which is more sour?	Drink 1	Drink 2
Which is more sour?	Drink 3	Drink 4
Which is more sour?	Fruit 1	Fruit 2
Which seems more watery?	Drink 1	Drink 2
Which seems more watery?	Drink 3	Drink 4
Which seems more watery?	Fruit 1	Fruit 2

Chocolate Group

Which do you think is healthier?	Drink 1	Drink 2
Which do you think is healthier?	Mousse 1	Mousse 2
Which do you think is healthier?	Chocolate 1	Chocolate 2
Which is sweeter?	Mousse 1	Mousse 2
Which is sweeter?	Chocolate 1	Chocolate 2
Which is sweeter?	Drink 1	Drink 2
Which is more "chocolatey"?	Chocolate 1	Chocolate 2
Which is more "chocolatey"?	Drink 1	Drink 2
Which is more "chocolatey"?	Mousse 1	Mousse 2
Which do you prefer?	Drink 1	Drink 2
Which do you prefer?	Mousse 1	Mousse 2
Which do you prefer?	Chocolate 1	Chocolate 2
Which is more cloying?	Drink 1	Drink 2
Which is more cloying?	Mousse 1	Mousse 2
Which is more cloying?	Chocolate 1	Chocolate 2
Which is more drinkable?	Drink 1	Drink 2
Which is more more-ish?	Mousse 1	Mousse 2
Which is more more-ish?	Chocolate 1	Chocolate 2
Which is thicker?	Drink 1	Drink 2
Which is thicker?	Mousse 1	Mousse 2
Which melts more in the mouth?	Chocolate 1	Chocolate 2
Which is richer?	Mousse 1	Mousse 2
Which is richer?	Chocolate 1	Chocolate 2
Which is richer?	Drink 1	Drink 2
Which is creamier?	Mousse 1	Mousse 2
Which is creamier?	Chocolate 1	Chocolate 2
Which is creamier?	Drink 1	Drink 2

Appendix 4
Obesity Pilot Study

Subjects

The sample consisted of 15 men[14] aged 23-66 years with a mean BMI of 25.54. Subjects were split into four groups: Healthy weight (N=7, BMI=21.95); overweight (N=5, BMI=26.88) and obese (N=2, BMI=36.55).

Method

Subjects were emailed 4 menus (Word documents) and an answer sheet. Each menu contained three or four (depending on the menu) binary choices between two foods, one of which was a "high-fat/unhealthy" food and one of which was a "low fat/healthy" food. Each choice indicated *when* the choices were being made for: immediate or delayed consumption. The subjects were instructed to make the choices on their answer sheet at certain times of day: before lunch, before dinner (when "fasted"), after lunch and after dinner (when "fed"). This was counterbalanced between subjects.

Results

There was a significant difference between choices made when deprived and those made when fed in the healthy weight group ($t[7]=2.518$, $p=0.04$) but not the

[14] It was thought at the time of piloting that the drug study would be conducted only with men, thus only men were tested in the pilot study.

overweight group (t[4]=0.513, p=0.635) and there was a trend in the Obese group (t[1]=9, p=0.07). There was no significant difference between choices for immediate consumption and choices for delayed consumption in any weight group (healthy: t[7]=-1.239, p=0.255; overweight: t[4]=0, p=1; obese: t[1]=-1.308, p=0.416).

Figure 6.3 indicates that, numerically, the expected pattern of results was revealed. Subjects were more likely to choose the high-fat food if they were making the choices while deprived (bottom figure) or for immediate consumption (top figure). This pattern was shown in the healthy-weight group and the obese group, but not in the overweight group.

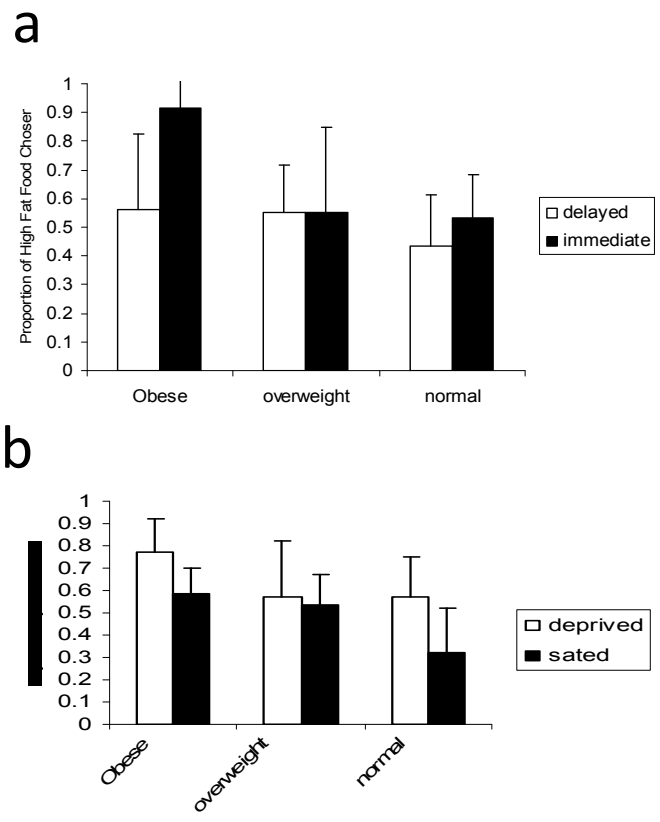

Figure 6.3. *The expected pattern of more choices of the high fat food option when food is to be received* ***a)*** *immediately* ***b)*** *and when in a deprived state (bottom) is shown in the obese and healthy-weight groups, but not in the overweight group.*