Individual differences in neural architecture supporting mental time travel

A thesis submitted for the degree of Doctor of Philosophy

School of Psychology, Cardiff University

January 2021

Samuel Ridgeway

Thesis Summary

Episodic and semantic memory have been cornerstones of memory research ever since they were first described in a seminal article by Endel Tulving in 1972. Later work by Tulving posited that particularly episodic memory supported mental time travel, a process by which humans could project the self across a conceptual lifespan (however modern research has emphasised the role of semantic memory in the process). Various neurocognitive models have been proposed that attempt to explain the component processes of mental time travel. While it is now recognized that a common 'core' brain network underlies memory, prospection, and imagination (Schacter et al., 2017), the neural substrates of the component processes that comprise the core network supporting memory-based simulations, and the extent to which they are dissociable, are still a matter of intense debate.

This thesis has demonstrated that combining diffusion MRI-based tractography with interview and self-report measures is a viable method for investigating the associations between interindividual differences in white matter microstructure and cognitive traits or tendencies related to mental time travel. The present findings provide support for the notion that episodic and semantic memory systems are at least partially separate and supported by different structurally instantiated neural pathways. However, it is also clear that they must interact and support each other within episodic construction and mental time travel.

Regarding the current models of mental time travel, the results of this thesis do not provide overwhelming support to any single model. However, some evidence has been provided (linking fornix-mediated hippocampal processing to spatial components of memory in particular) that might support the scene construction hypothesis (Hassabis & Maguire, 2007). Further, present findings did not show a significant association between semantic circuitry (mediated by the ILF) and episodic future thinking – which poses a challenge to the semantic scaffolding hypothesis (Irish & Piguet, 2013). However, this is consistent with Tulving's original notion of episodic and semantic memory (including autobiographical facts) being dissociable but interacting memory systems that are future as well as past directed.

Declaration and Statements

DECLARATION

This work has not been submitted in substance for any other degree or award at this or any other university or place of learning, nor is it being submitted concurrently for any other degree or award (outside of any formal collaboration agreement between the University and a partner organisation).

Signed: Sam Ridgeway Date: 27/01/2021

STATEMENT 1

This thesis is being submitted in partial fulfilment of the requirements for the degree of PhD.

Signed: Sam Ridgeway Date: 27/01/2021

STATEMENT 2

This thesis is the result of my own independent work/investigation, except where otherwise stated, and the views expressed are my own. Other sources are acknowledged by explicit references. The thesis has not been edited by a third party beyond what is permitted by Cardiff University's Use of Third Party Editors by Research Degree Students Procedure.

Signed: Sam Ridgeway Date: 27/01/2021

STATEMENT 3

I hereby give consent for my thesis, if accepted, to be available in the University's Open Access repository (or, where approved, to be available in the University's library and for inter-library loan), and for the title and summary to be made available to outside organisations, subject to the expiry of a University-approved bar on access if applicable.

Signed: Sam Ridgeway Date: 27/01/2021

WORD COUNT: 51,826 (Excluding summary, acknowledgements, declarations, contents pages, appendices, tables, diagrams and figures, references, bibliography, footnotes and endnotes)

Acknowledgements

I would like to thank my supervisors, Prof Andrew Lawrence and Dr Carl Hodgetts, for their insight and advice over the course of this PhD. Particularly given the difficulties of 2020 this has been much appreciated. I am also grateful to the ESRC Wales Doctoral Training Partnership that funded the project.

I would also like to thank the researchers in Cardiff whose knowledge helped form the approach to this project. I would also like to thank the lab group for their discussions and insight into their varying focuses, which helped contextualise my own work. Thanks especially to Prof Kim Graham, Alison Costigan, Angharad Williams, Bethany Coad, Vera Dehmelt, Ashvanti Valji, and Emma Craig.

Thanks as well to Sean, Theo, Morgan, and James who helped me stay sane over the last four years. Harry and Lizzie receive their credit pro rata.

I wish to thank my parents for supporting me on my whole journey. They have endured and I am grateful.

Finally, thank you Beth. I couldn’t have done this without you.

“With one singular exception, time's arrow is straight… When one thinks today about what one did yesterday, time's arrow is bent into a loop.” Endel Tulving (2002)

Preface

The results of Chapter 3 have been published in:

Williams, A. N., Ridgeway, S., Postans, M., Graham, K. S., Lawrence, A. D., & Hodgetts, C. J. (2020). The role of the pre-commissural fornix in episodic autobiographical memory and simulation. *Neuropsychologia*, 107457.

Content’s page

List of figures

List of tables and boxes

Chapter 1: General Introduction

1.1 General introduction to mental time travel

Although life is experienced one moment at a time, it would be too simplistic to suggest that humans exist only in the instant of the present — passively parsing and reacting to sensory stimuli as it occurs. Our behaviour is influenced by the knowledge that our lifespan stretches out both behind and ahead of us. As such, the life experience of any given person requires a temporal understanding of their past, present, and future. It has been argued that our ability to flexibly consider time and space, and our relative position within it, is a foundational element of our general cognitive abilities and self-conceptualisation capacity (Conway, Singer, & Tagini, 2004; D'Argembeau, 2020; Dafni-Merom & Arzy, 2020; Markowitsch & Staniloui, 2011; Suddendorf, Addis, & Corballis, 2009). Further, this is an ability that can be used on a broad scale — we can consider moments at either end of our lifespan, and at any temporal distance from the central 'present' instance. It is possible for us to remember a birthday party from our childhood and the act of eating breakfast this morning, using the same processes to support both (Conway, 2009; D'Argembeau, 2020; Monsa, Peer, & Arzy, 2020).

The capacity to represent ourselves across a cognitive timeline has been described as 'mental time travel' (Tulving, 1985, 2002a) or more generally as 'self-projection' (Buckner & Carroll, 2007) (see box 1.1 for a discussion on terminology). Tulving argued that the ability to travel 'mentally' through time would suggest three capacities of the mind. First, it would be necessary to experience time subjectively (i.e. to be able to reflect on experiences beyond 'implicit' forms of memory). Second, it would be necessary to be aware of when the subjectively experienced moment was occurring (in both the macro scale of past or future, and in more fine detail as to its temporal distance from the present). Finally, the thinker must have a concept of themself, and how they relate to their subjective sense of time. In Tulving's (2002a) own words "No traveller, no traveling".

Tulving described these as contributing to two separate concepts that underpinned mental time travel (Tulving, 2002b). Firstly, chronesthesia — a form of consciousness that allows individuals to think about subjective time (for a review see Szpunar, 2011); and secondly, autonoetic experience — a form of consciousness that allows individuals to understand their subjective experiences throughout time, and to perceive the present as a continuation of their past and a prelude to their future (Tulving, 2002b; Wheeler, Stuss, & Tulving, 1997). Tulving (2002b) described the subtle difference between his "esoteric concepts" stating "in autonoesis the emphasis is on awareness of *self,* albeit in subjective time, whereas in chronesthesia the emphasis is on awareness of *subjective time*, albeit in relation to self".

Fundamentally, mental time travel requires us to be able to disengage from our temporal present, and project ourselves into another period of conceptual time (Buckner & Carroll, 2007, see figure 1.1 for examples of self-projection). It has been associated with wider aspects of cognition, including the generative and creative aspects of language (Corballis, 2019); social cognition (Gaesser, 2020); and planning and decision making in novel environments (Brocas & Carrillo, 2018). The capacity for mental time travel emerges relatively early in human development, with evidence that children as young as four are able to consider their own futures (Suddendorf & Redshaw, 2013). It has been argued further that the ability might be formed even earlier than this, and that its detection is prevented by the inability of younger children to engage in the task at hand (Atance, 2015). Mental time travel has been proposed to be a uniquely human ability, and that our capacity to experience time subjectively is fundamental to the level of consciousness that separates us from other animals (Suddendorf & Corballis, 2007; Tulving, 2002a, 2005; but see Corballis, 2013, Clayton, Russell, & Dickinson, 2009; Martin-Ordas, 2020).

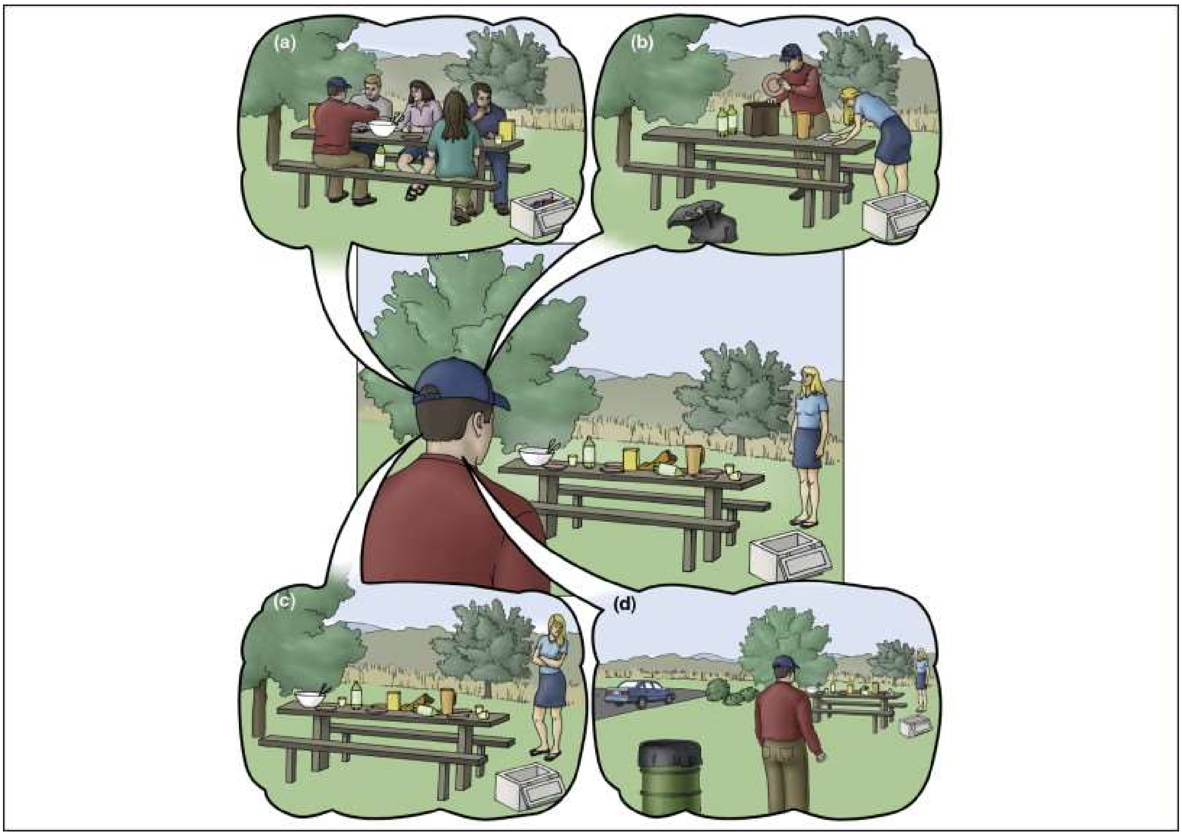


Figure 1.1 is reproduced from Buckner and Carroll (2007) and shows four forms of self-projection. Projections in (a) and (b) respectively show the person recalling a prior experience and simulating a potential future scenario. Further, this figure demonstrates how self-projection can occur without a shift in mental time in scenarios such as (c) which depicts the attempt to understand another's mental state and (d) in which navigational abilities are supported through the creation of a mental map of the area.

There has been some debate as to whether mental time travel is best considered a single ability, or an umbrella term that describes several underlying cognitive processes (Addis, 2018; Zheng, Luo, & Yu, 2014). It is possible, for instance, to consider the difference between future and past episodes as separating reality and fantasy (Johnson, Hashtroudi, & Lindsay, 1993; Suddendorf & Corballis, 2007). However, a growing body of research has demonstrated that these two processes share cognitive and neurological foundations, supporting the notion that 'mental time travel' represents a single continuous process (Addis, 2018, 2020; D'Argembeau, 2020; Dafni-Merom & Arzy, 2020; Zheng et al., 2014). As such, it is appropriate for a holistic examination of mental time travel to consider the directions in which constructions occur (i.e. both as autobiographical memory and future thinking (Addis, 2020; Schacter et al., 2012)). Further, it is important to consider the qualities and dimensions that exist within these constructs and how their demonstration or representation might provide additional insight into the individual and overarching processes in question.

Further it is important to conceptualise the nature in which subjective time is experienced. For example, autobiographical memory cannot simply be considered as a stream of episodes leading from our birth until our present. Instead it can be divided into various degrees of temporal specificity — covering minutes to whole sections of our lives (Conway, 2009; D'Argembeau, 2020). As such, we are able to remember the specific act of getting ready for our first day of school; and also to recall the morning routine we had over a period of months or years. It is possible for elements of our autobiographical memory to be further abstracted from specific times or events, such as being able to recall the colour of a school uniform. In Tulving's (1972) seminal work, he described this divide in declarative memory as reflecting "episodic" (tied to a specific spatiotemporal context) and "semantic" (decontextualized from spatiotemporal origin of acquisition) memory systems (for a historical review see Renoult & Rugg, 2020). Any given construction (e.g. autobiographical memory, counterfactual memory, or future simulation) is likely to contain both examples of episodic and semantic details, which help to scaffold or frame memories and simulations (Irish & Piguet, 2013; Schacter, Benoit, De Brigand, & Szpunar, 2015; Schacter, Benoit, & Spencer, 2017). It has been argued that episodes are integrated within the context of a person's life story, both for memories and imagined events, through higher order autobiographical knowledge (D'Argembeau & Mathy, 2011; Thomsen, 2015). As such, any study of mental time travel should consider, or at least be considered in the context of, the systems supporting its construction — i.e. representation of self, spatiotemporal context, and episodic and semantic memory systems.

Autonoetic consciousness was proposed by Tulving (1985) to vary across individuals. This is still held as one of the principal properties of autonoetic consciousness underpinning the capacity for mental time travel (Dafni-Merom & Arzy, 2020). Despite this, the study of individual differences in mental time travel capacity and its neural correlates remains in its infancy (for a review see Palombo, Sheldon, & Levine, 2018). These authors noted that common methods used to investigate autobiographical memory (such as quantitative interview techniques and self-reported trait-level questionnaires — discussed further below) are likely to be applicable within examining individual differences in this area. The present work represents a novel attempt to demonstrate that individual differences in the neural microstructure of healthy participants can be associated with traits and capacities associated with various aspects of mental time travel. The interindividual measurement of neural architecture will be assayed using diffusion weighted imaging, targeting tracts identified via prior research to be likely candidates for an anatomical association between areas relevant to the processing capacities of interest.

Box 1.1 A brief word on the terminology used in this thesis

Before continuing it is worth making a quick note of the terminology that will be used in this thesis. Prior research has used a number of terms (mental time travel, autonoetic consciousness, chronesthesia, autobiographical memory, episodic memory, episodic future thinking, prospection, self-projection, episodic construction, scene construction, and so on) that refer to processes that refer to similar (or in some cases identical) processes. To support the reader in understanding the present work, the terms that will be used across the project will be briefly identified here.

Please note that the terms that follow will be discussed and defined in more detail throughout this chapter (and the chapters that follow). Box 1.1 intends to ground the reader and may be used as a touchstone to clarify the content that follows.

The present project examines both past- and future-oriented cognition. In the same way that ***'memory'*** is used to talk about general reflections on the past, this thesis will use ***'prospection'*** or '***future thinking'*** to refer to general reflections on the future.

This thesis will use ***'mental time travel'*** to refer to mentation that decouples a person from the experienced present, and projects them to a point in their personal timeline such that that point is subjectively re/pre-experienced.

Mental time travel is considered to be a form of ***'autobiographical cognition'*** — that is, mental processing that supports a personal understanding of an individual's own life story across the full conceptual stretch of their lifespan.

Mental time travel further requires the ***'construction'*** of a specific and coherent mental episode (i.e. the mental representation of sensory and narrative details that constitute an 'occurrence'). Another common term is ***'simulation'*** which is used to describe a specific subset of constructions that the individual has not experienced (e.g. future narratives, counterfactual memory, etc).

Mental time travel is proposed to be supported by two systems: ***'episodic'*** — concerned with the procedural/contextual/narrative details of a spatiotemporally specific event; and ***'semantic'*** — concerned with facts and knowledge that are accessed outside of the spatiotemporal context of their acquisition.

'***Episodic construction'*** is a broad term that refers to the generation of specific and coherent mental episodes (i.e. the mental representation of sensory and narrative details that constitute an 'occurrence') and includes any construct that contains its own internal temporality. They are not necessarily tied to either memory or future thinking, nor are they necessarily personal (e.g. constructs that lack temporal context, are purely fantastical, etc).

Although 'episodic construction' will be used in discussing prior research, the focus of the empirical work in this thesis is on ***'autobiographical construction'*** (i.e. constructs that relate to an individual's experienced past or plausible future).

1.2 Autobiographical recall

As noted above, mental time travel takes place in both the past and the future. It is perhaps more natural to conceive of it in relation to the recollection and re-experiencing of prior episodes across our lifespan — 'episodic' autobiographical memory (Conway, 2001; for discussion see Renoult and Rugg, 2020). Even this unidirectional approach, however, might not fully encapsulate the particulars of the autobiographical memory system. Further to the recollection of specific episodes, autobiographical memory refers to our knowledge of our overall life story and an understanding of personal traits (Conway et al., 2004; Steiner et al., 2017). As such it engages both episodic and semantic memory systems (Fivush, 2011; Levine, Svoboda, Hay, Winocur, & Moscovitch, 2002; Renoult, Irish, Moscovitch, & Rugg, 2019). The integration of these separate strands of memory, along with a conceptualisation of the self, has been suggested to be fundamental to higher level cognitive processing relating to the social domain (Conway et al., 2004). These systems are used to substantiate our sense of who we are and how we can conceptually place ourselves in the world around us (Bluck, Alea, Habermas, & Rubin, 2005).

As autobiographical memory is an integrative process, it is important to consider the elements that support its function. In this context, the episodic memory system allows for recollections of specific events to be used both in isolation and combination as building blocks within the larger representation of the totality of an individual's past (Wheeler, 2000). Episodic memory refers to the ability to recall stimuli, actions, thoughts, and feelings that were directly experienced during a specific spatiotemporal event (Conway, 2009; Levine et al., 2002; Tulving, 2002a; see Renoult & Rugg, 2020 for discussion). Events, or 'episodes', are specific occurrences that are both discrete and unique. The nature of what defines an 'episode' is a contemporary focus of the field (e.g. Baldassano et al., 2017; D'Argembeau, 2020; Ezzyat & Davachi, 2011; Rubin & Umanath, 2015; Zacks, 2020). It is natural to consider these boundaries as temporal (e.g. Cohn-Sheehy & Ranganath, 2017) and episodes are commonly operationalised as salient occurrences occurring within a relatively short period of time (e.g. 24 hours — Conway, 2009; Levine et al., 2002). Further research has indicated that non-temporal factors (such as turns during navigation) can also form boundaries within events (Brunec et al., 2020; Clewett & Davachi, 2017). This emphasises the link between spatial and episodic memory and the importance of 'where' characteristics in mental time travel journeys (Dafni-Merom & Arzy, 2020; Robin, 2018; Tulving, 2005). As such, episodes might be considered the smallest unit of 'complete narrative' and are flexibly recombined to support a concept of the individual's experience in the context of their autobiographical memory (Burt, Kemp, & Conway, 2003; Cohn-Sheehy et al., 2020; Hohman, Peynircioğlu, Beason-Held, 2013).

The process by which episodic memories are experienced is fundamental to understanding the autobiographical memory system as a whole. Episodic memories should not be considered as analogous to television re-runs, as recollection does not occur as a complete re-experiencing of the remembered event. Instead, they are reconstructions stitched together from fragments derived from various modalities to produce a summary representation (Conway, 2009; Conway & Pleydell-Pearce, 2000; Schachter, Norman, & Koutstaal, 1998). Jeunehomme and D’Argembeau (2019) had participants experience a scripted event whilst wearing a camera so that they could compare later recall with an exact record of the event. They found that participants’ recollections displayed temporal discontinuities when compared to the recordings of their experience. In order for the scene to be conceived as coherent, participants used a form of ‘cognitive compression’ that facilitated accelerated playback during recollection. The constructive nature of episodic memory, as opposed to rote recall, has been proposed as fundamental in allowing for mental time travel to exist as a bidirectional process (Addis 2018; Schacter & Addis, 2007a, 2007b — the constructive episodic simulation hypothesis).

The second ‘branch’ of declarative memory is semantic memory, which deals with knowledge abstracted from the spatiotemporal context of its acquisitional origin (Moscovitch et al., 2005; Renoult & Rugg, 2020). Semantic memory can be considered an extremely ‘broad’ category in terms of both its cognitive scope and the brain regions that associate with it (Canessa et al., 2008). These authors described semantic memory as belonging to different categories, namely sensory, action and functional knowledge. These categories are each represented differently across the brain. For instance, posterior regions associated with sensory processing are also associated with sensory semantic memory (Canessa et al., 2008) whereas verbal semantic memory is associated with activation in frontal and temporal areas (Köylü et al., 2006). Further, it has been suggested that modality-specific features are supported by an amodal hub that supports conceptual knowledge shared between diverse semantic features (Patterson, Nestor, & Rogers, 2007; Rogers et al., 2004 — the hub-and-spoke hypothesis).

At first glance, semantic memory might seem misplaced within the scope of mental time travel —a process which indicates a spatiotemporal context by its very name. However, it has been suggested that semantic memory supports a sense of autobiographical knowledge through which episodic representations might be contextualised (D’Argembeau, 2020; Levine et al., 2004). This information relates to an individual’s semantic knowledge of their life story. Further, it refers to the conceptual knowledge of the ‘self’ and how this relates to external factors (e.g. close friends and family, work colleagues, and the world at large). Autobiographical memory can be considered as the retrieval of specific episodes constructed within a wider ‘contextual bedding’ provided by general semantic memory and specific autobiographical knowledge (Addis, 2018; Renoult et al., 2019). Further, it has been demonstrated that autobiographical memory can be primed simply by the activation of semantic memory itself (Mace, McQueen, Hayslett, Staley, & Welch, 2019).

Further research into semantic memory has suggested that semantic details in autobiographical constructions might be considered in terms of their degree of abstraction from the point of their spatiotemporal origin (Renoult, Davidson, Palombo, Moscovitch, & Levine, 2012; Renoult et al., 2016, see figure 1.2). This ranges from ‘general’ semantic knowledge (i.e. referring to information or facts that are common to a wider culture) to more ‘personal’ semantics (i.e. knowledge regarding the individual that has been abstracted from their experiences, such as common themes between events or knowledge of traits). Personal semantics are the main component of semantic details within autobiographical memory (Conway & Pleydell-Pearce, 2000). They share similarities with both episodic memory, as they are highly personal, and general semantic memory, as they are not tied to the specific spatiotemporal context in which they were acquired (Renoult et al., 2012).

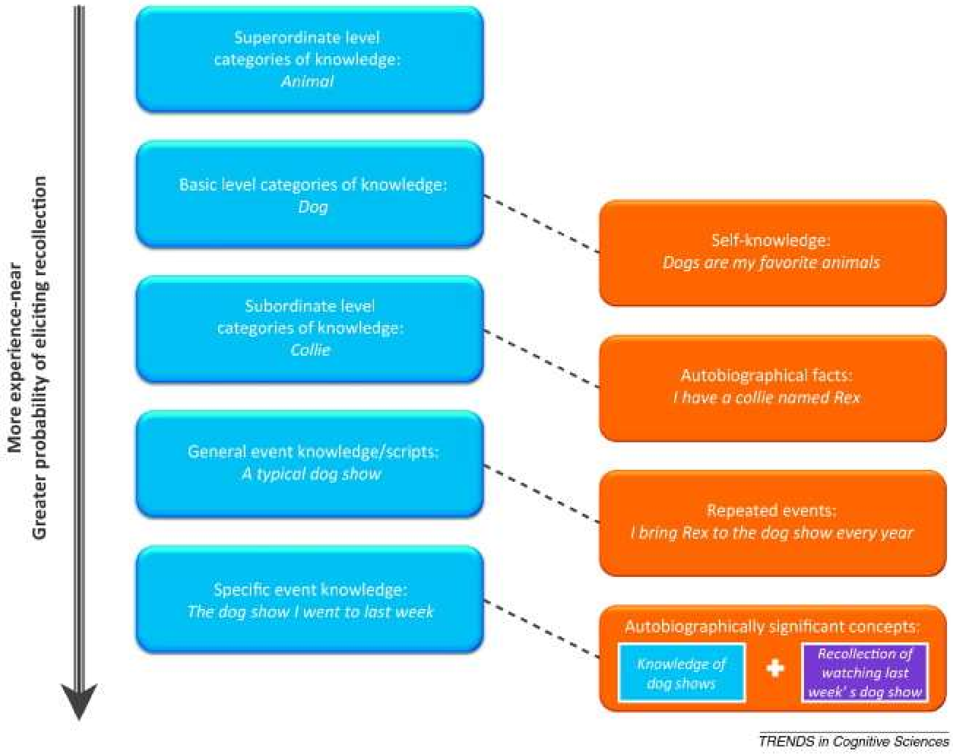


Figure 1.2 shows a continuum of abstraction within general (blue) and personal (orange) semantic details and is reproduced from Renoult et al. (2012). The greater the degree of abstraction from spatiotemporal origin, the less likely the memory is to elicit episodic recollection.

Whereas episodic and general semantic memory are relatively easy to classify (Levine et al., 2002; Renoult & Rugg, 2020; Tulving, 1972), personal semantic memory has provided researchers with more of a challenge. Kazui, Hashimoto, Hirono, and Mori (2003) reported that personal semantic memory performance correlated with both episodic and general semantic memory performance in Alzheimer's patients. These authors concluded that this demonstrated that personal semantic memory shared elements of both episodic and semantic memory. The experiment by Kazui et al. (2003) measured personal semantic memory using the Family Line Test (Kazui et al., 2000), which measured factual recall of information specific to the participant's life (e.g. name of spouse or grandchild). Information of this sort is quite clearly highly personal but has also been removed from the spatiotemporal context of its acquisitional origin. However, some of the items do contain elements of spatial (e.g. place of wedding) or temporal (e.g. first occupation) information. As such, it is possible to consider knowledge of extended lifetime periods or generalised memories of repeated events as existing under the umbrella of personal semantic memory (Renoult et al., 2012). These authors suggest that the key difference between episodic and personal semantic memory in this regard is temporal specificity. Personal semantic memory therefore can be conceived as dealing with concept-based or experience-far (i.e. abstract ideas such as traits and roles) and experience-near information (autobiographical facts more closely tied with spatiotemporal and perceptual details — Grilli & Verfaellie, 2014).

1.3 Autobiographical future thinking

So far, the focus has largely been on what can classically be considered as declarative memory — the combination of episodic and semantic frameworks that consist of our understanding of our experienced past (Davachi & Dobbins, 2008). However, mental time travel is bidirectional, and any discussion of the concept must also consider how these processes are reflected when directed towards the future. Indeed, it has been suggested that mental time travel, perhaps unintuitively, occurs more commonly as a consideration of the future than as a reflection of our past (Anderson & McDaniel, 2019; Gardner & Ascoli, 2015; Suddendorf & Corballis, 2007). Further it has been proposed that future thinking or 'prospection' involves flexible use of simulation, prediction, intention, and planning; and that both episodic and semantic systems were employed in these capacities (Addis, 2018, 2020; Szpunar, Spreng, & Schacter, 2014).

The ability to reflect on future scenarios through prospection allows us to simulate potential scenarios in our life before they occur. This allows us to consider the benefits and drawbacks of our potential choices, and to choose the manner in which we act. Research has suggested that prospection may have an influence on decision making and planning goal directed actions (Bulley, Henry, & Suddendorf, 2016; Bulley & Irish, 2018; Pezzulo & Rigoli, 2011). Its influence can also be seen in social actions — it is common enough for us to rehearse, to varying degrees of accuracy, how an argument with our boss or the presentation of a surprise gift might go. In this regard, further research has tied prospection to emotional regulation and empathy (Gaesser & Schacter, 2014; Gaesser, Dodds, & Schacter, 2017; Jing, Madore, & Schacter, 2016). It is proposed that the ability to pre-experience the future through mental time travel plays a role in the motivation for and management of human behaviour as an evolutionary process (Suddendorf et al., 2009).

Autobiographical future thinking represents a specific form of prospection that is characterised by the simulation of specific events that might plausibly take place in an individual's future (Atance & O'Neill, 2001; Suddendorf & Corballis, 2007; see also box 1.1). Autobiographical future thinking allows us to mentally pre-experience events and occurrences by integrating simulated sensory data, and by allowing us to reflect on the thoughts and feelings of the agents within the construction (D'Argembeau & Van der Linden, 2006). In this sense, this form of future-oriented cognition can be considered most similar to 'episodic' autobiographical memory.

Prospection is supported, as with declarative memory, by both episodic and semantic neurocognitive systems (D'Argembeau, 2020; Schacter et al., 2012; Szpunar et al., 2014). Indeed, shared deficits can be found to both past and future thinking in amnesic patients with hippocampal damage (Hassabis, Kumaran, Vann, & Maguire, 2007; Race, Keane, & Verfaellie, 2011, Tulving, 1985). Further, an extensive body of research has highlighted the cognitive similarities between autobiographical future thinking and autobiographical recall (Addis, 2018). The qualitative richness of prospection and recollection are found to vary similarly against temporal distance (D'Argembeau & Van der Linden, 2004). Further, phenomenological 'experiencing' is stronger for positive than negative scenarios for both recollection and prospection (Arnold, McDermott, & Szpunar, 2011; D'Argembeau & Van der Linden, 2004). Further, autobiographical future thinking and autobiographical recall have been found to show similar trajectories during both development (Busby & Suddendorf, 2005; Russell, Alexis, & Clayton, 2010) and ageing (Addis, Musicaro, Pan, & Schacter, 2010; Addis, Wong, & Schacter 2008).

As with autobiographical memory, semantic details in autobiographical future thinking can be considered separately as personal and general (La Corte & Piolino, 2016; Szpunar et al., 2014). Further, it has been suggested that personal semantics could be important when considering the temporal distance that a construction exists at in line with construal level theory (La Corte & Piolino, 2016; Trope & Liberman, 2003). The model proposed by La

Corte and Piolino, temporal distance in future thinking (TEDFIT), suggests that increasing temporal distance (from the present) is associated with a shift from episodic to semantic construction.

It has been proposed that mental episodes are constructed outside of a specific temporal context (Addis, 2018, 2020; Mullally & Maguire, 2014; Schacter et al., 2012). The sensation of specific personal temporality is then supported by the integration of autobiographical knowledge within the constructed episode (D'Argembeau, 2015, 2016). D'Argembeau and Mathy (2011) performed a series of experiments that showed that autobiographical future thinking was a process that began with accessing generalized personal knowledge before episodes were generated. Further these authors demonstrated that participants that had been cued with knowledge about their personal goals were able to generate future episodes more easily and in greater detail.

Tulving (1985) proposed that autonoetic experience requires both personal knowledge and self-consciousness. Contemporary work by D'Argembeau (2020) has suggested that the phenomenological experience of temporality during episodic constructions might be reliant on autobiographical knowledge. It has been argued that it is the autonoetic component of episodic memory, rather than the ability to recollect contextual detail, that is crucial in allowing an individual to project themself into their personal future (Klein, 2016). Further, it has been established that both lesion patients and healthy older adults find autobiographical future thinking more difficult than atemporal or fictious construction (Bertossi, Aleo, Braghittoni, & Ciaramelli, 2016; Rendell et al., 2012). This provides evidence that future-oriented mental time travel is not simply accessing the capacity for imagination or fantasy. Further work has shown that the autonoetic experience of imagine events is related to both the vividness of the construction and its relevance to personal goals (D'Argembeau & Van Der Linden, 2012; Lehner & D'Argembeau, 2016). It is possible, therefore, that mental time travel's bidirectional properties are supported through the integration of episodic and semantic details within autobiographical constructions.

1.4 Theories of mental time travel

Autobiographical memory and future thinking are linked by a shared constructive process (Addis 2020; Atance & O'Neill, 2001). However, the precise nature of their connection, and hence the capacity for mental time travel, is a matter of some debate. A growing body of research has produced various neurocognitive models that attempt to explain the cognitive processes and neurology that underpin this ability. The first noteworthy model was the *'constructive episodic simulation hypothesis'* (Schacter & Addis, 2007a; Schacter & Addis, 2007b; Schacter et al., 2012 — an updated form of this model was described by Addis, 2018, 2020 and is discussed further below). As suggested by its name, this model focuses on the episodic memory system and holds that it is sufficient for both reflection on past events and the simulation of plausible future scenarios.

The history of this model can be traced back to Bartlett (1932) who pioneered the field of memory research with his suggestion that memory is a process geared around generation rather than one of strict replay. This has been supported by evidence surrounding errors and distortions within memory, and how they can be cued or manipulated (e.g. Brainerd & Reyna, 2005; Loftus, 1973; Loftus & Pickrell, 1995). The constructive episodic simulation hypothesis holds that the ability to work across different periods of time is critical to the constructive memory system. It is proposed that the ability to consider the future is just an extension of this feature, and that memory and simulation are both built by flexibly recombining information from a shared store (Schacter et al., 2012 — see also Addis, 2018, 2020). The model conforms to the notion that episodic reconstruction is an adaptive feature of future planning (Suddendorf & Busby, 2003). The authors note that, although necessary for the ability, they do not consider future simulation to be the sole reason that episodic memory is a constructive process (Schacter & Addis, 2007b).

In line with these beliefs, it was held by the original form of the constructive episodic simulation hypothesis that autonoetic experience, or the conscious awareness of mental time travel, is not critical to the system's function (Schacter & Addis, 2007a, 2007b). Instead, a greater theoretical emphasis is placed upon the retrieval and integration of distinct elements within an episode. This argument has been supported by functional neuroimaging studies which established that activation could be identified across the default mode network for various mental simulations both when mental time travel was performed and when it was not (Buckner & Carroll, 2007; Hassabis et al., 2007). This model holds that the hippocampus plays a role in this process regarding the reintegration of episodic details to form a coherent episode (Eichenbaum & Cohen, 2001; Suddendorf & Corballis, 1997).

In addition to deficits in future thinking and the simulation of novel scenarios (Klein, Loftus, & Kihlstrom, 2002; Romero & Moscovitch, 2012; Tulving, 1985), amnesic patients with hippocampal damage show impairments in spatial navigation and scene construction (Burgess, Maguire, & O'Keefe, 2002). This contrasts with the proposed role of the hippocampus within a broader core network in the constructive episodic simulation hypothesis (Addis, Pan, Vu, Laiser, & Schacter, 2009; Thakral, Benoit, & Schacter, 2017; but see Addis 2018, 2020 for an updated account of this model). An alternate proposal that incorporates these deficits is the *'scene construction theory'* (Hassabis, Kumaran, & Maguire, 2007; Hassabis & Maguire, 2007; Mullally & Maguire, 2014). This theory holds that the hippocampus was primarily responsible for the construction of atemporal scenes that formed the foundation to temporally specific memories and simulations. As such, constructions would be grounded in a detailed and coherent spatial context derived from perceptual, semantic, and contextual information. The authors argue that this is a universal trait that might further tie together episodic memory and future thinking, spatial navigation, and even abstract fantasies and dreams (see also Spanò et al., 2020).

Scene construction is differentiated from general or 'simple' visual imagery through its access to higher level concepts and, hence, an increased level of complexity (Kosslyn, Ganis, & Thompson, 2001). Although the authors suggest that the hippocampus acts primarily in the construction of the scene, they consider that the broader concept of simulation is supported by regions across the medial temporal lobe and wider default network. For example, a process such as self-projection is supported by the wider network (Buckner & Carroll, 2007) and that this network integrates related processes within the specific context of episodic thinking. Self-projection might be valuable during the simulation of novel contexts and episodes. This has been further extrapolated to suggest simulation as a tool in understanding the mental states of others, however, conflicting evidence suggests that episodic construction and theory of mind are independent processes (Rosenbaum, Stuss, Levine, & Tulving, 2007).

Key to both the constructive episodic simulation and scene construction models is that both recall and prospection are supported by the same constructive processes. The rise of neuroimaging techniques has provided novel methods for investigating the similarities and differences between remembering the past and imagining the future. Although there has been a noted similarity in activated regions, there have been reports of differential activity within these networks and between these processes (Addis, Wong, & Schacter, 2007; Okuda et al., 2003). These two studies found convergent evidence that future thinking resulted in greater frontopolar and hippocampal activity in participants than a matched memory task. It should be noted that a difference in neural activity between the two processes is not inherently evidence that the above models are flawed. It was argued by Schacter and Addis (2007b, 2009) that this might instead reflect the different demands used within the same system of the two processes. For instance, greater constructive processes might explain the excess activity in simulation when compared with retrieval. This is reflected in the hippocampus performing more work to integrate novel constructions rather than accessing information that had been previously stored (Martin, Schacter, Corballis, & Addis, 2011). Schacter et al. (2012) suggest that a further confounding element has been noted as the difference in novelty between simulated future events and recalled autobiographical memories. It was found by Addis, Cheng, Roberts, and Schacter (2011a) that future thinking only elicited increased hippocampal activity in response to specific events (rather than general or routine). It was proposed that this reflected the additional requirements of constructions with high event specificity to have a greater number of novel associations between event details (see also Roberts, Schacter, & Addis, 2018).

Evidence from amnesic patients with hippocampal damage has also shown deficits in simulating future events or novel scenes (Klein et al., 2002; Mullally, Intraub, & Maguire, 2012; Romero & Moscovitch, 2012; Tulving, 1985). However, Squire et al. (2010) reported patients with hippocampal damage with varied deficits to their memory but an intact ability to simulate future scenarios. In particular, patient E.P. was reported to have extensive medial temporal lobe damage. He was impaired in his recent autobiographical memory but had intact remote autobiographical memory and future simulation. Schacter et al. (2012) proposed that this could fit with the constructive episodic hypothesis — noting that, even with hippocampal damage, it was possible to interpret these findings as showing that a relatively intact ability to retrieve episodic memories can support autobiographical future thinking.

However, an alternative explanation was put forward by Irish, Piguet and colleagues (2012a, 2012b, 2013) known as the *'semantic scaffolding hypothesis'*. This model was proposed following research into semantic dementia, in which semantic memory is impaired but episodic memory is left relatively intact, that demonstrated that patients with semantic dementia were impaired in future thinking tasks. This model proposed that autobiographical future thinking is reliant on the semantic memory system such that simulation consists of specific episodic details integrated into a framework of general and conceptual knowledge. Further study in healthy participants has found that cueing participants with details from their personal goals facilitated autobiographical future thinking (D'Argembeau & Demblon, 2012; D'Argembeau & Mathy, 2011).

Patients with semantic dementia show atrophy in anterior temporal lobes and experience deficits in the meaning of words, sensory objects, and concepts (for a review see Benhamou et al., 2020). Further it is associated with damage to regions in the default mode network, a neural network associated with mental time travel capacity (Irish, Piguet, & Hodges, 2012). Duval et al. (2012) performed a battery of tests in eight patients with semantic dementia in the early to moderate stage of the disease. Under investigation was the patients' structural and functional dimensions of self - respectively their mental self-representation and their consciousness. They demonstrated that the patients were impaired in the semantic aspects of their self-representation in both the past and future, although they were preserved in the present. Notably in the future, self-representation was impaired in both episodic and semantic contexts. It was further noted that self-projection and consciousness were only impaired in the aspects of the task relating to the future. Further, Irish, Addis, Hodges and Piguet (2012) tested semantic dementia patients with a modified version of the autobiographical interview to examine the richness of three recalled memories and three generated future events. These authors reported that, although recall was largely intact, patients showed impairments for future simulation. They argue that this demonstrates that the episodic memory system is not sufficient to support episodic future thinking, as argued by constructive episodic simulation hypothesis.

It was further noted by Irish and Piguet (2013) that the quality of responses differed in semantic dementia at a higher level than simply episodic or semantic details. The autobiographical interview (a technique for measuring autobiographical memory that is discussed further below) can be coded into two broad categories 'internal' (representing the episodic details referring to a singular target episode) and 'external' (details which do not pertain directly to this episode, such as semantic knowledge). It was noted that despite 'external' details being scored at a much higher rate than 'internal' details in the Irish et al. (2012a) autobiographical future thinking task, these details tended to be generated from recent unique or generally repeated events that were not relevant to the episode in the task. It was suggested by these authors that this might demonstrate the most accessible information available to participants attempting the task, and that it was used in place of the systems that would support healthy participants (such as abstracted representations supported by a semantic framework).

This finding led Irish and Piguet (2013) to conclude that semantic memory was particularly important to simulating novel future scenarios — that is in which participants have no prior experience and cannot rely on recycled episodic memory details. It is suggested that semantic memory, which by its very nature is abstracted from its acquisitional context and can therefore be applied to various contexts (Mion et al., 2010), provides 'raw' conceptual data that can be drawn upon to facilitate the generation of novel event construction (Binder & Desai, 2011). Irish et al. (2012a) found that 80% of autobiographical future thinking narratives produced by semantic dementia patients were reproductions of entire events they had previously experienced. This occurred despite the task instructions that explicitly directed them to create novel future scenarios. They concluded that novel scenarios require greater flexibility than the episodic memory system can provide on its own, and that semantic dementia patients' damage to areas supporting semantic memory prevent them from using these systems, as a neurotypical participant would, to generate future scenarios.

The constructive episodic simulation, episodic scene construction and semantic scaffolding models share a broad conceptual basis: autobiographical constructions rely on integrating episodic details within a broader contextual framework. The key distinction between the semantic scaffolding hypothesis and the other models is that it argues that the episodic content of autobiographical future thinking is supported specifically by semantic memory, whereas episodic recall is not. The other two models argue that both memory and future thinking are supported by the same processes. This conceptual difference is important to consider when evaluating both the noted similarities and differences between episodic recall and future thinking. For instance, the difference in episodic and semantic details given in past and future narratives (Irish et al., 2012a). This is supported by evidence that future narratives are found to be less specific than are recalled events (Anderson & Dewhurst, 2009). Neuroimaging research has also demonstrated differences between remembering the past and simulating the future in the medial temporal lobes (Okuda et al., 2003; Xu, Yuan, & Lei, 2016; Weiler, Suchan, & Daum, 2010). However, research by Palombo, Hayes, Peterson, Keane and Verfaellie (2018) suggested that this difference might be modulated by the demands of scene construction rather than future thinking per se (but see Roberts et al., 2018). Further, Addis (2018, 2020) argues that even though past and future thinking are supported by the same processes, that differences may still be found between the two cognitive tasks (e.g. Addis et al., 2011a).

As such, contemporary research has moved from a selective focus on episodic autobiographical memory and simulation (Hassabis & Maguire, 2007; Schacter & Addis, 2007b) and examined how both episodic and semantic systems might necessarily combine to support episodic constructions (Irish & Vatansever, 2020). A better reflection of modern research might be to consider the effects of temporality within episodic constructions. A revised version of the constructive episodic simulation hypothesis maintains that neither ‘time’ nor ‘travelling’ are essential aspects of mental time travel (Addis, 2018, 2020). The revisions to this model instead highlight the importance of general simulation (past, future, fantastical, etc) and the mental rendering of experience as vital coping mechanisms regarding the ‘ever-changing complexities of the present’ (but see Klein, 2016).

An alternative integrative model was proposed by D’Argembeau (2020) in which mental time travel is conceptualised as the capacity to navigate flexibly through hierarchical layers of autobiographical representation (relying on both episodic construction and autobiographical knowledge). The author notes that different forms of mental time travel resulted in different proportions of episodic details drawn from personal experience (as per Schacter & Addis, 2007b) and broader conceptual semantic knowledge (Irish & Piguet, 2013). This is underlined by the cross-modal nature of the representations, they require the integration of mental imagery (Pearson & Kosslyn, 2015) and specific information derived from systems supporting perception, action, and introspection (Barsalou, 2009).

The cognitive architecture underpinning mental time travel was proposed by D'Argembeau (2020) to be represented across several layers. Firstly, constructions of both past and future events are extrapolated from prior experiences (i.e. episodic memories) and recontextualised using semantic knowledge — the bias towards either system in any given context being dependent on the level of recontextualization required. Further, it is through autobiographical knowledge that temporal context is assigned to any given construction, and by which it is placed within a conceptualised personal timeline (extending into both the past and future). The author also posits that this might also cover the scope to which the construction covers (i.e. specific events, general occurrences, and lifetime periods). As such, this system looks to incorporate the many systems that associate with mental time travel and explain how flexibly engaging and integrating them may explain the intricate nature of the process.

1.5 Neural networks underlying episodic construction and autobiographical knowledge

Neuropsychological studies have demonstrated that patients with deficits in episodic or semantic memory both show deficits in autobiographical future thinking (Addis, Sacchetti, Ally, Budson, & Schacter, 2009; Irish et al., 2012a; Klein, Loftus, & Kihlstrom, 2002). Further, cognitive research has demonstrated that participants are able to provide more detail in future scenarios when the contextual setting is associated with richer personal memories (Robin & Moscovitch, 2014; Szpunar & McDermott, 2008). Finally, functional neuroimaging has shown overlapping activity between episodic memory, semantic memory, and autobiographical future thinking tasks in a wide array of regions including lateral temporal cortex and medial temporal lobes (Benoit & Schacter, 2015; Binder & Desai, 2011; Stawarczyk & D'Argembeau, 2015). It was further noted by these authors that the network engaged in both episodic recall and simulation overlapped with the default mode network (Raichle, 2015).

The neural correlates of episodic memory reveal that it is, in and of itself, a complex process that engages different regions based on the demands of the specific task at hand (Epelbaum et al., 2018). Using data from the Memento cohort, these authors demonstrated that different patterns of activity could be associated with episodic memory across different stages of its processing. Initial encoding was associated most strongly with parietal and temporal cortices; storage with entorhinal and parahippocampal areas; and retrieval with cortical thickness across frontal regions. This separation has previously been described as the 'attention-to-memory' model, which posits that parietal regions are used in directing top-down processes (Cabeza, Ciaramelli, Olson, & Moscovitch, 2008). In line with Tulving's (1983) hypothesis (i.e. of a specific 'retrieval mode' that supports episodic recall), it is possible to distinguish brain activation during episodic retrieval and working memory (Cabeza, Dolcos, Graham, & Nyberg, 2002).

Mental time travel is an integrative process that relies on an array of brain regions to support its function (Addis, 2020; D'Argembeau, 2020; Schacter et al., 2012). Early research suggested that episodic recall and future thinking were supported by a 'core network' that consisted of medial prefrontal cortex, lateral and medial parietal cortex, lateral and medial temporal lobes, and especially the hippocampus (Addis, Wong, & Schacter, 2007; Schacter, Addis, & Buckner, 2007; Suddendorf et al., 2009; Szpunar, Watson, & McDermott, 2007). This activity has been noted to overlap with the default mode network (Andrews-Hanna, Reidler, Sepulcre, Poulin, & Buckner, 2010; Østby et al., 2012; Schacter et al., 2007 — see figure 1.3). This network has been demonstrated to show high activity during rest, which decreases during tasks requiring attention to external stimuli (Andrews-Hanna, 2012; Buckner & DiNicola, 2019; Gusnard & Raichle, 2001). However, increased task activity in the default mode network has been tied to internal mentation (Andrews-Hanna, 2012) and other forms of high-level cognition (Mars et al., 2012; Spreng, Mar, & Kim, 2009). Evidence from thought sampling studies has indicated that participants tend to think about past or future events during rest blocks (Andrews-Hanna, Reidler, Huang, & Buckner, 2010; Stawarczyk, Majerus, Maj, van der Linden, & D'Argembeau, 2011). As such, it is plausible that rather than displaying a baseline activity, these studies indexed participants engaging in recall or prospection (Schacter et al., 2012).

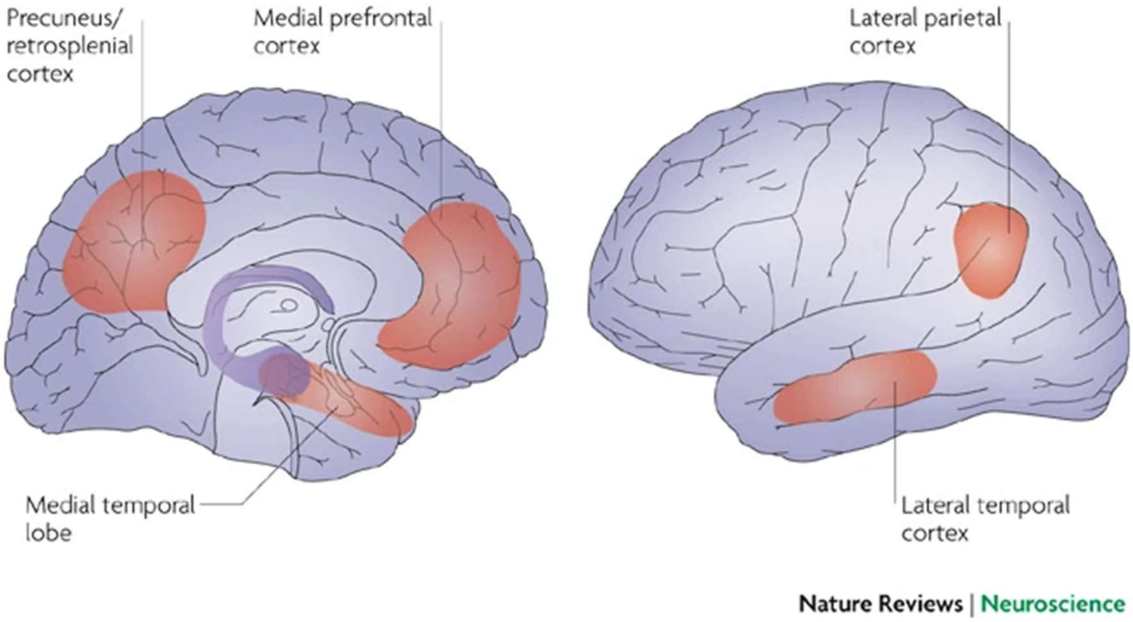


Figure 1.3 shows the core brain system proposed to support various forms of construction/simulation including mental time travel. Image reproduced from Schacter et al. (2007).

The diverse neural and cognitive nature of mental time travel processing has led to research examining the role of specific brain regions along with their relational activity with each other. The hippocampus has been identified as key within these networks, however, the specific role it plays has been the matter of some debate (Mullally & Maguire, 2014; Schacter et al., 2012). As above, key to early debate was the role of the hippocampus in spatial processing and the extent that this would be reflected within episodic constructions. Animal and human research has established that long-axis specialization exists within hippocampal function (Poppenk, Evensmoen, Moscovitch, & Nadel, 2013; Sekeres, Winocur, & Moscovitch, 2018). Anterior and posterior hippocampus have been respectively associated with general and specific processing in the realms of spatial representation (Baumann, Chan, & Mattingley, 2010; Ekstrom, Copara, Isham, Wang, & Yonelinas, 2011; Nadel, Hoscheidt, & Ryan, 2013). Further, anterior hippocampal processing has been associated with 'gist' processing whereas posterior hippocampus has been associated with 'detail' (Gutchess & Schacter, 2012; Hayes et al., 2011; Poppenk & Moscovitch, 2011; but see Roberts et al., 2018). Notably, anterior and posterior hippocampus have been associated with differential long-range connectivity (for a full review see Poppenk et al., 2013).

Further research has indicated that event segmentation might rely on functional connectivity between the hippocampus and posterior cortical regions (Baldassano et al., 2017; D'Argembeau, 2020; Ranganath & Ritchey, 2012). How boundaries are created between events have been noted as key to a wide range of temporalities within autobiographical memory (Burt, Kemp, & Conway, 2003; Cohn-Sheehy et al., 2020; D'Argembeau, 2020). This is further supported by reports of a specific hippocampal role in the recall of temporal sequences (Lehn et al., 2009) and in the representation of a temporal context in autobiographical memory (Cohn-Sheehy & Ranganath, 2017). As such, it is clear that the hippocampus is an important hub for processing related to mental time travel and that its specific function and role within different functional networks are vital to understanding the process.

Semantic memory processing is distributed widely across the cerebral cortex (Binder, Desai, Graves, & Conant, 2009) with evidence of different regions supporting modal specific and non-specific processing (Binder & Desai, 2011). Further, this processing has been shown to overlap with episodic memory and future thinking processing (Benoit & Schacter, 2015; Binder & Desai, 2011; Renoult et al., 2019; Stawarczyk & D'Argembeau, 2015). It has been proposed that the posterior regions linked with modal-specific processing might support the generation of sensory-perceptual content within mental time travel constructions (D'Argembeau, 2020; Gilmore et al., 2020).

A specific and direct contribution in personal semantic processing is likely to be played by the anterior temporal lobe (Grilli, Bercel, Wank, & Rapcsak, 2018; Martinelli, Sperduti, & Piolino, 2013). Further, this region is linked with higher-order processing of lifetime periods and other experience-near related personal semantic details (Grilli & Verfaellie, 2016). Resting state data has shown functional connectivity between the anterior temporal lobe and other regions connected with semantic cognition and unimodal processing (Irish, 2016; Jackson, Hoffman, Pobric, & Lambon Ralph, 2016). It has been proposed that the anterior temporal lobe might act as a hub that integrates modality-specific processing to create multimodal representations (Irish, 2016; Lambon Ralph, Jefferies, Patterson, & Rogers, 2017). In turn, this might allow for the region to support autonoetic experience within episodic construction by providing contextual information to support specific episodic processing (D'Argembeau, 2020; Gurguryan & Sheldon, 2019).

There are few studies in the present literature that have looked at how personal and general semantics might differ in neurofunctionality. Work by Coronel and Federmeier (2016) demonstrated that both general and personal semantic memories elicited an N400 response (an ERP commonly associated with semantic processing, see also Kutas & Federmeier, 2011) with shared latency and distribution. The authors concluded that personal and general semantics share fundamental functional and neurobiological mechanisms. This finding was supported by Renoult et al. (2016) who also found that personal and general semantic knowledge elicited an N400. This study also included a 'repeated events' category which also elicited an N400. These authors demonstrated that no difference could be found between ERPs generated from personal semantic knowledge or repeated events. However, the response to both of these differed from that of general semantic memory.

Further, it is possible to subdivide personal semantic details such that they might be considered more like episodic details or general semantic details (Renoult et al., 2012). A meta-analysis by Martinelli, Sperduti and Piolino (2013) suggested that as the levels of abstraction regarding autobiographical details increased, activation was seen to move from posterior to anterior structures. It has been shown that the left anterior temporal lobe (the proposed site for the semantic 'hub' — Patterson et al., 2007; Rogers et al., 2004) is associated with both general semantic details and personal semantic facts (Grilli, Bercel, Wank, & Rapcsak, 2018). In contrast, trait knowledge in particular might be mediated by the medial prefrontal cortex (Araujo, Kaplan, & Damasio, 2013; Martinelli et al., 2013). Finally, experience-near personal semantic details, which can be considered most similar to episodic memory, have also been associated with hippocampal processing (Grilli & Verfaellie, 2014).

The medial prefrontal cortex (mPFC) has been implicated as a central processing hub for the entirety of the default mode network (Andrews-Hanna, 2012). Functional connectivity has been established between mPFC and both hippocampus (Campbell, Madore, Benoit, Thakral, & Schacter, 2018; Jin & Maren, 2015; McCormick, St-Laurent, Ty, Valiante, & McAndrews, 2015; Sigurdsson & Duvarci, 2016) and anterior temporal lobes (Jackson, Bajada, Lambon Ralph, & Cloutman, 2020; Simmons, Reddish, Bellgowan, & Martin, 2010). Within mental time travel research, medial and ventromedial prefrontal cortex (vmPFC) have been associated with internal mentation, episodic construction and autonoesis (Bertossi et al., 2016a; Bertossi, Tesini, Cappelli, & Ciaramelli, 2016; Østby et al., 2012, Suddendorf et al., 2009; Wheeler et al., 1997). Participants with lesions to vmPFC display more severe deficits in autobiographical future thinking than in the creation of fictious experiences which might suggest a specific role for this region in autonoesis (Bertossi et al., 2016a). The mPFC has been implicated in contextual processing that integrates information from outside of specific events to associate them with higher order meaning (Krueger, Barbey, & Grafman, 2009; Preston & Eichenbaum, 2013; Lieberman, Straccia, Meyer, Du, & Tan, 2019). The region's role in higher order processing is further demonstrated by its support of chronological ordering and schematic knowledge in event segmentation (Baldassano, Hasson, & Norman, 2018; Liu, Shi, Cousins, Kohn, & Fernández, 2020; Stawarczyk, Bezdek, & Zacks, 2019). It has been suggested that the integration of autobiographical knowledge and concept of the self (i.e. processes supporting autonoesis) within episodic constructions might occur in mPFC (Craik et al., 1999; D'Argembeau, 2020; Demblon, Bahri, & D'Argembeau, 2016).

Wider research has also demonstrated that the default mode network is associated with activity in the frontoparietal control network (Christoff, Irving, Fox, Spreng, & Andrews-Hanna, 2016; Dixon et al., 2018; Smallwood, Brown, Baird, & Schooler, 2012). Resting state MR studies have shown functional connectivity between regions commonly associated with cognitive control, decision making, and goal directed activities (Spreng, Stevens, Chamberlain, Gilmore, & Schacter, 2010; Vincent, Kahn, Snyder, Raichle, & Buckner, 2008). D'Argembeau (2020) proposed that this might account for the difference between mental time travel as a spontaneous or a voluntary-and-directed action. As such, the frontoparietal control network might play an indirect role in mental time travel by allowing for a train of thought to be initiated and maintained. This is in line with the Tulving's (1983) proposed 'retrieval mode' — a cognitive state in which the retrieval of memory is prioritised (see also Kim, 2020 — RED model; Tarder-Stoll, Jayakumar, Dimsdale-Zucker, Günseli, & Aly, 2020). Further, the frontoparietal control network is particularly engaged when constructing novel future scenarios (Roberts et al., 2017). This was proposed by Addis (2020) to provide evidence that different types of mental time travel might be differently supported by the integration of the various neural networks.

1.6 Using diffusion-weighted magnetic resonance imaging (DWI) to study the structural connectivity of neurocognitive networks

Neuropsychology has a number of tools at its disposal with which to examine the 'neuro' components of its scope. In human subjects it is common to use functional neuroimaging techniques such fMRI, MEG, EEG and so on. The majority of neuroanatomical and structural work has historically been done post-mortem, commonly in animal models using invasive tract tracing techniques or via Klinger dissection and lesion-degeneration in humans (Jbabdi & Behrens, 2013). Further work has used inferential analysis to study deficits in the behaviours of lesion patients (Vaidya, Pujara, Petrides, Murray, & Fellows, 2019). This project instead focuses on diffusion MRI (dMRI), a non-invasive method that has become increasingly popular in the last decade that uses the diffusion properties of water in the brain to provide indices of structural connectivity *in vivo* (Jbabdi & Behrens, 2013).

Of particular relevance to the present analyses is diffusion tensor imaging (DTI). This is a method that makes use of the anisotropic nature of water displacement in white matter to virtually dissect 'tracts' or 'axonal connections' throughout the brain (Assaf & Pasternak, 2008). This allows researchers to understand the presence and extent of connections between different regions of the brain and to measure the microstructural properties of these connections, which are critical influences on inter-regional interactions in the brain (Johansen-Berg & Rushworth, 2009).

The degree of strength underpinning these neural networks can then be used to infer functional relations between the regions. As discussed above, a growing consensus considers that the capacity for mental time travel is supported by the interactions across distributed regions of the 'core network' (Addis, 2018; 2020; D'Argembeau, 2020; Schacter et al., 2012). The presence of anatomical connectivity is a prerequisite for the existence of functional networks, such that interactions across the network can be both rapid and efficient (Mesulam, 2012). This highlights the importance of (and hence the importance of study of) white matter tracts connecting regions of the core network in allowing the long-range internetwork communication. Importantly, the properties of structural connectivity can be used to understand a great extent of functional connectivity (Jbabdi & Behrens, 2013). Since structural and functional networks are mutually interdependent (Mesulam, 2012), the study of white matter enables us to infer 'structure-function' relationships that subserve mental time travel.

The combination of dMRI and tractography allow not only the reconstruction of major white-matter connections, but also provide measurements of microstructural features of those connections (Jbabdi & Behrens, 2013; Soares, Marques, Alves, & Sousa, 2013). For instance, certain aspects of diffusion, such as its anisotropy (see below), are thought to indicate axonal integrity at a microscopic level (Jbabdi & Behrens, 2013). Interindividual differences in such microstructural 'integrity' has been shown to relate to individual differences in cognition and personality in a number of domains (Forkel, Friedrich, de Schotten, & Howells, 2020). It has been suggested that this reflects the influence of microstructural integrity on synchronized network activity and communication (Pajevic, Basser, & Fields, 2014).

The white matter microstructural indices used in the present project, and hence the ones of particular focus, are fractional anisotropy (FA) and mean diffusivity (MD) (Basser, 1997). Fractional anisotropy refers to the degree to which diffusion is found to occur in any one given axis - a value of zero would imply no or equal restriction in any given direction, a value of one would suggest a unidirectional path. It is considered to measure fibre density, axonal diameter, and myelination in white matter (Alba-Ferrara & de Erausquin, 2013). Mean diffusivity provides a measure of the total diffusion within a voxel and is calculated by taking the mean of the diffusion in each of the three directions calculated in the tensor (the 'eigenvalues' — Clark et al., 2011). Given the nature of its output, that is as an *in vivo* measure of white matter anatomy and structural integrity, it is perhaps no surprise that DTI has widely been used in clinical work in which deficits to axonal integrity and general white matter damage might be expected (Beaulieu, 2002; Mori & Zhang, 2006; Sundgren et al., 2004). However, it has been increasingly used as a tool for examining individual differences in the neural correlates of cognitive capacities in healthy populations (Forkel et al., 2020).

Despite its ongoing and growing popularity and numerous advantages, the method has several inherent technical issues that govern certain aspects of its use (Jones, Knösche, & Turner, 2013; Soares, Marques, Alves, & Sousa, 2013). As tractography relies on measuring the movement of water molecules in brain tissue, its translation to a depiction of anatomical connectivity relies on a degree of procedural conjecture (Schilling et al., 2020). However, these authors further note that the connections derived from dMRI analysis can be highly accurate when combined with detailed anatomical knowledge. Further, although FA and MD are highly sensitive indices of white matter microstructure, they lack biological specificity (Beaulieu, 2002; Jones et al., 2013). For example, developmental variation in FA values can reflect differences in axonal packing density, calibre, myelination, spatial coherence, or changes in the number, size, and branching of glial cells (Jones et al. 2013). MD can be associated with edema, necrosis and cellularity (Alexander et al., 2011), though has also been shown to be sensitive in non-clinical settings (e.g. Hodgetts et al., 2015; 2017a; 2020). FA and MD are typically found to be inversely correlated (Vettel, Cooper, Garcia, Yeh, & Verstynen, 2017), and higher FA/lower MD typically associate with microstructural properties supporting efficient information transfer along white matter tracts (Beaulieu, 2002). Although the relationship is typically inverse, prior research has argued in favour of reporting multiple DTI measures to better characterise tissue microstructure (Alexander, Lee, Lazar, & Field, 2007).

1.7 Key white matter tracts of the 'core' network: the fornix and the inferior longitudinal fasciculus

1.7.1 Gross anatomy of the fornix

In line with prior research (e.g. Hodgetts et al., 2017a), the fornix is one of the primary neuroanatomical structures of interest in the present project. The fornix, derived from the Latin for 'arch', is a c-shaped structure that acts as the main output tract from the hippocampus (Raslau et al., 2015; see figure 1.4). It has been noted as part of the limbic system (Douet & Chang, 2015). Various lesion and functional imaging studies have associated it with a number of domains including recall memory (Tsivilis et al., 2008), navigation (Sutherland & Rodriguez, 1989), and the organisational aspects of food eating behaviour (Osborne & Dodek, 1986).

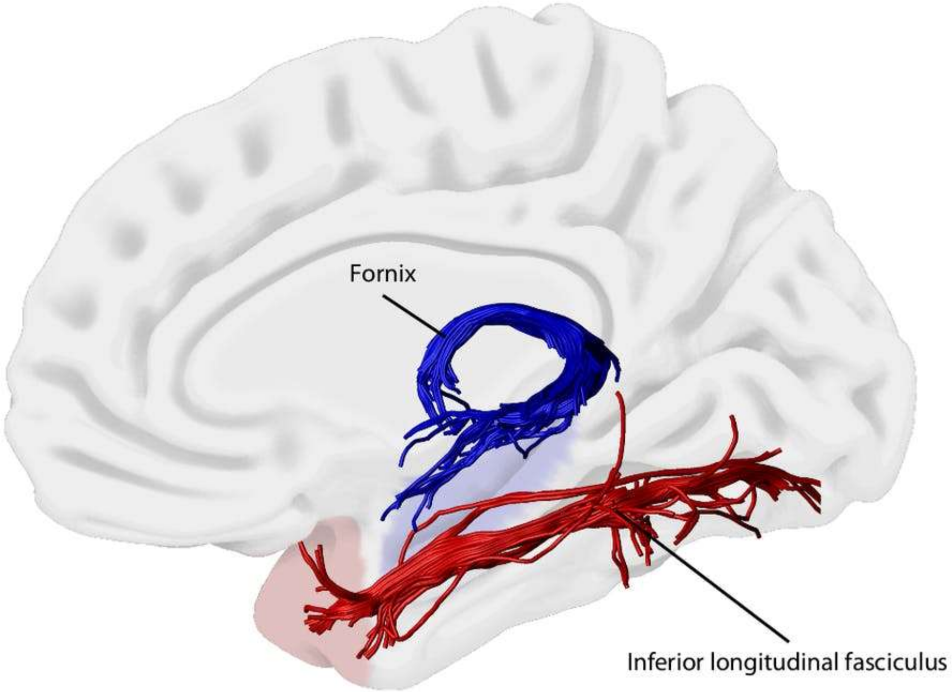


Figure 1.4 Shows a graphical representation of fornix and inferior longitudinal fasciculus white matter tracts. Reproduced from Hodgetts (2017).

The fornix consists of two largely ipsilateral bundles of white matter fibres (Griffiths, Batty, Reeves & Connolly, 2009). These fibres originate in the subicular cortex (specifically superior to the parahippocampal gyrus) and the pyramidal cells of the hippocampus. These fibres start to converge at the fimbria — a distinct bundle that sits medial surface of the alveus on the superior surface of the hippocampus (Raslau et al., 2015). The cross-sectional area of the fimbria increases as more fibres from the caudal extent of the hippocampus join with it. The two crura of the fornix (its most posterior portion) begin at the point where the hippocampus terminates.

Each crus of the fornix forms an arch underneath the splenium of the corpus callosum and head towards the midline. Griffiths et al. (2009) note that although strongly ipsilateral, there are a small number of fibres that cross the midline to form the fornical commissure. The fornices join in a region termed 'the body of the fornix' — in which separate identities are maintained laterally. The body of the fornix runs anterior to the inferior edge of the septum pellucidum. These separate once more in the vicinity of the rostral thalamus and form the two anterior columns of the fornix. The columns pass inferior towards the anterior commissure and split to form the two final projections of the fornix.

The majority of fibres pass caudal to the anterior commissure and terminate in the mammillary bodies. This has been termed the ‘post-commissural’ tract of the fornix. The remaining fibres form the pre-commissural tract and pass rostrally to the anterior commissure. These project to the hypothalamus, lateral septal nuclei, and lateral dorsal thalamus.

1.7.2 The Fornix: the primary axonal tract of the hippocampus

A ‘default mode’ or ‘core’ brain network, including medial prefrontal cortex and hippocampal regions, has been proposed that allows for the capacity of autobiographical memory, imagination, and other forms of mentation (Andrews-Hanna et al., 2010; Raichle, 2015; Schachter et al., 2012). The fornix is the primary axonal tract of the hippocampus, allowing for both the input and output of information (Amaral & Lavenex, 2007). Projections have been identified to prefrontal cortex, anterior thalamus, and mammillary bodies (for a review see Bubb, Kinnavane, & Aggleton, 2017). Further, diffusion imaging studies have highlighted the importance of the tract to the midline default mode network (Alves et al., 2019; Kernbach et al., 2018). These connections explain the disruptive effects of fornical lesions in primate and rodent models of episodic memory based on scene specific memory for objects (Gaffan, 1994; for a review see Benear, Ngo, & Olson, 2020).

Despite being an anatomical backbone of the default mode network, and implicated in amnesic syndrome (Benear et al., 2020), there have been few formal assessments of the impact of fornix damage on autobiographical memory and future thinking (but see Vann et al., 2009). Evidence from Tedder, Miller, Tu, Hornberger and Lah (2016) was taken from a patient (S.L.) who had localised damage to the fornix and mamillary bodies, but with spared hippocampi. This patient was diagnosed with Wernicke-Korsakoff’s syndrome and displayed both anterograde and retrograde amnesia. In a modified autobiographical interview, it was found that S.L. could not provide any details from the last two weeks or two years (note that the latter explicitly excluded memories from the last month). Further she was noted to have impaired recall of events taking place from her late 30s. Despite these deficits, she was noted to be able to produce normal numbers of event details in her descriptions of future events. Although this might be considered in the context of Irish and Piguet (2013) who found that episodic future thinking was often a display of repurposing recalled memories. It should also be noted that it would support the authors’ suggestion that semantic systems are largely responsible for generating novel future simulations. Taken as a whole it provides evidence that the non-hippocampal regions of the Papez circuitry might be critical only for event retrieval and not for future simulations.

Consistent with studies in lesion patients, a growing body of diffusion imaging studies have associated episodic memory with fornix microstructure indices in healthy adults (Rudebeck et al., 2009; Hodgetts et al., 2017a; for a review see Benear et al., 2020). Further, this work is supported by data in healthy aging populations, who show that respective decreases and increases in fornix FA and MD values correlate with changes in episodic memory capacity (Bennet, Huffman, & Stark, 2015; Metzler-Baddeley, Jones, Belaroussi, Aggleton, & O'Sullivan, 2011). Notably, however, developmental studies have not been able to replicate these findings in young children (Wendelken et al., 2015; but see Benear et al., 2020).

The fornix, however, contains two rostral divisions, these are known as the pre- and post-commissural fornices (see figure 1.5). The pre-commissural links to the prefrontal cortex, whereas the post-commissural fornix connects hippocampus to mammillary bodies and anterior thalamic nuclei (Aggleton, 2012; Christiansen et al., 2016). The distinct anatomical connectivity has led to varied lines of research examining if they might also be demonstrated to have differentiable functions (Christiansen et al., 2016; Coad et al., 2020; Williams et al., 2020). Indeed, studies in rats (e.g. Henderson & Greene, 1977; Thomas, 1978) demonstrated that localised damage to the pre-commissural fornix led to impairments in short term memory and avoidance learning tasks. Human patient studies have mainly focussed on damage to and abnormalities in the post-commissural fornix (Yeo, Seo, Kwon, & Jang, 2013). As such, it has been linked with deficits ranging from deficits in episodic memory in schizophrenia (Kuroki et al., 2006), anterograde and retrograde amnesia (Poreh et al., 2006), and diencephalic amnesia (Vann & Nelson, 2015). These studies provide two important considerations for the work in this project — firstly that caution must be taken when considering the 'functional' properties of the fornix considered as a single tract, and secondly that DTI is both viable for examining it and may also be sufficiently sensitive to examine finer grade details than traditional human lesion studies (as evaluation of the contribution of both the pre- and post-commissural fornix can be considered when conceptually it is justified).

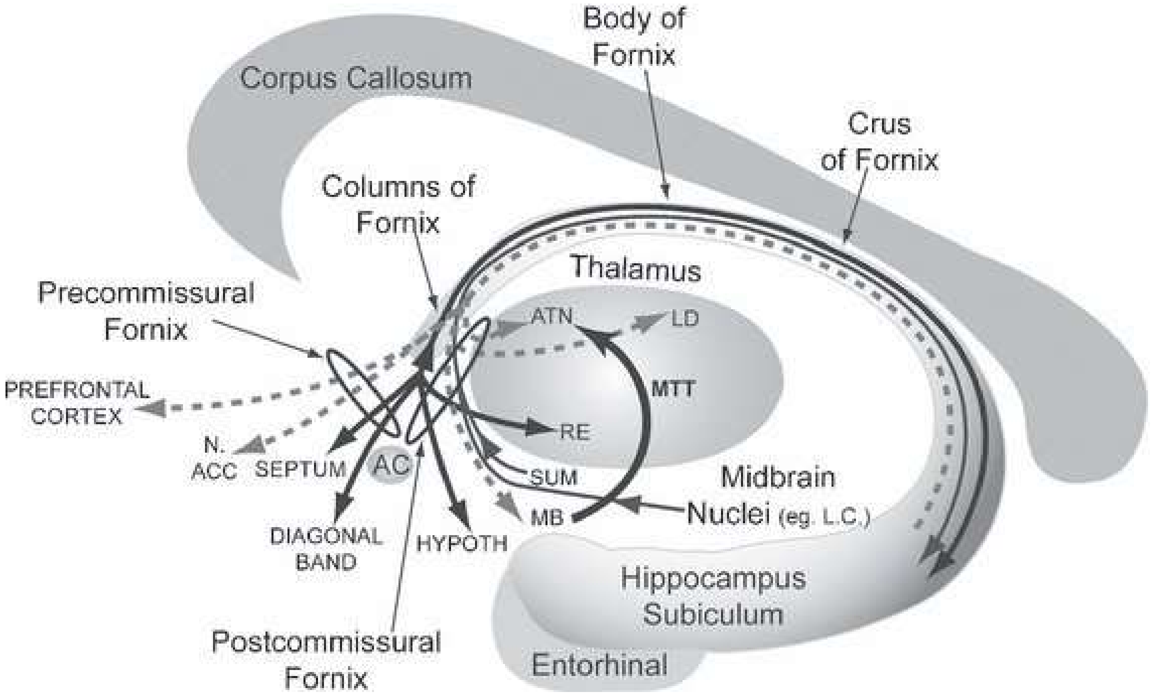


Figure 1.5 shows a diagrammatic representation of the location and subdivisions of the fornix. The arrows display connections between the fornix and hippocampal formations (dashed — solely efferent from hippocampal formations, narrow — solely efferent to hippocampal formations, wide — reciprocal connections). AC — anterior commissure; ATN — anterior thalamic nuclei; HYPOTH — hypothalamus; LC — locus coeruleus; LD — thalamic nucleus lateralis dorsalis; MB — mammillary bodies; MTT — mammillothalamic tract; RE — nucleus reuniens; SUM — supramammillary nucleus. Image reproduced from Aggleton et al. (2010).

1.7.3 Gross anatomy of the inferior longitudinal fasciculus

The inferior longitudinal fasciculus (ILF) is a long-range white matter tract that connects the occipital lobe to the anterior temporal lobe (Herbet, Zemmoura, Duffau, 2018; see figure 1.4). It was identified as far back as the 19th century (e.g. Burdach, 1822; Reil, 1812). The precise nature of the ILF has been under significant debate for the vast majority of its known existence (Herbet et al., 2018). Namely, the debate has focussed on whether the tract exists as a direct pathway from the occipital lobe to the anterior temporal lobe, or if it is instead representative of a collection of adjacent short-range u-fibres in series. However, more recent work has supported the idea that both sides of the argument could be held to be true — evidence has been provided that the ILF might have numerous terminals across the ventral temporal lobe and that as such it could be considered that both direct and indirect occipitotemporal pathways exists in the human brain (Bajada et al., 2016; Catani, Jones, Donato, & Ffytche, 2003).

1.7.4 Inferior longitudinal fasciculus: a key tract of the lateral temporal cortex and temporal pole

As the ILF represents the major pathway from the occipital lobe to the anterior temporal lobes, it has been proposed that it might reflect an anatomical route by which unimodal sensory information becomes integrated with, by nature amodal, semantic representations in a semantic hub based in the ventral anterior temporal lobes (Chen, Lambon Ralph, & Rogers, 2017; Lambon Ralph, Jefferies, Patterson, & Rogers, 2017).

The ILF has been associated with visual semantic processing in a picture naming task (Shin et al., 2019). These authors demonstrated a negative correlation between ILF FA and N400 latency and amplitude (i.e. that ILF structural coherence was associated with more efficient visual semantic processing). The N400 itself has been connected with autobiographical memory research, as it has been elicited in the processing of personal semantic details (Coronel & Federmeier, 2016; Renoult et al., 2016). Further research has established direct stimulation of the ILF during neurosurgery leads to semantic paraphasia during a picture naming task (Bello et al., 2007; but see Mandonnet, Nouet, Gatignol, Capelle, & Duffau, 2007; Vassal, Schneider, Sontheimer, Lemaire, & Nuti, 2013; for a review see Cocquyt et al., 2020). Research has also found that deficits to visual naming following a stroke are predicted by the degree of ILF damage, and that these are maintained when controlling for damage to anterior temporal lobe grey matter (Mehta et al., 2016).

Alterations to ILF microstructure have been found in patients with semantic dementia (Agosta et al., 2010). These patients, who present with deficits to semantic memory and future thinking but not to episodic memory, have provided valuable insights to the understanding of the constructs supporting mental time travel (Irish et al., 2012a). Further, ILF microstructure was positively correlated with increased semantic memory details provided by non-clinical participants in an autobiographical interview task (Hodgetts et al., 2017a). This growing body of research highlights the ILF as a key tract in order to investigate the neural underpinning of a semantic ‘framework’ that might be associated with the production of general semantic details and in supporting the production of future episodic and semantic detail in autobiographical future thinking.

1.8 ‘Naturalistic’ versus ‘laboratory’ task approaches in memory research

As a final note, it is important to reflect on the methodological decisions made in the approach to the cognitive measurements in this project. It is appropriate, therefore, to acknowledge the storied debate between the relative merits and failings of pursuing either an ecological (‘naturalistic’) or traditional (‘laboratory’) approach when considering how to examine the memory system (Banaji & Crowder, 1989, Conway, 1991; Neisser, 1978; see also accuracy vs quantity-oriented approaches to memory — Koriat & Goldsmith, 1994). The core tenets of the debate seek to add more or less weight to the advantages of examining how memory is used to support our daily lives, against the greater control and specificity that may be afforded by laboratory-based tasks (for a full review see Kvavilashvili & Ellis, 2004).

A meta-analysis performed by McDermott, Szpunar and Christ (2009) found that the two approaches could be differentially associated with a set of neural correlates. These authors found little overlap in brain activation when comparing the results of old/new recognition studies (representative of 'laboratory approaches') and the Galton-Crovitz cueing technique (representing naturalistic, autobiographical approaches — Crovitz & Schiffman, 1974). The former engaging areas such as the right middle frontal gyrus, precuneus and lateral parietal cortex, whereas the latter engaged the 'core' or 'default mode' network. As discussed above, this wide-ranging collection of regions including the lateral temporal cortices, mPFC, and hippocampus and has been associated with a variety of processes that might plausibly linked to mental time travel or self-projection, including daydreaming, mind wandering and creative thought, in addition to autobiographical memory and autobiographical future thinking (Addis et al., 2007; Szpunar et al., 2007; see Dafni-Merom & Arzy, 2020 for meta-analyses).

It has been concluded, therefore, that laboratory and naturalistic memory systems represent fundamentally different processes, and that consideration should be given as to the nature of memory being studied in any given piece of work (Roediger & McDermott, 2013). In line with these findings, a naturalistic method was adopted in order to best represent the process of mental time travel in an everyday setting. This should be considered in the use and conceptualisation of 'memory' across this project. Notably, in evaluating the different styles of mnemonic research, Tulving (1991) underscored the importance of both to the field and noted that "memory research is not a zero-sum game".

1.9 Studying individual differences in episodic constructions

Fundamental to original and contemporary conceptualisation of mental time travel was the idea that autonoetic consciousness would vary between individuals (Dafni-Merom & Arzy, 2020; Tulving, 1985). This is in line with wider cognitive capacities relating to executive control (Kane & Engle, 2002; Miyake & Friedman, 2012), working memory (Daneman & Carpenter, 1980; Unsworth & Engle, 2007) and mnemonic function (Kirchhoff, 2009; Miller, Donovan, Bennett, Aminoff, & Mayer, 2012). However, the study of individual differences in autobiographical memory remains in its relative infancy (for a review see Palombo et al., 2018c). It was noted by Palombo and colleagues that some evidence can be derived from cases with severely deficient or highly superior autobiographical memories (see also LePort, Stark, McGaugh, & Stark 2017; Palombo, Alain, Söderlund, Khuu, & Levine, 2015). Palombo and colleagues further identified the survey of autobiographical memory (SAM) and autobiographical interview (AI) as two techniques with which individual differences in autobiographical memory could be investigated.

1.9.1 The survey of autobiographical memory

The survey of autobiographical memory (SAM) is used to measure individual differences mnemonic traits or 'styles' of autobiographical retrieval and episodic construction (Palombo, Williams, Abdi, & Levine, 2013). These can be considered distinct from and complementary to the findings of performance- and laboratory-based measures of autobiographical memory (Palombo et al., 2015; Sheldon et al., 2018). For instance, performance-based measures of autobiographical memory (e.g. Levine et al., 2002) measure recall on specific (and likely highly salient) episodes, whereas trait mnemonics will inform the researcher of general capacity in the individual. It has been proposed that these traits are grounded in individual differences in brain structure and function (Palombo et al., 2018c; Sheldon, Farb, Palombo, & Levine, 2016). The SAM allows for individual assessment of episodic, semantic, and spatial memory as well as autobiographical future thinking (Palombo et al., 2013).

It has been suggested that trait episodic autobiographical memory represents an individual's ability to recollect episodic details supported by autonoetic subjective recall (Fan, Romero, & Levine, 2020). This is important in considering the mental time travel capacities of individuals might vary, despite similar performances on recall tasks. For instance, episodic recall can appear preserved if supported by non-episodic strategies such as a reliance on rehearsed constructions or familiarity without specific recall (Palombo, et al., 2015). Further, it has been suggested that the SAM, and hence trait autobiographical memory, might most closely associate with memory vividness rather than capacity (Clark & Maguire, 2020). As with any self-reported measure it is important to consider the participant's capacity for self-reflection. However, the work by Clark and Maguire suggests it is also important to consider the manner in which participants appraise their own capabilities.

1.9.2 The autobiographical interview

The autobiographical interview (AI) (Levine et al., 2002) is a semi-structured interview in which participants freely respond to prompts with descriptions of events from their past (Crovitz & Schiffman, 1974). The AI provides a wealth of information concerning elements of naturalistic autobiographical memory. It is one of the most used tools with which to examine autobiographical memory and episodic construction, having been administered in more than 200 studies to date (Miloyan, McFarlane, & Vasquez-Echeverria, 2019; Sheldon et al., 2018). These narratives are then examined with a coding scheme (Levine et al., 2002; Sheldon & Levine, 2016; see figure 1.6) which allows for the assessment of the richness of episodic detail provided by the participant. Importantly, the scoring method allows for the separation of episodic (i.e. events, sensory and mental state details specific to the episode) and non-episodic details (a combination of semantic and other information not directly related to the event). Within the coding scheme these are respectively referred to as 'internal' and 'external' details. For the sake of reliability, any detail that can reasonably be considered 'internal' is scored as such.

Although originally designed to study memory in aging populations (Levine et al., 2002), the AI has been developed and adapted to be used in many different forms of episodic construction including future thinking tasks (Addis et al., 2008; Miloyan et al., 2019; Sheldon et al., 2018). This is due to many and varied strengths that the method provides. Notably, it is data rich and allows for segmentation from broad scale episodic-semantic distinctions to much finer grain details. Research has demonstrated that the broad internal category has been demonstrated to be sensitive to the integrity of medial temporal lobe structures in both amnesic patients and healthy populations (Hodgetts et al., 2017a; Rosenbaum, Moscovitch, Foster, & Schnyer, 2008; Steinvorth, Levine, & Corkin, 2005). Despite the capacity for this analysis, however, it should be noted that issues with practicality can limit the depth to which analyses can be performed (Renoult et al., 2020). It should also be noted that the AI represents recall to specific memories rather than general autobiographical memory capacity.

The constructive nature of episodic recall means that the AI is vulnerable to biases and distortions that can rise through false memories. Although there is generally no way for an experimenter to verify the details provided by a participant, the accuracy of the method has been demonstrated when used to recall a scripted event (Diamond, Armson, & Levine, 2020). It might be considered, however, that the participant's subjective experience of memory is just as important to study as the degree of its objective truth. In this sense, it is more important that the participant gives an accurate account of events *as they recall them* than the accuracy of their recall per se. In this sense, it is important to consider whether differences in output are due to differences in mnemonic or narrative styles. It was further noted by Miloyan, McFarlane and Suddendorf (2019) that the AI is vulnerable to experimenter bias, particularly with regard to additional prompting from the experimenter. If the AI is to be considered an objective measure of subjective experience, it is clear that the influence of an experimenter prompting (made to improve the reliability of the method) should be carefully applied.

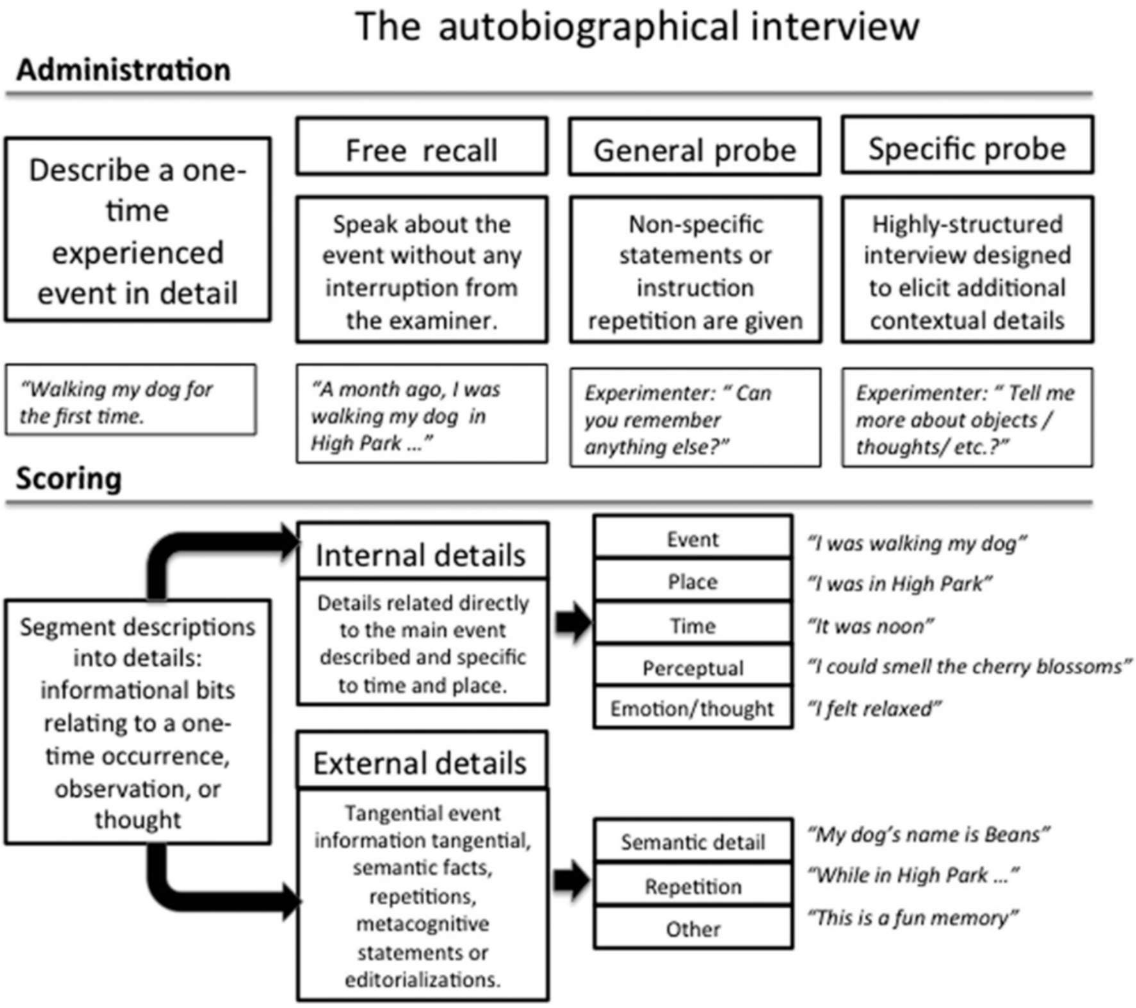


Figure 1.6 shows the general methodology of the AI and is reproduced from Sheldon and Levine (2016).

With regard to the differences between quality and quantity driven forms of autobiographical recall, it has been found that AI performance does not always correlate with SAM episodic self-report scores (Clark & Maguire, 2020; Palombo et al., 2013; but see Armson, Diamond, Levesque, Ryan, & Levine, 2021). In a reply to a preprint of the Clark and Maguire paper, Levine (2018) noted that the AI treats internal details as indexing the participant's capacity to recall contextual information relating to prior episodes, whereas the SAM episodic subscale is a trait-level measure of the subjective experience of recollection. He suggested that as such, an association between the two measures would not necessarily be expected (i.e. that subjective and objective measures of research might be considered separate but complementary). A key topic of investigation is if the same white matter tracts that mediate episodic and semantic recall capacity also subserve the subjective experience of mnemonic traits.

1.9.3 Alternative measures of autobiographical memory

The AI has been validated as a measure of individual differences and has been used in over 200 studies to cover a wide range of issues within autobiographical cognition (Miloyan, McFarlane, & Vasquez-Echeverria, 2019; Sheldon et al., 2018). The SAM represents a survey that measures both memory and future thinking, convenient to the overall aims of studying the bidirectional nature of mental time travel. Further, it has also been validated as a sensitive measure of individual differences in trait mnemonics in everyday life (Sheldon et al., 2016) — an important complementary measure to the task-based AI which focuses on the recall and simulation of specific autobiographical constructions.

An alternative method not used in the present analysis is the Memory Experiences Questionnaire (MEQ — Luchetti & Sutin, 2016; Sutin & Robins, 2007). Whereas the SAM indexes everyday trait mnemonics as described by Levine (Fan et al., 2020), the MEQ indexes 10 phenomenological qualities of autobiographical memory. It has been reported that memory experience surveys (of which the MEQ is an example) are influenced by beliefs about memory (Fitzgerald & Broadbridge, 2013). Recent research has indicated that stable individual differences can be established in memory phenomenology (Rubin, 2021). Further, evidence is emerging that unique neural correlates can be associated with subjective memory experience (Simons, Ritchey, & Fernyhough, 2021). Although these fall beyond the scope of this thesis, they will be important avenues of future research.

As an alternative to the AI approach, some studies have coded imagined atemporal scenarios (often in connection with scene construction — e.g. Hassabis et al., 2007). Unlike the AI, these have yet to be subjected to psychometric validation studies. Of particular importance to the present analyses, the scene construction method does not cover temporality within constructions. This was particularly important to the conceptual focus of the present work and made the AI a more natural choice of method.

1.10 Aims of the project

The present project uses an individual differences approach to investigate the relationship between white matter microstructure in two key tracts of the core network (i.e. the fornix and ILF) and the cognitive constructs that underlie the capacity for mental time travel. These will be measured both on a quantitative level (through use of a modified autobiographical interview) and as traits (using the survey of autobiographical memory).

As evidenced above, past and future episodic constructions share neurocognitive mechanisms. Therefore, it is expected in AI tasks that performance on past and future tasks will correlate within participants. Further, it is expected that they will share microstructure correlates — notably, fornix microstructure is anticipated to correlate with episodic memory measures and ILF microstructure with semantic memory. It is likely that the traits measured in chapter 2 by the SAM will also follow this pattern. However, in line with past research it is predicted that the associations between past and future thinking with white matter microstructure will be dissociable. Prior research indicates that while the two processes share neurocognitive mechanisms, these are employed differently or to different extents. It is expected, therefore, that weaker associations will be found for future than past thinking with fornix microstructure.

The project aims to provide novel insight into the similarities and differences of episodic past and future thinking. Further, it aims to use novel adaptations to existing methods to examine specific questions that remain as yet unanswered in the field. Chapter 4 proposes a novel coding scheme for the AI that will allow for investigation of the role of self-processing in episodic content of past and future autobiographical narratives, and whether it can be considered as a distinct construct in and of itself. Further, the nature of semantic processing will be examined in finer detail in chapter 5— investigating the neural correlates of personal and general semantic memory and how these might be differently or similarly supported. The project also aims to extend prior tractography-based research in the field by examining how episodic content might associate with a specific subcomponent of the fornix (i.e. the pre-commissural fornix — chapter 3). As such, this project aims to evaluate questions contemporary to the field and provide a basis for future research to explore further.

Chapter 2: Interindividual variation in fornix and ILF microstructure and mnemonic “traits” as measured with the survey of autobiographical memory

2.1 Introduction

The study of naturalistic or ‘everyday’ memory has long been distinguished from the memory examined by laboratory tasks (Conway, 1991; Neisser, 1978), with the two approaches providing complementary perspectives on autobiographical memory (Tulving, 1991). More recently, this has become a focus of cognitive neuroscientific methods, given the discovery of the default mode network and its reported association with autobiographical cognition (Philippi, Tranel, Duff, & Rudrauf, 2015; Spreng & Grady, 2010). The insight into cognitive processing provided by trait-based, individual differences measures of memory are distinct and complementary to both performance- and laboratory-based measures (Palombo et al., 2013). Trait-level autobiographical memory abilities or styles have been argued to reflect general tendencies in how individuals recall memories (Palombo, Sheldon, & Levine, 2018); this is in contrast to performance-based measures of autobiographical memory that involve the recall and description of a select few, typically over-rehearsed, events (e.g., Levine, Svoboda, Hay, Winocur, & Moscovitch, 2002). Like other traits, including emotion (Watson & Walker, 1996) and personality (Cobb-Clark & Schurer, 2012), it is likely that ‘trait mnemonics’ are grounded in individual differences in stable aspects of brain function and structure (see also Crawford, Muhlert, MacDonald, & Lawrence, 2020; Palombo et al., 2018c; Sheldon, Farb, Palombo, & Levine, 2016). Indeed, a study by Sheldon, Farb, Palombo, and Levine (2016) used a recently developed measure of trait autobiographical memory, the survey of autobiographical memory (SAM; Palombo, Williams, Abdi, & Levine, 2013; see below for details) to demonstrate that individual differences in capacity and bias towards aspects of everyday memory (episodic versus semantic) could be associated with different patterns of functional connectivity as measured using resting-state fMRI.

Individual differences in the subjective experience of remembering can be conceptualised by considering the qualities of the information stored following an event, how attempts to recall this event might be constrained or supported, how these might shape a person’s subjective experience of the past, and what effect this might have on the interpretation of stimuli in their experiential present or simulated future (Klein, 2015). This might appropriately be considered in terms of episodic and semantic memory systems (Tulving, 1972, 2002a) and differences between individuals in their capacity for, accuracy with, and reliance on these constructs.

The SAM is a reliable, valid method of interrogating a participant's self-reported reliance on both episodic-based remembering (recalling specific spatiotemporal event details) and semantic-based remembering (recalling facts) at the trait level (Palombo et al., 2013). It was used by Sheldon et al. (2016; see also Petrican, Palombo, Sheldon, & Levine, 2020) to associate self-reported mnemonic traits with functional connectivity of the medial temporal lobes in the resting state. It was found in this study that episodic autobiographical memory scores correlated positively with medial temporal lobe connectivity to posterior regions of the brain involved in sensory-perceptual and visual processing, consistent with the suggestion that episodic remembering is underscored by the reinstatement of past events in terms of vivid, contextual details or event specific information (Conway & Pleydell-Pearce, 2000). Individual differences in semantic remembering, on the other hand, were associated with functional connectivity between the medial temporal lobe and lateral temporal, inferior and middle prefrontal cortical regions implicated in controlled semantic cognition (Patterson, Nestor, & Rogers, 2007). This study acted as a further validation of the SAM as a reliable measure of mnemonic traits, and demonstrated it was possible for these traits to associate with neural correlates.

This double dissociation of general episodic and semantic remembering at the trait level is echoed in the findings of Hodgetts et al. (2017a) who used an adapted version of the Galton-Crovitz cueing paradigm (Crovitz & Schiffman, 1974) and the AI-based coding system (Levine et al., 2002) to parse specific autobiographical memories for episodic and semantic content. Individual differences in the amount of episodic and semantic detail produced in response to these cues were correlated with white matter microstructure of two key tracts of the default mode network, namely the fornix and inferior longitudinal fasciculus (ILF) (see chapter 1). It was found by Hodgetts and colleagues that individual differences in the production of episodic content within autobiographical memories significantly correlated with fornix but not ILF microstructure, whereas the reverse pattern was true for semantic details. The above studies add to the wealth of literature that has demonstrated dissociable neural correlates for episodic and semantic memory (e.g. Cabeza & Nyberg, 2000; Wiggs, Weisberg, & Martin, 1998), in line with Tulving's (2002a) suggestion that these are dissociable (if highly inter-relating) memory systems (see Renoult & Rugg, 2020 for discussion). Further, it was demonstrated by Hodgetts et al. that it is possible to assay interindividual differences in microstructure in memory-relevant white matter tracts in a healthy population using diffusion weighted imaging, and that this could specifically be related to differential aspects of autobiographical memory processing.

The SAM further identifies a participant's self-reported capacity for spatial memory relating primarily to navigation (Palombo et al., 2013; Fan, Abdi, & Levine, 2020). Effective navigation is facilitated through the use of cognitive maps (O'Keefe & Nadel, 1978; Murray, Wise, & Graham, 2017) (for a full review see Epstein, Patai, Julian, & Spiers, 2017). It is supported by both egocentric and allocentric coding systems (Galati et al., 2000). These are used in combination to maintain an awareness of ever-changing self-location (i.e. egocentric coding) with the relationship of external objects and entities with each other (i.e. allocentric coding). It has been noted that spatial and autobiographical memory show overlapping (Buckner & Carroll, 2007; Burgess, Becker, King, & O'Keefe, 2001; Maguire, 1997) but dissociable (Moscovitch et al., 2005) brain activation patterns. Relevant to the present analysis, a common overlap is noted to be found in hippocampal and parahippocampal regions (Moscovitch et al., 2005). Furthermore, Hodgetts et al. (2020) recently found that individual differences in spatial navigation in virtual reality was correlated with microstructure of the fornix in a similar way to individual differences in episodic autobiographical memory. It was concluded by the authors that the extended hippocampal network mediated by the fornix is critical to encoding, storing, and retrieving of both episodic and spatial memory, in line with cognitive map theory which proposes that we form a map-like representation of memories in both time and space; and that the processes supporting navigation through physical space also support navigation through our episodic memories (Epstein et al., 2017; O'Keefe & Nadel, 1978).

The final trait measured by the SAM is the self-reported ability to mentally construct future scenarios (Palombo et al., 2013). Palombo and colleagues note that although prospection is not a 'memory' it does engage similar systems as does the autobiographical memory system (this is reviewed in full in chapter 1). Despite the apparent overlap in future simulation, autobiographical memory, and spatial memory (Buckner & Carroll, 2007) it has been possible to also demonstrate that episodic future thinking relies on aspects of semantic thinking as well (Irish et al., 2012a). It has been proposed that this might reflect the differential expression of mental time travel into either the future or the past, and hence that these can be distinguished despite constructions otherwise closely resembling one another (D'Argembeau, 2020).

This study forms a combination of the proposals put forward by Sheldon et al. (2016) and Hodgetts et al. (2017a, 2020). As such it followed a correlative interindividual design, aimed at demonstrating the neural microstructure that might be implicated in trait-level differences between aspects of the subjective experience of autobiographical remembering. To serve this purpose, participants underwent DTI scanning, in which the tracts of interest were identified as being the fornix and the ILF, and then filled out the SAM. SAM scores were correlated with the microstructure of the identified tracts to establish if individual differences in white matter architecture were associated with self-reported mnemonic traits.

In line with the above research, and to the extent to which resting-state functional connectivity reflects structural connectivity (Suárez, Markello, Betzel, & Misic, 2020), it was predicted that episodic and spatial subcomponents of the SAM would correlate positively with fornix FA and negatively with fornix MD, but that these subscales would not correlate positively with ILF FA or negatively with ILF MD. Conversely it was predicted that individual differences in semantic ('fact-based') remembering would positively correlate with ILF FA and negatively correlate with ILF MD scores. It was predicted that the semantic subscale would not correlate positively with fornix FA or negatively with fornix MD. Finally, it was predicted that the future subscale of the SAM would be associated with both fornix and ILF microstructure (positively with FA and negatively with MD). This is in line with studies that have demonstrated that episodic future thinking engages brain regions that are classically associated with both episodic and semantic memory (Irish & Piguet, 2013; Schacter & Addis, 2007b).

2.2 Methods

2.2.1 Participants

Fifty-one healthy, right-handed, undergraduate, adult female participants (average age = 20 years SD = 1.1) took part in a self-report mnemonic traits and diffusion weight tractography study. Participants were recruited from Cardiff University. One participant did not fully complete the SAM, and their response to this section (the episodic subscale) was removed from the analysis. Two other participants showed extreme outlier values in their tractography indices (outside the range of the mean +/- 3 SD) and these values were also removed pairwise from the analysis. All participants gave informed consent (as approved by the Cardiff University Research Ethics Committee) and were paid approximately £25 for their participation.

2.2.2 Survey of autobiographical memory

The trait mnemonic styles of each participant were assessed using the 26-item version of the SAM (Palombo et al., 2013). For each item, participants were asked to consider whether they agreed or disagreed with a statement relating to an aspect of their memory and prospection using a five-point Likert scale (the full item list of items can be seen in Palombo et al., 2013).

The SAM is divided up into four sub-categories, referring to a participant's self-reported capacity for episodic (8 items), semantic (6 items), and spatial memory (6 items), as well as their ability to construct future events (6 items). The episodic and semantic categories follow the distinction made by Tulving (1985) as noted in chapter 1. Hence, they respectively refer to a participant's ability to recall details from a specific event (e.g. "When I remember events, I remember a lot of details"), and to acontextual factual recall (e.g. "I can learn and repeat facts easily, even if I don't remember where I learned them"). The 'spatial' memory scale can be conceptualised as referring to navigational ability rather than to the memory of a coherent 'scene' as described by the scene construction hypothesis of mental time travel (Rubin, 2020) (e.g. "In general, my ability to navigate is better than most of my family/friends"). Finally, the future subscale refers to a participant's general ability to construct detailed future events (e.g. "When I imagine an event in the future, I can picture people and what they look like"). The SAM has been shown to have excellent construct and external validity (Palombo et al., 2013; Fan et al., 2020; Petrican et al., 2020). Total scores on each of the four memory domains are derived using a weighting algorithm on the raw item ratings, developed during the original validation of the SAM (Palombo et al., 2013).

2.2.3 MRI data acquisition

Imaging data were acquired at Cardiff University's Brain Research Imaging Centre (CUBRIC) using a Siemens Magnetom Prisma 3 Tesla MRI scanner with a 32-channel head coil. T1-weighted structural 3D images were acquired using an MPRAGE sequence (224 axial slices, TR/TE = 2250/3.06ms, FOV = 256mm^2; slice thickness = 1mm; voxel size = 1mm^3, 9° flip angle).

Diffusion weighted imaging data were acquired using a multi-shell sequence (orientation = transversal/axial, 80 slices, TR/TE = 9400/67.0ms, FOV = 256mm^2, slice thickness = 2mm, voxel size = 2mm^3). Diffusion gradients were applied in (i) 30 isotropic directions (diffusion-weighted factor b = 1200sec/mm^2), (ii) in 60 isotropic directions (diffusion-weighted factor b = 2400sec/mm^2), and (iii) a volume without diffusion gradients (b = 0sec/mm^2).

2.2.4 MRI pre-processing

2.2.4.1 Diffusion MRI

FSL's Brain Extraction Tool (Smith, 2002) was used to subject a 'brain-tissue only' mask to T1-weighted structural images. Diffusion MRI (dMRI) data were pre-processed using ExploreDTIv4.8.3 (Leemans, Jeurissen, Sijbers, & Jones, 2009). Corrections were made to distortions arising from participant head motion and eddy currents. Free water contamination from cerebrospinal fluid is a noted issue for white matter pathways in proximity to the ventricles (e.g. the fornix). This has been shown to significantly affect delineation (Concha, Gross, & Beaulieu, 2005). The two-compartment 'Free Water Elimination' (FWE) procedure (Pasternak, Sochen, Gur, Intrator, & Assaf, 2009) was applied, therefore, to correct for voxel-wise partial volume artifacts arising from free water contamination. This allows for improved tract reconstruction and tissue specificity in Diffusion Tensor Imaging (DTI) (Albi et al., 2017; Pasternak et al., 2014). Following FWE, corrected diffusion tensor indices for FA and MD were calculated. FA reflects the degree to which diffusion is constrained to a single axis. MD ($10^{-3}mm^{2}s^{-1}$) is the combined average of axial (along the principal axis) and radial (along the orthogonal direction) diffusion (Vettel, Cooper, Garcia, Yeh, & Verstynen, 2017). The resulting free water corrected FA and MD maps were the inputs for the tractography analyses.

2.2.4.2 Tractography

Deterministic tractography was performed using the damped Richardson-Lucy spherical deconvolution (dRL-SD) algorithm. Spherical deconvolution allows for the estimation of fibre orientation distribution, and improved description of complex white matter anatomy (Dell'Acqua & Tournier, 2019). The step size was 0.5mm, and the fibre orientation density function amplitude threshold was 0.05. An angle threshold of 45° was used to prevent the reconstruction of anatomically implausible fibres. These are the default deterministic dRL streamline tractography parameters used at CUBRIC.

Waypoint region-of-interest (ROI) gates were drawn manually onto whole-brain free water corrected FA and MD maps to generate 3D fibre reconstructions of each tract-segment. The waypoint ROIs defined the tracts based on a ‘SEED’ point and Boolean logical operations: ‘NOT’ and ‘AND’. Tracts were retained (‘AND’) or excluded from the analyses (‘NOT’) dependant on the gates they passed through. These gates were then combined to reconstruct the tracts, as informed by anatomical plausibility (Schilling et al., 2020). Manual tractography was performed on a minimum of 15 subject so that a tract model could be calculated for automated tractography on all 51 data sets (Explore DTI; Parker et al., 2013). Visual inspection of each automatically generated tract allowed for the insertion of additional ‘NOT’ gates for erroneous fibres. Following the reconstruction of each pathway in each participant, mean FA and MD were calculated by averaging individual values at each 0.5mm step along the tracts.

2.2.4.3 Fornix

The fornix (see figure 1) was identified using the landmarks described in Catani and Thiebaut de Schotten (2008). From the mid sagittal slice, the coronal crosshair was placed approximately six voxels posterior to the anterior commissure. In the coronal plane, a single ‘AND’ gate was drawn around the fornix bundle where the anterior pillars enter the main body. Finally, 'NOT' gates were drawn around extraneous regions that were not part of the fornix.

2.2.4.4 Inferior longitudinal fasciculus

A two ROI approach was used in each hemisphere for the ILF (Hodgetts et al., 2017a; Wakana et al., 2007; see figure 1). The posterior edge of the cingulum bundle was initially identified on the sagittal plane. A SEED ROI was positioned at this location in the coronal plane that encompassed the whole hemisphere. A second ROI was drawn to isolate streamlines extending towards the anterior temporal lobes. This was positioned at the most posterior coronal slice in which the temporal and frontal lobes did not connect. An additional AND ROI was drawn here around the entire temporal lobe. As with the fornix, any anatomically implausible fibres were removed using additional NOT gates.

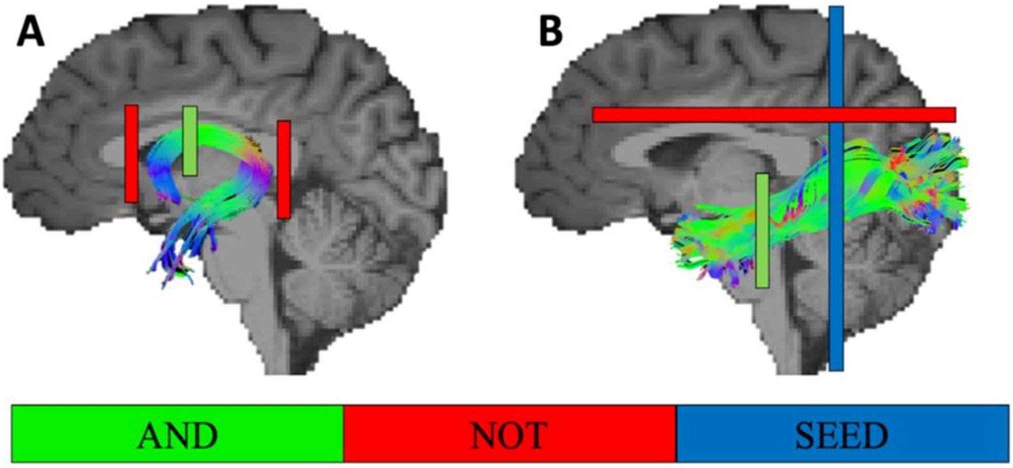


Figure 2.1. Automated tract reconstructions of the (a) fornix and (b) ILF. The ROIs used in creating each tract are displayed on each image. The tracts are displayed on the sagittal midline slices. Image reproduced from Valji et al. (2019).

2.2.5 Data handling

This analysis followed a correlational design in which the weighted sum scores from the SAM domains (i.e. episodic, semantic, spatial, and future categories) were compared with fornix and ILF microstructure FA and MD. In line with advice from modern statistical practice (Bender & Lange, 2001; Lakens et al., 2018) and prior research in the area (Hodgetts et al., 2017a), to control the family-wise error rate, a Bonferroni correction was performed using the number of white matter tracts of interest in this analysis (i.e. the fornix and the ILF), resulting in an $\alpha = 0.05/2 = 0.025$ for each SAM sub-domain. This was chosen to provide a measure of control for family wise errors, but so that it would not be too stringent given the modest sample size (i.e. to balance the possibility of type 1 and type 2 errors, considering the novelty of the approach — Lakens et al., 2018).

One participant had an incomplete SAM, and two produced outlier values in their ILF tract microstructure data (outside the range of the mean +/- 3 SD). These points were removed pairwise from the analysis to ensure that as much data was retained as possible. This is reported here in line with modern advice for good statistical practice (Valentine et al., 2018).

The SAM produces details regarding different trait aspects of a participant's memory through answers provided on a Likert scale. Therefore, they produce ordinal data and non-parametric comparisons are more appropriate (Kero & Lee, 2016). The comparisons in this analysis used Kendall's Tau, as research has shown it to be more robust and efficient than Spearman's rho due to its smaller gross error sensitivity and asymptotic variance (Croux & Dehon, 2010). Further it allows for Bayesian analysis to complement the main analyses (van Doorn, Ly, Marsman, & Wagenmakers, 2018; see figure 2.2 for an indication of how Bayes factors were interpreted). Despite using a non-parametric test, outliers were removed as they can affect the power of non-parametric analyses (e.g. due to measuring error during DTI) (Zimmerman, 1995).

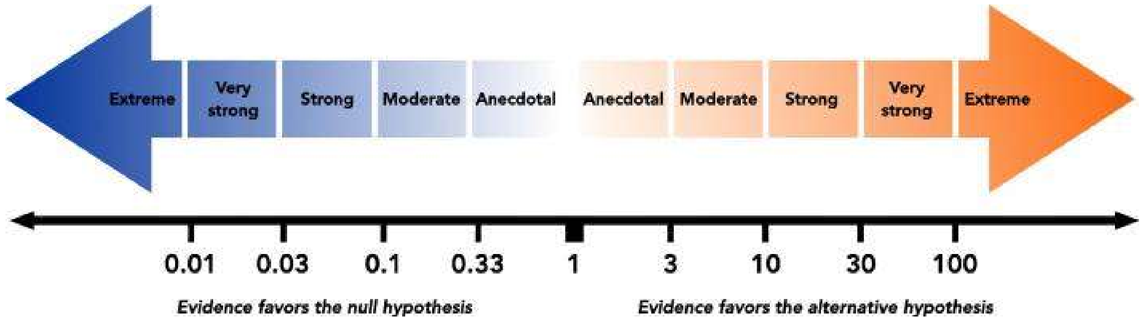


Figure 2.2 Shows the classification scheme for interpreting Bayes Factors (Lee & Wagenmakers, 2014), and is reproduced from Quintana and Williams (2018).

As higher values of FA are considered indicative of increased myelination and improved organization, cohesion, and compactness of white matter fibre tracts (Beaulieu, 2002; Fields, 2015), a positive association was predicted between fornix and ILF FA and their related SAM subcomponent scores. Conversely, an increase in MD shows greater axial and radial diffusion (i.e. the presence of more water). This has been associated with a reduction in conduction velocity along the tract (Beaulieu, 2002). As such, a negative association was predicted between participants' MD and their related scores in the SAM. Due to the directional nature of the present hypotheses, one-tailed Kendall's tau correlations were conducted between participants' scores on the SAM subcomponents and their DTI indices (Lakens, 2016).

Finally, Vovk-Sellke maximum p–ratios (VS-MPR) were computed: based on the p-value, the maximum possible odds in favour of H1 over H0 equals $1/(-e\, p \log(p))$ for $p \leq .37$, where log is the natural logarithm and e is its constant base (Benjamin & Berger, 2019). As such, the VS-MPR represents the largest odds in favour of the alternative hypothesis relative to the null hypothesis that is consistent with the observed data, and so is helpful in interpreting p-values.

2.3 Results

2.3.1 Intercorrelations within the SAM subscales

A positive correlation was found between participants' responses to the episodic and future (one-tailed Kendall's tau = 0.267, p = 0.003, VS-MPR = 19.351, BF$_{0+}$ = 14.112), episodic and semantic (one-tailed Kendall's tau = 0.209, p = 0.016, VS-MPR = 5.446, BF$_{0+}$ = 3.360) and spatial and future subscales (one-tailed Kendall's tau = 0.183, p = 0.032, VS-MPR = 3.372, BF$_{0+}$ = 2.036). No association was found between the episodic and spatial (one-tailed Kendall's tau = 0.018, p = 0.427, VS-MPR = 1.000, BF$_{0-}$ = 0.214), semantic and spatial (one-tailed Kendall's tau = 0.140, p = 0.076, VS-MPR = 1.880, BF$_{0-}$ = 0.943) or semantic and future subscales (one-tailed Kendall's tau = 0.151, p = 0.060, VS-MPR = 2.175, BF$_{0-}$ = 1.135). A correlation matrix produced in RStudio (2020) using GGally (Schloerke et al., 2011) is shown in figure 2.3. These findings are similar to previous reports (Palombo et al., 2013; Fan et al., 2020).

Figure 2.3 shows a Kendall's tau correlation matrix of the SAM subscales.

2.3.2 SAM subcomponent and fornix microstructure correlations

No significant correlations were found between fornix FA and the scores of the episodic (Figure 2.4.A. One-tailed Kendall's tau = 0.082, $p = 0.199$, VS-MPR = 1.145, $BF_{0+} = 0.416$), semantic (Figure 2.4.B. One-tailed Kendall's tau = -0.108, $p = 0.867$, VS-MPR = 1.000, $BF_{0+} = 0.090$), spatial (Figure 2.4.C. One-tailed Kendall's tau = -0.091, $p = 0.823$, VS-MPR = 1.000, $BF_{0+} = 0.099$) or future (Figure 2.4.D. One-tailed Kendall's tau = 0.174, $p = 0.037$, VS-MPR = 3.025, $BF_{0+} = 1.713$) subcomponents of the SAM.

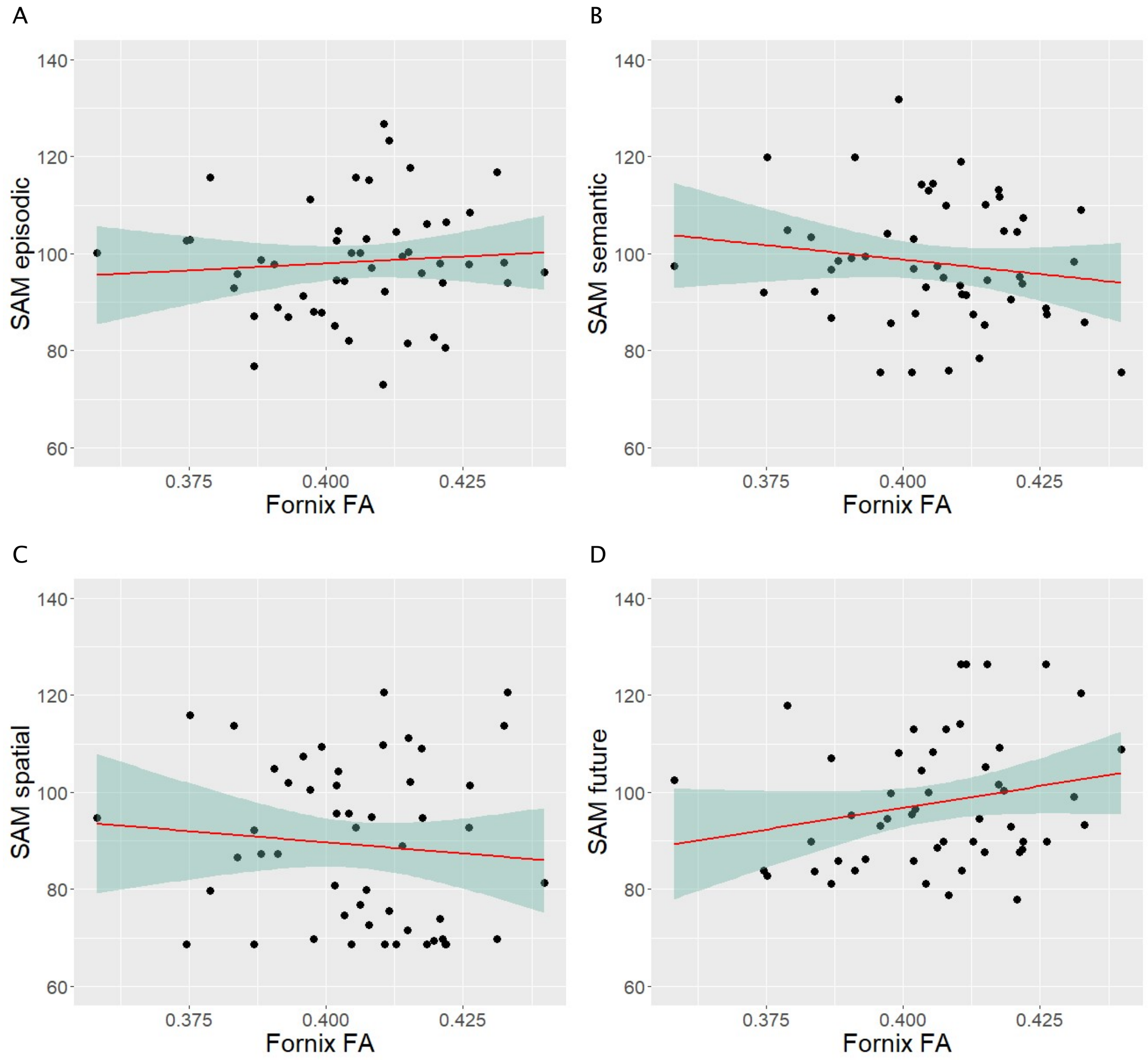


Figure 2.4 shows the correlations between fornix FA values and the scores produced on the SAM subscales A) episodic, B) semantic, C) spatial and D) future thinking. The shaded area represents the 95% CI.

A significant negative correlation was found between fornix MD microstructure and the spatial SAM subcomponent (Figure 2.5.C. One-tailed Kendall's tau = -0.246, *p* = 0.006, VS-MPR = 12.088, BF_{0-} = 9.012). Further a significant negative correlation was found between fornix MD and the future thinking subcomponent (Figure 2.5.D. One-tailed Kendall's tau = -0.248, *p* = 0.005, VS-MPR = 12.921, BF_{0-} = 9.012). No correlations were found for either episodic (Figure 2.5.A. One-tailed Kendall's tau = -0.083, *p* = 0.197, VS-MPR = 1.15, BF_{0-} = 0.420) or semantic (Figure 2.5.B. One-tailed Kendall's tau = -0.091, *p* = 0.173, VS-MPR = 1.212, BF_{0-} = 0.464) subcomponent scores.

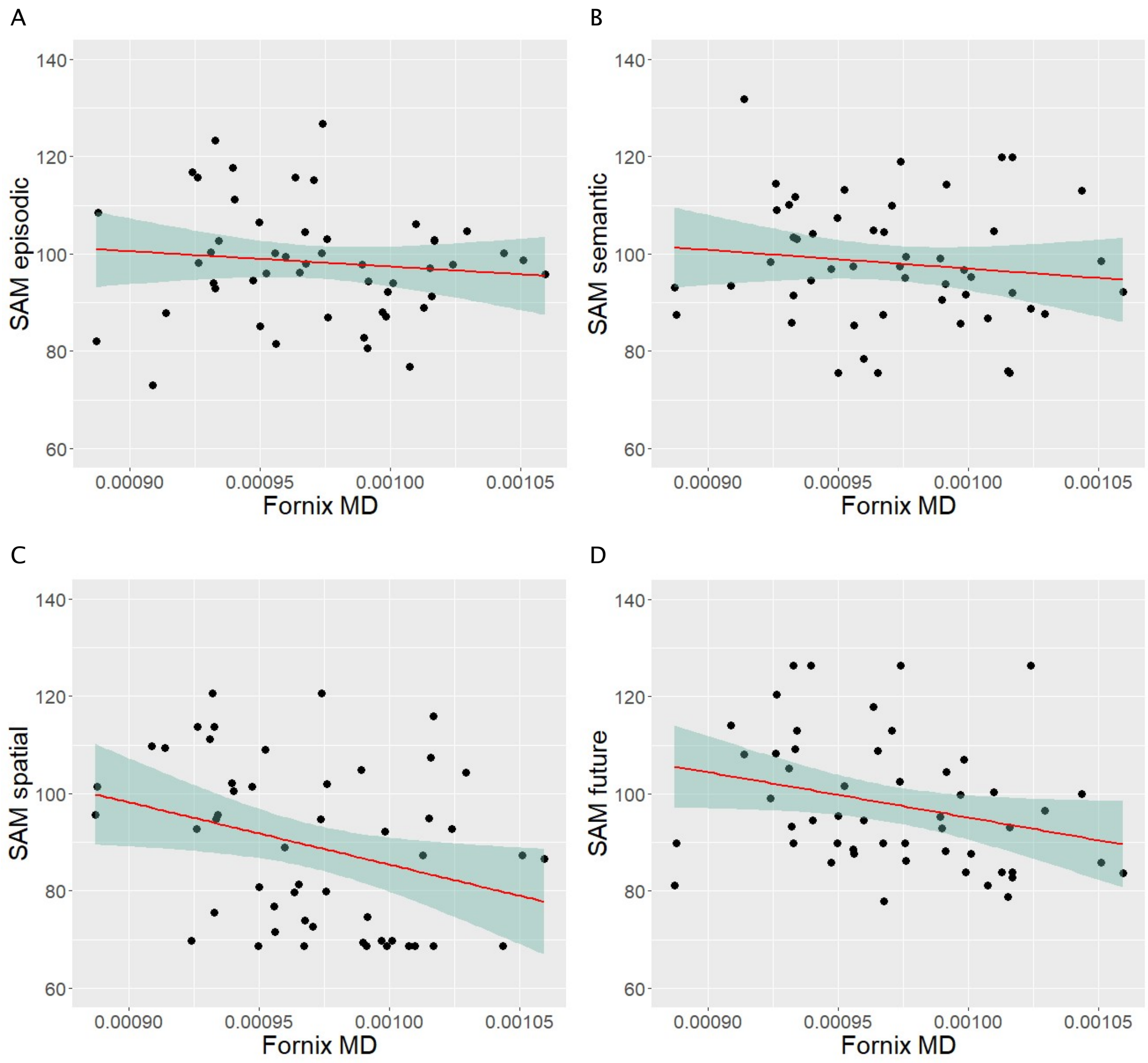


Figure 2.5 shows the correlations between fornix MD values and the scores produced on the SAM subscales A) episodic, B) semantic, C) spatial and D) future thinking. The shaded area represents the 95% CI.

2.3.3 SAM subcomponent and ILF microstructure correlations

No significant correlations were found between ILF FA and the scores of the episodic (Figure 2.6.A. One-tailed Kendall's tau = 0.107, $p = 0.141$, VS-MPR = 1.330, $BF_{0+} = 0.567$), semantic (Figure 2.6.B. One-tailed Kendall's tau = -0.035, $p = 0.640$, VS-MPR = 1.000, $BF_{0+} = 0.141$), spatial (Figure 2.6.C. One-tailed Kendall's tau = 0.159, $p = 0.054$, VS-MPR = 2.343, $BF_{0+} = 1.273$) or future (Figure 2.6.D. One-tailed Kendall's tau = 0.007, $p = 0.473$, VS-MPR = 1.000, $BF_{0+} = 0.194$) subcomponents of the SAM.

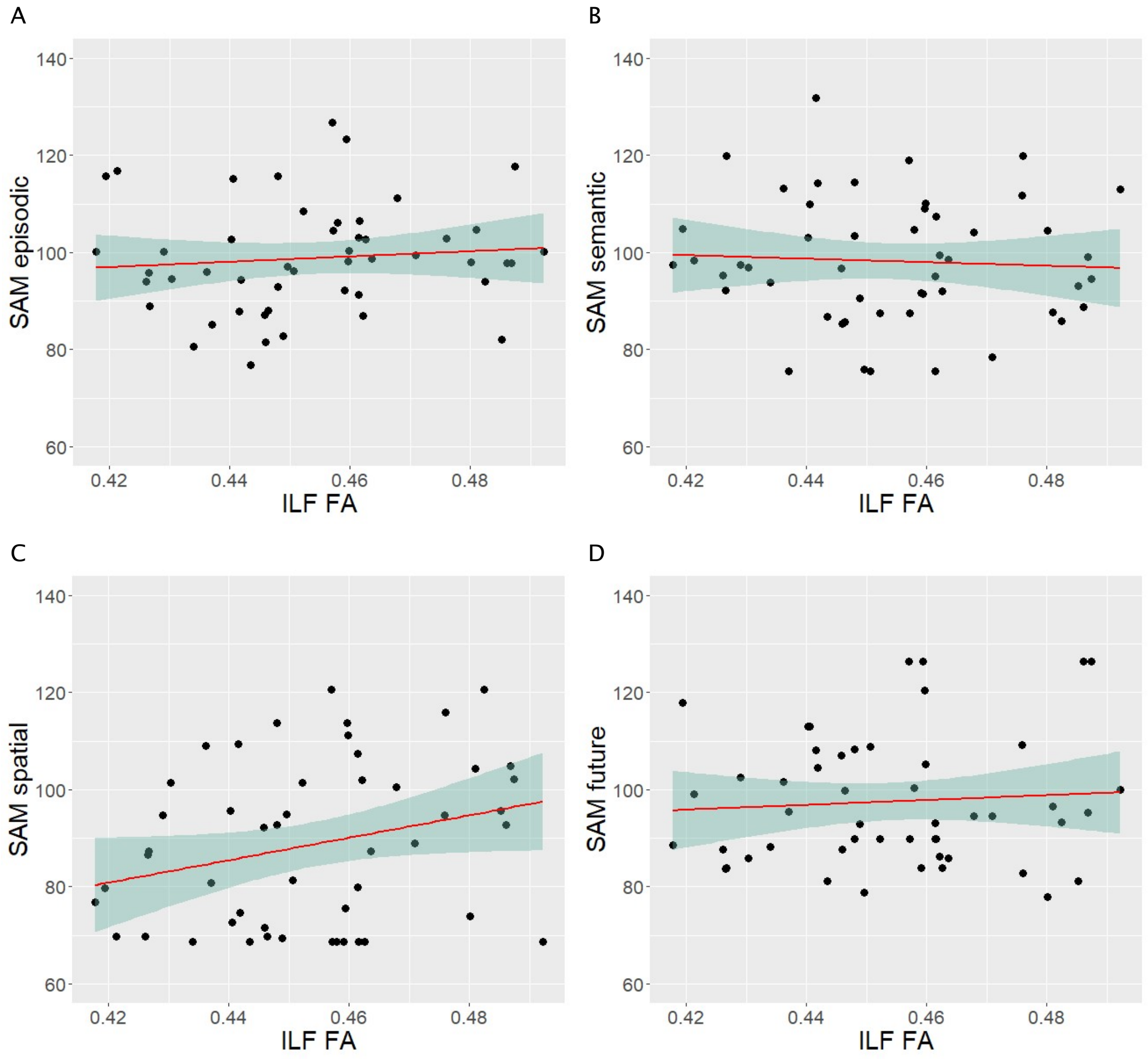


Figure 2.6 shows the correlations between ILF FA values and the scores produced on the SAM subscales A) episodic, B) semantic, C) spatial and D) future thinking. The shaded area represents the 95% CI.

Further, no significant correlations were found between ILF MD and the scores of the episodic (Figure 2.7.A. One-tailed Kendall's tau = -0.071, p = 0.238, VS-MPR = 1.077, BF_{0-} = 0.366), semantic (Figure 2.7.B. One-tailed Kendall's tau = -0.092, p = 0.172, VS-MPR = 1.214, BF_{0-} = 0.470), spatial (Figure 2.7.C. One-tailed Kendall's tau = -0.041, p = 0.337, VS-MPR = 1.004, BF_{0-} = 0.266) or future (Figure 2.7.D. One-tailed Kendall's tau = -0.140, p = 0.077, VS-MPR = 1.859, BF_{0-} = 0.926) subcomponents of the SAM.

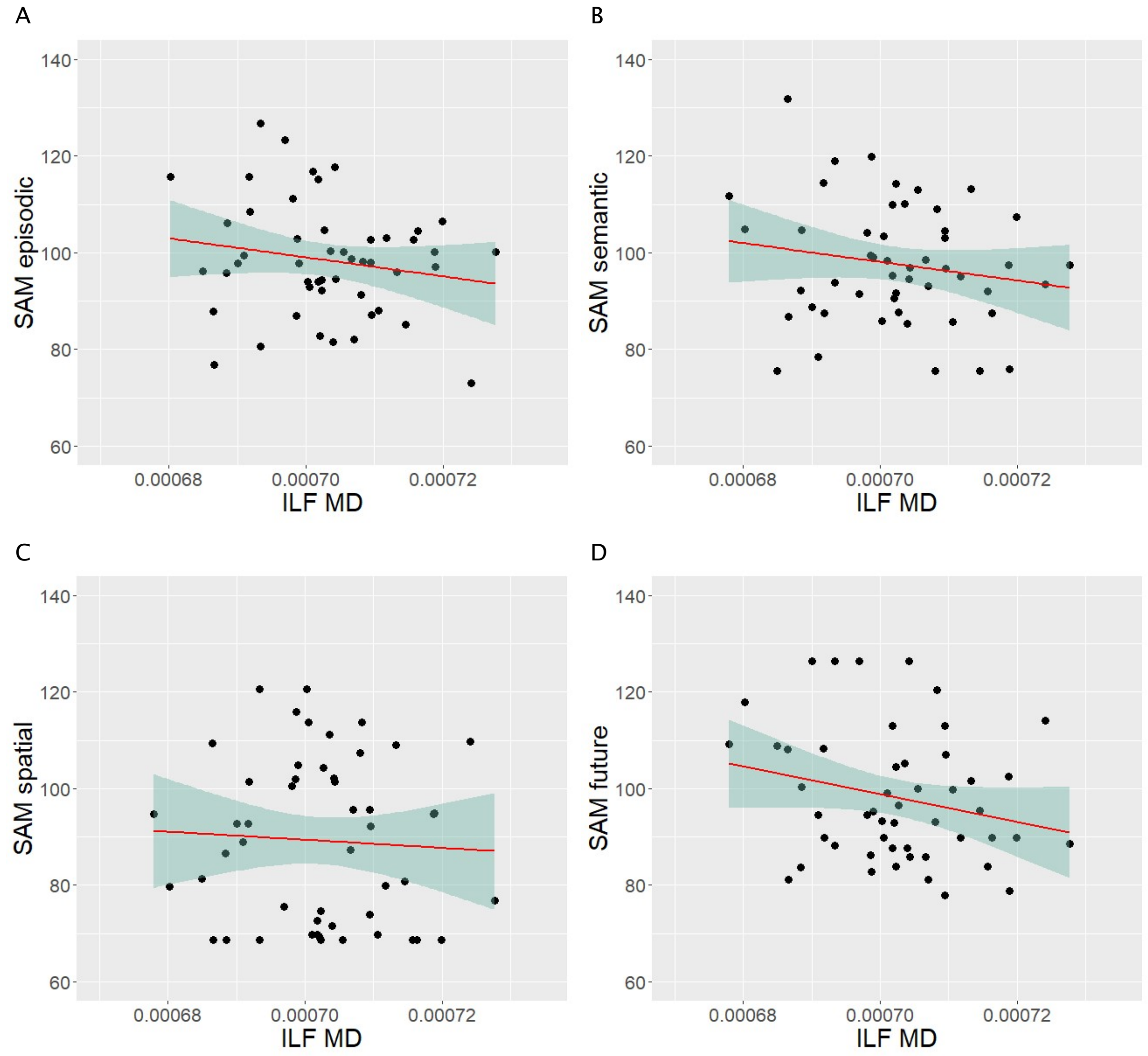


Figure 2.7 shows the correlations between ILF MD values and the scores produced on the SAM subscales A) episodic, B) semantic, C) spatial and D) future thinking. The shaded area represents the 95% CI.

2.3.4 Steiger's Z-test for key comparisons

The statistically significant findings in this analysis were subsequently analysed using Steiger's Z test (1980) to establish if two dependent correlations with a shared variable were significantly different. In this case, this meant comparing the correlation between the SAM subscale and the tract of interest with the correlation of that same subscale with the tract it was predicted not to correlate with. In order for these comparisons to be made it was necessary to convert Kendall's tau to Pearson's r, which was done following the formula presented in Walker (2003). The Steiger's z tests were then performed using the cocor webtool (Diedenhofen & Much, 2015).

A one-tailed Steiger's Z-test revealed that the difference between fornix and ILF MD associations with participants' scores on the spatial subscale of the SAM failed to reach statistical significance (z= -1.623, *p* = 0.052). Further, no significant difference was found between fornix and ILF MD values and the scores produced on the future subscale in a two-tailed test (z = -0.862, *p* = 0.194).

2.4 Discussion

This study set out to examine the relation between self-reported autobiographical memory traits (Palombo et al., 2018c) and the microstructure of two key white matter tracts, the fornix and the ILF, which have previously been shown to be differentially involved in the episodic vs. semantic aspects of autobiographical memory, respectively (Hodgetts et al., 2017a).

Contrary to predictions, the SAM-Episodic subscale did not positively correlate with fornix FA or negatively correlate with fornix MD values (Bayes factor analysis indicated anecdotal evidence in favour of the null hypothesis for both associations — BF ~ 0.4). The SAM-Episodic subscale did not correlate positively with ILF FA or negatively with ILF MD. Although this was broadly in line with predictions, Bayes factor analysis indicated only anecdotal evidence in favour of the null hypothesis in both associations (0.33 < BF < 0.6). In line with predictions, SAM-Semantic showed no positive association with fornix FA (Bayes factors indicated strong evidence in favour of the null — BF < 0.1). Although no negative association was found between SAM-Semantic and fornix MD, only anecdotal evidence was found in favour of the null (BF ~0.4). Contrary to predictions, SAM-Semantic did not correlate positively with ILF FA or negatively with ILF MD. Further, this analysis provided moderate evidence towards the null hypothesis regarding ILF FA (BF ~ 0.14). However, only moderate evidence was found to support the null for the association between SAM-Semantic and ILF MD (BF ~ 0.4). These findings do not support prior research that indicated that episodic and semantic memory can be generally associated with dissociable neural correlates (Cabeza & Nyberg, 2000), specifically when these were measured as traits using scores generated from the SAM (Sheldon et al., 2016) and that these could be associated with tract microstructure measures when measured using the autobiographical interview (Hodgetts et al., 2017a).

A significant negative correlation was established between fornix MD and two of the SAM subscales (i.e. SAM-Spatial and SAM-Future), and odds ratios/ Bayes Factors suggested moderate (BF ~ 10, indicated the correlation is 10 times more likely than the null) evidence for these correlations (Quintana & Williams, 2018). MD indicates the amount of water present in the tract and hence the lower proportion of axonal fibres (Beaulieu, 2002). Due to this it has primarily been used as a measure in neuro-atypical patients to provide a measure of the damage in their neuronal microstructure (e.g. Maggia et al., 2017) or the axonal thinning seen in aging brains (Garcia-Lazaro, Becerra-Laparra, Cortez-Conradis, & Roldan-Valadez, 2016). However, it has also been used as an indicator in healthy populations to indicate the efficiency of information transfer along a participant's white matter tracts (Beaulieu, 2002; Hodgetts et al., 2020). As such it is appropriate that the findings in the present sample of healthy, neurotypical participants can be analysed with regards to the associations that were produced (i.e. lower MD being indicative of higher self-report capabilities or tendencies).

Although a negative association was found between participants' self-reported navigational memory, as measured by the 'spatial' SAM subscale, and their fornix MD, this association did not significantly differ from the association between the spatial subscale and ILF MD (potentially reflecting a lack of sensitivity due to sample size). The present finding, therefore, provides moderate support for the notion that a greater reported capacity for navigational memory could be associated with higher neuronal information transfer efficiency across the fornix white matter tract (as per Beaulieu, 2002). Indeed, while the SAM is a self-reported measure of navigational ability, recent work has shown that SAM-spatial (but not SAM-episodic) scores relate to navigation performance (Clark et al., 2019; Selarka, Rosenbaum, Lapp, & Levine, 2019).

Prior research in animal models has demonstrated that fornical lesions are associated with impairments to spatial navigation ability (Cain, Boon, & Corcoran, 2006; De Bruin, Moita, De Brabander, & Joosten, 2001; Warburton & Aggleton, 1998) and place learning (Dumont, Amin, Wright, Dillingham, & Aggleton, 2015, O'Keefe, Nadel, Keightley, & Kill, 1975, Packard, Hirsh, & White, 1989), consistent with cognitive map theory. Research has demonstrated that cognitive map based navigational ability in humans is associated with hippocampal regions (Epstein et al., 2017; Moscovitch et al., 2005). Further, it has recently been demonstrated that fornix microstructure (specifically MD) is negatively associated with learning rate (i.e. with faster learning) in a virtual reality navigation task in healthy participants (Hodgetts et al., 2020). Consistent with the findings of the Hodgetts study, this analysis found that SAM-Spatial did not positively associate with ILF FA or negatively associate with ILF MD. Moderate evidence was found in favour of the null hypothesis for the association between SAM-Spatial and ILF MD ($BF < 0.33$), however, only anecdotal evidence was found for the association between SAM-Spatial and ILF FA ($BF \sim 1$). Hodgetts et al. suggested that together these findings show that, while visual object pathways are not important, the fornix might play a key role in mediating navigational learning. As such, the present findings support both the present hypotheses and the wider body of literature.

The association between fornix MD and the SAM spatial subscale but not the episodic subscale has further implications for the role of the fornix in episodic memory and mental time travel. In particular, as in previous studies with the SAM, present results suggest a dissociation, rather than an association, between self-reported episodic autobiographical memory and spatial abilities. This dissociation appears to run counter to claims that the processes supporting navigation through physical space also support navigation through our episodic memories (Epstein et al., 2017; Murray et al. 2018). However, a closer consideration of the data and the SAM itself suggest that the findings may not be strong evidence against theories suggesting a link between episodic and spatial abilities.

First it is important to consider the nature of the items comprising each SAM domain. The spatial subscale refers explicitly to memory relating to navigational occurrences and capabilities, whereas the episodic scale relates to perceptual details relating to objects, people and so on within an event, with no explicit mention of spatial context (Palombo et al., 2013). Although the fornix has previously been linked with autobiographical memory (e.g. Hodgetts et al., 2017a), it is possible that this link is not due to the event- and perceptual-related details that a person can recall (as implied by the episodic construction hypothesis (Schacter & Addis, 2007b). Instead, it is possible that the fornix plays a key role in creating a spatial framework in which autobiographical memories can be constructed (i.e. as described in both cognitive map theory but also in the scene construction hypothesis — Hassabis & Maguire, 2007). Indeed, Hodgetts et al. (2017a) found that fornix microstructure was selectivity linked to the recall of spatiotemporal details (but not other event details) in the AI. When investigating the criterion validity of the SAM, Palombo et al. (2013) found that scores on the spatial, but not the episodic, subscale of the SAM were significantly correlated with number of internal place details recalled in the AI, as well as with subjective ratings of the 'episodic richness' of autobiographical memories.

Further to this, it was found by Memel, Wank, Ryan and Grilli (2020) that the number of 'event elements' (i.e. perceptual details that related to people, objects, and other entities) produced in the AI showed a stronger association with microstructure of the uncinate fasciculus (a tract linking the entorhinal cortex with the prefrontal cortex - von der Heide, Skipper, Klobusicky, & Olson, 2013) than did spatiotemporal event details. This pattern was reversed for the fornix, which associated more strongly with spatiotemporal than event element details (see also Hodgetts et al., 2017a). Taken with the present results, that is the association between self-reported spatial but not episodic memory (the latter which in itself is more representative of the ‘event element’ concept described by these authors), it seems likely that different aspects of autobiographical memory (including mental time travel, scene, and event construction) are supported by different anatomical structures and connections. This in turn is consistent with the idea that amnesia results from damage to multiple distinct ‘memory’ systems (Gaffan, 2002; Murray, Wise, & Graham, 2017). Further research into this area could look to further elucidate the more specific nature of episodic processing and the distribution of structural networks that support it.

This conclusion can only be made in a tentative fashion, as it has been reported that participants are simply better at self-reporting their spatial navigation abilities in comparison to their other mnemonic traits (Kozlowski & Bryant, 1977), in part because objective feedback is more readily available for navigation (i.e., whether or not one has arrived at the destination) than for autobiographical memory (Fan et al., 2020). As such, it will be important to demonstrate that this finding can be demonstrated beyond the bounds of self-reported mnemonic traits.

Although it was predicted that the ‘episodic’ future thinking subscale would correlate with both the fornix and the ILF, an association could only be established between episodic future thinking traits and fornix MD. The association between the spatial memory and episodic future thinking domain of the SAM, along with their shared association with fornix MD suggests further support for both cognitive map and scene construction theories, as opposed to wider event construction accounts of the role of hippocampal circuitry (including the fornix) in autobiographical memory and future thinking. This result could in part be due to greater shared item content between the spatial and future items than between episodic and future items. For instance, one future item is "When I imagine an event in the future, I can picture the spatial layout” — it is possible that this explicitly relates to spatial memory capacity, rather than specifically engaging a participant’s ability to mental project the self into the future. However, a partial correlation found that a significant association was maintained between SAM-Future and fornix MD when controlling for the score on the spatial subscale (see supplementary results). Despite this, future research might consider constructing self-reported mnemonic traits scales in order to avoid any artificial or unnecessary crossover between the domain scales.

It was further predicted that episodic future thinking SAM subscale scores (but not episodic or spatial memory scores) would correlate with ILF microstructure on the basis that this tract is associated with semantic autobiographical memory (Hodgetts et al., 2017a) which has been proposed to provide a framework in which episodic future thinking can occur (Irish & Piguet, 2013). It was found that the SAM-Future subscale did not associate positively with

ILF FA or negatively with ILF MD. Notably, Bayes factor analysis indicated moderate evidence in favour of the null hypothesis (BF ~ 0.2) for the association between the future thinking subscale and ILF FA. However, only anecdotal evidence (BF ~ 0.9) supported the null hypothesis for the association between SAM-Future and ILF MD. Further, no positive association was found between future thinking and semantic subscales (albeit anecdotal evidence was found to support the alternate hypothesis — BF ~ 1). Taken on this basis, it might be possible to conclude that present results challenge the semantic scaffolding hypothesis. However, it was also found that the associations between the future thinking subscale and fornix and ILF MD did not significantly differ (although this may reflect a lack of sensitivity as no strong evidence was provided in favour of the null hypothesis). Further, SAM-Semantic was not found to associate either positively with ILF FA or negatively with ILF MD. As noted above, this runs contrary to prior research that has established inter-individual variation in the ILF as a marker of individual differences in behaviours reflecting semantic memory (Chen, Lambon Ralph, & Rogers, 2017; Hodgetts et al., 2017a). As such it is possible that the self-report measure is not best suited for identifying this cognitive ability and that the present results are not sufficiently strong to challenge the semantic framework hypothesis.

The use of the SAM can be considered both a strength and a limitation of the present study. As noted in Palombo et al. (2013) and Sheldon et al. (2016), we can on one hand be confident that the measure reflects a participant's 'natural' trait-like abilities or tendencies, as we are asking them to consider themselves in the context of their everyday life. However, the nature of self-report is to ask a participant to access and evaluate their abilities at a surface level. As such, a number of factors can influence the answer they give including a lack of self-awareness, a difference in opinion on how their ability would be reflected on a scale and even duplicity to avoid embarrassment in their assessment (Paulhus & Vazire, 2007). These factors are not fatal, as evidenced by the number of surveys that are carried out across many fields of research (Enkavi et al., 2019). However, it is important to consider them when evaluating the results of a study, especially when they do not seem to reflect the output of existing behavioural data.

An analysis performed by Clark and Maguire (2020) reported that memory questionnaires were associated with self-rated vividness of autobiographical memory, rather than the number of episodic details. They did find, however, that spatial tasks were found to validate findings made in relation to spatial memory (see also Palombo et al., 2013 as discussed above). As reflected earlier, this might be due to the increased salience of spatial memory (i.e. an individual who is lost has immediate and obvious feedback regarding their navigational ability, whereas the accuracy of episodic memories might not be checked/might not have a ‘verifiable’ standard to be checked against). Therefore, it can be considered that this method examines a specific aspect of mental time travel (which is proposed to reflect the vividness of constructions). This can be considered in light of Tulving’s (1991) article, which argued that “memory research is not a zero-sum game”, and that research can benefit from using a variety of methods. As such, the following chapters in this thesis will support the present findings by using complementary performance-based measures to provide converging evidence regarding the role of neural architecture in supporting the capacity for mental time travel (and the cognitive constructs that support it).

In conclusion, this analysis found significant associations between the spatial memory and episodic future thinking SAM subscales and fornix microstructure (MD). Further, the SAM-Future subscale did not associate positively with ILF FA or negatively with ILF MD. Taken together these findings support those accounts, including cognitive map theory (Epstein et al., 2017) and the scene construction model (Hassabis & Maguire, 2007) in which the extended hippocampal circuitry mediate by the fornix plays a key role in forming a spatially coherent context or scene, within which episodic constructions, both in the past and future, are formed. However, these findings are somewhat limited in scope due to the self-report nature of the study’s design, and a potential lack of sensitivity (as indicated by odds ratios, Bayes Factors). For instance, the expected relationships between episodic memory and the fornix, and semantic memory and the ILF were not found (albeit broadly with no strong evidence in favour of the null). It is possible that this is due in part to the relative limitations in self-knowledge of cognitive capacities outside of spatial domains (see also Arzy & Schacter, 2019). Further research will be important to examine whether these results are consistent in a task-based study.

2.5 Supplementary results

2.5.1 Partial correlation between future thinking subscale and ILF MD controlling for the spatial memory subscale

A significant negative association was found between the future thinking subscale and ILF MD when controlling for the influence of the spatial subscale (one-tailed Kendall’s partial tau = -0.213, $p = 0.015$; the partial correlation was completed in RStudio (2020) using the R package ppcor (Kim, 2015)).

Chapter 3: The role of the pre-commissural fornix in episodic autobiographical memory and future thinking

3.1 Introduction

As discussed in chapter 1, a key adaptive feature of human cognition is the ability to re-experience our personal histories and imagine the future in vivid detail — mental time travel (Suddendorf & Corballis, 2007; Tulving, 2005; Wheeler, Stuss, & Tulving, 1997). Various models have been proposed that seek explain the cognitive processes and neural mechanisms that support this capacity (reviewed in D'Argembeau, 2020). One such model is the constructive episodic simulation hypothesis, inspired by Tulving's notion of memory as mental time travel (see chapter 1), which holds that both memory and simulation are supported by the same processes and neural machinery (Addis, 2018; Schacter, et al., 2012). Neuroimaging research has demonstrated that such neural overlap exists between past and future thinking in a distributed set of brain regions, including the hippocampus and ventromedial prefrontal cortex (vmPFC) (Addis, Wong, & Schacter, 2007; Benoit & Schacter, 2015). This has been further supported by research that has demonstrated deficits to both episodic memory and future thinking following damage to the hippocampus and vmPFC (Kwan, Carson, Addis, & Rosenbaum, 2010; McCormick, Ciaramelli, De Luca, & Maguire, 2018; Race, Keane, & Verfaellie, 2011; but see Dede, Wixted, Hopkins, & Squire, 2016). This body of evidence has led to the suggestion that the hippocampus and vmPFC are key elements of a default (Andrews-Hanna, Reidler, Sepulcre, Poulin, & Buckner, 2010; Raichle, 2015) or 'core' network, that interact to support autobiographical memory and simulation (Schacter, et al., 2012; Schacter, Benoit, & Szpunar, 2017).

This distributed neural network approach (Mesulam, 1995; Sheldon, Fenerci, & Gurguryan, 2019; Tulving & Markowitsch, 1997) has been supported by converging streams of evidence in how recollections and simulations are constructed (Bellana, Liu, Diamond, Grady, & Moscovitch, 2017; Schacter, et al., 2012; Schacter, et al., 2017). Studies using functional magnetic resonance imaging (fMRI) have found increased functional connectivity between the hippocampus and vmPFC during both the retrieval of autobiographical memories (McCormick, St-Laurent, Ty, Valiante, & McAndrews, 2015) and the construction of episodic future events (Campbell, Madore, Benoit, Thakral, & Schacter, 2018). Further, resting-state functional connectivity between these regions has been shown to predict the episodic quality of individual's memories (Yang, Bossmann, Schiffhauer, Jordan, & Immordino-Yang, 2013).

The communication of information across networked areas depends on the organization and formation of the white matter connections between them (Jbabdi & Behrens, 2013; see chapter 1). Direct efferent anatomical connections from the hippocampus to the vmPFC have been revealed using invasive tract tracing techniques. In rats, the entire longitudinal extent of the subiculum/CA1 is connected with the vmPFC via the pre-commissural subdivision of the fornix. It is further noted that connectivity is strengthened progressively from dorsal to ventral hippocampus (Cenquizca & Swanson, 2007; Jay & Witter, 1991). These findings are echoed in primates, where the pre-commissural fornix provides an exclusive pathway from the subiculum (and CA1) divisions of the hippocampus to medial and, to a lesser extent, orbital prefrontal cortex (Aggleton, Wright, Rosene, & Saunders, 2015; Barbas & Blatt, 1995; Carmichael & Price, 1995). More projections are found in the anterior (equivalent to ventral in rats) than posterior (equivalent to dorsal in rats) hippocampus (Aggleton et al., 2015). In humans, white matter tracts and their microstructure can be studied non-invasively *in vivo* using diffusion-weighted magnetic resonance imaging (dMRI) (Jbabdi & Behrens, 2013, see chapter 1). This technique has been used to demonstrate hippocampus-PFC connections via the fornix (Croxson et al., 2005). Recent anatomically guided protocols have allowed for more refined segmentation of white matter tracts including the fornix, and work by Christiansen et al. (2016) demonstrated a selective reconstruction of pre-commissural versus post-commissural fornix fibres (see chapter 1). This allows for the direct structural connectivity of human hippocampus-PFC to be investigated in association with potential functional capacities underpinned by such connectivity.

By application of this novel anatomically informed tractography protocol, the role of the pre-commissural fornix in autobiographical past and future thinking was investigated using an individual differences design focusing not on self-report mnemonic traits (as in chapter 2) but rather on the recollection and simulation of specific and personal past and future events (Palombo, Sheldon, & Levine, 2018). Some of the data from the experiment described below have been reported in a prior publication (Hodgetts et al., 2017a), which examined the relationship between microstructure of the fornix as one unified bundle and episodic versus semantic autobiographical memory. Participants were asked to recall past experiences and generate future events using word-cues according to a modified Galton-Crovitz cue-word paradigm (Crovitz & Schiffman, 1974), which was then scored for episodic and semantic content using Levine and colleague’s (2002) AI scoring protocol (see chapter 1). White matter microstructure was assessed in these individuals using high angular resolution diffusion-weighted imaging (HARDI) and constrained spherical deconvolution tractography, which permits tracking through regions of crossing fibres (Dell'Acqua & Tournier, 2019).

Given the directed hippocampus-PFC functional connections identified above in relation to (re)constructing events in episodic memory and future thinking (Campbell, et al., 2018; McCormick, et al., 2015), it was hypothesized that individual differences in the number of internal details produced in both autobiographical memory and future thinking narratives would associate with pre-commissural fornix indices (positively with FA, and negatively with MD). The post-commissural fornix, which connects hippocampus to mammillary bodies and anterior thalamic nuclei (Aggleton, 2012; Christiansen, et al., 2016; Mathiasen, Louch, Nelson, Dillingham, & Aggleton, 2019), was used as a comparison tract for which no specific predictions were made.

3.2 Methods

3.2.1 Participants

Twenty-seven healthy undergraduates studying at Cardiff University (2 male; aged 18—22 years; mean = 19; SD = 1) were scanned at the Cardiff University Brain Research Imaging Centre (CUBRIC) and completed a Galton-Crovitz cue word paradigm (Crovitz & Schiffman, 1974). Informed consent was provided by each participant and the research was completed in accordance with the Cardiff University School of Psychology Research Ethics Committee guidelines.

All participants were included in the main analyses. One participant provided a number of autobiographical details that was 3 SD beyond the mean for the sample, however, they were not excluded as this was not considered to be due to experimental error. No outliers were detected in the tractography values produced in these analyses. This is reported here in line with modern advice for good statistical practice (Valentine et al., 2018).

3.2.2 AI Procedure

The AI method used in this thesis is an extension of the work done by Hodgetts et al. (2017a) — i.e. instead of focusing on autobiographical recall, this analysis examined autobiographical constructions in both the past and the future. Participants were given 1 minute to describe a specific and detailed episode for each of 10 cue-words. Cues were taken from three wordlists that were matched per semantic category (i.e. participants were instructed to describe an episode derived from either ‘holiday’, ‘vacation’ or ‘journey’ — for full word lists see appendix 1). If the episode lacked specificity or detail, the experimenter would prompt the participant in a non-specific manner in line with the original AI protocol (Levine et al., 2002).

The participants performed the experiment in three stages, presented in randomised order (autobiographical memory, autobiographical future thinking, and semantic definition). In each of the mental time travel tasks (i.e. autobiographical recall/future thinking), participants were not restricted to the time period in which their episode would be drawn from (i.e. their past/future narratives could relate to scenarios at any temporal distance from the present). A portable recording device (Zoom H1 Digital Field Recorder) was used to record each testing session for subsequent transcription and coding.

3.2.3 AI Scoring

The standardized AI scoring procedure (Levine et al., 2002) modified to examine future thinking (e.g. Race, Keane, & Verfaellie, 2011) was used. Participants' past and future narratives were segmented into distinct chunks of information in order to allow analysis of episodic and non-episodic detail within each. These chunks were typically characterized by grammatical clauses that referenced a unique occurrence, observation or thought (Levine, et al., 2002).

Two broad categories were used to categorize details: 'internal' details (which described the main event) and 'external' details (decontextualized information, including semantic details and information concerning extended events that are not specific in time and place, and repetitions). As the main event was required to refer to a specific time and place, and thus can be considered 'episodic' (Tulving, 2002a), it will be referred to as such from now on. As in prior work (see Levine, et al., 2002; Palombo et al., 2018a), if a participant described more than one event that was specific in time and place, the event that was described in the most detail was designated the main event and thus coded for 'episodic' details (the less detailed event was then coded as 'external' — see Levine, et al., 2002; Palombo et al., 2018a).

Along with spatiotemporal information, episodic details included specific information that directly described the identified main event (i.e. sensory details, occurrences, thoughts, and emotions, etc — Levine et al., 2002). In line with prior research (e.g. Hodgetts et al., 2017a; Levine et al., 2002), the broad categories of 'episodic' and 'external' details were also subdivided into several subcomponents. These subcomponents are fully listed and described with illustrative examples in table 3.1. However, in line with the recent recommendations of Renoult et al. (2020) this chapter used the combined 'internal' and 'external' scores for its analysis, in order to increase statistical power given the measurement error inherent to the extraction of these subcategories of event details from autobiographical narratives in healthy volunteers.

Table 3.1. Examples of internal (episodic) and external and details from past and future autobiographical narratives. The main event was required to refer to a specific time and place, and the specific event that was described in the most detail was coded as ‘internal’ and the other as ‘external’.

		Description	**Example**
Internal	*Event*	Activities, occurrences, actions, people present, reactions in others	*“so we'll probably have a celebration”*
	Time	Times, dates, days, seasons, years, indications of temporal order of events, frequencies, durations	*“On Friday”* *“before the end of term”* *“we'll probably spend about 2 hours there”*
	Place	Details pertaining to location including country, city/town, area, building, room, area within room, relative positioning to other people/objects	*“somewhere within Cardiff”* *“It won't be that far away”*
	Perceptual	Information perceived from sensory processes. Derived from but not limited to information regarding surroundings, individuals present, other's emotions, distances, weather, temperature.	*“in the sun”*
	Emotion/thought	Feelings and cognitive processes that occurred within the episode	*“when I get bored”*
External	*Semantic*	General and self-related knowledge, facts, opinions	*“That's one of my favourite films”*

Categorical	Any details (event, time, place, perceptual, emotion/thought) regarding repeated episodes of the same activity	*"go into the local cafes"*
Extended	Any details (event, time, place, perceptual, emotion/thought) regarding an episode that lasts for longer than 1 day or 24 h	*"I've got a plan… to go backpacking for 6 months"*
Repetitions	Details that have been mentioned previously within the episode	*n/a*
Tangential	Details not related to the main episode or have a weak connection	*n/a*
Other	Details not covered by other categories, including (but not limited to) retrospective comments about the episode or metacognitive statements	*"Does that count?"*

3.2.4 MRI data acquisition

All imaging data were acquired using a General Electric Healthcare (GE) 3-T HDx MRI system with an 8-channel receive-only head coil, at Cardiff University's Brain Research Imaging Centre (CUBRIC). High-resolution anatomical images were provided using a standard T1-weighted 3D FSPGR sequence (178 axial slices, 1mm isotropic resolution, TR/TE = 7.8/3.0s, FOV = 256 x 256 x 176mm, 256 x 256 x 176 data matrix, 20° flip angle).

High Angular Resolution Diffusion Image (HARDI) data (60 contiguous slices acquired along an oblique-axial plane with 2.4mm thickness and no gap, TE = 87ms; voxel dimensions = 2.4 x 2.4 x 2.4mm^3 412; FOV = 23 x 23 cm^2; 96 x 96 acquisition matrix) was acquired using a diffusion weighted single-shot spin-echo Echo-Planar Imaging (EPI) pulse sequence. The acquisition was cardiac gated, with 30 isotropic directions at b = 1200 s/mm^2. In addition, three non-diffusion weighted images were acquired with b = 0 s/mm^2.

3.2.5 MRI pre-processing

3.2.5.1 Diffusion MRI

Diffusion MRI (dMRI) data were pre-processed using ExploreDTIv4.8.3 (Leemans & Jones, 2009). Corrections were made to distortions arising from participant head motion and eddy currents. As previously noted, free water contamination from cerebrospinal fluid can affect delineation when reconstructing white matter pathways in proximity to the ventricles (e.g. the fornix; Concha et al., 2005). The two-compartment 'Free Water Elimination' (FWE) procedure (Pasternak et al., 2009) was applied to correct for voxel-wise partial volume artifacts arising from free water contamination. This allows for improved tract reconstruction and tissue specificity in Diffusion Tensor Imaging (DTI) (Pasternak et al., 2014; Albi et al., 2017). Following FWE, corrected diffusion tensor indices for FA and MD were calculated. The resulting free water corrected FA and MD maps were the inputs for the tractography analyses.

3.2.5.2 Tractography

Deterministic tractography was performed based on constrained spherical deconvolution (CSD) (Dell'Acqua & Tournier, 2019; Jeurissen, Leemans, Jones, Tournier, & Sijbers, 2011). CSD allows for bending/crossing/kissing fibres to be represented within individual voxels, as multiple peaks in the fibre orientation density function (fODF) can be extracted (Dell'Acqua & Tournier, 2019). The step size was 1mm, and the fODF amplitude threshold was 0.1. An angle threshold of 30° was used to prevent the reconstruction of anatomically implausible fibres.

Waypoint region-of-interest (ROI) gates were drawn manually onto whole-brain free water corrected FA and MD maps to generate 3D fibre reconstructions of each tract-segment. The waypoint ROIs defined the tracts based on a 'SEED' point and Boolean ('NOT' and 'AND') logical operations. Tracts were either retained ('AND') or excluded ('NOT') from the analyses dependant on which gates they passed through. These gates were then combined to reconstruct the tracts, as informed by anatomical plausibility (Schilling et al., 2020). Following the reconstruction of each pathway in each participant, mean FA and MD were calculated by averaging individual values at each 1mm step along the tracts.

3.2.5.3 Pre- and post-commissural fornix reconstruction

The reconstruction of the whole fornix was performed as described in chapter 2 (see figure 3.1). Following this the fornix was split, isolating the anterior body, by an ‘AND’ gate positioned at the point of the downward bend to the crus and fimbria of the fornix. In line with the protocol described in Christiansen, et al. (2016), fibres of the crus and fimbria of the fornix were excluded from the anterior-body and hence pre- and post- commissural fornix reconstructions. Partial volume effects due to the intermingling of the two fibre populations beyond the crus were, therefore, minimized (Saunders & Aggleton, 2007). In addition, this procedure avoided ‘jumping’ where tract voxels that pass close to, or across, neighbouring tract voxels ‘jump’ onto them (Jones & Cercignani, 2010). This split was conducted using the tract segmentation tool “splitter” within ExploreDTIv4.8.3.

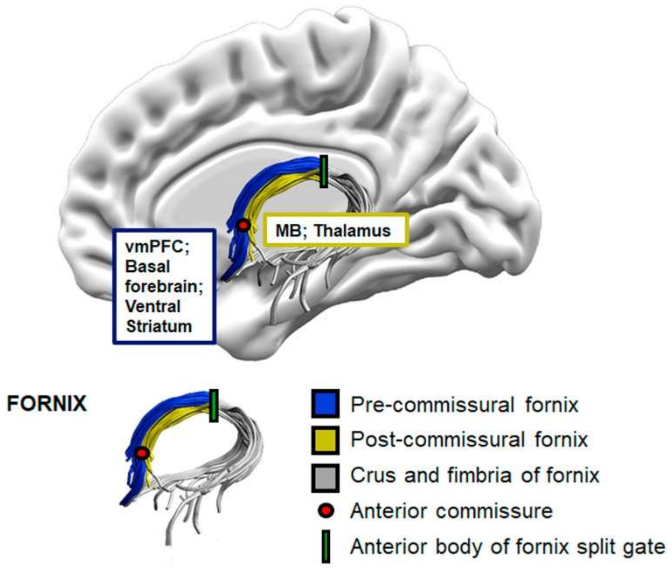


Figure 3.1. Schematic illustration of the anatomical landmarks for fornix tract subdivision and the connecting areas of interest (reproduced with permission from Williams et al., 2020; vmPFC = Ventromedial Prefrontal Cortex; MB = Mammillary Bodies).

The anterior body of the fornix was then divided into the pre- and post-commissural segments. This delineation took advantage of the manner in which the fibres separate at the anterior columns of the fornix. At this level, the segments contain approximately the same number of fibres (Powell, Guillery, & Cowan, 1957). The pre-commissural fornix was delineated by positioning an additional ‘AND’ gate on the coronal plane at the anterior commissure, as well as an additional ‘NOT’ gate meeting this ‘AND’ gate on the axial plane. For the post-commissural fornix reconstruction, the additional ‘NOT’ and ‘AND’ gates placed for reconstruction of the pre-commissural fornix were swapped (see Figure 3.2). Thus, for the pre-commissural fornix, tracts were included only if they extended anterior to the anterior commissure, and for the post-commissural fornix only tracts running posterior to the anterior commissure were retained (see Figure 3.3) (Christiansen, et al., 2016; Williams et al., 2020).

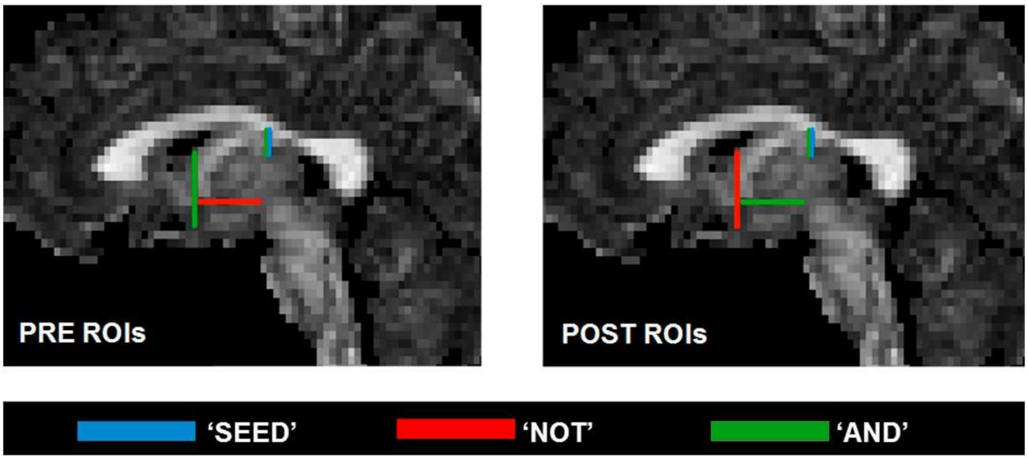


Figure 3.2. Waypoint region-of-interest (ROI) gates used for reconstructing the pre- and post-commissural fornix tract segments (Blue = SEED, Red = NOT, Green = AND) (reproduced from Williams et al., 2020).

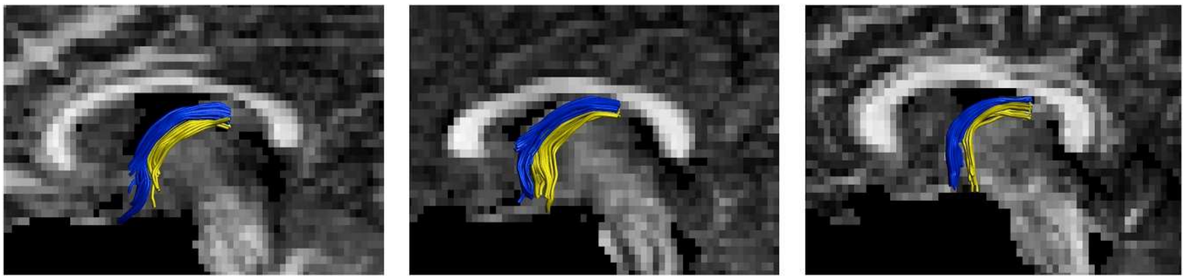


Figure 3.3. Example reconstructions for the pre- and post- commissural fornix segments (Blue = Pre, Yellow = Post) (reproduced from Williams et al., 2020).

3.2.5.4 Grey matter volumetrics

T1-weighted images were corrected for spatial intensity variations using FMRIB's Automated Segmentation Tool (FAST; Zhang, Brady, & Smith, 2001). Bilateral grey matter volumes (expressed as a proportion of estimated total intracranial volume) of the hippocampus were subsequently obtained using FMRIB's Integrated Registration & Segmentation Tool (FIRST; Patenaude, Smith, Kennedy, & Jenkinson, 2011). Volumes for the vmPFC ROI were derived using FreeSurfer (surfer.nmr.mgh.harvard.edu: Destrieux, Fischl, Dale, & Halgren, 2010), via summing volumes of the medial orbitofrontal cortex and rostral anterior cingulate cortex parcels.

3.2.6 Statistical Analyses

For each cued narrative, the numbers of episodic and external details were tallied, and the totals were then summed across the 10 narratives in each condition (past, future) to create total episodic and external AI scores for each condition for each participant to be used in analyses. The alpha level was set at $\alpha = 0.05$, as the primary tract of interest was the pre-commissural fornix. In addition, the post-commissural fornix was reported as a comparison tract.

Due to presence of outliers in the details generated in the AI non-parametric Kendall's tau correlations were conducted instead of Pearson correlations (which are "overly sensitive" to these, see Pernet, Wilcox, & Rousselet (2012)). Further, where appropriate the presence of outliers necessitated the use of Wilcoxon's signed rank test (Wilcoxon, 1945). Primary comparisons were made between the number episodic details produced and pre- and post-commissural fornix FA and MD values. These analyses were performed in JASP (2018, version 0.8.12). After transformation to a Pearson's r value (Walker, 2003), significant associations were tested using Steiger's Z-test (Steiger, 1980) using the cocor webtool (Diedenhofen & Musch, 2015). Partial correlations for key comparisons were completed in RStudio (2020) using the R package ppcor (Kim, 2015), and imputation was completed where appropriate using the R package 'mice' (van Buuren & Groothuis-Oudshoorn, 2011).

Consensus scoring was established based on the high inter-rater reliability (Cicchetti, 1994) from two raters who scored both the past and future events (intra-class correlation analysis, two-way random model: past (internal) r = 0.99; past (external) r = 1.0; future (internal) r = 0.78; future (external) r = 1.0). The values used are generated from a primary coder for autobiographical recall and future thinking narratives. The past condition uses the values generated in the original Hodgetts et al. (2017a) analysis (extending this analysis with a novel tractography approach). I was the primary coder for the future thinking narratives.

3.3 Results

3.3.1 Number of details produced (episodic and external) for the past and future narratives

Consistent with several previous studies (e.g. Addis, Sacchetti, Ally, Budson, & Schacter, 2009; Addis, et al., 2008; Race, et al., 2011; Wang et al., 2014), the total number of episodic details (summed across the 10 cue words) an individual recalled for the past (mean = 121.3, median = 114, SD = 40.8, range = 64–247) correlated strongly with the number of episodic details imagined for the future (mean = 59.3, median = 54, SD = 23.4, range = 27–105) (Figure 3.4A One-tailed Kendall's tau = 0.447, $p < 0.001$, VS-MPR = 82.26, $BF_{0+} = 81.7$).

Additionally, in line with those previous studies, there were significantly more episodic details given for the past in comparison to the future (Wilcoxon Signed Rank T(26) = 378.0, $p < 0.001$, VS-MPR = 9748, BF_{+0} = 4.084e+8).

The number of external details an individual recalled for the past (mean = 73.8, median = 71, SD = 39.0, range = 20–182) also correlated significantly with the number of external details imagined for the future (mean = 86.5, median = 75, SD = 40.8, range = 23–198) (Figure 3.4B. One-tailed Kendall's tau = 0.532, $p < 0.001$, VS-MPR = 714.5, BF_{0+} = 687.5). Again, in line with prior research (Irish & Piguet, 2013), significantly more external details were produced in the future than in the past narratives (Wilcoxon Signed Rank T(26) = 273.0, p = 0.022, VS-MPR = 4.323, BF_{+0} = 3.243).

The number of episodic details an individual recalled for the past did not correlate with the number of external details recalled for the past (one-tailed Kendall's tau = 0.146, $p < 0.144$, VS-MPR = 1.32, BF_{0+} = 0.730); nor, notably, did episodic future details correlate with external future details (one-tailed Kendall's tau = -0.058, p = 0.662, VS-MPR = 1.000, BF_{0+} = 0.183).

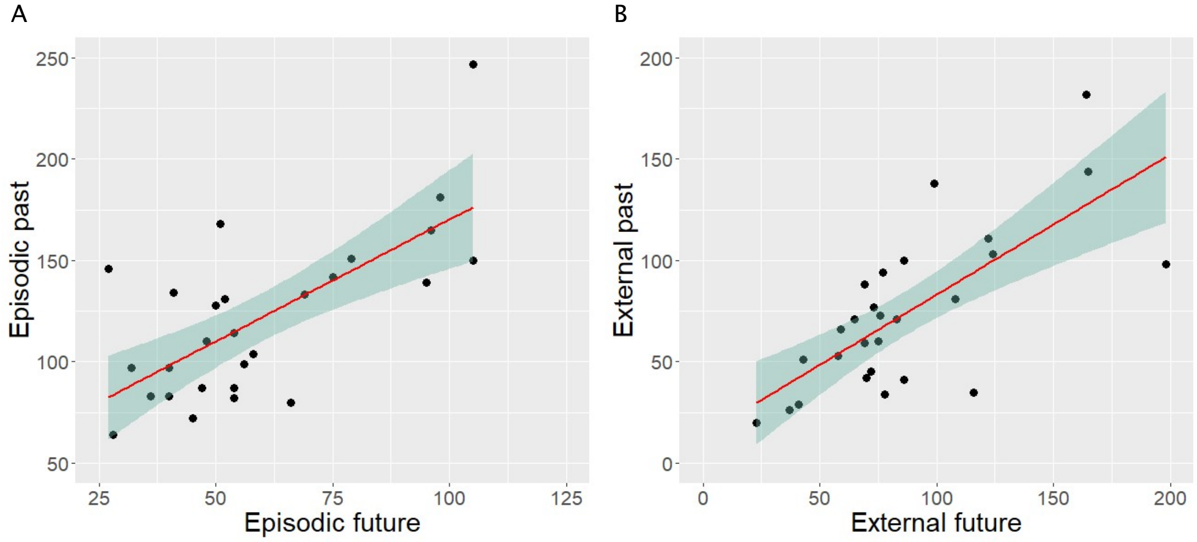


Figure 3.4 (A, B). Scatterplots depicting correlations between the number of details produced for the past versus the future AI narratives (A. Episodic, B. External) (N=27). Shading equals the 95% CI.

3.3.2 Correlations between pre- and post-commissural fornix microstructure indices

No significant correlation was found between pre-commissural fornix FA and post commissural fornix FA values (two-tailed Kendall's tau = 0.071, p = 0.620, VS-MPR = 1.000, BF_{10} = 0.282). However, a significant correlation was found for pre-commissural and post-commissural fornix MD (two-tailed Kendall's tau = 0.337. p = 0.014, VS-MPR = 6.198, BF_{10}

= 4.524). This is consistent with other work showing that white matter tracts tend to have consistent 'along-tract signature values' for MD but not FA (i.e. FA but not MD values vary along segments of specific tracts — Johnson et al., 2014; Yeatman, Wandell, & Mezer, 2014; see discussion). Due to the high correlation between MD values for the two fornix segments, the main analysis will focus on FA values (as these can be considered to have been adequately separated in the tractography).

3.3.3 Episodic past details and pre-/post-commissural fornix FA

A significant positive correlation was found between the number of past episodic details and pre-commissural fornix FA (Figure 3.5A. One-tailed Kendall's tau = 0.332, *p* = 0.008, VS-MPR = 9.753, BF_{0+} = 8.267). There was no significant correlation between post-commissural fornix FA and episodic past details (Figure 3.5B. One-tailed Kendall's tau = -0.011, *p* = 0.533, VS-MPR = 1.000, BF_{0+} = 0.232). The correlation between episodic past details and pre-commissural fornix FA was significantly greater than between episodic past details and post-commissural fornix FA (one-tailed Steiger z = 2.040, *p* = 0.021) (computed using 'cocor' webtool, Diedenhofen & Musch, 2015).

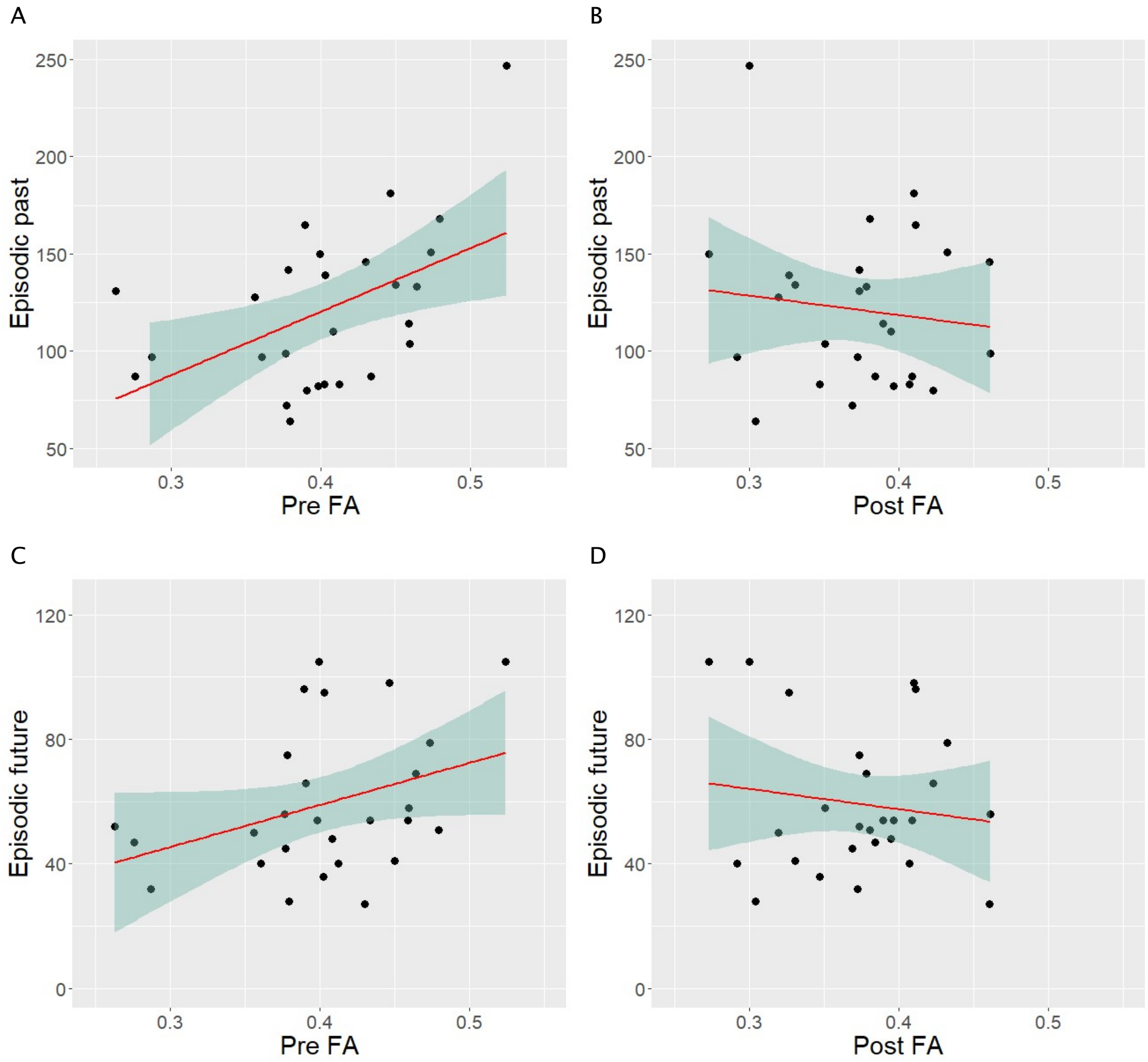


Figure 3.5 (A-D). Scatterplots depicting the correlations of episodic past (A, B) and future (C, D) AI details with pre-/post- commissural fornix microstructure (fractional anisotropy, FA). Number of episodic past/future details (summed over 10 cue words) is plotted on the y-axis (N=27). Shading equals the 95% CI.

3.3.4 Episodic future details and pre-/post-commissural fornix FA

The findings for the episodic future details showed a similar, albeit weaker pattern to those produced in the autobiographical recall task. A significant positive correlation was found between the total number of future episodic details produced and pre-commissural fornix FA values (Figure 3.5C. One-tailed Kendall's tau = 0.230, $p = 0.047$, VS-MPR = 2.543, BF_{0+} = 1.818). Further, no significant association was found between future episodic details and post-commissural fornix FA (Figure 3.5D. One-tailed Kendall's tau = 0.086, $p = 0.266$, VS-MPR = 1.045, BF_{0+} = 0.438). A one-tailed Steiger's Z test, however, showed no significant difference between the correlations of episodic future details and pre- and post-commissural fornix FA values (Steiger's Z = 0.846, *p* = 0.199).

Finally, a two-tailed Steiger's Z-test (Z = 0.954, *p* = 0.340) showed no significant difference between the correlations of pre-commissural fornix FA with the production of episodic past vs. episodic future details.

3.3.5 Influence of external details

It was found that in the autobiographical recall task, episodic details still showed a significant positive association with pre-commissural fornix FA when controlling for number of recalled external details (one-tailed Kendall's partial tau = 0.336, *p* = 0.008). However, it was found that in the future task that episodic details just failed to correlate with pre-commissural fornix FA when controlling for external details at the pre-specified alpha of 0.05 (one-tailed Kendall's partial tau = 0.229, *p* = 0.051).

3.3.6 Influence of grey matter volume

In order to run ppcor (Kim, 2015) the dataset can have no missing values. In the present dataset, one participant was removed from the dataset due to poor structural MR data quality. It was considered inappropriate to use listwise deletion as this would involve losing data that had been used in the original comparisons. Hence, the R package 'mice' (van Buuren & Groothuis-Oudshoorn, 2011) was used to allow for multiple imputation to generate a number for the missing hippocampal volume.

It was established that episodic details correlated with pre-commissural fornix FA values when controlling for hippocampal volume in both autobiographical recall (one-tailed Kendall's partial tau = 0.332, *p* = 0.009) and episodic future thinking tasks (one-tailed Kendall's partial tau = 0.257, *p* = 0.033). Further, the associations were maintained for both past (one-tailed Kendall's partial tau = 0. 340, *p* = 0.007) and future (one-tailed Kendall's tau = 0.236, *p* = 0.046) conditions when controlling for vmPFC volume.

3.3.7 Influence of verbal fluency

It has been suggested that non-episodic processes (including overall verbal fluency and narrative style) might play an influence on the similarities between remembering the past and imagining the future (Addis & Schachter, 2012; Schacter & Madore, 2016). Participants completed a measure of semantic verbal fluency ('category fluency'), as derived from the Delis-Kaplan Executive Function battery; (Ardila, Ostrosky-Solis, & Bernal, 2006; Delis, Kaplan, & Kramer, 2001) that required them to name as many unique animals as they could in one minute (mean = 13.41, SD = 2.17). It was found that a positive association was maintained between episodic details and pre-commissural fornix FA values when controlling for verbal fluency in both the past (one-tailed Kendall's tau = 0.351, $p = 0.006$) and future conditions (one-tailed Kendall's tau = 0.230, $p = 0.049$).

3.4 Discussion

A pattern of shared deficits in both the capacity to recollect prior personal experiences and simulate plausible future scenarios, known collectively as mental time travel, was first demonstrated in patient K.C. (Tulving 1985). Subsequent research in both this patient (Gao et al., 2020) and other populations (McCormick et al., 2018; Schacter et al., 2017) have identified two regions, the hippocampus and vmPFC, as supporting this ability. Evidence has emerged noting that the two areas are directly connected via the pre-commissural fornix (Aggleton et al., 2015), however, it is as yet unclear whether and to what extent this structural connectivity might mediate the episodic components of mental time travel.

The present project addressed this issue by applying a novel anatomically guided tractography protocol that allows for the separate in vivo reconstruction of pre- and post-commissural fornix fibres (Christiansen et al., 2016). A modified version of the Galton-Crovitz test (Crovitz & Shiffman, 1974; Hodgetts et al., 2017a) was used in order to produce cued narratives for matched past and future scenarios. These interviews were analysed using a validated coding scheme (Levine et al., 2002; Hodgetts et al., 2017a) to parse episodic and non-episodic details from each participant's transcribed interview. It was found that inter-individual variation in pre-commissural, but not post-commissural, fornix FA values were found to positively correlate with the amount of 'internal' episodic details produced in both past and future event constructions (Bayes factor analysis indicated moderate-to-strong support for the past association (BF ~ 8), though only anecdotal support for the association in the future (BF ~ 2)). Further, moderate evidence was found in the autobiographical memory task to support no positive association between the number of internal details and post-commissural fornix FA (BF <0.33). The 'internal' detail composite reflects components definitive of episodic memory as described by Tulving, considered to reflect the "what, where, and when" of episodic memory as well as the autonoetic component of re-experiencing (Tulving, 2002a), including recovery of perceptual, spatial, temporal, and emotional events (Renoult et al., 2020).

The current study therefore represents a novel finding that individual differences in the episodic content of both past and future thinking can be associated with the same underlying tract microstructure. Further, it provides structural evidence to support findings of the importance of individual differences in functional connectivity between the hippocampus and vmPFC (rather than the volumes of particular regions including the hippocampus) in mediating individual differences in episodic memory processes (Clark et al., 2020; Weisberg & Ekstrom, 2020).

The present results failed to demonstrate a statistical difference between the correlations of pre-commissural fornix and the number of details provided in participants' past and future task constructions, suggesting an equivalent role for hippocampal-prefrontal connectivity in past and future episodic thinking. However, the VS-MPR (also known as the Bayes Factor Bound, the maximum possible odds in favour of H1 over H0 based on the data — Benjamin & Berger, 2019) was somewhat stronger for the correlation of past than future episodic details. It is likely that this represents the finding in other studies that participants are able to provide more specific details for past than future events (e.g. Addis et al., 2009; Addis et al., 2008; Bertossi, Tesini, Cappelli, & Ciaramelli, 2016; Race et al., 2011; Wang et al., 2014;). In line with other research, it seems plausible that autobiographical future thinking required greater assistance from a semantic framework and the integration of more semantic details (D'Argembeau & Mathy, 2011; Irish & Piguet, 2013). The contribution of semantic details within past and future autobiographical constructions is discussed more fully in chapter 5.

It was further established that the link between pre-commissural fornix FA and the episodic content of past constructions is maintained when controlling for 'external' details. The external detail composite was originally intended to test the hypothesis that non-episodic processes (particularly semantic memory) were unaffected in conditions affecting episodic memory, and to assess overall verbosity as a potential confound in the interpretation of group or individual differences in internal detail production (Renoult et al., 2020). In healthy participants, external details are indeed primarily 'semantic' in nature, but they also include tangential or unrelated meta-cognitive commentary (Levine et al., 2002; Renoult et al., 2020). The current findings can then be taken to provide some support for Tulving's (e.g. 1983; 2002a) claims that episodic and semantic memory are distinct (albeit highly interactive) neurocognitive systems (see Renoult & Rugg, 2020 for discussion). Although this pattern was not maintained for episodic future details, a non-significant trend was still indicated by the partial correlation. As such these findings support earlier findings that non-episodic content for both past and future narratives is unaffected in patients with lesions to the hippocampus (Race et al., 2011) and vmPFC (Bertossi et al., 2016b). Further, these results may lend further support to the idea of a semantic framework that supports rather than controls the production of episodic details in future narratives (Irish & Piguet, 2013).

Taken together, these findings highlight the importance of hippocampus-vmPFC structural connectivity mediated by the pre-commissural fornix (Aggleton, et al., 2015; Cenquizca & Swanson, 2007), in episodic construction across past and future autobiographical events. Further, it builds upon fMRI studies that demonstrated functional connectivity between these regions is heightened during both the retrieval of autobiographical memories (McCormick et al., 2015) and the construction of future events (Campbell et al., 2018). It was noted in the Campbell et al. (2018) study, using dynamic causal modelling, that anterior hippocampus to vmPFC effective connectivity increased specifically during the initial construction of episodic future events. It is possible to conclude that event construction initiates in the hippocampus, and that vmPFC is engaged when additional episodic details become integrated. This conclusion is supported by wider studies into both humans and rodents that have shown hippocampal activity to precede medial PFC activity during memory retrieval (McCormick et al., 2015; Place, Farovik, Brockmann, & Eichenbaum, 2016). Optogenetic studies in mice (e.g. Ciocchi, Passecker, Malagon-Vina, Mikus, & Klausberger, 2015; Cohen & Meyer, 2020) have also shown that during memory retrieval ventral hippocampal signals carrying contextual information are sent directly to medial PFC, facilitating coordinated activity between these areas.

As previously noted (see chapter 1), there exists extensive debate as to the nature of the contributions of both the hippocampus and vmPFC to the episodic aspects of mental time travel (McCormick, et al., 2018; Robin & Moscovitch, 2017; Schacter, et al., 2017). Cognitive map theory posits that the hippocampus builds a unified (allocentric) representation of the spatial environment in order to navigate, and that this process is also used to support memory and guide future action in other cognitive domains (Ekstrom & Ranganath, 2018; Epstein et al., 2017). Scene construction theory holds that the anterior hippocampus and subiculum play a key role in forming (primarily egocentric) representations of spatially coherent scenes in memory, perception, and imagination (Gaffan & Gaffan, 1991; Hodgetts et al., 2017b; Zeidman & Maguire, 2016). These scenes are then proposed to provide a framework around which past and future episodes are constructed (Barry & Maguire, 2019; Murray, et al., 2017; Robin, 2018). Contrary to this, episodic or event construction hypothesis states that the (anterior) hippocampus houses a general relational processing mechanism that is key to construction of spatiotemporal contexts (Eichenbaum & Cohen, 2014). This region is also held to be responsible for further integration of other episodic details (e.g. objects, persons, etc.) into the constructed representation (Addis, 2018; Addis & Schacter, 2012; Schacter, et al., 2012; but see chapter 2).

The vmPFC's contribution to the construction of episodic content is instead linked with schematic representations, and particularly the self-schema (Buckner & Carroll, 2007;

D'Argembeau, 2013; Gilboa & Marlatte, 2017) (but see Ciaramelli et al., 2019). A study by Kurczek et al. (2015) compared the number of references to 'the self' made by patients with lesions to bilateral hippocampal regions or medial prefrontal cortex damage along with healthy controls. Patients with damage to the medial prefrontal cortex were found to include fewer self-representations ("I") in their autobiographical narratives than did healthy controls. Conversely, patients with hippocampal damage showed deficits to the number of episodic details in their narratives but maintained normal references to self within those. Tulving (2005) has emphasised the importance of 'self' within the consideration of autobiographical memory (see chapter 1). Prior research has suggested that hippocampal-mPFC connectivity (and in particular vmPFC) might serve in the construction of complex representations in which the self is oriented to a specific time, place, and 'context' (Murray et al., 2017). It has further been proposed that the hippocampus may then (following feedback from vmPFC by way of the thalamus and entorhinal cortices) act to constrain later retrieval and construction within the context of the established representation (Campbell, et al., 2018; Graham, Barense, & Lee, 2010; Place, et al., 2016; Preston & Eichenbaum, 2013). Hence, the construction of autobiographical episodes requires a sense of 'self' ("no traveller, no travelling" Tulving, 2002a), supported by a large-scale system involving interactions between the medial temporal lobe and the prefrontal cortices, that allows individuals to place themselves within the context of recombined episodic details in the formation of a coherent personal narrative (Tulving, 2005; Wheeler, et al., 1997). The role of 'self' representation within the context of episodic construction will be further examined in chapter 4.

The present findings support the role of the pre- but not post-commissural fornix, representing the structural connectivity from the hippocampus to the vmPFC and its role in self-representation, in episodic memory and future scenario construction. However, prior work, emphasised in cognitive map theory and animal models of amnesia, has suggested that spatial and contextual memory (which are related components to the overall output of an autobiographical episode) are mediated by the direct connectivity of the hippocampus to the mammillary bodies and thalamus (Aggleton & Brown, 1999; Aggleton, Saunders, & Vann, 2008; Parker & Gaffan, 1997; Rosenbaum, et al., 2014) via the post-commissural fornix (Aggleton, et al., 2010; Christiansen, et al., 2016; Mathiasen, et al., 2019; Vann & Nelson, 2015). The lack of emphasis placed on the role of this structure in the present analysis could be due to the nature of reconstructing the post-commissural fornix. The present reconstruction targeted the connection of the hippocampus to the hypothalamus and mammillary bodies, however, it excluded projections towards the anterior thalamic nuclei as these move towards posterior regions as the columns of the fornices descend (Aggleton, et al., 2010; Christiansen, et al., 2016; Poletti & Creswell, 1977). These thalamic fibres remain diffuse and do not form a discrete tract (Mathiasen, et al., 2019). Prior work has shown that hippocampal-thalamic interactions may be particularly important in spatial memory (Nelson, Kinnavane, Amin, O'Mara, & Aggleton, 2020), and thalamic damage is associated with deficits to episodic past and future thinking in humans (Irish, Hodges, & Piguet, 2013; Rosenbaum, et al., 2014). However, in addition to connections mediated by the post-commissural fornix, there exist a number of non-fornical connections between the hippocampus and anterior thalamic nuclei that serve episodic memory (Aggleton, et al., 2010; Bubb, Kinnavane, & Aggleton, 2017), which are not currently visible to dMRI based tractography.

In line with the present findings, Vann and colleagues have reported several studies that apply selective lesions to the descending post-commissural fornix columns in rats disconnecting subicular projections to the mammillary bodies (Vann, 2013; Vann, Erichsen, O'Mara, & Aggleton, 2011; Vann & Nelson, 2015). They found minimal impact to spatial memory tasks sensitive to mammillary body, mammillothalamic tract, anterior thalamic, and hippocampal lesions. Albeit derived from a single dissociation, these findings might suggest that hippocampal-mammillary connectivity, via the post-commissural fornix, is less important than hippocampal-vmPFC connectivity, via the pre-commissural fornix, when considering episodic memory and future thinking tasks that rely on constructive and self-referential processing — i.e. mental time travel. It is important to emphasize, however, that the current study did not find a strong dissociation between pre- and post-commissural fornix contributions to episodic past and future thinking, and other studies suggest a role for post-commissural fornix microstructure in episodic memory (Coad et al. 2020).

The present study is not without limitations, which should be used when considering its results and the design of future work. Due to the inter-correlation of the pre- and post-commissural fornix MD values, the present analysis has focussed largely on the pattern of associations presented by FA indices. Despite this, it should be noted that predicted effects such as an association between pre-commissural fornix and episodic details in autobiographical recall were established (for a full write up of the results of the MD indices see the supplementary results). Prior research has linked self-reported spatial memory on the SAM to the episodic richness of autobiographical memories (Palombo et al., 2013). To the extent that this project has associated both SAM-Spatial and episodic richness in autobiographical narratives with fornix microstructure, it can be considered that the results of chapters 2 and 3 align with one another. This is further supported by the association between fornix microstructure and episodic future thinking in both chapters (i.e. with SAM-Future and the episodic richness of autobiographical future thinking narratives). Although fornix associations have been identified with both self-reported and performance-based methods, the microstructure measures were not consistent between chapters (i.e. fornix MD negatively associated with SAM-Spatial/Future, and pre-commissural fornix FA associated with episodic richness in past/future autobiographical narratives). However, several unexpected results were also produced, for instance the lack of association between pre-commissural fornix MD and episodic details produced in future narratives. Further, it should also be noted that no association was found between SAM-Episodic and fornix FA/MD.

As noted in chapter 1, FA and MD are sensitive measures of fibre microstructure but both lack biological specificity. For example, FA values are influenced by myelination, axon diameter and packing density (Jones, Knösche, & Turner, 2013). Synchronous activity and effective communication between brain regions will be influenced by variation in these properties (Jbabdi & Behrens, 2013; Pajevic, Basser, & Fields, 2014). Further insight into the specific biological nature underlying associations between white matter microstructure and cognitive processing will be improved with the further development of multi-shell diffusion MRI and advanced biophysical modelling of the diffusion signal (Assaf, Johansen-Berg, & Thiebaut de Schotten, 2017).

Furthermore, diffusion properties are influenced not only by biological properties of the axons in a voxel (i.e. myelination, axonal density, and axonal diameter) but also by the geometric configuration of the axons (e.g. curvature, directional coherence and crossing fibre tracts — Johnson et al., 2014). This may be one reason why FA (diffusion directionality) in particular varies substantially along the trajectory of a tract (i.e. post-commissural vs. pre-commissural fornix) relative to overall diffusivity (as reflected in MD) (Johnson et al., 2014; see figure 3.6). Further, these differences may be reflected by different patterns of correlation between different tract microstructure measures and memory performance.

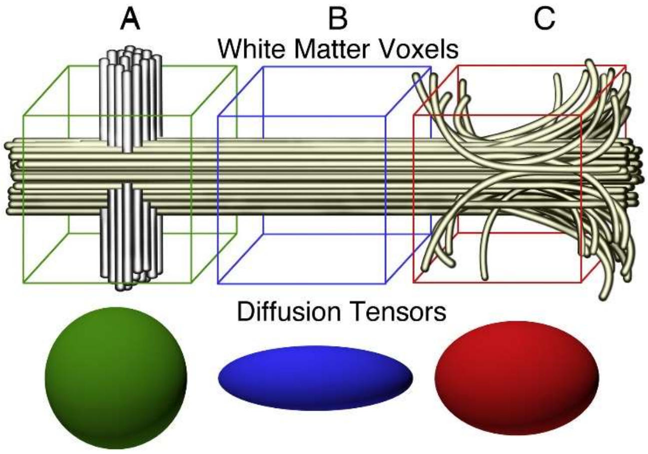


Figure 3.6 shows the effects of local environmental contributions to tract anisotropy and is reproduced from Johnson et al. (2014). Voxel A shows a target tract (yellow) crossing a separate tract (grey), which would result in low anisotropy measurements at this point. Voxel B contains only the tract of interest and would display high anisotropy. Voxel C shows axons from nearby grey matter joining the tract, as well as axons from the tract diverging to local grey matter targets. This would result in lowered anisotropy in this voxel.

The similarity between remembering past and simulating future events could be due to individual differences in non-episodic processes such as verbal fluency (Addis & Schacter, 2012) and narrative style (Gaesser, Sacchetti, Addis, & Schacter, 2011). However, it should also be noted that the findings were maintained when controlling both for 'external' details and for verbal fluency. Further, studies looking at patients with damage to the hippocampus (Race et al., 2011) and vmPFC (Bertossi, Candela, De Luca, & Ciaramelli, 2017) show that general narrative abilities do not account for deficits in episodic memory and future thinking. This work differs from the present study in that it reflects a patient population rather than individual differences in a neurotypical sample. As such, future work could examine healthy individuals in a manner that assesses non-episodic capabilities in line with this. It has been suggested that the field at large could be improved with access to nonverbal measures of both episodic memory and future thinking, and that the design of these will represent a significant advance for addressing gaps in the present state of the field (Wilkins & Clayton, 2019). It should be noted that this would allow for further investigation in non-human models, however, the extent to which non-humans are capable of mental time travel is the subject of intense debate (Corballis, 2019a, 2019b; Logan, 2014; Suddendorf & Corballis, 2007).

An assumption of the present study (and a point that was emphasized in the instructions) was that participants generated novel autobiographical future narratives. However, it is not possible to confirm that no 'recasting' of past events as future episodes occurred (Addis &

Schacter, 2012). Had this been the case, it would obviously inflate the similarity between past and future scores. This issue could be addressed in future using a ‘recombination’ paradigm, in which participants are explicitly required to use individual episodic details taken from different past events and then recombine them as a novel future episode (Addis, Pan, Vu, Laiser, & Schacter, 2009).

In conclusion, this experiment demonstrates a novel association between the white matter microstructure of the pre-commissural fornix and episodic autobiographical memory and future thinking. This demonstrates an anatomical mechanism by which hippocampal and vmPFC connectivity supports constructive episodic thinking. This novel finding extends the body of evidence suggesting that a core network supports the construction of both autobiographical recollections and hypothetical personal future events. Further, individual differences in structural connectivity reflect the richness with which individuals are able to describe these constructions and their capacity to achieve mental time travel.

3.5 Supplementary results

3.5.1 Episodic past details and pre-/post- commissural fornix MD

Significant negative correlations were found between both pre- (One-tailed Kendall's tau = -0.244, p = 0.038, VS-MPR = 2.957, B_{0-} = 2.176) and post-commissural fornix MD values (One-tailed Kendall's tau = 0.258, p = 0.030, VS-MPR = 3.478, B_{0-} = 2.625) and the number of episodic details produced in autobiographical recall narratives. There was no significant difference between the correlation for episodic past details and pre-commissural fornix MD was and that of episodic past details and post-commissural fornix MD (Steiger z = 0.111, p = 0.541).

3.5.2 Episodic future details and pre-/post- commissural fornix MD

No significant correlations were found between the number of episodic details produced in future thinking narratives and either pre-commissural (One-tailed Kendall's tau = 0.043, p = 0.623, VS-MPR = 1.000, B_{0-} = 0.197) or post-commissural fornix MD values (One-tailed Kendall's tau = 0.017, p = 0.550, VS-MPR = 1.000, B_{0-} = 0.225). A one-tailed Steiger's Z-test revealed no significant difference between the correlations of episodic future details and pre- and post-commissural fornix MD values (Steiger z = 0.201, p = 0.580).

Chapter 4: The role of the fornix in mediating the references to self and others within episodic content of autobiographical memory and future thinking

4.1 Introduction

A conscious awareness of the 'self' is emphasised as vital in Tulving's (1985, 2002a) concept for autonoesis and mental time travel ("no traveller, no travelling" — Tulving, 2002a). The fundamental requirement of self-processing within autobiographical memory has also been explicitly stated by cognitive theorists (Fivush, 2011; Rathbone, Moulin, & Conway, 2009). These theorists suggest that self-processing in this sense operates on the encoding, organisation, and retrieval of personally meaningful events. Further, the cognitive development of an autobiographical or "narrative" self (Arzy & Schacter, 2019; Fivush & Haden, 2003) is proposed as fundamental to the development of personal event memory (Prebble, Addis, & Tippett, 2013). Although several models emphasize a role of self-processing, the specific nature of this role is not always identified. It has been proposed that it might reflect the capacity to focus attention on self-mentation and the inner experience, allowing for autobiographical recall to be experienced as subjective time travel (D'Argembeau, Ortoleva, Jumentier, & Van der Linden, 2010; Lehner & D'Argembeau, 2016).

Autobiographical memory and a sense of 'self' have been found to develop contemporaneously (Howe & Courage, 1997). Fivush (2011) suggested that episodic memory (specifically recall for the "what, where and when of an experience") and autobiographical memory could be dissociable by the presence of self-processing (see also Brewer, 1986). The latter requiring autonoetic consciousness and contextual awareness of personal history. Evidence to support this theory has largely emerged from animal and developmental models (Bauer, Wenner, Dropik, & Wewerka, 2000; Clayton, Bussey, & Dickenson, 2003; Hampton, 2009; for a review see Fivush, 2011). Despite some suggestions that episodic memory is a uniquely human capacity (Suddendorf & Corballis, 2007; Tulving, 2002a), evidence has been found that animals are influenced by "what, where, when" (Clayton, Bussey, & Dickinson, 2003; Clayton & Dickinson, 1998; Malanowski, 2016). Further, developmental evidence has been found that shows infants are able to recall experiences before the development of a sense of self (Bauer, 2007; Bauer et al., 2000). Notably, this form of episodic memory emerges before the ability to order events on conventional timescales (Friedman, 2003; Pathman, Larkina, Burch, & Bauer, 2013). The capability to flexibly conceive of a personal timeline has been identified as important in mental time travel (D'Argembeau, 2020). As such, it is important to consider whether self-processing and episodic memory might be fully dissociable within autobiographical memory and other forms of mental time travel.

It is important to consider how self-related processing is similarly and differently represented in past and future oriented thinking. Autobiographical memories have been found to have more sensory details and references to specific episodes (Addis et al., 2008; Berntsen & Jacobsen, 2008; Grysman, Prabhakar, Anglin, & Hudson, 2013; see chapter 3) than do imagined future scenarios. Contrary to this, episodic future thinking has been associated with stronger feelings of personal significance than does episodic recall (Addis et al., 2008; D'Argembeau & Van der Linden, 2004). It has been proposed that this reflects closer ties between episodic future thinking and the self-schema (Berntsen & Bohn, 2010; Conway, 2005). Theoretical work has emphasised the bidirectional influence of self-related processing and autobiographical memory (Conway, 2005; Conway, Singer, & Tagini, 2004). Personal goals and motives, reflective of self-processing, have been shown to influence episodic future thinking (D'Argembeau & Mathy, 2011) and further evidence suggests that they have a greater effect on the structure of future oriented constructions than does episodic memory (Shao, Yao, Ceci, & Wang, 2010). This too has been identified as a bidirectional process, with the anticipation of significant future events playing a role in the development of a sense of self and self-identity (D'Argembeau, Lardi, & Van der Linden, 2012). It is possible that differences between past and future oriented mental time travel may reflect the differing levels of reliance on self-processing and the nuances of its application within the two tasks.

Linguistic analysis has been a common tool for measuring personality traits within psychological study (e.g. Twenge, Campbell, & Gentile, 2013; Vine, Boyd, & Pennebaker, 2020). In particular, the degree of self-processing employed by participants during autobiographical narratives has been measured through their use of self-talk and personal pronouns (Chaput et al., 2013; Lewis & Ramsay, 2004; Prebble et al., 2013). Prebble and colleagues proposed pronoun usage as a marker for autonoetic recollection (i.e. the explicit presence of the self or "I" within episodic memories) and used it to measure deficits to this in participants with autism spectrum disorder. Further this method has been used to measure self-processing in neuropsychological studies (Kurczek et al., 2015; Verfaellie, Wank, Reid, Race, & Keane, 2019). These studies demonstrated that patients with ventral medial prefrontal cortex (vmPFC) damage (but not patients with medial temporal lobe damage) show deficits to self-referential processing in comparison to control participants (but see Bertossi et al., 2016b).

Neuroimaging research has found that mPFC shows greater activation when participants are directed to consider their personal past and future than during non-personal past and future mentation (Abraham, Schubotz, & von Cramon, 2008). Finer detailed examination has specifically identified vmPFC in self-related processing (D'Argembeau, 2013; Denny, Kober, Wager, & Ochsner, 2012). Within the context of episodic construction, the vmPFC has been linked to demands on schematic representations (Gilboa & Marlatte, 2017; Robin & Moscovitch, 2017; Sheldon & Levine, 2016; van Kesteren, Ruiter, Fernández, & Henson, 2012) and in particular the self-schema (Buckner & Carroll, 2007; D'Argembeau, 2013). It has been suggested by Murray, Wise, and Graham (2017) that hippocampal-vmPFC connectivity serves the creation of complex conjunctive representations that places the self within specific time, place, and situational context. These conjunctive representations may subsequently constrain further retrieval and construction by the hippocampus (Campbell, Madore, Benoit, Thakral, & Schacter, 2018; Graham, Barense, & Lee, 2010; Place, Farovik, Brockmann, & Eichenbaum, 2016; Preston & Eichenbaum, 2013). Thus, the recall or simulation of autobiographical episodes involves a prefrontal 'self' system that can work in conjunction with the MTL system to help individuals recombine episodic details to construct a personally relevant past or future event (Tulving, 2005; Wheeler, Stuss, & Tulving, 1997). The vmPFC has been identified in functional neural networks that underlie default mode activity (Andrews-Hanna, Reidler, Sepulcre, Poulin, & Buckner, 2010; Raichle, 2015) and in particular episodic construction (Schacter et al. 2012; Schacter, Benoit, & Szpunar, 2017; see chapters 1 and 3). Therefore, it seems likely that this region supports autonoesis and self-related processing in the context of mental time travel and episodic construction.

The vmPFC has been identified by prior research as a core brain region with regard to processing information related to the future self and its goals (Ciaramelli, Anelli, & Frassinetti, 2021; D'Argembeau, 2013). Further research has reported greater activity in the vmPFC for future events than for non-temporally specific routine activities (D'Argembeau et al., 2010a). It has been proposed that the vmPFC plays a specific role in meaning generation (Roy et al., 2012), which has been proposed as relevant to the construction of relatively abstract future scenarios (in comparison to specific recalled events) (Palombo, Hayes, Peterson, Keane, & Verfaellie, 2018; Trope & Liberman, 2010). However, it has also been noted that reduced activation is found in this region regarding both personal characteristics (D'Argembeau et al., 2010b) and events (Mitchell, Schirmer, Ames, & Gilbert, 2011) in the future versus the present. It has been suggested that the more abstract nature of the future engenders a diminished role of 'self' compared with the demands of present thinking (D'Argembeau et al., 2010b; Palombo et al., 2018b). Further, D'Argembeau et al. (2010b) reported that vmPFC activity did not differ between past and future conditions.

The present analysis used a novel coding system to examine the number of references to self and others within episodic content derived from autobiographical recall and future thinking narratives. The primary focus of this analysis is self-reference (as an indicator of autonoetic experience — Prebble et al., 2013), other-references are included for contextual comparisons to be drawn. In line with prior research, this method used pronoun usage and self-talk to measure the degree of autonoesis displayed within an autobiographical narrative (e.g. Kurczek et al., 2015; Prebble et al., 2013; Verfaellie et al., 2019). A novel adaptation of the present method was to consider references with the participant as a central point of focus (an example is shown in figure 4.1) rather than using a simple word count generated by scoring explicit language. References were further considered at the level of linguistic richness in which they were described ('my friend' gives a clear indication of reference to both self and other, whereas 'Tony' refers only to another). In order to establish if this method is capable of separating a measure of 'self' from episodic content (and is not acting as a proxy measure for the latter), the number of internal details produced in each narrative will be used as a control variable. It is suggested that considering the 'richness' of details in this way might offer a benefit in comparison to examining a simple word count or ratios of personal pronouns, as it offers a broader metric for the presence of self within episodic construction (see Verfaellie et al., 2019).

In line with prior research, it is predicted that higher scores for both self and other details will be produced in the past condition than in the future condition due to the pattern of episodic content production in these tasks (Addis, Sacchetti, Ally, Budson, & Schacter, 2009; Addis, Wong, & Schacter, 2008; Berntsen & Bohn, 2010; Race, Keane, & Verfaellie, 2011; Wang, Capous, Koh, & Hou, 2014; see also chapter 3). However, prior work has also suggested that a higher degree of self-processing is associated with future than with past oriented tasks (D'Argembeau, 2012; 2013; D'Argembeau et al., 2012; Grysman et al., 2013). It is predicted that, when controlling for episodic content (i.e. self-references/internal details), more self-references will be made in the future than in the past condition. No specific predictions were made in past/future conditions for the production of other-references when controlling for episodic content (i.e. other-references/internal details).

Further, it is important to consider the potential effect of semantic processing in the conceptualisation of an autobiographical self. Notably, theoretical work has suggested that episodic and semantic self-knowledge form separate parts of a self-memory system (Conway, 2005; Conway & Pleydell-Pearce, 2000). Further models have examined the link between semantic knowledge and episodic self-knowledge, and how these might mediate a sense of 'identity' (Haslam, Jetten, Haslam, Pugliese, & Tonks, 2011). Renoult and colleagues (2012, 2016) argue that episodic and semantic memory systems might represent a spectrum within which purely episodic and general semantic details are bridged by personal semantics. These can be considered as appearing more episodic (e.g. memory for repeated events, etc) or semantic (e.g. autobiographical facts). This method sought to control for a semantic self-component by making a narrow focus on episodic content (i.e. the 'internal' content produced in the modified AI— see Levine et al. 2002; chapter 3). As such it was predicted that the number of self-references in both past and future conditions would correlate with internal but not external details produced by the participant.

The scores generated for self-references were then correlated with tractography indices. This took place in two stages. The first stage involved correlating self-references with fornix and ILF microstructure FA and MD values. The fornix has been established as a major white matter pathway in the default mode network that connects the hippocampus to vmPFC (Aggleton, Wright, Rosene, & Saunders, 2015; Kernbach et al., 2018; see chapter three). The vmPFC has been strongly associated with self-processing (D'Argembeau, 2013; Kurczek et al., 2015; Murray et al., 2017; Verfaellie et al., 2019) hence it was predicted that in both past and future conditions, the number of self-references would positively associate with fornix FA and negatively associate with fornix MD. In order to further demonstrate that this measure of self-processing was not influenced by semantic memory, it was predicted that self-references would not associate positively with ILF FA or negatively with ILF MD in either past or future conditions.

The second stage correlated self-references with pre- and post-commissural fornix FA (MD was not included due to cross-correlations between tracts with this measure, see chapter 3). The pre-commissural fornix is the major pathway from hippocampal regions to the vmPFC (see also Aggleton et al., 2015; Cenquizca & Swanson, 2007; Croxson et al., 2005), whereas the post-commissural fornix projects to the mammillary bodies (Aggleton, 2012). Therefore, it was predicted that self-references would positively correlate with pre- but not post-commissural fornix FA in both past and future conditions.

Further, in line with theoretical models that separate self-processing and 'what-where-when' episodic memory in mental time travel (Fivush, 2011) and considering the association between the fornix and episodic thinking (Hodgetts et al., 2017a; see chapter 3), it was predicted that the above associations (i.e. between self and whole/pre-commissural fornix microstructure) would be maintained when controlling for the number of episodic details produced by the participant (using partial correlations). To limit the number of comparisons in this analysis (i.e. in consideration of family wise errors, and issues with data dredging), this test was used only to validate significant associations. The maintenance of an effect with this control was proposed to demonstrate that these white matter pathways (i.e. whole/pre-commissural fornix) can be seen to separately support both self-processing and 'what-where-when' episodic thinking in autobiographical constructions.

The number of references made to others has been included in this analysis to allow for comparison with self-references. Prior research has indicated that other-processing is associated with dorsal medial prefrontal cortex (dmPFC — Denny et al., 2012; Wagner et al., 2012, 2019). However, this research also indicates that self- and other-processing is associated with a ventral-dorsal gradient in mPFC (i.e. other-processing is primarily associated with dmPFC but can also be associated with vmPFC to a lesser extent, with the reverse true for self-processing). No specific predictions were made as to associations between whole/pre-commissural fornix microstructure and other-references. However, it was predicted that self-references would show stronger whole/pre-commissural fornix tract associations than would other-references.

4.2 Method

4.2.1 Development of Scoring Protocol

This analysis used the scripts that had been coded for internal and external details in chapter 3 (in line with Hodgetts et al., 2017a; Levine et al., 2002). The number of self and other-references made within these internal details were tallied across each of the ten narratives to form separate counts for both past and future conditions for each participant. External details were not included so that details that did not directly pertain to episodic construction (and hence might involve semantic processing) would not be scored (Conway, 2005; Renoult et al., 2020).

The self was considered in line with general self-reference (e.g. Stone, Dunphy, & Smith., 1966) and included all personal pronouns (Prebble et al., 2013; Twenge et al., 2013). References to others were limited to entities given some form of agency within the narrative and included third person pronouns, references to names, titles, etc (Ross & Wang, 2010; Wang & Ross, 2005). Scoring was performed with an egocentric frame of reference — self and other-references were always considered relative to the participant rather than at the level of explicit language use (most commonly this occurs when the participant roleplays as someone else within their narrative, see figure 4.1 for an example). Entities had to be explicitly stated and references to self or other could not be inferred from the text (e.g. "the train was busy" implies the presence of others but does not directly refer to them — as such this was not included in the number of references to others).

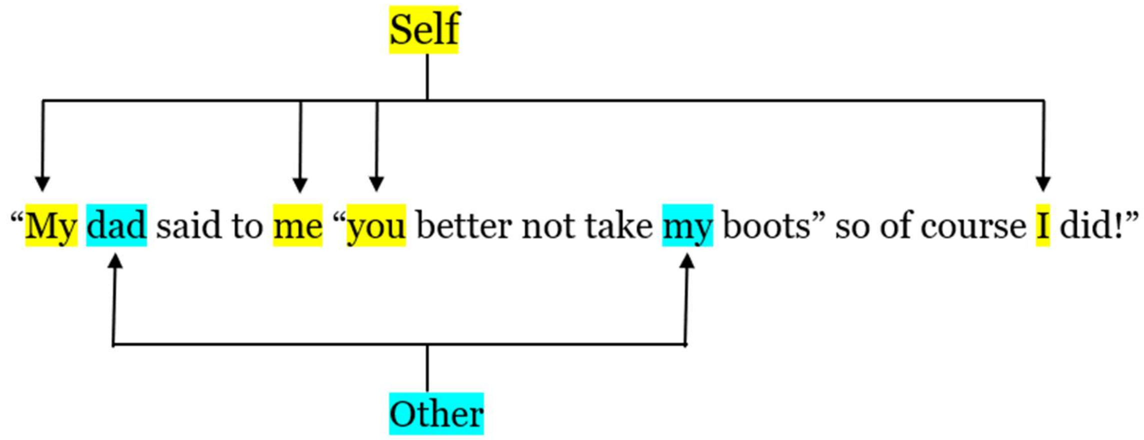


Figure 4.1 shows an example phrase that has been coded using the participant as the central point. In this example “my” is coded separately as a reference to both self and other. This differentiates the coding system from more simple or direct methods which would simply count an instance of “my” as self-processing.

Self and other-references were only scored if they were derived from a complete ‘idea’, that is the participant had to make a complete, coherent description, and repetition (e.g. through ‘false starts’ to phrases) was not further counted. The degree to which each full ‘idea’ could refer to the self or to other entities was, however, measured through the number of individual references to self and others within the idea (for instance “*She* introduced *her grandmother”* contains three ‘other’ references’). The full coding scheme is included in box 4.1.

Box 4.1 shows the full set of instructions provided to coders. Note: the 'collective-including-self' category was not used as part of the present analysis.

- There are three categories to be coded into
    - Self
        - I, me, my, etc
        - More rarely would include reference to self in the second or third person
    - Other
        - Counts towards references of specific living entities or groups of entities
            - "At the restaurant *they* gave us water" vs "At the restaurant the waiters were all very good, *they* brought us water"
        - Can include names, pronouns, roles (e.g. the waiter)
            - Entities can include living people, dead people, fictional characters, pets, animals
            - Plants, inanimate objects do not count
                - Animals as food would count as an inanimate object
            - Organisations/brands would not count under most circumstances. They would count if they are being used to refer to an entity as previously described
                - "There was a mascot race with Pepsi, Coke and Cadbury there. Pepsi won by a mile."
            - Entities cannot be 'inferred'
                - "The train was busy"
                    - 'busy' implies the presence of entities but these should not be scored as they are not specified
                    - This is because it isn't clear if it should 'other' or 'collective' in this case.
    - Collective-including-self
        - Any single reference that includes both self and another entity/entities.
        - We, our, etc

- Each detail should be scored separately within any given idea
    - "My dad and I bought our ice creams"
        - 2 self, 1 other, 1 collective
    - "She introduced her grandmother"
        - 3 other

- The categories are always to be considered from the point of view of the participant
    - "My dad said to me "you better not take my boots" so of course I did!"
        - 4 self, 2 other

- Must form a complete 'idea'
    - This means that 'false starts' would not be counted
    - "My hamster… I was… When I was young I went with my family to the pet shop and we got a hamster"
        - "My hamster" and "I was" don't form full 'ideas' and would be discounted from the scoring.
    - Similarly repetitions within an idea "I… I… I went to the shops" would only count once.

- Details appear either in the subject or object sections of a phrase
    - There can be multiple object to a verb, which need to be scored separately
        - "He gave *me* **my book"**
        - 'me' and 'my book' are separate details

- A reference is only counted in an episodic detail if it explicitly occurs in the temporal context of the episode.
    - "I remember going to the shops with my dad"
        - "I remember" would not count, as the self-reference occurs in the 'present'.
        - "with my dad" would count as it exists within the context of the episode.
    - "I think people were buying drinks" vs "I thought people were buying drinks"

4.2.2 MR imaging and tractography

The imaging data from this analysis is fully detailed in chapter 3. The reconstruction of the fornix and ILF followed the method described in chapter 2.

4.2.3 Statistical analyses

Kendall's tau correlations were performed due to the presence of outliers in the number of self and other-references (Pernet, Wilcox, & Rousselet, 2012). Primary comparisons were made between the number of self and other-references produced in episodic details in past and future narratives with fornix FA and MD values. The ILF is included as a comparison tract.

The alpha level was calculated using the number of tracts of interest in the analysis (i.e. the fornix) ($\alpha = 0.05$). Primary analyses were completed in JASP (2018, version 0.8.12). After transformation to a Pearson's r value (Walker, 2003), significant associations were tested using Steiger's Z-test (Steiger, 1980) using the cocor webtool (Diedenhofen & Musch, 2015). Partial correlations for key comparisons were completed in RStudio (2020) using the R package ppcor (Kim, 2015), and imputation was completed where appropriate using the R package 'mice' (van Buuren & Groothuis-Oudshoorn, 2011).

Consensus scoring was established based on the high level of agreement (Cicchetti, 1994) between two raters (intra-class correlation analysis, two-way mixed effects model: autobiographical self $r = 1.00$; autobiographical other $r = 0.96$; future self $r= 0.99$; future other $r= 0.98$).

4.3 Results

4.3.1 Number of self and other-references produced in internal content for both past and future narratives

The self and other-references were scored by totalling each respective reference across the ten cue words for both the autobiographical recall and future simulation tasks separately. The means and standard deviations are presented for these in table 4.1.

Table 4.1. Shows the mean, median, SD and range for the number of self and other-references made in episodic details produced across 10 autobiographical recall and future simulation AI narratives.

		Mean	Median	SD	Range
Autobiographical recall	*Self*	45.1	41	20.5	16–99
	Other	45.6	37	22.1	21–98
Future simulation	*Self*	23.7	22	10.6	10–48
	Other	17.0	15	11.2	3–47

A repeated measures ANOVA was performed to compare the mean scores produced in each condition. It was found that the present data violated the assumption of sphericity (Mauchly's W = 0.467, $p = 0.002$), and a Greenhouse-Geisser correction was used as the value ($\varepsilon = 0.744$) was less than 0.75 (Girden, 1992). The details across the four conditions were found to significantly differ (F (2.232, 58.034) = 45.30, $p < 0.001$, VS-MPR = 4.414+10, $\omega^2 = 0.618$). Post hoc Bonferroni comparisons revealed that no significant difference between self and other details in the autobiographical recall condition (t(26) = -0.184, $p = 1.000$, $d_z = -0.035$), however, significantly more self-references were produced than 'other' references in the future simulation task (t(26) = 3.630, $p = 0.007$, $d_z = 0.699$). It was found that more details were produced in the autobiographical task than the future task for both self (t(26) = 6.722, $p < 0.001$, $d_z = 1.294$) and other-references (t(26) = 9.117, $p < 0.001$, $d_z = 1.755$).

A significant positive correlation was found between the number of self-references made in past and future conditions (Figure 4.2A. Two-tailed Kendall's tau = 0.414, $p = 0.003$, VS-MPR = 22.38. $BF_{10} = 20.153$). The number of references to others was also found to positively associate between past and future narratives (Figure 4.2B. Two-tailed Kendall's tau = 0.454, $p = 0.001$, VS-MPR = 49.24. $BF_{10} = 48.54$). In the autobiographical recall condition, a positive association was found between the number of self and other-references (Figure 4.2C. Two-tailed Kendall's tau = 0.589, $p < 0.001$, VS-MPR = 1674. $BF_{10} = 1714$). Finally, a positive association was also found between the number of self and other-references produced in the future thinking task (Figure 4.2D. Two-tailed Kendall's tau = 0.558, $p < 0.001$, VS-MPR = 601.14. $BF_{10} = 711.68$).

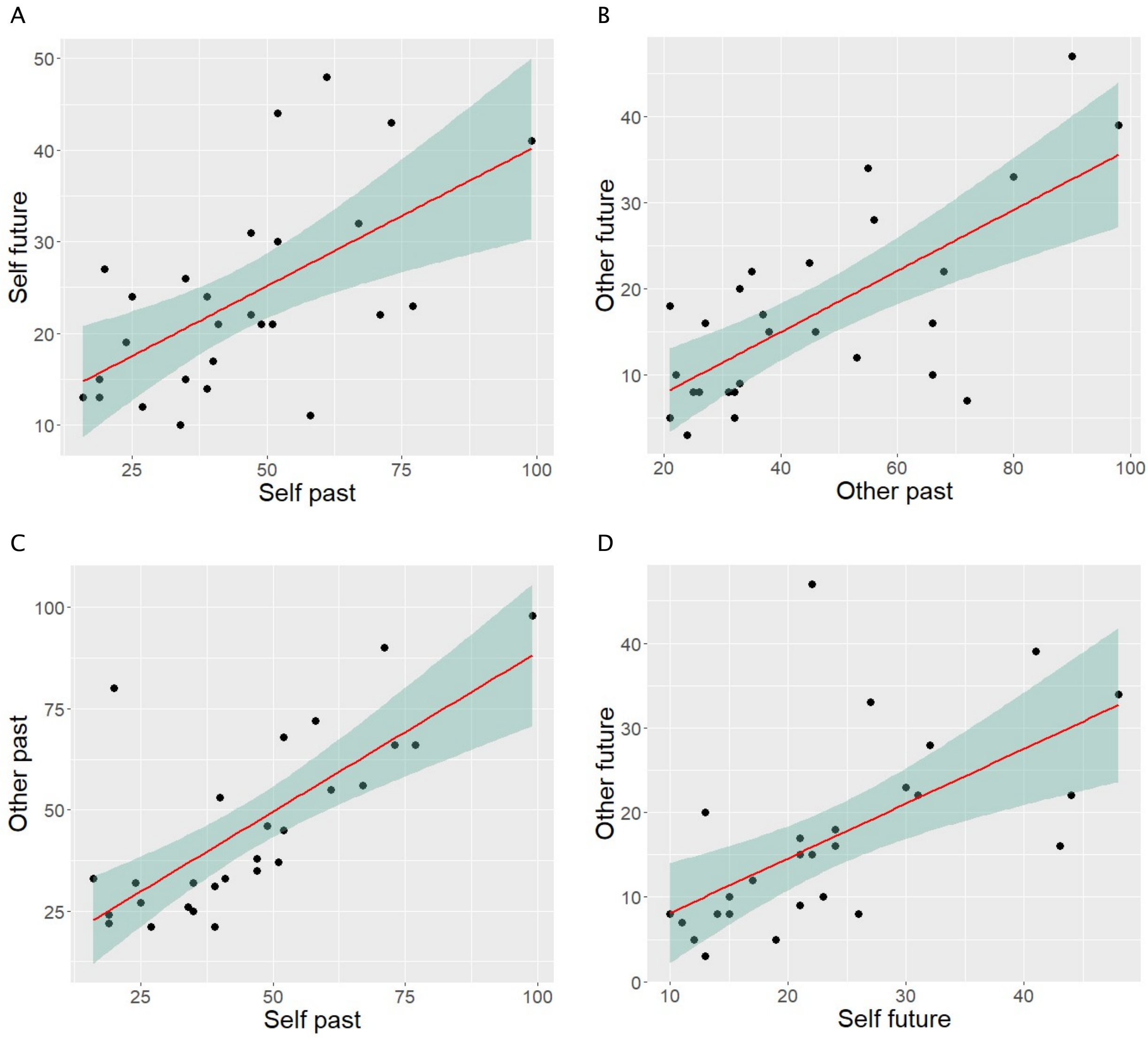


Figure 4.2. Shows the correlations between A) self-references in past and future conditions, B) other-references in past and future conditions, C) self and other-references in the past condition, D) self and other-references in the future condition. The shaded area represents the 95% CI.

4.3.2 Proportional self and other-references in past and future narratives

In order to control for the differing level of details produced in past and future tasks, another repeated measures ANOVA was performed using the mean scores generated from the number of self and other-references made divided by the number of internal details produced in the past and future tasks respectively (the scores generated from this are displayed in table 4.2). The data did not violate the assumption of sphericity (Mauchly's W = 0.813, p = 0.402). The details across the four conditions were again found to differ (F(3, 78) = 11.58, p < 0.001, VS-MPR = 12154, ω^2 = 0.279). Post hoc Bonferroni comparisons revealed that no significant difference between self and other details in the autobiographical recall condition (t(26) = 0.115, p = 1.000, d_z = 0.022), however, significantly more self-references were produced than 'other' references in the future simulation task (t(26) = 5.034, $p < 0.001$, $d_z = 0.969$). No significant difference between the 'self' details in the past and future condition (t(26) = -1.776, $p = 0.525$, $d_z = -0.341$). However, significantly more other-references were produced in the past than the future task (t(26) = 4.597, $p < 0.001$, $d_z = 0.885$).

Table 4.2. Shows the mean and SD for the controlled number of self and other-references made in episodic details produced across 10 autobiographical recall and future simulation AI narratives. These scores were transformed by dividing the number of self or other-references by the number of internal details produced in the respective past and future conditions.

		Mean	SD
Autobiographical recall	*Self*	0.37	0.10
	Other	0.37	0.09
Future simulation	*Self*	0.41	0.13
	Other	0.27	0.08

4.3.3 Correlation between self and other-references and the number of internal details

In the autobiographical recall task, a significant positive correlation was found between the number of internal details and both self (Figure 4.3A. Two-tailed Kendall's tau = 0.608, $p < 0.001$, VS-MPR = 3052.440, $BF_{10} = 3075.090$) and other-references (Figure 4.3B. Two-tailed Kendall's tau = 0.679, $p < 0.001$, VS-MPR = 31528.422, $BF_{10} = 30748.133$). This pattern was also found in the future thinking task, with positive associations found between the number of internal details produced and the number of self (Figure 4.3C. Two-tailed Kendall's tau = 0.530, $p < 0.001$, VS-MPR = 315.735, $BF_{10} = 327.901$) and other-references (Figure 4.3D. Two-tailed Kendall's tau = 0.685, $p < 0.001$, VS-MPR = 30386.920, $BF_{10} = 37778.529$).

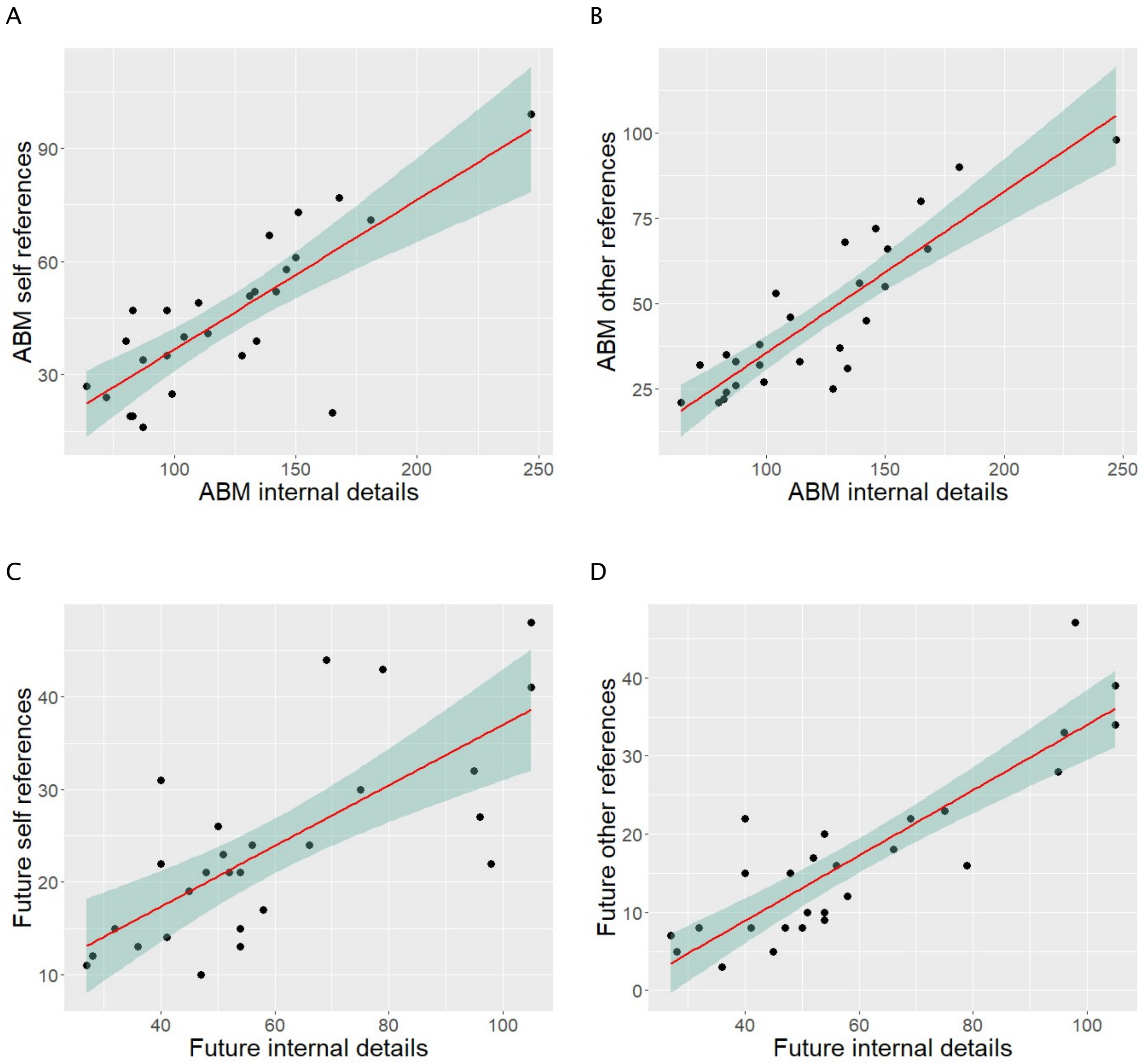


Figure 4.3. Shows the correlations between A) self-references and internal details in the past condition, B) other-references and internal details in the past condition, C) self-references and internal details in the future condition, D) other-references and internal details in the future condition. The shaded area represents the 95% CI.

4.3.4 Correlation between self and other-references and the number of external details

There was no significant correlation between either self (Figure 4.4A. Two-tailed Kendall's tau = 0.135, $p = 0.327$, VS-MPR = 1.007, $BF_{10} = 0.395$) or other-references (Figure 4.4B. Two-tailed Kendall's tau = 0.023, $p = 0.867$, VS-MPR = 1.000, $BF_{10} = 0.251$) and external details in autobiographical recall condition. Further, there was no significant correlation between either self (Figure 4.4C. Two-tailed Kendall's tau = -0.006, $p = 0.967$, VS-MPR = 1.000, $BF_{10} = 0.248$) or other-references (Figure 4.4D. Two-tailed Kendall's tau = -0.145, $p = 0.296$, VS-MPR = 1.021, $BF_{10} = 0.425$) in the autobiographical future thinking condition.

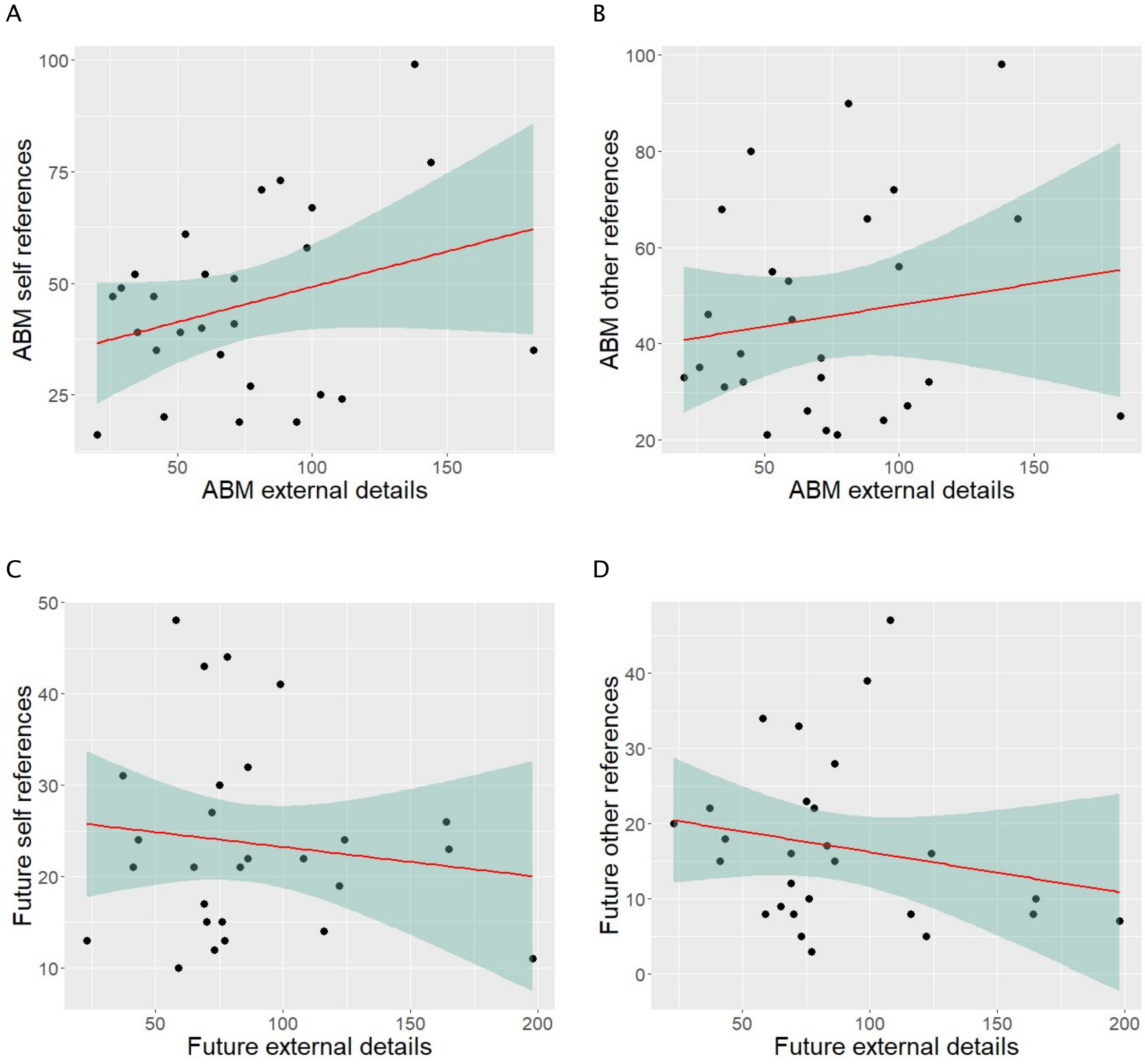


Figure 4.4. Shows the correlations between A) self-references and external details in the past condition, B) other-references and external details in the past condition, C) self-references and external details in the future condition, D) other-references and external details in the future condition. The shaded area represents the 95% CI.

4.3.5 Correlations between self and other-references and fornix and ILF microstructure

A significant association was found between fornix FA and the number of self-references made in the future thinking task (one-tailed Kendall's tau = 0.271, $p = 0.025$, VS-MPR = 4.009, $\mathrm{BF}_{0+} = 3.150$). Although not significant, weak correlations were established between the number of self-references in the autobiographical recall task for both fornix FA (one-tailed Kendall's tau = 0.212, $p = 0.061$, VS-MPR = 2.151, $\mathrm{BF}_{0+} = 1.474$) and MD (one-tailed Kendall's tau = -0.201, $p = 0.072$, VS-MPR = 1.942, $\mathrm{BF}_{0-} = 1.290$) values. No other significant or trend level associations were made with either fornix or ILF microstructure. A full display of Kendall's tau correlation values is shown in figure 4.2.

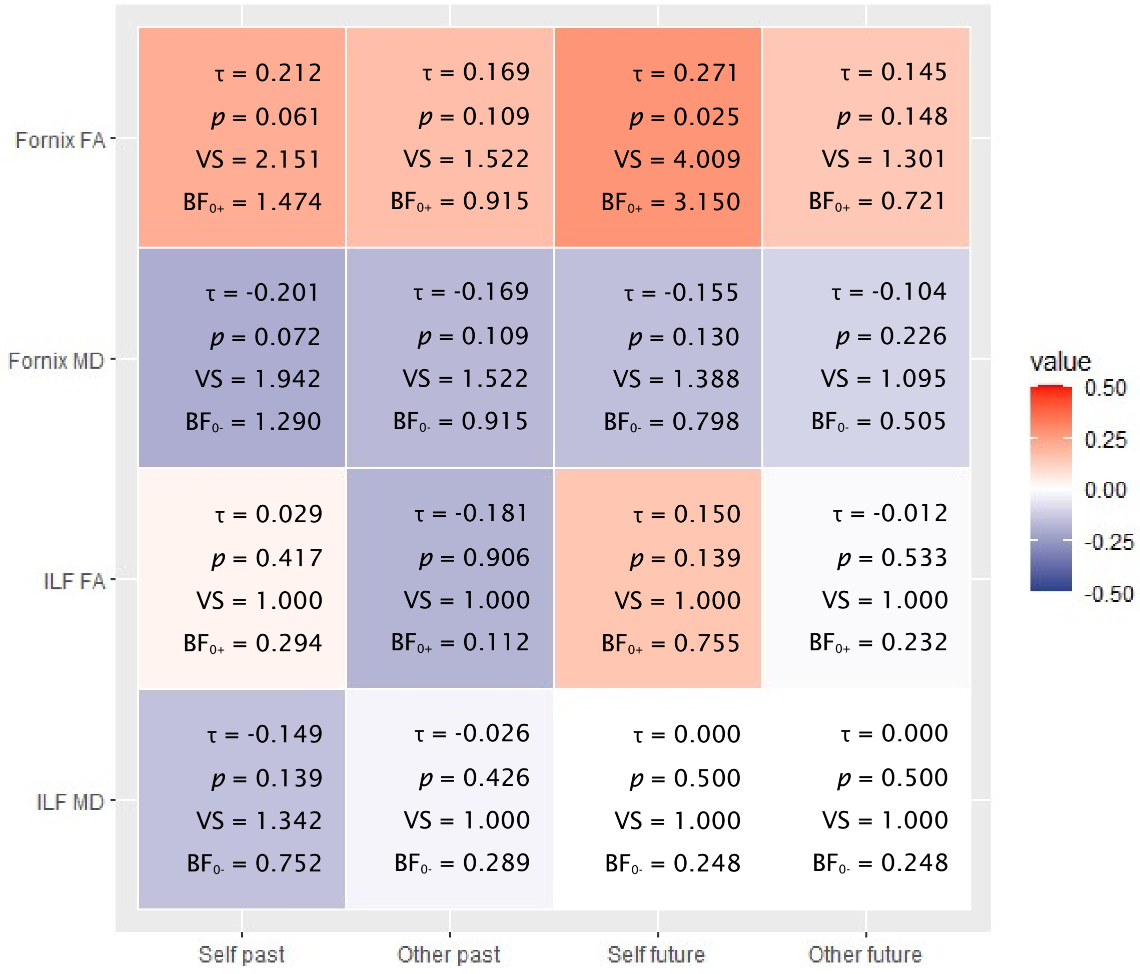


Figure 4.5. The one-tailed Kendall's tau correlations (τ) between self and other-references (both in autobiographical recall and simulation tasks) and fornix and ILF FA and MD. Also reported are *p* values (*p*), Vovk-Sellke maximum p-ratios (VS), and Bayes factors (BF$_{0+/-}$)

A one-tailed Steiger's Z test revealed no significant difference for the associations between self-references in the future condition and fornix and ILF FA values (z = 0.690, *p* = 0.245). Nor was the association in the future task between 'self' details and fornix FA greater than the association between other details and fornix FA (z = 1.438, *p* = 0.075).

4.3.5.1 Influence of episodic details and grey matter volume

The significant association was maintained between self-references in the future condition and fornix FA when controlling for the number of episodic details produced (one-tailed Kendall's partial tau = 0.259, *p* = 0.032). Further this association was found to be significant when controlling for hippocampal (one-tailed Kendall's partial tau = 0.288, *p* = 0.020) and vmPFC volume (one-tailed Kendall's partial tau = 0.260, *p* = 0.031).

However, a post-hoc test found no association between internal details and fornix FA when controlling for the number of self-references (two-tailed Kendall's partial tau = -0.056, p = 0.687).

4.3.6 Correlations between self and other-references and pre- and post-commissural fornix

In the autobiographical recall condition, a significant correlation was found between pre-commissural fornix FA and both self (Figure 4.6A. One-tailed Kendall's tau = 0.321, p = 0.010, VS-MPR = 8.175, BF_{0+} = 6.920) and other-references (Figure 4.6C. One-tailed Kendall's tau = 0.381, p = 0.003, VS-MPR = 22.623, BF_{0+} = 20.383). No association was found between post-commissural fornix in either the number of self (Figure 4.6B. One-tailed Kendall's tau = -0.057, p = 0.662, VS-MPR = 1.000, BF_{0+} = 0.183) or other-references (Figure 4.6D. One-tailed Kendall's tau = 0.072, p = 0.301, VS-MPR = 1.018, BF_{0+} = 0.393).

In the past condition, one tailed Steiger's z tests revealed a significant difference in the associations between pre- and post-commissural fornix FA for self (z = 2.420, p = 0.013) and other-references (z = 1.868, p = 0.031). No significant difference was found between the associations of self and other-references with pre-commissural fornix FA (z = -0.743, p = 0.771).

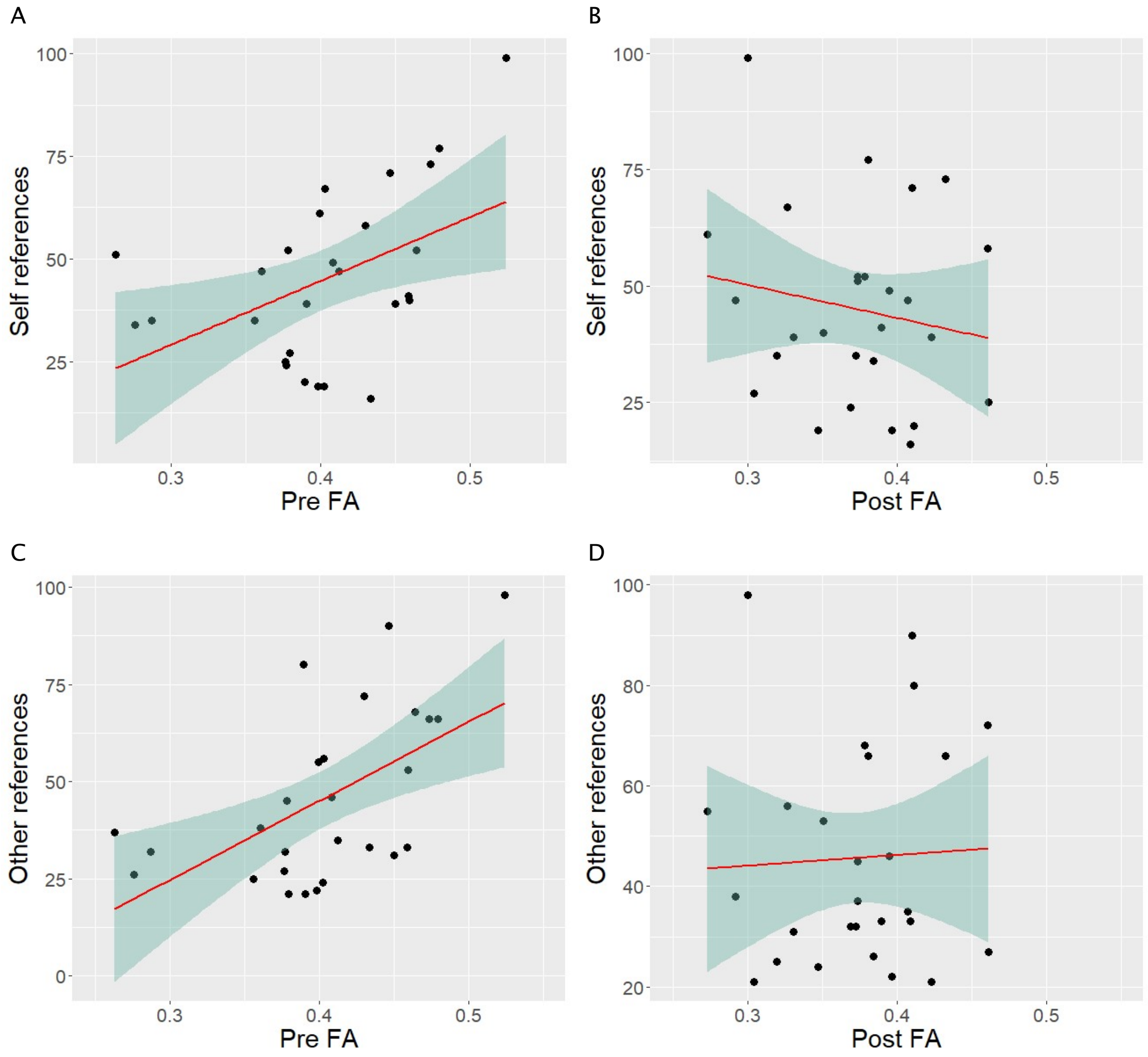


Figure 4.6 Shows the correlations between self (A, B) and other (C, D) references made within episodic details and pre-/post-commissural fornix FA values in the autobiographical recall condition.

In the future condition, no association was found between pre-commissural fornix FA and either the number of self (Figure 4.7A. One-tailed Kendall's tau = 0.173, p = 0.105, VS-MPR = 1.554, BF_{0+} = 0.949) or other-references (Figure 4.7C. One-tailed Kendall's tau = 0.174, p = 0.105, VS-MPR = 1.556, BF_{0+} = 0.959). No association was found between post-commissural fornix and either the number of self (Figure 4.7B. One-tailed Kendall's tau = -0.017, p = 0.550, VS-MPR = 1.000, BF_{0+} = 0.225) or other-references (Figure 4.7D. One-tailed Kendall's tau = 0.093, p = 0.252, VS-MPR = 1.059, BF_{0+} = 0.461).

Steiger's Z tests showed that there were no significant differences between past and future conditions for the association between self-references and pre-commissural fornix FA (z = 1.309, p = 0.095). However, a significantly larger association was found in the past than the future condition for the association between other-references and pre-commissural fornix FA (z = 1.949, p = 0.025).

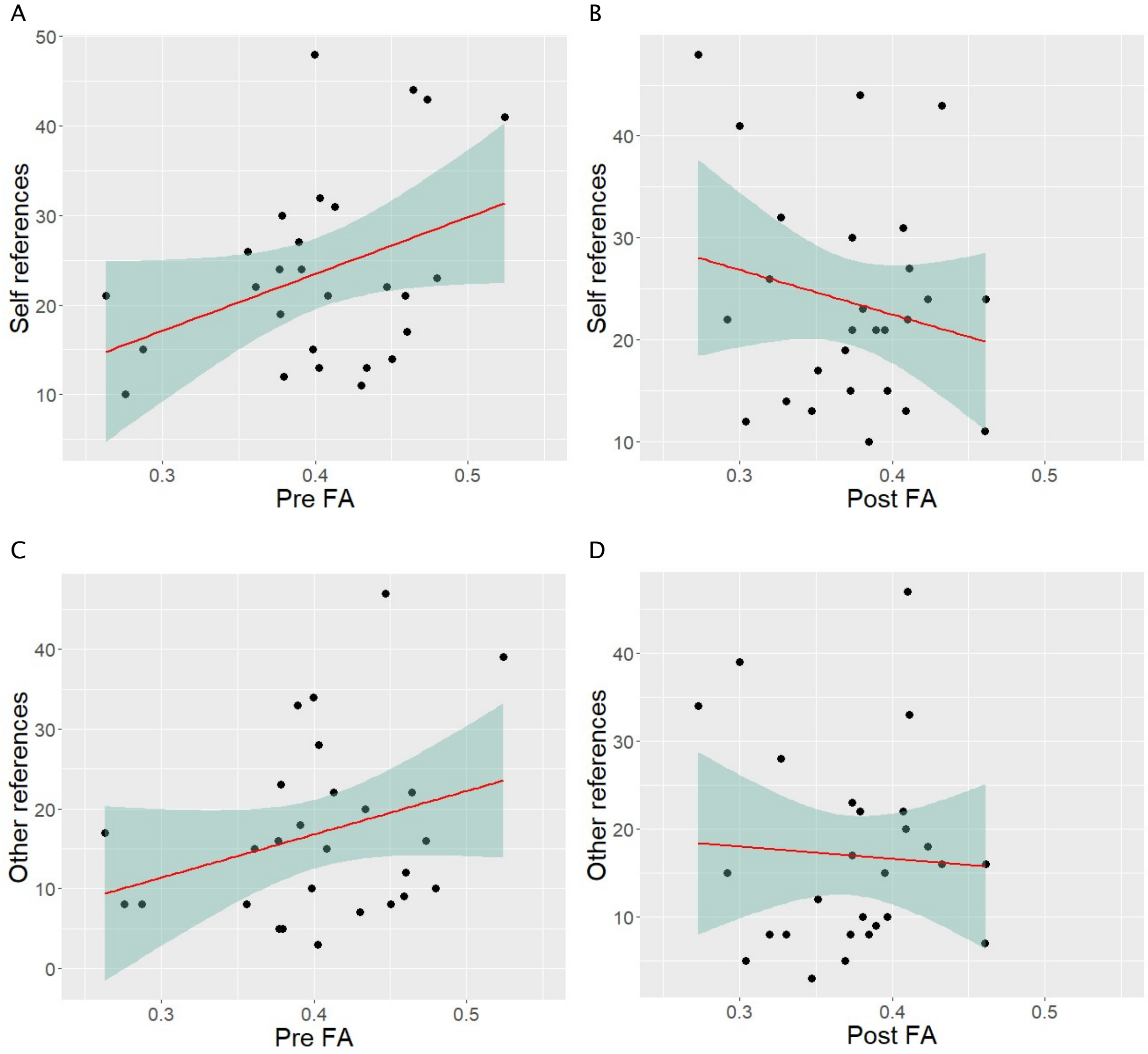


Figure 4.7. Shows the correlations between self (A, B) and other (C, D) references made within episodic details and pre-/post-commissural fornix FA values in the future thinking condition.

4.3.6.1 Influence of episodic details and grey matter volume

Significant associations were maintained between pre-commissural fornix and self (one-tailed Kendall's partial tau = 0.325, p = 0.020) and other-references (one-tailed Kendall's partial tau = 0.374, p = 0.007) when controlling for hippocampal grey matter volume in the autobiographical recall condition. Further, the association were maintained when controlling for vmPFC grey matter volume in this condition for both self (one-tailed Kendall's partial tau = 0.323, p = 0.021) and other (one-tailed Kendall's partial tau = 0.390, p = 0.005) references.

No significant association was found in the past condition between pre-commissural fornix FA values and either the number of self (one-tailed Kendall's partial tau = 0.159, p = 0.243) or other-references (one-tailed Kendall's partial tau = 0.225, p = 0.107) when controlling for the number of internal details.

4.4 Discussion

This chapter aimed to demonstrate a novel coding scheme investigating the degree of autonoesis in autobiographical recall and future thinking by examining participants' use of episodic self-reference. As in chapter 3, participants were tasked with a modified autobiographical interview that required them to both recall autobiographical memories and construct plausible future scenarios (see also Hodgetts et al., 2017a; Williams et al., 2020). These narratives were transcribed and then scored using the novel coding scheme to measure the degree of self-related language used by participants from an egocentric perspective. This allowed for the examination of behavioural patterns, along with correlations with white matter tracts to investigate the potential role of identified neural networks in supporting self-processing (and therefore autonoesis) in mental time travel.

In line with predictions, it was found that participants produced more references to self and other in the autobiographical recall task than in the autobiographical future thinking condition. This was in line with prior research which has established that past oriented tasks provide greater level of detail and specificity than do future oriented tasks (e.g. Addis et al., 2008; 2009; Race et al., 2011; Wang et al., 2014). When controlling for the amount of episodic content produced in each condition, it was found that self-references did not differ in past and future tasks. Further, in the future thinking task it was found that significantly more references were made to self than to others. In the autobiographical recall task no significant difference was found between the number of references to self and others. These findings demonstrate that self-referential but not other-referential processing is preserved in future thinking when compared with autobiographical recall. It is proposed that this reflects a higher degree of importance and salience attached to self-related processing in future thinking in comparison to recall. Although not entirely in line with predictions (i.e. that future thinking would show higher proportional self-references than did recall), this can be considered in line with prior research that has highlighted the different role of self-processing between past and future thinking (Addis et al., 2008; D'Argembeau, 2013; D'Argembeau & Van der Linden, 2004). It is possible that this might reflect uniquely future oriented demands as planning, which require more focus on self-relevance than does the recall of prior events. However, the importance of self-related processing to mental time travel as a whole is underlined by the fact that past and future references to 'self' did not differ when controlling for episodic content.

Theoretical work has suggested that autobiographical memories might separately contain 'episodic-self' and 'where-what-when' episodic details (Fivush, 2011). Further, it has been suggested that the self-processing may also be supported by semantic systems (Conway, 2005, Conway & Pleydell-Pearce, 2000). In order to focus solely on the episodic-self, only internal details were used for this analysis (see Levine et al., 2002). In line with predictions, it was found that self-references details correlated with the number of internal but not external details produced by participants. Moderate evidence was found in favour of the null hypothesis (BF < 0.33) when correlating self-references in future thinking narratives with external content. However, only anecdotal evidence was found in favour of the null (BF ~ 0.4) for the association between self-references and external details in the recall task. This provides a measure of confidence that self-reference scores generated by the present coding scheme were not unduly influenced by semantic processing. However, future research in a larger sample size (with greater statistical power) will be needed to confirm this finding.

The present analysis focussed on a putative episodic-self, which is proposed to be separable from semantic self-processing (Conway, 2005; Conway & Pleydell-Pearce, 2000; Fivush, 2011). The ILF has been associated with semantic processing (e.g. Agosta et al., 2010; Hodgetts et al., 2017a; Shin et al., 2019). Notably in Hodgetts et al. (2017a) the tract was associated with the number of semantic details produced in an autobiographical narrative. These details are likely to contain an element of self-processing in the form of self-knowledge and other related personal semantic details. As such, it was considered an appropriate tract to use in comparisons designed to demonstrate the lack of semantic processing in this method. In line with predictions, self-references were not found to associate positively with ILF FA or negatively with ILF MD values. This is strengthened by Bayesian analysis that found moderate evidence to support the null hypothesis (BF < 0.3) for the association between self-references in the autobiographical memory task and ILF FA, and self-references in the autobiographical future thinking task and ILF MD. Only anecdotal evidence was found in favour of the null hypothesis (BF ~ 0.7) for self-references in the autobiographical memory task and ILF MD, and self-references in the autobiographical future thinking task and ILF FA. Collectively, it is proposed that these results indicate that the self-reference measure used in the present analysis reflected self-processing that was not supported by a semantic system.

A significant positive association was found between fornix FA and the number of self-references made in the future thinking condition (Bayes factor analysis indicated moderate support for the alternate hypothesis — BF ~ 3). This effect was maintained when controlling for hippocampal and vmPFC grey matter volume. Further, this effect was maintained when controlling for episodic content. However, a partial correlation between internal details and fornix FA in the future condition was found to be non-significant when controlling for self-references. This demonstrates that the predicted effect for self-processing could not be found independent of the link with episodic function. As such, present findings do not support research that claims episodic memory might differentially contain procedural and self-related content (Fivush, 2011). No further significant directional associations were found between fornix FA and MD values and the task performance measures. However, weak correlations (Kendall's tau ~ 0.2) were identified between self-references in the autobiographical memory task and fornix FA and MD. It is possible that the present study did not have sufficient statistical power to establish this as a significant association. As such, present findings provide only limited support for prior research that has indicated a relationship between self-reference in autobiographical narratives and vmPFC (Kurczek et al., 2015; Verfaellie et al., 2019). Further this can similarly be considered in the broader association between self-processing and vmPFC identified in other studies (e.g. D'Argembeau, 2013; Murray et al., 2017).

A Steiger's Z test found no significant difference between fornix FA association with self-references than other-references in the future thinking condition. However, the VS-MPR value did support a stronger association for self than other. To some extent, a similar pattern could be seen with VS-MPR values indicating stronger self than other-reference associations with fornix FA/MD. However, these were largely marginal and are not offered as strong evidence of the overall pattern. It should be considered that these results provide limited evidence to the prediction that self-references would show stronger associations with fornix microstructure than would other-references (in line with Denny et al., 2012; Wagner et al., 2012). It is suggested that the present analysis was not sufficiently sensitive to these differences to establish this pattern, and that future work with a larger sample (and greater statistical power) is needed to clarify these relationships.

Finer-grained analysis was possible by further splitting the fornix into pre- and post-commissural components (Christiansen et al., 2016; see chapter 3). In line with predictions, a positive association was found between self and pre-commissural fornix FA in the autobiographical recall task (Bayes factor analysis indicated moderate support for this association — BF ~ 7). Although this effect was maintained when controlling for hippocampal and vmPFC grey matter volume, no significant association was found when controlling for episodic content — contrary to hypotheses. In line with the above analysis, this finding suggests the present cannot support the model proposed by Fivush (2011) in which episodic memory can be dissociated between procedural and self-related components.

Against predictions, no positive association was found between pre-commissural fornix FA and self-references in the autobiographical future thinking condition. Although Bayes factor analysis did not provide strong evidence in favour of the null hypothesis (BF ~ 1). It is possible that this might reflect the greater episodic specificity found in autobiographical memory as opposed to episodic future thinking (Berntsen & Bohn, 2010). Further, this could be due to a rehearsal effect if autobiographical memories serve a more social function than future oriented thinking (Alea & Bluck, 2003). However, a Steiger's Z test did not demonstrate a significant difference between pre-commissural fornix associations with self-references in the autobiographical recall or future thinking conditions.

In line with predictions, no positive association was found between post-commissural fornix FA and self-references in either the past or future conditions. Further, Bayes factor analysis indicated there was moderate evidence in favour of the null hypothesis (BF ~ 0.2). Further, a Steiger's Z test showed a significant difference between self-reference associations with pre-commissural and post-commissural fornix FA association. As stated in chapter 3, the pre-commissural fornix projects to mPFC in a gradient with more projections to vmPFC and fewer to dorsal mPFC (Aggleton et al., 2015; Cenquizca & Swanson, 2007; Croxson et al., 2005) whereas the post-commissural fornix projects to the mammillary bodies (Aggleton, 2012). This provides further support for an association between vmPFC and self-referential processing in autobiographical recall.

Against predictions, VS-MPR showed a stronger association between pre-commissural fornix FA for other-references than for self-references in the autobiographical memory condition (albeit a Steiger's Z test revealed no difference between these associations). In the future thinking condition, no difference was found between pre-commissural fornix associations with self or other-references. As such these findings do not support prior research that indicated a stronger association between self-processing than other-processing with vmPFC (Denny et al., 2012; Wagner et al., 2012).

Overall, the white matter tract associations do not support a separable role of the whole/ pre-commissural fornix in episodic memory and self-processing in autobiographical recall and future simulation. However, the present findings, along with those of chapter 3, do suggest that fornix microstructure does play a role in episodic recall and future thinking. Further, it is likely that these do also reflect autonoesis and hence a self-processing component. The present findings also support the notion that self-related processing in episodic constructions can be measured separately to semantic self-processing, providing support to theoretical accounts (Conway, 2005; Conway & Pleydell-Pearce, 2000). Taken as a whole, the present results can be considered to align with Tulving's proposal for mental time travel, in that they demonstrate a strong interaction between spatiotemporal episodic and self-referential content (Tulving, 2005). However, they can also be explained by scene construction theory, which holds that scene construction itself is egocentric by its very nature (Mullally & Maguire, 2014).

When the results were analysed using self-other ratios scores (in line with vmPFC lesions studies - Kurczek et al., 2015; Verfaellie et al., 2019; see supplementary results) a significant association was found solely between self-references in the past condition and ILF FA. Future research might examine whether these different forms of data handling act as measures of subtly different processes. The overall pattern of these results might reflect a lack of power in the present analysis, and it is likely that a clearer pattern of results could be identified if the use of larger scale sample populations could be implemented. This is likely to be a key area for future research to consider with regards to associations with episodic narratives. Although clearly data rich, the method suffers from a degree of noise that can affect its effectiveness in smaller sample studies.

Another factor to consider regarding present findings is the use in this analysis of a broad definition of both 'self' and 'other' references. A recently published analysis by Tackman et al. (2019) showed that the type of language used in an analysis can affect the associations developed from it. They examined the use of 'I-talk' within depression and split this into smaller subcomponents of personal pronoun use (e.g. I) and the use of personal possessive pronouns (e.g. my). They found that the former but not the latter correlated with depression. Further work in this area has indicated that the use of "I" is associated positively with negative memories and negatively with positive memories in patients with major depressive disorder (Himmelstein, Barb, Finlayson, & Young, 2018). As such, it is possible that different forms of self-talk might associate with different aspects of cognition (e.g. valence). This is further supported by the findings of Twenge et al. (2013) who associated the change in pronoun use with a respective change in cultural tendencies. Future work could look to examine whether our effects are maintained across specific subcomponents of self-referential analysis, and how this might reflect the combinational nature of some references (e.g. when referring to both self and other in the context of a possession, or the interdependent and independent aspects of self and how these might vary across cultures Shao, Yao, Ceci, & Wang, 2010; Wang, 2016).

Further, the present study did not control for ‘psychological distance’ (see Liberman & Trope, 2008; Trope & Liberman, 2003). This is a term that describes ways (e.g. temporal, spatial, socially, etc) that an event can be removed from a person’s present experiences. It was suggested by Mitchell et al. (2011) that episodic future thinking becomes increasingly difficult as a simulated experience becomes further distanced from a person’s general experiences. As such it might be considered that the ‘self’ in the distant past and future might be processed more in line with being a ‘different person’. Further, these authors suggested that a psychological difference might exist between present and future self. The present analysis found that future oriented thinking used a greater proportion of self-references than references to others, whereas no difference was found in the past condition. This might be seen as a challenge to the viewpoint offered by these authors. However, as no temporal restriction or controls were used in the narratives produced in the present study, it was not possible to examine the difference between self-oriented processing in near and far future. Whereas it seems unlikely that the self in the far future is processed like a different person, it is still possible that a weighting of self-relevance could be seen with time. Further, present results could be due to participants using more temporally distant events for their past than their future constructions. As such it is suggested that future research would benefit from measuring the degree of psychological distance present in each construction.

The present coding system was designed primarily to examine the degree of self-processing and self-reference that was produced in past and future episodic narratives. The purpose of scoring the references to other was primarily to act as a comparison for the main focus of the analysis. To that end, a participant using a phrase such as “my teacher” was considered to have lexically demonstrated the presence of ‘self’ within the narrative (i.e. that they stated a personal relationship to the ‘other’ entity was used to demonstrate their placement of ‘self’ within the conceptual framework of their narrative). As such, no distinction was made regarding the quality of ‘other’ referenced in the narratives. A meta-analysis by Murray et al. (2012) showed that a distinction could be found between others that were ‘close to self’ or public. Both ‘close other’ and ‘self’ demonstrated vmPFC activation whereas ‘public other’ showed more dmPFC activation. As such, the degree of vmPFC activation is moderated by the degree of inclusion of close others to a person’s sense of self (see also D’Argembeau, 2013). The present coding scheme did not control for this (i.e. “my brother” and “my waiter” would be scored identically, though the former is more likely to have a stronger connection to a person’s self-concept). The present coding scheme could be adapted in order to examine the degree of separation from self that is present in references made to other entities. This would extend the present analysis, whilst allowing it to maintain the focus on conceptual self-placement within the episodic narrative. It is possible that this might help to show a separation between intrinsically 'self' and 'other' related processing might associate with white matter tractography.

The demographic nature of the sample population used in this study might also be considered a limitation. As noted above, and in line with D'Argembeau's (2013) concept of 'inclusion within self-concept', different cultures have been found to process self and others in different ways (Han & Ma, 2014; Shao et al., 2010; Wang, 2016). The cultural background of participants was not considered and, as such, could not form part of the final analyses. Further to this, Shao et al. (2010) identified that self-related processing also varies between sexes. These researchers found that men showed greater degree of personal focus in descriptions of events and themselves in past, present and future tasks. The sample used in the present analysis was almost entirely female (25 female, 2 male participants). As such, present findings are best considered in relation to this population. Future research might aim for a more balanced sample and might particularly examine if behavioural differences between sexes might also be reflected in differences in white matter neuroarchitecture.

Finally, the results of the present study might be considered within the context of mixed findings in other research using self-references (Bertossi et al., 2016b; Kurczek et al., 2015; Verfaellie et al., 2019). It was found by Kurczek et al. (2015) that vmPFC lesion patients used a lower proportion of personal pronouns than did controls and patients with medial temporal lobe damage. However, this result was not corroborated by Bertossi et al. (2016b) who found no deficit in their vmPFC lesion patients. Further study by Verfaellie et al. (2019) showed that both vmPFC and medial temporal lobe lesion patients used a lower proportion of self-referential pronouns than did healthy controls. However, this analysis found no difference between in the proportion of self-references recorded between the patient groups. The reasons for the inconsistency in findings between these studies require careful consideration.

Firstly, it is important to consider that evidence from lesion populations by their very nature lack a degree of control (i.e. in the nature of the lesion, severity of deficits and so on). Further these studies found opposing patterns of results for the number of episodic details produced in a future thinking task — a deficit was identified by Bertossi et al. (2016b) but not by Kurczek et al. (2015). Further a study by Verfaellie et al. (2019) found that neurotypical participants produced more episodic details when describing events relating to the self than to another. This 'self-benefit' was maintained in patients with medial temporal lobe damage but not in patients with damage to vmPFC. Clearly, this demonstrates that the self-reference results were not the only inconsistent findings between these studies. As such, this does not preclude the production of self-reference as a tool with which to examine self-related processing in episodic narratives. However, it might also be considered that self-references are a somewhat blunt instrument when measuring the capacity for self-projection or reflection (Prebble et al., 2013; Twenge et al., 2013). For instance, it would not inform an experimenter about higher order cognitive processes (for example a participant's choice to tell a story in such a way that shows them in a positive light). Future work might seek to establish a more defined connection between the use of self-referential language and how it relates to self-processing. In particular, it is suggested that qualitative measures could be used in conjunction to provide complementary evidence regarding the precise nature of self-related processing in episodic narratives.

In conclusion, behavioural evidence has been found that a higher proportion of self-references (in comparison to references to others) are made in autobiographical future thinking and autobiographical recall. This supports prior evidence that the role of the 'self' differs between past and future aspects of mental time travel (e.g. Addis et al., 2008; D'Argembeau, 2013; D'Argembeau & Van der Linden, 2004). It was predicted that fornix microstructure indices would correlate with the number of self-references produced in both past and future tasks (and that this association would be stronger than those with other-references). Although some evidence was found for this association, the comparison was not maintained when controlling for episodic content. This can be seen as providing support for Tulving's concept of mental time travel, which proposed of episodic spatial details and self-referential processing as being highly interwoven (Tulving, 2005). These results can also be considered to support scene construction theory, which emphasizes the egocentric nature of scene construction (Mullally & Maguire, 2014). Future research should seek to clarify inconsistent findings within self-referential analyses. Further, the use of complementary qualitative data would provide further insight to the nuances of the self and self-related processing in mental time travel.

4.5 Supplementary results

4.5.1 Descriptive statistics and correlations using self-other ratio scores

Prior work in lesion patients (e.g. Bertossi et al., 2016b; Verfaellie et al., 2019) has examined self-related processing using the proportion of self and other-references (calculated as 'self' or 'other' divided by 'self + other'). The descriptive statistics for these are displayed in table 4.3. Paired samples t tests were performed to compare the ratio scores. The primary comparisons of interest were between self-references in the past and future task, self and other-references in the past task and self and other-references in the future task — as such the alpha level was set to $\alpha = 0.05/3 = 0.017$.

Table 4.3. Shows the mean and SD for self and other ratio scores (calculated as 'self' or 'other' divided by 'self + other').

		Mean	SD
Autobiographical recall	*Self*	0.50	0.09
	Other	0.50	0.09
Future simulation	*Self*	0.61	0.11
	Other	0.39	0.11

It was found that the proportion of self-references in the future condition was significantly higher than references to others (t(26) = 4.899, $p < 0.001$, VS-MPR = 835.427, d = 0.943). No significant difference was found between the proportion of self and other-references in the past condition (t(26) = -0.038, $p = 0.970$, VS-MPR = 1.000, d = -0.007). The proportion of self-references was found to be significantly higher in the future than in the past (t(26) = 4.655, $p < 0.001$, VS-MPR = 469.241, d = -0.896).

A significant positive association was found between self-references ILF FA in the autobiographical recall condition (one-tailed Kendall's tau = 0.362, $p = 0.004$, VS-MPR = 17.152, $BF_{0+} = 14.114$). No further significant associations were found for either FA or MD metrics.

Chapter 5: The role of the fornix and ILF in the production of personal and general semantic details in autobiographical memory and future thinking

5.1 Introduction

It is commonly understood that both autobiographical memories and episodic future constructions are multifaceted in their composition (i.e. they comprise of both episodic and semantic content — D'Argembeau, 2020; Devitt, Addis, & Schacter, 2017). While much research into mental time travel has focussed on the role of episodic memory (e.g. Schacter & Addis, 2007b; Tulving, 2002a), there is increasing interest in the role of semantic memory, particularly with regard to thinking about the future (Klein, 2013; Irish & Piguet, 2013). The role of the semantic memory system within the construction of episodic narratives across the lifespan has been discussed by a number of models — the *constructive episodic simulation hypothesis* (Addis, 2018; 2020; Schacter & Addis, 2007b); the *scene construction hypothesis* (Hassabis & Maguire, 2007; Mullally & Maguire); the *semantic scaffolding hypothesis* (Irish & Piguet, 2013); and the *self-memory system model* (Conway & Pleydell-Pearce, 2000). Although its contribution to episodic constructions has been acknowledged, the precise contribution of semantic memory to mental time travel (and more specifically episodic future thinking) has not yet been identified.

The role of semantic processing in episodic construction and mental time travel has been a recent focus of the field (for reviews see D'Argembeau 2020; Schacter et al., 2012). Key findings have been found in patients with semantic dementia, a neurodegenerative disease characterised by atrophy in anterior temporal lobes and associated with deficits in understanding the meaning of words, sensory objects, and concepts with a relative sparing of episodic memory (Benhamou et al., 2020). Despite the preservation of episodic memory, patients with semantic dementia have been demonstrated to show deficits in episodic future thinking (Duval et al., 2012; Irish et al., 2012a). Studies in healthy individuals have found that cueing participants with autobiographical knowledge and personal goals guided episodic construction in future scenarios (D'Argembeau & Demblon, 2012; D'Argembeau & Mathy, 2011). Functional neuroimaging work has shown overlapping activation in episodic and semantic future thinking tasks (Abraham, Schubotz, & von Cramon, 2008). Further work has suggested that anterior temporal lobe activity supports future thinking based on semantic memory (Addis et al., 2007; Addis, Roberts, & Schacter, 2011; Irish et al., 2012a). As such, semantic memory has been proposed by various models to play a role within the contextualisation of episodic systems and might be fundamental to experiencing chronesthesia (Addis, 2018; 2020; D'Argembeau, 2020; Irish & Piguet, 2013; Mullally & Maguire, 2014; Schacter et al., 2017). In particular, the semantic scaffolding hypothesis holds that semantic knowledge provides a framework by which past and future episodic constructions are supported (Irish & Piguet, 2013).

Episodic constructions in the form of autobiographical memories and simulated future scenarios are formed of episodic and semantic content (Devitt et al., 2017). This content is readily accessed by narratives produced in AI tasks (e.g. Addis et al., 2008; Hodgetts et al., 2017a; Levine et al., 2002). Prior work by Hodgetts et al. (2017a) demonstrated that ILF microstructure mediated individual differences in the semantic, but not episodic, component of autobiographical memories produced in an AI task.

Up to this point of the project, semantic details have been considered in broad rather than specific scope. In the context of the AI, semantic details are grouped in with other tangential details in the 'external' category (Levine et al., 2002). However, a growing body of research has examined how semantic memory within episodic constructions might be divided into further subcategories. It is proposed that semantic memory could instead be considered as a collective term for both 'personal' and 'general' semantic details (Renoult, Davidson, Palombo, Moscovitch, & Levine, 2012; Renoult et al., 2016; Renoult, Irish, Moscovitch, & Rugg, 2019). The primary distinction between personal and general semantics is that the former is highly idiosyncratic and can retain some aspect of its acquisitional context, whereas the latter are culturally shared and acontextual. Further, it has been suggested by Renoult et al. (2012) that personal semantics can be considered to show aspects of both episodic (as they relate specifically to the life story of the individual) and semantic memory (as they are do not pertain to a specific spatiotemporal contextual point). Further research in amnesic patients has shown that personal semantic memory can be maintained, along with a concept of self, in the absence of episodic memory (Rathbone, Moulin, & Conway, 2008; for a review see Grilli & Verfaellie, 2014).

The nature of the divide between personal and general semantic processing is a topic of recent research. One suggestion is that personal semantic processing is not separate from but instead a subcomponent of general semantic processing (Grilli, Bercel, Wank, & Rapcsak, 2018; Renoult et al., 2012). Grilli et al. (2018) found that damage to the left ventral anterior lobe was associated with impaired recall of autobiographical facts. It was reported by Maguire and Frith (2003) that general and personal semantics elicited differential though overlapping functional activity — with a greater response being found in left lateralised medial prefrontal cortex, retrosplenial cortex and temporal pole in personal compared with general semantic processing. Notably medial prefrontal cortex (and more specifically left vmPFC) has been associated with self-processing (D'Argembeau & Salmon, 2012; Murray et al., 2012; see also chapter 4), which might explain the differences in otherwise similar functional activity. This is also consistent with the idea of a broader semantic network or hub as discussed in chapter 1 (see also Patterson et al., 2007; Rogers et al., 2004). Further, an ERP study by Coronel and Federmeier (2016) has demonstrated that both personal preference and general semantic statements elicited an N400 response with similar latency and distribution. It was concluded by these authors that personal and general semantics share functional and neurobiological features.

Of note within the study by Maguire and Firth (2003) is that left lateralised medial prefrontal cortex, retrosplenial cortex and temporal pole were also active during episodic memory (see also Grilli et al., 2018). This could be differentiated from personal semantic memory by a greater degree of activation and further activation of the hippocampus. This allowed an alternate interpretation of the findings above to suggest that personal semantics existed on a spectrum of increasing abstraction from episodic to general semantic memories (Renoult et al., 2012; see figure 5.1).

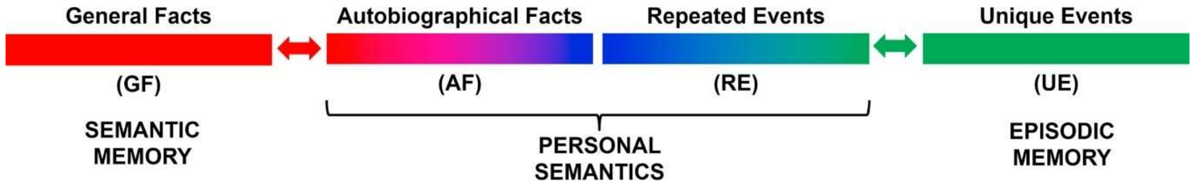


Figure 5.1 shows a proposed spectrum of abstraction within memory content. Personal semantic content can be considered to more closely resemble either general semantics (i.e. autobiographical facts) or episodic content (i.e. memory of repeated events). This figure is reproduced from Renoult et al. (2016).

In line with the spectrum theory, it is important to consider what specifically constitutes a personal semantic detail. Renoult et al. (2012) suggests that personal semantics might consist of autobiographical facts, self-knowledge, and repeated and extended events. Whereas the first two clearly align with semantic memory, the latter appear to show more similarities with episodic memory. For instance, they still are described with contextual information from a first-person perspective (Conway & Pleydell-Pearce, 2000; Robinson & Swanson, 1993) — in this sense they are considered to be 'experience-near' (whereas autobiographical facts lack spatiotemporal context and are 'experience-far' - Grilli et al., 2018; Grilli & Verfaellie, 2014). However, prior research has demonstrated that repeated events are not recalled as clearly as unique events nor show the same level of personal significance (Addis, Moscovitch, Crawley, & McAndrews, 2004; Holland, Addis, & Kensinger, 2011; Levine et al., 2004). Further, they have been described as summaries of the episodes produced from the characteristics shared between them (Neisser, 1981). As such Renoult et al (2016) aptly described these as "constellations of separate but similar episodes" — entities that are considered whole when seen in the context of the sum of their separate parts. Neuroimaging data has shown that functional activity differs between autobiographical facts and repeated events largely in the hippocampus and medial temporal lobe (Addis et al., 2004; Holland et al., 2011). However, these studies also note that unique events generated greater activity in the left parahippocampal gyrus, left temporoparietal junction, right inferior temporal cortex, and fusiform gyri. Hence although repeated events are dissociable from both episodic memory and general semantics, they may share some elements of episodic processing.

In line with the findings of Coronel and Federmeier (2016), Renoult et al. (2016) demonstrated that personal semantics could be distinguished from episodic and semantic memory in an ERP study. Against the authors' predictions, no difference was found between the autobiographical facts and repeated events (identified as two subcategories of personal semantics). It was noted by the authors that this was found despite the repeated events in their study having been restricted to occurrences within the past year. The authors had expected that this time limit would have limited the degree of semanticisation in comparison to events tied to even earlier memories, which should have made an effect more likely to be found. They did note that the presence of everyday activities within their repeated events might have meant that their time limit was not rigidly adhered to. Although this shows that repeated events can be clearly considered as part of a 'personal semantics' category, it does not support the existence of a spectrum on which they exist.

The final model explaining the relationship between episodic, personal, and general semantic memory is a component process model (Moscovitch, Cabeza, Winocur, & Nadel, 2016). This model holds that each of these are supported to differing degrees by wide ranging but shared cognitive processes. These include self-reflection, sensory-perceptual imagery, spatial/temporal features, emotional valence, potential to elicit recollection, and their typical perspective (i.e. they are mentally experienced in the first or third person). This can most easily be considered in the case of comparing the form and neural processing of unique and repeated events. Both reflect direct experiences and elicit overlapping but differential results as measured in behavioural (Conway & Pleydell-Pearce, 2000; Robinson

& Swanson, 1993) and functional neural imaging domains (Addis et al., 2004; Holland et al., 2011).

The present experiment has two broad aims. Firstly, to create a coding scheme in which the subcomponents of semantic memory can be examined in AI transcripts. Secondly to establish if individual differences between the levels of these details can be associated with interindividual differences in white matter microstructure. Some of the data presented in this chapter was previously published by Hodgetts et al. (2017a), who demonstrated that ILF microstructure mediates individual differences in the production of semantic details during autobiographical recall. As noted by Tanguay (2018), the experiment by Hodgetts and colleagues did not look to differentiate the mix of general semantics, self-knowledge, and autobiographical facts within this category (nor did it include the details coded as repeated or extended events). Further, the experiment focussed only on autobiographical recall and did not include future thinking (Addis et al., 2008).

In the present analysis, the scripts produced in the autobiographical interviews were reanalysed to examine the level of 'personal' and 'general' semantic details produced by each participant for both past and future events. Details that would have been marked as 'semantic' in the Hodgetts et al. (2017a) were split into 'personal' and 'general' subcomponents. General semantic details related to knowledge that would be culturally shared (Renoult et al., 2012). The 'personal semantic' category included both autobiographical facts (e.g. "my first pet was named Sophie") and self-knowledge (regarding information such as personal traits, roles, etc). Personal semantic knowledge could include details that were indirectly related to the self — this is in line with the definition of autobiographical knowledge given by Renoult et al. (2020) but different to the procedure followed by Strikwerda-Brown, Mothakunnel, Hodges, Piguet, and Irish (2019) which defined anything not directly related to the self as 'general semantics'. In line with prior research (Renoult et al., 2012; Renoult et al., 2016), a 'total' personal semantic score was calculated by adding the extended and repeated event details (in the Hodgetts et al. coding system as 'extended' and 'categorical') produced by each participant to the personal semantic facts and self-knowledge identified above. In line with findings from Irish and Piguet (2013), it was predicted that the future thinking task would produce significantly more personal and general semantic details than would the autobiographical memory task (as this would demonstrate a greater reliance on semantic processing and the creation of a scaffold within which future episodic content could be more easily produced).

If personal semantics can be considered a bridge between general semantic and episodic processing (representing the degree of abstraction from the original context of their acquisition — Renoult et al., 2012; 2016) then it should be expected that their neural correlates will reflect this. Prior research has respectively identified associations between episodic and semantic memory content with fornix and ILF microstructure respectively (Hodgetts et al., 2017a; see also chapter 3). As such, it was predicted that personal semantic content (which can be considered to align with episodic details in that repeated and extended events retain some of their acquisitional context) would associate in both past and future tasks with fornix and ILF microstructure (positively with FA and negatively with MD). General semantics, which are considered to be fully abstracted from the spatiotemporal origin, were predicted to associate positively with ILF FA and negatively with ILF MD in both past and future conditions. It was predicted that general semantic content would not correlate positively with fornix FA or negatively with fornix MD values in either the past or future condition.

In the second stage of analysis, personal semantic details were divided into two subcategories based on their level of abstraction from contextual origin: self-knowledge and autobiographical facts (PSk — as would have been identified as ‘semantic’ in the Hodgetts et al. (2017a) coding scheme and subcategorised as ‘personal’ in this analysis) and repeated and extended events (RE — ‘categorical’ and ‘extended’ components of the external category in the Hodgetts et al. system). It was predicted that the autobiographical task would show significantly more RE than PSk details, as this was the more ‘episodic-like’ category and would follow the episodic pattern shown in chapter 3. Further it was predicted that the opposite pattern would be true in the future condition, that more PSk than RE details would be produced.

It was predicted that both PSk and RE details would correlate positively with ILF FA and negatively with ILF MD in both past and future conditions. It was further proposed that PSk details might be considered to show a greater level of abstraction and decontextualization than RE details (due to the latter retaining some level of contextual detail regarding their episodic origin — i.e. their experience-near nature would align them more closely with previous findings relating to episodic details). Therefore, it was predicted that PSk details would not associate positively with fornix FA or negatively with fornix MD, whereas RE details were predicted to correlate positively with fornix FA and negatively with fornix MD.

The semantic framework or scaffold hypothesis has suggested that ‘episodic’ future thinking is particularly supported by the semantic memory system (Irish & Piguet, 2013). The previous analyses have demonstrated that more general facts, autobiographical facts, and self-knowledge are produced in the future thinking condition than in the autobiographical condition, consistent with this hypothesis. A final comparison with which to test this theory correlated ILF microstructure with internal details produced in past and future narratives. Part of the data used for this analysis has been produced in Hodgetts et al. (2017a), which showed no association between ILF microstructure and episodic details in autobiographical recall. As such, it was predicted that the number of episodic details produced in a future thinking task would associate positively with ILF FA and negatively with ILF MD.

5.2 Methods

5.2.1 Scoring

The scripts (both for autobiographical memory and future thinking) were collected from those previously scored with a standardized AI scoring procedure (Hodgetts et al., 2017a; Levine et al., 2002; see chapter 3). This involved highlighting within each answer a primary and unique 'event' to be used for the 'internal' category. This was then further segmented for episodic details (regarding spatiotemporal, perceptual, emotional, etc details). Details that were not under this umbrella were recorded as 'external'.

Important to this analysis was the 'semantic' subcategory of external details. These details were examined and separated into either 'personal' or 'general' categories (for examples see table 5.1). The 'personal' category was operationalised as facts relating to or knowledge of a participant's own life story. In line with Renoult et al. (2020) (but unlike Strikwerda-Brown et al., 2019), this could include autobiographical facts that were indirectly related to the self. Remaining semantic details were classified as 'general semantics'.

As discussed above there has been some evidence that personal semantic details consist not only of self-knowledge (as is measured by the original Levine et al. scoring system) but also of repeated and extended events (Renoult et al., 2012; Renoult et al., 2016; Tanguay, 2018). These are also coded for in the Hodgetts et al. (2017a) coding system as 'categorical' and 'extended' details (in this coding system 'extended' events explicitly last for longer than 24 hours — for examples see table 5.1). These were also collected to be added to each participant's personal semantic knowledge score to provide a 'total' personal semantic score.

Table 5.1. Examples of personal and general semantic details as they might appear in episodic narratives

		Description	**Example**
Personal semantics	*Autobiographical facts*	Self-relevant factual content that is detached from its acquisitional context	*"My first pet was named Sophie"*
	Self-knowledge	Self-concept and personal identity. Regards knowledge of one's traits, attributes, etc	*"I work well under pressure"*
	Repeated events	Any details (event, time, place, perceptual, emotion/thought) regarding repeated episodes of the same activity	*"I played that album to death"*
	Extended events	Any details (event, time, place, perceptual, emotion/thought) regarding an episode that lasts for longer than 1 day or 24 h	*"I've got a plan… to go backpacking for 6 months"*
General semantics		General knowledge, facts, etc. Abstracted from original spatiotemporal context and culturally shared (i.e. they do not relate to the self)	*"Time travel is a staple of science fiction"*

5.2.2 MR imaging and tractography

The process by which imaging data was collected for this analysis (and the method by which tractography was performed) is fully detailed in chapter 3. Reconstruction of the fornix and ILF are described in chapter 2. The pre- and post-commissural fornix reconstructions were performed as described in chapter 3.

5.2.3 Statistical Analyses

Personal and general semantic details were tallied across the ten cued narratives for both past and future conditions to create the personal and general semantic scores for each participant. Personal semantic details consisted of a total addition of ‘personal semantic knowledge’, “extended” and “categorical” details from the modified Levine et al. (2002) coding scheme. The alpha level was set at $\alpha = 0.025$, as associations were predicted with both the fornix and ILF.

Due to presence of outliers in the details generated in the AI, non-parametric Kendall’s tau correlations were conducted instead of Pearson correlations (which are “overly sensitive” to these) (Pernet, Wilcox, & Rousselet, 2012). Where appropriate, this also necessitated the use of Wilcoxon Signed Rank tests (Wilcoxon, 1945). Primary comparisons were made between personal semantic and general semantic scores and ILF and fornix microstructure for both past and future conditions. All analyses were performed in JASP (2018, version 0.8.12). After transformation to a Pearson’s r value (Walker, 2003), significant differences between correlations were tested for using Steiger’s Z-test (Steiger, 1980) as implemented in the cocor webtool (Diedenhofen & Musch, 2015). Partial correlations for key comparisons were completed in RStudio (2020) using the R package ppcor (Kim, 2015), and imputation was completed where appropriate using the R package ‘mice’ (van Buuren & Groothuis-Oudshoorn, 2011).

Consensus scoring was established based on the agreement between two raters using intra-class correlation analysis. First, it was established that the scoring of external details was consistent between raters (intra-class correlation analysis, two-way mixed effects model: past semantic $r = 0.99$; future semantic $r = 0.85$; past categorical $r = 0.98$; future categorical $r = 0.93$; past extended $r = 0.97$; future extended $r = 0.86$). The reliability of subcategorising semantic details was tested by a second rater coding the details identified as ‘semantic’ by the primary rater (myself) as being either ‘personal’ or ‘general’ (intra-class correlation analysis, two-way mixed effects model: past personal semantic $r = 0.98$; future personal semantic $r = 0.88$; past general semantic $r = 0.97$; future general semantic $r = 0.67$). As such it was established that the coders showed good to excellent agreement across all categories in the analysis (Cicchetti, 1994).

5.3 Results

5.3.1 Number of personal and general semantic details produced for the past and future narratives

The mean, median, SD and range for total personal and general semantic details produced in both autobiographical recall and future simulation tasks are shown in table 5.2. A Kendall's tau correlation matrix showed positive associations between all detail outputs in this task (see figure 5.2).

Table 5.2. Displays the mean, median, SD and range for personal and general semantic details produced in past and future narratives

		Mean	Median	SD	Range
Autobiographical recall	*Personal*	54.7	49	29.9	15–136
	General	4.8	4	4.0	0–15
Future simulation	*Personal*	51.5	47	23.0	16–111
	General	11.4	11	8.1	1–35

A repeated measures ANOVA was performed to compare each of the mean scores. It was found that these violated the assumption of sphericity (Mauchly's W = 0.138, $p < 0.001$) and Greenhouse-Geisser correction was used as the value ($\varepsilon = 0.619$) was less than 0.75 (Girden, 1992). The means produced were found to significantly differ (F (1.86, 48.27) = 79.88, $p < 0.001$, VS-MPR = 7.225e+12, $\omega^2 = 0.743$).

Post hoc Bonferroni comparisons were used to compare the present findings with prior research. Irish and Piguet (2013) reported that more semantic details were produced in future simulation than in episodic recall (see also Devitt et al., 2017). The present results show that more general semantic details were included in the future narratives than in autobiographical recall (t=5.139, $p < 0.001$, $d_z = 0.989$). However, no difference was found between the number of personal semantic details produced in both past and future conditions (t= 0.702, $p = 1.000$, $d_z = 0.135$). It was further reported by Conway and Pleydell-Pearce (2000) that autobiographical constructions tend to show more personal than general semantic detail. The present findings found that this was the case both for the past (t= 9.453, $p < 0.001$, $d_z = 1.819$) and future conditions (t= 11.484, $p < 0.001$, $d_z = 2.210$).

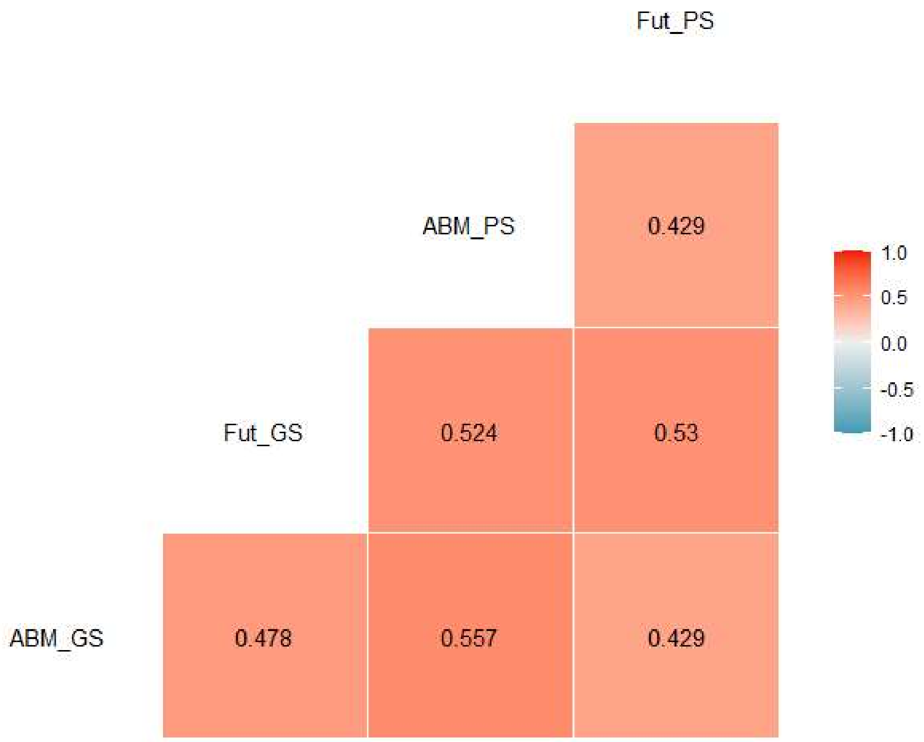
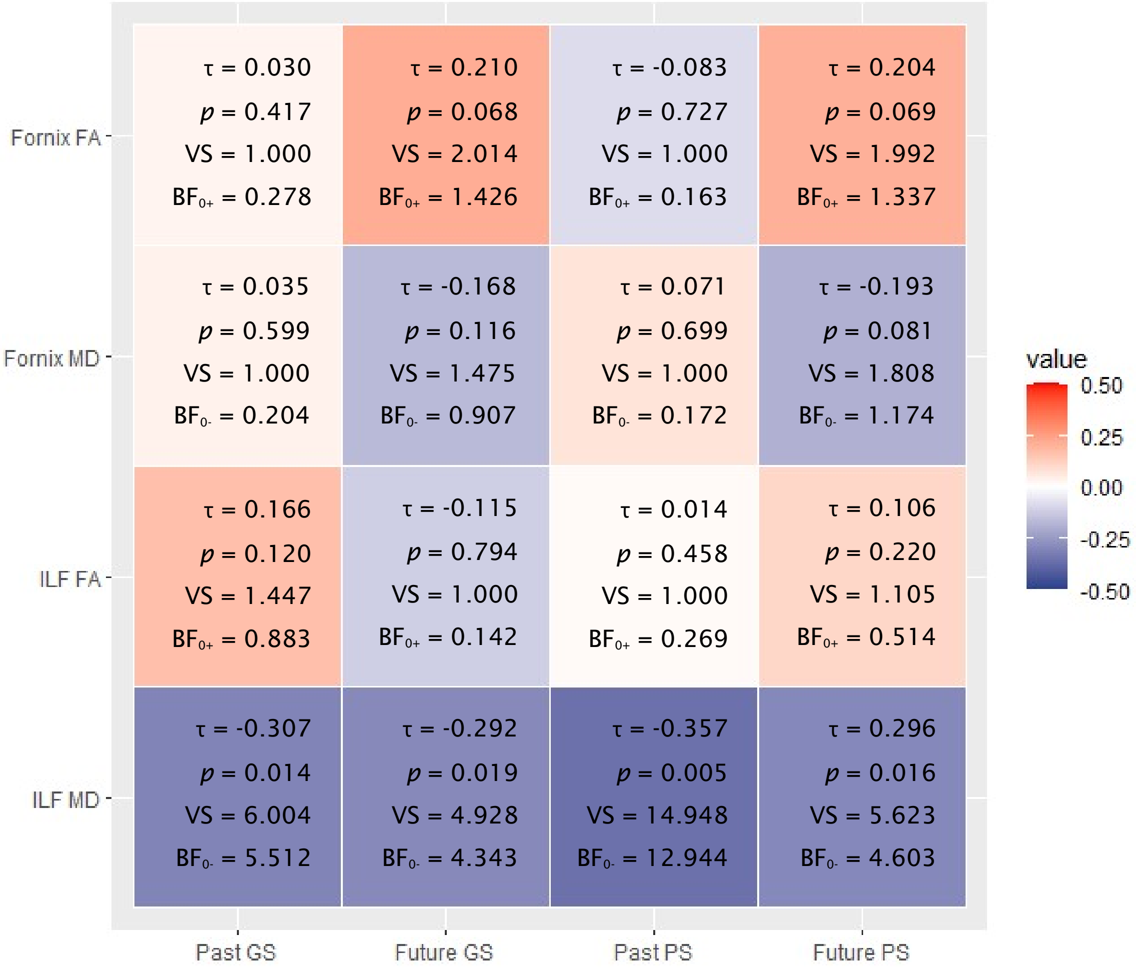


Figure 5.2. Shows the Kendall's tau correlation matrix between general and personal semantic details produced in autobiographical recall and future simulations. The correlations between future and past personal semantics; and future personal and past general semantic (p=0.002, two-tailed). All other correlations (p < 0.001, two-tailed). Produced in RStudio (2020) using GGally (Schloerke et al., 2011).

5.3.2 Personal and general semantic detail correlations with fornix and ILF microstructure

Significant negative correlations were found between ILF MD and the number of general semantic knowledge details in both the autobiographical memory (one-tailed Kendall's tau = -0.307, p = 0.014, VS-MPR = 6.004, BF_{0-} = 5.512) and future thinking tasks (one-tailed Kendall's tau = -0.292, p = 0.019, VS-MPR = 4.928, BF_{0-} = 4.343). Further, significant negative correlations were found for total personal semantic details with ILF MD in both past (one-tailed Kendall's tau = -0.357, p = 0.005, VS-MPR = 14.948, BF_{0-} = 12.944) and future tasks (one-tailed Kendall's tau = -0.296, p = 0.016, VS-MPR = 5.623, BF_{0-} = 4.603).

No significant correlations were found between personal or general semantic details and ILF FA in either the autobiographical memory or future thinking task. Further no correlations were found in either task for personal and general semantics with either fornix FA or MD microstructure (these are displayed in full in figure 5.3).



	Past GS	Future GS	Past PS	Future PS
Fornix FA	$\tau = 0.030$ $p = 0.417$ VS = 1.000 $BF_{0+} = 0.278$	$\tau = 0.210$ $p = 0.068$ VS = 2.014 $BF_{0+} = 1.426$	$\tau = -0.083$ $p = 0.727$ VS = 1.000 $BF_{0+} = 0.163$	$\tau = 0.204$ $p = 0.069$ VS = 1.992 $BF_{0+} = 1.337$
Fornix MD	$\tau = 0.035$ $p = 0.599$ VS = 1.000 $BF_{0-} = 0.204$	$\tau = -0.168$ $p = 0.116$ VS = 1.475 $BF_{0-} = 0.907$	$\tau = 0.071$ $p = 0.699$ VS = 1.000 $BF_{0-} = 0.172$	$\tau = -0.193$ $p = 0.081$ VS = 1.808 $BF_{0-} = 1.174$
ILF FA	$\tau = 0.166$ $p = 0.120$ VS = 1.447 $BF_{0+} = 0.883$	$\tau = -0.115$ $p = 0.794$ VS = 1.000 $BF_{0+} = 0.142$	$\tau = 0.014$ $p = 0.458$ VS = 1.000 $BF_{0+} = 0.269$	$\tau = 0.106$ $p = 0.220$ VS = 1.105 $BF_{0+} = 0.514$
ILF MD	$\tau = -0.307$ $p = 0.014$ VS = 6.004 $BF_{0-} = 5.512$	$\tau = -0.292$ $p = 0.019$ VS = 4.928 $BF_{0-} = 4.343$	$\tau = -0.357$ $p = 0.005$ VS = 14.948 $BF_{0-} = 12.944$	$\tau = 0.296$ $p = 0.016$ VS = 5.623 $BF_{0-} = 4.603$

Figure 5.3. The one-tailed Kendall's tau correlations (τ) between personal and general semantic details (both in autobiographical recall and simulation tasks) and fornix and ILF FA and MD. Also reported are *p* values (*p*), Vovk-Sellke maximum *p*-ratios (VS), and Bayes factors ($BF_{0+/-}$)

One-tailed Steiger's Z tests revealed significant differences between the associations of general semantic details in the past condition with ILF and fornix MD values (z = -2.04, *p* = 0.022) but no significant difference future general semantics between these two tracts (z = -0.749, *p* = 0.227). A two-tailed Steiger's Z test revealed a significant difference between the associations of personal semantic details recalled in the past condition with ILF and fornix MD (z = -2.58, *p* = 0.010). Finally, a two-tailed Steiger's Z test found a significant difference between the associations of the personal semantic details found in the future condition with ILF and fornix MD (z = -2.25, *p* = 0.025).

5.3.2.1 Influence of verbal fluency

Using the R package ppcor (Kim, 2015) it was established that all significant associations were preserved when controlling for the effect of verbal fluency. Therefore, significant negative correlations were found between ILF MD and general semantic details in the past (one-tailed Kendall's tau = -0.303, $p = 0.015$) and future conditions (one-tailed Kendall's tau = -0.290, $p = 0.019$), and personal semantic details in the past (one-tailed Kendall's tau = -0.357, $p = 0.005$) and future conditions (one-tailed Kendall's tau = -0.292, $p = 0.018$).

5.3.2.2 Post-hoc analysis: influence of ILF lateralisation

Prior research has found evidence that semantic processing is associated with left lateralisation (Grilli et al., 2018; Rice et al., 2015). Further, Hodgetts et al. (2017a) found that semantic details were more strongly associated with left ILF FA than right ILF FA, however, this difference was not significant. As such, it was considered important to further investigate the potential effect of lateralisation in the present analysis. To this end, the number of personal and general semantic details were correlated with both left and right ILF MD in both past and future tasks (the analysis was limited to MD values, as these had indicated significant associations in the initial analysis).

Significant negative correlations were found between left ILF MD values and the number of general semantic produced in the past (one-tailed Kendall's tau = -0.396, $p = 0.002$, VS-MPR = 25.044, $BF_{0-} = 27.501$) and future conditions (one-tailed Kendall's tau = -0.369, $p = 0.004$, VS-MPR = 15.631, $BF_{0-} = 16.138$). Further, left ILF MD was found to negatively correlate with the number of personal semantic details produced in both the past (one-tailed Kendall's tau = -0.454, $p < 0.001$, VS-MPR = 104.785, $BF_{0-} = 97.291$) and future conditions (one-tailed Kendall's tau = -0.296, $p = 0.016$, VS-MPR = 5.623, $BF_{0-} = 4.603$).

No significant associations were found between right ILF MD and the number of general semantic produced in either the past (one-tailed Kendall's tau = -0.136, $p = 0.167$, VS-MPR = 1.231, $BF_{0-} = 0.665$) or future conditions (one-tailed Kendall's tau = -0.080, $p = 0.285$, VS-MPR = 1.028, $BF_{0-} = 0.417$). Further, no significant associations were found between right ILF MD and the number of personal semantic details produced in either the past (one-tailed Kendall's tau = -0.186, $p = 0.088$, VS-MPR = 1.725, $BF_{0-} = 1.090$) or future conditions (one-tailed Kendall's tau = -0.141, $p = 0.153$, VS-MPR = 1.280, $BF_{0-} = 0.695$).

One-tailed Steiger's Z tests revealed significant differences between the associations of left and right ILF MD values with the number of general semantic details produced in the past condition ($z = -2.020$, $p = 0.022$); the associations of left and right ILF MD values with the number of general semantic details produced in the future condition ($z = -2.228$, $p = 0.013$); the associations of left and right ILF MD values with the number of personal semantic details produced in the past condition ($z = -2.121$, $p = 0.017$). No significant difference was found between the associations of left and right ILF MD values with the number of personal semantic details produced in the future condition (z = -1.182, p = 0.119).

5.3.3 Personal semantic subcomponent details produced for autobiographical recall and future simulation narratives

The mean, median, SD and range for the number of personal semantic RE and PSk details produced in both autobiographical recall and future simulation tasks are shown in table 5.3. A repeated measures ANOVA was performed to compare the mean scores produced in each condition. It was found that these violated the assumption of sphericity (Mauchly's W = 0.182, $p < 0.001$) and Greenhouse-Geisser correction was used as the value ($\varepsilon = 0.609$) was less than 0.75 (Girden, 1992). The means produced were found to significantly differ (F (1.83, 47.53) = 55.64, $p < 0.001$, VS-MPR = 1.160e+10, $\omega^2 = 0.667$).

In line with predictions, it was found that significantly more RE details were produced than PSk details in the autobiographical recall task (t(26) = 9.26, $p < 0.001$, $d_z = 1.782$). Further it was found that significantly more RE details were found in the past than in the future condition (t(26) = 8.13, $p < 0.001$, $d_z = 1.565$). It was found that in the future condition, significantly more PSk than RE details were produced (t(26) = 7.50, $p < 0.001$, $d_z = 1.443$). Finally, it was found that significantly more PSk details were produced in the future than in the past condition (t(26) = 8.62, $p < 0.001$, $d_z = 1.659$).

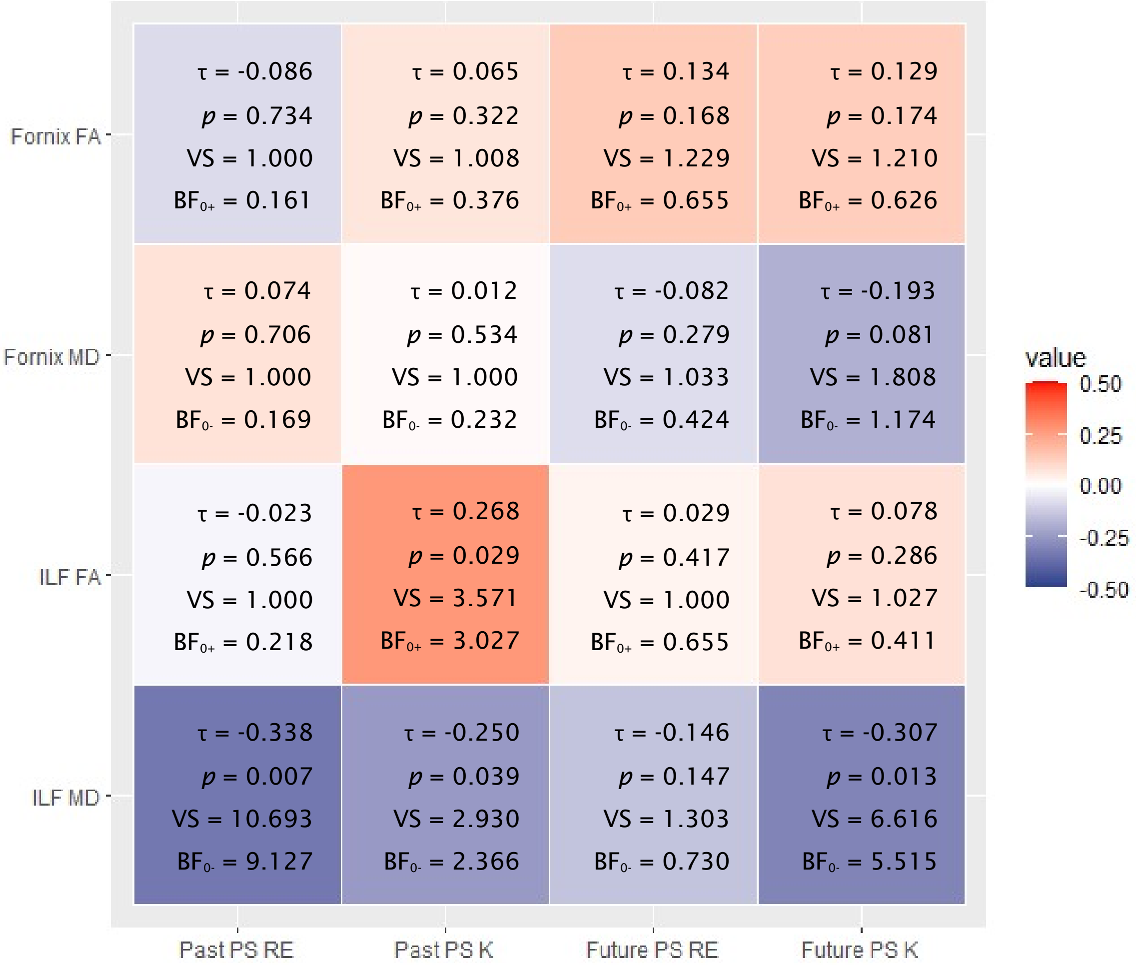
Table 5.3. Displays the mean, median, SD and range for personal and general semantic details produced in past and future narratives

		Mean	Median	SD	Range
Autobiographical recall	*RE*	48.4	48	27.3	11–126
	PSk	6.3	5	4.7	0–18
Future simulation	*RE*	11.9	12	6.6	0–27
	PSk	39.6	34	19.5	15–87

A positive correlation was found between PSk and RE details produced in the autobiographical recall condition (two-tailed Kendall's tau = 0.358, p = 0.012, VS-MPR = 7.154, BF_{10} = 6.667). No association was found between PSk and RE produced in the future condition (two-tailed Kendall's tau = 0.271, p = 0.054, VS-MPR = 2.344, BF_{10} = 1.629). The number of RE details produced in past and future conditions showed a significant positive association (two-tailed Kendall's tau = 0.290, p = 0.038, VS-MPR = 2.961, BF_{10} = 2.152). Finally, no association was found in the number of PSk details produced in the past and future conditions (two-tailed Kendall's tau = 0.111, p = 0.436, VS-MPR = 1.000, BF_{10} = 0.340).

5.3.4 Personal semantic subcomponent correlations with fornix and ILF microstructure

Significant negative associations were found between past RE details and ILF MD (one tailed Kendall's tau = -0.338, p = 0.007, VS-MPR = 10.693, BF_{0-} = 9.127) and future PSk details and ILF MD (one tailed Kendall's tau = -0.307, p = 0.013, VS-MPR = 6.616, BF_{0-} = 5.515). All other associations were non-significant (p > 0.025). The full output of these correlations is displayed in Figure 5.4.



	Past PS RE	Past PS K	Future PS RE	Future PS K
Fornix FA	τ = -0.086 p = 0.734 VS = 1.000 BF_{0+} = 0.161	τ = 0.065 p = 0.322 VS = 1.008 BF_{0+} = 0.376	τ = 0.134 p = 0.168 VS = 1.229 BF_{0+} = 0.655	τ = 0.129 p = 0.174 VS = 1.210 BF_{0+} = 0.626
Fornix MD	τ = 0.074 p = 0.706 VS = 1.000 BF_{0-} = 0.169	τ = 0.012 p = 0.534 VS = 1.000 BF_{0-} = 0.232	τ = -0.082 p = 0.279 VS = 1.033 BF_{0-} = 0.424	τ = -0.193 p = 0.081 VS = 1.808 BF_{0-} = 1.174
ILF FA	τ = -0.023 p = 0.566 VS = 1.000 BF_{0+} = 0.218	τ = 0.268 p = 0.029 VS = 3.571 BF_{0+} = 3.027	τ = 0.029 p = 0.417 VS = 1.000 BF_{0+} = 0.655	τ = 0.078 p = 0.286 VS = 1.027 BF_{0+} = 0.411
ILF MD	τ = -0.338 p = 0.007 VS = 10.693 BF_{0-} = 9.127	τ = -0.250 p = 0.039 VS = 2.930 BF_{0-} = 2.366	τ = -0.146 p = 0.147 VS = 1.303 BF_{0-} = 0.730	τ = -0.307 p = 0.013 VS = 6.616 BF_{0-} = 5.515

Figure 5.4. The one-tailed Kendall's tau correlations (τ) between PSk and RE details (both in autobiographical recall and simulation tasks) and fornix and ILF FA and MD. Also reported are p values (p), Vovk-Sellke maximum p-ratios (VS), and Bayes factors ($BF_{0+/-}$)

Steiger's Z tests revealed that the associations between RE details generated in the past condition with fornix and ILF MD values were significantly different (z = -2.478, p = 0.007). However, no difference was found between the associations of future PSk details with fornix and ILF MD values (z = -0.693, p = 0.244).

5.3.4.1 Influence of verbal fluency

Partial correlations showed that significant associations were maintained for ILF MD and RE in the past condition (one-tailed Kendall's tau = -0.336, p = 0.08) ILF MD and PSk in the future condition (one-tailed Kendall's tau = -0.303, p = 0.015).

5.3.5 Correlations between internal details and ILF microstructure

No significant association was found between ILF FA and the number of episodic details produced in either the past (Figure 5.5A. One-tailed Kendall's tau = -0.132, p = 0.831, VS-MPR = 1.000, BF_{0+} = 0.133) or future (Figure 5.5B. One-tailed Kendall's tau = -0.080, p = 0.721, VS-MPR = 1.000, BF_{0+} = 0.165) conditions. Further, no significant association was found between ILF MD and the number of episodic details produced in either the past (Figure 5.5C. One-tailed Kendall's tau = -0.137, p = 0.158, VS-MPR = 1.261, BF_{0+} = 0.673) or future (Figure 5.5D. One-tailed Kendall's tau = -0.006, p = 0.483, VS-MPR = 1.000, BF_{0+} = 0.256) conditions.

Steiger's Z tests revealed that no difference was found for episodic detail associations with ILF FA in past condition and future conditions (z = 0. 477, p = 0.317). Further, no difference was found for episodic detail associations with ILF MD in past condition and future conditions (z = 1.201, p = 0.115).

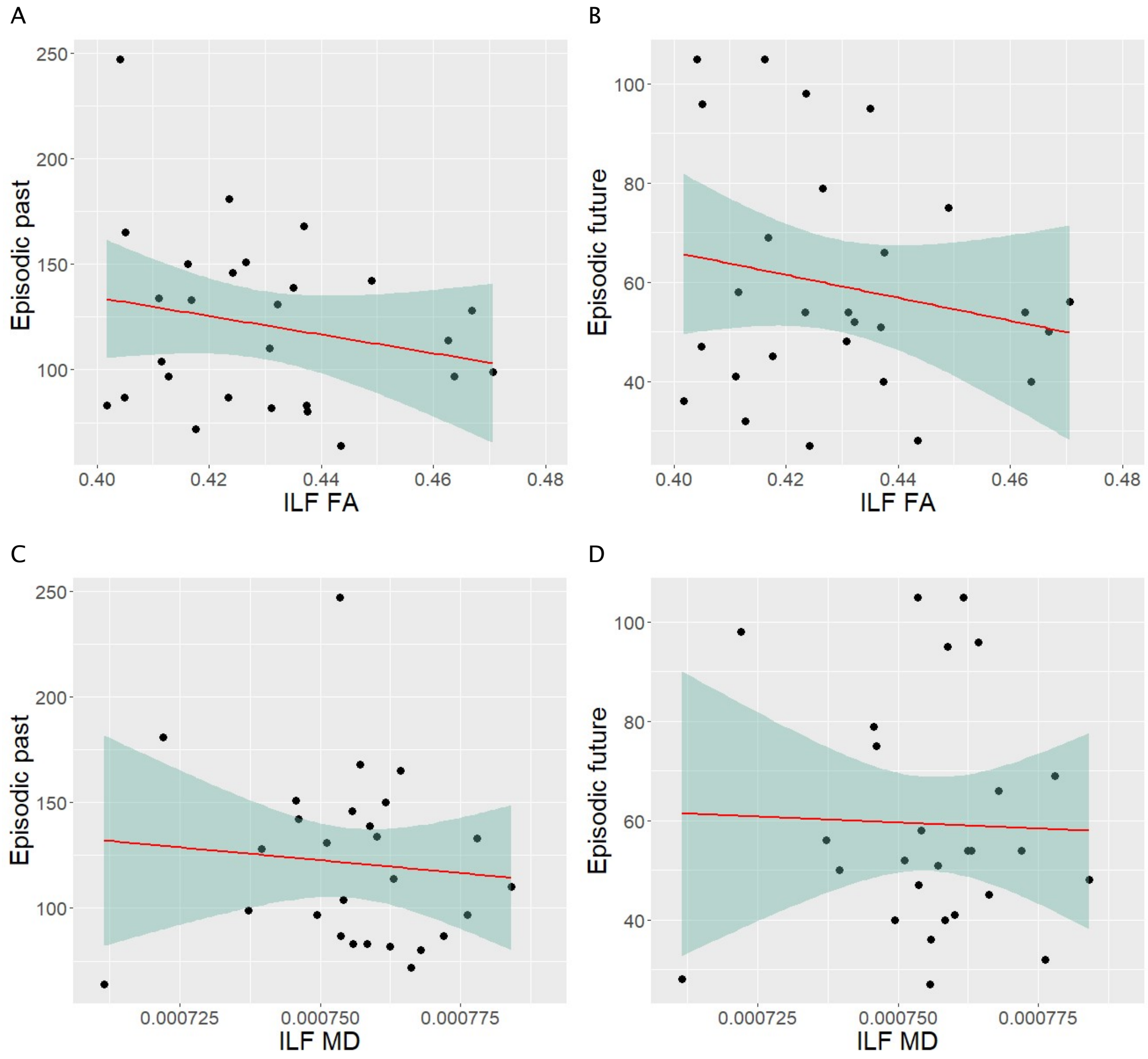


Figure 5.5 (A-D). Scatterplots depicting the correlations of ILF FA (A, B) and MD microstructure (C, D) against the number of episodic details produced in past and future AI tasks. Number of episodic past/future details (summed over 10 cue words) is plotted on the y-axis (N=27). Shading equals the 95% CI.

5.4 Discussion

Although a key focus within mental time travel research is temporality and episodic memory, evidence has also emerged that the atemporal semantic memory system is vital to its effective function (Irish & Piguet, 2013). Research using AI has often considered semantic details as being homogenous or part of a broader category (e.g. Hodgetts et al., 2017a; Levine et al., 2002). However, a growing body of research has looked to subdivide the semantic details produced in episodic construction (Renoult et al., 2012; 2016) and in particular during AI (Renoult et al., 2020; Strikwerda-Brown et al., 2019). These details have been identified as personal and general semantics and various models have been proposed to explain how episodic, personal semantic and general semantic memory systems are combined within episodic constructions (Conway, 2001; D'Argembeau, 2020; Irish et al., 2012a; Renoult et al., 2012; 2016). The present project used this research to inform the development of a coding scheme related to the identification of personal and general semantic details produced in AI narratives.

It has been found that future thinking generates a higher number of external (see chapter 3) and semantic details (Irish & Piguet, 2013). The present study demonstrated that a greater number of general semantic details were produced in the future thinking than the autobiographical recall task. Further, although no difference was found in total personal semantic scores, the past condition showed a greater level of RE and the future condition a greater level of PSk (the latter results is particularly interesting given the conceptual similarities between PSk and general semantics). As such, these findings broadly support present predictions (with the exception that no difference was found between total personal semantic details produced in past and future conditions). Taken as a whole, these findings can be considered consistent with the idea that semantic content, and particularly 'experience-far' content, is of particular importance to autobiographical future thinking. Further, it supports the view of Renoult et al. (2012) that RE details may be more closely aligned with episodic memory (which has also been noted to be more prevalent in past rather than future thinking — e.g. Addis et al., 2008).

In line with predictions, the present analysis found that both total personal semantic and general semantic details negatively correlated with ILF MD values in both past and future tasks. Bayes factors broadly indicated moderate support for this association (BF ~ 5), although strong evidence was found associating total personal semantic details produced in the past condition and ILF MD (BF ~ 13). However, the predicted positive association between personal and general semantics and ILF FA values was not established. Further, moderate evidence was even found in favour of the null hypothesis (BF < 0.33) regarding associations between ILF FA and general semantic details in the future thinking condition, and personal semantic details in the autobiographical condition. This emphasises the difficulty that can arise when working with DTI metrics, and the importance of reporting multiple measures where possible (see Johnson et al., 2014; chapter 3). Taken as a whole, it is suggested that this does support an association between personal and general semantic detail production in autobiographical constructions, however, it does highlight the need for better understanding in the precise nature of the biological attributes that underlie microstructure-cognition associations.

Fornix FA did not correlate positively with either general or personal semantic details produced in either the past or future condition. Further, fornix MD did not correlate negatively with either general or personal semantic details produced in either the past or future condition. Moderate evidence (BF < 0.33) was found against associations of fornix FA and MD values with personal and general semantic details produced in the autobiographical memory narrative. In the future thinking condition, Bayes factors indicated only anecdotal support for the null hypothesis for the association between general semantic details and fornix MD (BF ~ 0.9). In the future thinking condition anecdotal evidence was found supporting a positive association between fornix FA and total personal/general semantic details (BF ~ 1.4). Further, anecdotal evidence was found supporting a negative association between fornix MD and personal semantic details in the future thinking condition (BF ~ 1.2). This supports the prediction that there would be no positive/negative association between fornix FA/MD respectively and general semantics (although only in the autobiographical memory condition). However, it was also predicted that personal semantic details would associate with fornix microstructure — in line with prior research that had suggested that personal semantic details might be considered to share some features of episodic memory, and that they might exist on a spectrum of abstraction between general semantic and episodic memory (Maguire & Frith, 2003; Renoult et al., 2012; 2016). The full pattern of these findings instead supports the conclusion that personal semantics are a subcomponent of the general semantic system (Grilli et al., 2018).

A post-hoc analysis indicated that both personal and general semantic details produced in autobiographical recall and future thinking narratives were negatively associated with left ILF MD. No negative association was found between these details and right ILF MD (Bayes factor analyses did not find evidence in favour of the null — BF > 0.33). Further, Steiger's Z tests generally indicated that significant differences could be found between the associations of left and right ILF MD, and personal/general semantic details produced in both conditions. As such, present results support the notion that individual differences in both personal and general semantics as measured by the AI are mediated by left ILF connectivity with the semantic hub in the ventral anterior temporal lobe (Grilli et al., 2018; Rice et al., 2015; see also Chen et al., 2017; Patterson et al., 2007; Rogers et al., 2004).

Personal semantics themselves can be further subdivided into autobiographical facts, self-knowledge, and repeated and extended events. The former of these can be considered close to semantic memory in their form, whereas the latter show relative similarities to episodic memory (Renoult et al., 2012). Functional neuroimaging research has shown that activity differs between autobiographical facts and repeated events in the hippocampus and medial temporal lobe (Addis et al., 2004; Holland et al., 2011). However, an ERP study by Renoult et al. (2016) failed to show functional differences between repeated events and autobiographical facts. It was predicted that repeated and extended events would show an association with fornix microstructure, but that all personal semantic subcomponents would associate with ILF microstructure.

As predicted, a negative association was found between ILF MD and RE details in the autobiographical recall narratives (BF ~10), and PSk details in the autobiographical future thinking narratives (BF ~ 5). Although not significant ($\alpha > 0.025$), moderate evidence (BF > 3) was found associating ILF FA with PSk details produced in the past condition. However, contrary to predictions, no other personal semantic subcomponents were found to associate with ILF microstructure. In fact, moderate evidence (BF < 0.33) was found in favour of the null hypothesis when testing for a positive association between ILF FA and RE details produced in the past condition. These results provide weak evidence of a link between ILF microstructure (most likely MD) and the subcomponents of personal semantic processing. However it seems likely that the present study is underpowered for this effect, and future studies with larger samples will be needed to confirm these associations.

VS-MPR did indicate that a stronger association was found between ILF MD values and RE details in the past condition than in the future condition, and conversely that a stronger association was found between ILF MD and PSk details in the future condition than in the past condition. Together with the behavioural findings reported above, it is possible that the 'knowledge' based (or acontextual) personal and general semantic processing form the basis of a semantic framework that enables episodic future thinking. Future research might examine if patients with deficits in semantic memory show differential deficits in the subcomponents of personal semantics. Indeed a preprint by Strikwerda-Brown, Hodges, Piguet and Irish (2020) has proposed a new fine-grained taxonomy (NExt) with which to examine external details. These authors suggest that further analysis of 'external' content in the AI will provide novel insight due to the wealth of detail pertaining directly to the participant's life story. Notably, their results demonstrate an effect by which episodic memory might serve to support 'semantic-like' recall in patients with semantic dementia. This finding supports the idea that episodic and semantic systems are highly interactive, though dissociable at behavioural and neural level.

No positive/negative associations were found respectively between fornix FA or MD and the personal semantic subcomponent details produced in either autobiographical recall or future thinking narratives. Although this was predicted for PSk details, Bayes factors did not provide strong evidence to support a lack of association. Moderate evidence was found in favour of the null hypothesis for the tested negative association between PSk details in the past condition and fornix MD (BF ~ 0.23). However, only anecdotal evidence was found in favour of the null hypothesis for the tested positive association between PSk details produced in the past and future condition and fornix FA (0.33 < BF < 0.63). Further, these results were against the prediction that RE details would associate with fornix microstructure. In fact, Bayes factor analysis supported the null hypothesis for the proposed positive fornix FA and negative fornix MD associations with RE details in the past condition (BF < 0.17). However, only anecdotal evidence in favour of the null was found for proposed positive fornix FA and negative fornix MD associations with RE details in the future condition (BF ~ 0.5).

These results align with the findings of Coronel and Federmeier (2016) who found that personal and general semantics showed overlapping ERP responses and suggested that the two shared fundamental neurobiological underpinnings (see also Grilli et al., 2018). Coronel and Federmeier's findings should be considered in the context of their experimental paradigm. These authors only used a single form of personal semantic information (the participant's reported personal preferences) in their analysis. As such, this finding might only reflect that this form of personal semantic processing shares the neural correlates of general semantic processing. However, as noted above a number of studies have successfully differentiated different forms of semantic processing at the neural level (e.g. Addis et al., 2004; Maguire & Frith, 2003; Renoult et al., 2016). Research by Mace, McQueen, Hayslett, Staley and Welch (2019) showed that conceptual semantic processing (in response to both lexical and non-lexical stimuli) primed voluntary and involuntary autobiographical recall. It is suggested that this phenomenon might in part explain the results of functional studies (whereas this would not be apparent in the present work that associated neural architecture with detail production in AI narratives). Finally, it is important to consider that functional and structural neuroconnectivity are not perfectly aligned between the two processes. This is suggested as the categories were shown to differ at a behavioural level but not at neural level employed in this analysis (see also Conway & Pleydell-Pearce, 2000; D'Argembeau, 2013; Irish & Piguet, 2013).

Episodic details produced in the future thinking task were not found to associate positively with ILF FA or negatively with ILF MD. Further in both cases, Bayes factors (BF < 0.33) provided moderate support in favour of the null hypothesis (i.e. that there is no positive/negative association between internal details and ILF FA/MD respectively). This can be taken as a specific challenge to the semantic framework hypothesis, which suggested that episodic future thinking is heavily reliant on the semantic memory system (Irish & Piguet, 2013). These findings must be considered within the context of prior research — they reflect a healthy population, whereas Irish's model was developed from work with semantic dementia patients (but see D’Argembeau & Demblon, 2012; D’Argembeau & Mathy, 2011). It is possible that healthy brains do not directly rely on semantic memory, such that it dictates the level of or capacity for episodic future. However, the system might be important for establishing a future temporality such that healthy future thinking cannot be supported without it. The balance of present findings suggest that personal semantic and episodic systems are highly interactive but dissociable. As such, the deficits displayed by patients with semantic might reflect an incapability to properly engage their episodic system with the task requirements of creating potential episodic future scenarios.

Irish et al. (2012a) showed that 80% of future simulations generated by semantic dementia patients were reproductions of entire events that they had experienced. It is unknown in the present sample to what extent participants were creating novel constructions or relying on and repurposing pre-lived scenarios. This is a limitation of the present task and should be considered when evaluating the present findings. This issue can be addressed using a recombination task (see Addis, Musicaro, Pan, & Schacter, 2010). Further insight might be made by controlling for the degree of novelty within a constructed future scenario. Prior research has identified that the degree of novelty in a constructed future episode moderated the contribution of episodic and semantic systems (Wang, Yue, & Huang, 2016). These findings suggest that future research might also consider the qualities of the constructed future scenarios, and the contribution made to these by both episodic and semantic systems. In particular, these might provide further insight into the relationships between general semantic, personal semantic, and episodic memory.

It is important to consider how the present approach compared to that of contemporary research. This coding scheme was developed parallel to those of Strikwerda-Brown et al. (2019) and Renoult et al. (2020), and although largely similar, the three are not precisely congruous. For example, in Strikwerda-Brown et al. personal semantic details required the detail to be explicitly self-relevant. This was not the case in the present scheme, or in Renoult et al., which allowed for autobiographical facts to indirectly relate to the self. Further, neither the present method nor the taxonomy proposed by Strikwerda-Brown et al. separated autobiographical facts and self-knowledge, however, these were separately recorded by Renoult and colleagues. The differences between coding schemes are due to a lack of consensus on key definitions and concepts within the field. Further consideration might be made of the baseline task instructions for conducting an AI. Participants are asked to focus on providing as much episodic detail as possible, which might impact the number of semantic details they produce. Moving forward, it will be important to establish a consensus on the definitions, scoring and testing methods used in this field of research.

In the present analysis personal semantic details were grouped to allow for a binary comparison between 'episodic-like' and 'semantic-like' details. It was predicted that this would allow the present analysis to establish if interindividual differences in white matter microstructure supported the existence of an episodic-semantic spectrum relating to autobiographical processing. The 'semantic-like' category was formed of autobiographical facts and self-knowledge, as these details were proposed to relate less to their contextualised, episodic origins than did the 'episodic-like' details (i.e. repeated and extended events). Further to conceptual similarities, these groupings were informed by research that had identified overlapping neural correlates (e.g. Maguire & Frith, 2003; Renoult et al., 2012). However, a growing body of work has demonstrated that autobiographical facts and self-knowledge can be differentiated on a neural level (Grilli et al., 2018; Klein & Lax, 2010; Marquine et al., 2016; Renoult et al., 2016; Tanguay et al., 2018; Tanguay, Palombo, Atance, Renoult, & Davidson, 2020). Work with lesion patients has demonstrated that damage to left (but not right) anterior ventral lobe is associated with deficits to autobiographical facts but not self-knowledge (Grilli et al., 2018; but see Renoult et al., 2012), whereas knowledge of personal traits was found to be impaired with damage to mPFC (Marquine et al., 2016). The findings of the present analysis might suggest that both autobiographical facts and self-knowledge were associated with ILF and not fornix microstructure. However, as they were grouped together it is impossible to judge the individual contributions to these findings (for example it could be that a greater number of autobiographical facts were produced than the number of self-knowledge details, and that it was this bias that predicated the pattern of associations). Future work should look to adapt the current approach, so that autobiographical facts and self-knowledge are recorded separately. This would allow for clarification on the neural substrates supporting the production of these details in healthy participants. Further, the role of the mPFC in self-knowledge (using e.g. an "I am" self-statement task), and how this relates to aspects of episodic self-processing, including goals and emotions (D'Argembeau, 2020) could be a focus for future research.

In conclusion, overlapping neural correlates are associated with the production of personal and general semantics in episodic construction (i.e. they are mediated by left ILF connectivity to the anterior temporal lobe). However, a clear difference has been established between the white matter associations of personal semantics and episodic details (see also chapter 3). This finding was maintained even when examining the most 'episodic-like' aspects of personal semantics (i.e. repeated and extended events). The results of this analysis challenge the idea of an episodic-semantic spectrum of abstraction, and instead support personal semantics as a subdomain of general semantic processing (Grilli et al., 2018; Renoult et al., 2012). These results suggest mental time travel is supported by a broad autobiographical network composed of dissociable but interactive components (D'Argembeau, 2020; Tulving, 2005). Further, behavioural evidence provides some support for the semantic scaffolding hypothesis (although tract associations seemed largely to challenge this account). Finally, it will be important for future research to form a consensus on the definition of key concepts and the methods by which scripts are coded.

Chapter 6: General Discussion

6.1 Overview of the project

Episodic and semantic memory have been cornerstones of memory research ever since they were first described in a seminal article by Endel Tulving (1972). Later work by Tulving (1985, 2002a, 2005) posited that particularly episodic memory supported mental time travel, a process by which humans could project the self across a conceptual lifespan (however later work has emphasised the role of semantic memory in the process — Conway & Pleydell-Pearce, 2000; D'Argembeau, 2020; Irish & Piguet, 2013; Klein 2013). Tulving suggested that the capacity to project an aspect of the self across both lived and potential experiences was fundamental to the separation of human consciousness from that of other life forms. Over time the field of mental time travel research has expanded and associated the construct with aspects of high-level human cognition - including decision making in novel environments (Brocas & Carrillo, 2018) and the creative aspects of language (Corballis, 2019). Further work has examined the brain regions and functional networks that support mental time travel (or self-projection more broadly), which has seen the development of neurocognitive models seeking to explain the ability (e.g. Carroll & Buckner, 2007; D'Argembeau, 2020; Irish & Piguet, 2013; Klein, 2013; Maguire & Mullally, 2014; Schacter & Addis, 2007b). Still, fundamental questions remain. While it is now recognized that a common 'core' brain network underlies memory, prospection, and imagination (Schacter et al., 2017), the neural substrates of the component processes that comprise the core network supporting memory- based simulations, and the extent to which they are dissociable, are still a matter of intense debate (D'Argembeau, 2020; Mullally & Maguire, 2014; Schacter et al., 2012).

The present project used an individual differences approach to investigate the relationship between white matter microstructure in two key tracts of the core network (i.e. the fornix, the main tract of the episodic hippocampal network, and the ILF, the main tract of the ventral semantic network - Alves et al., 2019; Hodgetts et al., 2017a; Schacter et al., 2012) and key component cognitive processes that have been suggested to support mental time travel. The focus on neuroarchitecture in a healthy population (i.e. not using either functional imagining or lesion patients) is a relatively novel approach in autobiographical memory research (see also Hebscher et al., 2018; Hodgetts et al., 2017a; Williams et al., 2020). The analyses within this project are proposed to complement wider research (Nyberg, 1996) and provide further context for questions regarding the underlying neurocognitive features of mental time travel or self-projection more broadly.

Further, this thesis aimed to investigate mental time travel as a bidirectional process (i.e. investigating both the personal past and future). The research carried out by Hodgetts and colleagues (2017a) provided a conceptual and practical foundation for the general approach of this thesis. However, their work only examined autobiographical recall and did not include a task based on 'episodic' future thinking (Atance & O'Neil, 2001). The present thesis represents an extension of this approach and allowed for a fuller examination of mental time travel in a broader scope, encompassing imagining as well as remembering. Further to this, novel coding schemes for the modified Autobiographical Interview (Levine et al. 2002) were developed and employed such that finer-grained answers could be provided to more specific questions about the component cognitive processes and representations supporting mental time travel. In particular, the extent to which self-relevance and autonoetic consciousness (Fivush, 2011; Tulving, 2005) are part of and support mental time travel were examined. Further, this more focused approach allowed for investigation into the role of episodic and semantic processing, including personal semantic memory, within autobiographical constructions. Understanding the specific nature of these component processes is vital for the evaluation of contemporary models of mental time travel.

Another important aspect of the present project was the combined approach of using both self-reported trait-based and performance-based measures of autobiographical memory and future thinking. This was achieved by using a self-reported index of trait mnemonics, the survey of autobiographical memory (SAM; Palombo et al., 2013), in addition to the modified AI detailed above. Whereas historical work might have seen these approaches to be naturally opposed (Banaji & Crowder, 1989; Conway, 1991; Neisser, 1978), they are better considered as complementary methods that are able to answer specific questions that the other cannot (Tulving, 1991). This combined approach was important regarding a holistic examination of mental time travel and allowed present findings (derived from self-report of the subjective experience of mental time travel and task-based measures examining specific component cognitive processes) to be interpreted in a broader fashion than if one method had been pursued alone.

6.2 Summary of experimental chapters and main findings

6.2.1 Interindividual variation in fornix and ILF microstructure and mnemonic "traits" as measured with the survey of autobiographical memory

As noted above, subjective or self-reported measures of memory (such as the present work on mnemonic traits, which are thought to index stable individual differences in subjective mnemonic experiences) are a valuable tool in complement to laboratory- and performance-based measures of autobiographical cognition (Palombo et al., 2013). In particular, trait-based measures are proposed to assay general mnemonic styles whereas performance-based measures are proposed to be more heavily influenced by the recall of a select few events (Palombo, Sheldon, & Levine, 2018). The SAM allows for the inspection of self-reported mnemonic traits (episodic, semantic, and spatial/navigational) and prospection tendencies. In line with other stable traits, for example relating to emotion (Watson & Walker, 1996) and personality (Cobb-Clark & Schurer, 2012), individual differences in trait mnemonics are likely to be grounded in stable aspects of brain function and structure (see also Crawford, Muhlert, MacDonald, & Lawrence, 2020; Sheldon, Farb, Palombo, & Levine, 2016).

The present research aimed to extend this prior work by demonstrating that individual differences in white matter microstructure of key tracts in the 'core' network could be associated with trait mnemonics as measured by the SAM. Prior research by Hodgetts and colleagues (2017a) demonstrated that a double dissociation could be found between episodic and semantic detail production in an autobiographical memory task (the AI) and their association with the fornix (the key white matter tract linking the hippocampus with the rest of the core network — Alves et al., 2019) vs. the ILF (the key white matter tract of the ventral semantic system — Alves et al., 2019), respectively.

Various neurocognitive models have been proposed that attempt to explain the component processes of mental time travel. Episodic construction (Schacter & Addis, 2007b) and scene construction accounts (Hassabis & Maguire, 2007) have emphasised the importance of the hippocampus in constructing both past and future events. The latter account, alongside cognitive map theory (Epstein et al., 2017), further emphasises a more select role in the spatial components of constructive memory. While Tulving (2002a) (consistent with Hodgetts et al., 2017a) has emphasized the distinction between episodic and semantic memory systems in mental time travel, recent work with semantic dementia patients has provided some evidence that semantic memory might play a specific role in episodic future thinking, suggesting a common neural substrate upon which both semantic and episodic future thinking rely (Irish et al., 2012a; Irish & Piguet, 2013). In line with the previous findings of Hodgetts et al. (2017a), it was predicted that fornix microstructure would associate with episodic memory, spatial memory, and future thinking. By contrast, ILF microstructure was predicted to associate with semantic memory (as in Hodgetts et al., 2017a) but also potentially with future thinking - as suggested by Irish & Piguet (2013).

It was found that significant associations exist between fornix microstructure and the SAM measures of spatial memory and episodic future thinking (BF ~ 10 indicated a strong support for the alternate hypothesis). Notably, however, no associations were found between either episodic or semantic memory and any of the white matter indices used in the analysis. Hence, the results can be considered to provide converging evidence for neurocognitive models that propose that the extended hippocampal circuitry mediated by the fornix plays a role in forming a spatially coherent scene (or map, context, etc) in which episodic constructions are formed (Epstein et al., 2017; Hassabis & Maguire, 2007; Murray, Wise, & Graham, 2018). It was proposed that the lack of expected associations might be due to issues with criterion validity and capacity for accurate self-knowledge outside of particularly mnemonic domains.

6.2.2 The role of the pre-commissural fornix in episodic autobiographical memory and future thinking

The next stage of the project adopted a task-based approach, to allow for a complementary examination of autobiographical memory and episodic future thinking. Participants completed a modified form of the autobiographical interview (AI) (Levine et al., 2002; Addis et al., 2008). The past component of the AI was used by Hodgetts et al. (2017a) to establish that fornix FA values associated with the production of 'internal' (episodic) details during recall in an AI task. In an extension to this, the present analysis examined both autobiographical recall and episodic future thinking, to examine the extent to which they share neural substrates.

Further, the research by Hodgetts et al. (2017a) examined the fornix as a unified bundle. Prior research, however, has indicated that episodic recall and prospection are both linked with activity in, and functional connectivity between, the hippocampus and vmPFC (Andrews-Hanna et al., 2010; Campbell et al., 2018; Schacter et al., 2012). Using a novel anatomically guided tractography protocol, based on findings in nonhuman primates that the fornix can be divided into pre- and post-commissural sections (which respectively link the hippocampus to the vmPFC and mammillary bodies — Aggleton et al., 2015), it became possible to test for a specific role of hippocampal-vmPFC structural connectivity in mental time travel. Based on prior functional MRI and patient-lesions findings, it was predicted that pre-commissural, but not post-commissural, fornix would associate with episodic details produced in both past and future AI tasks.

In line with predictions, it was found that pre-commissural, but not post-commissural, fornix microstructure associated with episodic details produced in both past and future episodic constructions. Further, it was established that these results were maintained when controlling for non-episodic narrative content, verbal fluency and hippocampal/vmPFC grey matter volumes. It is also worth noting that results were stronger in the past than in the future condition — Bayes factor analysis indicated moderate support in the past condition (BF ~ 8) but only anecdotal support in the future condition (BF ~ 2). However, a Steiger's Z test did not find a significant difference between these associations. It is suggested that the greater task difficulty of future thinking (Anderson, Dewhurst, & Nash, 2012) introduces more noise into the analysis, and that present work would benefit from replication with a larger sample (discussed further in analysis of general approach below — section 6.4).

Overall, this experiment provided important novel evidence that a structurally supported pathway between hippocampus and vmPFC supported the construction of past events and future scenarios, consistent with the idea (Schacter et al., 2012; Tulving, 2002a) of a more general system for personal mental time travel.

6.2.3 The role of the fornix in mediating the references to self and others within episodic content of autobiographical memory and future thinking

Tulving (1985, 2002a) identified self-projection as vital for the capacity for mental time travel — in his own words, "no traveller, no travelling". Theoretical work has further proposed that separate and differentiable components of episodic memory might regard 'where-what-when' and 'self' information (Fivush, 2011). As such, it has been proposed that personal event memory is developed alongside a sense of autobiographical self (Arzy & Schacter, 2019; Fivush & Haden, 2003; Prebble, Addis, & Tippett, 2013), or that autobiographical memory is 'self-referential' (Brewer, 1986). Further research has highlighted that 'episodic' and 'semantic' self-processing can be considered as separate concepts (Conway, 2005; Conway & Pleydell-Pearce, 2000).

Prior research into episodic self-processing has examined self-talk and pronoun usage (Chaput et al., 2013; Kurczek et al., 2015; Prebble et al., 2013; Verfaellie et al., 2019). This approach formed the basis of a novel coding system, which aimed to use linguistic self-referencing to evaluate the degree of autonoetic consciousness within the internal ('episodic') content of past and future narratives. This coding system was applied to the past and future narratives produced by participants in chapter 3. In line with prior research (Addis, Sacchetti, Ally, Budson, & Schacter, 2009; Addis, Wong, & Schacter, 2008; Berntsen & Bohn, 2010; Race, Keane, & Verfaellie, 2011; Wang, Capous, Koh, & Hou, 2014), it was predicted that participants would produce more self-references in the past than future condition. However, in line with recent research which has emphasised the extent to which personal goals heavily influence episodic future thinking (D'Argembeau, 2012; 2013; D'Argembeau et al., 2012; Grysman et al., 2013), it was predicted that the future thinking condition would display more self-references than the past condition proportional to the degree of episodic detail production. In line with these predictions, it was found that more self and other details were produced in the autobiographical recall task (in line with the typically greater episodic detail of past vs. future constructions). Contrary to predictions, self-references were produced in similar proportions to overall episodic content in both past and future conditions. However, the future thinking narratives produced fewer references to others than did the past. It was concluded that the preservation of self-references (vs other-references) in the future thinking supported prior research that had emphasised its importance in this capacity.

The neuroanatomical aspect of this chapter was primarily influenced by research that has identified the vmPFC as a core brain region in processing information related to the self, particularly the future self and its goals (Ciaramelli et al., 2021; D'Argembeau, 2013; Denny et al., 2012; Wagner et al., 2012). Further, this brain region has previously been identified in the default mode network (Andrews-Hanna, Reidler, Sepulcre, Poulin, & Buckner, 2010; Raichle, 2015) and the related core network that supports episodic construction (Schacter et al. 2012; Schacter, Benoit, & Szpunar, 2017). In line with this research, it was predicted that self-references would associate with fornix microstructure (which links hippocampal regions with default regions of mPFC — Aggleton, Wright, Rosene, & Saunders, 2015; Kernbach et al., 2018). Finer detailed analysis predicted that associations would be made with pre-commissural but not post commissural fornix (the former projects to the vmPFC whereas the latter projects to the mamillary bodies — Aggleton, 2012; Christiansen et al., 2016). Further, it was predicted that partial correlations controlling respectively for the number of internal details and self-references would maintain the association found for each in this analysis. Finally, it was predicted that self-references would show stronger associations with whole/pre-commissural fornix microstructure than would other-references (each are respectively represented in a ventral-dorsal gradient in vmPFC — Denny et al., 2012; Wagner et al., 2012). As such, this would demonstrate that fornix microstructure separately supports both 'what-where-when' and 'self-related' episodic content (to the extent that these are in fact dissociable). As the analysis used only internal content (to avoid contamination by personal semantic memory e.g. trait references), it was further predicted that no positive/negative association would be found with ILF FA/MD respectively.

A significant positive association (BF ~ 3 indicates moderate support for alternate hypothesis) was found between fornix microstructure (FA) and the number of self-references made in the future thinking task (in line with findings by Ciaramelli et al., 2021). Pre-commissural fornix FA was found to correlate positively with the number of self (BF ~ 7) and other-references (BF ~ 20) in the autobiographical recall condition of the AI. However, associations were significant when controlling associations for internal episodic details. As such it was concluded that fornix microstructure was associated with both episodic detail recall (including spatiotemporal details) and the episodic self, but that these could not be identified separately. To the extent that episodic spatial details and self-reference are highly interwoven, the findings are consistent with both Tulving's idea of mental time travel (Tulving, 2005) and could also be accounted for by scene construction theory, which emphasizes the egocentric (self-referential) nature of scene construction (Mullally & Maguire, 2014). No positive/negative associations were found between self or other references and ILF FA/MD respectively. This finding suggested that self-references in episodic content were not supported by personal semantic memory (e.g. trait knowledge, autobiographical facts, etc).

A key conclusion of this analysis was that future work might consider a qualitative aspect of self-reference and autonoetic consciousness rather than rely solely on quantitative measures. This is in line with the inconsistent findings from patients with hippocampal and vmPFC damage (Bertossi et al., 2016b; Kurczek et al., 2015; Verfaellie et al., 2019). It is proposed that considering the depth and complexity of self-involvement and evaluation within episodic constructions might provide insight into the precise nature of these processes and their relation to other component processes of mental time travel. Further, it might allow for a more nuanced examination of the neural correlates of these processes and how they are supported within structurally underpinned functional neural networks.

6.2.4 The role of the fornix and ILF in the production of personal and general semantic details in autobiographical memory and future thinking

By its nature mental time travel is a temporal, contextual process, however, episodic constructions always include atemporal, acontextual semantic details (Levine et al., 2002). The role of the semantic memory system within the construction of episodic narratives across different periods of the lifespan has been discussed by a number of models (constructive episodic simulation hypothesis (Addis, 2018; 2020; Schacter & Addis, 2007b); scene construction hypothesis (Hassabis & Maguire, 2007); semantic scaffolding hypothesis (Irish & Piguet, 2013); and self-memory system model (Conway & Pleydell-Pearce, 2000). Evidence from semantic dementia patients has supported the idea that semantic memory is fundamental to episodic future thinking (Irish et al., 2012a; see also D'Argembeau, 2020).

Within the context of the AI, semantic details have been considered monolithic (and are sometimes even presented with other 'irrelevant' or 'external' details produced by the participant) (e.g. Hodgetts et al., 2017a; Levine et al., 2002). Research has found that these details can be subdivided and has suggested that these subdivisions might demonstrate a spectrum between episodic and semantic processing (Renoult et al., 2012, 2020; Tanguay et al., 2018, 2020). To test this, the AI scripts were recoded for personal and general semantic details. The general semantic category consisted of facts and knowledge that was not directly relevant to the participant's self-concept (i.e. details that were abstracted from their acquisitional context and considered culturally shared rather than idiosyncratic). Personal semantics included autobiographical facts and self-knowledge but also details pertaining to repeated and extended events (Renoult et al., 2012; 2016; 2020).

Personal semantics have been suggested to show more elements of episodic processing (e.g. their fundamental requirement of self-reference, the degree of original spatiotemporal context found in extended and repeated events, etc) than does general semantic processing (Renoult et al., 2012). In line with this, and prior research that has linked episodic AI content with fornix microstructure and semantic AI content with ILF microstructure, it was predicted that personal semantics would associate with both fornix and ILF indices. General semantics were predicted to associate with the ILF but not the fornix (as in Hodgetts et al., 2017a). Further, the subcomponents of personal semantics can be considered more (i.e. repeated and extended events) or less (i.e. autobiographical facts and self-knowledge) related to their contextualized, episodic origins. A second set of analyses predicted that the former but not the latter would correlate with fornix microstructure (both aspects of personal semantics were expected to correlate with ILF microstructure). Finally, it was predicted that episodic future details would associate with ILF microstructure (as in Irish & Piguet, 2013).

In line with the semantic scaffolding hypothesis (Irish & Piguet, 2013), it was found that a greater number of general semantic details were produced in the episodic future thinking task than in the autobiographical recall task. No significant difference was found in the number of personal semantic details produced in past or future conditions, suggesting a similar contribution of autobiographical knowledge to past and future constructions (D'Argembeau, 2020). However, it was found that a greater number of repeated and extended event details were produced in recall than in prospection. The opposite was true with autobiographical facts and self-knowledge, which were produced more in the future condition than in the past. This also supports the semantic scaffolding hypothesis, as it suggests that acontextual and abstract information is used more to support autobiographical future thinking than autobiographical recall. Further, this might be considered to support the idea that repeated events represent a form of personal semantic processing that is more closely aligned with episodic memory (see Renoult et al., 2012), as autobiographical recall narratives produced both more internal content and repeated/extended event details than did autobiographical future thinking narratives.

Correlations with DTI metrics showed that both personal and general semantic details, for past and future, associated with ILF but not fornix microstructure. This finding was broadly maintained when examining the subcomponents of personal semantics (i.e. associations with ILF but not fornix). These findings show that despite behavioural findings of a close interaction, nevertheless episodic and semantic systems could be differentiated at a neural level even in episodic future thinking. Further, no positive/negative association could be found between ILF FA/MD and the production of episodic details in either the past or future condition (in fact, Bayes factors generally indicated evidence in favour of the null hypothesis — BF < 0.33). These findings do not support those of Irish et al. (2012a) who reported that episodic content in future thinking but not recall was correlated with lateral temporal lobe damage in semantic dementia. Instead they are consistent with Tulving's notion of interacting but dissociable, episodic, and semantic memory systems underpinning mental time travel (Tulving, 2002a).

The totality of the present findings suggest that personal semantics should perhaps best be considered a component of the general semantic system. Notably this held even for repeated and extended events, which are the most episodic-like component of personal semantic processing (Renoult et al., 2012). Both personal and general semantics are proposed to be mediated by ILF connectivity with the semantic hub in left ventral anterior temporal lobe (see also Grilli et al., 2018). However, it should be noted that the present analysis did not separate autobiographical facts and self-knowledge — as has been done in other coding systems (Renoult et al., 2020). Prior research has demonstrated that these have different neural correlates (Grilli et al., 2018; Klein & Lax, 2010; Marquine et al., 2016; Renoult et al., 2016). In particular, self-knowledge has been associated with mPFC (Marquine et al., 2016) and autobiographical facts have been associated with left anterior ventral lobe (Grilli et al., 2018). Examining how these aspects might be differentially supported by neural architecture, and in particular, the apparently unique role of the mPFC in self-knowledge (using e.g. an "I am" self-statement task), and how this relates to aspects of episodic self-processing, including goals and emotions (D'Argembeau, 2020) is an important topic for future research.

6.3 Overall contribution of present findings

The first notable finding of this project was an association between the spatial memory and future thinking subscales of the SAM and interindividual variation in fornix microstructure (MD) values. This provides a measure of support for the scene construction hypothesis, which holds that hippocampal circuitry plays a vital role in the construction of a contextually coherent 'scene' in which autobiographical memories and future projections can be constructed (Hassabis et al., 2007; Hassabis & Maguire, 2007, Mullally & Maguire, 2014). However, no positive/negative association was found between episodic memory traits and fornix FA/MD — as was predicted in line with not only the scene construction hypothesis but all neurocognitive models of mental time travel (D'Argembeau, 2020; Irish et al., 2012; Schacter & Addis, 2007b). Further, this result did not support the findings of Hodgetts et al. (2017a; see also Memel et al., 2020), which established that episodic autobiographical memory (particularly spatiotemporal AI details) were associated with interindividual fornix microstructure variation. The results of chapters 3 and 5 also demonstrated that (pre-commissural) fornix and ILF microstructure could be associated with both episodic and semantic details produced in autobiographical recall and future simulations. As such, it is suggested that conclusions should not be made in isolation when considering the associations found between SAM subscales and white matter microstructure.

Indeed, a comparison of the results from chapters 2 and 3 shows a somewhat mirrored pattern. In chapter 2, an association was found between episodic future thinking but not episodic memory traits and fornix microstructure. Whereas in chapter 3, although both past and future conditions showed positive associations between the number of episodic details produced and pre-commissural fornix microstructure, a stronger association was found in the past than in the future condition. Prior research has indicated that participants generally produce more episodic, including spatial, details in memory recall than in future simulation tasks (e.g. Addis, Sacchetti, et al., 2009; Addis, et al., 2008; Bertossi, et al., 2016a; Race, et al., 2011), which could account for this finding. That the pattern is reversed in the present SAM findings suggests that conclusions should carefully consider what the SAM measures. It was reported by Kozlowski and Bryant (1977) that participants were better able to report spatial navigation abilities than other cognitive traits. Notably, the future thinking scale also included a spatial component (“*When I imagine an event in the future, I can picture the spatial layout”*). In contrast, the ‘episodic’ scale of the SAM makes no explicit reference to spatial details of episodic memories, which could explain a lack of association with hippocampal circuitry according to the scene construction hypothesis. This finding was supported by Clark and Maguire (2020) who reported that spatial tasks commonly supported spatial memory. However, these authors also reported that memory questionnaires correlated with the vividness of an autobiographical memory rather than the level of episodic detail production, suggesting that the SAM and AI are measuring different aspects of mental time travel.

Further, no positive/negative association was found respectively between ILF FA/MD and the SAM semantic subscale. However, an association between semantic AI details and ILF microstructure has been identified previously by Hodgetts et al. (2017a), and further validated by the results in chapter 5. Prior research has found an association between ILF microstructure and lexicosemantic performance (Agosta et al., 2010; Marcotte et al., 2017). Further, Nugiel, Alm and Olson (2016) reported that performance on a verb generation task (that indexes semantic control — Snyder & Munakata, 2008; Snyder et al., 2010) associated with ILF microstructure. Given the fact that the AI is a narrative-based task, and that the number of details produced were taken as a measure of depth of or inclination towards semantic processing, it is possible that this could explain the difference in the findings between these two chapters. The extent to which the SAM semantic scale actually measures semantic memory, as opposed to e.g. beliefs about memory, is unclear (Palombo et al., 2013). Overall, it seems clear that the SAM findings in this project demonstrate that it is a viable method but that further validation is required to establish the precise nature of what it measures, how it relates to other aspects of memory performance and phenomenology (e.g. the "remember" vs. "know" distinction (Evans & Wilding, 2012; Tulving, 1985), and self-rated phenomenology ("vividness" and "presence" — Mather et al. 1997)), and what conclusions can be drawn from such results.

It was found by Hodgetts et al. (2017a) that the number of episodic and semantic details produced in an AI associated respectively with fornix and ILF microstructure. These findings have been supported and extended by the present results in chapters 3 and 5. These chapters examined performance in both autobiographical recall and future thinking task variants of the AI. The consistency between the brain-behaviour correlations for the past and future conditions supports the idea that a mental time travel or constructive memory system supports episodic constructions in both temporal directions. Subtle differences were noted between past and future tasks, for instance stronger associations were noted for both episodic and semantic details in the past than in the future condition. Although this might have been expected for episodic details (the production of which are more associated with recall than future simulation - e.g. Addis, Sacchetti, et al., 2009; Addis, et al., 2008; Bertossi, et al., 2016a; Race, et al., 2011), this pattern was not anticipated for semantic details (which Irish & Piguet (2013) reported show relatively increased production in future thinking than recall). It is possible that this reflects an element of noise introduced by the varying task difficulties — future thinking is generally accepted to be a more difficult task than is recall (Anderson et al., 2012). The strength of association against the degree of relative production is an area of potential focus of future research. In addition, future work might vary the timescale of past and future constructions, given that episodic and semantic detail vary as a function of temporal distance from the present with greater episodic specificity for near versus far events (Addis & Schacter, 2008; La Corte & Piolino, 2016).

VS-MPR outputs (i.e. the odds in favour of the hypothesis relative to the null, or the Bayes Factor bound) were used in chapter 3 to support the semantic scaffolding hypothesis of episodic future thinking (see Irish & Piguet, 2013). Further, it was found in chapter 5 that ILF microstructure was associated with the production of semantic details in both past and future conditions, consistent with an important contribution of semantic memory to future thinking (Schacter et al., 2012). In line with the semantic scaffolding hypothesis it was predicted that internal (episodic) details produced in the future thinking task would correlate with ILF microstructure, however, no such association was found (indeed Bayes factor analyses provided evidence in favour of the null hypothesis). Although a different pattern of semantic details was found between past and future conditions, the evidence across this study did not provide strong support for key aspects of the semantic scaffolding hypothesis, specifically the idea that semantic and episodic memory are part of the same neurocognitive system (see also Irish & Vatansever, 2020). Rather, the results tended to support Tulving's view (2002a) that episodic and semantic memory are dissociable, but interacting, components of mental time travel.

Nevertheless, there is a growing body of work in the domain of personal semantics examining the concept of a spectrum between episodic and semantic memory systems, along which details can be considered in terms of the precision of their temporospatiality and abstraction (Renoult et al., 2012; Renoult, Irish, Moscovitch, & Rugg, 2019; Tanguay et al., 2018). Although some functional evidence has been found that can distinguish details along this spectrum (e.g. Maguire & Frith, 2003; Tanguay, 2018) these findings have not been consistent (Coronel & Federmeier, 2016; Renoult et al., 2016). The findings of chapter 5 did not provide evidence to support this account (i.e. that some aspects of personal semantics, particular those that retain contextual detail, are closely aligned with episodic memory systems). This finding is given particular weight as episodic and semantic details could be consistently associated with target tracts. Therefore, if a spectrum did exist, and was supported by a neurological basis, it would be expected that the present method should have been able to demonstrate it. Instead, the findings of the present project provide support for the notion that personal semantics are a subcomponent of the general semantic system (Grilli et al., 2018). Both of these are proposed to be mediated by ILF connectivity to the semantic hub in the ventral anterior temporal lobe (see also Patterson et al., 2007; Rogers et al., 2004).

However, the present results also failed to demonstrate a more commonly found distinction between personal (idiosyncratic) and general (culturally shared) semantic memory (Grilli et al., 2018). In the case of the latter this might be due to the insensitivity of the present method in differing neural associations with self and other processing (see chapter 4), for example. It is possible that this shows a limitation in the present method to fully measure and isolate the different components and representations at hand. Self-projection has been described as fundamental to the process of mental time travel (Tulving, 2002a), and the lack of sensitivity to it in the present method is a clear weakness. This is an area that future research might give particular focus towards.

A further consideration for the present work is that, to maximize statistical power, and in line with the theoretical approach of Tulving, the episodic details are treated as a monolith. No further consideration is made for the different qualities (spatial, temporal, perceptual, etc.) they pertain to and are coded for using the adapted coding scheme we followed (Hodgetts et al., 2017a; Levine et al., 2002). However, evidence has suggested that the quality of details produced in an autobiographical task can be influenced by the contextual nature of the prompt (Sheldon, Gurguryan, Madore, & Schacter, 2019). Further, research by Memel, Wank, Ryan and Grilli (2020) has noted that the association between fornix FA and episodic details is especially strong for the spatiotemporal subcomponent of these, consistent with the findings reported here for the SAM. It seems likely that research in this field can investigate more specific hypotheses and that the method is sufficiently sensitive to find evidence in support of these. However, this will require far larger samples to have sufficient power to examine relations between multiple components of mental time travel and multiple white matter tracts underpinning the core or default network, going beyond the targeted, hypothesis driven approach adopted in this thesis.

6.4 Analysis of the general approach

Perhaps the clearest take away from the overall pattern of results is that they reflect the traditional trade-off between the more ecologically valid conclusions that can be drawn from a naturalistic data source, but also the lack of control that they show in relation to more traditional laboratory-based approaches (Neisser, 1978; Banaji & Crowder, 1989, Conway, 1991). In line with prior research (e.g. McDermott et al., 2009), it can confidently be concluded that the present results reflect individual differences in traits relating to episodic construction and mnemonic strategies. Further, the present findings demonstrate that these traits and abilities or tendencies can be associated with interindividual variation in the microstructure of white matter tracts of healthy individuals, which has important implications for cognitive network neuroscience in general, and the role of white matter architecture in particular (Filley & Fields, 2016; Weisberg & Ekstrom, 2020).

The alpha levels used to test for statistical ‘significance’ (but see Lakens et al., 2018) were set using the number of tract(s) of interest in each analysis (i.e. either one or two, leaving an alpha level of 0.05/0.025). It must be considered that this figure did not map onto the number of comparisons that were made within the analyses (i.e. the alpha level might have been more conservatively set in line with the number of microstructure measures used or the number of hypotheses made). As such, it is important to consider that the alpha-levels set might have underestimated the familywise error rate (and increased the likelihood of type one errors). However, it was considered that stringent alpha-levels might instead bias the analyses towards excessive likelihood of type two errors (Lakens et al. 2018). This was considered to be particularly important when considering the novelty of these investigations (i.e. associating trait mnemonics as measured by the SAM with individual differences in white matter tract microstructure and developing novel AI coding protocols with which to examine specific cognitive components supporting mental time travel). As such, the findings of this thesis are presented with a measure of caution (i.e. regarding the possibility that they have underestimated the familywise error rate). They will require replication in high-powered studies with larger sample sizes.

It is important to consider possible explanations for the inconsistent pattern of results found throughout this project. Although some patterns emerged in relation to tract microstructure-cognition associations, these were not replicated in both microstructure measures, nor were patterns consistent between chapters. A sensitivity analysis can be used post-hoc to determine the effect sizes that a study can reliably detect (Perugini, Gallucci, & Costanti, 2018). Sensitivity analyses (run in GPower 3.1 — Faul, Erdfelder, Buchner & Lang, 2009) indicated that the analyses used were suitably powered for approximately a medium effect size in chapter 2 ($\rho = 0.38$ — $\alpha = 0.025$, $1-\beta = 0.8$, $n = 51$), and larger effect sizes in chapter 3 ($\rho = 0.46$ — $\alpha = 0.05$, $1-\beta = 0.8$, $n = 27$), chapter 4 ($\rho = 0.46$ — $\alpha = 0.05$, $1-\beta = 0.8$, $n = 27$) and chapter 5 ($\rho = 0.51$ — $\alpha = 0.025$, $1-\beta = 0.8$, $n = 27$). When converted to Kendall's tau (Walker, 2003), this indicated that the present study was adequately powered to investigate effect sizes of $\tau \sim 0.259$, $\tau \sim 0.317$ and $\tau \sim 0.353$. The effect sizes reported tended to be smaller than these, which indicates that the present project lacked a degree of statistical power. It is highly recommended that larger sample sizes are used moving forwards, to ensure adequate statistical power can be achieved.

While the sample size used for chapters 3, 4 and 5 was comparable to related investigations (e.g. Palombo et al., 2018a; Postans et al., 2014), replicable and precise results are more likely when statistical power is high (Button, et al., 2013; Yarkoni, 2009). However, the evidential value of an experiment is not simply measured by power (Dienes & McLatchie, 2018; Wagenmakers et al., 2015). Modern statistical methods have recommended the use of Bayes factors and likelihood ratios to test the extent to which a given data set provides evidence for or against a null hypothesis (Benjamin & Berger, 2019; Dienes & McLatchie, 2018; Wagenmakers et al., 2015). The present project has presented both Bayes factors and VS-MPRs where possible for its comparisons. This is a notable strength regarding the extent to which the strength of any given finding can be considered and what conclusions can be drawn. Nevertheless, as stated above, large sample sizes are now required to address the questions raised here, although it is reassuring that converging evidence is coming from massive data sets such as UK Biobank (Spreng et al., 2020).

As with any experimentation, the methods used in the present project have their own limitations. First and foremost, it is not currently possible to form a clear biological interpretation of the individual differences found in the reported white matter diffusion metrics. It has been noted that FA and MD typically display an inverse relationship, in which higher FA and lower MD are associated with more efficient information transfer along tracts (Beaulieu, 2002). Further, high FA is associated with high myelin density and highly directional tract orientation profiles, whereas MD is associated with low myelin density and diffuse distributions of orientation profiles (Seehaus et al., 2015). However, the precise nature of variation between FA and MD profiles is still difficult to interpret even in this context. For instance, FA has been shown to be sensitive to variation in fibre microstructure but has been linked with myelination, axon diameter and packing density, axon permeability and fibre geometry (Jones et al., 2013). Whereas MD has been associated with edema, necrosis and cellularity (Alexander et al., 2011). Future studies will rely on the development of these techniques to ensure that a better understanding of the biological specifics allow for more precise interpretations of neurocognitive findings. In particular, the development of new diffusion MR sequences, alongside biophysical models for estimating biologically specific properties of the white matter from dMRI data, such as neurite density and orientation (Zhang, Schneider, Wheeler-Kingshott, & Alexander, 2012), hold great promise for illuminating the biological variation that underpins individual differences in cognitive function. However, gains in biological specificity may come at the cost of sensitivity, and the results presented here again highlight the continued utility of tensor-based microstructure metrics. These approaches could usefully be extended to large lifespan samples to study the development and degeneration of the white matter pathways underpinning mental time travel across the lifespan, which might have implications for the understanding of developmental and neurodegenerative brain disorders impacting autobiographical memory (Adlam, Malloy, Mishkin, & Vargha-Khadem, 2009; Strikwerda-Brown, Grilli, Andrews-Hanna, & Irish, 2019).

As noted above, although FA and MD are typically expected to display an inverse relationship, they are sensitive to different aspects of the underlying biology of white matter tract microstructure (Alexander et al., 2007). It has been argued, therefore, that it is beneficial to report both measures to allow for more precise interpretation (Alexander et al., 2007; Johnson et al., 2014). Indeed, there are numerous examples of this advice being followed in research associating tract microstructure with spatial and autobiographical memory measures (e.g. Hodgetts et al., 2015; 2017a; 2020; Postans et al., 2014; Memel et al., 2020). In line with this research, the present thesis predicted that task performance/self-reported capacity would positively correlate with FA and negatively correlate with MD. In line with Hodgetts et al. (2017a), the results of chapters 3, 4 and 5 showed that generally stronger effects were found in FA metrics for the fornix and MD metrics for the ILF. This is perhaps not surprising, given the overlap in the datasets between these analyses – however, it was a result that was found to be consistent in the future thinking datasets. However, this pattern was not universal within the project. Chapter 2 demonstrated that self-reported capacity for spatial memory and episodic future thinking were associated with fornix MD but not FA. The first of these findings can be considered in line with prior research, which has indicated that scene/navigational processing is more strongly associated with fornix MD than FA (Hodgetts et al., 2015; 2020; Postans et al., 2014). However, it is difficult to interpret the association with episodic future thinking in these terms (especially given that SAM-Episodic did not associate with either fornix FA or MD, and that both episodic memory and future thinking were associated more strongly with fornix FA in the AI research in this project). It is possible that this reflects differences in how self-report/performance-based measures are supported by fornix microstructure (although, as noted above, it is difficult to speculate on the precise biological nature by which this would be mediated). However, it has been noted that DTI is a method that is susceptible to noise, artifacts, and other measurement issues (Alexander et al., 2007; Chamberland et al., 2019). The variation of FA and MD associations between analyses (both within this thesis and the wider body of literature noted above) highlights the importance of reporting (where possible) more than one diffusion parameter (Alexander et al., 2007; Johnson et al., 2014). Taken as a whole, these findings highlight a limitation of DTI in its current state, and the importance of developing ever better protocols to allow for more specificity in interpreting its outputs.

Another limitation is that tractography accuracy is rater-and protocol-dependent, and future research would benefit from fully automated methodology. Nevertheless, when guided by detailed anatomical knowledge, as was the case in this thesis, tractography can be highly accurate (Schilling et al., 2020). Further, it has been suggested that microstructure can vary along an individual tract, based on the underlying anatomy, and so averaging microstructure values along a tract may be problematic (Alexander et al., 2011; Johnson et al., 2014). Where possible this has been addressed in this project (i.e. separating the fornix into pre- vs. post-commissural segments), which can be considered a strength of the current thesis. However, it is clear that moving forwards it will be important to establish a clear understanding of both the biological markers that are being measured, and the true nature of the underlying anatomical fibre pathways. This will allow for a clearer understanding of the neurological underpinnings of the cognitive processes of interest.

A final weakness of tractography in its present state, is that it is unable to establish the directionality of communication between regions (Cloutman & Lambon Ralph, 2012; Gutierrez et al., 2020). This is particularly relevant to mental time travel research as the directionality of hippocampal-vmPFC communication has been the subject of much debate (Campbell et al., 2018; Monk, Dalton, Barnes, & Maguire, 2021). It will be important for future work to address this issue by adopting a multi-modal imaging approach in which functional and structural imaging is combined (e.g. Hodgetts et al., 2015).

As mentioned above, the present experiments were also limited as they did not control for, or manipulate, temporal distance from the present. D'Argembeau, Xue, Lu, Van der Linden, and Bechara (2008) noted that more immediate decisions showed a double dissociation in activation to emotional events in the near future and far future between the caudate and anterior vmPFC, respectively. Further, the increase in psychological distance might alter the difficulty of the task and the manner in which processing is supported (Mitchell et al., 2011). Finally, the semantic system might be more heavily recruited in events that are at a further psychological distance or that are more 'novel' (see Irish & Piguet, 2013). Further research could examine if a gradient exists along which immediate knowledge, far reaching speculation and acontextual fantasy might be placed. This might also prove to be indicative of a participant's ability to flexibly and creatively construct future scenarios.

Further, it is possible to question the limits of such constructive abilities in terms of their basis in or adherence to reality. It has been found that the construction of fictious events shares similar activation across the default mode network as does episodic recall and future thinking, despite the inherent differences in self-projection and specific temporality (Hassabis, Kumaran, & Maguire, 2007; Maguire & Mullally, 2013; Schacter et al., 2012). This is important when considering the putative difference in restriction between autobiographical recall and future thinking - if memory accuracy is a given, then the latter must have fewer constraints (Van Boven, Kane & McGraw, 2009). However, a symmetry between the temporal directions is restored by evidence from research into episodic counterfactual thinking (De Brigard & Parikh, 2019). These authors suggest that this process (by which a participant imagines how events *could* have gone) is linked to the above processes and their neural correlates. Although all of these show similarities (they produce temporally experienced episodes outside of the present context), they are different in terms of the level of self-projection, temporal specificity, and adherence to reality. Future research might further investigate these subfactors when considering mental time travel and episodic construction as neurocognitive processes.

6.5 Strengths and weaknesses of the Autobiographical Interview

The AI is a method that has been widely used since it was first described by Levine et al. (2002) (for a review see Sheldon et al., 2018). A strength of the present research is that the approach followed (where possible and applicable) the advice for AI research proposed by Miloyan, McFarlane and Vásquez-Echeverria (2019). This meta-analysis of AI research concluded that bias could be introduced via coding behaviours and the implementation of statistical analyses. In order to maintain a strong methodological basis, present analyses were always tested for inter-rater reliability and partial correlations were used to ensure that findings were not unduly biased by external factors. This is particularly relevant to the findings of chapter 4 and demonstrates the need for strict standards and clear reporting. As such, the findings and conclusions of the present thesis are presented with confidence in that they can provide a basis for future investigations.

Although the AI has been a noted success in autobiographical memory and episodic future thinking research (Sheldon et al., 2018), it is not a method without its own limitations. For instance, the present method compared the number of details produced by participants as a marker of the richness of their narrative and hence their memory. This does not, however, provide any indication of how accurate this recall was. Recent research by Diamond, Armson and Levine (2019) tested this by examining participants' recall of real-world events after delays of between two days and three years. The events in question were reported as 'complex' but 'controlled and verifiable'. These authors found that fewer episodic details were produced as time passed but that these details remained highly accurate. However, the degree to which this varies between individuals is likely to be relevant to the present design and is a factor that might be of interest as a control measure in future research.

Further, the authors reported that the decrease in episodic details is due to 'forgetting', although plausible this is not the only viable explanation. An alternative semi structured interview technique is the Test Episodique de Mémoire du Passé Autobiographique (TEMPau; Piolino et al., 2003), this method further included a scale in which participants indicted if they 'remembered', 'knew' or 'guessed' at details produced within their recollections as a measure of episodicity and the degree mental time travel (Tulving, 1985; Evans & Wilding, 2012). It is possible that the decrease in details produced is due to diminished confidence in recollection over time — as opposed to details that can explicitly no longer be remembered. In the context of the present work, it is possible that a greater production of details does not reflect a greater capacity for episodic memory, but a greater confidence in the specific details at hand. This highlights that the AI is ultimately an indirect method of measuring cognitive abilities. Nevertheless, our findings are convergent with those using task-based measures of episodic memory more generally (e.g. Rudebeck et al., 2009).

A potential avenue for further research is the of use automated coding schemes (for example natural language processing tools such as SÉANCE (Crossley, Kyle, & McNamara, 2017)). These tools offer much with regards to reducing the legwork associated with analysing AI transcripts, which in turn will allow for the analysis of far larger datasets. Not only would this mean that more participants might be recruited, it also could be used to examine other data sources that are as yet untapped (e.g. social media, email or text logs might allow for the analysis of an equally valid but less commonly tested form of communication). However, when considering the raw numerical advantage of this method, it is also important to consider the relative lack of contextual or interpretative analysis in such automated approaches that can easily be performed by a human coder using consensus coding techniques (Levine et al., 2002). This is already apparent in the loss of other features of communication (tone, body language, etc) when examining a transcribed interview. The development of more sophisticated coding tools (likely assisted by machine learning algorithms (Al Marouf, Hossain, Sarker, Pandey, & Siddiquee, 2019; Pearl & Steyvers, 2013)) will certainly be of interest to researchers in this field.

The AI is also, by its nature, a language-based measure of autobiographical memory, which takes place in the context of a social interaction (i.e. there is an interviewer and interviewee). When autobiographical memories are narrated, autobiographical memory is confounded with narrative skills (Bartoli & Smorti, 2019) and also with norms for self-disclosure (Skowronski & Walker, 2004), which may vary as a function of gender (Grysman & Denney, 2017). This limitation has been addressed to some extent by using a control measure of verbal fluency, and a different (albeit self-reported) non-interview measure of memory traits. Further issues can be seen in populations that have difficulty in communicating, for example in studies on young children (Atance, 2015; Prabhakar, & Ghetti, 2020) and autism (Marini et al., 2016). The issue of language in the study of autobiographical memory urgently requires new methods to be developed, although to the extent that autobiographical memories, as distinct from episodic memories, are necessarily organised through language, which provides them with a narrative structure that shapes the life story (Fivush 2011), this task may prove difficult, if not impossible.

6.6 Future directions of mental time travel research

Along with the analysis of the methods and findings of the present project, it is important to consider where mental time travel research might progress from here. The present method employed a naturalistic design, in which participants' cognitive traits or tendencies were measured through self-report and a semi structured interview. A further step in this regard would be to consider the 'brain-as-predictor' approach (Berkman & Falk, 2013). These authors characterised this approach as bridging the gap between traditional psychological research and cognitive neuroscience, by seeking the neural correlates of real-world behaviours. This method has already been used in examining health-related behaviours (e.g. in relation to giving up smoking (Falk, Berkman, Whalen, & Lieberman, 2011) and predicting consumer choices (Levy, Lazzaro, Rutledge, & Glimcher, 2011). Future research might consider examining memories produced in the real world (e.g. on social media) (including collective memories) as a viable method for furthering naturalistic study (Siegelman & Baldassano, 2020).

An alternative to fully naturalistic studies is to consider how laboratory tasks can be adapted to be 'more real'. Examples of this have been seen into research into alcohol that has included the use of a 'simulated bar' (e.g. Jones, Rose, Cole, & Field, 2013; Dallas et al., 2014). Within the context of memory research, Jeunehomme and D'Argembeau (2019) used wearable cameras and had participants experience a scripted event. This allowed the researchers to be certain of what participants experienced and how they experienced it. The greater control within this study allowed for the examination of an issue (temporality within scenes) that would otherwise be very difficult to examine in a more natural setting. Further, Nielson et al. combined real-world navigation with wearable camera to explore the resolution of spatial memory representations along the long axis of the hippocampus (Nielson, Smith, Sreekumar, Dennis, & Sederberg, 2015). Virtual reality technology further has the potential to experimentally manipulate the experience of mental time travel and its relation to spatial memory (e.g. via "teleportation") (Deuker, Bellmund, Schröder, & Doeller, 2016). Rather than being considered as opposed sides, it is clear that a blend of naturalistic and laboratory-based tasks will allow for a more holistic examination of the specific processes at work in episodic construction and mental time travel.

A final avenue that future research might consider is what the neural effects of training might have in participants. This is particularly relevant given the present use of DTI, which has been noted to be sensitive to training related plasticity in both rats (Hofstetter & Assaf, 2017) and humans (Oechslin, Gschwind, & James, 2018). This technique might allow for examination of how the microstructure of the fornix and ILF change in relation to changes in task performance after directed training, addressing issues of causality (Bertolero & Bassett, 2020). Further, this approach allows for the examination of the effects of specific training (e.g. in narrative production, language skills, self-projection, etc) and what following changes in neural architecture might reveal about their role in cognition.

6.7 Conclusion

"Past and future events loom large in much of human thinking, giving rise to cultural, religious, and scientific concepts about origins, destiny, and time itself" (Suddendorf & Corballis, 1997). The study of individual differences is pivotal for a full description of the cognitive and neural substrates of mental time travel. This thesis has demonstrated that combining diffusion MRI-based tractography with interview and self-report measures is a viable method for investigating the associations between interindividual differences in white matter microstructure and cognitive traits or tendencies related to mental time travel (Tulving, 2005). Hence this should be considered a valuable approach for wider neurocognitive network research. However, further study must be done to identify the specific biological markers that underpin various diffusion metrics. It will also be important to consider how in turn these mechanistically support functional brain network and ultimately cognitive function (Bertolero & Bassett, 2020). The present findings provide support for the notion that episodic and semantic memory systems are at least partially separate and supported by different structurally instantiated neural pathways. However, it is also clear that they must interact and support each other within episodic construction and mental time travel (D'Argembeau, 2020; Schacter et al., 2012), which will require complementary functional and dynamic approaches to investigate. Regarding the current models of mental time travel, the results of this thesis do not provide overwhelming support to any single model. However, some evidence has been provided (linking fornix-mediated hippocampal processing to spatial components of memory in particular) that might support the scene construction hypothesis (Hassabis & Maguire, 2007). Further, present findings did not show a significant association between semantic circuitry (mediated by the ILF) and episodic future thinking — which poses a challenge to the semantic scaffolding hypothesis (Irish & Piguet, 2013). However, this is consistent with Tulving's original notion of episodic and semantic memory (including autobiographical facts) being dissociable but interacting memory systems that are future as well as past directed (Tulving, 2002a). Specific gaps have been identified within the field for future research, particularly with regard to considering how new technology and new experimental techniques could benefit the field, so that ultimately we can come to understand the neurocognitive mechanisms underpinning the uniquely human ability to "mentally roam at will over what has happened, as readily as over what might happen" (Tulving, 2002a).

References

Abraham, A., Schubotz, R. I., & von Cramon, D. Y. (2008). Thinking about the future versus the past in personal and non-personal contexts. *Brain Research*, *1233*, 106-119.

Addis, D. R. (2018). Are episodic memories special? On the sameness of remembered and imagined event simulation. *Journal of the Royal Society of New Zealand*, *48*(2-3), 64-88.

Addis, D. R. (2020). Mental Time Travel? A Neurocognitive Model of Event Simulation. *Review of Philosophy and Psychology*, *11*(2), 233–259.

Addis, D. R., & Schacter, D. (2012). The hippocampus and imagining the future: where do we stand? *Frontiers in Human Neuroscience*, *5*, 173.

Addis, D. R., Cheng, T., P. Roberts, R., & Schacter, D. L. (2011a). Hippocampal contributions to the episodic simulation of specific and general future events. *Hippocampus*, *21*(10), 1045-1052.

Addis, D. R., Moscovitch, M., Crawley, A. P., & McAndrews, M. P. (2004). Recollective qualities modulate hippocampal activation during autobiographical memory retrieval. *Hippocampus*, *14*(6), 752-762.

Addis, D. R., Musicaro, R., Pan, L., & Schacter, D. L. (2010). Episodic simulation of past and future events in older adults: Evidence from an experimental recombination task. *Psychology and Aging*, *25*(2), 369.

Addis, D. R., Pan, L., Vu, M. A., Laiser, N., & Schacter, D. L. (2009). Constructive episodic simulation of the future and the past: Distinct subsystems of a core brain network mediate imagining and remembering. *Neuropsychologia*, *47*(11), 2222-2238.

Addis, D. R., Roberts, R. P., & Schacter, D. L. (2011b). Age-related neural changes in autobiographical remembering and imagining. *Neuropsychologia*, *49*(13), 3656-3669.

Addis, D. R., Sacchetti, D. C., Ally, B. A., Budson, A. E., & Schacter, D. L. (2009). Episodic simulation of future events is impaired in mild Alzheimer's disease. *Neuropsychologia*, *47*(12), 2660-2671.

Addis, D. R., Wong, A. T., & Schacter, D. L. (2007). Remembering the past and imagining the future: common and distinct neural substrates during event construction and elaboration. *Neuropsychologia*, *45*(7), 1363-1377.

Addis, D. R., Wong, A. T., & Schacter, D. L. (2008). Age-related changes in the episodic simulation of future events. *Psychological Science*, *19*(1), 33-41.

Aggleton, J. P. (2012). Multiple anatomical systems embedded within the primate medial temporal lobe: implications for hippocampal function. *Neuroscience & Biobehavioral Reviews*, *36*(7), 1579-1596.

Aggleton, J. P., & Brown, M. W. (1999). Episodic memory, amnesia and the hippocampal-anterior thalamic axis. *Behavioral and Brain Sciences*, *22*(3), 425-444.

Aggleton, J. P., O'Mara, S. M., Vann, S. D., Wright, N. F., Tsanov, M., & Erichsen, J. T. (2010). Hippocampal–anterior thalamic pathways for memory: uncovering a network of direct and indirect actions. *European Journal of Neuroscience*, *31*(12), 2292-2307.

Aggleton, J. P., Saunders, R. C., & Vann, S. D. (2008). Using hippocampal amnesia to understand the neural basis of diencephalic amnesia. *Handbook of Behavioral Neuroscience*, *18*, 503-632.

Aggleton, J. P., Wright, N. F., Rosene, D. L., & Saunders, R. C. (2015). Complementary patterns of direct amygdala and hippocampal projections to the macaque prefrontal cortex. *Cerebral Cortex*, *25*(11), 4351-4373.

Agosta, F., Henry, R. G., Migliaccio, R., Neuhaus, J., Miller, B. L., Dronkers, N. F., ... & Gorno-Tempini, M. L. (2010). Language networks in semantic dementia. *Brain*, *133*(1), 286-299.

Al Marouf, A., Hossain, R., Sarker, M. R. K. R., Pandey, B., & Siddiquee, S. M. T. (2019, February). Recognizing Language and Emotional Tone from Music Lyrics using IBM Watson Tone Analyzer. In *2019 IEEE International Conference on Electrical, Computer and Communication Technologies (ICECCT)* (pp. 1-6). IEEE.

Albi, A., Pasternak, O., Minati, L., Marizzoni, M., Bartrés-Faz, D., Bargallo, N., ... & Fiedler, U. (2017). Free water elimination improves test–retest reproducibility of diffusion tensor imaging indices in the brain: a longitudinal multisite study of healthy elderly subjects. *Human Brain Mapping*, *38*(1), 12-26.

Alea, N., & Bluck, S. (2003). Why are you telling me that? A conceptual model of the social function of autobiographical memory. *Memory*, *11*(2), 165-178.

Alexander, A. L., Hurley, S. A., Samsonov, A. A., Adluru, N., Hosseinbor, A. P., Mossahebi, P., ... & Field, A. S. (2011). Characterization of cerebral white matter properties using quantitative magnetic resonance imaging stains. *Brain Connectivity*, *1*(6), 423-446.

Alexander, A. L., Lee, J. E., Lazar, M., & Field, A. S. (2007). Diffusion tensor imaging of the brain. *Neurotherapeutics*, *4*(3), 316-329.

Alves, P. N., Foulon, C., Karolis, V., Bzdok, D., Margulies, D. S., Volle, E., & de Schotten, M. T. (2019). An improved neuroanatomical model of the default-mode network reconciles previous neuroimaging and neuropathological findings. *Communications Biology*, *2*(1), 1-14.

Amaral, D., & Lavenex, P. (2007). *Hippocampal neuroanatomy*. In P. Andersen, R. Morris, D. Amaral (Eds.) & T. Bliss & J. O'Keefe (Ed.), *The Hippocampus Book* (p. 37–114). Oxford University Press.

Anderson, F. T., & McDaniel, M. A. (2019). Hey buddy, why don't we take it outside: An experience sampling study of prospective memory. *Memory & Cognition*, *47*(1), 47-62.

Anderson, R. J., & Dewhurst, S. A. (2009). Remembering the past and imagining the future: Differences in event specificity of spontaneously generated thought. *Memory*, *17*(4), 367-373.

Anderson, R. J., Dewhurst, S. A., & Nash, R. A. (2012). Shared cognitive processes underlying past and future thinking: The impact of imagery and concurrent task demands on event specificity. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *38*(2), 356.

Andrews-Hanna, J. R. (2012). The brain's default network and its adaptive role in internal mentation. *The Neuroscientist*, *18*(3), 251-270.

Andrews-Hanna, J. R., Reidler, J. S., Huang, C., & Buckner, R. L. (2010). Evidence for the default network's role in spontaneous cognition. *Journal of Neurophysiology*, *104*(1), 322-335.

Andrews-Hanna, J. R., Reidler, J. S., Sepulcre, J., Poulin, R., & Buckner, R. L. (2010). Functional-anatomic fractionation of the brain's default network. *Neuron*, *65*(4), 550-562.

Araujo, H. F., Kaplan, J., & Damasio, A. (2013). Cortical midline structures and autobiographical-self processes: an activation-likelihood estimation meta-analysis. *Frontiers in Human Neuroscience*, *7*, 548.

Ardila, A., Ostrosky-Solís, F., & Bernal, B. (2006). Cognitive testing toward the future: The example of Semantic Verbal Fluency (ANIMALS). *International Journal of Psychology*, *41*(5), 324-332.

Armson, M. J., Diamond, N. B., Levesque, L., Ryan, J. D., & Levine, B. (2021). Vividness of recollection is supported by eye movements in individuals with high, but not low trait autobiographical memory. *Cognition*, *206*, 104487.

Arnold, K. M., McDermott, K. B., & Szpunar, K. K. (2011). Imagining the near and far future: The role of location familiarity. *Memory & Cognition*, *39*(6), 954-967.

Arzy, S., & Schacter, D. L. (2019). Self-agency and self-ownership in cognitive mapping. *Trends in Cognitive Sciences*, *23*(6), 476-487.

Assaf, Y., & Pasternak, O. (2008). Diffusion tensor imaging (DTI)-based white matter mapping in brain research: a review. *Journal of Molecular Neuroscience*, *34*(1), 51-61.

Assaf, Y., Johansen-Berg, H., & Thiebaut de Schotten, M. (2019). The role of diffusion MRI in neuroscience. *NMR in Biomedicine*, *32*(4), e3762.

Atance, C. M. (2015). Young children's thinking about the future. *Child Development Perspectives*, *9*(3), 178-182.

Atance, C. M., & O'Neill, D. K. (2001). Episodic future thinking. *Trends in Cognitive Sciences*, *5*(12), 533-539.

Bajada, C. J., Haroon, H. A., Azadbakht, H., Parker, G. J., Lambon Ralph, M. A., & Cloutman, L. L. (2017). The tract terminations in the temporal lobe: Their location and associated functions. *Cortex*, *97*, 277-290.

Baldassano, C., Chen, J., Zadbood, A., Pillow, J. W., Hasson, U., & Norman, K. A. (2017). Discovering event structure in continuous narrative perception and memory. *Neuron*, *95*(3), 709-721.

Baldassano, C., Hasson, U., & Norman, K. A. (2018). Representation of real-world event schemas during narrative perception. *Journal of Neuroscience*, *38*(45), 9689-9699.

Banaji, M. R., & Crowder, R. G. (1989). The bankruptcy of everyday memory. *American Psychologist*, *44*(9), 1185.

Barbas, H., & Blatt, G. J. (1995). Topographically specific hippocampal projections target functionally distinct prefrontal areas in the rhesus monkey. *Hippocampus*, *5*(6), 511-533.

Barry, D. N., & Maguire, E. A. (2019). Remote memory and the hippocampus: a constructive critique. *Trends in Cognitive Sciences*, *23*(2), 128-142.

Barsalou, L. W. (2009). Simulation, situated conceptualization, and prediction. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *364*(1521), 1281-1289.

Bartlett, F. C. (1932). *Remembering: A study in experimental and social psychology*. Cambridge University Press.

Bartoli, E., & Smorti, A. (2019). Facing the language-memory problem in the study of autobiographical memory. *Integrative Psychological and Behavioral Science*, *53*(3), 374-396.

Basser, P. J. (1997). New histological and physiological stains derived from diffusion-tensor MR images. *Annals of the New York Academy of Sciences*, *820*(1), 123-138.

Bauer, P. J., Wenner, J. A., Dropik, P. L., Wewerka, S. S., & Howe, M. L. (2000). Parameters of remembering and forgetting in the transition from infancy to early childhood. *Monographs of the Society for Research in Child Development*, i-213.

Baumann, O., Chan, E., & Mattingley, J. B. (2010). Dissociable neural circuits for encoding and retrieval of object locations during active navigation in humans. *NeuroImage*, *49*(3), 2816-2825.

Beaulieu, C. (2002). The basis of anisotropic water diffusion in the nervous system–a technical review. *NMR in Biomedicine: An International Journal Devoted to the Development and Application of Magnetic Resonance In Vivo*, *15*(7-8), 435-455.

Bellana, B., Liu, Z. X., Diamond, N. B., Grady, C. L., & Moscovitch, M. (2017). Similarities and differences in the default mode network across rest, retrieval, and future imagining. *Human Brain Mapping*, *38*(3), 1155-1171.

Bello, L., Gallucci, M., Fava, M., Carrabba, G., Giussani, C., Acerbi, F., ... & Gaini, S. M. (2007). Intraoperative subcortical language tract mapping guides surgical removal of gliomas involving speech areas. *Neurosurgery*, *60*(1), 67-82.

Bender, R., & Lange, S. (2001). Adjusting for multiple testing—when and how? *Journal of Clinical Epidemiology*, *54*(4), 343-349.

Benear, S. L., Ngo, C. T., & Olson, I. R. (2020). Dissecting the fornix in basic memory processes and neuropsychiatric disease: A review. *Brain Connectivity*, *10*(7), 331-354.

Benhamou, E., Marshall, C. R., Russell, L. L., Hardy, C. J., Bond, R. L., Sivasathiaseelan, H., ... & Razi, A. (2020). The neurophysiological architecture of semantic dementia: spectral dynamic causal modelling of a neurodegenerative proteinopathy. *Scientific Reports*, *10*.

Benjamin, D. J., & Berger, J. O. (2019). Three recommendations for improving the use of p-values. *The American Statistician*, *73*(sup1), 186-191.

Bennett, I. J., Huffman, D. J., & Stark, C. E. (2015). Limbic tract integrity contributes to pattern separation performance across the lifespan. *Cerebral Cortex*, *25*(9), 2988-2999.

Benoit, R. G., & Schacter, D. L. (2015). Specifying the core network supporting episodic simulation and episodic memory by activation likelihood estimation. *Neuropsychologia*, *75*, 450-457.

Berkman, E. T., & Falk, E. B. (2013). Beyond brain mapping: Using neural measures to predict real-world outcomes. *Current Directions in Psychological Science*, *22*(1), 45-50.

Berntsen, D., & Bohn, A. (2010). Remembering and forecasting: The relation. *Memory & Cognition*, *38*(3), 265-278.

Berntsen, D., & Jacobsen, A. S. (2008). Involuntary (spontaneous) mental time travel into the past and future. *Consciousness and Cognition*, *17*(4), 1093-1104.

Bertolero, M. A., & Bassett, D. S. (2020). On the nature of explanations offered by network science: A perspective from and for practicing neuroscientists. *Topics in Cognitive Science*, *12*(4), 1272-1293.

Bertossi, E., Aleo, F., Braghittoni, D., & Ciaramelli, E. (2016a). Stuck in the here and now: Construction of fictitious and future experiences following ventromedial prefrontal damage. *Neuropsychologia*, *81*, 107-116.

Bertossi, E., Candela, V., De Luca, F., & Ciaramelli, E. (2017). Episodic future thinking following vmPFC damage: impaired event construction, maintenance, or narration? *Neuropsychology*, *31*(3), 337.

Bertossi, E., Tesini, C., Cappelli, A., & Ciaramelli, E. (2016b). Ventromedial prefrontal damage causes a pervasive impairment of episodic memory and future thinking. *Neuropsychologia*, *90*, 12-24.

Binder, J. R., & Desai, R. H. (2011). The neurobiology of semantic memory. *Trends in Cognitive Sciences*, *15*(11), 527-536.

Binder, J. R., Desai, R. H., Graves, W. W., & Conant, L. L. (2009). Where is the semantic system? A critical review and meta-analysis of 120 functional neuroimaging studies. *Cerebral Cortex*, *19*(12), 2767-2796.

Bluck, S., Alea, N., Habermas, T., & Rubin, D. C. (2005). A tale of three functions: The self–reported uses of autobiographical memory. *Social Cognition*, *23*(1), 91-117.

Brainerd, C. J., & Reyna, V. F. (2005). *The science of false memory* (Vol. 38). Oxford University Press.

Brewer, W. F. (1986). *What is autobiographical memory?* In D. C. Rubin (Ed.), *Autobiographical Memory* (p. 25–49). Cambridge University Press.

Brocas, I., & Carrillo, J. D. (2018). A Neuroeconomic Theory of Mental Time Travel. *Frontiers in Neuroscience*, *12*, 658.

Brunec, I. K., Ozubko, J. D., Ander, T., Guo, R., Moscovitch, M., & Barense, M. D. (2020). Turns during navigation act as boundaries that enhance spatial memory and expand time estimation. *Neuropsychologia*, 107437.

Bubb, E. J., Kinnavane, L., & Aggleton, J. P. (2017). Hippocampal–diencephalic–cingulate networks for memory and emotion: An anatomical guide. *Brain and Neuroscience Advances*, *1*, 2398212817723443.

Buckner, R. L., & Carroll, D. C. (2007). Self-projection and the brain. *Trends in Cognitive Sciences*, *11*(2), 49-57.

Buckner, R. L., & DiNicola, L. M. (2019). The brain's default network: updated anatomy, physiology and evolving insights. *Nature Reviews Neuroscience, 20*(10), 593-608.

Bulley, A., & Irish, M. (2018). The functions of prospection–variations in health and disease. *Frontiers in Psychology*, *9*, 2328.

Bulley, A., Henry, J., & Suddendorf, T. (2016). Prospection and the present moment: The role of episodic foresight in intertemporal choices between immediate and delayed rewards. *Review of General Psychology*, *20*(1), 29-47.

Burdach, K. F. (1822). Vom Baue und Leben des Gehirns, second volume. *Dyk'schen Buchhandlung, Leipzig*.

Burgess, N., Becker, S., King, J. A., & O'Keefe, J. (2001). Memory for events and their spatial context: models and experiments. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *356*(1413), 1493-1503.

Burgess, N., Maguire, E. A., & O'Keefe, J. (2002). The human hippocampus and spatial and episodic memory. *Neuron*, *35*(4), 625-641.

Burt, C. D., Kemp, S., & Conway, M. A. (2003). Themes, events, and episodes in autobiographical memory. *Memory & Cognition*, *31*(2), 317-325.

Busby, J., & Suddendorf, T. (2005). Recalling yesterday and predicting tomorrow. *Cognitive Development*, *20*(3), 362-372.

Button, K. S., Ioannidis, J. P., Mokrysz, C., Nosek, B. A., Flint, J., Robinson, E. S., & Munafò, M. R. (2013). Confidence and precision increase with high statistical power. *Nature Reviews Neuroscience*, *14*(8), 585-585.

Cabeza, R., & Nyberg, L. (2000). Neural bases of learning and memory: functional neuroimaging evidence. *Current Opinion in Neurology*, *13*(4), 415-421.

Cabeza, R., Ciaramelli, E., Olson, I. R., & Moscovitch, M. (2008). The parietal cortex and episodic memory: an attentional account. *Nature Reviews Neuroscience*, *9*(8), 613-625.

Cabeza, R., Dolcos, F., Graham, R., & Nyberg, L. (2002). Similarities and differences in the neural correlates of episodic memory retrieval and working memory. *NeuroImage*, *16*(2), 317-330.

Cain, D. P., Boon, F., & Corcoran, M. E. (2006). Thalamic and hippocampal mechanisms in spatial navigation: a dissociation between brain mechanisms for learning how versus learning where to navigate. *Behavioural Brain Research*, *170*(2), 241-256.

Campbell, K. L., Madore, K. P., Benoit, R. G., Thakral, P. P., & Schacter, D. L. (2018). Increased hippocampus to ventromedial prefrontal connectivity during the construction of episodic future events. *Hippocampus*, *28*(2), 76-80.

Canessa, N., Borgo, F., Cappa, S. F., Perani, D., Falini, A., Buccino, G., ... & Shallice, T. (2008). The different neural correlates of action and functional knowledge in semantic memory: an FMRI study. *Cerebral Cortex*, *18*(4), 740-751.

Catani, M., & De Schotten, M. T. (2008). A diffusion tensor imaging tractography atlas for virtual in vivo dissections. *Cortex*, *44*(8), 1105-1132.

Catani, M., Jones, D. K., Donato, R., & Ffytche, D. H. (2003). Occipito-temporal connections in the human brain. *Brain*, *126*(9), 2093-2107.

Cenquizca, L. A., & Swanson, L. W. (2007). Spatial organization of direct hippocampal field CA1 axonal projections to the rest of the cerebral cortex. *Brain Research Reviews*, *56*(1), 1-26.

Chamberland, M., Raven, E. P., Genc, S., Duffy, K., Descoteaux, M., Parker, G. D., ... & Jones, D. K. (2019). Dimensionality reduction of diffusion MRI measures for improved tractometry of the human brain. *NeuroImage*, *200*, 89-100.

Chaput, V., Amsellem, F., Urdapilleta, I., Chaste, P., Leboyer, M., Delorme, R., & Goussé, V. (2013). Episodic memory and self-awareness in Asperger Syndrome: Analysis of memory narratives. *Research in Autism Spectrum Disorders*, *7*(9), 1062-1067.

Chen, L., Lambon Ralph, M. A., & Rogers, T. T. (2017). A unified model of human semantic knowledge and its disorders. *Nature Human Behaviour*, *1*(3), 1-10.

Chen, L., Ralph, M. A. L., & Rogers, T. T. (2017). A unified model of human semantic knowledge and its disorders. *Nature Human Behaviour*, *1*(3), 1-10.

Christiansen, K., Aggleton, J. P., Parker, G. D., O'Sullivan, M. J., Vann, S. D., & Metzler-Baddeley, C. (2016). The status of the precommissural and postcommissural fornix in normal ageing and mild cognitive impairment: An MRI tractography study. *NeuroImage*, *130*, 35-47.

Christoff, K., Irving, Z. C., Fox, K. C., Spreng, R. N., & Andrews-Hanna, J. R. (2016). Mind-wandering as spontaneous thought: a dynamic framework. *Nature Reviews Neuroscience*, *17*(11), 718-731.

Ciaramelli, E., Anelli, F., & Frassinetti, F. (2021). An asymmetry in past and future mental time travel following vmPFC damage. *Social Cognitive and Affective Neuroscience*, *16*(3), 315-325.

Ciaramelli, E., De Luca, F., Monk, A. M., McCormick, C., & Maguire, E. A. (2019). What" wins" in VMPFC: Scenes, situations, or schema? *Neuroscience & Biobehavioral Reviews*, *100*, 208-210.

Cicchetti, D. V. (1994). Guidelines, criteria, and rules of thumb for evaluating normed and standardized assessment instruments in psychology. *Psychological Assessment*, *6*(4), 284.

Ciocchi, S., Passecker, J., Malagon-Vina, H., Mikus, N., & Klausberger, T. (2015). Selective information routing by ventral hippocampal CA1 projection neurons. *Science*, *348*(6234), 560-563.

Clark, I. A., & Maguire, E. A. (2020). Do questionnaires reflect their purported cognitive functions? *Cognition*, *195*, 104114.

Clark, I. A., Hotchin, V., Monk, A., Pizzamiglio, G., Liefgreen, A., & Maguire, E. A. (2019). Identifying the cognitive processes underpinning hippocampal-dependent tasks. *Journal of Experimental Psychology: General*, *148*(11), 1861.

Clark, I. A., Monk, A. M., Hotchin, V., Pizzamiglio, G., Liefgreen, A., Callaghan, M. F., & Maguire, E. A. (2020). Does hippocampal volume explain performance differences on hippocampal-dependant tasks? *NeuroImage*, *221*, 117211.

Clark, K. A., Nuechterlein, K. H., Asarnow, R. F., Hamilton, L. S., Phillips, O. R., Hageman, N. S., ... & Narr, K. L. (2011). Mean diffusivity and fractional anisotropy as indicators of disease and genetic liability to schizophrenia. *Journal of Psychiatric Research*, *45*(7), 980-988.

Clayton, N. S., & Dickinson, A. (1998). Episodic-like memory during cache recovery by scrub jays. *Nature*, *395*(6699), 272-274.

Clayton, N. S., Bussey, T. J., & Dickinson, A. (2003). Can animals recall the past and plan for the future? *Nature Reviews Neuroscience*, *4*(8), 685-691.

Clayton, N. S., Russell, J., & Dickinson, A. (2009). Are animals stuck in time or are they chronesthetic creatures? *Topics in Cognitive Science*, *1*(1), 59-71.

Clewett, D., & Davachi, L. (2017). The ebb and flow of experience determines the temporal structure of memory. *Current Opinion in Behavioral Sciences*, *17*, 186-193.

Cloutman, L. L., & Lambon Ralph, M. A. (2012). Connectivity-based structural and functional parcellation of the human cortex using diffusion imaging and tractography. *Frontiers in Neuroanatomy*, *6*, 34.

Coad, B. M., Craig, E., Louch, R., Aggleton, J. P., Vann, S. D., & Metzler-Baddeley, C. (2020). Precommissural and postcommissural fornix microstructure in healthy aging and cognition. *Brain and Neuroscience Advances*.

Cobb-Clark, D. A., & Schurer, S. (2012). The stability of big-five personality traits. *Economics Letters*, *115*(1), 11-15.

Cocquyt, E. M., Lanckmans, E., van Mierlo, P., Duyck, W., Szmalec, A., Santens, P., & De Letter, M. (2020). The white matter architecture underlying semantic processing: A systematic review. *Neuropsychologia*, *136*, 107182.

Cohen, A. O., & Meyer, H. C. (2020). Ventral Hippocampus Projections to Prelimbic Cortex Support Contextual Fear Memory. *Journal of Neuroscience*, *40*(44), 8410-8412.

Cohn-Sheehy, B. I., & Ranganath, C. (2017). Time regained: how the human brain constructs memory for time. *Current Opinion in Behavioral Sciences*, *17*, 169-177.

Cohn-Sheehy, B. I., Delarazan, A. I., Crivelli-Decker, J. E., Reagh, Z. M., Mundada, N. S., Yonelinas, A. P., ... & Ranganath, C. (2021). Narratives bridge the divide between distant events in episodic memory. *Memory & Cognition*, 1-17.

Concha, L., Gross, D. W., & Beaulieu, C. (2005). Diffusion tensor tractography of the limbic system. *American Journal of Neuroradiology*, *26*(9), 2267-2274.

Conway, M. A. (1991). In defense of everyday memory. *American Psychologist, 46*(1), 19–26.

Conway, M. A. (2001). Sensory–perceptual episodic memory and its context: Autobiographical memory. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *356*(1413), 1375-1384.

Conway, M. A. (2005). Memory and the self. *Journal of Memory and Language*, *53*(4), 594-628.

Conway, M. A. (2009). Episodic memories. *Neuropsychologia*, *47*(11), 2305-2313.

Conway, M. A., & Pleydell-Pearce, C. W. (2000). The construction of autobiographical memories in the self-memory system. *Psychological Review*, *107*(2), 261.

Conway, M. A., Singer, J. A., & Tagini, A. (2004). The self and autobiographical memory: Correspondence and coherence. *Social Cognition*, *22*(5: Special issue), 491-529.

Corballis, M. C. (2013). Mental time travel: a case for evolutionary continuity. *Trends in Cognitive Sciences*, *17*(1), 5-6.

Corballis, M. C. (2019). Language, memory, and mental time travel: An evolutionary perspective. *Frontiers in Human Neuroscience*, *13*, 217.

Corballis, M. C. (2019). Mental time travel, language, and evolution. *Neuropsychologia*, *134*, 107202.

Coronel, J. C., & Federmeier, K. D. (2016). The N400 reveals how personal semantics is processed: Insights into the nature and organization of self-knowledge. *Neuropsychologia*, *84*, 36-43.

Craik, F. I., Moroz, T. M., Moscovitch, M., Stuss, D. T., Winocur, G., Tulving, E., & Kapur, S. (1999). In search of the self: A positron emission tomography study. *Psychological Science*, *10*(1), 26-34.

Crawford, B., Muhlert, N., MacDonald, G., & Lawrence, A. D. (2020). Brain structure correlates of expected social threat and reward. *Scientific Reports*, *10*(1), 1-13.

Crossley, S. A., Kyle, K., & McNamara, D. S. (2017). Sentiment Analysis and Social Cognition Engine (SEANCE): An automatic tool for sentiment, social cognition, and social-order analysis. *Behavior Research Methods*, *49*(3), 803-821.

Croux, C., & Dehon, C. (2010). Influence functions of the Spearman and Kendall correlation measures. *Statistical Methods & Applications*, *19*(4), 497-515.

Crovitz, H. F., & Schiffman, H. (1974). Frequency of episodic memories as a function of their age. *Bulletin of the Psychonomic Society*, *4*(5), 517-518.

Croxson, P. L., Johansen-Berg, H., Behrens, T. E., Robson, M. D., Pinsk, M. A., Gross, C. G., ... & Rushworth, M. F. (2005). Quantitative investigation of connections of the prefrontal cortex in the human and macaque using probabilistic diffusion tractography. *Journal of Neuroscience*, *25*(39), 8854-8866.

D'Argembeau, A. (2015). Knowledge structures involved in episodic future thinking. *Reasoning as Memory*, Psychology Press. 128-145.

D'Argembeau, A. (2016). The role of personal goals in future-oriented mental time travel. *Seeing the Future: Theoretical Perspectives on Future-Oriented Mental Time Travel*, Oxford University Press. 199-214.

D'Argembeau, A., & Demblon, J. (2012). On the representational systems underlying prospection: Evidence from the event-cueing paradigm. *Cognition*, *125*(2), 160-167.

D'Argembeau, A., & Salmon, E. (2012). The neural basis of semantic and episodic forms of self-knowledge: insights from functional neuroimaging. *Sensing in Nature*, 276-290.

D’Argembeau, A., & Van der Linden, M. (2004). Phenomenal characteristics associated with projecting oneself back into the past and forward into the future: Influence of valence and temporal distance. *Consciousness and Cognition*, *13*(4), 844-858.

D’Argembeau, A., & Van der Linden, M. (2006). Individual differences in the phenomenology of mental time travel: The effect of vivid visual imagery and emotion regulation strategies. *Consciousness and Cognition*, *15*(2), 342-350.

D’Argembeau, A., Ortoleva, C., Jumentier, S., & Van der Linden, M. (2010b). Component processes underlying future thinking. *Memory & Cognition*, *38*(6), 809-819.

D’Argembeau, A., Xue, G., Lu, Z. L., Van der Linden, M., & Bechara, A. (2008). Neural correlates of envisioning emotional events in the near and far future. *NeuroImage*, *40*(1), 398-407.

Dafni-Merom, A., & Arzy, S. (2020). The radiation of autonoetic consciousness in cognitive neuroscience: A functional neuroanatomy perspective. *Neuropsychologia*, 107477.

Daneman, M., & Carpenter, P. A. (1980). Individual differences in working memory and reading. *Journal of Memory and Language*, *19*(4), 450.

D'Argembeau, A. (2012). Autobiographical memory and future thinking. In D. Berntsen & D. C. Rubin (Eds.), *Understanding autobiographical memory: Theories and Approaches* (p. 311–330). Cambridge University Press.

D'Argembeau, A. (2013). On the role of the ventromedial prefrontal cortex in self-processing: the valuation hypothesis. *Frontiers in Human Neuroscience*, *7*, 372.

D'Argembeau, A. (2020). Zooming In and Out on One's Life: Autobiographical Representations at Multiple Time Scales. *Journal of Cognitive Neuroscience*, 1-19.

D'Argembeau, A., & Mathy, A. (2011). Tracking the construction of episodic future thoughts. *Journal of Experimental Psychology: General*, *140*(2), 258.

D'Argembeau, A., Lardi, C., & Van der Linden, M. (2012). Self-defining future projections: Exploring the identity function of thinking about the future. *Memory*, *20*(2), 110-120.

D'Argembeau, A., Stawarczyk, D., Majerus, S., Collette, F., Van der Linden, M., & Salmon, E. (2010c). Modulation of medial prefrontal and inferior parietal cortices when thinking about past, present, and future selves. *Social Neuroscience*, *5*(2), 187-200.

D'Argembeau, A., Stawarczyk, D., Majerus, S., Collette, F., Van der Linden, M., Feyers, D., ... & Salmon, E. (2010a). The neural basis of personal goal processing when envisioning future events. *Journal of Cognitive Neuroscience*, *22*(8), 1701-1713.

Davachi, L., & Dobbins, I. G. (2008). Declarative memory. *Current Directions in Psychological Science*, *17*(2), 112-118.

De Brigard, F., & Parikh, N. (2019). Episodic counterfactual thinking. *Current Directions in Psychological Science*, *28*(1), 59-66.

de Bruin, J. P., Moita, M. P., de Brabander, H. M., & Joosten, R. N. (2001). Place and response learning of rats in a Morris water maze: differential effects of fimbria fornix and medial prefrontal cortex lesions. *Neurobiology of Learning and Memory*, *75*(2), 164-178.

De Erausquin, G. A., & Alba-Ferrara, L. (2013). What does anisotropy measure? Insights from increased and decreased anisotropy in selective fiber tracts in schizophrenia. *Frontiers in integrative neuroscience*, *7*, 9.

Dede, A. J., Wixted, J. T., Hopkins, R. O., & Squire, L. R. (2016). Autobiographical memory, future imagining, and the medial temporal lobe. *Proceedings of the National Academy of Sciences*, *113*(47), 13474-13479.

Delis, D. C., Kaplan, E., & Kramer, J. H. (2001). *Delis-Kaplan Executive Function System (D–KEFS)* [Database record]. APA PsycTests.

Dell'Acqua, F., & Tournier, J. D. (2019). Modelling white matter with spherical deconvolution: How and why? *NMR in Biomedicine*, *32*(4), e3945.

Demblon, J., Bahri, M. A., & D'Argembeau, A. (2016). Neural correlates of event clusters in past and future thoughts: How the brain integrates specific episodes with autobiographical knowledge. *NeuroImage*, *127*, 257-266.

Denny, B. T., Kober, H., Wager, T. D., & Ochsner, K. N. (2012). A meta-analysis of functional neuroimaging studies of self-and other judgments reveals a spatial gradient for mentalizing in medial prefrontal cortex. *Journal of Cognitive Neuroscience*, *24*(8), 1742-1752.

Destrieux, C., Fischl, B., Dale, A., & Halgren, E. (2010). Automatic parcellation of human cortical gyri and sulci using standard anatomical nomenclature. *NeuroImage*, *53*(1), 1-15.

Deuker, L., Bellmund, J. L., Schröder, T. N., & Doeller, C. F. (2016). An event map of memory space in the hippocampus. *eLife*, *5*, e16534.

Devitt, A. L., Addis, D. R., & Schacter, D. L. (2017). Episodic and semantic content of memory and imagination: A multilevel analysis. *Memory & Cognition*, *45*(7), 1078-1094.

Diamond, N. B., Armson, M. J., & Levine, B. (2020). The truth is out there: Accuracy in recall of verifiable real-world events. *Psychological Science*, *31*(12), 1544-1556.

Diedenhofen, B., & Musch, J. (2015). cocor: A comprehensive solution for the statistical comparison of correlations. *PLOS ONE*, *10*(4), e0121945.

Dienes, Z., & McLatchie, N. (2018). Four reasons to prefer Bayesian analyses over significance testing. *Psychonomic Bulletin & Review*, *25*(1), 207-218.

Dixon, M. L., De La Vega, A., Mills, C., Andrews-Hanna, J., Spreng, R. N., Cole, M. W., & Christoff, K. (2018). Heterogeneity within the frontoparietal control network and its relationship to the default and dorsal attention networks. *Proceedings of the National Academy of Sciences*, *115*(7), E1598-E1607.

Douet, V., & Chang, L. (2015). Fornix as an imaging marker for episodic memory deficits in healthy aging and in various neurological disorders. *Frontiers in Aging Neuroscience*, *6*, 343.

Dumont, J. R., Amin, E., Wright, N. F., Dillingham, C. M., & Aggleton, J. P. (2015). The impact of fornix lesions in rats on spatial learning tasks sensitive to anterior thalamic and hippocampal damage. *Behavioural Brain Research*, *278*, 360-374.

Duval, C., Bejanin, A., Piolino, P., Laisney, M., De La Sayette, V., Belliard, S., ... & Desgranges, B. (2012). Theory of mind impairments in patients with semantic dementia. *Brain*, *135*(1), 228-241.

Duval, C., Desgranges, B., de La Sayette, V., Belliard, S., Eustache, F., & Piolino, P. (2012). What happens to personal identity when semantic knowledge degrades? A study of the self and autobiographical memory in semantic dementia. *Neuropsychologia*, *50*(2), 254-265.

Eichenbaum, H., & Cohen, N. J. (2001). *Oxford psychology series; no. 35. From conditioning to conscious recollection: Memory systems of the brain*. Oxford University Press.

Eichenbaum, H., & Cohen, N. J. (2014). Can we reconcile the declarative memory and spatial navigation views on hippocampal function? *Neuron*, *83*(4), 764-770.

Ekstrom, A. D., & Ranganath, C. (2018). Space, time, and episodic memory: The hippocampus is all over the cognitive map. *Hippocampus*, *28*(9), 680-687.

Ekstrom, A. D., Copara, M. S., Isham, E. A., Wang, W. C., & Yonelinas, A. P. (2011). Dissociable networks involved in spatial and temporal order source retrieval. *NeuroImage*, *56*(3), 1803-1813.

Enkavi, A. Z., Eisenberg, I. W., Bissett, P. G., Mazza, G. L., MacKinnon, D. P., Marsch, L. A., & Poldrack, R. A. (2019). Large-scale analysis of test–retest reliabilities of self-regulation measures. *Proceedings of the National Academy of Sciences*, *116*(12), 5472-5477.

Epelbaum, S., Bouteloup, V., Mangin, J. F., La Corte, V., Migliaccio, R., Bertin, H., ... & Memento Study group. (2018). Neural correlates of episodic memory in the Memento cohort. *Alzheimer's & Dementia: Translational Research & Clinical Interventions*, *4*, 224-233.

Epstein, R. A., Patai, E. Z., Julian, J. B., & Spiers, H. J. (2017). The cognitive map in humans: spatial navigation and beyond. *Nature Neuroscience*, *20*(11), 1504.

Evans, L. H., & Wilding, E. L. (2012). Recollection and familiarity make independent contributions to memory judgments. *Journal of Neuroscience*, *32*(21), 7253-7257.

Ezzyat, Y., & Davachi, L. (2011). What constitutes an episode in episodic memory? *Psychological science*, *22*(2), 243-252.

Falk, E. B., Berkman, E. T., Whalen, D., & Lieberman, M. D. (2011). Neural activity during health messaging predicts reductions in smoking above and beyond self-report. *Health Psychology*, *30*(2), 177.

Fan, C. L., Abdi, H., & Levine, B. (2020). On the relationship between trait autobiographical episodic memory and spatial navigation. *Memory & Cognition*, 1-11.

Fan, C. L., Romero, K., & Levine, B. (2020). Older adults with lower autobiographical memory abilities report less age-related decline in everyday cognitive function. *BMC Geriatrics*, *20*(1), 1-12.

Faul, F., Erdfelder, E., Buchner, A., & Lang, A. G. (2009). Statistical power analyses using G* Power 3.1: Tests for correlation and regression analyses. *Behavior Research Methods*, *41*(4), 1149-1160.

Fields, R. D. (2015). A new mechanism of nervous system plasticity: activity-dependent myelination. *Nature Reviews Neuroscience*, *16*(12), 756-767.

Filley, C. M., & Fields, R. D. (2016). White matter and cognition: making the connection. *Journal of Neurophysiology*, *116*(5), 2093-2104.

Fitzgerald, J. M., & Broadbridge, C. L. (2013). Latent constructs of the autobiographical memory questionnaire: A recollection-belief model of autobiographical experience. *Memory*, *21*(2), 230-248.

Fivush, R. (2011). The development of autobiographical memory. *Annual Review of Psychology*, *62*, 559-582.

Fivush, R., & Haden, C. A. (Eds.). (2003). *Autobiographical memory and the construction of a narrative self: Developmental and cultural perspectives*. Psychology Press.

Forkel, S. J., Friedrich, P., de Schotten, M. T., & Howells, H. (2020). White matter variability, cognition, and disorders: a systematic review. *medRxiv*.

Friedman, W. J. (2003). The development of a differentiated sense of the past and the future. *Advances in Child Development and Behavior*, *31*, 229-269.

Gaesser, B. (2020). Episodic mindreading: Mentalizing guided by scene construction of imagined and remembered events. *Cognition*, *203*, 104325.

Gaesser, B., & Schacter, D. L. (2014). Episodic simulation and episodic memory can increase intentions to help others. *Proceedings of the National Academy of Sciences*, *111*(12), 4415-4420.

Gaesser, B., Dodds, H., & Schacter, D. L. (2017). Effects of aging on the relation between episodic simulation and prosocial intentions. *Memory*, *25*(9), 1272-1278.

Gaesser, B., Sacchetti, D. C., Addis, D. R., & Schacter, D. L. (2011). Characterizing age-related changes in remembering the past and imagining the future. *Psychology and Aging*, *26*(1), 80.

Gaffan, D. (1994). Scene-specific memory for objects: a model of episodic memory impairment in monkeys with fornix transection. *Journal of Cognitive Neuroscience*, *6*(4), 305-320.

Gaffan, D. (2002). Against memory systems. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *357*(1424), 1111-1121.

Gaffan, D., & Gaffan, E. A. (1991). Amnesia in man following transection of the fornix: a review. *Brain*, *114*(6), 2611-2618.

Galati, G., Lobel, E., Vallar, G., Berthoz, A., Pizzamiglio, L., & Le Bihan, D. (2000). The neural basis of egocentric and allocentric coding of space in humans: a functional magnetic resonance study. *Experimental Brain Research*, *133*(2), 156-164.

Gao, A. F., Keith, J. L., Gao, F. Q., Black, S. E., Moscovitch, M., & Rosenbaum, R. S. (2020). Neuropathology of a remarkable case of memory impairment informs human memory. *Neuropsychologia*, *140*, 107342.

Garcia-Lazaro, H. G., Becerra-Laparra, I., Cortez-Conradis, D., & Roldan-Valadez, E. (2016). Global fractional anisotropy and mean diffusivity together with segmented brain volumes assemble a predictive discriminant model for young and elderly healthy brains: A pilot study at 3T. *Functional Neurology*, *31*(1), 39.

Gardner, R. S., & Ascoli, G. A. (2015). The natural frequency of human prospective memory increases with age. *Psychology and Aging*, *30*(2), 209.

Gilboa, A., & Marlatte, H. (2017). Neurobiology of schemas and schema-mediated memory. *Trends in Cognitive Sciences*, *21*(8), 618-631.

Gilmore, A. W., Quach, A., Kalinowski, S. E., Gotts, S. J., Schacter, D. L., & Martin, A. (2020). Dynamic content reactivation supports naturalistic autobiographical recall in humans. *Journal of Neuroscience*, *41*(1), 153-166.

Girden, E. R. (1992). *ANOVA: Repeated Measures* (No. 84). Sage publications, Inc.

Graham, K. S., Barense, M. D., & Lee, A. C. (2010). Going beyond LTM in the MTL: a synthesis of neuropsychological and neuroimaging findings on the role of the medial temporal lobe in memory and perception. *Neuropsychologia*, *48*(4), 831-853.

Griffiths, P. D., Batty, R., Reeves, M. J., & Connolly, D. J. (2009). Imaging the corpus callosum, septum pellucidum and fornix in children: normal anatomy and variations of normality. *Neuroradiology*, *51*(5), 337-345.

Grilli, M. D., & Verfaellie, M. (2014). Personal semantic memory: insights from neuropsychological research on amnesia. *Neuropsychologia*, *61*, 56-64.

Grilli, M. D., & Verfaellie, M. (2016). Experience-near but not experience-far autobiographical facts depend on the medial temporal lobe for retrieval: Evidence from amnesia. *Neuropsychologia*, *81*, 180-185.

Grilli, M. D., Bercel, J. J., Wank, A. A., & Rapcsak, S. Z. (2018). The contribution of the left anterior ventrolateral temporal lobe to the retrieval of personal semantics. *Neuropsychologia*, *117*, 178-187.

Grysman, A., & Denney, A. (2017). Gender, experimenter gender and medium of report influence the content of autobiographical memory report. *Memory*, *25*(1), 132-145.

Grysman, A., Prabhakar, J., Anglin, S. M., & Hudson, J. A. (2013). The time travelling self: Comparing self and other in narratives of past and future events. *Consciousness and Cognition*, *22*(3), 742-755.

Gurguryan, L., & Sheldon, S. (2019). Retrieval orientation alters neural activity during autobiographical memory recollection. *NeuroImage*, *199*, 534-544.

Gusnard, D. A., & Raichle, M. E. (2001). Searching for a baseline: functional imaging and the resting human brain. *Nature Reviews Neuroscience*, *2*(10), 685-694.

Gutchess, A. H., & Schacter, D. L. (2012). The neural correlates of gist-based true and false recognition. *NeuroImage*, *59*(4), 3418-3426.

Gutierrez, C. E., Skibbe, H., Nakae, K., Tsukada, H., Lienard, J., Watakabe, A., ... & Doya, K. (2020). Optimization and validation of diffusion MRI-based fiber tracking with neural tracer data as a reference. *Scientific Reports*, *10*(1), 1-18.

Hampton, R. R. (2009). Multiple demonstrations of metacognition in nonhumans: Converging evidence or multiple mechanisms? *Comparative Cognition & Behavior Reviews*, *4*, 17.

Han, S., & Ma, Y. (2014). Cultural differences in human brain activity: a quantitative meta-analysis. *NeuroImage*, *99*, 293-300.

Haslam, C., Jetten, J., Haslam, S. A., Pugliese, C., & Tonks, J. (2011). ‘I remember therefore I am, and I am therefore I remember’: Exploring the contributions of episodic and semantic self-knowledge to strength of identity. *British Journal of Psychology*, *102*(2), 184-203.

Hassabis, D., & Maguire, E. A. (2007). Deconstructing episodic memory with construction. *Trends in Cognitive Sciences*, *11*(7), 299-306.

Hassabis, D., Kumaran, D., & Maguire, E. A. (2007). Using imagination to understand the neural basis of episodic memory. *Journal of Neuroscience*, *27*(52), 14365-14374.

Hassabis, D., Kumaran, D., Vann, S. D., & Maguire, E. A. (2007). Patients with hippocampal amnesia cannot imagine new experiences. *Proceedings of the National Academy of Sciences*, *104*(5), 1726-1731.

Hayes, J. P., LaBar, K. S., McCarthy, G., Selgrade, E., Nasser, J., Dolcos, F., & Morey, R. A. (2011). Reduced hippocampal and amygdala activity predicts memory distortions for trauma reminders in combat-related PTSD. *Journal of Psychiatric Research*, *45*(5), 660-669.

Hebscher, M., Levine, B., & Gilboa, A. (2018). The precuneus and hippocampus contribute to individual differences in the unfolding of spatial representations during episodic autobiographical memory. *Neuropsychologia*, *110*, 123-133.

Henderson, J., & Greene, E. (1977). Behavioral effects of lesions of precommissural and postcommissural fornix. *Brain Research Bulletin*, *2*(2), 123-129.

Herbet, G., Zemmoura, I., & Duffau, H. (2018). Functional anatomy of the inferior longitudinal fasciculus: from historical reports to current hypotheses. *Frontiers in Neuroanatomy*, *12*, 77.

Himmelstein, P., Barb, S., Finlayson, M. A., & Young, K. D. (2018). Linguistic analysis of the autobiographical memories of individuals with major depressive disorder. *PLOS ONE*, *13*(11), e0207814.

Hodgetts, C. J. (2017). How we discovered that brain connections shape memories. *The Conversation*. https://theconversation.com/how-we-discovered-that-brain-connections-shape-memories-80506

Hodgetts, C. J., Postans, M., Shine, J. P., Jones, D. K., Lawrence, A. D., & Graham, K. S. (2015). Dissociable roles of the inferior longitudinal fasciculus and fornix in face and place perception. *eLife*, *4*, e07902.

Hodgetts, C. J., Postans, M., Warne, N., Varnava, A., Lawrence, A. D., & Graham, K. S. (2017a). Distinct contributions of the fornix and inferior longitudinal fasciculus to episodic and semantic autobiographical memory. *Cortex*, *94*, 1-14.

Hodgetts, C. J., Stefani, M., Williams, A. N., Kolarik, B. S., Yonelinas, A. P., Ekstrom, A. D., ... & Graham, K. S. (2020). The role of the fornix in human navigational learning. *Cortex*, *124*, 97-110.

Hodgetts, C. J., Voets, N. L., Thomas, A. G., Clare, S., Lawrence, A. D., & Graham, K. S. (2017b). Ultra-high-field fMRI reveals a role for the subiculum in scene perceptual discrimination. *Journal of Neuroscience*, *37*(12), 3150-3159.

Hofstetter, S., & Assaf, Y. (2017). The rapid development of structural plasticity through short water maze training: A DTI study. *NeuroImage*, *155*, 202-208.

Hohman, T. J., Peynircioğlu, Z. F., & Beason-Held, L. L. (2013). Flexibility of event boundaries in autobiographical memory. *Memory*, *21*(2), 249-260.

Holland, A. C., Addis, D. R., & Kensinger, E. A. (2011). The neural correlates of specific versus general autobiographical memory construction and elaboration. *Neuropsychologia*, *49*(12), 3164-3177.

Howe, M. L., & Courage, M. L. (1997). The emergence and early development of autobiographical memory. *Psychological Review*, *104*(3), 499.

Irish, M. (2016). Semantic memory as the essential scaffold for future-oriented mental time travel. *Seeing the Future: Theoretical Perspectives on Future-Oriented Mental Time Travel*, 389-408.

Irish, M., & Piguet, O. (2013). The pivotal role of semantic memory in remembering the past and imagining the future. *Frontiers in Behavioral Neuroscience*, *7*, 27.

Irish, M., & Vatansever, D. (2020). Rethinking the episodic-semantic distinction from a gradient perspective. *Current Opinion in Behavioral Sciences*, *32*, 43-49.

Irish, M., Addis, D. R., Hodges, J. R., & Piguet, O. (2012a). Considering the role of semantic memory in episodic future thinking: evidence from semantic dementia. *Brain*, *135*(7), 2178-2191.

Irish, M., Hodges, J. R., & Piguet, O. (2013). Episodic future thinking is impaired in the behavioural variant of frontotemporal dementia. *Cortex*, *49*(9), 2377-2388.

Irish, M., Piguet, O., & Hodges, J. R. (2012b). Self-projection and the default network in frontotemporal dementia. *Nature Reviews Neurology*, *8*(3), 152-161.

Jackson, R. L., Bajada, C. J., Lambon Ralph, M. A., & Cloutman, L. L. (2020). The graded change in connectivity across the ventromedial prefrontal Cortex reveals distinct subregions. *Cerebral Cortex*, *30*(1), 165-180.

Jackson, R. L., Hoffman, P., Pobric, G., & Lambon Ralph, M. A. (2016). The semantic network at work and rest: differential connectivity of anterior temporal lobe subregions. *Journal of Neuroscience*, *36*(5), 1490-1501.

Jay, T. M., & Witter, M. P. (1991). Distribution of hippocampal CA1 and subicular efferents in the prefrontal Cortex of the rat studied by means of anterograde transport of Phaseolus vulgaris-leucoagglutinin. *Journal of Comparative Neurology*, *313*(4), 574-586.

Jbabdi, S., & Behrens, T. E. (2013). Long-range connectomics. *Annals of the New York Academy of Sciences*, *1305*(1), 83.

Jeunehomme, O., & D'Argembeau, A. (2019). The time to remember: Temporal compression and duration judgements in memory for real-life events. *Quarterly Journal of Experimental Psychology*, *72*(4), 930-942.

Jeurissen, B., Leemans, A., Jones, D. K., Tournier, J. D., & Sijbers, J. (2011). Probabilistic fiber tracking using the residual bootstrap with constrained spherical deconvolution. *Human Brain Mapping*, *32*(3), 461-479.

Jin, J., & Maren, S. (2015). Prefrontal-hippocampal interactions in memory and emotion. *Frontiers in systems neuroscience*, *9*, 170.

Jing, H. G., Madore, K. P., & Schacter, D. L. (2016). Worrying about the future: An episodic specificity induction impacts problem solving, reappraisal, and well-being. *Journal of Experimental Psychology: General*, *145*(4), 402.

Johansen-Berg, H., & Rushworth, M. F. (2009). Using diffusion imaging to study human connectional anatomy. *Annual Review of Neuroscience*, *32*, 75-94.

Johnson, M. K., Hashtroudi, S., & Lindsay, D. S. (1993). Source monitoring. *Psychological Bulletin*, *114*(1), 3.

Johnson, R. T., Yeatman, J. D., Wandell, B. A., Buonocore, M. H., Amaral, D. G., & Nordahl, C. W. (2014). Diffusion properties of major white matter tracts in young, typically developing children. *NeuroImage*, *88*, 143-154.

Jones, A., Rose, A. K., Cole, J., & Field, M. (2013). Effects of alcohol cues on craving and ad libitum alcohol consumption in social drinkers: the role of disinhibition. *Journal of Experimental Psychopathology*, *4*(3), 239-249.

Jones, D. K., & Cercignani, M. (2010). Twenty-five pitfalls in the analysis of diffusion MRI data. *NMR in Biomedicine*, *23*(7), 803-820.

Jones, D. K., Knösche, T. R., & Turner, R. (2013). White matter integrity, fiber count, and other fallacies: the do's and don'ts of diffusion MRI. *NeuroImage*, *73*, 239-254.

Kane, M. J., & Engle, R. W. (2002). The role of prefrontal Cortex in working-memory capacity, executive attention, and general fluid intelligence: An individual-differences perspective. *Psychonomic Bulletin & Review*, *9*(4), 637-671.

Kazui, H., Hashimoto, M., Hirono, N., & Mori, E. (2003). Nature of personal semantic memory: Evidence from Alzheimer's disease. *Neuropsychologia*, *41*(8), 981-988.

Kazui, H., Hashimoto, M., Hirono, N., Imamura, T., Tanimukai, S., Hanihara, T., ... & Mori, E. (2000). A study of remote memory impairment in Alzheimer's disease by using the family line test. *Dementia and Geriatric Cognitive Disorders*, *11*(1), 53-58.

Kernbach, J. M., Yeo, B. T., Smallwood, J., Margulies, D. S., De Schotten, M. T., Walter, H., ... & Bzdok, D. (2018). Subspecialization within default mode nodes characterized in 10,000 UK Biobank participants. *Proceedings of the National Academy of Sciences*, *115*(48), 12295-12300.

Kero, P., & Lee, D. (2016). Likert is Pronounced" LICK-urt" not" LIE-kurt" and the Data are Ordinal not Interval. *Journal of Applied Measurement*, *17*(4), 502-509.

Kim, H. (2020). An integrative model of network activity during episodic memory retrieval and a meta-analysis of fMRI studies on source memory retrieval. *Brain Research*, *1747*, 147049.

Kim, S. (2015). ppcor: an R package for a fast calculation to semi-partial correlation coefficients. *Communications for Statistical Applications and Methods*, *22*(6), 665.

Kirchhoff, B. A. (2009). Individual differences in episodic memory: The role of self-initiated encoding strategies. *The Neuroscientist*, *15*(2), 166-179.

Klein, S. B. (2013). The complex act of projecting oneself into the future. *Wiley Interdisciplinary Reviews: Cognitive Science*, *4*(1), 63-79.

Klein, S. B. (2015). What memory is. *Wiley Interdisciplinary Reviews: Cognitive Science*, *6*(1), 1-38.

Klein, S. B. (2016). Autonoetic consciousness: Reconsidering the role of episodic memory in future-oriented self-projection. *Quarterly Journal of Experimental Psychology*, *69*(2), 381-401.

Klein, S. B., & Lax, M. L. (2010). The unanticipated resilience of trait self-knowledge in the face of neural damage. *Memory*, *18*(8), 918-948.

Klein, S. B., Loftus, J., & Kihlstrom, J. F. (2002). Memory and temporal experience: The effects of episodic memory loss on an amnesic patient's ability to remember the past and imagine the future. *Social Cognition*, *20*(5), 353-379.

Koriat, A., & Goldsmith, M. (1994). Memory in naturalistic and laboratory contexts: Distinguishing the accuracy-oriented and quantity-oriented approaches to memory assessment. *Journal of Experimental Psychology: General*, *123*(3), 297.

Kosslyn, S. M., Ganis, G., & Thompson, W. L. (2001). Neural foundations of imagery. *Nature Reviews Neuroscience*, *2*(9), 635-642.

Köylü, B., Trinka, E., Ischebeck, A., Visani, P., Trieb, T., Kremser, C., ... & Benke, T. (2006). Neural correlates of verbal semantic memory in patients with temporal lobe epilepsy. *Epilepsy Research*, *72*(2-3), 178-191.

Kozlowski, L. T., & Bryant, K. J. (1977). Sense of direction, spatial orientation, and cognitive maps. *Journal of Experimental Psychology: Human Perception and Performance*, *3*(4), 590.

Krueger, F., Barbey, A. K., & Grafman, J. (2009). The medial prefrontal Cortex mediates social event knowledge. *Trends in Cognitive Sciences*, *13*(3), 103-109.

Kurczek, J., Wechsler, E., Ahuja, S., Jensen, U., Cohen, N. J., Tranel, D., & Duff, M. (2015). Differential contributions of hippocampus and medial prefrontal Cortex to self-projection and self-referential processing. *Neuropsychologia*, *73*, 116-126.

Kuroki, N., Kubicki, M., Nestor, P. G., Salisbury, D. F., Park, H. J., Levitt, J. J., ... & Shenton, M. E. (2006). Fornix integrity and hippocampal volume in male schizophrenic patients. *Biological Psychiatry*, *60*(1), 22-31.

Kutas, M., & Federmeier, K. D. (2011). Thirty years and counting: finding meaning in the N400 component of the event-related brain potential (ERP). *Annual Review of Psychology*, *62*, 621-647.

Kwan, D., Carson, N., Addis, D. R., & Rosenbaum, R. S. (2010). Deficits in past remembering extend to future imagining in a case of developmental amnesia. *Neuropsychologia*, *48*(11), 3179-3186.

La Corte, V., & Piolino, P. (2016). On the Role of Personal semantic memory and temporal distance in episodic future thinking: the TEDIFT model. *Frontiers in Human Neuroscience*, *10*, 385.

Lakens, D. (2016). One-sided tests: Efficient and underused [Blog post]. In *The 20% Statistician*. https://daniellakens.blogspot.com/2016/03/one-sided-tests-efficient-and-underused.html

Lakens, D., Adolfi, F. G., Albers, C. J., Anvari, F., Apps, M. A., Argamon, S. E., ... & Zwaan, R. A. (2018). Justify your alpha. *Nature Human Behaviour*, *2*(3), 168-171.

Lambon Ralph, M. A., Jefferies, E., Patterson, K., & Rogers, T. T. (2017). The neural and computational bases of semantic cognition. *Nature Reviews Neuroscience*, *18*(1), 42.

Lee, M. D., & Wagenmakers, E. J. (2014). *Bayesian cognitive modeling: A practical course*. Cambridge University Press.

Leemans A., Jeurissen B., Sijbers J., Jones D.K. (2009) ExploreDTI: A graphical toolbox for processing, analyzing, and visualizing diffusion MR data. In: *Proceedings of the 17th Annual Meeting of International Society of Magnetic Resonance Medicine, Hawaii*. p. 3537

Leemans, A., & Jones, D. K. (2009). The B-matrix must be rotated when correcting for subject motion in DTI data. *Magnetic Resonance in Medicine: An Official Journal of the International Society for Magnetic Resonance in Medicine*, *61*(6), 1336-1349.

Lehn, H., Steffenach, H. A., van Strien, N. M., Veltman, D. J., Witter, M. P., & Håberg, A. K. (2009). A specific role of the human hippocampus in recall of temporal sequences. *Journal of Neuroscience*, *29*(11), 3475-3484.

Lehner, E., & D'Argembeau, A. (2016). The role of personal goals in autonoetic experience when imagining future events. *Consciousness and Cognition*, *42*, 267-276.

LePort, A. K., Stark, S. M., McGaugh, J. L., & Stark, C. E. (2017). A cognitive assessment of highly superior autobiographical memory. *Memory*, *25*(2), 276-288.

Levine, B. (2018). Peer commentary on "Do questionnaires reflect their purported cognitive functions?" by Clark, I. A. & Maguire, E. A. https://www.biorxiv.org/content/10.1101/583690v1

Levine, B., Svoboda, E., Hay, J. F., Winocur, G., & Moscovitch, M. (2002). Aging and autobiographical memory: dissociating episodic from semantic retrieval. *Psychology and Aging*, *17*(4), 677.

Levine, B., Turner, G. R., Tisserand, D., Hevenor, S. J., Graham, S. J., & McIntosh, A. R. (2004). The functional neuroanatomy of episodic and semantic autobiographical remembering: a prospective functional MRI study. *Journal of Cognitive Neuroscience*, *16*(9), 1633-1646.

Levy, I., Lazzaro, S. C., Rutledge, R. B., & Glimcher, P. W. (2011). Choice from non-choice: predicting consumer preferences from blood oxygenation level-dependent signals obtained during passive viewing. *Journal of Neuroscience*, *31*(1), 118-125.

Lewis, M., & Ramsay, D. (2004). Development of self-recognition, personal pronoun use, and pretend play during the 2nd year. *Child Development*, *75*(6), 1821-1831.

Liberman, N., & Trope, Y. (2008). The psychology of transcending the here and now. *Science*, *322*(5905), 1201-1205.

Lieberman, M. D., Straccia, M. A., Meyer, M. L., Du, M., & Tan, K. M. (2019). Social, self,(situational), and affective processes in medial prefrontal Cortex (MPFC): Causal, multivariate, and reverse inference evidence. *Neuroscience & Biobehavioral Reviews*, *99*, 311-328.

Liu, W., Shi, Y., Cousins, J. N., Kohn, N., & Fernandez, G. (2020). Hippocampal-medial prefrontal event segmentation and integration contribute to episodic memory formation. *bioRxiv*.

Loftus, E. F. (1973). Activation of semantic memory. *The American Journal of Psychology*, 331-337.

Loftus, E. F., & Pickrell, J. E. (1995). The formation of false memories. *Psychiatric Annals*, *25*(12), 720-725.

Logan, C. J. (2014). Making progress in non-human mental time travel. *Frontiers in Psychology*, *5*, 305.

Luchetti, M., & Sutin, A. R. (2016). Measuring the phenomenology of autobiographical memory: A short form of the Memory Experiences Questionnaire. *Memory*, *24*(5), 592-602.

Mace, J. H., McQueen, M. L., Hayslett, K. E., Staley, B. J. A., & Welch, T. J. (2019). Semantic memories prime autobiographical memories: General implications and implications for everyday autobiographical remembering. *Memory & Cognition*, *47*(2), 299-312.

Maggia, C., Mistral, T., Doyle, S., Forbes, F., Krainik, A., Galanaud, D., ... & Payen, J. F. (2017, September). Traumatic Brain Lesion Quantification based on Mean Diffusivity Changes. In *International MICCAI Brain Lesion Workshop* (pp. 88-99). Springer, Cham.

Maguire, E. A. (1997). Hippocampal involvement in human topographical memory: evidence from functional imaging. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *352*(1360), 1475-1480.

Maguire, E. A., & Frith, C. D. (2003). Aging affects the engagement of the hippocampus during autobiographical memory retrieval. *Brain*, *126*(7), 1511-1523.

Maguire, E. A., & Mullally, S. L. (2013). The hippocampus: a manifesto for change. *Journal of Experimental Psychology: General*, *142*(4), 1180.

Malanowski, S. (2016). Is episodic memory uniquely human? Evaluating the episodic-like memory research program. *Synthese*, *193*(5), 1433-1455.

Mandonnet, E., Nouet, A., Gatignol, P., Capelle, L., & Duffau, H. (2007). Does the left inferior longitudinal fasciculus play a role in language? A brain stimulation study. *Brain*, *130*(3), 623-629.

Markowitsch, H. J., & Staniloiu, A. (2011). Memory, autonoetic consciousness, and the self. *Consciousness and Cognition*, *20*(1), 16-39.

Marquine, M. J., Grilli, M. D., Rapcsak, S. Z., Kaszniak, A. W., Ryan, L., Walther, K., & Glisky, E. L. (2016). Impaired personal trait knowledge, but spared other-person trait knowledge, in an individual with bilateral damage to the medial prefrontal cortex. *Neuropsychologia*, *89*, 245-253.

Mars, R. B., Neubert, F. X., Noonan, M. P., Sallet, J., Toni, I., & Rushworth, M. F. (2012). On the relationship between the "default mode network" and the "social brain". *Frontiers in Human Neuroscience*, *6*, 189.

Martin, V. C., Schacter, D. L., Corballis, M. C., & Addis, D. R. (2011). A role for the hippocampus in encoding simulations of future events. *Proceedings of the National Academy of Sciences*, *108*(33), 13858-13863.

Martinelli, P., Sperduti, M., & Piolino, P. (2013). Neural substrates of the self-memory system: New insights from a meta-analysis. *Human Brain Mapping*, *34*(7), 1515-1529.

Martin-Ordas, G. (2020). It is about time: Conceptual and experimental evaluation of the temporal cognitive mechanisms in mental time travel. *Wiley Interdisciplinary Reviews: Cognitive Science*, e1530.

Mather, M., Henkel, L. A., & Johnson, M. K. (1997). Evaluating characteristics of false memories: Remember/know judgments and memory characteristics questionnaire compared. *Memory & Cognition*, *25*(6), 826-837.

Mathiasen, M. L., Louch, R. C., Nelson, A. D., Dillingham, C. M., & Aggleton, J. P. (2019). Trajectory of hippocampal fibres to the contralateral anterior thalamus and mammillary bodies in rats, mice, and macaque monkeys. *Brain and Neuroscience Advances*, *3*, 2398212819871205.

McCormick, C., Ciaramelli, E., De Luca, F., & Maguire, E. A. (2018). Comparing and contrasting the cognitive effects of hippocampal and ventromedial prefrontal cortex damage: a review of human lesion studies. *Neuroscience*, *374*, 295-318.

McCormick, C., St-Laurent, M., Ty, A., Valiante, T. A., & McAndrews, M. P. (2015). Functional and effective hippocampal–neocortical connectivity during construction and elaboration of autobiographical memory retrieval. *Cerebral Cortex*, *25*(5), 1297-1305.

McDermott, K. B., Szpunar, K. K., & Christ, S. E. (2009). Laboratory-based and autobiographical retrieval tasks differ substantially in their neural substrates. *Neuropsychologia*, *47*(11), 2290-2298.

Mehta, S., Inoue, K., Rudrauf, D., Damasio, H., Tranel, D., & Grabowski, T. (2016). Segregation of anterior temporal regions critical for retrieving names of unique and non-unique entities reflects underlying long-range connectivity. *Cortex*, *75*, 1-19.

Memel, M., Wank, A. A., Ryan, L., & Grilli, M. D. (2020). The relationship between episodic detail generation and anterotemporal, posteromedial, and hippocampal white matter tracts. *Cortex*, *123*, 124-140.

Mesulam, M. (2012). The evolving landscape of human cortical connectivity: facts and inferences. *NeuroImage*, *62*(4), 2182-2189.

Mesulam, M. M. (1995). Structure and function of cholinergic pathways in the cerebral Cortex, limbic system, basal ganglia and thalamus of the human brain. *Psychopharmacology: The Fourth Generation of Progress*.

Metzler-Baddeley, C., Jones, D. K., Belaroussi, B., Aggleton, J. P., & O'Sullivan, M. J. (2011). Frontotemporal connections in episodic memory and aging: a diffusion MRI tractography study. *Journal of Neuroscience*, *31*(37), 13236-13245.

Miller, M. B., Donovan, C. L., Bennett, C. M., Aminoff, E. M., & Mayer, R. E. (2012). Individual differences in cognitive style and strategy predict similarities in the patterns of brain activity between individuals. *NeuroImage*, *59*(1), 83-93.

Miloyan, B., McFarlane, K. A., & Suddendorf, T. (2019). Measuring mental time travel: Is the hippocampus really critical for episodic memory and episodic foresight? *Cortex*, *117*, 371-384.

Miloyan, B., McFarlane, K., & Vásquez-Echeverría, A. (2019). The adapted Autobiographical interview: A systematic review and proposal for conduct and reporting. *Behavioural Brain Research*, *370*, 111881.

Mion, M., Patterson, K., Acosta-Cabronero, J., Pengas, G., Izquierdo-Garcia, D., Hong, Y. T., ... & Nestor, P. J. (2010). What the left and right anterior fusiform gyri tell us about semantic memory. *Brain*, *133*(11), 3256-3268.

Mitchell, J. P., Schirmer, J., Ames, D. L., & Gilbert, D. T. (2011). Medial prefrontal Cortex predicts intertemporal choice. *Journal of Cognitive Neuroscience*, *23*(4), 857-866.

Miyake, A., & Friedman, N. P. (2012). The nature and organization of individual differences in executive functions: Four general conclusions. *Current Directions in Psychological Science*, *21*(1), 8-14.

Monk, A. M., Dalton, M. A., Barnes, G. R., & Maguire, E. A. (2021). The Role of Hippocampal–Ventromedial Prefrontal Cortex Neural Dynamics in Building Mental Representations. *Journal of Cognitive Neuroscience*, *33*(1), 89-103.

Monsa, R., Peer, M., & Arzy, S. (2020). Processing of Different Temporal Scales in the Human Brain. *Journal of Cognitive Neuroscience*, *32*(11), 2087-2102.

Mori, S., & Zhang, J. (2006). Principles of diffusion tensor imaging and its applications to basic neuroscience research. *Neuron*, *51*(5), 527-539.

Moscovitch, M., Rosenbaum, R. S., Gilboa, A., Addis, D. R., Westmacott, R., Grady, C., ... & Nadel, L. (2005). Functional neuroanatomy of remote episodic, semantic and spatial memory: a unified account based on multiple trace theory. *Journal of Anatomy*, *207*(1), 35-66.

Mullally, S. L., & Maguire, E. A. (2014). Memory, imagination, and predicting the future: a common brain mechanism? *The Neuroscientist*, *20*(3), 220-234.

Mullally, S. L., Intraub, H., & Maguire, E. A. (2012). Attenuated boundary extension produces a paradoxical memory advantage in amnesic patients. *Current Biology*, *22*(4), 261-268.

Murray, E. A., Wise, S. P., & Graham, K. S. (2017). *The evolution of memory systems: ancestors, anatomy, and adaptations*. Oxford University Press.

Murray, E. A., Wise, S. P., & Graham, K. S. (2018). Representational specializations of the hippocampus in phylogenetic perspective. *Neuroscience Letters*, *680*, 4-12.

Murray, R. J., Schaer, M., & Debbané, M. (2012). Degrees of separation: a quantitative neuroimaging meta-analysis investigating self-specificity and shared neural activation between self-and other-reflection. *Neuroscience & Biobehavioral Reviews*, *36*(3), 1043-1059.

Nadel, L., Hoscheidt, S., & Ryan, L. R. (2013). Spatial cognition and the hippocampus: the anterior–posterior axis. *Journal of Cognitive Neuroscience*, *25*(1), 22-28.

Neisser, U. (1978). Memory: What are the important questions? In M. M. Gruneberg, P. E. Morris, & R. N. Sykes (Eds.), *Practical aspects of memory* (pp. 3-24). London: Academic Press.

Neisser, U. (1981). John Dean's memory: A case study. *Cognition*, *9*(1), 1-22.

Neisser, U. (1982). Memory: What are the important questions. *Memory observed: Remembering in natural contexts*, 3-19.

Nelson, A. J., Kinnavane, L., Amin, E., O'Mara, S. M., & Aggleton, J. P. (2020). Deconstructing the direct reciprocal hippocampal-anterior thalamic pathways for spatial learning. *Journal of Neuroscience*, *40*(36), 6978-6990.

Nielson, D. M., Smith, T. A., Sreekumar, V., Dennis, S., & Sederberg, P. B. (2015). Human hippocampus represents space and time during retrieval of real-world memories. *Proceedings of the National Academy of Sciences*, *112*(35), 11078-11083.

Nugiel, T., Alm, K. H., & Olson, I. R. (2016). Individual differences in white matter microstructure predict semantic control. *Cognitive, Affective, & Behavioral Neuroscience*, *16*(6), 1003-1016.

Nyberg, L. (1996). Classifying human long-term memory: Evidence from converging dissociations. *European Journal of Cognitive Psychology*, *8*(2), 163-184.

Oechslin, M. S., Gschwind, M., & James, C. E. (2018). Tracking training-related plasticity by combining fMRI and DTI: the right hemisphere ventral stream mediates musical syntax processing. *Cerebral Cortex*, *28*(4), 1209-1218.

O'Keefe, J., & Nadel, L. (1978). *The hippocampus as a cognitive map*. Oxford: Clarendon Press.

O'Keefe, J., Nadel, L., Keightley, S., & Kill, D. (1975). Fornix lesions selectively abolish place learning in the rat. *Experimental Neurology*, *48*(1), 152-166.

Okuda, J., Fujii, T., Ohtake, H., Tsukiura, T., Tanji, K., Suzuki, K., ... & Yamadori, A. (2003). Thinking of the future and past: The roles of the frontal pole and the medial temporal lobes. *NeuroImage*, *19*(4), 1369-1380.

Osborne, B., & Dodek, A. B. (1986). Disrupted patterns of consummatory behavior in rats with fornix transections. *Behavioral and neural biology*, *45*(2), 212-222.

Østby, Y., Walhovd, K. B., Tamnes, C. K., Grydeland, H., Westlye, L. T., & Fjell, A. M. (2012). Mental time travel and default-mode network functional connectivity in the developing brain. *Proceedings of the National Academy of Sciences*, *109*(42), 16800-16804.

Packard, M. G., Hirsh, R., & White, N. M. (1989). Differential effects of fornix and caudate nucleus lesions on two radial maze tasks: evidence for multiple memory systems. *Journal of Neuroscience*, *9*(5), 1465-1472.

Pajevic, S., Basser, P. J., & Fields, R. D. (2014). Role of myelin plasticity in oscillations and synchrony of neuronal activity. *Neuroscience*, *276*, 135-147.

Palombo, D. J., Alain, C., Söderlund, H., Khuu, W., & Levine, B. (2015). Severely deficient autobiographical memory (SDAM) in healthy adults: A new mnemonic syndrome. *Neuropsychologia*, *72*, 105-118.

Palombo, D. J., Bacopulos, A., Amaral, R. S., Olsen, R. K., Todd, R. M., Anderson, A. K., & Levine, B. (2018a). Episodic autobiographical memory is associated with variation in the size of hippocampal subregions. *Hippocampus*, *28*(2), 69-75.

Palombo, D. J., Hayes, S. M., Peterson, K. M., Keane, M. M., & Verfaellie, M. (2018b). Medial temporal lobe contributions to episodic future thinking: Scene construction or future projection? *Cerebral Cortex*, *28*(2), 447-458.

Palombo, D. J., Sheldon, S., & Levine, B. (2018c). Individual differences in autobiographical memory. *Trends in Cognitive Sciences*, *22*(7), 583-597.

Palombo, D. J., Williams, L. J., Abdi, H., & Levine, B. (2013). The survey of autobiographical memory (SAM): A novel measure of trait mnemonics in everyday life. *Cortex*, *49*(6), 1526-1540.

Parker, A., & Gaffan, D. (1997). Mamillary body lesions in monkeys impair object-in-place memory: functional unity of the fornix-mamillary system. *Journal of Cognitive Neuroscience*, *9*(4), 512-521.

Parker, G. D., Marshall, D., Rosin, P. L., Drage, N., Richmond, S., & Jones, D. K. (2013). Fast and fully automated clustering of whole brain tractography results using shape-space analysis. *Proceedings of the International Society for Magnetic Resonance in Medicine. Salt Lake City, USA*, *778*.

Pasternak, O., Maier-Hein, K., Baumgartner, C., Shenton, M. E., Rathi, Y., & Westin, C. F. (2014). The estimation of free-water corrected diffusion tensors. In *Visualization and Processing of Tensors and Higher Order Descriptors for Multi-Valued Data* (pp. 249-270). Springer, Berlin, Heidelberg.

Pasternak, O., Sochen, N., Gur, Y., Intrator, N., & Assaf, Y. (2009). Free water elimination and mapping from diffusion MRI. *Magnetic Resonance in Medicine: An Official Journal of the International Society for Magnetic Resonance in Medicine*, *62*(3), 717-730.

Patenaude, B., Smith, S. M., Kennedy, D. N., & Jenkinson, M. (2011). A Bayesian model of shape and appearance for subcortical brain segmentation. *NeuroImage*, *56*(3), 907-922.

Pathman, T., Larkina, M., Burch, M. M., & Bauer, P. J. (2013). Young children's memory for the times of personal past events. *Journal of Cognition and Development*, *14*(1), 120-140.

Patterson, K., Nestor, P. J., & Rogers, T. T. (2007). Where do you know what you know? The representation of semantic knowledge in the human brain. *Nature Reviews Neuroscience*, *8*(12), 976-987.

Paulhus, D. L., & Vazire, S. (2007). The self-report method. *Handbook of research methods in personality psychology*, *1*, 224-239.

Pearl, L., & Steyvers, M. (2013). “C’mon–You Should Read This”: Automatic Identification of Tone from Language Text. *International Journal of Computational Linguistics (IJCL)*, *4*(1), 12-30.

Pearson, J., & Kosslyn, S. M. (2015). The heterogeneity of mental representation: Ending the imagery debate. *Proceedings of the National Academy of Sciences*, *112*(33), 10089-10092.

Pernet, C. R., Wilcox, R. R., & Rousselet, G. A. (2013). Robust correlation analyses: false positive and power validation using a new open source matlab toolbox. *Frontiers in Psychology*, *3*, 606.

Perugini, M., Gallucci, M., & Costantini, G. (2018). A Practical primer to power analysis for simple experimental designs. *International Review of Social Psychology, 31*(1), Article 20.

Petrican, R., Palombo, D. J., Sheldon, S., & Levine, B. (2020). The Neural Dynamics of Individual Differences in Episodic Autobiographical Memory. *eNeuro*, *7*(2).

Pezzulo, G., & Rigoli, F. (2011). The value of foresight: how prospection affects decision-making. *Frontiers in Neuroscience*, *5*, 79.

Philippi, C. L., Tranel, D., Duff, M., & Rudrauf, D. (2015). Damage to the default mode network disrupts autobiographical memory retrieval. *Social Cognitive and Affective Neuroscience*, *10*(3), 318-326.

Piolino, P., Desgranges, B., Belliard, S., Matuszewski, V., Lalevée, C., De La Sayette, V., & Eustache, F. (2003). Autobiographical memory and autonoetic consciousness: triple dissociation in neurodegenerative diseases. *Brain*, *126*(10), 2203-2219.

Place, R., Farovik, A., Brockmann, M., & Eichenbaum, H. (2016). Bidirectional prefrontal-hippocampal interactions support context-guided memory. *Nature Neuroscience*, *19*(8), 992-994.

Poletti, C. E., & Creswell, G. (1977). Fornix system efferent projections in the squirrel monkey: an experimental degeneration study. *Journal of Comparative Neurology*, *175*(1), 101-127.

Poppenk, J., & Moscovitch, M. (2011). A hippocampal marker of recollection memory ability among healthy young adults: contributions of posterior and anterior segments. *Neuron*, *72*(6), 931-937.

Poppenk, J., Evensmoen, H. R., Moscovitch, M., & Nadel, L. (2013). Long-axis specialization of the human hippocampus. *Trends in Cognitive Sciences*, *17*(5), 230-240.

Poreh, A., Winocur, G., Moscovitch, M., Backon, M., Goshen, E., Ram, Z., & Feldman, Z. (2006). Anterograde and retrograde amnesia in a person with bilateral fornix lesions following removal of a colloid cyst. *Neuropsychologia*, *44*(12), 2241-2248.

Postans, M., Hodgetts, C. J., Mundy, M. E., Jones, D. K., Lawrence, A. D., & Graham, K. S. (2014). Interindividual variation in fornix microstructure and macrostructure is related to visual discrimination accuracy for scenes but not faces. *Journal of Neuroscience*, *34*(36), 12121-12126.

Powell, T. P. S., Guillery, R. W., & Cowan, W. M. (1957). A quantitative study of the fornixmamillo-thalamic system. *Journal of Anatomy*, *91*(Pt 4), 419.

Prabhakar, J., & Ghetti, S. (2020). Connecting the dots between past and future: constraints in episodic future thinking in early childhood. *Child Development*, *91*(2), e315-e330.

Prebble, S. C., Addis, D. R., & Tippett, L. J. (2013). Autobiographical memory and sense of self. *Psychological Bulletin*, *139*(4), 815.

Preston, A. R., & Eichenbaum, H. (2013). Interplay of hippocampus and prefrontal Cortex in memory. *Current Biology*, *23*(17), R764-R773.

Quintana, D. S., & Williams, D. R. (2018). Bayesian alternatives for common null-hypothesis significance tests in psychiatry: a non-technical guide using JASP. *BMC Psychiatry*, *18*(1), 178.

Race, E., Keane, M. M., & Verfaellie, M. (2011). Medial temporal lobe damage causes deficits in episodic memory and episodic future thinking not attributable to deficits in narrative construction. *Journal of Neuroscience*, *31*(28), 10262-10269.

Raichle, M. E. (2015). The brain's default mode network. *Annual Review of Neuroscience*, *38*, 433-447.

Ranganath, C., & Ritchey, M. (2012). Two cortical systems for memory-guided behaviour. *Nature Reviews Neuroscience*, *13*(10), 713-726.

Raslau, F. D., Augustinack, J. C., Klein, A. P., Ulmer, J. L., Mathews, V. P., & Mark, L. P. (2015). Memory part 3: the role of the fornix and clinical cases. *American Journal of Neuroradiology*, *36*(9), 1604-1608.

Rathbone, C. J., Moulin, C. J., & Conway, M. A. (2009). Autobiographical memory and amnesia: Using conceptual knowledge to ground the self. *Neurocase*, *15*(5), 405-418.

Reil, J. C. (1812). Nachträge zur anatomie des grossen und kleinen Gehirns. *Archiv für die Physiologie*, *11*(3), 345-376.

Rendell, P. G., Bailey, P. E., Henry, J. D., Phillips, L. H., Gaskin, S., & Kliegel, M. (2012). Older adults have greater difficulty imagining future rather than atemporal experiences. *Psychology and Aging*, *27*(4), 1089.

Renoult, L., & Rugg, M. D. (2020). An historical perspective on Endel Tulving's episodic-semantic distinction. *Neuropsychologia*, *139*, 107366.

Renoult, L., Armson, M. J., Diamond, N. B., Fan, C. L., Jeyakumar, N., Levesque, L., ... & Levine, B. (2020). Classification of general and personal semantic details in the Autobiographical Interview. *Neuropsychologia*, *144*, 107501.

Renoult, L., Davidson, P. S., Palombo, D. J., Moscovitch, M., & Levine, B. (2012). Personal semantics: at the crossroads of semantic and episodic memory. *Trends in Cognitive Sciences*, *16*(11), 550-558.

Renoult, L., Irish, M., Moscovitch, M., & Rugg, M. D. (2019). From knowing to remembering: the semantic–episodic distinction. *Trends in Cognitive Sciences*, *23*(12), 1041-1057.

Renoult, L., Tanguay, A., Beaudry, M., Tavakoli, P., Rabipour, S., Campbell, K., ... & Davidson, P. S. (2016). Personal semantics: Is it distinct from episodic and semantic memory? An electrophysiological study of memory for autobiographical facts and repeated events in honor of Shlomo Bentin. *Neuropsychologia*, *83*, 242-256.

Rice, G. E., Lambon Ralph, M. A., & Hoffman, P. (2015). The roles of left versus right anterior temporal lobes in conceptual knowledge: an ALE meta-analysis of 97 functional neuroimaging studies. *Cerebral Cortex*, *25*(11), 4374-4391.

Roberts, R. P., Schacter, D. L., & Addis, D. R. (2018). Scene construction and relational processing: Separable constructs? *Cerebral Cortex*, *28*(5), 1729-1732.

Roberts, R. P., Wiebels, K., Sumner, R. L., van Mulukom, V., Grady, C. L., Schacter, D. L., & Addis, D. R. (2017). An fMRI investigation of the relationship between future imagination and cognitive flexibility. *Neuropsychologia*, *95*, 156-172.

Robin, J. (2018). Spatial scaffold effects in event memory and imagination. *Wiley Interdisciplinary Reviews: Cognitive Science*, *9*(4), e1462.

Robin, J., & Moscovitch, M. (2014). The effects of spatial contextual familiarity on remembered scenes, episodic memories, and imagined future events. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *40*(2), 459.

Robin, J., & Moscovitch, M. (2017). Details, gist and schema: hippocampal–neocortical interactions underlying recent and remote episodic and spatial memory. *Current Opinion in Behavioral Sciences*, *17*, 114-123.

Robinson, J. A., & Swanson, K. L. (1993). Field and observer modes of remembering. *Memory*, *1*(3), 169-184.

Roediger, H. L., & McDermott, K. B. (2013). Two types of event memory. *Proceedings of the National Academy of Sciences*, *110*(52), 20856-20857.

Rogers, T. T., Lambon Ralph, M. A., Garrard, P., Bozeat, S., McClelland, J. L., Hodges, J. R., & Patterson, K. (2004). Structure and deterioration of semantic memory: a neuropsychological and computational investigation. *Psychological Review*, *111*(1), 205.

Romero, K., & Moscovitch, M. (2012). Episodic memory and event construction in aging and amnesia. *Journal of Memory and Language*, *67*(2), 270-284.

Rosenbaum, R. S., Gao, F., Honjo, K., Raybaud, C., Olsen, R. K., Palombo, D. J., ... & Black, S. E. (2014). Congenital absence of the mammillary bodies: a novel finding in a well-studied case of developmental amnesia. *Neuropsychologia*, *65*, 82-87.

Rosenbaum, R. S., Moscovitch, M., Foster, J. K., Schnyer, D. M., Gao, F., Kovacevic, N., ... & Levine, B. (2008). Patterns of autobiographical memory loss in medial-temporal lobe amnesic patients. *Journal of Cognitive Neuroscience*, *20*(8), 1490-1506.

Rosenbaum, R. S., Stuss, D. T., Levine, B., & Tulving, E. (2007). Theory of mind is independent of episodic memory. *Science*, *318*(5854), 1257-1257.

Ross, M., & Wang, Q. (2010). Why we remember and what we remember: Culture and autobiographical memory. *Perspectives on Psychological Science*, *5*(4), 401-409.

Rubin, D. C. (2020). The ability to recall scenes is a stable individual difference: Evidence from autobiographical remembering. *Cognition*, *197*, 104164.

Rubin, D. C. (2021). Properties of autobiographical memories are reliable and stable individual differences. *Cognition*, *210*, 104583.

Rubin, D. C., & Umanath, S. (2015). Event memory: A theory of memory for laboratory, autobiographical, and fictional events. *Psychological Review*, *122*(1), 1.

Rudebeck, S. R., Scholz, J., Millington, R., Rohenkohl, G., Johansen-Berg, H., & Lee, A. C. (2009). Fornix microstructure correlates with recollection but not familiarity memory. *Journal of Neuroscience*, *29*(47), 14987-14992.

Russell, J., Alexis, D., & Clayton, N. (2010). Episodic future thinking in 3-to 5-year-old children: The ability to think of what will be needed from a different point of view. *Cognition*, *114*(1), 56-71.

Saunders, R. C., & Aggleton, J. P. (2007). Origin and topography of fibers contributing to the fornix in macaque monkeys. *Hippocampus*, *17*(5), 396-411.

Schacter, D. L., & Addis, D. R. (2007a). The ghosts of past and future. *Nature*, *445*(7123), 27-27.

Schacter, D. L., & Addis, D. R. (2007b). The cognitive neuroscience of constructive memory: remembering the past and imagining the future. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *362*(1481), 773-786.

Schacter, D. L., & Madore, K. P. (2016). Remembering the past and imagining the future: Identifying and enhancing the contribution of episodic memory. *Memory Studies*, *9*(3), 245-255.

Schacter, D. L., Addis, D. R., & Buckner, R. L. (2007). Remembering the past to imagine the future: the prospective brain. *Nature Reviews Neuroscience*, *8*(9), 657-661.

Schacter, D. L., Addis, D. R., Hassabis, D., Martin, V. C., Spreng, R. N., & Szpunar, K. K. (2012). The future of memory: remembering, imagining, and the brain. *Neuron*, *76*(4), 677-694.

Schacter, D. L., Benoit, R. G., & Szpunar, K. K. (2017). Episodic future thinking: Mechanisms and functions. *Current opinion in behavioral sciences*, *17*, 41-50.

Schacter, D. L., Benoit, R. G., De Brigard, F., & Szpunar, K. K. (2015). Episodic future thinking and episodic counterfactual thinking: Intersections between memory and decisions. *Neurobiology of Learning and Memory*, *117*, 14-21.

Schacter, D. L., Norman, K. A., & Koutstaal, W. (1998). The cognitive neuroscience of constructive memory. *Annual Review of Psychology*, *49*(1), 289-318.

Schilling, K. G., Petit, L., Rheault, F., Remedios, S., Pierpaoli, C., Anderson, A. W., ... & Descoteaux, M. (2020). Brain connections derived from diffusion MRI tractography can be highly anatomically accurate—if we know where white matter pathways start, where they end, and where they do not go. *Brain Structure and Function*, *225*(8), 2387-2402.

Schloerke, B., Crowley, J., Cook, D., Hofmann, H., Wickham, H., Briatte, F., ... & Larmarange, J. (2011). Ggally: Extension to ggplot2.

Seehaus, A., Roebroeck, A., Bastiani, M., Fonseca, L., Bratzke, H., Lori, N., ... & Galuske, R. (2015). Histological validation of high-resolution DTI in human post mortem tissue. *Frontiers in Neuroanatomy*, *9*, 98.

Sekeres, M. J., Winocur, G., & Moscovitch, M. (2018). The hippocampus and related neocortical structures in memory transformation. *Neuroscience letters*, *680*, 39-53.

Selarka, D., Rosenbaum, R. S., Lapp, L., & Levine, B. (2019). Association between self-reported and performance-based navigational ability using internet-based remote spatial memory assessment. *Memory*, *27*(5), 723-728.

Shao, Y., Yao, X., Ceci, S. J., & Wang, Q. (2010). Does the self drive mental time travel? *Memory*, *18*(8), 855-862.

Sheldon, S., & Levine, B. (2016). The role of the hippocampus in memory and mental construction. *Annals of the New York Academy of Sciences*, *1369*(1), 76-92.

Sheldon, S., Diamond, N. B., Armson, M. J., Palombo, D. J., Selarka, D., Romero, K., ... & Levine, B. (2018). Assessing Autobiographical Memory: Implications for Understanding the Underlying Neurocognitive Mechanisms. *Stevens' Handbook of Experimental Psychology and Cognitive Neuroscience*, *1*, 1-34.

Sheldon, S., Farb, N., Palombo, D. J., & Levine, B. (2016). Intrinsic medial temporal lobe connectivity relates to individual differences in episodic autobiographical remembering. *Cortex*, *74*, 206-216.

Sheldon, S., Fenerci, C., & Gurguryan, L. (2019). A neurocognitive perspective on the forms and functions of autobiographical memory retrieval. *Frontiers in systems neuroscience*, *13*, 4.

Sheldon, S., Gurguryan, L., Madore, K. P., & Schacter, D. L. (2019). Constructing autobiographical events within a spatial or temporal context: a comparison of two targeted episodic induction techniques. *Memory*, *27*(7), 881-893.

Shin, J. B., Rowley, J., Chowdhury, R. A., Jolicoeur, P., Klein, D., Grova, C., ... & Kobayashi, E. (2019). Inferior longitudinal fasciculus' role in visual processing and language comprehension: a combined MEG-DTI study. *Frontiers in Neuroscience*, *13*, 875.

Siegelman, M., & Baldassano, C. (2020). Remembering together. *Nature human behaviour*, *4*(2), 132-133.

Sigurdsson, T., & Duvarci, S. (2016). Hippocampal-prefrontal interactions in cognition, behavior and psychiatric disease. *Frontiers in systems neuroscience*, *9*, 190.

Simmons, W. K., Reddish, M., Bellgowan, P. S., & Martin, A. (2010). The selectivity and functional connectivity of the anterior temporal lobes. *Cerebral Cortex*, *20*(4), 813-825.

Simons, J., Ritchey, M., & Fernyhough, C. (2021). Brain mechanisms underlying the subjective experience of remembering. https://psyarxiv.com/3642t/

Skowronski, J. J., & Walker, W. R. (2004). How describing autobiographical events can affect autobiographical memories. *Social Cognition*, *22*(5: Special issue), 555-590.

Smallwood, J., Brown, K., Baird, B., & Schooler, J. W. (2012). Cooperation between the default mode network and the frontal–parietal network in the production of an internal train of thought. *Brain research*, *1428*, 60-70.

Smith, S. M. (2002). Fast robust automated brain extraction. *Human Brain Mapping*, *17*(3), 143-155.

Snyder, H. R., & Munakata, Y. (2008). So many options, so little time: The roles of association and competition in underdetermined responding. *Psychonomic Bulletin & Review*, *15*(6), 1083-1088.

Snyder, H. R., Hutchison, N., Nyhus, E., Curran, T., Banich, M. T., O'Reilly, R. C., & Munakata, Y. (2010). Neural inhibition enables selection during language processing. *Proceedings of the National Academy of Sciences*, *107*(38), 16483-16488.

Soares, J., Marques, P., Alves, V., & Sousa, N. (2013). A hitchhiker's guide to diffusion tensor imaging. *Frontiers in neuroscience*, *7*, 31.

Spanò, G., Pizzamiglio, G., McCormick, C., Clark, I. A., De Felice, S., Miller, T. D., ... & Maguire, E. A. (2020). Dreaming with hippocampal damage. *eLife*, *9*, e56211.

Spreng, R. N., & Grady, C. L. (2010). Patterns of brain activity supporting autobiographical memory, prospection, and theory of mind, and their relationship to the default mode network. *Journal of Cognitive Neuroscience*, *22*(6), 1112-1123.

Spreng, R. N., Dimas, E., Mwilambwe-Tshilobo, L., Dagher, A., Koellinger, P., Nave, G., ... & Bzdok, D. (2020). The default network of the human brain is associated with perceived social isolation. *Nature Communications*, *11*(1), 1-11.

Spreng, R. N., Mar, R. A., & Kim, A. S. (2009). The common neural basis of autobiographical memory, prospection, navigation, theory of mind, and the default mode: a quantitative meta-analysis. *Journal of Cognitive Neuroscience*, *21*(3), 489-510.

Spreng, R. N., Stevens, W. D., Chamberlain, J. P., Gilmore, A. W., & Schacter, D. L. (2010). Default network activity, coupled with the frontoparietal control network, supports goal-directed cognition. *NeuroImage*, *53*(1), 303-317.

Stawarczyk, D., & D'Argembeau, A. (2015). Neural correlates of personal goal processing during episodic future thinking and mind-wandering: An ALE meta-analysis. *Human Brain Mapping*, *36*(8), 2928-2947.

Stawarczyk, D., Bezdek, M. A., & Zacks, J. M. (2019). Event representations and predictive processing: The role of the midline default network core. *Topics in Cognitive Science*.

Stawarczyk, D., Majerus, S., Maj, M., Van der Linden, M., & D'Argembeau, A. (2011). Mind-wandering: Phenomenology and function as assessed with a novel experience sampling method. *Acta Psychologica*, *136*(3), 370-381.

Steiger, J. H. (1980). Tests for comparing elements of a correlation matrix. *Psychological Bulletin*, *87*(2), 245.

Steiner, K. L., Thomsen, D. K., & Pillemer, D. B. (2017). Life story chapters, specific memories, and conceptions of the self. *Applied cognitive psychology*, *31*(5), 478-487.

Steinvorth, S., Levine, B., & Corkin, S. (2005). Medial temporal lobe structures are needed to re-experience remote autobiographical memories: evidence from HM and WR. *Neuropsychologia*, *43*(4), 479-496.

Stone, P. J., Dunphy, D. C., & Smith, M. S. (1966). *The general inquirer: A computer approach to content analysis*. M.I.T. Press.

Strikwerda-Brown, C., Grilli, M. D., Andrews-Hanna, J., & Irish, M. (2019). “All is not lost”—Rethinking the nature of memory and the self in dementia. *Ageing research reviews*, *54*, 100932.

Strikwerda-Brown, C., Hodges, J., Piguet, O., & Irish, M. (2020, September 28). Examining the episodic-semantic interplay during future thinking – A reanalysis of external details. https://doi.org/10.31234/osf.io/9yszk

Strikwerda-Brown, C., Mothakunnel, A., Hodges, J. R., Piguet, O., & Irish, M. (2019). External details revisited–A new taxonomy for coding 'non-episodic' content during autobiographical memory retrieval. *Journal of neuropsychology*, *13*(3), 371-397.

Suárez, L. E., Markello, R. D., Betzel, R. F., & Misic, B. (2020). Linking structure and function in macroscale brain networks. *Trends in Cognitive Sciences*.

Suddendorf, T., & Busby, J. (2003). Mental time travel in animals? *Trends in Cognitive Sciences*, *7*(9), 391-396.

Suddendorf, T., & Corballis, M. C. (1997). Mental time travel and the evolution of the human mind. *Genetic, social, and general psychology monographs, 123(2)*, 133–167.

Suddendorf, T., & Corballis, M. C. (2007). The evolution of foresight: What is mental time travel, and is it unique to humans? *Behavioral and brain sciences*, *30*(3), 299-313.

Suddendorf, T., & Redshaw, J. (2013). The development of mental scenario building and episodic foresight. *Annals of the New York Academy of Sciences*, *1296*(1), 135-153.

Suddendorf, T., Addis, D. R., & Corballis, M. C. (2009). Mental time travel and the shaping of the human mind. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *364*(1521), 1317-1324.

Sundgren, P. C., Dong, Q., Gomez-Hassan, D., Mukherji, S. K., Maly, P., & Welsh, R. (2004). Diffusion tensor imaging of the brain: review of clinical applications. *Neuroradiology*, *46*(5), 339-350.

Sutherland, R. J., & Rodriguez, A. J. (1989). The role of the fornix/fimbria and some related subcortical structures in place learning and memory. *Behavioural Brain Research*, *32*(3), 265-277.

Sutin, A. R., & Robins, R. W. (2007). Phenomenology of autobiographical memories: The memory experiences questionnaire. *Memory*, *15*(4), 390-411.

Szpunar, K. K. (2011). On subjective time. *Cortex*, *47*(3), 409-411.

Szpunar, K. K., & McDermott, K. B. (2008). Episodic future thought and its relation to remembering: Evidence from ratings of subjective experience. *Consciousness and Cognition*, *17*(1), 330-334.

Szpunar, K. K., Spreng, R. N., & Schacter, D. L. (2014). A taxonomy of prospection: Introducing an organizational framework for future-oriented cognition. *Proceedings of the National Academy of Sciences*, *111*(52), 18414-18421.

Szpunar, K. K., Watson, J. M., & McDermott, K. B. (2007). Neural substrates of envisioning the future. *Proceedings of the National Academy of Sciences*, *104*(2), 642-647.

Tackman, A. M., Sbarra, D. A., Carey, A. L., Donnellan, M. B., Horn, A. B., Holtzman, N. S., ... & Mehl, M. R. (2019). Depression, negative emotionality, and self-referential language: A multi-lab, multi-measure, and multi-language-task research synthesis. *Journal of Personality and Social Psychology*, *116*(5), 817.

Tanguay, A. (2018). *The Neural Correlates of Personal Semantics* (Doctoral dissertation, Université d'Ottawa/University of Ottawa).

Tanguay, A. F., Palombo, D. J., Atance, C. M., Renoult, L., & Davidson, P. S. (2020). Scrutinizing the grey areas of declarative memory: Do the self-reference and temporal orientation of a trait knowledge task modulate the Late Positive Component (LPC)? *Neuropsychologia*, *142*, 107444.

Tanguay, A. N., Benton, L., Romio, L., Sievers, C., Davidson, P. S., & Renoult, L. (2018). The ERP correlates of self-knowledge: Are assessments of one’s past, present, and future traits closer to semantic or episodic memory? *Neuropsychologia*, *110*, 65-83.

Tarder-Stoll, H., Jayakumar, M., Dimsdale-Zucker, H. R., Günseli, E., & Aly, M. (2020). Dynamic internal states shape memory retrieval. *Neuropsychologia*, *138*, 107328.

Team, R. (2015). RStudio: integrated development for R. *RStudio, Inc., Boston, MA URL http://www. rstudio. com*, *42*, 14.

Tedder, J., Miller, L., Tu, S., Hornberger, M., & Lah, S. (2016). Into the future with little past: exploring mental time travel in a patient with damage to the mammillary bodies/fornix. *The Clinical Neuropsychologist*, *30*(2), 334-349.

Thakral, P. P., Benoit, R. G., & Schacter, D. L. (2017). Imagining the future: The core episodic simulation network dissociates as a function of timecourse and the amount of simulated information. *Cortex*, *90*, 12-30.

Thomas, G. J. (1978). Delayed alternation in rats after pre-or postcommissural fornicotomy. *Journal of Comparative and Physiological Psychology*, *92*(6), 1128.

Thomsen, D. K. (2015). Autobiographical periods: A review and central components of a theory. *Review of General Psychology*, *19*(3), 294-310.

Trope, Y., & Liberman, N. (2003). Temporal construal. *Psychological Review*, *110*(3), 403.

Trope, Y., & Liberman, N. (2010). Construal-level theory of psychological distance. *Psychological Review*, *117*(2), 440.

Tsivilis, D., Vann, S. D., Denby, C., Roberts, N., Mayes, A. R., Montaldi, D., & Aggleton, J. P. (2008). A disproportionate role for the fornix and mammillary bodies in recall versus recognition memory. *Nature Neuroscience*, *11*(7), 834.

Tulving, E. (1972). Episodic and semantic memory. *Organization of Memory*, *1*, 381-403.

Tulving, E. (1983) Elements of Episodic Memory. *Oxford University Press, Oxford.*

Tulving, E. (1985). Memory and consciousness. *Canadian Psychology/Psychologie Canadienne*, *26*(1), 1.

Tulving, E. (1991). Memory research is not a zero-sum game. *American Psychologist, 46*(1), 41–42.

Tulving, E. (2002a). Episodic memory: From mind to brain. *Annual Review of Psychology*, *53*(1), 1-25.

Tulving, E. (2002b). *Chronesthesia: Conscious awareness of subjective time.* In D. T. Stuss & R. T. Knight (Eds.), *Principles of frontal lobe function* (p. 311–325). Oxford University Press.

Tulving, E. (2005). *Episodic Memory and Autonoesis: Uniquely Human?* In H. S. Terrace & J. Metcalfe (Eds.), *The missing link in cognition: Origins of self-reflective consciousness* (p. 3–56). Oxford University Press.

Tulving, E., & Markowitsch, H. J. (1997). Memory beyond the hippocampus. *Current Opinion in Neurobiology*, *7*(2), 209-216.

Twenge, J. M., Campbell, W. K., & Gentile, B. (2013). Changes in pronoun use in American books and the rise of individualism, 1960-2008. *Journal of Cross-Cultural Psychology*, *44*(3), 406-415.

Unsworth, N., & Engle, R. W. (2007). On the division of short-term and working memory: an examination of simple and complex span and their relation to higher order abilities. *Psychological Bulletin*, *133*(6), 1038.

Vaidya, A. R., Pujara, M. S., Petrides, M., Murray, E. A., & Fellows, L. K. (2019). Lesion studies in contemporary neuroscience. *Trends in Cognitive Sciences*, *23*(8), 653-671.

Valentine, K. D., Buchanan, E. M., Cunningham, A., Hopke, T., Wikowsky, A., & Wilson, H. (2018). Have psychologists increased reporting of outliers in response to the reproducibility crisis? *Social and Personality Psychology Compass*, e12591.

Valji, A., Priemysheva, A., Hodgetts, C. J., Costigan, A. G., Parker, G. D., Graham, K. S., ... & Gruber, M. J. (2019). Curious connections: white matter pathways supporting individual differences in epistemic and perceptual curiosity. *bioRxiv*, 642165.

Van Boven, L., Kane, J., & McGraw, A. P. (2009). Temporally asymmetric constraints on mental simulation: Retrospection is more constrained than prospection. *Handbook of imagination and mental simulation*, Psychology Press. 131-147.

van Buuren, S., & Groothuis-Oudshoorn, K. (2011). mice: Multivariate imputation by chained equations in R. *Journal of Statistical Software*, 45(3), 1-67.

Van Doorn, J., Ly, A., Marsman, M., & Wagenmakers, E. J. (2018). Bayesian inference for Kendall's rank correlation coefficient. *The American Statistician*, *72*(4), 303-308.

Van Kesteren, M. T., Ruiter, D. J., Fernández, G., & Henson, R. N. (2012). How schema and novelty augment memory formation. *Trends in Neurosciences*, *35*(4), 211-219.

Vann, S. D. (2013). Dismantling the Papez circuit for memory in rats. *eLife*, *2*, e00736.

Vann, S. D., & Nelson, A. J. (2015). The mammillary bodies and memory: more than a hippocampal relay. In *Progress in Brain Research* (Vol. 219, pp. 163-185). Elsevier.

Vann, S. D., Erichsen, J. T., O'Mara, S. M., & Aggleton, J. P. (2011). Selective disconnection of the hippocampal formation projections to the mammillary bodies produces only mild deficits on spatial memory tasks: implications for fornix function. *Hippocampus*, *21*(9), 945-957.

Vann, S. D., Tsivilis, D., Denby, C. E., Quamme, J. R., Yonelinas, A. P., Aggleton, J. P., ... & Mayes, A. R. (2009). Impaired recollection but spared familiarity in patients with extended hippocampal system damage revealed by 3 convergent methods. *Proceedings of the National Academy of Sciences*, *106*(13), 5442-5447.

Vassal, F., Schneider, F., Sontheimer, A., Lemaire, J. J., & Nuti, C. (2013). Intraoperative visualisation of language fascicles by diffusion tensor imaging-based tractography in glioma surgery. *Acta Neurochirurgica*, *155*(3), 437-448.

Verfaellie, M., Wank, A. A., Reid, A. G., Race, E., & Keane, M. M. (2019). Self-related processing and future thinking: Distinct contributions of ventromedial prefrontal Cortex and the medial temporal lobes. *Cortex*, *115*, 159-171.

Vettel, J. M., Cooper, N., Garcia, J. O., Yeh, F. C., & Verstynen, T. D. (2017). White Matter Tractography and Diffusion-Weighted Imaging. *eLS*, 1-9.

Vincent, J. L., Kahn, I., Snyder, A. Z., Raichle, M. E., & Buckner, R. L. (2008). Evidence for a frontoparietal control system revealed by intrinsic functional connectivity. *Journal of Neurophysiology*, *100*(6), 3328-3342.

Vine, V., Boyd, R. L., & Pennebaker, J. W. (2020). Natural emotion vocabularies as windows on distress and well-being. *Nature Communications*, *11*(1), 1-9.

Von Der Heide, R. J., Skipper, L. M., Klobusicky, E., & Olson, I. R. (2013). Dissecting the uncinate fasciculus: disorders, controversies and a hypothesis. *Brain*, *136*(6), 1692-1707.

Wagenmakers, E. J., Beek, T. F., Rotteveel, M., Gierholz, A., Matzke, D., Steingroever, H., ... & Pinto, Y. (2015). Turning the hands of time again: a purely confirmatory replication study and a Bayesian analysis. *Frontiers in Psychology*, *6*, 494.

Wakana, S., Caprihan, A., Panzenboeck, M. M., Fallon, J. H., Perry, M., Gollub, R. L., ... & Blitz, A. (2007). Reproducibility of quantitative tractography methods applied to cerebral white matter. *NeuroImage*, *36*(3), 630-644.

Walker, D. A. (2003). JMASM9: converting Kendall's tau for correlational or meta-analytic analyses. *Journal of Modern Applied Statistical Methods*, *2*(2), 26.

Wang, Q. (2016). Remembering the self in cultural contexts: A cultural dynamic theory of autobiographical memory. *Memory Studies*, *9*(3), 295-304.

Wang, Q., & Ross, M. (2005). What we remember and what we tell: The effects of culture and self-priming on memory representations and narratives. *Memory*, *13*(6), 594-606.

Wang, Q., Capous, D., Koh, J. B. K., & Hou, Y. (2014). Past and future episodic thinking in middle childhood. *Journal of Cognition and Development*, *15*(4), 625-643.

Wang, T., Yue, T., & Huang, X. T. (2016). Episodic and semantic memory contribute to familiar and novel episodic future thinking. *Frontiers in Psychology*, *7*, 1746.

Warburton, E. C., & Aggleton, J. P. (1998). Differential deficits in the Morris water maze following cytotoxic lesions of the anterior thalamus and fornix transection. *Behavioural Brain Research*, *98*(1), 27-38.

Watson, D., & Walker, L. M. (1996). The long-term stability and predictive validity of trait measures of affect. *Journal of Personality and Social Psychology*, *70*(3), 567.

Weiler, J. A., Suchan, B., & Daum, I. (2010). When the future becomes the past: Differences in brain activation patterns for episodic memory and episodic future thinking. *Behavioural Brain Research*, *212*(2), 196-203.

Weisberg, S. M., & Ekstrom, A. D. (2021). Hippocampal volume and navigational ability: The map (ping) is not to scale. *Neuroscience & Biobehavioral Reviews.*

Wendelken, C., Lee, J. K., Pospisil, J., Sastre III, M., Ross, J. M., Bunge, S. A., & Ghetti, S. (2015). White matter tracts connected to the medial temporal lobe support the development of mnemonic control. *Cerebral Cortex*, *25*(9), 2574-2583.

Wheeler, M. A. (2000). *Episodic memory and autonoetic awareness*. In E. Tulving & F. I. M. Craik (Eds.), *The Oxford handbook of memory* (p. 597–608). Oxford University Press.

Wheeler, M. A., Stuss, D. T., & Tulving, E. (1997). Toward a theory of episodic memory: the frontal lobes and autonoetic consciousness. *Psychological Bulletin*, *121*(3), 331.

Wiggs, C. L., Weisberg, J., & Martin, A. (1998). Neural correlates of semantic and episodic memory retrieval. *Neuropsychologia*, *37*(1), 103-118.

Wilcoxon, F. (1945). Individual Comparisons by Ranking Methods. *Biometrics Bulletin, 1*(6), 80-83.

Wilkins, C., & Clayton, N. (2019). Reflections on the spoon test. *Neuropsychologia*, *134*, 107221.

Williams, A. N., Ridgeway, S., Postans, M., Graham, K. S., Lawrence, A. D., & Hodgetts, C. J. (2020). The role of the pre-commissural fornix in episodic autobiographical memory and simulation. *Neuropsychologia*, 107457.

Xu, X., Yuan, H., & Lei, X. (2016). Activation and connectivity within the default mode network contribute independently to future-oriented thought. *Scientific Reports*, *6*, 21001.

Yang, X. F., Bossmann, J., Schiffhauer, B., Jordan, M., & Immordino-Yang, M. H. (2013). Intrinsic default mode network connectivity predicts spontaneous verbal descriptions of autobiographical memories during social processing. *Frontiers in Psychology*, *3*, 592.

Yarkoni, T. (2009). Big correlations in little studies: Inflated fMRI correlations reflect low statistical power—Commentary on Vul et al.(2009). *Perspectives on Psychological Science*, *4*(3), 294-298.

Yeatman, J. D., Wandell, B. A., & Mezer, A. A. (2014). Lifespan maturation and degeneration of human brain white matter. *Nature Communications*, *5*(1), 1-12.

Yeo, S. S., Seo, J. P., Kwon, Y. H., & Jang, S. H. (2013). Precommissural fornix in the human brain: a diffusion tensor tractography study. *Yonsei Medical Journal*, *54*(2), 315-320.

Zacks, J. M. (2020). Event perception and memory. *Annual Review of Psychology*, *71*, 165-191.

Zeidman, P., & Maguire, E. A. (2016). Anterior hippocampus: the anatomy of perception, imagination and episodic memory. *Nature Reviews Neuroscience*, *17*(3), 173-182.

Zhang, H., Schneider, T., Wheeler-Kingshott, C. A., & Alexander, D. C. (2012). NODDI: practical in vivo neurite orientation dispersion and density imaging of the human brain. *NeuroImage*, *61*(4), 1000-1016.

Zhang, Y., Brady, M., & Smith, S. (2001). Segmentation of brain MR images through a hidden Markov random field model and the expectation-maximization algorithm. *IEEE Transactions on Medical Imaging*, *20*(1), 45-57.

Zheng, H., Luo, J., & Yu, R. (2014). From memory to prospection: what are the overlapping and the distinct components between remembering and imagining? *Frontiers in Psychology*, *5*, 856.

Zimmerman, D. W. (1995). Increasing the power of nonparametric tests by detecting and downweighting outliers. *The Journal of Experimental Education*, *64*(1), 71-78.