Detail and Temporal Structure in Memory for Real-World Experiences: Age- and time-related changes

by

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Abstract

Episodic memory was initially defined as our ability to relive event-specific details and to remember the temporal context in which those details occurred. A rich tradition of laboratory studies has focused on memory organization, but the to-be-remembered stimuli bore little resemblance to real-world experiences. Conversely, autobiographical memory studies provide greater ecological validity but are limited in their measurement of recall organization. In this dissertation, I report three behavioural experiments that examine temporal structure in memory for real-world episodes, its relation to memory detail, and how these dimensions change with increasing age and remoteness. Chapter 2 describes an experiment probing remote temporal order and item recognition memory for objects encountered in a museum exhibit, using photographs of the exhibit and similar lures. Lure discrimination declined more than temporal order memory across a lifespan sample, although aging was associated with decreased flexibility in reconstructing order. Chapter 3 investigated how memory for the details and temporal structure of a single extended event change over time, using verbal true/false tests and a within-subjects delay manipulation. Memory for specific details declined rapidly whereas memory for temporal order was stable from 1 hour to 1 month and increased significantly overnight. Aging was associated with a marked decline in order memory at all delays, in contrast to a subtler and time-dependent decline in detail memory. Chapter 4 describes a study examining spontaneous temporal organization in free recall of extended real-world episodes. Younger and older adults tended to cluster their recall according to temporal proximity with a forward-going bias, extending principles of recall dynamics in laboratory studies to autobiographical-like memory. Moreover, more temporally organized memories were also denser in episodic detail, suggesting a relationship between structure and phenomenology within single recall narratives. Overall, these studies bridge a gap between laboratory memory and autobiographical memory literatures and methods, and provide a richer picture both of how we remember past episodes, and how we fail to do so. More specifically, they suggest that temporal organization is a critical determinant of memory success and quality over long timescales and is particularly vulnerable to age-related decline.

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Chapter 1
General Introduction

All conscious experiences occur once. Yet most of us can, to some degree, relive earlier “slice[s] of experience frozen in time” (Tulving, 1984), that occurred minutes, days, or decades ago. These episodic memories, though not perfect copies of the experiences they represent (Bartlett, 1932; Schacter, Norman, & Koutstaal, 1998), are often vivid and rich in multisensory details (e.g. sights, sounds, body positions, thoughts and feelings). But episodic memories are not just free-floating slices – they are temporally extended, and linked to other memories. Reliving one moment brings into focus other moments that were nearby, spreading along a path carved by temporal proximity (Howard & Kahana, 2002; Tulving, 1984). In this way, episodic memory is like mental time travel to the past and then through it (Hasselmo, 2009; Tulving, 2002).

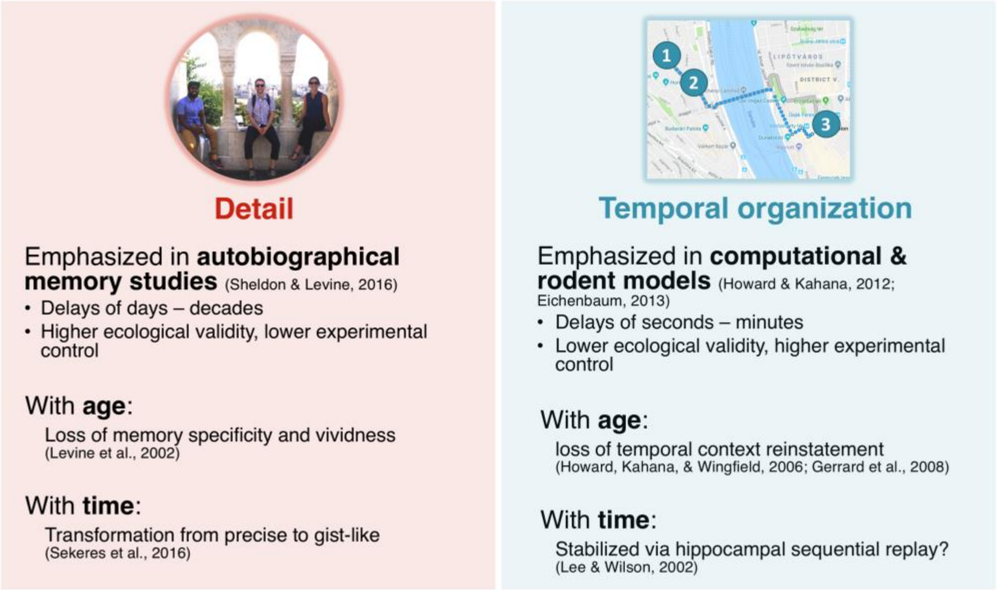
These two components – recovering the details of a past experience and its temporal context – jointly constitute Endel Tulving’s original definition of episodic memory, which he wrote, “…is successful if the person can describe the perceptible properties of the event and more or less accurately specify its temporal relations to other events” (Tulving, 1972, p. 388). Episodic memory is thus defined by both its content and organization. These components are also each thought to be core functions of the hippocampus, the brain structure most critical for enabling and shaping episodic memory. I will refer to these components as detail and temporal structure.

Not all memories are episodic. Semantic memory, for instance, refers to general knowledge about the world and oneself that is not indexed to any specific past experience (Renoult, Davidson, Palombo, Moscovitch, & Levine, 2012; Tulving, 1972). Movement through semantic memory space follows meaning-based rather than temporal associations (Collins & Loftus, 1975). One reason for focusing on episodic memory is that it is disproportionately disrupted in aging (Levine, Svoboda, Hay, Winocur, & Moscovitch, 2002; Nilsson et al., 1997), and further in Alzheimer’s Disease (Bäckman, Small, & Fratiglioni, 2001), due in large part to age- and dementia-related atrophy of the hippocampus (Gorbach et al., 2016; Leal & Yassa, 2015; Raz et al., 2005). Accordingly, in healthy older aging and Alzheimer’s Disease, memories tend to become both detail-impoverished (Barnabe, Whitehead, Pilon, Arsenault-Lapierre, & Chertkow, 2012; Levine et al., 2002) and temporally disorganized (Allen, Morris, Stark, Fortin, & Stark, 2015; Bellassen, Iglói, de Souza, Dubois, & Rondi-Reig, 2012).

Yet on the face of it, it is not obviously clear how or why the content and organization of memory should be connected, either in behaviour or underlying neurophysiology. In principle, retrieval can succeed or fail along either dimension: we may vividly flash back to a particular experience without remembering what happened before or after, or faithfully remember a sequence of events bereft of any perceptual or affective detail. Despite proposed connections between detail and temporal structure in episodic memory, these two dimensions have mostly been explored in separate, parallel literatures (Figure 1).

Details are the focus of autobiographical memory studies, in which the events in question are participants' experiences from their personal lives, retrospectively sampled from their life history. We routinely recall dozens of specific perceptual, contextual and emotional details in these memories (Levine et al., 2002). Researchers cannot, however, objectively measure the accuracy or resolution with which a memory corresponds to the experience it represents, neither in details (e.g. "her jacket was red-orange with black buttons") nor temporal structure (e.g. "we walked on the beach *and then* ate pizza"), because personal experiences are uncontrolled and unverifiable. Consequently, autobiographical memory details tend to be analyzed as discrete bits measured by their quantity (Koriat & Goldsmith, 1996). Temporal structure, on the other hand, is the focus of much rodent and laboratory research on episodic memory (Eichenbaum, 2013; Healey, Long, & Kahana, 2018). In these studies, memory for trajectories through a maze or lists of experimental stimuli is typically measured at delays of seconds or minutes. Control over encoding and retrieval conditions in these studies affords precise modeling of the ways in which structure in experience transforms into structure in memory, revealing striking aspects of memory organization in behaviour and brain activity (Polyn & Cutler, 2017). On the other hand, the events in question bear little resemblance to complex human experiences from our lives outside the laboratory (but see Uitvlugt & Healey, 2018), and studies of recall organization have usually ignored recall phenomenology (but see Sadeh, Moran, & Goshen-Gottstein, 2014).

This discrepancy may be limiting our understanding of core mechanisms underlying episodic memory as it manifests in day-to-day life, including its neural mechanisms, and its dysfunction in healthy and pathological aging. To bridge this gap, I devised a series of controlled real-world encoding paradigms, pairing the richness of autobiographical memory studies with the control of laboratory experiments. This allowed me to investigate detail and temporal structure in memories for extended, one-shot real-world events.



Detail

Emphasized in **autobiographical memory studies** (Sheldon & Levine, 2016)
- Delays of days – decades
- Higher ecological validity, lower experimental control

With **age**:
Loss of memory specificity and vividness (Levine et al., 2002)

With **time**:
Transformation from precise to gist-like (Sekeres et al., 2016)

Temporal organization

Emphasized in **computational & rodent models** (Howard & Kahana, 2012; Eichenbaum, 2013)
- Delays of seconds – minutes
- Lower ecological validity, higher experimental control

With **age**:
loss of temporal context reinstatement (Howard, Kahana, & Wingfield, 2006; Gerrard et al., 2008)

With **time**:
Stabilized via hippocampal sequential replay? (Lee & Wilson, 2002)

Figure 2.1. Overview of research on detail (left) and temporal organization (right) in episodic memory.

In this introduction, I will begin with overviews of the literature on detail and temporal structure in episodic memory (summarized in Figure 1.1), including neural mechanisms and age- and time-related changes. I will then outline empirical and theoretical differences between naturalistic and laboratory approaches to measuring episodic memory, making a case for the importance of bridging the gap between the two. Finally, I will outline my line of research.

1.1 Detail in episodic memory

1.1.1 Theory and background

Episodic memory entails re-experiencing the details of a past event. Tulving suggested that episodic memory, as a memory system distinct from semantic and procedural systems, is uniquely characterized by “autonoetic consciousness”, the awareness of the self as a continuous entity across time (Tulving, 1985). We recover not just the content of a past event but the conscious experience of it (Moscovitch, 1995, 2008), knowing that it occurred to an earlier version of ourselves, with some proportion of its perceptual, contextual or affective detail.

In recognition memory experiments, episodic retrieval (i.e. recollection) has been dissociated from non-episodic retrieval processes using various methods. The Remember/Know procedure (Gardiner, 1988; Tulving, 1985) relies on participants’ self-reported memory state:

‘remembering’ entails recognizing an item based on re-experiencing specific details from the encoding context, and ‘knowing’ entails recognition based on an acontextual feeling of oldness. Source memory tasks probe recollection objectively, operationalizing it as recognition of an old item accompanied by accurate retrieval of particular experimenter-defined stimulus features (e.g. the item’s colour or location on the screen) (Jacoby, 1991; Johnson, Hashtroudi, & Lindsay, 1993)**.** Importantly, even strong or confident feelings of familiarity, unaccompanied by specific details, rely on different (non-hippocampal) neural mechanisms than recollection (Yonelinas, Aly, Wang, & Koen, 2010). The number of specific perceptual details distinguishes true from false memories (Brewer, 1988; Norman & Schacter, 1997; Schooler, Gerhard, & Loftus, 1986) and memory for real from imagined events (Johnson, Foley, Suengas, & Raye, 1988).

Vivid episodic retrieval depends on visual imagery in particular (Brewer & Pani, 1996; Greenberg & Knowlton, 2014; Rubin, Schrauf, & Greenberg, 2003; St-Laurent, Moscovitch, Levine, & McAndrews, 2009), and more specifically on the ability to mentally reconstruct visual scenes (Clark et al., 2019; Rubin, Deffler, & Umanath, 2019). Scenes confer a “viewpoint-specific, quasi-perceptual experience of past events” (King, Trinkler, Hartley, Vargha-Khadem, & Burgess, 2004, p. 415). A recent study demonstrated strikingly high degrees of detail and spatial precision in participant’s memories for real-world scenes by measuring participants’ drawings of them (Bainbridge, Hall, & Baker, 2019). After a distraction-filled delay, participants reliably drew many specific objects from the 30 encoded scenes, with few schema-based intrusions, and with high degrees of precision in object location and size. This study extended similar findings from recognition memory suggesting that episodic memory has a massive storage capacity for precise visual detail (Brady, Konkle, Alvarez, & Oliva, 2008).

Details, and the sense of reliving they engender, are at the heart of episodic autobiographical memory, our memory for specific past experiences. They are what separates one experience from another (Mitchell & Johnson, 2009). Autobiographical memory is considered to be a hierarchical knowledge base, spanning multiple levels of specificity (Conway & Pleydell-Pearce, 2000) and types of information (Levine et al., 2002), where episodic memory refers to the “experience-near”, sensory-perceptual, “minutia” of specific experiences (Conway, 2001). Details are the main currency of analysis in the Autobiographical Interview (AI) scoring method (Levine et al., 2002), in contrast to earlier methods that focused on the number of memories retrieved (Crovitz & Schiffman, 1974; for review, see Sheldon et al., 2018). In the AI, participants recall memories freely, and then with probing for specific details. Transcribed memories are decomposed into discrete informational units that are categorized as either internal (episodic; specific to the event being described) or external (relating to a different event, or non-episodic; semantic, metacognitive, repetitions, etc.). Internal details are further categorized according to their type (event, place, time, perceptual, or thought/emotional). The AI thus reveals the interplay of episodic and non-episodic processes contributing to single recall narratives, and objectively quantifies the phenomenology of retrieval.

Through the lens of the AI, impairments in episodic autobiographical memory manifest as reductions in the number or proportion of internal details, often with elevated external details, indicating an episodic-to-semantic or detailed-to-schematic shift. Such impairments in memory specificity are observed in aging (Addis, Wong, & Schacter, 2008; Levine et al., 2002; St. Jacques & Levine, 2007), Alzheimer's Disease (Barnabe et al., 2012; Meulenbroek et al., 2010), amnestic Mild Cognitive Impairment (aMCI; Bastin et al., 2013; Murphy, Troyer, Levine, & Moscovitch, 2008; Tramoni et al., 2012), frontotemporal dementia (McKinnon et al., 2008), temporal lobe epilepsy (TLE) (St-Laurent et al., 2009), depression (Soderlund et al., 2008) and other psychiatric disorders (for review, see Sheldon et al., 2018). As reviewed below, these impairments in detailed retrieval are linked to structural and functional declines in the hippocampus and its interactions with the cortex.

1.1.2 Neural mechanisms: The hippocampus as a detail generator

Retrieving prior experiences requires that their constituent features be bound together, then coherently reinstated. Decades of research on both humans and animals has suggested that the medial temporal lobes (MTL), especially the hippocampal formation (dentate gyrus, CA fields and subiculum; hereafter called the hippocampus), serves this function in virtue of its internal circuitry and connectivity with distributed cortical regions.

Anatomically, the hippocampus has reciprocal connections with neocortical association areas via the surrounding MTL cortex and anterior thalamic nuclei (Aggleton & Brown, 1999; Eichenbaum, 2000). It is located at the top of a bidirectional multisensory hierarchy; the perirhinal and parahippocampal cortices receive input from unimodal and polymodal sensory areas, respectively, and these two streams converge in the hippocampus (Eichenbaum, Yonelinas, & Ranganath, 2007). The hippocampus, then, "receives input from essentially the entire brain in a small number of synapses" (Howard, Fotedar, Datey, & Hasselmo, 2005), and its connectivity is thus "ideal for making the widely distributed associations between the many different, contemporaneously experienced stimuli making an event" (Aggleton & Brown, 1999).

Computational models of the hippocampus have formalized the processes by which it supports detailed remembering. One class of models suggests that hippocampal cell ensembles form sparse indices of distributed neocortical activity patterns representing the various idiosyncratic features of a given experience (Marr, 1971; McClelland, McNaughton, & O'Reilly, 1995; Teyler & Rudy, 2007). Similar experiences are "pattern-separated" by the sparse and randomly assigned projections from the dentate gyrus to cell ensembles in CA3, which differentiate overlapping input patterns (Norman & O'Reilly, 2003; Treves & Rolls, 1994). Recurrent connections within CA3 act as an autoassociative or attractor network, enabling rapid formation of "whole scene or snapshot-like" associations and, subsequently, autocompletion of whole indices when cued by one of their elements (Treves & Rolls, 1994). Autocompleted hippocampal indices reinstate the original cortical activity patterns (Marr, 1971; Moscovitch, 2008; Norman & O'Reilly, 2003), reversing the information flow governing perception (Damasio, 1989; Linde-Domingo, Treder, Kerrén, & Wimber, 2019). Notably, in these models, the hippocampus binds elements that are temporally coincident or occurring within milliseconds, and retrieval manifests as simultaneous activation of multiple CA3 ensembles triggering simultaneous reactivation throughout cortex (Damasio, 1989; Treves & Rolls, 1994). Hippocampal circuity, therefore, allows for the idiosyncratic details of one-time experiences to be stored as integrated snapshots, kept distinct from similar experiences, and reactivated with high fidelity.

Accordingly, structural damage to the hippocampus compromises detailed episodic retrieval. In autobiographical memory studies, amnesia patients with hippocampal damage recall fewer internal details and as many or more external details as controls (Steinvorth, Levine, & Corkin, 2005). Perceptual details in particular are lost with hippocampal damage (Greenberg, Eacott, Brechin, & Rubin, 2005; St-Laurent, Moscovitch, Jadd, & McAndrews, 2014; St-Laurent, Moscovitch, & McAndrews, 2016) and patients exhibit difficulty reconstructing or imagining coherent visual scenes (Hassabis, Kumaran, Vann, & Maguire, 2007). An overarching function of the hippocampus, then, may be the generation and binding of details into coherent event representations (Rosenbaum, Gilboa, Levine, Winocur, & Moscovitch, 2009), or similar alternatives – for example, relational binding (Howard Eichenbaum & Cohen, 2014), high resolution binding (Yonelinas, 2013) or scene construction (Maguire, Intraub, & Mullally, 2015).

Neuroimaging evidence supports and extends findings from neuropsychology. In terms of brain structure, individual differences in the integrity of the fornix, the main output pathway of the hippocampus, are associated with differences in the number of internal but not external details in autobiographical memories (Hodgetts et al., 2017). In fMRI studies, hippocampal activity scales parametrically with subjective ratings of detail during episodic autobiographical retrieval (Addis et al., 2004), and is greater for highly vivid versus less vivid memories (Gilboa, Winocur, Grady, Hevenor, & Moscovitch, 2004; Sheldon & Levine, 2013). Similarly, the degree to which whole-brain functional networks converge on the hippocampus (using graph theory measures) is greater during more vivid retrieval of scene pictures (Geib, Stanley, Wing, Laurienti, & Cabeza, 2015). Critically, hippocampal sensitivity to memory detail or vividness is generally invariant of event recency (Gilboa et al., 2004; Sheldon & Levine, 2013), uniqueness (i.e. specific versus repeated; (Addis, Moscovitch, Crawley, & McAndrews, 2004)) and temporal orientation (i.e. remembering the past versus imagining the future; see Schacter, Addis, & Szpunar, 2017 for review), suggesting that its engagement is driven by the process of binding and reinstating details.

Given the complex and multidimensional nature of episodic and autobiographical memory retrieval, networks beyond the hippocampus are involved. Both laboratory (Rugg & Vilberg, 2012) and autobiographical (Svoboda, McKinnon, & Levine, 2006) measures of episodic retrieval elicit activity in a network that also overlaps with the canonical default mode network (Raichle et al., 2001; but see Bellana, Liu, Diamond, Grady, & Moscovitch, 2016), including the medial prefrontal and parietal cortices and angular gyri. Furthermore, conjuring sensory details in memory or imagination recruits activity in early sensory regions (Bone et al., 2018; Danker & Anderson, 2010). Accordingly, vivid episodic retrieval recapitulates distributed cortical brain patterns observed during perception of complex events (Buchsbaum, Lemire-Rodger, Fang, & Abdi, 2012), with greater encoding-retrieval neural similarity predicting more objectively detailed (St-Laurent, Abdi, Bondad, & Buchsbaum, 2014) and subjectively vivid (St-Laurent, Abdi, & Buchsbaum, 2015) memories. Oscillatory phase coherence is a candidate mechanism for hippocampal-cortical coordination. The magnitude of phase coherence in hippocampal, medial prefrontal and medial parietal theta oscillations is diagnostic of source memory success (Guderian & Düzel, 2005) and correlates with subjective ratings of visual imagery during autobiographical retrieval (Fuentemilla, Barnes, Düzel, & Levine, 2014). Phase alignment is thought to facilitate detailed remembering by synchronizing firing across regions (Fries, 2015).

In sum, the hippocampus – by virtue of its interactions with cortex – evolved the ideal circuitry for storing and synchronously reactivating the details of one-time events, re-experienced as scenes in one's mind's eye, akin to Tulving's slices of experience frozen in time.

1.1.3 Effects of aging and remoteness

Normal healthy aging is reliably associated with a disproportionate decline in episodic relative to non-episodic (e.g. semantic and procedural) memory, with the population-average onset of decline often beginning around age 60 (Leal & Yassa, 2015; Nyberg, 2016). In longitudinal studies, the hippocampus is one of the most pronounced sites of atrophy in the brain, with annual volume decreases ranging from 0.7% - 2.0% (compared to 4.66% in Alzheimer's Disease (Barnes et al., 2009) and accelerating with age (Fjell et al., 2009; Raz et al., 2005). Prefrontal structural integrity (Raz et al., 2005) and functional hippocampal-prefrontal interactions (Salami, Pudas, & Nyberg, 2014; St. Jacques, Rubin, & Cabeza, 2012) also reliably decline with age. Hippocampal decline, however, more reliably predicts cognitive decline, particularly in episodic memory (Gorbach et al., 2016; Hedden et al., 2014; Kaup, Mirzakhanian, Jeste, & Eyler, 2011). A finer-grained understanding of how episodic memory changes over the healthy lifespan may improve intervention in pathological aging and diagnosis of it. At the same time, aging can be used as a model for increasing our understanding of basic episodic memory mechanisms.

One hallmark of aging is a loss of detail and specificity in episodic memory. Across measures, older adults exhibit a decline in recollection with spared familiarity relative to younger adults (Yonelinas, 2002). Age-related hippocampal volume reduction correlates with decreased recollection but not familiarity, whereas the reverse pattern is observed in the entorhinal cortex (Yonelinas et al., 2007). Accordingly, older adults tend to report fewer 'remember' responses and an equal or greater proportion of 'know' responses (Java, 1996; Prull, Dawes, Martin, Rosenberg, & Light, 2006). Their self-reported recollection, however, sometimes matches that of younger adults despite objectively poorer performance, perhaps particularly when retrieving complex naturalistic events (Diamond, Abdi, & Levine, *in prep.;* Robin & Moscovitch, 2017; St-Laurent, Abdi, et al., 2014; St. Jacques, Montgomery, & Schacter, 2015). This pattern highlights the importance of measuring the accuracy of recalled details. To this end, in Chapter 3 we combine the Remember/Know procedure with verifiable cued recall of specific event details.

Using objective measures, aging is associated with reduced source or contextual memory but spared acontextual recognition of old items, suggesting a decline in binding together multiple perceptual details as a coherent whole (Hashtroudi, Johnson, & Chrosniak, 1989; Naveh-Benjamin, 2000; Spencer & Raz, 1995). Corresponding age-related declines are observed in neural reactivation during mental replay of video clips (St-Laurent, Abdi, et al., 2014). Critically, though, item discrimination does decline with age across species when lures and old items are similar, indicating age-reductions in pattern separation, linked to abnormality in the DG/CA3 circuit (Johnson et al., 2017; Reagh et al., 2018; Yassa, Mattfeld, Stark, & Stark, 2011).

Recent findings suggest that the age-related decline may be best-characterized by a loss of episodic memory precision. When modelling precision using continuous response measures, both contextual (i.e. spatial location; Nilakantan, Bridge, Vanhaerents, & Voss, 2018) and item-based (i.e. colour and orientation; Korkki, Richter, Jeyarathnarajah, & Simons, 2018) memory representations lose precision with age, even when dichotomous measures of recollection success are matched across age groups. This finding suggests that when older adults remember past events, their memories are fuzzier or less perceptually detailed than those of younger adults. Accordingly, in autobiographical recall and related mental simulations, older adults produce fewer internal details and more external details, indicating a shift towards more semantic or gist-based event representations (Spreng et al., 2017). This age-related decline in the representational quality of episodic memory, in addition to altered strategic monitoring processes (Cohn, Emrich, & Moscovitch, 2008), renders older adults more susceptible to false recognition (Trelle, Henson, Green, & Simons, 2017), particularly when old and new information share perceptual and/or conceptual overlap (Koutstaal & Schacter, 1997), as seen in Chapter 2 (Diamond, Romero, Jeyakumar, & Levine, 2018). In sum, with advancing age, memories lose detail and specificity, becoming unyoked from the specific perceptual details of past events.

Within individuals, memories tend to transform over time in a manner that is similar to lifespan changes reviewed above. That is, individual episodic memories tend to lose specific perceptual details over time while retaining gist (Reyna & Brainerd, 2002; Sekeres et al., 2016; Wiltgen & Silva, 2007; Winocur & Moscovitch, 2011). In laboratory studies, measures of recollection consistently decrease more than familiarity over delays ranging from days to weeks (for review, see Sadeh, Ozubko, Winocur, & Moscovitch, 2014). In one recent example of this phenomenon, a one-month versus one-day delay elicited increased false alarms to semantically related lure photographs that carried the gist but not the details of specific photographs encoded earlier (Dandolo & Schwabe, 2018). These findings echo recent studies using more naturalistic film clips as encoding material: participants recall fewer perceptual details (Sekeres et al., 2016) and commit more false recognition of altered details (Furman, Dorfman, Hasson, Davachi, & Dudai, 2007) over time, but recall and recognition of high level plot information changes little.

Diary studies confirm that episodic autobiographical events are also forgotten over time, though perhaps at a shallower rate than laboratory stimuli (Brewer, 1988; Linton, 1975; Rubin & Wenzel, 1996; Wagenaar, 1986). Less is known about the manner in which autobiographical versus laboratory memories transform with time, because personal memories are (1) usually unverifiable, (2) highly heterogeneous within and across participants, and (3) participants are rarely tested on the same event at multiple timepoints. A recent study from our lab overcame problems 1 and 2 by capitalizing on a scripted and homogeneous real-life event experienced by many people, finding reduced accuracy (based on true/false statements) for event details over delays of months-to-years (Armson, Abdi, & Levine, 2017). We build on this finding in Chapter 3 by testing memory at hours-to-weeks-long delays within subjects. Importantly, the effect of remoteness on episodic detail accuracy depends on how it is measured. In free recall, participants spontaneously regulate the "grain size" of their memories (Goldsmith, Koriat, & Pansky, 2005), recalling fewer and more general details with time but maintaining accuracy in details that are recalled (Diamond, Armson, & Levine, *in prep).* In recognition and cued recall studies, participants become more susceptible to false details over time (Barclay & Wellman, 1986).

Loss of episodic detail over time is likely due to molecular-level weakening of hippocampal traces, both by passive decay and active overwriting mechanisms (Barry & Maguire, 2018; Richards & Frankland, 2017). Accordingly, hippocampal activation declines as recollection fades from minutes-to-weeks long delays (Viskontas, Carr, Engel, & Knowlton, 2009). The transformation of memories from detailed to gist-like is accompanied by a shift in their neural basis, from the hippocampus to the ventromedial prefrontal cortex (Winocur & Moscovitch, 2011). However, hippocampal necessity (in neuropsychological studies) and activity (in neuroimaging studies) does not decrease over time when remote memories remain detailed or vivid (Winocur & Moscovitch, 2011; for meta-analysis see Yonelinas, Ranganath, Ekstrom, & Wiltgen, 2019). The process of systems consolidation may unfold over months or years (Dudai, Karni, & Born, 2015), though human neuroimaging studies have rarely measured memory performance (in terms of objective accuracy) at such long delays.

Together, the above-reviewed studies indicate that episodic memory can be measured as the retrieval of integrated perceptual details, that a core function of the hippocampus is the binding and reinstatement of these details, and that details tend to fade with age and time. There are, however, two main limitations in this literature. First, laboratory stimuli may fail to capture the complexity and richness of memory for every real-life experiences. On the other hand, in studies of autobiographical memory, recalled details are usually opaque to accuracy measurement. Second, although naturalistic memories unfold over time, methodological limitations often prevent analysis of how recall dynamics map onto the dynamics of the encoded episode.

1.2 Temporal structure in episodic memory

1.2.1 Theory and background

> "Imagine a past devoid of time information: a rich store of memories, some vivid, detailed, and steeped in affect, but all free-floating entities unattached to any time. This peculiar sort of memory would be like a jumbled box of snapshots, all clearly belonging to our past but resistant to any attempts at dating or sequencing. It is readily apparent that this is nothing like human memory…" (Friedman, 1993, p. 44)

Although episodic memory is often measured as the ability to recall the details of discrete stimuli, there is considerable evidence that episodes are neurocognitively represented as extended and structured sequences of events. Tulving suggested that "organization of knowledge in the episodic system is temporal: One event precedes, cooccurs, or succeeds another in time" (1984, p. 225). Researchers using rodent models of episodic memory have long emphasized temporal structure as a critical component (Buzsáki & Tingley, 2018; Jensen & Lisman, 1996; Levy, 1996; Wallenstein, Eichenbaum, & Hasselmo, 1998), likely because their subjects are often encoding and retrieving extended goal-directed episodes. For instance: "episodic memory includes the capacity to mentally retrace trajectories through previously visited locations, including re-experiencing specific stimuli encountered on this trajectory, and the relative timing of events" (Hasselmo, 2009, p. 559), and "the basic structure of episodic memory is a temporally extended representation that distinguishes the beginning from the end of an event" (Ferbinteanu, Kennedy, & Shapiro, 2006, p. 691). In recent years there has been an explosion of human behavioural and neuroimaging work on how temporal context shapes episodic memory (for reviews, see: (Clewett & Davachi, 2017; Davachi & DuBrow, 2015; Ekstrom & Ranganath, 2017; Healey et al., 2018; Palombo & Verfaellie, 2017; Ranganath & Hsieh, 2016).

Time has been operationalized many different ways in episodic memory experiments. For clarity, I am not focusing on memory for time per se, for 'when' past events occurred as measured by clocks and calendars. Events are not time-stamped in memory, and absolute time is neither a memorable feature of past events nor an effective retrieval cue, relative to other event features (Brewer, 1988; Underwood, 1977; Wagenaar, 1986). In his influential review of memory and time, Friedman concluded that "time is invariably the worst possible cue for recalling events" (Friedman, 2004, p. 134). Rather, my focus is on the temporal structure, or organization, of episodic memories – that is, how we remember the order of events with respect to each other. As I will argue, temporal structure is a fundamental organizing principle of how we remember episodes, central to the contribution of the hippocampus, and key to understanding age-related decline in episodic memory.

In contrast to remembering absolute dates and times, which is effortful and inferential (Friedman, 1993), we automatically and universally recover temporal structure when we remember past episodes (Healey et al., 2018). For example, people spontaneously cluster their free recall of past events according to their encoded temporal proximity (Kahana, 1996) (see Figure 1.2A). On the flip side, discriminating the order of events becomes more difficult the closer they were in time (Skowronski, Walker, & Betz, 2003; St. Jacques, Rubin, LaBar, & Cabeza, 2008; Templer & Hampton, 2013), an extension of the symbolic distance effect (Moyer & Bayer, 1976). Remembering the order of items that were close in time is thought to rely more on contextual reconstruction processes than items that were further away, for which order can be inferred by comparing the feeling of recency or memory strength for each item (Friedman, 1993; St. Jacques, Rubin, LaBar, & Cabeza, 2008). In addition to clustering memory by temporal proximity, we also spontaneously recall events in their original order – that is, with a forward-going bias (Anderson & Conway, 1993; Brunec et al., 2015; Kahana, 1996). Accordingly, recognition memory of single items is better when successive recognition cues are presented in their encoded order (Light & Schurr, 1973) or from proximal list positions (Schwartz, Howard, Jing, & Kahana, 2005).

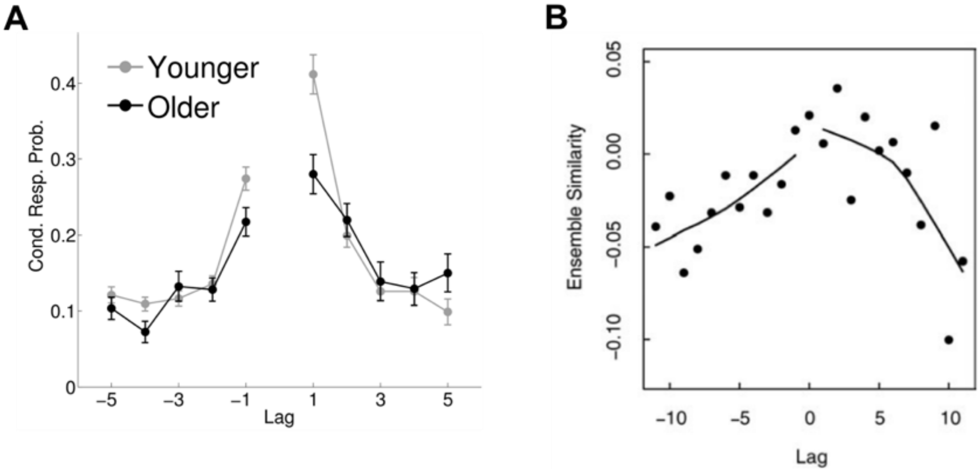


Figure 2.2. ***A.*** The influence of temporal context on free recall, as measured by lag-conditional response probability, is reduced in older adults. ‘Lag’ refers to the encoded distance, in ordinal positions, from a given recalled word. The probability of transitioning from one word to another is conditional on the lag between them. ***B.*** similar pattern observed in intracranial recordings from the medial temporal lobe during a continuous recognition task; repeated images trigger neural reinstatement of the ensemble activity pattern accompanying before and after the target stimulus, with similarity dropping off as a function of lag. Figure *A* edited and reproduced from Healey & Kahana (2016). Figure *B* reproduced from Howard et al. (2012).

These two phenomena – contiguity and forward asymmetry – have been thoroughly described in word list recall (Kahana, 1996), one of the oldest and most frequently used tasks in the history of episodic memory research. An influential class of computational models – the Temporal Context Model (Howard & Kahana, 2002) and updated versions of it (Lohnas, Polyn, & Kahana, 2015; Polyn, Norman, & Kahana, 2009; Sederberg, Howard, & Kahana, 2008) – suggest that, during encoding, stimuli become associated with a slowly drifting internal context representation, and that recalling a given item reinstates its surrounding context, iteratively cueing items that were nearby (see Figure 1.2A). Across manipulations, organization by contiguity and forward asymmetry is consistently observed in nearly every participant (Healey & Kahana, 2014), and the magnitude of participants’ contiguity effect predicts their overall recall performance, whereas semantic clustering – an orthogonal form of recall organization – does not (Sederberg, Miller, Howard, & Kahana, 2010).

One might suppose that such strong effects of temporal organization might be due to the artificial conditions of list-learning paradigms, where discrete and arbitrary stimuli are presented one-after-another in rapid succession over many trials (Hintzman, 2016). Here, item sequence is an unusually salient and strategically beneficial dimension against an unusually low-dimensional background. Yet evidence suggests that temporal context reinstatement is timescale-invariant – for instance, it explains the dynamics of search through autobiographical memory, where events are separated by weeks to years (Moreton & Ward, 2010), and through memory for public news stories, even when accounting for semantic associations (Uitvlugt & Healey, 2018). Little is known, however, about the temporal structure or “micro-time” (Hassabis & Maguire, 2007), of single real-life episodes, the prototypical unit of autobiographical memory. This dearth of knowledge occurs because experimenters are usually blind to the temporal structure in such episodes. In Chapter 4, we measured temporal structure, along with detail, in free recall for single extended real-world events.

Critically, theories of temporal memory based on direct item-to-item associations (e.g. associative chaining; Lewandowsky & Murdock, 1989), binding of items to a discrete ordinal positions (positional coding; Yntema & Trask, 1963), or familiarity-based feelings of recency (Friedman, 1993) cannot account for the forward asymmetry and timescale-invariance of the contiguity effect (Healey et al., 2018). Rather, the evidence supports the idea that episodic memory, when successful, reactivates not just a single slice but rather a temporally structured stream of past experiences.

1.2.2 Neural mechanisms: The hippocampus as a sequence generator

For decades, research on the hippocampus focused on its role in representing space, motivated by the finding of place cells that fire in specific locations (Moser, Kropff, & Moser, 2008; O’Keefe & Dostrovsky, 1971). More recent evidence suggests, however, that the hippocampus codes for the spatiotemporal organization of experience (Eichenbaum, 2017) – that the temporal dimension is complementary or superordinate to the spatial one. For instance, the hippocampus codes a given location differently when embedded in different behavioural trajectories, depending on the direction of travel, the subsequent turn or decision to be made, or the ultimate goal or reward

(Shapiro, Kennedy, & Ferbinteanu, 2006; Wood, Dudchenko, & Eichenbaum, 1999). The representation of place, in other words, depends on where you or your rat are coming from and where you are going. Even considering spatial environments alone, a recent model suggests that place cells do not code for metric spatial information but rather environment topology, or "the connections between portions of a given environment and the sequence in which they are experienced", adding that "the reason we include temporal sequence along with more conventional spatial relationships is because movement through space takes place over time; sequence thus embodies connectivity" (Dabaghian, Brandt, & Frank, 2014). More recently, time cells in the hippocampus were discovered, firing at specific moments in delays or temporally structured experiences irrespective of location (for review, see Eichenbaum, 2013).

If the structural connectivity of the hippocampus makes it ideal for binding details, its physiology makes it ideal for forming, stabilizing and retrieving representations of event sequences. Certain models suggest that the CA3 subfield is a heteroassociative rather than an autoassociative network, forming asymmetric links across ensembles representing different events, preserving the ordinal structure of temporally extended activity patterns (Jensen & Lisman, 1996; Levy, 1996; Lisman, 1999). During navigation, cycles of the hippocampal theta rhythm nest sequences of place cell activity representing the animal's recent past, present, and future locations, ordered along the theta phase (Dragoi & Buzsáki, 2006; O'Keefe & Recce, 1993). These theta sequences emerge only in familiar routes (Feng, Silva, & Foster, 2015), and at decision points they depict possible (and actually taken) paths ahead (Wikenheiser & Redish, 2015), indicating that they reflect a kind of "recall mode…a rapid, time-compressed readout of memory sequences" (Jensen & Lisman, 1996). Furthermore, once an animal learns a route, place fields skew backwards such that a cell begins firing in advance of the location it initially represented, suggesting they represent a prediction of upcoming locations based on experience (Mehta, Quirk, & Wilson, 2000; Stachenfeld, Botvinick, & Gershman, 2017). This pattern is echoed in human single cell recordings during repeated presentations of a movie (Paz et al., 2010). Similarly, fluctuations in hippocampal BOLD signal during spoken recall predict whether the next-recalled word will come from a nearby list position (temporal context reinstatement), whereas perirhinal activity, for instance, predicts recall success irrespective of temporal context (Kragel, Morton, & Polyn, 2015).

During sharp-wave ripples – massively synchronous bursts of cortically-projecting hippocampal activity observed during sleep and post-encoding rest periods – cells fire in sequences that recapitulate earlier behavioural episodes (for reviews, see Buzsáki, 2015; Joo & Frank, 2018). These replay events can represent extended remote behavioural trajectories that are untethered to the animal's current position (Gupta, van der Meer, Touretzky, & Redish, 2010; Karlsson & Frank, 2009), and they are predictive of and necessary for subsequent memory-guided behaviour (Jadhav, Kemere, German, & Frank, 2012; Pfeiffer & Foster, 2013). They are thus thought to be a mechanism of episodic retrieval, and also storage, by compressing event sequences occurring at the timescale of experience (seconds-to-minutes) down to the millisecond-level timescale at which synaptic plasticity operates (Buzsáki & Moser, 2013). Notably, in monkeys, sharp-wave ripples immediately precede BOLD signal increases in the default mode network, overlapping with the recollection and autobiographical memory networks (Kaplan et al., 2016). Based on the foregoing, Buzsáki and colleagues argue that the hippocampus is fundamentally a "sequence generator" (Buzsáki & Tingley, 2018), providing "organised access (in spatiotemporal trajectories) to neocortical representations" (Friston & Buzsáki, 2016), and that its essential contribution to episodic memory is described by this general function.

Evidence from human fMRI supports the hypothesis that the hippocampus mediates memory for temporal order. For example, hippocampal activation is observed during explicit order memory judgements (Ekstrom & Bookheimer, 2007; Ekstrom, Copara, Isham, Wang, & Yonelinas, 2011; Konishi, Asari, Jimura, Chikazoe, & Miyashita, 2006; Lehn et al., 2009; Wang & Diana, 2017a), especially when contrasting contextual with strategy- or item-based order retrieval (Konishi et al., 2006; Lehn et al., 2009). It is also greater for order judgements of shorter-lag item pairs, consistent with the notion that ordering more proximal items places greater demands on recollection or reconstructing the encoding context (Wang & Diana, 2017b). Hippocampal activity patterns code the order of items in specific sequences, such that different sequences containing a common set of elements are represented differently (Hsieh, Gruber, Jenkins, & Ranganath, 2014; Kalm, Davis, & Norris, 2013), echoing journey-dependent spatial coding in rodents discussed above. The hippocampus also extracts temporal structure implicitly, both in statistical learning and one-trial learning paradigms (Kumaran & Maguire, 2006; Schapiro, Turk-Browne, Norman, & Botvinick, 2016; Shanks, Channon, Wilkinson, & Curran, 2006).

Neural signatures of correct temporal context retrieval and lag-sensitivity are often observed in distributed cortical networks beyond the hippocampus, with regions varying by task (Hsieh & Ranganath, 2015; St. Jacques et al., 2008; Wang & Diana, 2017b). In particular, the medial prefrontal cortex is often co-implicated with the hippocampus (Jenkins & Ranganath, 2016). In rodent studies, mPFC dynamics are often entrained by hippocampal dynamics (Hyman, Zilli, Paley, & Hasselmo, 2005; Jones & Wilson, 2005), exhibiting similar sequential firing and replay patterns (Euston, Gruber, & McNaughton, 2012; Tiganj, Jung, Kim, & Howard, 2017).

A signature of temporal context, as described by the Temporal Context Model based on behavioural data, is observable in populations of hippocampal neurons during encoding. In a sequence learning task in rodents, Manns, Howard, & Eichenbaum (2007) found that hippocampal activity patterns represented individual items but also gradually drifted over the course of a sequence sampling period, such that hippocampal representation of items became more dissimilar as the temporal lag between them increased. This lag-sensitivity in hippocampal activity patterns predicted subsequent accuracy in discriminating the order of items (selecting the earlier one). Human fMRI studies subsequently revealed similar evidence for a drifting temporal context representation in the hippocampus that supports temporal memory. For instance, the degree of drift in multivoxel hippocampal patterns across pairs of items predicts subsequent behavioural judgements of their relative order (DuBrow & Davachi, 2014; Jenkins & Ranganath, 2010) and distance (Deuker, Bellmund, Schröder, & Doeller, 2016; Ezzyat & Davachi, 2014).

The hippocampus reinstates these context representations at retrieval. For instance, using fMRI, Nielson and colleagues (2015) presented participants with images captured by a lifelogging camera worn during their everyday lives for a month. Though presentation order was random and there was no explicit demand on memory search, neural similarity in the anterior hippocampi scaled with objective spatial and temporal similarity between pairs of photographs, on the scale of kilometers and days. This suggests that memories are organized by spatiotemporal proximity in the hippocampus, mirroring the behavioural contiguity effect discussed above. More direct observations of a ‘neural contiguity effect’, using standard laboratory recall and recognition tasks, have been observed in fMRI (Kragel et al., 2015), intracranial (Folkerts, Rutishauser, & Howard, 2018; Howard, Viskontas, Shankar, & Fried, 2012) and electrocorticographic recordings (Manning, Polyn, Baltuch, Litt, & Kahana, 2011; Yaffe et al., 2014). For instance, free or cued recall of a given list item not only reactivates the brain state that accompanied encoding of that item, but also reactivation of nearby items decreasing as a function of lag in both directions (see Figure 1.2B). Such neural contiguity effects are only observed on correct recall trials and are predictive of behavioural contiguity effects (Manning et al., 2011; Yaffe et al., 2014). These studies further demonstrate the importance of temporal context in how laboratory episodes are represented.

Early neuropsychological studies on temporal memory focused on the effects of frontal lobe lesions, though these findings may be explained by more general executive function deficits (McAndrews & Milner, 1991; Shimamura, Janowsky, & Squire, 1990). More recently, temporal context memory deficits were observed in patients with selective hippocampal or encompassing medial temporal lobe lesions, without frontal lobe pathology or executive function deficits, and with spared recognition of single items (Downes, Mayes, MacDonald, & Hunkin, 2002; Mayes et al., 2010; Spiers, Burgess, Hartley, Vargha-Khadem, & O'Keefe, 2001). Nonetheless, temporal context memory may be most impaired in patients with co-ocurring hippocampal and frontal lobe damage (Shimamura et al., 1990). Huppert and Piercy (1978) cleverly orthogonalized item trace strength and temporal context, finding that repeated presentation of more remote stimuli led amnesia patients to believe they were presented more recently, indicating that their recency judgements are based on trace strength and not temporal context. Fortin, Agster and Eichenbaum (2002) found similar deficits in rodents with selective hippocampal lesions, who had impaired memory for sequential order but intact recognition memory of single items, and intact influence of recency on recognition. Monkeys with hippocampal lesions exhibit the same pattern (Templer & Hampton, 2013). These findings suggest that the hippocampus is necessary for an allocentric sense of time – that is, for the order of items with respect to each other – but not for a sense of oldness or recency.

More direct evidence for an impairment in temporal context per se was recently demonstrated using computational modeling of word list recall (Palombo, Lascio, Howard, & Verfaellie, 2018). Patients with selective hippocampal lesions exhibited selective deficits in the temporal contiguity effect, indicating a failure to reinstate temporal context at retrieval. Similarly, electrical brain stimulation of the MTL in epilepsy patients transiently scrambles recall output order, presumably by disrupting the endogenous hippocampal dynamics that guide contextual recall organization (Goyal et al., 2018). Finally, preliminary evidence suggests that these findings extend to memory for more naturalistic events. Even under conditions in which hippocampal amnesia patients recalled as many details as controls from a staged real-life event, the order in which they recalled those details was unrelated to their encoded order (Dede, Frascino, Wixted, & Squire, 2016). St-Laurent and colleagues (2011) found similar results in TLE patients, thought they could not measure temporal order accuracy objectively. Similar though more nuanced patterns of temporal disorganization are observed in healthy aging.

1.2.3 Effects of aging and remoteness

In addition to difficulty in retrieving episodic details, older adults' memories tend to become less spatiotemporally organized. Recent theoretical and empirical work has highlighted the vulnerability of temporal order memory to aging, and argued for the utility of temporal order tests in particular for characterizing normal versus pathological aging and establishing cross-species correspondence (Allen et al., 2015; Allen, Morris, Mattfeld, Stark, & Fortin, 2014; Fouquet, Tobin, & Rondi-Reig, 2010).

Aging, like amnesia, is associated with a reduction in the tendency to organize free recall by temporal context (Howard, Kahana, & Wingfield, 2006; Healey & Kahana, 2016). An analogue of this effect is found in rodent physiological recordings of the hippocampus: during rest periods after a navigation task, aged rats show as much hippocampal ensemble reactivation as younger rats (Gerrard, Kudrimoti, Mcnaughton, & Barnes, 2001), but their reactivation patterns lack sequence structure and they have corresponding post-sleep memory deficits (Gerrard, Burke, McNaughton, & Barnes, 2008). In humans, aging is often associated with reduced accuracy on order recognition tasks for verbal (Fabiani & Friedman, 1997), spatial (Tolentino, Pirogovsky, Luu, Toner, & Gilbert, 2012), and pictorial (Roberts, Ly, Murray, & Yassa, 2014) stimuli. The pattern of errors made by older adults indicates that they rely on item-position associations (e.g. knowing that X was in the third position) and have difficulty remembering temporal relations among items (Allen et al., 2015). A meta-analysis of aging studies on associative versus item memory (Old & Naveh-Benjamin, 2008) found stronger age-related declines in memory for temporal associations than other any other form of associative binding. Temporal and spatial context retrieval correlate with hippocampal volume, which is reduced in older adults (Rajah, Kromas, Han, & Pruessner, 2010)

Relatively less is known about how the temporal structure, compared to detail, of episodic memory changes over time. Memory for the absolute date and time of personal events decays relatively rapidly (Barclay & Wellman, 1986; Friedman, 2004), as does memory for the specific ordinal positions of event components (Burt, Kemp, & Conway, 2008; Burt, Watt, Mitchell, & Conway, 1998). Although, in word list recall studies, organization by temporal context is relatively robust to varying delays between encoding and recall and between the encoded items themselves (Howard & Kahana, 1999; Howard, Youker, & Venkatadass, 2008), though the delays in these studies are still on the order of seconds or minutes. There is evidence for temporal organization across separate autobiographical events separated by days, weeks or years (Moreton & Ward, 2010; Nielson et al., 2015; Uitvlugt & Healey, 2018). But it is unclear, in humans, how the temporal organization of single extended real-world experiences changes over long delays.

After encoding a given event, and particularly during sleep, certain aspects of experience are thought to be actively restructured and strengthened whereas others are thought to be actively purged (Dudai et al., 2015; Hardt, Nader, & Nadel, 2013; Richards & Frankland, 2017; Winocur & Moscovitch, 2011). Evidence from rodents and humans suggests that sequence structure in particular may benefit from post-encoding rest and sleep (Drosopoulos, Windau, Wagner, & Born, 2007; Griessenberger et al., 2012; Inostroza & Born, 2013), likely by means of compressed replay of recent event sequences in the hippocampus, propagating to the cortex (Joo & Frank, 2018; Kumaran, Hassabis, & McClelland, 2016). When storing or transforming one-time experiences, why does the healthy brain preserve ordinal structure of once-experienced events? One potential explanation is that sequence structure facilitates prediction and simulation of future episodes (Buckner, 2010; Stachenfeld et al., 2017). Across the studies in this thesis, we measure temporal organization in memory at delays ranging from 1 hour to 1 month, and in Chapter 3 in particular, we investigate how memory for details and temporal order change over time within subjects, with the prediction that temporal order will be better preserved over time.

1.3 The relationship between detail and temporal structure

As reviewed above, episodic memory retrieval has been defined by the recovery of specific details from one-time experiences along with their temporal context. Though studies of episodic memory tend to focus on one of these components or the other, they show parallel patterns. They both depend on the hippocampus, in virtue of its circuitry which is ideal for binding and reinstating different elements of experience, and both are vulnerable to age-related decline. Yet there is little evidence about the relationship between detail and temporal structure in episodic memory. Do they rely on common mechanisms? What is the relationship between reinstating static, co-occurring associations comprising a snapshot of experience versus dynamic associations bridging across time?

One class of evidence for a connection between detail and temporal structure comes from the Remember/Know paradigm, where 'Remember' responses are associated with a stronger contiguity effect (Sadeh, Moran, et al., 2014) and greater sequence reconstruction accuracy (Perfect, Mayes, Downes, & Van Eijk, 1996) than 'Know' responses. Since 'Remember' responses are a subjective index of retrieving details from the encoding trial in question, these findings suggest that more detailed retrieval triggers greater reinstatement of surrounding temporal context. Complementary findings have been found using vividness (Burt et al., 2008) and confidence ratings (Schwartz et al., 2005). A recent study using intracranial recordings (Folkerts et al., 2018) found that the neural contiguity effect was specific to highest-confidence 'old' responses, which the authors take to indicate recollection. Notably, recognition trials with lower confidence ratings were accompanied by an anti-contiguity effect, in that reactivation was lower for items from more proximal list positions. Howard and Eichenbaum (2013) concluded that recollecting detailed features of an individual item is an expression of the same neural phenomenon as recovering an item's surrounding temporal context. However, the quality and accuracy of details retrieved on 'Remember' and high confidence trials are unclear, given the subjective nature of these responses, and it is possible that participants make these responses on the basis of retrieving temporal contextual information itself.

On the other hand, detail and temporal structure in episodic memory are not always tied together. For instance, as mentioned above, Dede and colleagues (2016) found that amnesia patients recalled a real-life event with as many multimodal details as controls who were tested at a longer delay, but in an order that bore no resemblance to the encoded order. A similar dissociation of detail and temporal structure is seen, for example, in traumatic memories, which can be extremely vivid and detailed yet temporally disorganized and fragmented (Brewin, 2014). Wegner and colleagues (1996) found a similar pattern in experimentally-induced intentional memory suppression for a movie. After watching the movie, participants were either instructed to think about the movie throughout the day, suppress thoughts about the movie, or were assigned to a control condition. Relative to other conditions, suppression instructions impaired memory for the movie's sequence structure, but did not affect recognition, cued recall, or free recall of specific scene details. They wrote, “Victims of traumatic events often describe their recollections of these episodes as fragmentary, more like snapshots or slides than the replay of a continuous experience…an episode that one doesn't want to think about comes apart in memory somehow, breaking into pieces that no longer flow together” (Wegner et al., 1996, p. 680).

Based on these patterns, Brewin (2014) argued that long-term perceptual memory is in fact a distinct system from episodic memory, with the former generating detailed, sensory-near and inflexible representations, and the latter contextualized, hippocampus-dependent representations (Brewin, Gregory, Lipton, & Burgess, 2010; but see Rubin et al., 2016). This recent model built on an established one suggesting that the hippocampus stores map-like, allocentric representations of events (i.e. viewpoint-independent relations), whereas the medial parietal cortex implements egocentric representations used in imagining and re-experiencing the products of retrieval (Burgess, Becker, King, & O’Keefe, 2001; Byrne, Becker, & Burgess, 2007). Finally, sequence structure can be learned and expressed in memory unconsciously while remaining hippocampus-dependent (Schendan, Searl, Melrose, & Stern, 2003; Shanks et al., 2006), whereas details form the basis of conscious recollection.

In sum, there is little evidence about the relationship between detail and temporal structure in episodic memory, and what evidence exists reveals both associations and dissociations. The relationship between these dimensions within single memories is particularly under-explored, despite the fact that naturalistic episodic memories are highly rich and structured.

1.4 Remembering naturalistic versus laboratory episodes

The relative merits of naturalistic and laboratory memory assessment have been debated for decades (Banaji & Crowder, 1989; Koriat & Goldsmith, 1996; Neisser, 1978; Tulving, 1991), the former emphasizing ecological validity and the latter emphasizing experimental control (for review, see Kvavilashvili & Ellis, 2004). Over this time there has been an increasing focus on investigating memory for naturalistic content (see Figure 1.3). Relative to laboratory stimuli, autobiographical events tend to be more remote (and therefore span a larger search space; Chen, Gilmore, Nelson, & McDermott, 2017)), as well as more emotional, personally significant, and self-referential (Cabeza & St. Jacques, 2007). Furthermore, patterns of age-related memory change sometimes vary considerably across naturalistic and laboratory measures of ostensibly the same construct (e.g. Diamond, Abdi, & Levine, *in prep*; Rendell & Thomson, 1999).

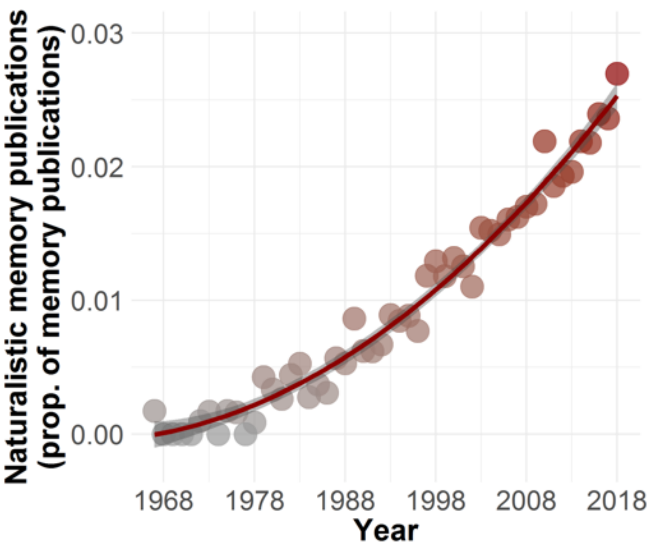


Figure 2.3. Increase in naturalistic memory publications over time. Circles depict, for each year, the proportion of memory-related publications (PubMed search = 'memory') which were framed as being naturalistic (PubMed search = 'memory AND (naturalistic OR autobiographical OR real-world OR "real world"'). The data are best fit with a model including linear and quadratic relationships between year and proportion ($F(2,49) = 1016$, adjusted $R^2 = .976$, $p < .001$). The red line depicts the orthogonal quadratic term fit ($\beta = .193$, $t(49) = 8.791$, $p < .001$) and the grey shaded area depicts the 95% confidence interval around the line.

Consistent with these suggested differences, brain network patterns during retrieval of autobiographical versus laboratory-style events diverge, with the former eliciting greater activity or discriminability in the hippocampus and cortical recollection network (Cabeza et al., 2004; Chen et al., 2017; Chow, Westphal, & Rissman, 2018; Monge, Wing, Stokes, & Cabeza, 2017; Summerfield, Hassabis, & Maguire, 2009; for earlier meta-analyses, see Gilboa, 2004; McDermott, Szpunar, & Christ, 2009). On the other hand, when laboratory retrieval tasks tap contextual recall or subjective re-experiencing, the associated pattern of brain activation is similar to that engaged by autobiographical memory (Kim, 2015; Rissman, Chow, Reggente, & Wagner, 2016; Rugg & Vilberg, 2012).

More direct experimental manipulations of the contextual features that vary between naturalistic and laboratory event encoding have been conducted in the spatial memory literature. For instance, a factor analysis showed that different patterns of spatial memory emerged from real-world navigation versus virtual reality and passive video watching, due in part to processing at different spatial scales. This echoes comparisons of real-world and virtual reality in rodent (Aghajan et al., 2015) and monkey (Thome et al., 2017) research in which virtual reality altered or reduced hippocampal spatial coding mechanisms which are thought to underlie human episodic memory encoding (Buzsáki & Moser, 2013). Memory based on real-world exploration is aided by more visually distinctive encoding contexts (Denis, Mores, & Gras, 2014; Uttl & Graf, 1993) and the contribution of idiothetic cues not available in most laboratory encoding paradigms (Taube, Valerio, & Yoder, 2013). In general, in real-world versus laboratory environments, items are embedded in richer and more distinct pools of contextual information.

Real-world encoding conditions also allow for active exploration, rather than the passive viewing conditions typical of most laboratory encoding paradigms. Volitional control over stimulus sampling improves associative memory recall compared to passive encoding by virtue of increased hippocampal interactions with prefrontal and other regions (Voss, Gonsalves, Federmeier, Tranel, & Cohen, 2011). Neural signatures of physical action and volitional control at encoding are reactivated during retrieval (Nyberg et al., 2001; Voss, Galvan, & Gonsalves, 2011) suggesting that non-perceptual aspects of active encoding may form part of a richer memory trace that supports subsequent retrieval (Engelkamp & Zimmer, 1989). Self-motion produces better relational memory for stimulus arrays than volitional control alone (i.e. actively rotating the stimulus array without self-motion) or passive transport in a wheelchair (Holmes, Newcombe, & Shipley, 2018; Wang & Simons, 1999). These results are consistent with evidence from rodents, in which passive or restricted movement reduces or alters hippocampal mapping of events (Song, Kim, Kim, & Jung, 2005; Terrazas, 2005). In monkeys, unconstrained locomotion in large-scale space engages greater posterior hippocampal activity, linked to recollection and fine-grained event representations (Brunec, Bellana, et al., 2018; Poppenk, Evensmoen, Moscovitch, & Nadel, 2013), compared to constrained or passive locomotion through the same space (Engle et al., 2016). In general, based on the foregoing, it is reasonable to suppose that properties characteristic of real-world experience, compared to typical passive laboratory conditions or even virtual reality, should facilitate subsequent episodic memory (Diamond et al., *in prep*).

These differences may be magnified for representations of temporal context, given that standard trial-based laboratory paradigms are particularly unlike naturalistic experience in their temporal structure and in the manner in which temporal gaps are bridged. Shapiro and colleagues introduced a distinction between events and episodes, suggesting that "Events can be momentary, but episodes are typically prolonged and include a linked series of events that continue through time" (Shapiro et al., 2006). There has been a recent surge in behavioural and neuroimaging studies devising new methods to measure temporal context memory for real-world episodes (Dede et al., 2016; Denis et al., 2014; Griffiths, Mazaheri, Debener, & Hanslmayr, 2016; Jeunehomme & D'Argembeau, 2018; Nielson et al., 2015; St. Jacques et al., 2008).

I developed and validated such a paradigm in my MA and early PhD research, building on earlier work in the lab by Michael Armson (Armson et al., 2017), which capitalized on a pre-existing event that was highly scripted and homogenous across participants – Baycrest's mask-fit test, mandated for all employees. Armson and colleagues developed a test of memory for the event using true/false questions about perceptual and event details, and participants were tested at delays ranging from one month to several years. The test was validated by the expected deleterious effect of delay. I built on this paradigm by designing, for experimental purposes, a real-life walking tour of the artwork and exhibits on the first floor Baycrest Hospital – a visually rich environment with many idiosyncratic and distinctive art pieces. A museum-style audio guide controlled item sequence and viewing duration. We created a content-matched virtualized version of the same tour captured in static photographs, and tested younger and older adults in each condition on the same recognition test for specific details from the tour. After a two-day delay, we found greater memory accuracy and subjective re-experiencing for the real-world tour, and different patterns of age-related decline across the conditions (Diamond et al., *in prep*).

In using controlled real-world encoding paradigms, we can pair the richness and ecological validity of autobiographical memory methods with the control of laboratory studies. The element of control allows us to supplement subjective ratings of detail and vividness with objective measurement of detail accuracy. Furthermore, by controlling the sequence structure of the encoding episode, we can co-opt tools and ideas from the laboratory and animal model literatures to investigate temporal structure in real-world human memories. This allows us to explore the relationship between detail and temporal structure within memories for extended, one-shot, real-world episodes, how these dimensions of episodic memory change over the lifespan, and how they change over naturalistic timescales (i.e. days to months).

The first study in this thesis (Chapter 2) used a museum exhibit at the Ontario Science Centre (‘Brain: The inside story’) containing visually distinctive and idiosyncratic items in an immersive environment. The second and third studies (Chapters 3 and 4) used the Baycrest Tour paradigm, including a second version of the tour built on the second floor. The sequence structure of all three events (the Brain exhibit and Baycrest Tour 1 & 2) was dictated by the track-like layout of the physical spaces, analogous to unidirectional tracks used in rodent studies, and by additional experimental procedures – a scavenger-hunt style pamphlet cueing participants’ attention to specific items in the Brain exhibit, and an audio guide for the Baycrest tours. In all studies, encoding of temporal order information was incidental.

1.5 Overview of studies

In Chapter 2, I present the results of a study assessing age-related change in remote memory for the temporal order of items comprising a real-world episode, as contrasted with recognition memory for the items themselves. Specifically, we used a picture-based recognition paradigm to investigate temporal associative recognition and item recognition across a lifespan sample. Months after encoding, we presented participants with pairs of photographs from a previously visited museum exhibit, manipulating the order and distance of the items, along with similar lure photographs (taken from an un-visited, but thematically related, exhibit). This design allowed us to investigate both explicit memory for the temporal order of a one-shot real-world event, as well as the implicit influence of cue order and distance on order and item recognition. We hypothesized that aging would be associated with a decline particularly in temporal associative recognition. This was not the case. This study is published (Diamond et al., 2018), and is included in this thesis without changes.

Having investigated memory for temporal order at a remote (3 months) delay in Chapter 2, Chapter 3 presents the results of a study investigating how memory for temporal order versus local details change over time. Previous evidence reliably suggests that memories lose detail and precision over time, but little is known about how memory for temporal context changes over time. Here, we probed accuracy along these two dimensions at multiple delays (1 hour, 1 day, 1 week, and 4 weeks) in a within-subjects design using a true/false cued recall paradigm, building on Armson et al. (2017) and Diamond et al. (*in prep)*. Based on models of consolidation, we hypothesized that temporal order memory would be better retained over time than detail memory, and that this difference would be maximally expressed overnight (between the 1 hour and 24 hour tests) with intervening sleep. We also tested older adults, allowing for an exploratory comparison of age-related decline not just in detail and temporal order memory accuracy, but also time-related transformation along these dimensions.

One reason for the importance of free recall in episodic memory research is that it “reveals structure and organization in memory through the ways items tend to cluster in recall sequences” (Polyn et al., 2009). Autobiographical memory is also studied using free recall, but organization within events (akin to words within lists) is rarely investigated. In this study, we investigated hallmarks of temporal context reinstatement borrowed from the word-list learning literature. Furthermore, we paired these measures with standard measures of episodic detail richness using the Autobiographical Interview scoring method (Levine et al., 2002), allowing us to test the relationship between these dimensions within memories. We used pre-existing data from younger and older adults tested at delays of 2 days or 1 week, allowing us to test hypotheses concerning age-related changes in both dimensions of recall. We hypothesized that classic contiguity and forward asymmetry effects would be observed in recall of real-world episodes at naturalistic delays, and that more detail-rich memories would be more temporally organized.

Chapter 2
Lifespan changes in temporal associative versus item recognition

2

2.1 Abstract

Normal aging is typically associated with reduced ability to reconstruct the spatiotemporal context of past events, a core component of episodic memory. However, little is known about our ability to remember the order of events comprising extended real-world experiences and how this ability changes with age. We leveraged the richness and structure of a museum exhibit to address this question. Three months after visiting the exhibit, 141 adults aged 18-84 completed a test of spatiotemporal order memory and old/new recognition using pictures from the exhibit and similar lures, from which measures of associative and item memory were derived. Order discrimination accuracy was modulated by inter-item order and distance in younger and older adults, extending findings from recognition of laboratory stimuli at short delays to remote real-world experiences. In contrast to established findings from laboratory-based assessments, we observed a significant effect of aging on item memory driven by increased lure susceptibility, but no age-related reduction in spatiotemporal associative memory. These findings present novel insights into different components of memory for real-world experiences at naturalistic timescales and across the lifespan.

2.2 Introduction

Episodic memory is defined by the ability to recover the spatial and temporal context of specific past experiences (Tulving, 1972). Age-related reductions in memory for spatiotemporal contextual details are observed for both laboratory (e.g. Allen, Morris, Stark, Fortin, & Stark, 2015; Fabiani & Friedman, 1997) and naturalistic events (e.g. Levine, Svoboda, Hay, Winocur, & Moscovitch, 2002), yet there is little connection between the methods used across these two testing platforms. Laboratory methods can objectively measure and manipulate the accuracy and spatiotemporal organization of retrieval with respect to the encoded episodes, but sequences of laboratory stimuli bear little resemblance to the sequences of events, places and actions that define everyday experiences. On the other hand, studies of real-life events (i.e., autobiographical memory) typically rely on free recall or subjective ratings that preclude objective measurement. Heterogeneity in the remoteness, content and context of participants’ personal autobiographical memories exacerbates this problem, especially in the context of cognitive aging studies. Consequently, still little is known about how we retrace trajectories through past real-world experiences and how this ability changes with age.

Naturalistic events unfold over time in rich and immersive spatial contexts. Memory for such events can reveal crucial component processes of episodic memory, particularly the reconstruction of dynamic spatiotemporal representations (Buzsáki & Llinás, 2017). Across species, spatial and temporal contexts form scaffolds for episodic memories (Ranganath & Hsieh, 2016; J. Robin, Wynn, & Moscovitch, 2015) and they are shaped by actions, goals and exploration (Howard Eichenbaum & Cohen, 2014; Shapiro et al., 2006). In particular, properties characteristic of naturalistic encoding such as volitional control, self-initiated movement, curiosity and goal-directedness modulate hippocampal-neocortical interactions that support episodic memory encoding, and increase subsequent retrieval performance relative to passive encoding baselines (Cornwell, Johnson, Holroyd, Carver, & Grillon, 2008; Gruber, Gelman & Ranganath, 2014; Kaplan et al., 2012; Voss, Gonsalves, Federmeier, Tranel, & Cohen, 2011). These and other related processes are often studied in isolation in the laboratory but are jointly constitutive of everyday experiences. Furthermore, direct experience in real-world space produces qualitatively different spatial memory representations than desktop paradigms (virtual reality and video; Hegarty, Montello, Richardson, Ishikawa, & Lovelace, 2006). Consequently, it is not surprising that autobiographical and laboratory memory tasks sometimes show little overlap in terms of brain activity patterns (H.-Y. Chen et al., 2017), with greater activity in regions related to spatial reconstruction during retrieval of autobiographical episodes than even detail-rich videos (St-Laurent et al., 2016), and hippocampal recordings in rodents and primates reveal different firing patterns during real-world versus virtual exploration (Aghajan et al., 2015; Thome et al., 2017). Thus, certain mechanisms supporting spatiotemporal context encoding and retrieval may be systematically missed by conventional laboratory encoding paradigms.

To bridge the gap between laboratory and naturalistic methods for investigating spatiotemporal information in episodic memory, researchers have recently used verifiable real-world encoding paradigms (Griffiths et al., 2016; Nielson et al., 2015; St. Jacques et al., 2008), although aging effects in such methods remain largely unexplored. In the present study, we used an exhibit at the Ontario Science Centre (“Brain: The Inside Story”) as a rich, dynamic, large-scale and yet controlled one-shot episode for investigating spatiotemporal context memory in a sample of healthy adults ranging in age from 18-84. As a unique and precisely dated event, we were able to probe memory at 2 – 4 months post-encoding, a critical period for memory consolidation (when extrapolated from animal research; Bontempi, Laurent-Demir, Destrade, & Jaffard, 1999; Winocur, Moscovitch, Caruana, & Binns, 2005; see (Sheldon & Levine, 2013) that is rarely tested in most laboratory methods (where memory is usually assessed at seconds- or minutes-long delays) or in autobiographical memory paradigms, where highly personally significant events are often probed years or decades after their occurrence.

As an ancillary goal, we also investigated whether order memory accuracy was sensitive to the spatiotemporal distance between items encountered in the exhibit, as has been previously shown at both laboratory (stimuli separated by seconds) and autobiographical (events separated by days-to-years) timescales (e.g. Curran & Friedman, 2003; Skowronski, Walker, & Betz, 2003; St. Jacques et al., 2008; Underwood, 1977), and whether distance sensitivity changed with age (Fabiani & Friedman, 1997; Perlmutter, Metzger, Nezworski, & Miller, 1981; Roberts et al., 2014; Tolentino et al., 2012). An effect of distance on ordinal discrimination of the exhibit items at our months-long delay would provide novel evidence regarding the durability of memory for spatiotemporal relations within single extended events.

Using photographs from the exhibit along with lures from a separate but similar exhibit, we devised a novel online test of old/new recognition and spatiotemporal order memory, allowing us to test predictions concerning age-related deficits for associative (context) versus item (content) memory. According to the associative deficit hypothesis (Naveh-Benjamin, 2000) and related theories (Hashtroudi, Johnson, et al., 1989; Spencer & Raz, 1995), age-related changes in spatiotemporal associative memory arise from older adults' impairment in binding together and subsequently retrieving associations among items, with spared acontextual recognition memory for the items themselves. Memory for ordinal associations is unique in that the to-be-bound items were not experienced simultaneously, so the associative link must bridge a temporal (and, in our case, spatial) gap. In a meta-analysis of aging studies on associative versus item memory, Old and Naveh-Benjamin (2008) found stronger age-related declines in temporal associative memory than other forms of associative binding. The general finding of age-impaired temporal associative memory (and associative memory in general) and spared item memory has received a great deal of empirical support from studies that probed memory for discrete laboratory stimuli (i.e., experimenter-generated lists of words or images).

Certain laboratory encoding manipulations can attenuate age-related associative memory declines, including implicit promotion of deep encoding or contextual binding (Skinner & Fernandes, 2009; Perfect & Dasgupta, 1997), self-referential encoding (Dulas, Newsome, & Duarte, 2011), distinctive encoding environments (Uttl & Graf, 1993) and active participation in event encoding (Cheke, 2016; Hashtroudi, Parker, Luis, & Reisen, 1989). In passive laboratory tasks, older adults may fail to spontaneously engage in adaptive encoding processes that younger adults engage automatically (e.g. Craik, 1986). It is unclear to what degree findings of age effects on temporal associative memory generalize to memory for naturalistic experiences, in which stimuli are meaningfully (rather than arbitrarily) linked, spatiotemporal context is continuous and actively generated rather than discrete and passively perceived, sequence structure is implicit rather than strategically salient (Hintzman, 2016), and the pool of contextual information that defines each episode is comparatively rich. We reasoned that the ecologically valid conditions of our paradigm would implicitly engage active encoding processes that would attenuate the age-related decline often observed in laboratory studies. The nature of the encoding experience also allowed us to explore age effects on spatiotemporal episodic memory across naturalistic timescales.

2.3 Methods

The "Brain: The inside story" exhibit.

The *"Brain: The inside story*" is a traveling exhibit that was housed at the Ontario Science Centre from November 19, 2014 to March 29, 2015, with recruitment for the initial phase of this study occurring on weekends and civic holidays from February 14 – March 29, 2015. The Ontario Science Centre is a leading attraction in Toronto with an estimated 1 million visitors annually and numerous permanent and temporary exhibits running simultaneously. It is therefore a useful venue to recruit a large sample of adults for research participation. Approximately 164,000 individuals visited the Brain exhibit, which contained perceptually rich educational information about the brain (e.g., sensory, memory and emotional function) aimed at a general audience.

Visitors to the "Brain: The Inside Story" exhibit were recruited by the researchers prior to entering the exhibit at a table just outside the exhibit entrance (to the left of the map in Figure 2.1, between the entrance (above) and exit (below) doors). Next to the table was a poster advertising a “Real-world memory experiment” for adults 18 years and older and the gift-card lottery compensation (see below). Participants were told that participation would involve following a scavenger hunt-style pamphlet guide that would not significantly alter their experience of the exhibit, and that to be eligible for compensation they would have to provide their name and email (among other information) for a follow-up questionnaire to be completed online in the future. Interested participants were given a pamphlet containing multiple-choice questions about the appearance of 17 items in the exhibit, which were selected as targets based on their distinctiveness and spacing. Participants were told that the questions were ordered according to the exhibit layout. They were instructed to find each item, examine it as they would normally, and answer the multiple-choice question (e.g. “Look at the display called “Evolving Emotions”. Which of the following is NOT displayed here? (a) White rhino; (b) California seahare; (c) Green iguana; (d) Northern racoon”) before moving to the next item. They were asked not to revisit items. They were instructed to fill out the pamphlet alone, and upon exiting the exhibit, to enter the time and then return the pamphlet to the researchers at the recruitment station. Notably, they were neither explicitly instructed to encode the target stimuli nor their order. The multiple-choice questions could be answered correctly with minimal effort, and were constructed to confirm participants’ minimally sufficient attention to the target stimuli in a specified order (also dictated by the track-like physical layout of the exhibit).

Prior to entering the exhibit, participants also indicated on the pamphlet their name, sex, age, email address and entry time, and provided ratings on a 6-point Likert scale of their initial level of curiosity about the exhibit content. Upon exiting, participants recorded their exit time and rated their post-encoding curiosity about the content they encountered. Encoding duration was defined as the total time spent in the exhibit. In exchange for completing and submitting the pamphlet, participants were entered into a draw to win one of three gift cards ($200, $50, $50) to local shopping centres.

Participants

1131 participants turned in completed pamphlets at the end of the exhibit ($M_{\text{age}} = 38.64$, $SD = 13.2$). Of these, 1019 participants scored at least 15/17 on the pamphlet questions (and thus sufficiently attended to the items) and were later invited by email to complete an online memory test for the Brain Exhibit. In exchange for completion of the online test, participants were offered a $10 gift card to Amazon.com or iTunes. 169 successfully completed the test. This participation rate is not surprising given that the barrier to submitting a pamphlet was intentionally low (the recruitment table was immediately outside the exhibit entrance and the pamphlet was simple and unobtrusive), while still leading potential compensation, and that those who submitted pamphlets were a sample of adults with no pre-existing intention of participating in research. The pamphlet submission process was a way of building a pool of eligible participants rather than expected participants.

Of 169 participants who completed the online test, 9 were excluded for health reasons and one participant was excluded for having previously visited the exhibit from which the lure items were drawn (see below). We also took into consideration responses to lure trials as an empirical measure of compliance. Based on analysis of the distribution these responses, we excluded participants who correctly rejected fewer than three of sixteen (18.75%) of the lure trials, which was deemed to reflect lack of engagement with the test, misunderstanding of instructions, or abnormally poor lure discrimination. This resulted in the exclusion of 18 participants (11.3% of the sample; $M_{\text{age}} =$ 44.10 years, SD = 16.67, range = 19-77; 12 participants had 0 correct rejections, 5 had one correct rejection, and one had 2 correct rejections).

After these exclusions, 141 participants were included in the analyses (See Table 2.1 for descriptive statistics and Figure S1 for a correlation matrix including associative and item memory scores). Comparing the final 141 participants to the remainder of the 1019 participants who scored 15 or higher on the pamphlet (and thus can be said to have complied with the encoding instructions) but did complete the online test, the final participants did not differ in age ($M_{completed}$ = 40.43 years, SD = 13.21; $M_{NotCompleted}$ = 38.56 years, SD = 13.78; $t(182) = 1.5$, p = .136) nor encoding duration ($M_{completed}$ = 51.53 minutes, SD = 34.3; $M_{NotCompleted}$ = 53.04 minutes, SD = 34.69; $t(187) = .48$, p = .632). The final participants had marginally higher curiosity ratings ($M_{completed}$ = 5.23, SD = 0.86; $\mathrm{M}_{\mathrm{NotCompleted}}$ = 5.06, SD = 1.01; $t(187) = 2.02$, p = .045) though this difference was very small (d = .17). Our sample size of 141 exceeds Cohen’s (1992) recommendation of N = 85 to reliably detect a medium sized population correlation at power = .8 and $\alpha = .05$.

This study was approved by the research and ethics boards at the University of Toronto and Baycrest Health Sciences. All participants gave informed consent prior to participating in both phases of the experiment.

Table 2.1

Descriptive statistics

Variable	Mean or count	*SD*	IQR
Age (years)	40.87	13.89	28-49
Gender (M/F/prefer not to respond)	33 / 106 / 2		
Handedness (R/L/A)	127 / 12 / 2		
Education (years)	.17	3.89	16-19
PHQ-9 score	3.21	4.02	0-4
Lifetime history of anxiety (Y/N)	39 / 102		
Encoding – Test delay (days)	100.64	14.55	73-133
Encoding duration (minutes)	52.91	33.71	27-70
Curiosity rating (/6)	5.22	1.65	5-6

Materials

Test stimuli were photographs taken from in front of target items at an angle and distance that was similar to how participants would have encountered them in the exhibit. Target stimuli comprised pictures of 16 items from the Ontario Science Centre exhibit (one of the original 17 target items was not included because it was found to be unsuitable as a photographic visual cue). Lure stimuli were 16 pictures of items taken from the “Your Brain” exhibit at the Franklin Institute in Philadelphia, and from other similar brain exhibit pictures found online. We selected these stimuli for their feasibility as lures based on pilot data.

Procedure

Two to four months after visiting the exhibit, participants meeting inclusion criteria were invited by email to complete the online memory test. Participants completed a brief health history screening form online, including history of neurological illness (stroke, epilepsy, neurodegenerative disease or any condition requiring brain surgery, traumatic brain injury with a loss of consciousness > 15 minutes), psychotic disorder requiring hospitalization, active drug or alcohol abuse or other major health condition affecting cognition. They also completed the Patient Health Questionnaire (PHQ–9; Kroenke, Spitzer & Williams, 2001), a screening measure for depression, and a binary question about lifetime history of anxiety ("Have you ever suffered from significant anxiety that interfered with your functioning?"). Participants were instructed to complete the test in one sitting in a quiet room without assistance from others.

Participants completed an old/new and spatiotemporal order recognition task, conducted via the Qualtrics platform (www.qualtrics.com). Participants were shown pairs of pictures and had to indicate whether or not the item pairs were shown in the same order as encountered in the exhibit (i.e., intact or re-ordered) or if either of the items was not from the Brain Exhibit (i.e., new). There were 16 intact, 16 re-ordered, and 16 new pairs in total. Participants clicked either 'Correct order', 'Wrong order' or 'New'. Participants were instructed to respond 'New' if either picture was not at the brain exhibit, but both pictures were in fact new on these trials. In addition, we varied the spatiotemporal distance of old (intact and re-ordered) pairs, such that half of the old pairs consisted of adjacent target items in the exhibit (i.e., near pairs) and half consisted of items with 2 intervening target items between them (i.e., far pairs) (see Figure 1). For both old and new pairs, individual items appeared in multiple pairs, but each pair appeared in a given order only once. It is worth noting that in an fMRI study of spatial/temporal order memory with a similar design, where individual items were repeated in multiple unique combinations, task-critical medial temporal and prefrontal brain regions were not sensitive to individual item repetitions (Ekstrom, Copara, Isham, Wang, & Yonelinas, 2011). Accordingly, tasks of this nature are thought to tap into processing of item associations, which were trial-unique, over and above the constituent items.

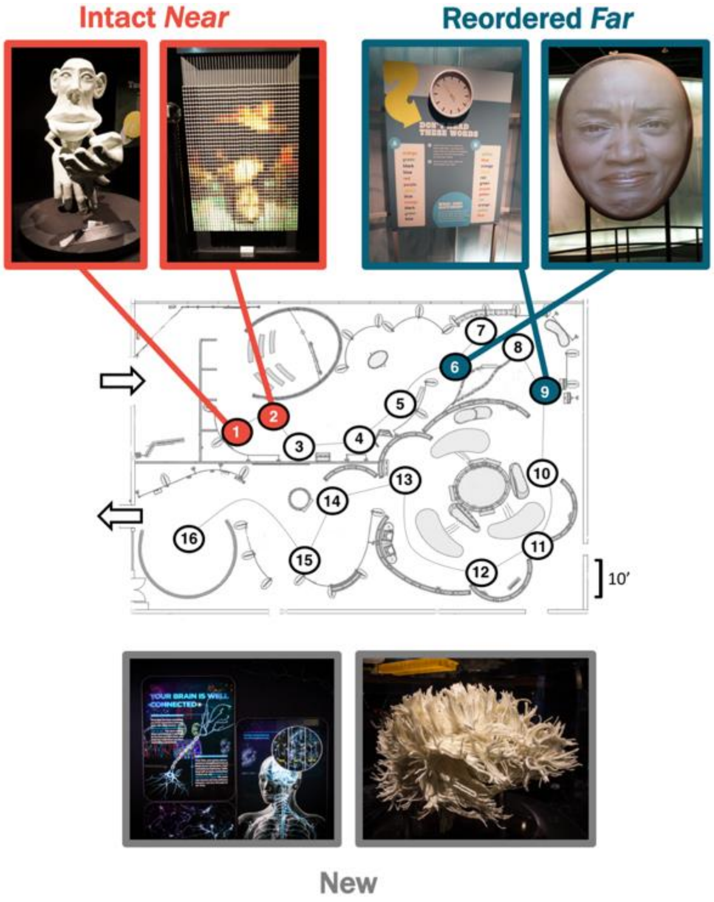


Figure 2.1. Diagram outlining three example stimulus pairs from the recognition memory test. The map depicts the structure of the exhibit and numbered red circles depict the approximate location of each target item and the order in which they were viewed. (A) Near (adjacent) and intact (in the correct order, from left to right); (B) Far (two intervening target items) and re-ordered (in the wrong order from left to right); (C) Lure pair (new pictures drawn from a different brain museum exhibit). All photo stimuli were the same size; images are cropped and re-sized here for display purposes.

Data analysis

Before extracting estimates of associative and item memory and investigating their relationship to aging, we characterized performance on our novel old/new and spatiotemporal order memory test by modelling performance as a function of age (continuous between-subjects regressor) and our memory cue manipulations (categorical within-subjects factors). We fit the data with linear mixed effects models using the lmer() function within the lme4 (Bates, Mächler, Bolker, & Walker, 2015) and lmerTest (Kuznetsova, Brockhoff, & Christensen, 2016) packages in the R programming language, first at the highest level of cue pair validity (i.e., intact/reordered/new) and then within 'old' pairs (intact/reordered and near/far). In both models, we averaged performance over trials of each type within participants. Participants were modelled with a random intercept and significance tests using the Satterthwaite approximation for degrees of freedom, which produces relatively conservative Type 1 error rates (Luke, 2017). We used a similar model to investigate the interaction between age and error types. Age was mean-centred in all models. Post-hoc Welch's t-tests (degrees of freedom rounded to the nearest whole number) were Bonferroni-corrected for multiple comparisons. We report Cohen's d estimates of effect size. When measuring associations between task performance and age, we computed Kendall's rank correlation (tau) in addition to Pearson's *r* when score distributions were highly non-normal due to ties at floor or ceiling. All significance tests were two-tailed.

We adapted the logic of process dissociation (Jacoby, 1991)to calculate independent estimates of associative and item memory under a signal detection framework (for similar approaches, see: Cohn, Emrich, & Moscovitch, 2008; Troyer, D'Souza, Vandermorris, & Murphy, 2011; Troyer et al., 2012; Wolk, Signoff, & DeKosky, 2008; Yonelinas, Regehr, & Jacoby, 1995). Specifically, we computed associative memory (associative d´) as the standardized proportion of hits to intact and reordered pairs minus the standardized proportion of order errors (see Equation 1), thereby isolating accurate spatiotemporal context memory over and above item recognition.

$$Z\left(\frac{P(\text{'}intact\text{'} \mid intact) + P(\text{'}reordered\text{'} \mid reordered)}{2}\right) - Z\left(\frac{P(\text{'}intact\text{'} \mid reordered) + P(\text{'}reordered\text{'} \mid intact)}{2}\right) \qquad (1)$$

Item memory (item d´) was calculated as a standard old/new discrimination score.

$$Z(P(\text{'intact'} \mid \text{intact})) - Z(P(\text{'intact'} \mid \text{new})) \qquad (2)$$

Hit rates of 100% and false alarm rates of 0% were corrected by artificially adding half of one miss or false alarm, respectively (*P_{hit} = 1 corrected to 1-1/(2N) and P_{FA} =1 corrected to 1/(2N), where N is the number of eligible trials)* (Macmillan & Creelman, 2005).

We note that in previous studies where estimates of item and associative memory or recollection and familiarity were extracted from a single test using 'exclusion test' conditions from the process dissociation procedure (Jacoby, 1991; Troyer et al., 2011; Wolk et al., 2008), there are typically two response options (e.g., 'old' and 'new'). Participants are instructed to respond 'old' selectively to old stimuli presented in the correct context (‘intact’, in the present study) and to respond ‘new’ to both totally new test stimuli and old test stimuli presented in the incorrect context; therefore, hits only include correct recognition based on item and context. The inclusion of third response option in the present study (‘reordered’) allows one to dissociate correct rejections based on context violations (‘reordered’ | reordered) versus lures (‘new’ | new), as well as more inclusive operationalizations of misses (‘new’ | intact or reordered) and false alarms (‘intact’ or ‘reordered’ | new), but raises the question of how to theoretically integrate ‘reordered’ hits into previously established formulas. We reasoned that, from the perspective of associative memory, intact and reordered hits similarly signal correct recognition of the items and their spatiotemporal context (and the converse, order errors, signal recognition in the absence of context). Conversely, we used a standard measure of item memory consistent with previous studies (Troyer et al., 2012; Troyer et al., 2011; Wolk et al., 2008), based on a dual-process signal detection model (Yonelinas et al., 1995), including only ‘intact’ responses to intact pairs (hits) and new pairs (false alarms). We reasoned that from the perspective of item memory, ‘intact’ and ‘reordered’ responses do not equally signal familiarity for the items irrespective of their spatiotemporal context. Accordingly, of false alarms to new trials, ‘intact’ responses were more prevalent than ‘reordered’ responses (M_{intact} = 12.41% of new trials, $M_{\text{reordered}}$ = 7.18%; $t(140) = 4.498$, $p < .001$). We report results using alternative formulas in the Supplementary Material (Appendix A, Figure S2; Associative$_2$ = Z(*P*(‘intact’ | intact)) – Z(*P*(‘intact’ | reordered)), consistent with previous studies; Item$_2$ = Z(*P*(‘intact’ or ‘reordered’ | intact or reordered)) – Z(*P*(‘intact’ or ‘reordered’| new)), isolating old/new discrimination irrespective of old pair order; Item$_3$ = Z(*P*(order errors))– Z(*P*(‘intact’ or ‘reordered’ | new)), isolating old/new discrimination in the *absence* of associative memory). The main findings held under all operationalizations of item and associative memory. A broader examination of test responses is considered in our error type analyses.

To investigate the unique effect of aging and potential contributions from other variables on memory, we conducted separate multiple regressions upon associative and item memory estimates, modelling age as our regressor of interest in addition to demographic and health information (sex, handedness, years of education, depression [PHQ-9 score] and anxiety) and extraneous memory-related factors (remoteness, encoding duration and pre-encoding curiosity ratings) (see Table 2.1). As encoding duration, PHQ-9 scores, education, and curiosity were significantly skewed, these scores were square root (education) or log (encoding duration, PHQ-9, and curiosity) transformed for the purposes of regression analysis.

We also recorded response times (RT). Our main purpose in assessing RT was to assess task compliance and confirm validity of the responses, given that testing was unsupervised. We expected to find that reaction times would be sensitive to our manipulation of cue validity (old vs. new), order (intact vs. re-ordered) and distance (near vs. far). These findings would further support our use of the internet testing platform. Analyses were restricted to correct trials.

Mirroring our analyses of recognition memory performance (see Data Analysis and Results), we first modelled participant-wise median RT as a function of pair type (intact, re-ordered or new; within-subjects factor) and age (between-subjects regressor). There were main effects of pair type ($F(2,274) = 22.66$, $p < .001$), where both new and re-ordered trials elicited faster responses than intact trials ($t(138) = 5.62$, $p < .001$, $d = .48$, and $t(138) = 6.57$, $p < .001$, $d = .56$, respectively) and age ($F(1,137) = 51.02$, $p < .001$), whereby response times increased with age ($r = .52$, $p < .001$). The interaction between age and pair type was not significant ($F(2,274) = 2.35$, $p = .097$) (see Table 2.2).

Next, we investigated RT within the old pairs as a function of age, order (intact vs. re-ordered) and distance (near vs. far). Four participants had zero correct trials in a given cell – they were included in the model but not in the post-hoc t-tests. In addition to main effects of age ($F(1,133) = 39.01$, $p < .001$) and order ($F(1,399) = 59.05$, $p < .001$) as above, there was a significant interaction between age and order ($F(1,399) = 7.79$, $p = .006$) such that the age-related increase in RT was slightly greater for intact ($r = .41$, $p < .001$) versus reordered trials ($r = .37$, $p < .001$). Furthermore, there was a main effect of distance ($F(1,399) = 63.63$, $p < .001$) where responses were faster for far than for near pairs ($t(134) = 8.91$, $p < .001$, $d = .33$), extending previous findings. There was also an interaction between order and distance ($F(1,399) = 7.47$, $p = .007$). Far re-ordered pairs elicited the fastest responses (all *p's* < .001 uncorrected) and near intact pairs elicited the slowest responses (all *p*'s < .001 uncorrected). That participants' response times were sensitive to our context manipulation and exhibited expected effects of item distance supports the contention that participants completed the online test according to instructions, with high compliance, and that their responses were valid at the item level.

Table 2.2

Mean (M) and standard deviation (SD) of participant-wise median response times for each pair type.

Pair type	***M(s)***	***SD(s)***
Intact near	9.73	5.31
Intact far	7.34	3.94
Reordered near	7.37	3.77
Reordered far	6.10	3.40
New	6.63	3.96

2.4 Results

We first characterized performance on our recognition memory test at the highest level by modelling accuracy as a function of age and the three main pair types (intact, reordered and new). There were main effects of age ($F(1,139) = 21.75$, $p < .001$), with overall accuracy decreasing as a function of age ($r = -.37$, $p < .001$), and pair type ($F(2,278) = 75.03$, $p < .001$), where new pairs elicited greater accuracy than both intact ($t(140) = 7.43$, $p < .001$, $d = .63$) and reordered pairs ($t(140) = 10.37$, $p < .001$, $d = .87$), and intact trials elicited greater accuracy than reordered trials ($t(140) = 4.36$, $p < .001$, $d = .37$). Furthermore, there was an interaction between pair type and age ($F(2,278) = 9.38$, $p < .001$), such that increasing age predicted lower accuracy on new ($r = -.39$, $p < .001$) and re-ordered ($r = -.25$, $p = .003$), but not intact ($r = -.14$, $p = .094$) pairs (see Figure 2.2).

Within the old pairs, we modelled accuracy as a function of age and pair order (intact vs. reordered) and pair distance (near vs. far). In keeping with the above results, there were significant main effects of age ($F(1,139) = 7.38$, $p = .007$,) and pair order ($F(1,417) = 17.76$, $p < .001$). There was also a main effect of distance ($F(1,417) = 45.12$, $p < .001$), whereby far pairs elicited greater accuracy than near pairs (*t*(140) = 7.21, *p* < .001, *d* = .61), and no interaction between distance and age (*F*(1,417) = .22, *p* = .64), consistent with previous findings that the benefit of greater inter-item distance to accurate contextual retrieval is age-invariant (Fabiani & Friedman, 1997; Perlmutter et al., 1981; Tolentino et al., 2012). There were no interactions between pair order and age (*F*(1,417) = 2.37, *p* = .12), pair order and distance (*F*(1,417) = .62, *p* = .43), nor was there a three-way interaction (*F*(1,417) = 2.73, *p* = .099) (see Figure 2.2).

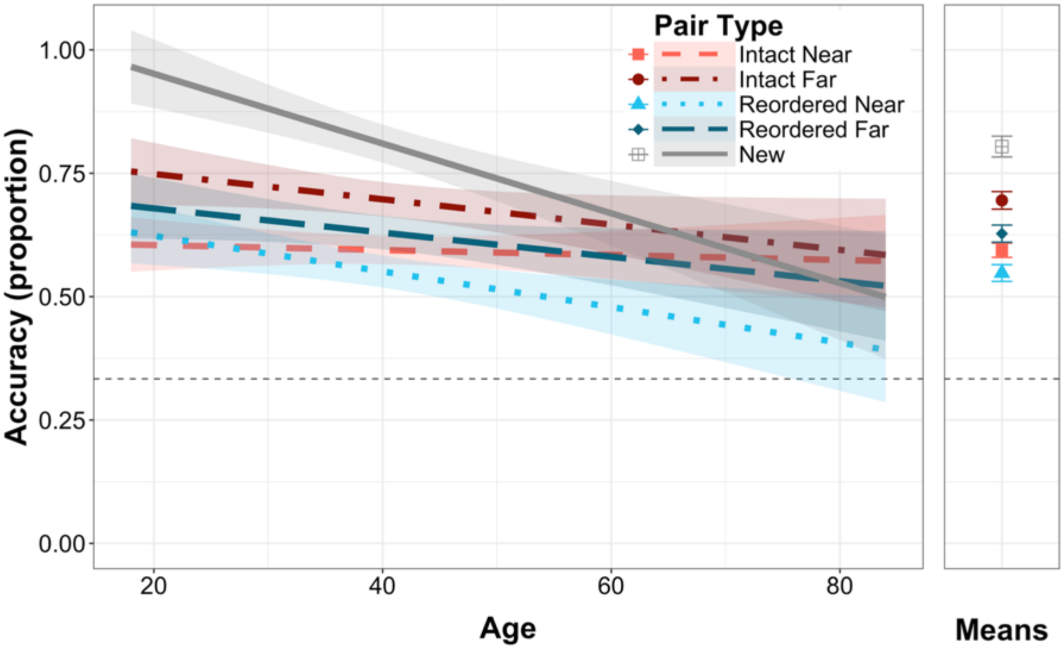


Figure 2.2. Performance on each trial type. Left: correlation of performance on each trial type with age (shaded region displays 95% confidence interval around linear model trend lines). Right: circles display whole-sample means and lines represent standard errors of the means. The dotted black line (accuracy = 0.33) signifies chance performance.

Modelling the effect of age on associative and item memory using multiple regressions, age was not significantly associated with associative memory (β = -.16, *t* = -1.55, *p* = .124, semi-partial *r* = -.14), though there was a trend towards a reduction with age. There was a non-significant trend towards better associative memory with greater total encoding duration (β = .18, *t* = 1.90, *p* = .06, semi-partial *r* = .17), consistent with previous findings of encoding duration at the item level (Vilberg & Rugg, 2009). None of the other predictors (sex, handedness, years of education, depression, anxiety, remoteness, encoding duration and pre-encoding curiosity ratings) was significant (all *p*'s > .25). The variance inflation factors (VIF) for age and total encoding duration were 1.29 and 1.17, respectively, ruling out potential issues of collinearity (VIF for all other variables < 1.4).

For item memory, age was a significant predictor of performance ($\beta = -.34$, t = -3.48, $p = .001$, semi-partial r = -.29). Age had a stronger than expected negative association with item memory. Years of education was positively associated with item memory ($\beta = .22$, t = 2.51, $p = .014$, semi-partial $r = .21$). No other variables predicted item memory performance (all p's > .15).

Scatterplots showing the zero-order correlations between age and associative memory versus item memory are presented in Figure 2.3. To compare associative and item memory, we modelled memory type (associative vs. item) as a within-subjects factor and age as a continuous predictor of performance. We found main effects of age ($F(1,139) = 9.48$, $p = .003$), wherein overall memory performance decreased with age ($r = -.25$, $p = .003$), and a main effect of memory type ($F(1,139) = 311.54$, $p < .001$), wherein item memory ($M = 1.73$, $SD = .89$) was greater than associative memory ($M = .83$, $SD = .66$) overall ($t(140) = 17.03$, $p < .001$, $d = 1.43$), which is unsurprising given that item memory is thought to be less effortful (Jacoby, 1991; Old & Naveh-Benjamin, 2008). There was a significant interaction between memory type and age ($F(1,139) = 11.44$, $p < .001$), such that age was negatively associated with item memory ($r = -.30$, $R^2 = .09$, $p < .001$) but not associative memory ($r = -.14$, $R^2 = .02$, $p = .09$) and the coefficients were significantly different from each other ($Z = 2.53$, $p = .012$,; Steiger, 1980). Removal of the oldest participant (84 years old) did not significantly alter the results of the aforementioned analyses (with participant removed: Associative $r = -.13$, $p = .124$; Item $r = -.29$, $p < .001$), and alternative associative and item memory formulas produced similar coefficients (see Appendix A, Figure S2). Given that associative memory was poorer than item memory overall, we assessed the possibility that it was at chance, which would artificially eliminate the possibility of observing an age-related decline. We tested whether scores at the low (18-35 years old) and high extremes of the age sample (60+ years old) were significantly above zero. Associative memory in both the youngest ($M = .93$, $SD = .65$; $t(50) = 10.16$, $p < .001$) and oldest adults ($M = .73$, $SD = .74$; $t(17) = 4.23$, $p < .001$) was significantly above chance (see Appendix A, Figure S3).

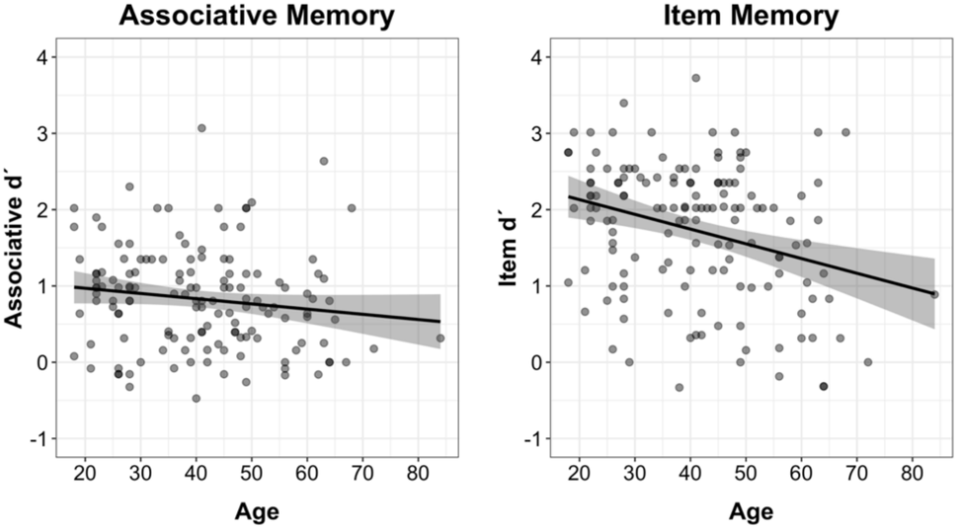


Figure 2.3. Scatterplots displaying zero-order correlations between age and associative (left; r = -.143, p = .09) and item (right; r = -.302, p < .001) memory. Dots represent individual participants. Shaded region displays 95% confidence interval around a linear model trend line.

To further unpack the nature of memory decisions driving the observed age effects on item vs. associative memory, we investigated the types of errors contributing to these scores. We operationally defined three broad classes of errors: order errors ('reordered' responses to intact pairs and 'intact' responses to reordered pairs, isolating spatiotemporal context error in the presence of accurate old/new recognition), misses ('new' responses to old [intact and re-ordered] pairs) and false alarms (old ['intact' and 'reordered'] responses to lures). Modelling error type as a within-subjects categorical regressor and age as a continuous regressor yielded main effects of age ($F(1,139) = 25.78$, $p < .001$) and error type ($F(2,278) = 97.50$, $p < .001$), with order errors being more common than both misses ($t(140) = 19.45$, $p < .001$, $d = 1.64$) and false alarms ($t(140) = 5.90$, $p < .001$, $d = .5$), and false alarms being more common than misses ($t(140) = 5.92$, $p < .001$, $d = .5$). Furthermore, there was a significant interaction between age and error type ($F(2,278) = 15.94$, $p < .001$), with age positively associated with increasing proportion of misses (r = .27, $p = .001$; tau = .16, $p = .011$) and false alarms (r = .39, $p < .001$; tau = .26, $p < .001$) but not order errors (r = .04, $p = .602$) (see Figure 2.4).

To reconcile our observation of age-related decline in performance on reordered trials with the contrasting stability in associative memory and order errors, we ran exploratory correlations between age and the two types of errors one can make on reordered trials: false alarms ('intact' |

reordered) and misses (‘new’ | reordered). We found that aging was associated with an increase in misses (*r* = .28, *p* < .001; *tau* = .18, *p* = .005) but not false alarms (*r* = .09, *p* = .305; *tau* = .08, *p* = .18) on reordered trials, although these correlations were not significantly different from each other (Z = 1.65, *p* = .099).

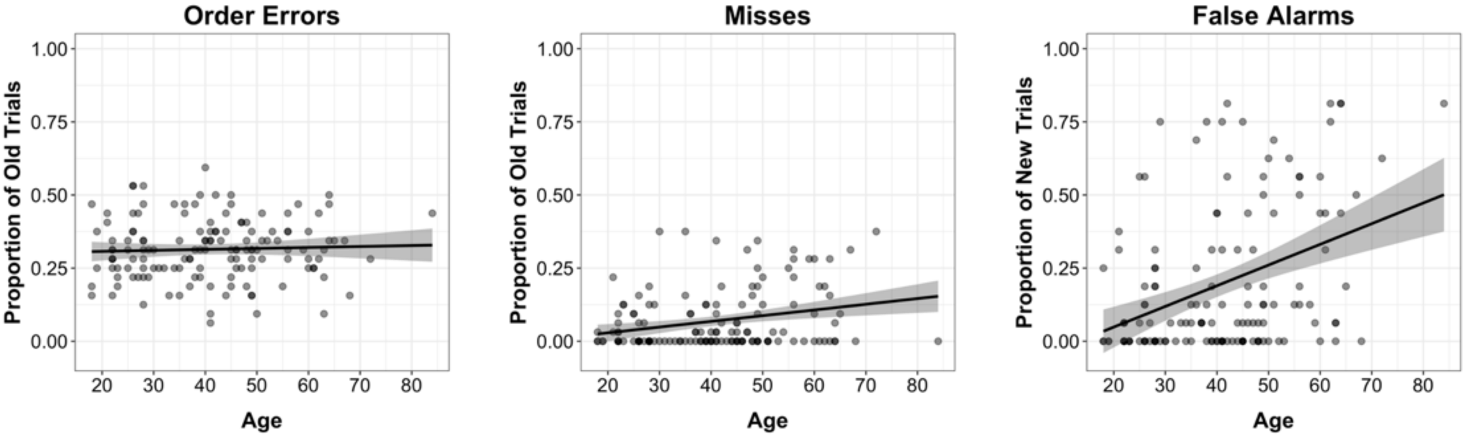


Figure 2.4. Correlations between age and error types (Order errors: r = .044, p = .6; Misses: r = .27, p = .001, tau = .16, p = .011; False Alarms: r = .39, p < .001, tau = .26, p < .001). Each error type is calculated as a proportion of the number of appropriate trials. Dots represent individual. Shaded region displays 95% confidence interval around a linear model trend line.

While our continuous age sample provides a unique window into changes in distinct retrieval processes across the lifespan, most of the literature motivating this research models age as categorical younger and older groups. Thus, to facilitate interpretation and comparison with related studies, we analyzed and visualized associative and item memory scores, as well as error types, using canonical younger (18-35 years) and older (60+ years) groups. Consistent with the above findings, there was an interaction between age group and memory type, wherein item discrimination was significantly lower in older adults (*d* = .84; 44.44% lower than younger adults) but associative memory was not (*d* = .26; 20.98% lower than younger adults; Figure S3). There was also an interaction between age and error type, wherein older adults exhibited a two-fold increase in misses and a three-fold increase in false alarms relative to younger adults, with no difference in order errors (see Appendix A, Figure S4).

2.5 Discussion

We attempted to enhance concordance between laboratory and naturalistic methods of memory assessment using a novel, one-shot, real-world episode (exploring a museum exhibit) prospectively for subsequent memory testing. Spatiotemporal associative memory and item memory were assessed with a recognition memory paradigm using target and lure photographs, allowing us to dissociate, in a large lifespan sample, age effects on item discrimination and spatiotemporal order retrieval.

Contrary to an extensive literature documenting age-related deficits in associative memory (Old & Naveh-Benjamin, 2008), there was no significant effect of age on spatiotemporal associative memory using adaptations of standard process-dissociation measures. Accordingly, there was no age-related increase in order errors, and the implicit effect of inter-item distance on order memory accuracy and response times did not interact with age. Conversely, we found a significant reduction in item memory over the lifespan driven primarily by a marked increase in susceptibility to false alarm to novel lures. Lure susceptibility could not be accounted for by more liberal response criteria in older adults because aging also was associated with increased misses. While previous studies have reported age-related reductions in temporal order memory alongside item memory reductions (Newman, Allen, & Kaszniak, 2001) and false alarm increases (Daum, Gräber, Schugens, & Mayes, 1996), we are not aware of any prior report of a greater age-related reduction in item versus associative memory. This dissociation challenges the notion that age-related declines in memory for content, where observed, are necessarily driven by impairments in memory for context (Dumas & Hartman, 2003).

Spatiotemporal associative memory

The attenuated age effects on associative memory in the present study may be attributable to encoding factors that promote subsequent associative memory, such as active exploration and goal-directed movement (Kaplan et al., 2012; Plancher et al., 2012; Voss et al., 2011). In exploration of environmental-scale spaces, spatial and temporal relationships are actively constructed via self-motion rather than passively perceived (Buzsáki & Llinás, 2017), enhancing relational memory (Wang & Simons, 1999) due to contributions of vestibular, kinesthetic and proprioceptive cues (Taube et al., 2013). Active exploration may automatically recruit hippocampally mediated associative processing circuits and strategies that younger but not older adults typically engage spontaneously in impoverished encoding conditions. For instance, passive transport in a wheelchair disrupts the formation of spatial representations in older adults relative to younger adults but both groups perform similarly when actively navigating (Adamo, Briceno, Sindone, Alexander, & Moffat, 2012; Allen, Kirasic, Rashotte, & Haun, 2004). A review of earlier spatial memory literature found that older adults perform similar to younger adults in real-life but not laboratory environments due to greater distinctiveness of contexts in which items are embedded in real life environments (Uttl & Graf, 1993).

The exhibit items were not only linked by participants' physical locomotion but also by semantic similarity, in contrast to typical associative memory studies using intentionally arbitrary stimuli. Semantic relatedness among studied items has been shown to facilitate the formation of temporal contextual associations during encoding by encouraging reactivation of previously encountered related items (Tzeng & Cotton, 1980). One might also suspect that prior knowledge about museum exhibits could lend schematic support to associative memory, for older adults in particular (Castel, 2005). However, such knowledge would neither bear on the idiosyncratic details of these particular items nor their sequence, and therefore would not have systematically altered temporal order judgements in this study.

Intentional encoding of associations has been found to benefit younger adults more than older adults and thereby increase the age-related gap in associative memory (Old & Naveh-Benjamin, 2008). In our study, the encoding instructions explicitly cued attention towards perceptual features of the exhibit items, but not their order. It could be argued that this difference explains the observed age-related decline in item memory and stability in associative memory. Even in previous studies, however, where associative memory was incidentally encoded and item memory was intentionally encoded, associative memory still declined with age as much as, or more than, item memory (Old & Naveh-Benjamin, 2008; Schmitter-Edgecombe & Simpson, 2001). Regarding temporal associations in particular, evidence for effects of intentional versus incidental encoding has been debated (Michon & Jackson, 1984; Naveh-Benjamin, 1990; R. T. Zacks, Hasher, Alba, Sanft, & Rose, 1984), with intentional encoding sometimes boosting temporal order memory in both younger and older adults (Schmitter-Edgecombe & Simpson, 2001) and sometimes in neither (Kausler, Lichty, & Davis, 1985), and with age effects typically observed either way (Kausler & Wiley, 1990). Therefore, based on the literature, one would expect to observe an age-related decline in temporal associative memory based on incidental encoding alone.

At test, naturalistic photographs of the items (including their immediate local contexts) were likely potent retrieval cues, triggering implicit context reinstatement and providing retrieval support that may also have conferred greater benefits to older than to younger adults (Cohn et al., 2008). In previous studies, context reinstatement has been found to improve recognition performance in older adults as much or more than in younger adults, in some cases ameliorating the age gap altogether (Craik & Schloerscheidt, 2011; Naveh-Benjamin & Craik, 1995; J. Robin & Moscovitch, 2017). Consistent with this interpretation, we found that performance on intact pairs was stable with age but performance on reordered pairs – where the constituent items were valid cues but the spatiotemporal context was violated – declined. The age-related decline in performance on reordered trials was driven by increased misses, but not order errors, and is therefore not inconsistent with the main finding of preserved spatiotemporal associative recognition memory in older adults. This finding could be related to reduced flexibility in spatiotemporal relational representations with age (Etchamendy, Konishi, Pike, Marighetto, & Bohbot, 2012), such that aging spares recognition of intact contextual cues but impairs flexible reconstruction of these cues, leading older adults to perceive old-but-reconfigured elements as new. We would predict steeper age-related reductions in spatiotemporal contextual memory for the exhibit had we used a task that placed higher demands than recognition on self-initiated processing and strategic retrieval (Cohn et al., 2008; Craik, 1986), for instance free recall (e.g. (Dumas & Hartman, 2003; Levine et al., 2002) or serial order reconstruction (e.g. Kausler & Wiley, 1990; Schmitter-Edgecombe & Simpson, 2001), or with speeded rather than self-paced response windows (Roberts et al., 2014). Given that we did not implement an immediate test, another possibility is that forgetting over the months-long delay interval rendered our test less sensitive to age differences in associative memory that may have been apparent at shorter delays. We cannot rule out this possibility, although prior studies suggest that temporal order memory for both laboratory stimuli and naturalistic actions performed in the laboratory decays at similar rate in younger and older adults (Kausler & Wiley, 1990; Perlmutter et al., 1981).

Item memory

The age-related increase in lure susceptibility is consistent with recent cross-species evidence that aging affects discrimination of familiar from novel information due to changes in medial temporal lobe circuits responsible for high-level object representation, especially when familiar and novel items have high feature overlap (Burke et al., 2011; Reagh et al., 2016; Ryan et al., 2012; Yeung, Ryan, Cowell, & Barense, 2013; Johnson et al., 2017). Combined with age-related source monitoring impairments, this may produce elevated false recognition (Hashtroudi, Johnson, et al., 1989; Schacter, Koutstaal, Johnson, Gross, & Angell, 1997). This view is contrasted with the notion that age-related changes are due to a weakening of memory traces.

Previous studies have shown that false recognition of events can be induced in older adults, for instance by watching naturalistic videos and then reviewing plausible lure photos that were not in fact in the videos (Schacter et al., 1997). In the present study, we found age-related increases in lure susceptibility without any manipulation to promote it, alongside largely preserved associative memory for valid memoranda. Given that both valid memoranda and lures in the present study were naturalistic photos depicting brain-themed museum exhibit items, it is likely that perceptual and conceptual similarity between targets and lures, and corresponding over-reliance on gist information during discrimination, contributed to the increase in false recognition with age (Koutstaal & Schacter, 1997; Pidgeon & Morcom, 2014). Our findings are more consistent with models of aging emphasizing mnemonic discrimination impairments than with the associative deficit hypothesis (Naveh-Benjamin, 2000), but more work is necessary to adjudicate between these views.

Task compliance

Regarding our paradigm, as the memory test was conducted online and was unsupervised (see Armson, Abdi, & Levine, 2017, for a similar approach), it is crucial to determine that participants responded in a valid and reliable manner. We ruled out inattentive or random responding by excluding those who performed very poorly on discrimination of new items. Sensitivity in participants’ response times to our old/new and context manipulation helped to establish task compliance. Furthermore, we replicated established effects of context reinstatement, in that performance was greater on intact compared to reordered trials, and age-invariant sensitivity to inter-item distance (i.e., better performance and faster responses on far than on near pairs) in line with previous studies (Fabiani & Friedman, 1997; Perlmutter et al., 1981; St. Jacques et al., 2008; Tolentino et al., 2012; but see Campbell, Trelle, & Hasher, 2014). These results build upon recent work using large-scale real-world encoding paradigms to explore spatiotemporal organization in episodic memories (Griffiths et al., 2016; Nielson et al., 2015; St. Jacques et al., 2008). We extend the results of these studies, which tested memory for events in familiar environments at shorter delays, to a cognitive aging context and show some preservation of spatiotemporal order memory for the elements of a one-shot episode at a longer delay and finer spatiotemporal scale than previously reported. Even on the most difficult adjacent re-ordered pairs, thought to require fine-grained episodic reconstruction (Curran & Friedman, 2003; St. Jacques et al., 2008), performance was well above chance (whole-sample mean = .55; chance = .33).

Limitations

The influence of naturalistic encoding processes *per se* on the present findings remains speculative; inclusion of a comparable and time-matched laboratory assessment would help to establish the specificity of the observed effects to naturalistic events. Furthermore, unlike previous studies, we could not dissociate spatial and temporal aspects of memory organization (e.g. Allen et al., 2015; St. Jacques et al., 2008) – accurate associative retrieval could involve retracing the egocentric trajectory of target items and/or by remembering their allocentric spatial locations in a map-like representation. Nevertheless, the architectural structure of museum exhibits makes them useful in particular for testing naturalistic spatiotemporal memory and facilitating translation between rodent models and human research (Zisch, Gage, & Spiers, 2014). It is also not clear to what degree order memory performance in the present task generalizes to other forms of associative memory (see Old & Naveh-Benjamin, 2008) or mnemonic context more broadly (Stark, Reagh, Yassa, & Stark, 2017). Nor is it clear to what degree successful associative memory involved subjective recollection of the encoding episode. Indeed, recent work suggests that ordinal associative memory (at short delays) may not depend on recollection (Brunec, Ozubko, Barense, & Moscovitch, 2017). Future work is necessary to determine the strategies and phenomenological states accompanying spatiotemporal context retrieval and how they change with age.

Another potential limitation concerns the representativeness of the sample in the present study. Although the sample and recruitment method are different from the typical aging study recruiting younger adults from a pool of undergraduates, usually psychology students, and older adults from research participant databases, the Ontario Science Centre is a highly generic and popular attraction in Toronto. There is no reason to suspect that recruitment from such an attraction is less representative of the general population than typical recruitment methods. Indeed, several high impact memory studies have used museum exhibits in naturalistic encoding paradigms (e.g. Aggleton & Waskett, 1999; Henkel, 2013; St. Jacques, Olm, & Schacter, 2013), and prior visits to museum exhibits are often used as cues in autobiographical memory studies (e.g. Hassabis, Kumaran, Vann, & Maguire, 2007; Robin & Moscovitch, 2014)) for their assumed universality.

A second concern about the present sample is that it lacks representation at the older end of the age spectrum. We would expect to observe a decline in spatiotemporal associative memory at the higher end of the age spectrum had our sample included more participants in that range. However, one would expect continued decline in item memory as well. Moreover, the age distribution in our sample is comparable to that of many laboratory studies reporting age-related declines in spatiotemporal memory and associative memory (see Old & Naveh-Benjamin, 2008). Finally, continuous lifespan investigations of associative versus item memory (Bender, Naveh-Benjamin, & Raz, 2010) and corresponding brain atrophy (Raz et al., 2005) found incremental changes beginning in early adulthood and accelerating in middle rather than late age. Therefore, to the extent that significant age-related declines in temporal associative memory are expected based on the literature, they should be detectable in the present sample. Nonetheless, we cannot make inferences about memory changes in older age (i.e., 70 years and older) based on the present sample.

Finally, the effect of aging on associative memory could in principle be artificially truncated by the lower performance of younger adults in associative versus item memory. This procedure would affect comparisons of the associative and item memory slopes. Therefore, the magnitude of this difference should be interpreted with caution. Yet despite the long delay and fine grain at which ordinal discrimination was tested, older adults' performance was well above chance (associative d´ = .73 in participants 60+ years old). The null effect of age on associative memory cannot be explained by the lower overall performance on associative memory, unless there was a feature of the task that selectively reduced younger adults' performance. Moreover, the dissociation between age effects on associative and item memory is supported by multiple lines of evidence: there was no age-related increase in order errors, where the distribution is well off of floor and ceiling, and the influence of inter-item distance on ordinal discrimination did not interact with age.

Conclusions

Laboratory research has demonstrated that spatiotemporal context is a fundamental component of episodic memory (Howard & Kahana, 2002a; Ranganath & Hsieh, 2016; Tulving, 1972), and it is assumed that this contextual detail is a core feature of our personal memories from months and years ago. Due to methodological limitations, however, little is known about memory for the order of real-world experiences over delays typical of everyday episodic memory, and how this capacity changes with age. The present study provides further validation for assessing memory using verifiable real-world events (see also Armson et al., 2017; St. Jacques, Montgomery, & Schacter, 2015)). We found that memory for the fine-grained spatiotemporal structure of a real-world event persists over months in both younger and older adults, and that increased lure susceptibility in older adults reverses the classic pattern of item and associative memory changes observed in laboratory studies of aging. Future work in this vein will contribute to understanding normal versus pathological memory changes in aging and how they manifest in day-to-day life.

Chapter 3
Differential consolidation of detail and temporal structure

3

3.1 Abstract

Episodic memory is defined both by reliving the details of specific moments in time (e.g. a new acquaintance's name and the colour of her shirt) and retrieving the temporal contextual relations among these moments. Previous research has found that different types of information are forgotten at different rates, but it is not clear how the details and the sequence structure of a single complex event are forgotten over time. In samples of younger and older adults, we measured memory for the details and sequence structure of an immersive real-world event at four time-points within subjects (1 hour, 24 hours, 1 week and 4 weeks). The spacing of tests was designed to probe memory change overnight, thought to be a critical period for consolidation, as well as in the subsequent days weeks. In younger adults, detail memory accuracy and subjective recollection declined across all tests. Conversely, sequence memory accuracy was stable from first to last tests and increased above-baseline overnight. Aging was associated with a subtle and time-dependent decline in detail memory in addition to a large decrement in sequence memory at all delays. Together, these results suggest that consolidation may confer greater stability to the spatiotemporal structure of events than their idiosyncratic details, and that such spatiotemporal structure may be particularly vulnerable to age.

3.2 Introduction

Episodic memory entails storing and then coherently reactivating associations among the co-occurring details of an experience (e.g. the name of a painting and its colours, or the smell of the cafeteria and a thought you had while there) (Horner & Burgess, 2013; McClelland, McNaughton, & O'Reilly, 1995; Tulving, 1972). Memory for these specific details, when bound together, underlies our subjective sense of re-experiencing specific moments in time (Meiser, Sattler, & Weißer, 2008; Mitchell & Johnson, 2009; Tulving, 1985). A second defining component of episodic memory is that experiences are remembered in temporal relation to each other (Tulving, 1972). Retrieving one experience often evokes, in order, the extended sequence of events in which it was embedded (Howard & Kahana, 2002a), imbuing specific memories with a sense of "beforeness and afterness" (Conway, 2009).

Convergent evidence from human and animal research suggests that the hippocampus is necessary for the formation and retrieval of both static or atemporal detail associations and sequential associations (Davachi & DuBrow, 2015; Eichenbaum et al., 2007; Ranganath & Hsieh, 2016). Accordingly, it has been speculated that they are two behavioural expressions of a common neural phenomenon (Howard & Eichenbaum, 2013). Tests of episodic memory, however, usually probe memory for static detail associations or spatiotemporal associations, but not both. In principle memory can succeed or fail along either dimension (see Figure 3.1). Indeed, models of hippocampal function link different components of its circuitry to forming and retrieving scene- or snapshot-like memories (Treves & Rolls, 1994) versus sequential associations across memories (Lisman, 1999). Yet little is known about the relationship between memory for the details and memory for the sequence structure of extended episodes, and in particular, about how these components of episodic memory change over time.

Between encoding and retrieval, episodic memories change. They are transient, for one – most attended information is rapidly forgotten (Ebbinghaus, 1913; Schacter, 1999; Wixted, 2004) - yet forgetting is neither passive nor indiscriminate (Richards & Frankland, 2017; Sadeh, Ozubko, et al., 2014). Memories transform systematically over time (Sekeres et al., 2018; Winocur & Moscovitch, 2011) and repeated retrievals (Antony, Ferreira, Norman, & Wimber, 2017), stabilizing certain dimensions or features of experience and discarding others in a manner that is shared across individuals (Chen et al., 2016). By tracking change in different components of complex event memories over time, we can shine a light on the underlying mechanics of this transformation process. In this study, we explored how memory for the details and sequence structure of a real-world experience transform within younger and older individuals over timescales ranging from an hour to a month.

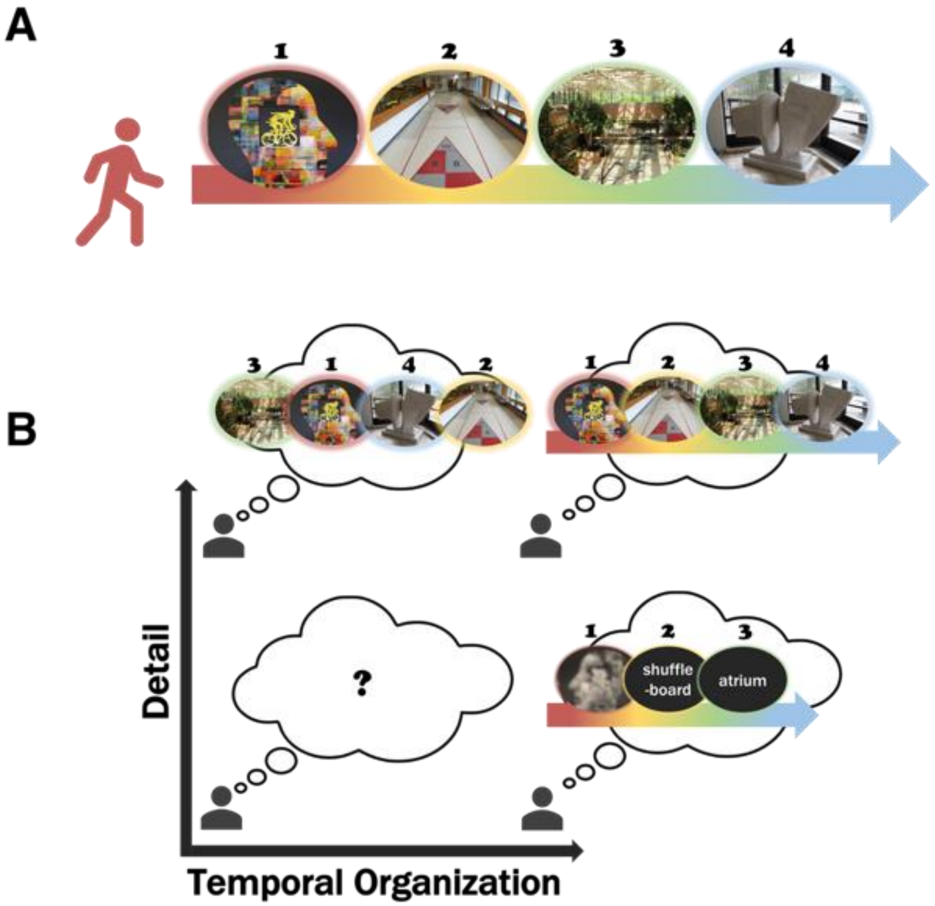


Figure 3.1. *A.* Schematic depiction of episodic memory encoding. Items are encountered in spatial and temporal succession, and are associated with a drifting representation of spatiotemporal context (the gradient-coloured arrow). The order of events is indicated by the number labels and the colours. *B.* Schematic depiction of episodic memory retrieval success as measured along two dimensions: the recovery of event specific details (*y*-axis), and memory for temporal relations (*x*-axis). *Top right*: Memory can be both detailed (as indicated by high-fidelity retrieval of the four items) and temporally organized (as indicated by retrieval of items in their original order, thought to be driven by retrieval of extended spatiotemporal context). *Top left:* Memory can be detailed, but temporally disorganized (spatiotemporal context is not retrieved and thus items are out of order). *Bottom right:* Memory can be temporally organized but detail-impoverished. Loss of details is represented by the degraded (loss of colour) and altered (orientation flipped) copy of the first item, the lack of perceptual detail in items 2 and 3, and the altogether forgetting of item 4.

It is well-established that memories tend to lose detail over time, transforming from perceptually-rich and specific to gist-like and generalized (Hardt et al., 2013; Reyna & Brainerd, 1995; Winocur & Moscovitch, 2011). In studies using video or text narrative stimuli, specific details (e.g. names and perceptual details) are forgotten at a faster rate, over days to months, than the gist, plot, or meaning of the stories (Furman et al., 2007; Sekeres et al., 2016; Stanhope, Cohen, & Conway, 1993; Thorndyke, 1977). These findings are echoed in traditional laboratory studies across species, in which memory for particular stimulus configurations and details decline more, and faster, than memory for the individual stimuli or their global characteristics (Dandolo & Schwabe, 2018; Riccio, Ackil, & Burch-Vernon, 1992; Talamini & Gorree, 2012; Wiltgen & Silva, 2007; for review, see Sadeh, Ozubko, Winocur, & Moscovitch, 2016). Consistent with loss of detail, self-reported subjective recollection declines with time, whereas familiarity is less affected (Sadeh et al., 2014; Tulving, 1985). One concern with many of these studies is that the component of memory that declines more tends to be the more difficult one on average.

This time-dependent shift in the representational quality of a memory mirrors a shift in their neural basis from the hippocampus to the cortex, which in turn is thought to reflect a shift from high-resolution but interference-prone to low-resolution but stable formats (Dudai, 2004; McClelland et al., 1995; Sekeres et al., 2018; Winocur & Moscovitch, 2011). Since the distributed cortical representations underlying the various details of each experience converge in the hippocampus (Marr, 1971; McClelland et al., 1995; Moscovitch, 2008), access to these bound details is lost as the hippocampal trace decays (Hardt et al., 2013). Yet, although the hippocampus is also necessary for representing the order of events in memory, there is little evidence about how this dimension of episodic memory changes with time.

Sequence structure is a key component of mechanisms of consolidation at the physiological level. During online behaviour and subsequent sleep, hippocampal cells that had encoded specific locations or events are replayed repeatedly and in order, ‘squeezing’ sequences occurring at the timescale of experience (seconds or minutes) into the timeframe at which synaptic plasticity operates (Buzsáki & Moser, 2013; Skaggs & McNaughton, 1996). These replayed trajectories, particularly during sleep, are necessary for stabilizing memory for spatiotemporal associations formed earlier (Drieu, Todorova, & Zugaro, 2018; Girardeau, Benchenane, Wiener, Buzsáki, & Zugaro, 2009; Lee & Wilson, 2002), and the degree to which replay events preserve their encoded order predicts subsequent spatial memory in the Morris swim task (Gerrard, Burke, McNaughton, & Barnes, 2008; for related evidence in humans, see Zhang, Deuker, & Axmacher, 2017). Therefore, sequence structure may benefit from post-encoding consolidation processes, particularly sleep, relative to other episodic information.

Accordingly, in humans, memory for spatiotemporal relations can improve over post-encoding rest periods (Craig, Dewar, Della Sala, & Wolbers, 2015; Craig, Wolbers, Achtzehn, Strickland, & Dewar, 2019) and sleep strengthens memory for sequences of stimuli when compared to matched periods of wakefulness (Drosopoulos et al., 2007; Griessenberger et al., 2012). Similarly, sleep benefits route memory in virtual spatial environments (Noack, Schick, Mallot, & Born, 2017; Peigneux et al., 2004). In certain cases, the influence of temporal organization on behaviour emerges after 24 hours but not after shorter within-session delays (Braun, Wimmer, & Shohamy, 2018), together suggesting some kind of offline restructuring that strengthens temporal (or spatiotemporal) associations. Little is known, however, about how the change in sequence memory over time, often focusing on effects of post-encoding sleep, relates to the change in memory for specific details, often measured at longer timescales. Relatedly, it is unclear how to reconcile the view that time and sleep decontextualize memory, stripping away details and extracting gist (Feld & Born, 2017; Lewis & Durrant, 2011; McClelland et al., 1995), with the view that offline replay stabilizes spatiotemopral associations (Joo & Frank, 2018; O'Neill, Pleydell-Bouverie, Dupret, & Csicsvari, 2010). Even less is known about how these components change in memory for real-world experiences.

Personal experiences are forgotten less, and at slower rates, relative to laboratory stimuli (Rubin & Wenzel, 1996), often exhibiting impressive retention when cued after years-long delays (Brewer, 1988; Linton, 1975; Wagenaar, 1986). These studies, however, have mostly used diary methods, limiting the generalizability of the events in question and the precision with which memory can be assessed. Our lab recently validated the use of more controlled recognition-style true/false memory tests to probe specific details of staged event, finding an expected decline in accuracy over delays ranging from one month to several years (Armson et al., 2017). By including test probes about the spatiotemporal relations among pairs of items at varying distances, and manipulating the retention interval within subjects, we can more rigorously measure change in episodic memory for a naturalistic event over time.

How should aging affect forgetting of detail and sequence information? Limited evidence from rodents suggests that forgetting rates increase with aging, reflected in faster decay at the level of hippocampal synapses (Barnes & McNaughton, 1985). Regarding sequence memory, young and aged rats exhibit similar magnitudes of place cell reactivation during sleep (Gerrard et al., 2001), yet the sequential organization of reactivation is markedly reduced in aged rats, commensurate with spatial navigation deficits following sleep (Gerrard et al., 2008). In humans, however, when accounting for differences in acquisition rate, aging is often associated neither with faster forgetting in the short (Geffen, Moar, O'Hanlon, Clark, & Geffen, 1990; Youngjohn & Crook, 1993) nor long term (Fjell et al., 2005), though findings vary widely according to testing procedures and delays used (for review, see Elliott, Isaac, & Muhlert, 2014). Most studies have used traditional recognition or recall paradigms. Dissociating retention of different types of hippocampus-dependent episodic memory for a naturalistic event over longer time scales may reveal novel insights about whether and how aging affects consolidation. Furthermore, by contrasting effects of aging with those of increasing remoteness, we can tease apart memory changes due to age-related neurobiological alterations from those related to memory weakening (Heyworth & Squire, 2019).

In the present study, we tested memory for the details and sequence structure of a controlled, one-time real-world episode in younger and older adults. We investigated the transformation of these components over time, implementing trial-unique tests at four time-points within subjects (1 hour, and at 24 hours, 1 week and 4 weeks after encoding), allowing us to test predictions about memory change related to sleep and longer delays. We hypothesized that sequence memory would be more stable than detail memory over time, and that this difference would be maximally expressed in the change overnight (from 1 hour to 24 hours).

3.3 Methods

Participants

57 younger adult participants (M_{age} = 22.74 years, SD = 3.59; $M_{\text{Education}}$ = 15.26, SD = 1.75) and 48 older adult participants (M_{age} = 72.69 years, SD = 4.61; $M_{\text{Education}}$ = 15.81, SD = 2.80) were tested. Testing at the three remote delays (1 day, 1 week, and 4 weeks) was conducted online and unsupervised. We monitored responses on these measures for evidence of lack of engagement, which could influence performance on subsequent tests. We excluded participants who scored

2.5 standard deviations below mean overall accuracy for their age group on any of the four memory tests, which we take to reflect a reasonable probability of inattentive responding. This resulted in the exclusion of two younger participants (one responded accurately on 51.5% of trials on the 24 hour test, and the other 38.9% on the 4 week test), Additionally, one younger participant was excluded for failing to complete all 4 memory tests within the appropriate time windows, and one was excluded for technical issues during testing (the headphones malfunctioned). Of the older participants, 1 was excluded for failing to complete all 4 memory tests within the appropriate time windows. Seven participants were excluded for scoring below 26 on the Montreal Cognitive Assessment (MOCA), the recommended cut-off for separating cognitively healthy adults from those at-risk of cognitive impairment (Nasreddine et al., 2005), and an additional 2 older participants were excluded for having clinical diagnoses of amnestic Mild Cognitive Impairment that were not known at the time of testing. There were no test performance outliers among the remaining older adults, reinforcing that our exclusion criterion screened participants with inattentive responding rather than poor performance due to age-related memory impairment. After exclusions, data from 53 younger adults (M_{age} = 22.60 years, SD = 3.23; $M_{\text{Education}}$ = 15.40, SD = 1.67) and 38 older adults (M_{age} = 72.66 years, SD = 4.67; $M_{\text{Education}}$ = 15.84, SD = 2.86) were included.

All participants were recruited via the Rotman Research Institute participant database at Baycrest Health Sciences Centre or from advertisements online and in the Toronto community, and were screened for history of neurological or psychiatric illness, active significant medical illness or substance abuse. Participants were fluent English speakers, had normal or corrected-to-normal vision and hearing, and were not colour-blind. Finally, all participants were screened for prior exposure to the second floor of Baycrest Hospital (where the tour took place). Participants gave informed consent in accordance with institutional guidelines, and were compensated upon completion of the study.

Materials

The encoding event

Participants underwent an audio-guided real-world walking tour of the artwork on the second floor of Baycrest Hospital (see Figure 3.2). Participants were instructed to examine different target items (e.g. paintings, portraits, and sculptures). Participants were aware that they were in a memory experiment but no instructions were given regarding the nature of the test. In this sense, sequence memory encoding was fully incidental. The audio guide and the unidirectional structure of the route controlled the sequence structure of the experience, and ensured that all participants encoded the target items and for a set duration. The tour took on average 20.53 minutes (*SD* = 1.61) for younger adults and 22.66 minutes (*SD* = 3.40) for older adults.

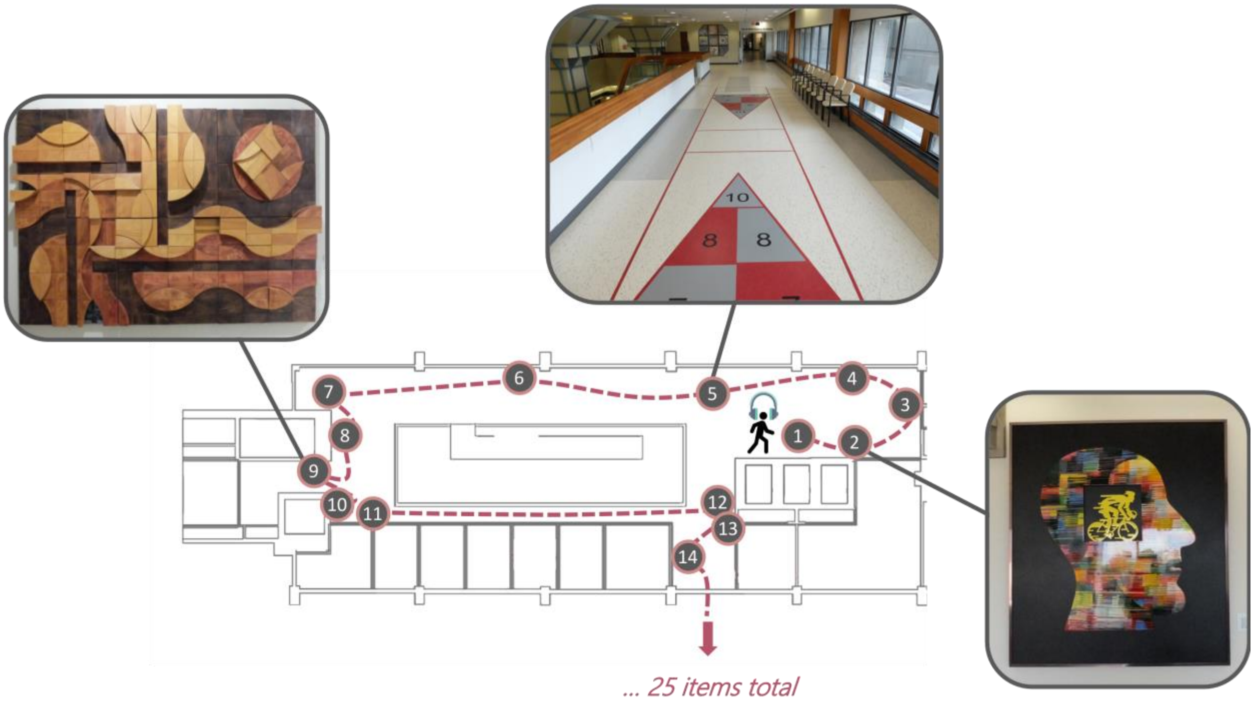


Figure 3.2. Depiction of part of the tour route (dashed line), including locations and ordinal positions of target items (numbered circles), and photographs of selected target items, including selections of the audio guide content.

The audio guide was recorded and edited using Audacity (http://audacity.sourceforge.net/). There was one male narrator. The audio guide was broken down into multiple tracks, each associated with an item. Each track was initiated by the participant by pressing a button on the MP3 player. Upon arrival at target items, the guide instructed participants to examine them, followed by a silent period in the recording, and then directed participants to the next item. The guide thus controlled the encoding duration for each item, while the separate tracks allowed for individual differences in walking speed between items. For some items, the guide provided information (e.g. about the artist) or cued participants' attention to certain features. Participants were given extensive instructions before the tour began, and they were given an opportunity to practice using the MP3 player to control the audio guide. The experimenter unobtrusively observed participants to verify that they followed the instructions.

The memory tests

The memory tests were implemented in Qualtrics (https://www.qualtrics.com/), an online survey platform. Previous work from our laboratory validated the use of online testing using recognition memory experiments (Armson et al., 2017; Diamond et al., 2018). They consisted of true/false statements pertaining to either event and perceptual details ('detail statements'; e.g. "The sculpture called One Nine North is dark red") or the spatiotemporal order of pairs of items from the tour ('sequence statements'; e.g. "You encountered the sculpture called One Nine North before the Spiro Family Gardens painting"). Whereas some detail statements referred to information that was not specific in place and time (e.g. "You were asked to note the time twice"), sequence statements referred to pairs of specific items for which encoding was ensured by the audio guide. There were 25 such target items, each of which had a clear ordinal position in the tour. Sequence statements were binned into three levels of lag, or ordinal distance: 'Near' pairs had 0 or 1 intervening target items, 'medium' pairs had 2-3 intervening target items, and 'far' pairs had 4-6 intervening target items.

False detail statements were created by altering details of tour elements and were non-redundant with respect to true statements – no two statements referred to the same detail. Most detail statements referred to item features, rather than whole items, so that there were multiple T/F statements for most target items in the tour (e.g. one statement about the colour of a particular piece of art and another about its shape). Previous research has demonstrated that distinct details of real-world stimuli are forgotten at different rates (Brady, Konkle, Alvarez, & Oliva, 2013). False sequence statements simply reversed the true order of item pairs. These, too, were non-redundant with respect to true statements.

On each trial, participants were presented with a statement and responded 'true' or 'false'. They were then cued to rate the subjective quality of their memory using the Remember/Know/Guess procedure (Gardiner, Ramponi, & Richardson-Klavehn, 1998), which builds on the standard Remember/Know procedure (Gardiner, 1988; Tulving, 1985) by purifying Know responses of guesses. 'Remember' responses indicate subjective re-experiencing of the items in question and 'Know' responses indicate a feeling of familiarity in the absence of re-experiencing. Subjective ratings were gathered for both detail and sequence trials to equate their trial structure. However, since the interpretation of such ratings for sequence statements is unclear given that they each refer to two tour items, only RKG ratings for detail statements are analyzed here. Beyond including a “Guess” option, the present RKG method is different from most previous applications of this method in two ways. First, RK or RKG responses are typically employed in old/new recognition paradigms where they characterize subjective memory for whole stimuli, whereas here are made at the featural level (e.g. a target item’s colour). Participants were thus instructed to report “remembering” when they made their true/false responses on the basis of re-experiencing the detail in question – for instance, by ‘seeing’ the detail in their mind’s eye, or by remembering a thought they had about it. They were instructed to report ‘knowing’ when they had a feeling, even a strong feeling, that a given item was true or false without re-experiencing the detail in question. In the experiment, we used the terms ‘Memory Type A' and ‘Memory Type B’ to avoid contamination by pre-experimental associations with the words ‘Remember’ and ‘Know’. To ensure that participants understood these instructions, they were asked to verbally justify their subjective ratings in a set of practice questions. Second, in contrast to old/new paradigms where subjective ratings are only gathered for “old” responses, Remember/Know/Guess responses were gathered for “false” as well as “true” responses, on the basis that false statements altered features of otherwise valid memoranda and thus would similarly require recollection of the true item feature in question.

In total, there were 276 true/false statements (141 true and 135 false; 137 detail and 139 sequence). They were split into 4 test forms with 69 statements each (see Appendix B for all items and description of from creation procedure). The forms contained similar numbers of true/false and detail/sequence statements, number of sequence statements at each lag level, and number of statements referring to each target item in the tour. They were also balanced according to overall accuracy and subjective ratings based on pilot data collected at a 1 day delay (see Appendix B). Each test form began with the same set of instructions.

Questionnaires and neuropsychological tests

Participants completed a battery of questionnaires, including the Survey of Autobiogrpahical Memory (SAM) (Palombo, Williams, Abdi, & Levine, 2012), a self-report measure of trait memory ability along four dimensions (episodic, spatial, future and semantic), the Object-Spatial and Verbal Imagery Questionnaire (OSIVQ), the Questionnaire upon Mental Imagery (QMI), and the Big Five Inventory personality test. They also completed a face-name associative memory test, during which participants are presented with pairs of faces and names, and then at test are presented with intact face-name pairs, recombined face-name pairs, and novel faces and names. They are instructed to respond ‘Yes’ if the face and name were presented together earlier, or ‘No’ if the face and name are new or were not paired together. Using the logic of process dissociation, this test yields scores of associative (p(‘Intact’ | Intact) – p(‘Intact’ | Recombined)) and item memory (p(‘Intact’ | Intact) – p(‘Intact’ | New)). Participants also completed a battery of online neuropsychological tests implemented in the Cambridge Brain Sciences platform. This battery included an object-location paired associates memory test, a grammatical reasoning test, a mental rotation test, and an odd-one-out test (https://www.cambridgebrainsciences.com/science/tasks). These data were collected as part of a multi-study data collection effort, and only questionnaires and tests of *a priori* interest were analyzed here. These were: the episodic and spatial dimensions of the SAM, the object and spatial components of the OSIVQ, face-name associative memory and object-location associative memory. Older adults also completed the Montreal Cognitive Assessment (MoCA) prior to the beginning of the experiment.

Procedure

Participants entered Baycrest such that the tour location was avoided. They were given instructions about the tour and were familiarized with the audio guide. They then completed the tour independently, with an experimenter unobtrusively following to ensure adherence to the protocol and to address potential technical issues. Following the tour, they returned to the testing room and completed the battery of questionnaires and neuropsychological tests. This phase was intentionally interposed between the tour and the first test to interrupt active rehearsal and specifically to reduce the effect of recency on spatiotemporal order judgements. Test 1 began after participants completed the intervening battery, rather than after a set period of time. Consequently, there was variability in the exact duration of this delay (M_{younger} = 47.53 minutes, SD = 8.30 minutes; M_{older} = 61.72 minutes, SD = 10.75 minutes). We refer to the first test delay as ‘1 hour’ for brevity. Participants were then given instructions about the memory tests including practice items, after which they completed the first test. Although the first test was completed in the laboratory, it was implemented online in Qualtrics like the following three tests which participants completed remotely. The order of forms across tests 1-4 was counter-balanced across participants using a Latin square design, creating four different form orders (ABDC, BCAD, CDBA, DCAB) to which participants were randomly assigned.

Participants had been made aware of the timing of the four tests in advance, and were scheduled based on their reported availability during those times. For each remote test (24 hours, 1 week and 4 weeks), they were sent a link to the appropriate form on the evening before each scheduled test day, along with their time window to complete the test. The window was from 2 hours before to 1 hour after the time at which their tour was completed, on the day of the test (e.g. test 2 = 22-25 hours after completion of the tour). Though this specific window was always communicated to participants, tests completed at delays within 15% of this target time were accepted. The spacing of the four delay periods (1 hour, 24 hours, 1 week and 4 weeks) was designed to reflect established estimates of the rate of forgetting, following an exponential or power function (Wixted, 2004).

Analysis

We used multilevel logistic regression analyses using the *glmer* software from the lme4 package (Bates et al., 2015) in R. This allowed us to predict accuracy (correct vs. incorrect) on a trial-wise basis from both delay (1 hr, 24 hrs, 1 wk, and 4 wks) and information type (detail vs. sequence). We modelled delay as a linear predictor. Significant negative linear trends were interpreted as reflecting an exponential-like forgetting rate given the spacing of the four delay periods. Post-hoc *t* tests were Bonferroni-corrected for multiple comparisons – we report Bonferroni-corrected p-values. For between-subjects comparisons, we used Welch's t-tests by default which are more robust to unequal variance across groups. We used Cohen's *d* to measure effect size, as implemented in the *effsize* package in R.

3.4 Results

Items and forms

We first conducted an item analysis, averaging item-wise accuracy over age groups and delays. Of the original pool of 276 items, three had average proportion accuracy scores lower than .4 and were removed: one was an erroneous duplicate, one concerned a tour feature (the location of a garbage bin) that was altered over the course of testing, and one was vaguely worded. Average accuracy for the remaining 273 items is displayed in Figure 3.3. A 2(information type: detail vs. sequence) X 2 (validity: true vs. false) ANOVA revealed neither an effect of information type (*F*(1, 269) = .32, *p* = .57) nor item validity (*F*(1, 269) = .42, *p* = .52), nor an interaction (*F*(1, 269) = .005, *p* = .95). Notably, there was greater inter-item variability for detail than for sequence, consistent with the fact that detail items concerned different types of idiosyncratic features (e.g. colours, orientations, locations, auditory information and actions) whereas sequence items were all ordinal judgements of the same form (i.e. You encountered *X* before *Y*).

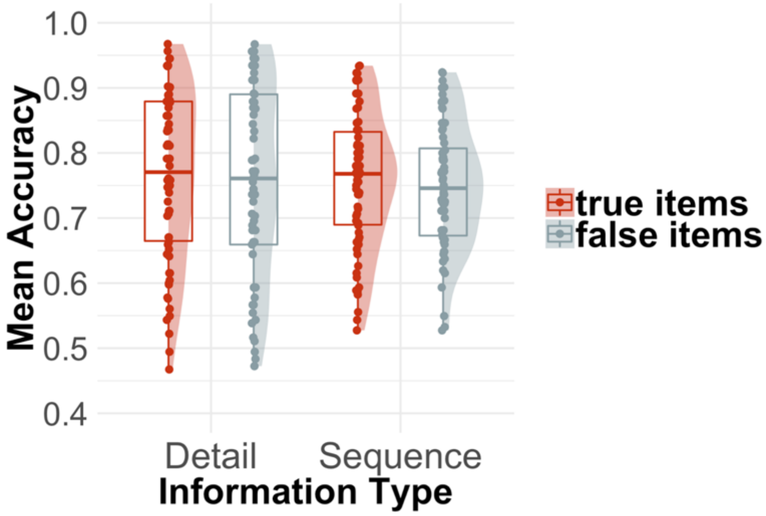


Figure 3.3. Proportion of accurate responses elicited by each true/false statement, split by detail and sequence statements. Boxplots, smoothed distributions (shaded regions), and individual items (dots) are presented.

Items were sorted into four test forms, the order of which was counter-balanced across participants. The test forms were balanced based on pilot data collected at a 24 hour delay. See Appendix B for more information about the pilot study and the creation of the four test forms. To investigate the possibility of form differences and potential interactions with delay in the final sample, we conducted a linear mixed effects model predicting participant-wise accuracy from form, delay and information type (detail vs. sequence). There was no effect of form (*F*(3,665.96) = 2.12, *p* = .097), indicating similar overall accuracy across forms (M_{FormA} = .77, *SD* = .12; M_{FormB} = .75, *SD* = .11; M_{FormC} = .76, *SD* = .11; M_{FormD} = .75, *SD* = .10). Moreover, form did not interact with delay (*F*(3, 669.37) = .72, *p* = .540) nor information type (*F*(3,622.02) = .95, *p* = .416), suggesting that the four forms behaved similarly across delays and produced similar patterns of detail and sequence memory performance overall. Nonetheless, we accounted for variance across forms in subsequent analyses by including a random intercept for form.

Younger adults: Transformation of detail versus sequence memory

To investigate how memory for details and sequence structure transformed over time, we conducted a multi-level logistic regression, modelling accuracy on trial-by-trial basis as a function of delay and information type, with random intercepts for subject and form (Fig. 3.4). There were main effects of delay ($\chi^2(1) = 61.09$, $p < .001$) and information type ($\chi^2(1) = 13.00$, $p < .001$). Concerning delay, overall performance was greater at 1 hour compared to 1 week ($t(52) = 3.43$, p = .007, $d = .47$) and 1 month ($t(52) = 6.97$, p < .001, $d = .95$), at 24 hours compared to 1 week ($t(52) = 4.76$, p = .007, $d = .65$) and 1 month ($t(52) = 7.45$, p < .001, $d = 1.02$), and at 1 week compared to 1 month ($t(52) = 3.28$, p = .011, $d = .45$; p-values Bonferroni-corrected for 6 comparisons) (see Fig. 3.4A). Concerning information type, averaging over all tests, sequence memory ($M = .79$, $SD = .13$) was better than detail memory ($M = .77$, $SD = .08$), though this difference was small ($t(52) = 2.49$, p = .016, $d = .34$). Critically, these effects were qualified by a crossover interaction between information type and delay ($\chi^2(1) = 46.81$, $p < .001$), whereby detail memory declined across tests and sequence memory did not. Detail memory significantly declined across all delays (p's: <.001 - .007, d's: .47 - 1.15) except 1 hour to 24 hours ($p = .225$, $d = .29$; Bonferroni-corrected for 6 comparisons), but sequence memory only declined from 24 hours to 4 weeks ($p = .016$, $d = .43$; Bonferroni-corrected for 6 comparisons), with no decline from the first to last tests ($p \sim 1$, $d = .03$). Consistent with the results from the item analysis above, at the subject level, true versus false trials did not change differently across tests for either detail ($\chi^2(1) = 1.70$, $p = .193$) or sequence items ($\chi^2(1) = .71$, $p = .399$). This means that the decline in detail memory over time was driven in equal part by misses (responding ‘false’ to a true item) and false alarms (responding ‘true’ to a false item).

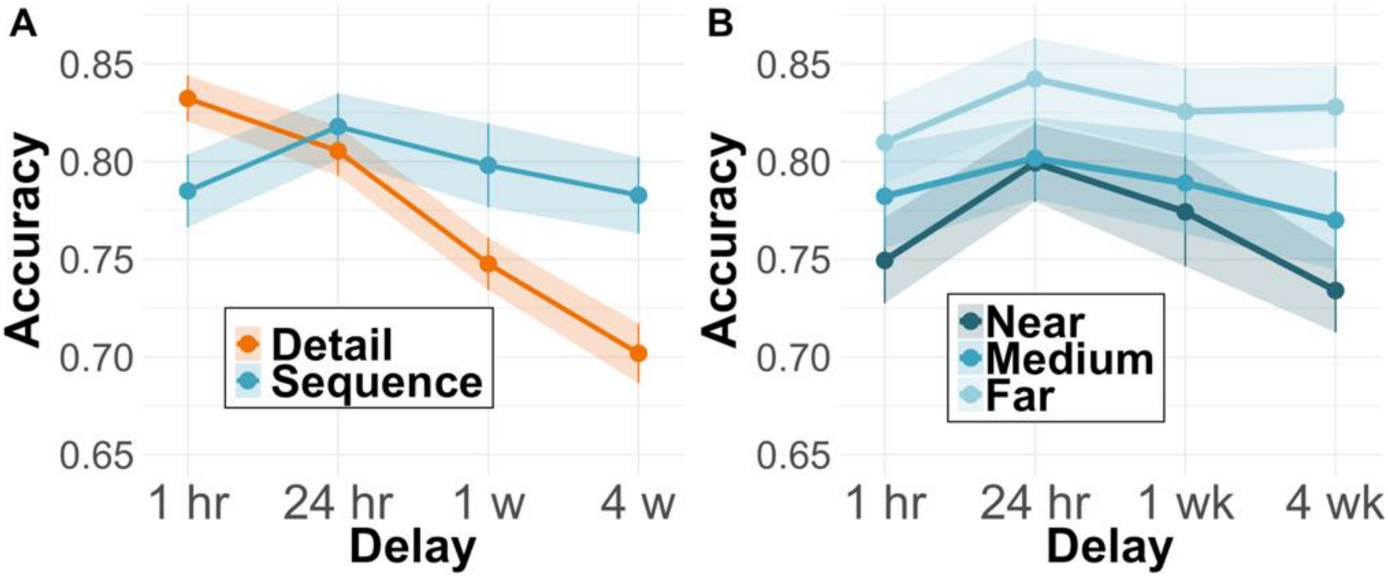


Figure 3.4. *A:* Detail versus sequence memory accuracy by delay. *B*: Sequence memory accuracy by inter-item lag in sequence items. Dots depict sample means, and shaded regions depict between-subjects standard error at each delay.

We considered that the contrasting forgetting curves for detail and sequence memory could be partly due to a difference in how these types of information were shaped by repeated testing, rather than by time per se. This is because sequence statements, though trial unique, involved pairwise recombinations of a common set of tour elements (e.g. "You encountered *A* before *B* and "You encountered *C* before *A)*, whereas detail statements each concerned a specific detail from the tour, though multiple details were tested about each target item (e.g. colour, size, etc.). Furthermore, it is possible that retrieving the order of elements with non-contiguous ordinal positions (e.g. *A* and *D*) involves recall of the intervening trajectory (i.e. *A*-*B*-*C*-*D*), benefiting sequence memory for those intervening temporal associations. Sequence statements may therefore have more inter-trial redundancy than detail statements. We reasoned that if this alone drove the difference in retention of detail and sequence memory, sequence memory should improve more than detail memory across trials within a test. To test this possibility, we ran a multi-level logistic regression predicting accuracy on each trial of the first test (1 hour) as a function of trial number and information type (detail vs. sequence), with random intercepts for subject and test item. Note that trial order was randomized for each participant, so test items appeared in different trial positions across subjects. There was a main effect of information type ($\chi^2(1) = 9.53$, $p = .002$), in that detail accuracy ($M = .83$, $SD = .09$) was higher than sequence accuracy on the first test (*M* = .78, *SD* = .14; *t*(52) = 3.33, *p* = .002, *d* = .35). However, there was neither an effect of trial number (χ^2(1) = .003, *p* = .954), nor an interaction between information type and trial number (χ^2(1) = 1.41, *p* = .234). Moreover, this model did not fit the data better than a null model excluding trial number as a predictor (with trial number: AIC = 3349.3; without trial number: AIC = 3346.7; χ^2(2) = 1.36, *p* = .507). Detail and sequence memory accuracy, therefore, did not change differently over the course of trials in the first test. Consequently, inter-trial redundancy in sequence trials alone cannot explain the difference between detail and sequence memory.

Younger adults: Lag effect on sequence memory

Previous studies have demonstrated an effect of inter-item lag on memory for spatiotemporal order (e.g. Diamond, Romero, Jeyakumar, & Levine, 2018). We binned lag into three levels (near, medium and far) to have a sufficient number of trials in each test form. We ran a multi-level logistic regression modelling accuracy on trial-by-trial basis as a function of delay and lag, with random intercepts for subject and form. There was a main effect of lag, (χ^2(2) = 33.48, *p* < .001), wherein far pairs elicited greater overall accuracy than both medium (*t*(52) = 3.69, *p* = .002 , *d* = .51) and near pairs (*t*(52) = 6.69, *p* < .001, *d* = .92), but near and medium pairs did not elicit different accuracy levels (*t*(52) = 2.03, *p* = .143 , *d* = .28; Bonferroni-corrected for 3 comparisons) (Fig. 3.4B). We considered the possibility that nearer pairs – tapping finer-grained spatiotemporal context representations – would decline more over time than coarser-grained far pairs. This was not the case – there was no interaction with delay (χ^2(2) =1.58, *p* = .454), suggesting that although finer-grained representations of spatiotemporal context are remembered worse overall, they are not forgotten faster than coarser-grained representations.

Younger adults: Transformation overnight

Given *a priori* interest in overnight memory transformation from the first to the second test, we next investigated data from these two tests alone. We repeated the above multi-level logistic regression modelling accuracy on trial-by-trial basis as a function of delay (1 hr and 24 hours only) and information type, with random intercepts for subject and form. Effects of delay (χ^2(1) = .08, *p* = .775) and information type (χ^2(1) = 3.70, *p* = .055) were not significant, though there was a trend towards the latter, with detail memory (*M* = .82, *SD* = .08) numerically exceeding sequence memory (*M* = .80, *SD* = .12) on average over the first two tests. Critically, there was a significant crossover interaction between delay and information type ($\chi^2(1) = 11.03$, $p < .001$): whereas detail memory trended towards a decline overnight ($M_{1hr} = .832$, $M_{24\text{hr}} = .805$; $t(52) = 2.13$, $p = .075$, $d = .29$), sequence memory significantly increased ($M_{1hr} = .785$, $M_{24\text{hr}} = .818$; $t(52) = 2.44$, $p = .037$, $d = .33$; Bonferroni-corrected for two comparisons) (Fig. 3.5A). Overnight change scores for detail and sequence accuracy were significantly different from each other ($M_{DetDiff} = -.027$; $M_{SeqDiff} = +.033$; $t(52) = 3.24$, $p = .002$, $d = .45$) (Fig. 3.5B). Although these effects were small, they were reliable: 37 participants (69.8% of younger sample) exhibited a decline in detail memory overnight, and 34 exhibited an above-baseline improvement in sequence memory (64.2% of younger sample). Overnight change in detail and sequence memory were not correlated across subjects ($r(51) = .002$, p = .986), suggesting that there was not a trade-off mechanism.

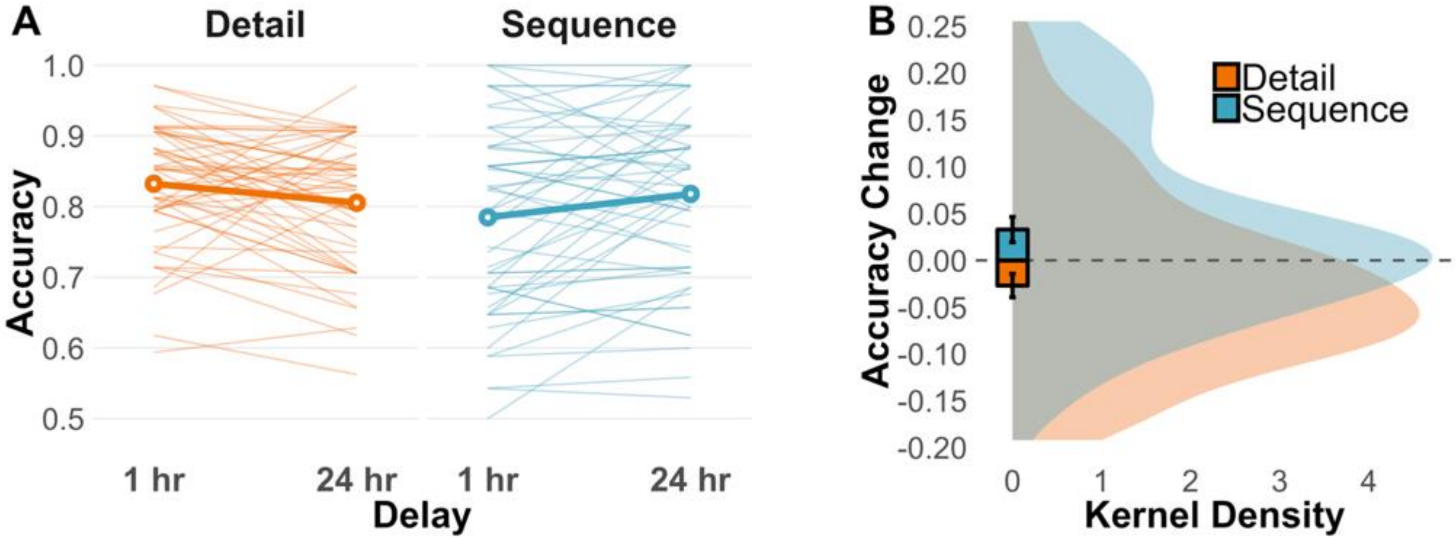


Figure 3.5. *A:* Detail and sequence memory accuracy at 1 hour and 24 hours. Circles and thick lines depict group-averaged performance and thin lines depict individual participants. *B*: Overnight change scores (24 hours – 1 hour) for detail and sequence memory accuracy. Coloured bars and error bars depict group-averaged change scores and between-subjects standard errors, and kernel density plot depicts the distribution of the detail versus sequence change scores.

Younger adults: Subjective memory by delay

Remember/Know/Guess (R/K/G) ratings for detail trials are presented in Figure 3.6, split by correct (left) and incorrect (right) responses. We modelled Remember vs. Know as a binary outcome, as a function of delay and accuracy, with random intercepts for subject and form. We left Guess ratings out of the model so that Remember and Know proportions could vary independently. There were main effects of accuracy ($\chi^2(1) = 201.52$, $p < .001$) and delay ($\chi^2(1) = 81.93$, $p < .001$) but no interaction ($\chi^2(1) = 1.80$, $p = .179$). Remember ratings were more prevalent on correct ($M = .63$, $SD = .15$) versus incorrect trials ($M = .31$, $SD = .22$; $t(52) = 15.28$, $p < .001$, $d = 2.09$), whereas Know ratings were more prevalent on incorrect ($M = .26$, $SD = .15$) versus correct trials ($M = .19$, $SD = .10$; $t(52) = 4.53$, $p < .001$, $d = .62$) (see Fig. 3.6). It is visually apparent that Guess ratings increased even more than Know ratings from accurate to inaccurate trials. Regarding delay, Remember ratings declined across tests. Declines were significant between 1 hour and 1 week ($p = .017$, $d = .43$), 1 hour and 1 month ($p < .001$, $d = .66$), 24 hours and 1 week ($p < .001$, $d = .71$), and 24 hours and 4 weeks ($p < .001$, $d = 1.0$; Bonferroni-corrected for 6 comparisons). Know ratings exhibited the opposite relationship with delay: they significantly rose from 1 hour to 1 week ($p = .034$, $d = .40$), 24 hours to 1 week ($p = .004$, $d = .50$), and 24 hours to 1 month ($p = .007$, $d = .47$; Bonferroni-corrected for 6 comparisons). The same overall pattern of decreasing Remember and increasing Know ratings with delay was observed within accurate trials only ($\chi^2(1) = 73.83$, $p < .001$) (see Fig. 3.6A), suggesting that even correct memory for event-specific details is accompanied by less frequent subjective re-experiencing with time.

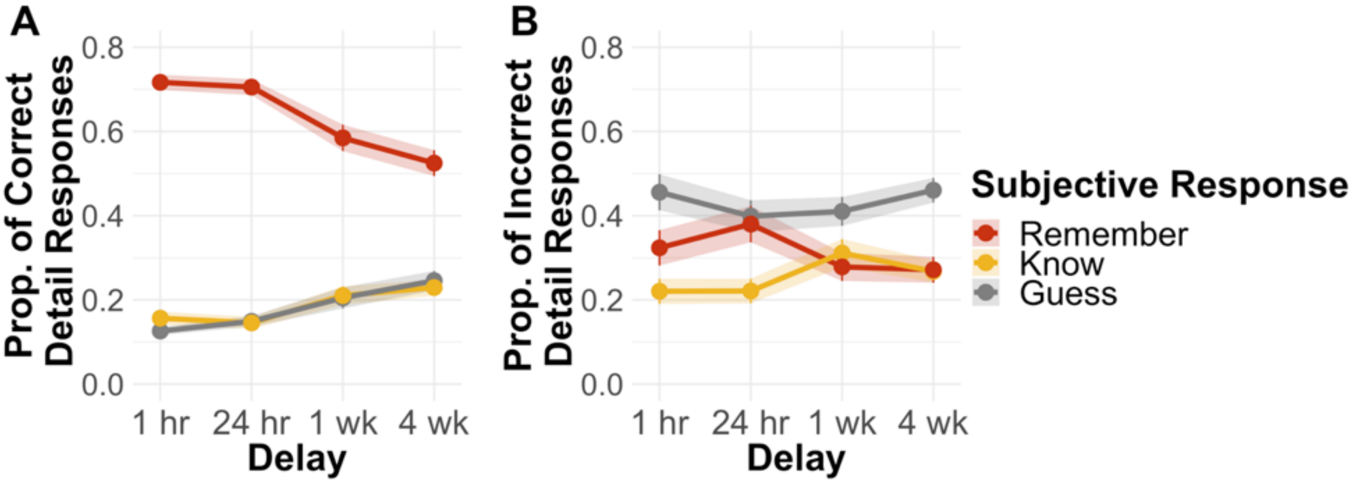


Figure 3.6. Subjective memory ratings (Remember / Know / Guess), as a proportion of correct (***A***) and incorrect (***B***) detail trials, by delay.

Younger adults: Relation to trait mnemonics and neuropsychological test performance

To facilitate interpretation of our novel measures of detail and sequence memory, in addition to Remember responses, we investigated their relationship to related measures of trait mnemonics and imagery (SAM episodic, SAM spatial, OSIVQ object and OSIVQ spatial), and to standardized neuropsychological tests of episodic memory (face-name associative memory and object-location associative memory). The item memory score extracted from the face-name memory test was not included because performance was at ceiling. Measures of detail accuracy, sequence accuracy, and subjective re-experiencing (Remember responses as a proportion of correct detail responses) were taken from the first test only. We reasoned that these scores had the most straightforward interpretation, given that scores on subsequent tests or the average of all tests would include the effects of delay and repeated testing. We predicted in particular that SAM episodic scores, measuring self-reported trait episodic memory ability, would be related to detail memory, and that SAM spatial scores, measuring self-reported trait allocentric navigation ability, would be related to sequence memory. One participant was missing questionnaire data due to administrative error, leaving 52 participants in these analyses.

We began with a data-driven approach, using a canonical correlation to analyze the relationship between our test variables (detail accuracy, sequence accuracy and re-experiencing) and questionnaire and neuropsychological data. Multivariate tests of dimensionality, as shown in Table 3.1, indicate that the first canonical dimension was statistically significant at the .05 level. The second dimension was marginally significant (p = .087), and we interpret it exploratorily. The third was not significant (p = .218). Table 3.2 shows the standardized canonical coefficients, which can interpreted similarly to standardized regression coefficients in a multiple regression, for the first two dimensions across both sets of variables. Dimension 1 was most strongly influenced by sequence accuracy (.97) among the test variables, and self-rated trait allocentric spatial memory (SAM spatial; .63) and objective associative memory performance (face-name = .47; object-location = .30)) among the questionnaire and neuropsychological variables. Dimension 2 was mostly strongly influenced by Remember responses (-1.03) among the test variables, and object imagery (OSIVQ object = -.67) and self-rated trait episodic memory ability (SAM episodic = -.55) among the questionnaire and neuropsychological variables. Figure 3.7A visualizes the canonical loadings, reflecting raw correlations between the original variables and the canonical variate of the test variable set, along Dimensions 1 and 2.

Table 3.1

Tests of canonical dimensions

Dimension	Canonical corr.	Wilk's Lambda	F	DF1	DF2	P
1	.67	.39	2.70	18	122.11	.0007
2	.46	.70	1.73	10	88.00	.087
3	.34	.88	1.50	4	45.00	.218

Table 3.2

Standardized canonical coefficients

Variables	Dimension	
Test variables	1	2
Detail accuracy	.13	.45
Sequence accuracy	.97	-.25
Remember responses	-.32	-1.03
Questionnaires & Neuropsychological Tests		
SAM episodic	-.30	-.55
SAM spatial	.63	.24
OSIVQ object	.03	-.67
OSIVQ spatial	.09	.12
Object-loc. assoc. memory	.30	-.43
Face-name assoc. memory	.47	.02

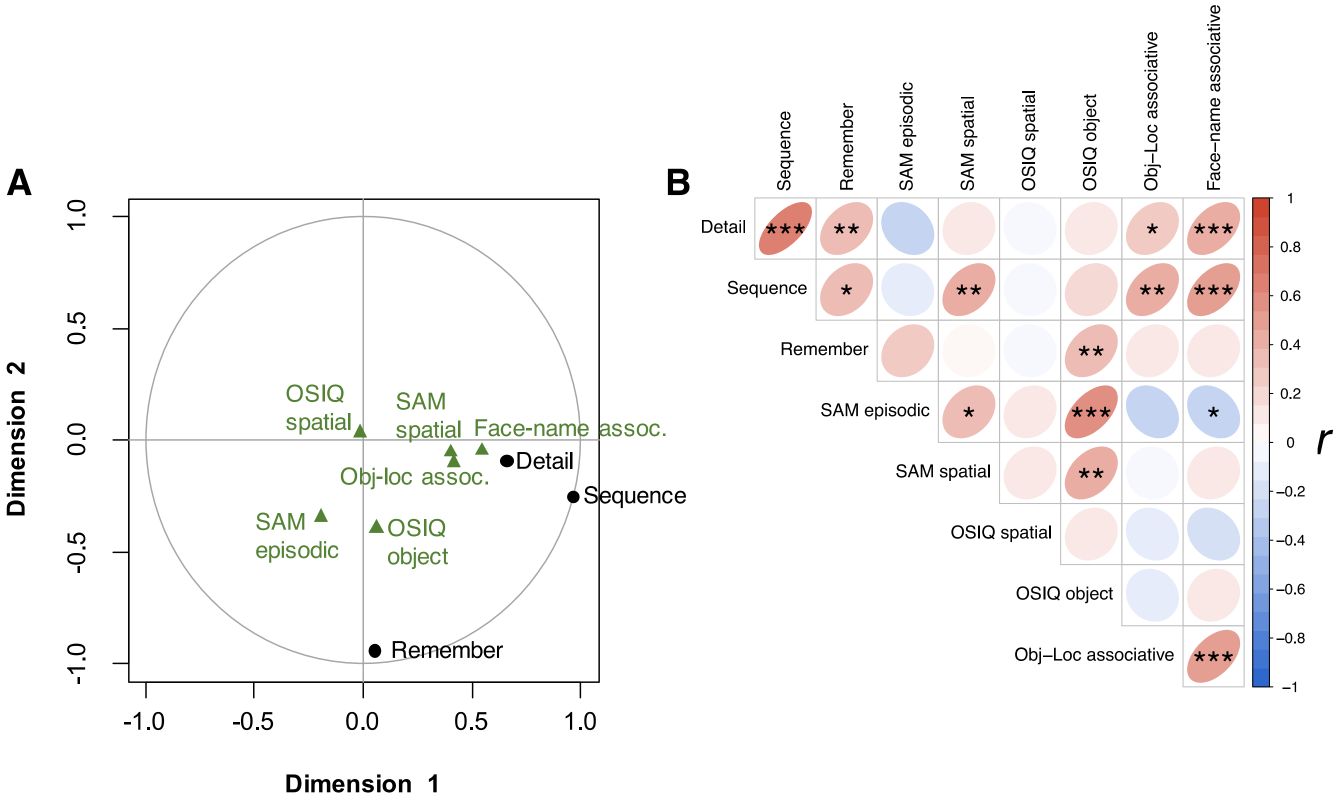


Figure 3.7. Relationships among detail accuracy, sequence accuracy, Remember responses, and questionnaire and neuropsychological variables. *A.* Canonical correlation relating test measures (detail accuracy, sequence accuracy, and Remember responses; test 1 only) and standardized trait and neuropsychological measures. Canonical loadings, representing the correlations between each set of raw variables and the canonical variate of the test variable set, are depicted for Dimensions 1 and 2. Test variables are black circles, and questionnaire and neuropsychological variables are green triangles. *B.* Correlation matrix depicting bivariate Pearson's correlations among all variables (**p < .05;* ***p* < .01; ****p* < .001).

Figure 3.7B displays bivariate Pearson correlations among all variables. As predicted sequence memory accuracy was positively associated with SAM spatial scores (*r*(50) = .40, *p* = .004), reflecting trait allocentric navigation ability. However, detail memory was not associated with SAM episodic scores, in fact trending towards a negative relationship (*r*(50) = -.24, *p* = .08). The strong positive association between detail and sequence memory is to be expected given that both kinds of trials shared an underlying demand on remembering the names of the target items.

Age effects on the transformation of detail versus sequence memory

To investigate how age affects the transformation of detail and sequence memory over time, we repeated the model above but included age as a factor (see Figure 3.8). Focusing on the model terms involving age, there was a main effect of age ($\chi^2(1) = 10.62$, $p = .001$) in that older adults performed worse than younger adults overall ($t(84.78) = 3.29$, $p = .001$, $d = .69$). There was also an interaction between age and information type ($\chi^2(1) = 47.76$, $p < .001$), in that older adults had significantly worse overall sequence memory ($t(82.20) = 3.97$, $p < .001$, $d = .84$) but not detail memory accuracy ($t(86.44) = 1.70$, $p = .09$, $d = .35$; Bonferroni-corrected for two comparisons) compared to younger adults. Parsed another way, whereas younger adults' sequence memory significantly though trivially exceeded their detail memory (see above), older adults' sequence memory was significantly worse than their detail memory, and by a notable margin ($t(37) = 4.10$, $p < .001$, $d = .66$). There was also a significant interaction between age and delay ($\chi^2(1) = 6.68$, $p = .009$): younger adults exhibited a trend towards a greater memory decline from the first to last test than older adults ($t(76.54) = 1.87$, $p = .065$, $d = .40$), though this is because younger adults' overall memory was initially higher ($t(85.15) = 3.72$, $p < .001$, $d = .77$). These effects were qualified by a three-way interaction between age, information type and delay ($\chi^2(1) = 5.52$, $p = .02$), suggesting that age effects on forgetting over time were different for detail versus sequence memory. We parsed this three-way interaction by investigating the interaction between age and delay within detail and sequence memory separately.

In detail memory, there was an interaction between age and delay ($\chi^2(1) = 10.88$, $p < .001$). Younger adults exhibited a steeper decline from first to last test than older adults ($t(80.75) = 3.34$, $p = .001$, $d = .71$) (Fig. 3.8, left). Accordingly, younger adults significantly out-performed older adults at the first test only ($t(84.58) = 2.90$, $p = .019$, $d = .61$; Bonferroni-corrected for 4 comparisons), and the effect of age shrank as a function of time ($d_{24hr} = .42$, $d_{1wk} = .25$, $d_{4wk} = .09$). In sequence memory, on the other hand, there was no interaction between age and delay ($\chi^2(1) = .08$, $p = .784$).

We considered whether the age-associated decline in accuracy was driven differently by responses to true versus false statements. There was an interaction between age and item validity (true vs. false) ($\chi^2(1) = 15.46$, $p < .001$), whereby aging was associated with poorer accuracy on false statements ($t(87.23) = 3.43$, $p = .002$, $d = .71$) but not true statements ($t(88.49) = 1.89$, $p =$

.125, *d* = .38; Bonferroni-corrected for 2 comparisons). There was no three-way interaction with information type ($\chi^2(1) = .16$, $p = .692$), suggesting that this pattern was similar for detail and sequence trials. Therefore, the negative effect of age on memory accuracy overall was driven by vulnerability to accept altered details and temporal relations as true.

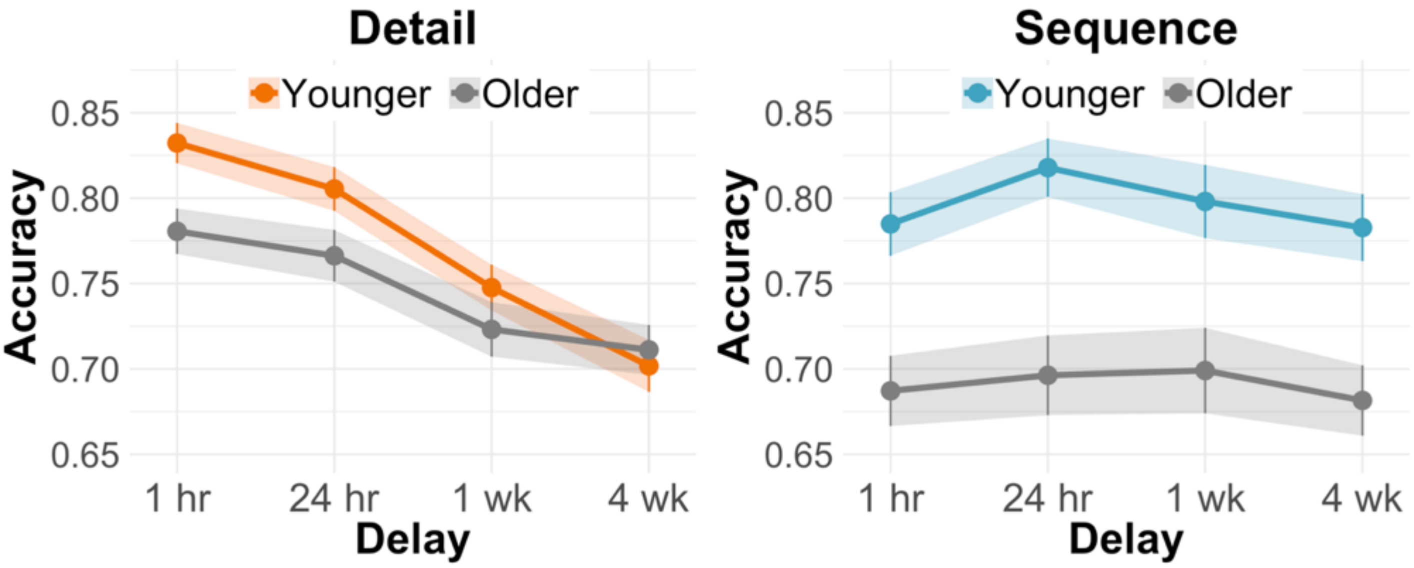


Figure 3.8. Detail versus sequence memory accuracy by age and delay. Younger participants' data are copied from Figure 3.4A for convenience.

Older adults, unlike younger adults, did not exhibit an interaction between delay and information type overnight (tests 1 and 2 only; $\chi^2(1) = 1.01$, $p = .314$). However, in separate models of detail and sequence memory including age as factor, interactions between age and delay were not significant (detail: $\chi^2(1) = .84$, $p = .360$; sequence: $\chi^2(1) = 2.14$, $p = .143$). Thus while older adults' did not exhibit different patterns of change in detail and sequence memory overnight, their overnight change in each memory type separately was not different from younger adults'.

Age effects on the effect of lag on sequence memory

As in younger adults, the effect of lag on sequence memory was significant in the older adult sample ($\chi^2(2) = 11.53$, $p = .003$), and there was no interaction between lag and delay ($\chi^2(2) = .37$, $p = .831$). Modelling the effect of age, there was no interaction between lag and age ($\chi^2(2) = 2.82$, $p = .244$), suggesting that younger and older adults' sequence memory was similarly modulated by spatiotemporal distance (Fig. 3.9).

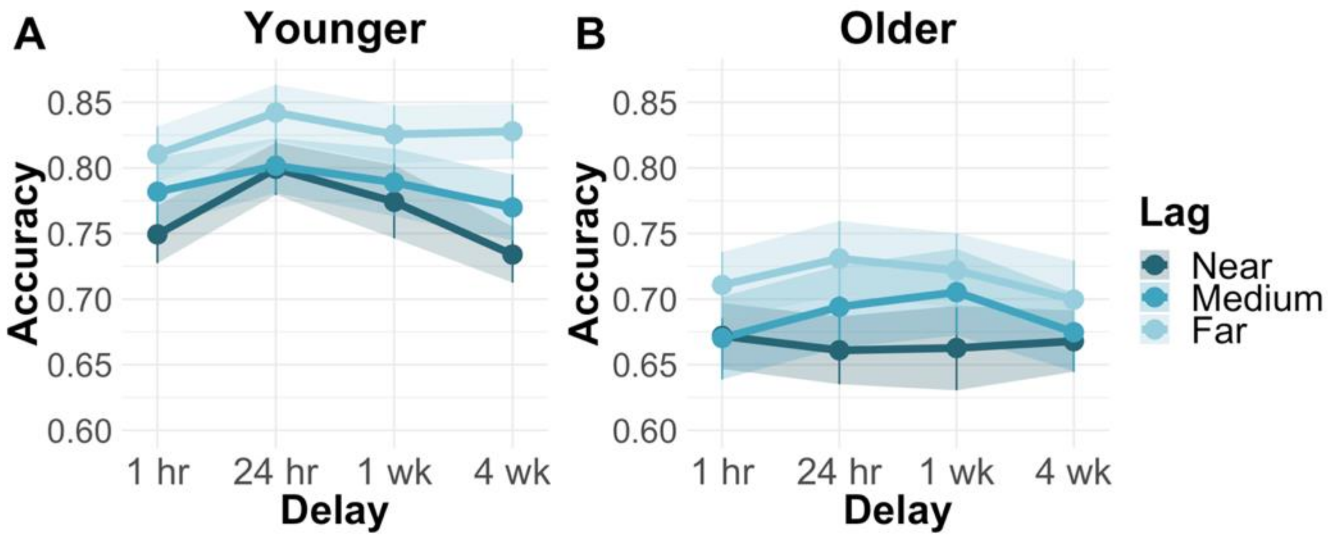


Figure 3.9. The effect of inter-item lag on sequence memory accuracy, split by age and delay. Younger participants' data are copied from Figure 3.4B for convenience, though the y-axis is extended downward to accommodate older adults' performance on near lag trials.

Age effects on subjective memory

Having already investigated the effects of age on accuracy, we investigated the effects of age on subjective memory ratings for accurate detail trials, again focusing on Remember and Know (see Figure 3.10). Including age as a factor in the model described above, there was no main effect of age ($\chi^2(1) = 1.49$, $p = .222$) nor was there an interaction between age and delay ($\chi^2(1) = .06$, $p = .546$). This suggests that younger and older adults self-report similar proportions of Remember and Know responses overall and exhibited similar changes in Remember and Know responses over time, in contrast to age differences in objective memory accuracy.

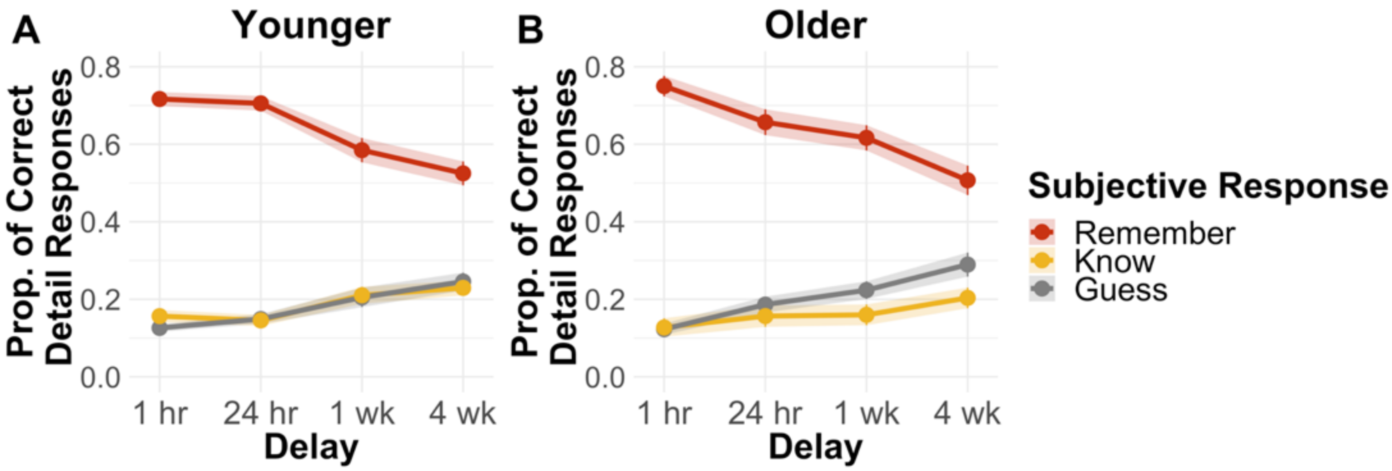


Figure 3.10. Subjective memory ratings (Remember / Know / Guess), as a proportion of correct (A, left) trials, split by age and delay. Younger participants' data are copied from Figure 3.6A for convenience.

We repeated the analyses of individual differences (canonical correlation and bivariate correlations) in the sample of older adults. No dimensions were significant in canonical correlation results. Bivariate correlations were similar overall, though were generally smaller with fewer reaching significance. Though, notably, the neuropsychological test of object-location associative memory correlated with sequence memory as in younger adults ($r(36) = .37$, $p = .02$).

3.5 Discussion

Using novel true/false tests probing memory for details and sequence structure of a one-shot real-world episode, we found that detail memory declined significantly within-subjects from 1 hour to 1 month, with self-reported recollection of details following a similar trend, whereas sequence memory exhibited no decline from the first test to the last. Moreover, we observed a crossover interaction overnight whereby sequence memory significantly improved above baseline whereas details were forgotten. Finally, while the effect of age on detail memory was subtle and time-dependent, aging was associated with a marked decrement in sequence memory at all delays. These results suggest that different components of extended real-world episodes are differentially vulnerable to decline with increasing time and age.

The dissociation between retention of detail and sequence information builds on decades-old findings that different elements of complex events are forgotten at different rates (Stanhope et al., 1993; Thorndyke, 1977). Critically, detail memory accuracy initially exceeded sequence memory accuracy before deteriorating. The difference in forgetting rates cannot, therefore, be attributed to differences in overall difficulty. Considering the spacing of our four timepoints, the rate of detail loss was initially rapid and decelerated with time, following classic forgetting curves observed in the laboratory (Ebbinghaus, 1913; Wixted, 2004). Similarly, accurate detail responses were decreasingly based on self-reported recollection of the encoding experience and increasingly on familiarity. Together, these results build on previous cross-species evidence that episodic memories tend to lose detail and vividness with time (Heyworth & Squire, 2019; Sekeres et al., 2016; Winocur & Moscovitch, 2011).

The time-related forgetting of details is qualified by the preservation of temporal structure in memory across tests, including an above-baseline improvement from one hour to 24 hours. Although sequence memory declined from its peak at 24 hours to the final test at 4 weeks, retention of sequence information was stable from the first test to the last, as was the effect of spatiotemporal distance on order judgements. Consistent with established findings (Moyer & Bayer, 1976; St. Jacques et al., 2008), the shortest-lag order judgements elicited the lowest accuracy, yet performance on these trials, too, was stable across tests. This suggests that sequence structure is not retained simply because it is relatively coarser or more gist-like dimension of episodic memory – even high-resolution representations of sequence structure, referring to local portions of the tour route, were retained over time. The surprising degree of stability in temporal order accuracy stands in contrast to other forms of temporal memory, such as absolute dates or the specific ordinal positions of events, which decline more rapidly (Barclay & Wellman, 1986; Burt et al., 1998; Linton, 1975). On the other hand, our findings are consistent with recent evidence that free recall of real-world events tends to lose detail but retain temporal structure over months and years (Heyworth & Squire, 2019). Though beyond the scope of the present study, these findings raise questions about the adaptive value of retaining fine-grained sequence structure in episodic memory, particularly for one-time experiences. One possibility is that remembered sequences are the building blocks of predictions and simulations of future events (Buckner, 2010; Lisman & Redish, 2009). Furthermore, memories are only useful for guiding decisions to the degree that they preserve the sequence of actions and events that led to rewards, and reward value is often only clear in retrospect (Braun et al., 2018).

The significant increase in sequence memory overnight is consistent with models of consolidation based on rodent electrophysiology suggesting that hippocampal replay during sleep supports memory for encoded spatiotemporal relations (O'Neill et al., 2010). It is thought that sleep preferentially consolidates interconnections across memories (Lewis & Durrant, 2011). Reliving a particular snapshot of experience (e.g. looking at a painting) involves associating or re-associating multiple features (Mitchell & Johnson, 2009), but the end product is a unified memory, often experienced as a coherent, static scene (Horner & Burgess, 2013; Maguire & Mullally, 2013; Rubin et al., 2019). The temporal structure of an episode, on the other hand, is never experienced in and of itself (Polyn & Cutler, 2017) but rather is inherently built up out of relations or interconnections across memories. The relative stability of temporal structure over time is consistent with evidence for time- and sleep-related consolidation of forms of latent structure that are built up over time or across trials, such as hierarchical and spatial relations (Coutanche, Gianessi, Chanales, Willison, & Thompson-Schill, 2013; Ellenbogen, Hu, Payne, Titone, & Walker, 2007). However, it is important to emphasize that any conclusions about sleep based on the present data are premature, as we neither measured nor manipulated sleep. Our lab is now testing the effects of sleep more directly.

The dissociation in forgetting of details and sequence structure is notable given the similarity in the way they were cued. All test trials were verbal true/false statements referring to specific artwork and items from the tour by name. Detail and sequence trials, therefore, shared an underlying item-name associative memory demand. Accordingly, detail and sequence memory accuracy loaded on a dimension with neuropsychological tests of associative memory. Subjective re-experiencing, on the other hand, loaded on an orthogonal dimension with measures of self-rated episodic memory ability and object imagery, highlighting a divide between objective and subjective measures of memory. As predicted, sequence memory accuracy was corelated with self-rated allocentric spatial memory ability as measured by the SAM spatial dimension (Palombo et al., 2012), raising the possibility that accurate order judgments benefit from one's ability to process map-like representations of the tour route in memory. While the online and unsupervised administration of three remote tests (24 hours, 1 week, and 4 weeks) limited experimental control, we have previously validated similar online testing procedures (Armson et al., 2017; Diamond et al., 2018).

It is important to consider the effects of repeated testing on performance on the three remote tests. Retrieval practice effects, whereby retrieving studied information facilitates long-term retention of it, are strong and reliable (Karpicke & Roediger, 2008). Every test trial was unique in the present experiment, but the effects of retrieval also spread to non-tested but episodically-linked information (Karpicke, Lehman, & Aue, 2014). Therefore, the observed forgetting curves very likely over-estimate retention at 24 hours, 1 week or 1 month. However, the key comparison was between detail and sequence trials, which were inter-mixed on each test. Even though every sequence memory trial involved a unique pair of target items, one might suspect that these trials would benefit more from repeated testing because accurate order memory for non-contiguous items can solved by associative inference if one remembers the order of intervening items (i.e. if I know that A came before B, and B before C, I can infer that A came before C). Similarly, evidence suggests that temporal order judgements reactivate intervening items (DuBrow & Davachi, 2014), and that re-exposure to portions of stimulus sequences improves later memory for other stimuli in the sequence that were not re-exposed (Smith, Hasinski, & Sederberg, 2013). We do not think that repeated testing affects interpretation of sequence versus detail retention for three reasons. First, if there was more retrieval-induced facilitation across sequence trials, this should be apparent across trials within one test. We found that this was not the case – neither detail nor sequence memory performance improved across trials. Second, reactivating or predicting untested sequence information requires memory for the sequence structure of the event, and is itself of interest in a test of sequence memory. Third, similar associative spreading or pattern completion should also occur for detail trials – for instance, a test probe about the colour of a painting likely influences a subsequent test probe about the orientation of the same painting (Horner & Burgess, 2013), and details of nearby items for that matter.

Aging was associated with a greater impairment in sequence memory than detail memory. This dissociation is consistent with an early meta-analysis by Spencer and Raz (1995), who categorized contextual information as either stimulus-bound (e.g. colour, shape, size, modality) or spatiotemporal. They found reliably larger age effects on memory for spatiotemporal context compared to stimulus-bound context which, they suggest, reflects the fact that spatiotemporal context can more easily become disengaged from the content itself. In the present study, older adults' memory for specific details far exceeded their memory for the order in which those details were encoded, suggesting age-related change in the organization, over and above the content, of memory. This pattern is similar to recent findings in patients with hippocampal damage (Dede et al., 2016), raising the possibility that these age effects are partly attributable to age-related degradation of the hippocampus (Leal & Yassa, 2015).

We considered that older adults might exhibit a relative decline in sequence memory overnight, given age-associated disorganization in hippocampal replay in rodents (Gerrard et al., 2008) and evidence for sleep-related associative memory impairments in humans (Mander et al., 2013). This was not the case: despite having much poorer sequence memory overall, aging was not associated with greater forgetting of sequence information overnight, nor at longer delays. This pattern is consistent with previous aging findings on forgetting in general (Fjell et al., 2005; Rubin & Wenzel, 1996) and temporal order memory in particular (Kausler & Wiley, 1990). Older adults did not exhibit the overnight increase in sequence memory observed in younger adults, though this interaction was not statistically significant. These results may suggest that the age-related decline in sequence memory manifests principally during encoding, perhaps as an impairment in linking incoming information to an extended temporal context representation, or a narrower bandwidth in that temporal context representation (Healey & Kahana, 2016; Howard et al., 2006). On the other hand, we cannot rule out the possibility that older adults rapidly lost sequence information in the hour between encoding and the first test, due to either decay or retroactive interference caused by the intervening neuropsychological battery.

Aging was also associated with a time-dependent decline in detail memory: the age gap was significant at the earliest delay and shrunk with time, disappearing by one month. In this sense, older adults forgot less than younger adults over time, though their memory was initially less detailed. It is well-established that older adults exhibit difficulty in coherently retrieving multiple features of a given even (Chalfonte & Johnson, 1996), and their autobiographical memories tend to be less detailed and more schematic (Levine et al., 2002). The present findings suggest that as memories shift from perceptually rich to more gist-based representations in all subjects, the age gap may shrink accordingly. Yet why was the age gap eliminated at more remote tests, when age-related declines in autobiographical memories are reliably observed in months- and years-old memories? The retrieval support conferred by the test cues may have benefited older adults disproportionately (Craik, 1986).

In contrast to time-dependent age effects on detail memory, there were no age differences in subjective recollection at any time point, in line with previous findings of subjective-objective episodic memory decoupling with age (Duarte, Henson, & Graham, 2008; Robin & Moscovitch, 2017; St. Jacques et al., 2015). It is important to keep in mind that ‘Remember’ responses were measured as a proportion of accurate detail responses, controlling for differences in accuracy across groups. The dissociation between age-related decline in detail accuracy and preservation in self-reported recollection, particularly at the earliest test, could reflect non-criterial recollection of features not probed by the true/false detail statements among older adults. A ‘Remember’ response may be based, for instance, on memory for specific thoughts and feelings, which tend to be more prevalent older adults’ event memories (Hashtroudi, Johnson, & Chrosniak, 1990). Alternatively, this pattern could reflect age-related alterations in metamemory or retrieval monitoring (Mitchell & Johnson, 2009; Wong, Cramer, & Gallo, 2012).

In conclusion, different components of episodic memory for an extended one-shot event were forgotten at different rates. Specific perceptual and event details declined rapidly, whereas memory for spatiotemporal relations remained stable from one hour to one month and increased significantly overnight, suggesting that consolidation confers greater benefit to spatiotemporal structure compared to idiosyncratic details. The age-associated reduction in episodic memory was not driven by faster forgetting, but rather by a subtle decline in memory for details at the earliest delays and a marked decline in memory for spatiotemporal relations at all delays.

Chapter 4
Temporal dynamics in autobiographical recall: Effects of aging and relation to episodic richness

4

4.1 Abstract

Verbal recall of past experiences is often richly detailed and temporally structured – we do not just retrieve slices of experience abstracted out of time, but rather extended events that unfold over the course of a narrative. There is a long tradition of research on temporal organization in recall of laboratory stimuli, but very little is known about temporal organization in recall of real-world experiences, where the focus is usually on memory detail. In the present study, we sought to bridge a gap between laboratory and autobiographical memory recall methods by probing memory for an immersive and dynamic, yet controlled, real-world event, allowing us to pair measures of temporal organization and detail richness derived from laboratory (word list) and autobiographical paradigms, respectively. 119 participants freely recalled such events: younger and older adults at a delays of 2 day, or younger adults at a delay of 1 week. Aging was associated with a loss of detail richness, extending established findings, as well as a loss of temporal context reinstatement, as indicated by reductions in the tendency to organize recall by the contiguity and order of items at encoding. Nonetheless, across age groups, measures of detail and temporal organization were positively correlated, suggesting a connection between the structure of an event in memory and the richness with which it is relived.

4.2 Introduction

> “Time is what keeps everything from happening at once.” - Ray Cummings, 1921

We often recall experiences from our past in the form of extended narratives, dwelling on certain details and then jumping in time and space to others. These memories are considered episodic to the degree that they are populated by event-specific details (e.g. perceptions, thoughts and feelings) and located in subjective time relative to other experiences (Tulving, 1972). Both of these memory components – detail and temporal organization – depend on the hippocampus (Long & Kahana, 2018; Sheldon & Levine, 2016), which exhibits functional decline in older age (Leal & Yassa, 2015; Rosenzweig & Barnes, 2003). Accordingly, episodic memories become both detail-impoverished and temporally disorganized in older relative to younger adults (Healey & Kahana, 2016; Levine et al., 2002). Yet these dimensions have for the most part been explored in separate literatures using incompatible methods. And despite the rich detail and temporal structure inherent in everyday real-world experiences, little is known about temporal structure in recall of real-world experiences, about how temporal structure is related to the resolution with which these experiences are recalled, and whether and how these two components come apart in older age.

Free recall dynamics reveal underlying structure in memory in the way that participants spontaneously transition from one item to another (Polyn et al., 2009). Decades of laboratory recall studies using word lists as stimuli reveal a tendency to structure recall according to the relative temporal proximity (the contiguity effect) and order of items at encoding (Kahana, 1996). These effects guided influential temporal context models of episodic memory (e.g. Howard & Kahana, 2002a; Lohnas et al., 2015; Polyn et al., 2009; Sederberg et al., 2008) suggesting that during encoding items become associated to a slowly drifting internal context representation – a recency-weighted history of mental activity. Later, recalling an item triggers a "jump back in time" to an earlier state of context, iteratively cueing items that were nearby and thus shared contextual overlap, with a forward bias. The canonical measurement of temporal organization is the lag-conditional response probability (lag-CRP) function (Kahana, 1996), the probability of transitioning from one item to another conditional on their distance (lag) and direction (before or after) at encoding. The canonical signature of temporal context reinstatement is a peak in the lag-CRP function at lags of +/- 1, dropping off with increasing lag, with higher recall probability in the forward direction (see Figure 1.2).

Among healthy younger adults, temporal contiguity and forward asymmetry are universal in word list recall studies (present in over 95% of participants; Healey & Kahana, 2014), and the magnitude of temporal clustering predicts overall recall quantity whereas semantic clustering does not (Sederberg et al., 2010). Older adults, however, show significantly weaker temporal organization (Kahana, Howard, Zaromb, & Wingfield, 2002), caused by a reduction in the degree to which items reinstate their surrounding temporal context (Howard, Kahana, & Wingfield, 2006; but see Healey & Kahana, 2016, for additional factors). Conversely, these studies found no such age differences in probability of first recall and serial position curves, reflecting where participants initiate their recall and which items tend to be recalled overall, respectively. Thus it is particularly when recall dynamics – how one moves through memory – are taken into account that age decrements are observed. This same overall pattern is observed in amnesia patients with medial temporal lobe damage (Palombo et al., 2018), suggesting it is a fundamental indicator of episodic memory failure. These findings parallel age-related declines observed in temporal context recognition tasks (Allen, Morris, Stark, Fortin, & Stark, 2015; Fabiani & Friedman, 1997; but see Chapter 2: Diamond, Romero, Jeyakumar, & Levine, 2018).

Discrete experimental stimuli (e.g. words), though, are unlike experiences from our lives outside the laboratory. For one, laboratory recall studies typically employ delays of seconds or minutes on the high end, whereas personal episodes are often recalled after days, weeks and decades. Nonetheless, there is also evidence for temporal organization in the network of autobiographical memories spanning our whole lives (Barsalou, 1988; Friedman, 2004). That is, forward chronology and temporal contiguity shape the order in which participants' freely recall separate events across their autobiographical timeline (Bruce & Van Pelt, 1989; Moreton & Ward, 2010), and time is superordinate to other dimensions along which people search for autobiographical memories (Barsalou, 1988; Linton, 1986). Although temporal proximity is confounded by semantic similarity in these studies (Hintzman, 2016), Uitvlugt and Healey (2018) found the canonical contiguity effect in participants' recall of public news events separated by months or years even when controlling for semantic similarity. Another potential confounding factor with such events is temporal schema (Friedman, 2004). That is, public events may be organized according to the calendar or to proximity to personal and public temporal landmarks such as birthdays and holidays rather than by temporal contextual relations between events per se.

Moreover, these studies treat events as discrete, countable units measured in binary fashion (i.e. remembered or not), analogous to word stimuli in laboratory studies. Yet naturalistic episodes are continuous and multidimensional, permitting many possible narrative descriptions varying in detail and specificity (Heusser, Fitzpatrick, & Manning, 2018; Koriat & Goldsmith, 1996). While macro-scale temporal organization across autobiographical events has been studied (e.g. Barsalou, 1988; Moreton & Ward, 2010; Nielson, Smith, Sreekumar, Dennis, & Sederberg, 2015), little is known about micro-scale temporal organization in recall of single extended real-world episodes, despite such units being the basic unit of episodic and autobiographical memory (Anderson & Conway, 1993; Ferbinteanu et al., 2006). Episodic memory is thought to co-opt neurophysiological mechanisms evolved for navigation through physical space (Buzsáki &

Moser, 2013), promoting “mental time travel” along “spatiotemporal trajectories” (Hasselmo, 2009; Tulving, 2002), but there is little empirical evidence that naturalistic human episodic memories unfold in this way. Relatedly, there is little evidence about how such spatiotemporal structure in autobiographical memories relates to memory detail and phenomenology.

As in word list learning paradigms, free recall is a dominant memory elicitation method in the autobiographical memory literature, in which participants routinely recall specific past experiences in rich multimodal detail. The Autobiographical Interview scoring method (Levine et al., 2002) decomposes recall narratives into their constituent units of information and classifying them as either internal (spatiotemporally specific to the episode being described) or external (referring to a different event, semantic information about the world or oneself, or metacognitive information). Aging and memory disorders are associated with a reduction in episodic or internal details (e.g. perceptual, emotional and contextual details) and a concomitant elevation in external details (Addis et al., 2008; Levine et al., 2002; Sheldon et al., 2018). Although recall of autobiographical episodes is self-evidently highly dynamic and structured, with events spanning dozens of minutes or hours and involving action and location-change, such information is opaque to the standard autobiographical memory assessment as the events are recalled retrospectively, and are therefore uncontrolled and unverifiable. That is, researchers cannot objectively map structure in recall back onto the structure of the original experience. Consequently, autobiographical memories are often measured as atemporal counts of different types of details, like “a jumbled box of snapshots” (Friedman, 1993, p. 44).

In one study of temporal organization within autobiographical episodes, free recall and forward recall instructions produced similar detail production rates, and higher rates than instructions to recall in reverse-order or by non-temporal dimensions like centrality (Anderson & Conway, 1993). Free recall and forward recall for a given event also produced similar output orders, suggesting that chronological time may be the principal dimension underlying organization of specific episodes. St-Laurent and colleagues (2011) measured temporal organization in autobiographical memories with experimenter-ratings of temporal resolution and coherence and by inferring order errors based on internal inconsistency (St-Laurent et al., 2011). Yet without control over encoding, one cannot objectively measure the degree to which the temporal structure of the encoding episode shapes subsequent recall.

Other studies have measured temporal order accuracy more objectively by comparing recall order to encoded order verified against prospectively collected diary records (Thaiss & Petrides, 2008) or controlled staged events (Dede et al., 2016; Heyworth & Squire, 2019). These studies, however, did not measure hallmark temporal proximity-related signatures of temporal context reinstatement. Dissociations of detail and temporal organization, including cases of preserved ordering but reduced episodic detail (St-Laurent et al., 2011) and the opposite (Dede et al., 2016) have been demonstrated in patients with medial temporal lobe damage. Yet, consistent with Tulving's original definition, recollection of specific episodic details and recovery of temporal context are presumed to be related, or even "reflections of the same neural phenomenon" (Howard & Eichenbaum, 2013). If this is the case, density or richness of episodic detail should be associated with spontaneous temporal organization. Yet, to our knowledge, there is no direct evidence for this prediction.

In the present studies, we developed methods for simultaneously measuring temporal dynamics and detail composition in single extended recall narratives, pairing methods from the word list and autobiographical memory literatures. We applied these methods to recall data that were previously collected for different purposes. In Study 1, we assessed free recall of a controlled real-world walking tour in younger and older adults after a two-day delay. In addition to standard measures of detail richness, comparison of the freely recalled sequence to the encoded event sequence enabled a fine-grained analysis of temporal organization, including effects of proximity and order, using established methods from the word-list learning literature. We hypothesized that previous findings of age-reduced internal detail density (Levine et al., 2002) and temporal organization (Howard et al., 2006) and in autobiographical and laboratory recall would be observed under the present staged event paradigm. In Study 2, we replicated findings of temporal contextual organization in a larger independent sample of younger adults recalling a different tour event at a one-week delay. Having derived hallmark measures of episodic detail and temporal context reinstatement from these staged events, we investigated the hypothesis that more detailed memories would exhibit greater temporal contextual organization.

4.3 Study 1: Methods

Participants

The younger group included 22 participants (M_{age} = 23.81 years, SD_{age} = 3.92, $M_{\text{education}}$ = 15.64 years, $SD_{\text{education}}$ = 1.09) and the older group included 22 participants (Mage = 69.00, SDage = 3.07, $M_{\text{education}}$ = 16.56, $SD_{\text{education}}$ = 3.73), one of whom was excluded for revisiting the tour area between encoding and recall sessions, two of whom were excluded for unusually poor neuropsychological test performance. An additional older participant was excluded from analyses due to insufficient recall quantity (see below). All participants were recruited via the Rotman Research Institute Participant Database at Baycrest Health Sciences Centre and from advertisements in the Toronto community, and were screened for history of neurological or psychiatric illness, active significant medical illness or substance abuse. Participants were fluent English speakers, had normal or corrected-to-normal vision and hearing, were not colour-blind and gave informed consent in accordance with institutional guidelines. Participants with prior exposure to the tour area were excluded.

Materials and Procedure

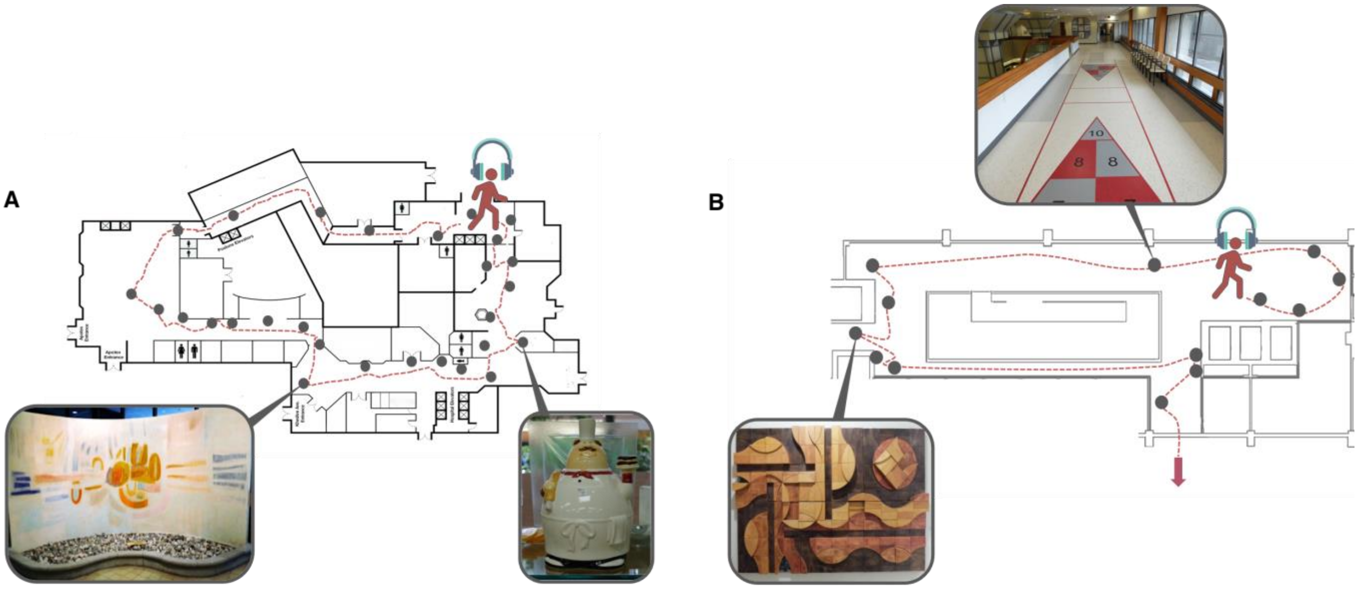
Both studies consisted of two phases: a controlled real-world encoding phase, and a retrieval phase during which participants freely recalled their tour experience. Prior to encoding, participants both completed a neuropsychological assessment battery, including the Rey Auditory Learning Verbal Test (RAVLT), Brief Visuospatial Memory Questionnaire (BVMT), face-name associative memory (Troyer et al., 2012), Symbol Digit Modalities Test (SDMT), verbal fluency (FAS), and the Shipley Vocabulary Test.

Encoding Phase

Participants underwent an audio-guided walking tour of artwork and assorted items on the first floor of Baycrest Hospital (Baycrest Tour 1.0; Figure 4.1A). The route formed a loop through several different sections of the building. Participants were instructed to approach different target items, but the overall route was unidirectional. Thus the physical structure of the tour route, along with the audio guide, controlled the sequence structure of the experience. Participants were instructed to examine different target items (e.g. paintings, portraits, and exhibits) and complete different tasks (e.g. locate a particular individual in a frame of portraits, or locate a particular item in the gift shop). In the middle of the tour, participants had a scripted interaction with a research confederate, during which the confederate asked a series of questions. Baycrest Tour 1.0

took an average of 23.0 minutes (SD = 3.0) for younger adults and 27.15 minutes (SD = 4.32) for older adults.

The audio guide was recorded and edited using Audacity (http://audacity.sourceforge.net/). It was narrated by four different speakers (two female and two male). Each section of the audio guide was broken down into multiple tracks, each associated with an item. Each track was initiated by the participant by pressing a button on the MP3 player. Upon arrival at target items, the guide instructed participants to examine them, followed by a silent period in the recording, and then directed participants to the next item. For some items, the guide provided information (e.g. about the artist) or cued participants' attention to certain features. Participants in both conditions were given extensive instructions before the tour began, and they were given an opportunity to practice using the MP3 player to control the audio guide. Specifically, participants were informed that they would be tested for their memory of the tour, and that they should pay close attention to the material contained in the audio guide. The experimenter unobtrusively observed participants to verify that they followed the instructions.



C

Internal– event 4

"…I stood in front of the I guess it's called the Heritage Museum. I remember

Internal – thought

wanting to go in because there was something that looked interesting. It was one

Internal – perceptual Internal – event

of those mutli-coloured and shiny things behind the glass but I didn't go in.

Internal – event 6 Internal – place 7 Internal – place 8

Walked passed the piano, passed the marketplace. I went into the gift store and

Internal – event

I was instructed to look for the fat ceramic chef and to pay attention to it…I

Internal – event 9 External – semantic

walked across, looked at Andy Warhol portraits. I like Andy Warhol a lot…"

Figure 4.1. *A and B.* Maps of the two tour events with photographs of example items. Grey circles indicate approximate locations of main items. *A:* Baycrest Tour 1.0 was experienced by the younger and older participants. There were 27 universal items with defined ordinal positions. Participants were instructed, for example, to find the chef cookie jar in the gift shop (8th item; right photograph) and examine a large curved painting called 'Let There be Light' (15th item; left photograph). *B:* Baycrest Tour 2.0 was experienced by the Study 2 participants. It was split into two sections; only section 1 is depicted here. Participants were instructed, for example, to stand in the red number 8 in the shuffleboard game (5th item), and to examine a wall-mounted wood sculpture (8th item). *C*. Example recall narrative for Baycrest Tour 1.0. In this segment, the participant recalls 9 internal details and 1 external detail. Their recall vector is [4,6,7,8,9]. Note that they skipped the 5th item in the tour.

Retrieval Phase

Participants returned to the lab after 2 days. They were asked to freely recall their experience of the tour (instruction: “Tell me everything you can remember about the tour”). They completed a true/false memory test consisting of 40 true and 40 false statements about details from the tour (e.g., “The piano was black”) before performing free recall. False statements were created by altering the details of true statements. This true/false memory test was conducted for the purposes of another study. In Study 2, we report recall data from participants who performed free recall for a different tour with no intervening true/false test. Participants in Study 1 were also asked to recall a time-matched personal event, with the order of recall (tour versus personal) counter-balanced across participants. Data from the time-matched personal events are not included in this report. They received the standard Autobiographical Interview administration, including a General probe (“Is there anything else you can tell me about this event”) following free recall for participants with limited output during Free Recall, as well as a subsequent Specific Probe for particular kinds of details. Given that our present interest is in spontaneous memory organization, only data from free recall and general probe are analyzed here. All participants’ recall sessions were audio recorded and transcribed.

Analysis

To measure memory detail, we used the AI scoring method. Transcribed recall narratives are broken down into discrete informational units/clauses, and categorized as either internal or external. Internal details are episodic and specific in space and time to the event in question. External details are not specific to the event in question – they may be semantic details (describing general features of oneself or the world that are not specific in space and time), repetitions, metacognitive statements (e.g. “I’m not sure”), or episodic details about different events. Internal details are further categorized as event, place, time, perceptual, or emotion/thought. Memories were scored by N.D. and research assistants, all of whom were trained on the method and achieved intraclass correlation coefficients of .90 or higher for the internal and external detail composite scores. Each scorer completed 20 transcripts from a reliability set, and ICCs were computed with reference to trained scorers’ data. The ratio of internal-to-total details measures the proportion of all details in a memory that refer to specific episodic information, unbiased by group differences in event content and individual differences in verbosity.

We augmented the AI scoring method to investigate temporal organization. In recall of word lists or other standard laboratory stimuli, the items are discrete and occupy clearly defined serial positions (i.e. first, second, third, …). In recall of naturalistic episodes, particularly real-life experiences, perceptual experience is continuous rather than discrete, and the ‘stimuli’ include any attended feature of experience. We defined items as the elements of each tour to which the audio guide explicitly cued participants’ attention, ensuring that they were encoded by all participants in the first place, and in a specified order. These time-tagged items have clearly-defined and homogenous ordinal positions. There were 27 such items in Baycrest Tour 1.0. We coded participants’ first mention of any of these items with its ordinal position. Because a given naturalistic event can be described in myriad ways, ‘mentioning’ was defined as any reference to an item that would be unambiguous to a listener who was familiar with the tour. Thus for each memory, we derived a vector of time-tags, or ordinal positions, representing the items that person recalled and the order in which they were recalled.

To measure temporal organization, we submitted the recall vectors to analysis of lag-conditional response probability (lag-CRP; Kahana, 1996), which is the canonical measure of temporal context reinstatement in recall. Lag-CRP measures the probability of transitioning from a recalled item i to the next-recalled item $i + 1$ as a function of their distance (lag) and order at encoding (described in greater detail in Results). We also derived overall measures of temporal clustering (tendency to successively recall temporal nearby items; Polyn et al., 2009) and forward asymmetry (tendency to make forward transitions) in recall. We measured lag-CRP and temporal clustering using publicly available MATLAB scripts from the Behavioural Toolbox v1.01 from the Computational Memory Lab (http://memory.psych.upenn.edu/Software).

To derive stable measures of temporal organization, we decided a priori to exclude recall trials with fewer than 5 time-tagged items (i.e. 4 transitions). This resulted in the exclusion of one older adult, leaving 18 older adults in the final sample.

4.4 Study 1: Results

Neuropsychological test performance

Younger and older participants' neuropsychological test performance is reported in Table 4.1. As expected, older adults performed worse than younger adults on all tests of memory and executive functioning, but not verbal fluency (FAS), in which there was no age difference, nor vocabulary (Shipley Vocabulary Test), in which older adults out-performed younger adults.

Table 4.1

Neuropsychological test performance in younger and older groups

Test	Younger Mean (SD)	Older Mean (SD)	Uncorrected P-value	Cohen's d
RAVLT: learning trials 1-5	59.27 (7.12)	53.47 (7.40)	.015	.80
RAVLT: delayed recall	12.86 (2.01)	11.47 (2.04)	.034	.69
RAVLT: recognition hits-FA	14.04 (1.13)	12.42 (2.69)	.022	.81
BVMT: total learning	26.68 (4.08)	19.37 (7.99)	.001	1.18
BVMT: delayed recall	10.59 (1.47)	7.05 (3.03)	< .001	1.52
Face-name associative memory	.83 (.16)	.66 (.25)	.022	.81
SDMT: delayed recall[a]	7.32 (2.36)	3.78 (2.34)	< .001	1.51
SDMT: Total correct	60.45 (8.24)	45.42 (10.99)	< .001	1.63
Trails: B – A (s)	28.32 (7.45)	36.58 (18.09)	.076	-.61
FAS: total correct	43.50 (12.63)	42.79 (10.46)	.84	.06
Shipley: total correct	29.52 (4.49)	35.84 (3.37)	< .001	-1.58

[a] At the end of the neuropsychological test session, participants were presented with each of the symbols and had to recall the corresponding digit.

Details

Table 4.2 presents an overview of summary statistics and age effects on detail and temporal organization. Differences between age groups were assessed with Welch's t-tests.

Table 4.2

Measures of detail and temporal context reinstatement (* = significant age-related reduction).

Measure	**Younger Mean [SD]**	**Older Mean [SD]**
Detail measures		
Internal detail count	92.45 [9.54]	72.44 [11.85]
External detail count	14.27 [3.56]	23.72 [4.61]
Internal/total detail proportion	.87 [.06]	.74 [.15] *
Temporal context measures		
Temporal clustering	.87 [.10]	.75 [.17] *
Forward asymmetry	84 [.12]	.72 [.16] *
Explicit sequence errors (/transitions)	.04 [.06]	.06 [.08]

The balance of internal and external details, measured as the internal-to-total detail ratio, is commonly used to measure the episodic detail richness of autobiographical memories. It reliably differentiates younger from older adults and healthy from episodic memory-impaired populations (e.g. Barnabe, Whitehead, Pilon, Arsenault-Lapierre, & Chertkow, 2012; Davidson et al., 2008; Kurczek et al., 2015; Levine et al., 2002; Meulenbroek et al., 2010), while controlling for individual differences in verbosity. Younger adults had considerably higher internal detail proportions than older adults ($t(22.03) = 3.05$, $p < .001$, $d = 1.35$), replicating the established negative effect of age on episodic detail richness (see Figure 4.2B).

We also replicated the interaction between age and detail type on raw detail counts ($F(1,38) = 17.29$, $p < .001$) reported previously (Addis et al., 2008; Levine et al., 2002) (see Figure 4.2A), with older adults reporting fewer internal details and more external details than younger adults, though neither of these differences were significant when correcting for multiple comparisons (internal: *t*(26.90) = 1.88, *p* = .141, *d* = .60; external: *t*(37.93) = 2.18, *p* = .072, *d* = .69; p-values Bonferroni-corrected for two comparisons). Analyses were performed on log-transformed internal and external detail counts to correct for significant positive skewness.

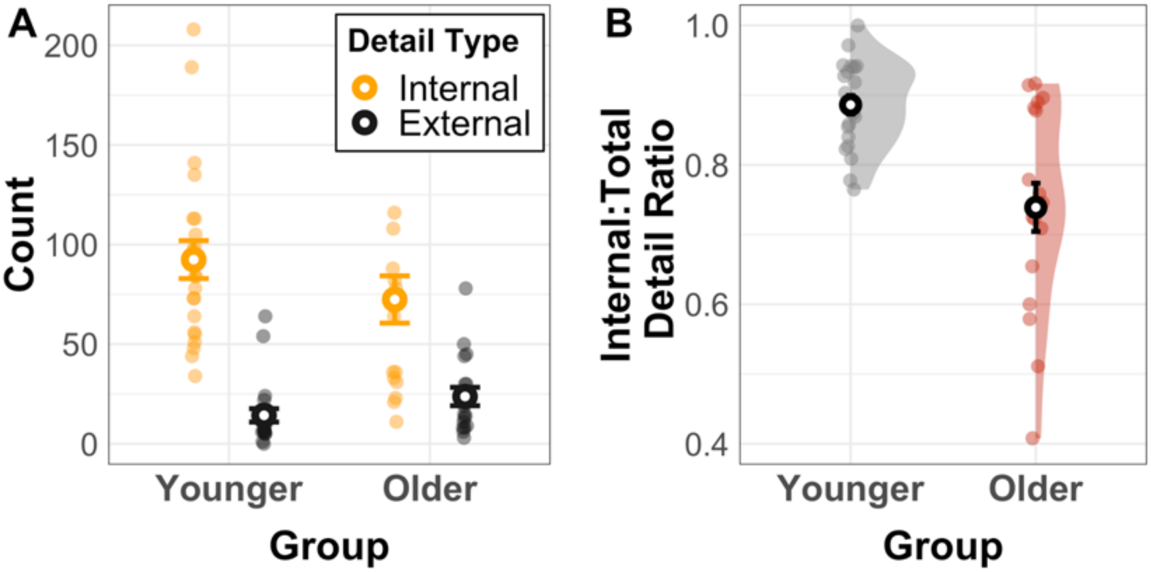


Figure 4.2. ***A.*** Raw internal and external detail counts across groups. ***B.*** Episodic detail richness, measured as internal detail proportion. Black dots with white fill depict group means. Coloured dots depict individual subjects, and are slightly horizontally jittered to reveal overlap. Error bars depict standard errors. Shaded regions in B depict the smoothed distribution of each group along the y-axis.

Temporal organization

We measured conditional response probability as a function of lag (lag-CRP), which measures the probability of transitioning from an item i to the next-recalled item i + 1 as a function of their distance (lag) and order at encoding. For instance, a lag of +1 represents a forward transition from a given item to the item that occurred next during the tour, whereas a lag +2 represents a forward transition that skipped an intervening item (e.g. from the 5th encoded item to the 7th encoded item). Negative lags indicate transitions made in the backwards direction, opposite the encoded order. The CRP value is calculated as, for each lag, the number of transitions made divided by the number of transitions that were available. Repetitions are excluded and thus unavailable. For each participant, values of zero for a given lag indicate that the participant had an opportunity to make that transition but did not. Lags that were never possible are NA, rather than 0. For example, if a participant recalls every encoded item in perfect order, beginning at the first item, there was never an opportunity to make a transition in the backwards direction, and all negative lags would be NA for that participant. The analysis therefore considers at every transition which items have already been recalled. This accounts for individual differences in the overall number of items recalled, and differences in the number of items in each event.

Figure 4.3 presents the average lag-CRP curves for younger and older groups. Both groups exhibit the two typical features of the lag-CRP curve: (1) the contiguity effect, whereby transition probability peaks for neighbouring items and declines as a function of distance in both directions, and (2) forward asymmetry, whereby forward transitions were more common than backwards transitions.

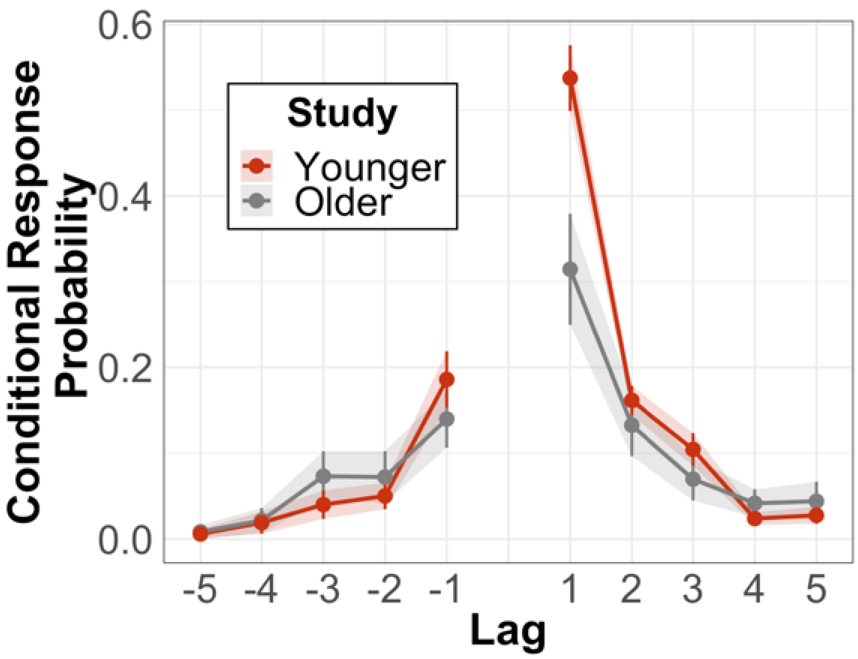


Figure 4.3. Lag-conditional response probabilities split by group. Error bars are bootstrap-derived standard errors (1000 resamples).

Age differences in the lag-CRP curves are visually apparent, particularly at Lag +1. To test the effect of age, we ran participant-wise linear regressions predicting CRP from lag. We did this separately for positive (1 to 6) and negative (-1 to -6) lags (Kahana et al., 2002; Sadeh, Moran, et al., 2014). This measure produced a coefficient for each participant, in each direction, representing the steepness of their CRP curve (the change in recall probability as a function of increasing lag). Participants with no above-zero CRP values in either direction were excluded from analysis of that direction. In the positive direction, 2 older participants were excluded and in the negative direction, 3 younger and 4 older participants were excluded. Group differences in coefficients were compared with t-tests. For positive lags, younger adults (*M* = -.12, *SD* = .04) had steeper curves than older adults (*M* = -.07, *SD* = .07; *t*(25.58) = 2.57, *p* = .016, *d* = .88). There was no age difference in the negative direction (younger: *M* = -.040, *SD* = -.032; older: *M* = -.033, *SD* = .025; *t*(30.80) = .71, *p* = .483, *d* = .24). We note that previous studies took a similar approach to analyzing differences in lag-CRP curves, though they fit power functions to the curves rather than linear models (Kahana et al., 2002; Sadeh, Moran, et al., 2014). We opted for a more theoretically neutral linear model, given the novelty of our encoding conditions and encoding-recall delay.

We next derived overall temporal clustering and forward asymmetry scores for each participant. The temporal factor (Polyn et al., 2009) calculates, for each transition, the proportion of possible transition distances that are greater than the observed transition distance. Averaging over all transitions in a memory, it outputs a single proportion score representing the tendency to successively recall items that were nearer in space and time. A score of 1 indicates that the participant always made the shortest transition available, and a score of 0.5 indicates chance-level temporal clustering. Consistent with the peaked lag-CRP curves, both groups exhibited greater-than-chance temporal clustering (p’s < .001), but there was a group difference in the degree of temporal clustering (Fig. 4.4A). Younger adults clustered more than older adults *t*(26.85) = 2.62, *p* = .014, *d* = .87), indicating a large negative effect of age on temporal context reinstatement.

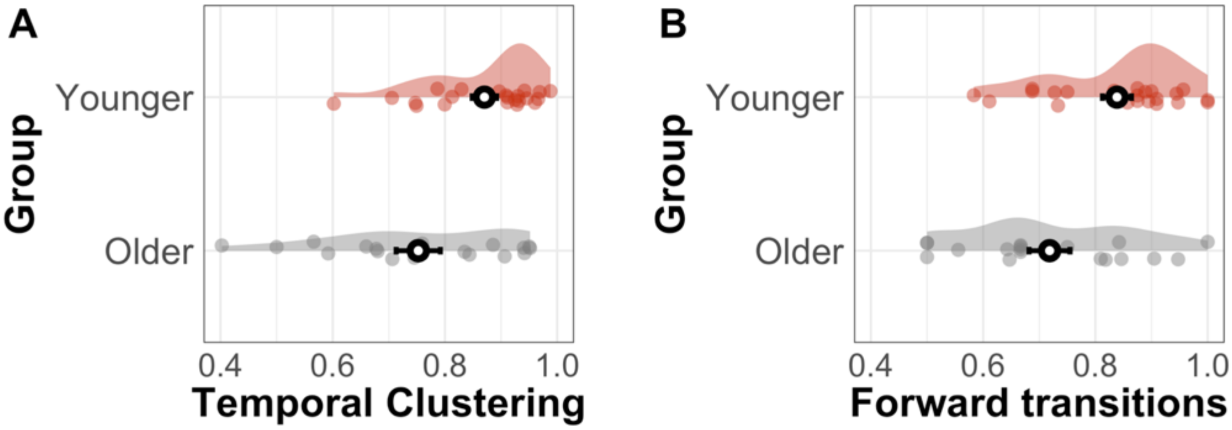


Figure 4.4. ***A.*** Temporal clustering. A score of .5 indicates chance-level temporal clustering, and a score of 1 indicates that every recall made transition was the shortest available one. ***B.*** Forward asymmetry, measured as the proportion of all transitions that moved forward in time with respect to the encoded order. A score of .5 indicates recall transitions were made in backward and forward directions with equal probability, and a score of 1 indicates that only forward transitions were made.

Forward asymmetry was calculated as the proportion of all transitions that moved forward in time with respect to the encoded order, excluding repetitions. Younger and older adults both exhibited greater-than-chance forward asymmetry (*p*'s < .001), but groups differed here, too (Fig. 4.4B). Younger adults exhibited significantly higher forward asymmetry than older adults (*t*(31.76) = 2.69, *p* = .011, *d* = .87), indicating that age was associated with a large reduction in the tendency to recall in chronological order.

We supplemented the analysis of forward asymmetry, which measures spontaneous recovery of the encoded temporal order, with analysis of explicit sequence errors, which were defined as any explicit reference to temporal order (e.g. using clauses such as "and then", "after", "before", etc.) that were verifiably incorrect. These were rare (younger: *M* = .73, *SD* = 1.12; older: *M* = .94, *SD* = 1.51). In contrast to the deleterious effect of age on spontaneous forward asymmetry, there was no difference between age groups in explicit sequence errors (Mann-Whitney U test: U = 191, *p* = .838, *d* = .17). To account for the fact that younger adults recalled more time-tagged items overall, and thus had more opportunities to make explicit sequence errors, we repeated this analysis with each participants' number of sequence errors adjusted for the number of transitions they made. There were no group differences on this measure either (U = 186, *p* = .791, *d* = .17).

Serial position effects

We have focused on group differences in the contextual dynamics of recall, as evidenced by the lag-CRP curves, temporal clustering and forward asymmetry. The observed age effects, however, could be linked to features of recall aside from its dynamics – for instance, which items are recalled, and from which ordinal position one initiates recall. Figure 4.5A shows serial position curves for each age group (Fig. 8). Consistent with established findings, younger and older adults exhibit similar primacy and recency effects (Healey & Kahana, 2016; Howard et al., 2006), with older adults recalling fewer items overall. We note that the shape of these serial position curves should be interpreted cautiously, as unlike laboratory stimuli, the items comprising the tour were not matched in their perceptual features, nor visual or environmental saliency, nor were they equidistant from each other. However, given that younger and older adults were exposed to the same event, the similarity in their serial position curves is noteworthy.

Figure 4.5B shows the proportion of participants in each group who began recall at each serial position (probability of first recall (PFR) curves**)**. Consistent with established findings, younger and older adults PFR curves are nearly identical (Healey & Kahana, 2016; Howard et al., 2006). Nearly all participants exhibit a strong primacy effect**,** initiating recall at the first or second tour item.

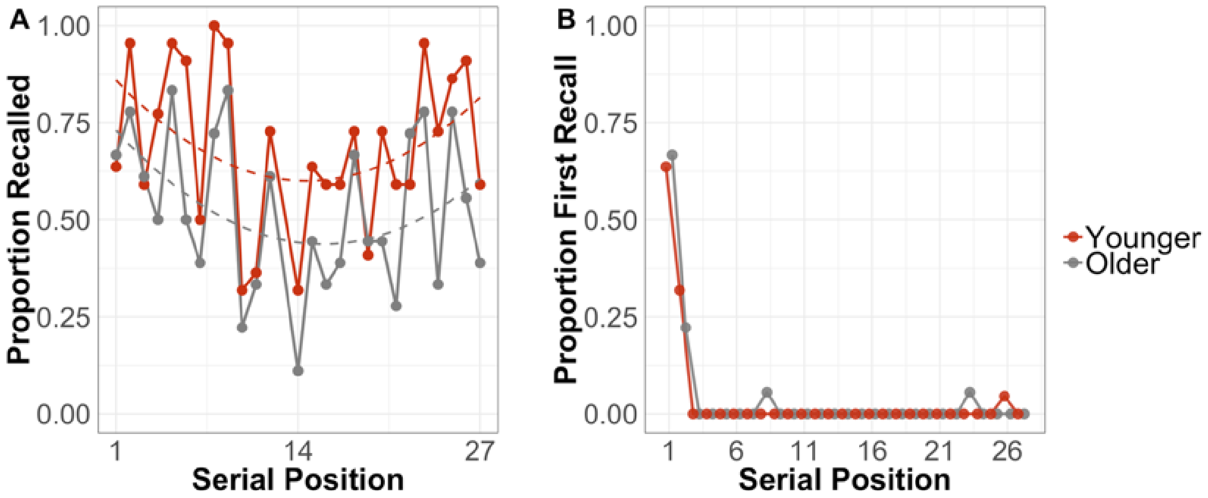


Figure 4.5. ***A.*** Serial position curves. Dots depict group averages. Dashed line depicts the quadratic fit for each group. ***B.*** Proportion of participants initiating recall at each serial position. Dots are slightly horizontally offset for each group to reveal overlap.

4.5 Study 1: Interim summary

Study 1 demonstrated that in addition to the established age-related reduction in episodic detail richness in naturalistic recall, older adults also exhibit more temporally disorganized recall. Specifically, older adults' recall transitions ‘jump’ larger spatiotemporal distances than younger adults’, and they are less likely to retrace the episode in the order in which it was encoded. This age-related decline is specific to measures of spontaneous temporal organization – older adults did not make more explicit sequence errors, nor did they differ in which items they recalled nor where they imitated recall.

As mentioned above, younger and older participants completed the same true/false memory test of tour details prior to recalling the tour event. This test may have contaminated recall and altered the temporal dynamics measures, particularly because true/false test items were presented in random order without regard to the order in which items were encoded. One might suspect that older adults would be more susceptible to retroactive interference effects of the true/false test on memory for the tour. On the other hand, older adults have been shown to be less susceptible to both the enhancing and distorting effects of memory reactivation (St. Jacques et al., 2015). We cannot address this concern empirically, but the age-related reduction in temporal organization observed here closely mirrors established findings from the word-list learning literature, and is consistent with our predictions derived from theoretical and neurobiological models of aging. Nonetheless, we acknowledge that our application of measures of temporal dynamics is novel and would optimally be tested in free recall without a prior recognition memory test. In experiment 2, we analyzed recall data collected from a larger independent younger adult sample who recalled a different event with no intervening testing. This enabled us to internally validate our measures of naturalistic recall dynamics. Furthermore, leveraging this larger sample, we tested the hypothesis that episodic detail richness would be positively associated with temporal contextual organization across subjects.

4.6 Study 2: Methods

Participants

The Study 2 sample included 90 younger participants (M_{age} = 24.84 years, SD_{age} = 4.65, $M_{\text{education}}$ = 16.55 years, $SD_{\text{education}}$ = 2.82, 60 females). 11 of these participants were excluded for insufficient recall quantity according to the threshold described in experiment 1 (see below). Participants were screened for the same exclusion criteria as in Study 1.

Materials and Procedure

Encoding phase

Study 2 participants underwent a different audio-guided tour, this one on the second floor of Baycrest Hospital (Baycrest Tour 2.0; Figure 4.1B). There was no confederate interaction, and the guide narrator was one male, but it was otherwise similar to Baycrest Tour 1.0. For the purposes of a different experiment, Baycrest Tour 2.0 was split into two sections. Participants completed one section of the tour, were taken to a testing room to complete a battery of tests and questionnaires for approximately 45 minutes, and then completed the other section. The order of the sections was counter-balanced across participants. There were 13 time-tagged items in section 1 and 18 time-tagged items in section 2. Section 1 took 9.12 minutes on average (*SD* = 1.27), and section 2 took on average 10.17 minutes (*SD* = 1.95).

Retrieval phase

Participants only conducted Free Recall (they did not undergo General Probe nor Specific probe) after a 1 week delay. They neither completed the intervening true/false test nor the time-matched personal event recall. For the purposes of a separate experiment, these participants underwent eye-tracking during recall, using a head-mounted EyeLink system. They recalled each section of the tour separately, with the order of recall (section 1 versus section 2) counter-balanced across participants. During the first-recalled section, participants could move their eyes freely (free viewing). During the second-recalled section, participants were instructed to restrict their viewing patterns (fixed-viewing). As detailed below, eye movements did occur in the fixed viewing condition, albeit within a restricted range. As a result, fixation had little effect on recall measures (Armson, 2018). Specifically, there was no detectable effect of viewing condition on measures of memory detail and temporal organization, so we included data from both recalls in the present study.

Analysis

We used the same measures of detail and temporal organization from Study 1. As in Study 1, we excluded recall trials with fewer than four transitions between time-tagged items. Here, this resulted in the exclusion of both recall trials for 11 participants, and one recall trial for 17 participants. For clarity, after exclusions, there were 79 participants in Study 2, 62 with two recall trials and 17 with one, and trials excluded for this reason were also excluded from the analyses of details.

To investigate whether participants' recall organization was affected by the difference between the tour sections, owing to their differing structure and number of items, or the eye movement manipulation, we conducted linear mixed effects models separately predicting temporal clustering and forward asymmetry from tour section (section 1 vs. section 2) and viewing condition (free vs. fixed). There was neither an effect of section ($F(1, 67.90) = .38$, $p = .54$) nor viewing condition ($F(1, 67.90) = .82$, $p = .37$) on temporal clustering. Similarly, forward asymmetry was unaffected by these manipulations ($F(1, 66.98) = 1.19$, $p = .28$, and $F(1, 67.90) = .83$, $p = .36$, for tour section and viewing condition, respectively). Therefore, we conducted all analyses of detail and temporal organization on each recall trial separately and then averaged the resulting scores for each participant. For participants with only one recall trial with at least 4 transitions, that trial was carried forward.

4.7 Study 2: Results

Detail

Study 2 participants recalled on average 39.2 (*SD* = 2.19) internal details and 8.47 (*SD* = .81) external details on average (averaged over tour section, as described above). Their internal-to-total detail proportion was .83 (*SD* = .10).

Temporal organization

The lag-CRP curve (Figure 4.6) exhibited the canonical shape, indicating that participants transitioned between items according to their temporal proximity and with a forward bias. In spite of the differences in events and testing methods, the lag-CRP curve obtained in this study mirrored that obtained for younger (but not older) participants in Study 1. Temporal clustering (*M* = .82, *SD* = .09; Figure 4.7A) and forward asymmetry (*M* = .85, *SD* = .12; Figure 7B) were greater than chance (*p*'s < .001). Post-hoc comparisons between the two tour events (restricted to young participants from Study 1) indicated that forward asymmetry was not different across the two tours (*t*(32.93) = .41, *p* = .684, *d* = .1), while temporal clustering was lower in Study 2 participants (*t*(30.44) = 2.27, *p* = .039, *d* = .59). It is unknown if this is an effect of delay, differences between the two tours (Baycrest Tour 1.0 versus 2.0), or other differences methodological differences across studies (e.g. the use of any eye tracker).

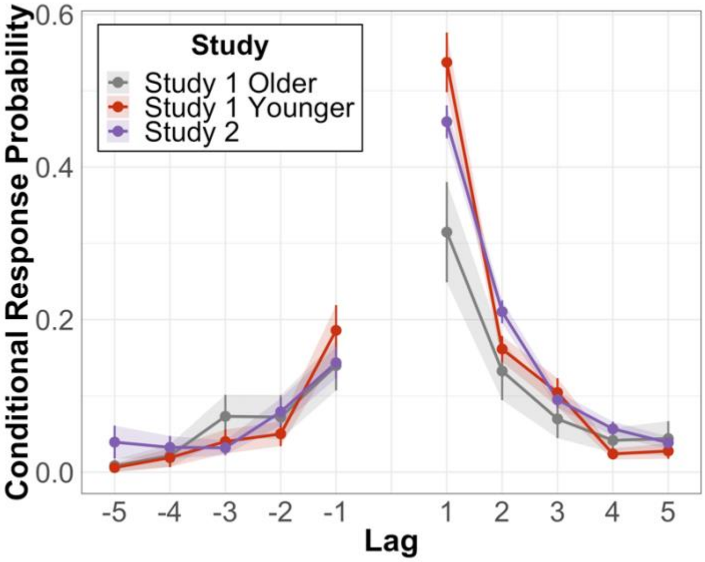


Figure 4.6. Lag-conditional response probability for Study 2 participants (purple). The lag-CRP curves from Study 1 younger (red) and older (grey) participants are reproduced here to facilitate visual comparison.

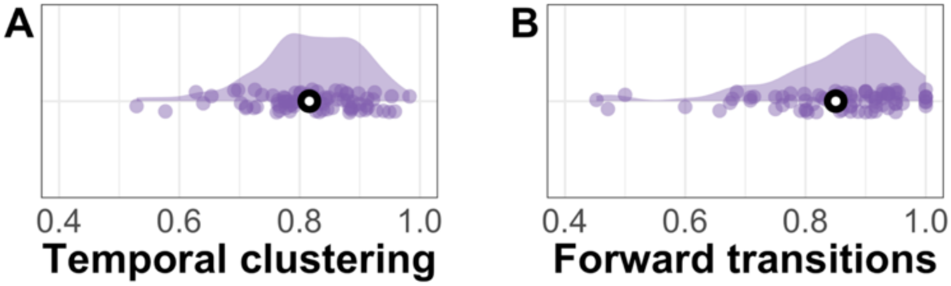


Figure 4.7. ***A.*** Temporal clustering. ***B.*** Proportion of forward-going transitions. Both measures were analyzed and visualized using the same methods from Study 1.

Relating detail and temporal organization

We hypothesized that greater temporal context reinstatement, as measured by temporal clustering and forward asymmetry, would be associated with more episodically detail-rich recall. We tested this hypothesis by merging all three groups of participants across both studies. We ran separate linear mixed effects models predicting detail count from temporal clustering (Figure 4.8A) and forward asymmetry (Figure 4.9A), with each model also including group (Study 1 older, Study 1 younger, and Study 2 younger), detail type (internal and external), and all interactions. As above, internal and external detail counts were log transformed to produce normal distributions. Post-hoc Pearson correlations were conducted on raw data.

There was a significant interaction between temporal clustering and detail type ($F(1,113) = 11.56$, $p < .001$), whereby temporal clustering was positively associated with internal details ($r(117) = .28$, $p = .002$) but not external details ($r(117) = -.12$, $p = .195$), and these coefficients were significantly different from each other ($Z = 5.63$, $p < .001$; (Steiger, 1980)) (see Figure 4.8A). No other model terms were significant. Critically, the absence of an interaction between group and temporal clustering ($F(2,113) = 0.21$, $p = .814$) or the three-way interaction including detail type ($F(2,113) = 0.34$, $p = .710$) suggests that the relationship between temporal clustering and details did not vary across groups. To further clarify this finding, we tested the association between temporal clustering and the internal:total detail ratio, again including group in the model (Figure 4.8B). Temporal clustering was significantly associated with internal:total detail proportion ($F(1,113) = 32.32$, $p < .001$; $r(117) = .45$, $p < .001$). There was no interaction between temporal clustering and group ($F(2,113) = 1.15$, $p = .322$), though we visualized and analyzed each group separately for transparency and completeness. Temporal clustering and internal detail proportion were not significantly associated within the younger group ($r(20) = .15$, $p = .50$), likely because of a ceiling effect in internal detail proportion, as can be seen in Figure 4.8B. In the older and Study 2 groups, who had greater variance in internal detail proportion, the association between temporal clustering and internal detail proportion was significant ($r(16) = .53$, $p = .025$, and $r(77) = .35$, $p = .002$, respectively).

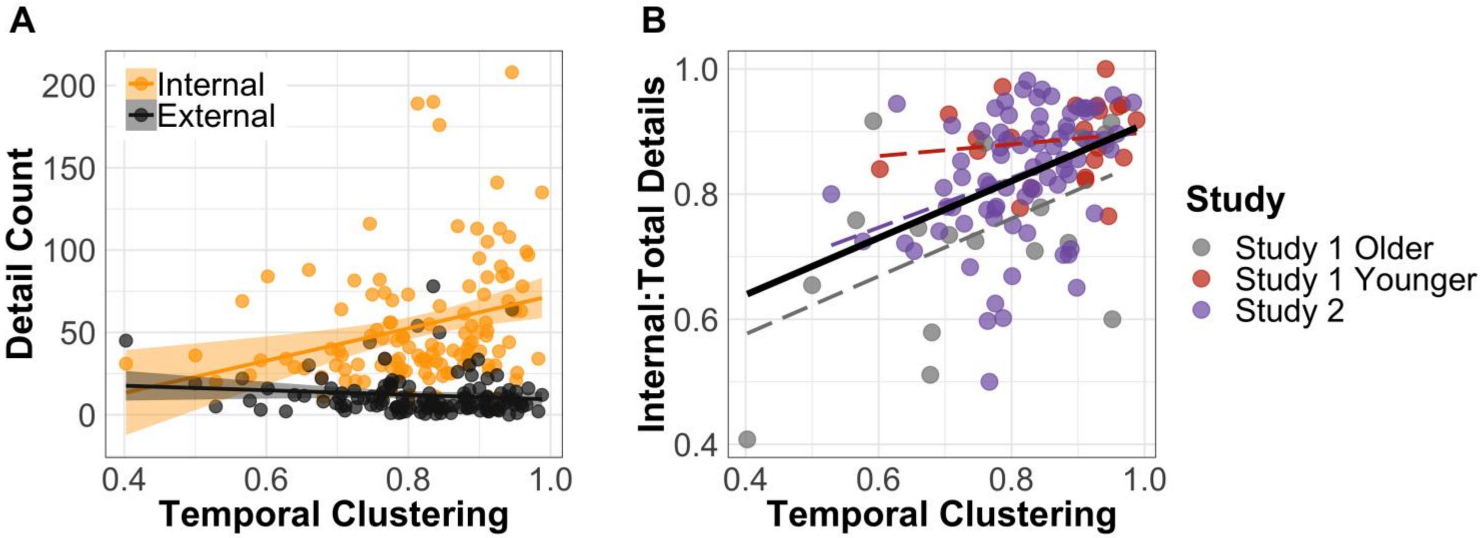


Figure 4.8. ***A.*** Relationship between temporal clustering and internal versus external details in each participant, collapsing across groups. ***B:*** Relationship between temporal clustering and internal detail proportion. Linear trendlines for each group are shown in colour with dashed lines. The solid black line is the linear trendline for the whole sample (r(117) = .45, p < .001).

We followed the same logic with forward asymmetry. As with temporal clustering, there was a significant interaction between forward asymmetry and detail type (*F*(1,113) = 12.28, *p* < .001), and no other model terms were significant. However, unlike temporal clustering, forward asymmetry was not correlated with internal details (*r*(117) = .04, *p* = .684), but was significantly negatively correlated with external details (*r*(117) = -.26, *p* = .004) (Fig. 4.9A). These coefficients were significantly different from each other (*Z* = 4.17, *p* < .001). Testing temporal clustering versus forward asymmetry directly, temporal clustering had a significantly greater association with internal details than forward asymmetry (*Z* = 2.86, *p* = .004), though they did not significantly differ in their relationship to external details (*Z* = 1.66, *p* = .096). Here too, forward asymmetry was significantly associated with internal:total detail proportion (*F*(1,113) = 36.75, *p* < .001; *r*(117) = .47, *p* > .001), and the interaction with group was not significant (*F*(2,113) = 1.89, *p* = .15). As with temporal clustering, the correlation between forward asymmetry and internal:total detail proportion was not significant within the younger group due to restricted range (*r*(20) = .13, *p* = .56), but it was significant within both older (*r*(16) = .53, *p* = .025) and Study 2 groups (*r*(77) = .43, *p* < .001) (Fig. 4.9B).

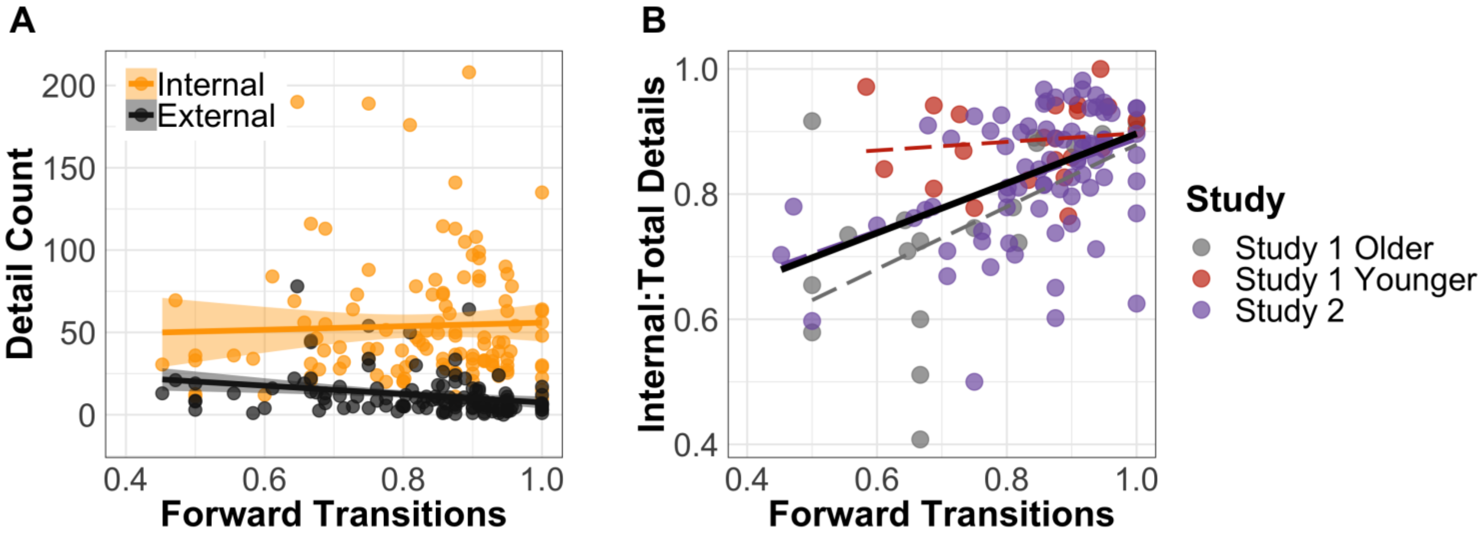


Figure 4.9. ***A.*** Relationship between forward asymmetry and internal versus external details in each participant, collapsing across groups. ***B.*** Relationship between forward asymmetry and internal detail proportion. Linear trendlines for each group are shown in colour with dashed lines. The solid black line is the linear trendline for the whole sample (r(117) = .47, p < .001).

Although temporal clustering and forward asymmetry were significantly correlated with each other (*r*(117) = .55, *p* < .001), they each explained unique variance in internal detail proportion when modelled together in a multiple regression (temporal clustering: β = .29, *t* = 2.93, *p* = .004; forward asymmetry: β = .33, *t* = 3.39, *p* < .001), suggesting that they are capturing different aspects of temporal structure, within single memories, that predict detail richness. This is consistent with their different relationships to internal and external details. There was no interaction between them (β = .04, *t* = .42, *p* = .673).

Lastly, to visualize the relationship between episodic detail richness and temporal context reinstatement, we re-plotted lag-CRP curves collapsing across group, binned by internal detail proportion quintiles across (Fig. 4.9A). Quintiles line up in gradient-like fashion at lag +1, further highlighting the relationship between overall detail richness and temporal context reinstatement. This pattern may be driven in part by age differences, but the same general pattern obtained within the Study 2 sample (Figure 4.9B).

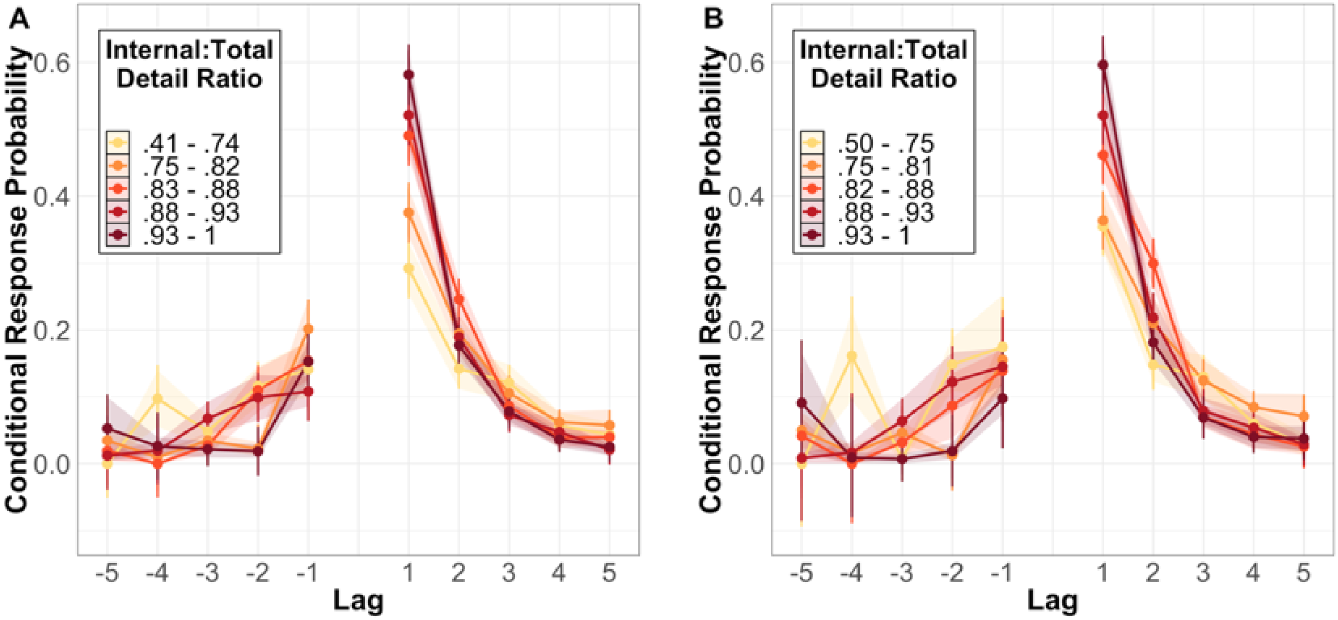


Figure 4.10. ***A***. Lag-CRP curves binned by internal detail proportion quintiles collapsing across all three groups (N = 119). ***B.*** Same as A, but with Study 2 participants only (N = 79). Error bars are bootstrap-derived standard errors (1000 resamples).

4.8 Discussion

In the present study, we sought to bridge a gap between laboratory and autobiographical recall in order to simultaneously measure detail and temporal organization in free recall of extended, one-time real-world episodes. To measure temporal organization objectively and at a fine-grain, we staged real-world events in which participants actively ambulated in large-scale spaces, encoding many distinctive art pieces and other items in a programmed sequence. Replicating prior findings in autobiographical free recall of participant-selected events, we found that production of internal (but not external) details was reduced in older relative to younger adults (Levine et al., 2002). All groups spontaneously clustered their recall according to temporal proximity with a forward-going bias, extending established findings with laboratory material at short delays to naturalistic recall at multi-day delays. Aging was associated with temporal disorganization of memory. Group differences were specific to spontaneous temporal organization, reflected in free recall transitions, as all groups made similarly few explicit sequence errors. Finally, internal detail proportion was significantly correlated with measures of temporal organization, suggesting that events remembered with greater temporal organization are also richer in episodic detail.

The Autobiographical Interview scoring method has been used to quantify the detail composition of memories and related mental representation in over 170 studies (Sheldon et al., 2018; autobiographicalinterview.com), but it is blind to intra-event temporal dynamics. That is, standard autobiographical memory measures cannot objectively distinguish two memories with similar detail counts but different degrees of temporal organization. By leveraging the known sequence structure of the encoded episodes, we were able to link detail to temporal context in a more fully articulated description of episodic autobiographical memory. Visual investigation of the scatterplots above shows many participants whose recall organization exceeded their detail and vice versa, raising the possibility that simultaneous measurement of these two dimensions may provide better characterization of individual and group differences in episodic memory.

These findings build on other recent work extending temporal context effects in laboratory recall to real-world event recall (Cortis Mack, Cinel, Davies, Harding, & Ward, 2017; Jeunehomme & D'Argembeau, 2018a; Moreton & Ward, 2010; Nielson et al., 2015; Uitvlugt & Healey, 2018). Here, we report spontaneous temporal context reinstatement, as measured by a strong tendency to cluster items according to spatiotemporal proximity in their order of occurrence, within memory of single extended events at naturalistic delays (2 days or 1 week). Given the long delays (by laboratory standards) between encoding and recall, these results suggest that temporal organization is not a by-product of recency effects or relative differences in trace strength among tour items, but rather a jump back in time to the state of temporal context present during encoding (Howard & Kahana, 2002a).

It has been suggested that temporal organization in autobiographical memory is based on the association between specific event components (e.g. spilling wine when the waiter is taking an order) and schematic points in generalized knowledge about event structure, or scripts (e.g. the waiter takes orders before the start of the meal), rather than temporal relations among event components themselves (Anderson & Conway, 1993; Burt et al., 1998). By design, however, the components of our tour paradigm were idiosyncratic and arbitrarily related. Temporal organization in the present data, therefore, cannot be driven by script-like knowledge beyond generalized notions of the beginning and end of a tour. One may ask, then, what the important differences are between the present naturalistic encoding paradigm and standard laboratory stimuli with no schematic organization. One essential difference is the manner in which temporal associations are formed. In the present paradigm, participants moved from one item to another, and indeed, many participants freely recalled their trajectories between items, noting information about distance, body position, and perceptual information encountered along the way. This is in contrast to empty inter-stimulus intervals in standard laboratory paradigms. While we discretized our recall data and marked ordinal positions for the purposes of analysis, the original experience and the recall narrative itself were continuous.

We note that our encoding paradigms, being essentially unidirectional tracks, confound space and time. Several virtual reality studies have orthogonalized spatial and temporal structure during encoding, finding that spatial proximity also shapes recall organization when accounting for temporal proximity (Miller, Lazarus, Polyn, & Kahana, 2013), with spatial and temporal memory tasks recruiting dissociable neural networks (Ekstrom & Bookheimer, 2007; Ekstrom et al., 2011). We use the term 'temporal organization' for convenience because, although target items were encountered in different allocentric spatial locations, it is the order of such locations that is of interest. Indeed, the underlying hippocampal computations may be best explained as representing event sequence rather space or time per se (Buzsáki & Tingley, 2018). Temporal clustering and forward-bias in recall were likely enhanced by environmental features that contribute to segmenting and structuring the neural and behavioural representation of events, including spatial boundaries (Horner, Bisby, Wang, Bogus, & Burgess, 2016; Radvansky & Copeland, 2006), turns (Janzen & van Turennout, 2004; Schinazi & Epstein, 2010), and goals (McKenzie & Buzsaki, 2016; for discussion, see Brunec, Moscovitch, & Barense, 2018). More concretely, our tour routes unfolded over environmental-scale space, in that participants had to walk from item-to-item to see them all, but they included vista-scale sub-spaces in which some sequences of items could be seen from a given perspective or with head turn. Furthermore, intrinsic processes implicated in real-world more than laboratory encoding conditions, such as volitional control and self-motion (Aghajan et al., 2015; Holmes et al., 2018; Kaplan et al., 2012; Winter, Mehlman, Clark, & Taube, 2015), may also facilitate the integration of event components across time. Further work is necessary to understand how different environmental features and component processes shape the way information is strung together across time, and how dimensions beyond temporal order (e.g. space, semantic associations and narrative structure) compete for influence on memory organization with complex events.

Our finding of an age-related reduction in spontaneous temporal organization, manifesting as a shallower lag-CRP function in the forward direction and reduced clustering and forward asymmetry scores, extends established laboratory findings (Howard et al., 2006; Kahana et al., 2002; Healey & Kahana, 2016). In keeping with these studies, age groups had similar serial position and probability of first recall curves, suggesting that differences in recall dynamics were not due to differences in where recall began or which items were recalled overall. In a computational model of word list recall data, Howard and colleagues (2006) attributed this pattern to an age-related impairment in the degree to which retrieved items reinstated their surrounding temporal context, which they ascribed to hippocampal decline (Leal & Yassa, 2015; Rosenzweig & Barnes, 2003). Indeed, a similar overall pattern was recently observed in medial temporal lobe amnesia patients (Palombo et al., 2018). Notably, aging is also associated structural decline of the prefrontal cortex (Raz et al., 2005), which has also been implicated in representing temporal context (Jenkins & Ranganath, 2010; Polyn & Kahana, 2008). Whereas hippocampal and prefrontal cortical damage both produce deficits in spontaneous recovery of temporal context (Dede et al., 2016; Palombo et al., 2018), prefrontal patients can exhibit normal temporal context memory when encouraged to use certain strategies (McAndrews & Milner, 1991; Thaiss & Petrides, 2008). It is unclear which deficit – a basic impairment in temporal context memory versus a strategic one – characterizes older adults' performance here. In Chapter 4, we find a marked age-related decline in memory for temporal structure when cued, suggesting that the present data more likely reflect age-related hippocampal alterations.

The positive relationship between temporal organization and detail richness builds on previous work suggesting that memory organization shapes access to details (Anderson & Conway, 1993). In her diary studies, Linton (1986) noticed that searching in forward chronological order brought different types of memory content to mind than alternative search dimensions such as category, even when these searches converged on the same overall events. More recently, recognition studies have reported a relationship between temporal context reinstatement and subjective re-experiencing. For instance, the contiguity effect, manifesting in behavioural and neural data, is triggered selectively by highest confidence recognition trials (Folkerts et al., 2018; Schwartz et al., 2005) – though the degree to which confidence tracks detail or re-experiencing is unclear (Yonelinas, Aly, Wang, & Koen, 2010). Similarly, personal photographs recognized with higher vividness ratings are ordered more accurately (Burt et al., 2008). In a recall study, Sadeh, Moran, & Goshen-Gottstein (2014) found that recalled words accompanied by subjective sense of recollection as indexed by 'Remember' responses were accompanied by a larger contiguity effect than recalled words accompanied by an acontextual feeling of familiarity ('Know' responses; Tulving, 1985). 'Remember' responses are supposed to be based on retrieval of details from the encoding episode. But these ratings are subject to different interpretations and, being subjective, can decouple from objective detail retrieval (Yonelinas, 2001), particularly in older adults (Diamond, Abdi, & Levine, in prep; McCabe, Roediger, McDaniel, & Balota, 2009). It is possible that participants make these responses on the basis of retrieving temporal contextual information itself. Conversely, the Autobiographical Interview scoring method used in the present study provides an objective measure of the preponderance of unique episode-specific details in a memory.

Participants who exhibited greater temporal clustering produced more internal but not external details, suggesting that the degree to which recall dynamics reflect spatiotemporal proximity is associated with the amount of episodic content (specific perceptual, affective and event details) recalled. It is known that items in closer proximity to 'now' are retrieved or imagined in richer contextual detail (Trope & Liberman, 2010), analogous to finer hippocampal representations of nearby locations during online memory-guided spatial navigation (Buzsáki & Moser, 2013). Jumping back in time to an earlier moment from the encoding episode – an earlier 'now' – may bring moments that were nearby into higher resolution, but only to the degree that items were initially bound to their surrounding spatiotemporal contexts. If this is the case, reduced temporal context binding and/or reinstatement in older adults (Howard et al., 2006) could explain the typical age-related reduction in internal details (Addis et al., 2008; Levine et al., 2002). In other words, though older adults begin recall like younger adults, they may benefit less from spreading activation through contextually-linked items, relatively stranding them in recall islands. A corollary of this decrement would be increased demands for multiple deliberate recall initiation attempts, with which older adults struggle (Craik, 1986), with initiation attempts jumping around more in space and time. Nonetheless, we can only speculate about the casual direction, if there is one, between temporal organization and detail richness. A causal relationship could be tested more directly by manipulating temporal context reinstatement cues (e.g. by manipulating the presentation order of recognition cues) and investigating the effects on memory detail, and vice versa (e.g. by testing the influence of verbal versus pictorial cues on memory for order).

Greater forward asymmetry was also associated with greater episodic detail richness, but this association was driven by a reduction in external details rather than an elevation in internal details. Excessive external details can reflect over-reliance reliance on semantic information (Spreng et al., 2017) or poor cognitive control (Levine, 2004; McKinnon et al., 2008, 2014). It is possible that external detail interjections interrupt the forward flow of temporal context, truncating memory search. Alternatively, participants with temporally disorganized memories may terminate memory search earlier and compensate with additional non-episodic information. Future analyses of the dynamics of internal and external details, reflecting how participants move ‘in’ and ‘out’ of the flow of an extended event memory or simulation, may reveal a complimentary dimension of naturalistic recall. One overarching interpretation is that whereas temporal clustering is more automatic (to the degree that strong temporal associations were formed in the first place) and dependent on hippocampal dynamics, chronologically-ordered search is more strategic and dependent on cognitive control mechanisms coordinated by prefrontal cortex (Badre & Wagner, 2007; Vriezen & Moscovitch, 1990). This interpretation would be consistent with the association between temporal clustering and detail generation, on the one hand, and forward asymmetry and external detail suppression, on the other.

We note that there is no statistical reason to think that increased richness would necessarily produce more temporally organized narratives. Our measures of temporal organization were output-bound (Koriat & Goldsmith, 1996), controlling for the number of items recalled. Lag-conditional response probabilities and temporal clustering are both computed on a transition-by-transition basis, adjusting for the number of available transitions at every point, and forward asymmetry was computed as a proportion of recalled items. Thus, while temporally structured recall was richer in episodic detail, these two constructs are not overlapping. In other words, it is possible to recall a richly detailed memory that is poorly organized, as is sometimes observed, in hippocampal amnesia and post-traumatic stress disorder (Brewin, 2014; Dede et al., 2016), for example, and vice versa.

Our staged events were designed to extend measures of recall dynamics to recall of all real-world experiences, but they are not necessarily representative of everyday autobiographical episodes. Although encoding of temporal structure was implicit, the novelty, artificial control over route structure, and emphasis on navigation in these events likely inflated the accuracy and resolution of temporal organization in recall. Studies using wearable camera technology offer useful alternative methods for measuring and manipulating temporal context in memory for more representative of everyday autobiographical episodes (Chow & Rissman, 2017; Jeunehomme &

D’Argembeau, 2018b; St. Jacques & Schacter, 2013), though they must tolerate heterogeneity within and across participants. Our paradigm reflects a compromise between experimental control and naturalistic encoding.

In conclusion, participants recapitulate encoded trajectories in recall of real-world episodes, clustering successive items according to temporal proximity and recalling events in chronological order. Both of these features of temporal organization are compromised in older age, despite the fact that younger and older adults recall the same items overall and initiate recall at the start of the event. This suggests that aging is associated in particular with a decline in the temporal organization of extended episodes in memory. Finally, measures of spontaneous temporal organization are associated with the density of episodic details in recall, suggesting a link between episodic memory quality and organization.

General Discussion

5

There were four main goals of this thesis. The first goal was to investigate temporal structure in memory for extended one-time experiences. The second goal was to investigate how temporal structure shapes the way in which such experiences are remembered. The third goal was to investigate whether memories become spatiotemporally disorganized in older age and, if so, how. The fourth was a methodological precursor to the first three: to develop controlled yet naturalistic real-world encoding paradigms, allowing us to pair the rigour of laboratory-based methods with the richness and ecological validity of autobiographical memory methods. In this final chapter, I will synthesize the results from these studies, try to reconcile their inconsistencies, and discuss the ways in which spatiotemporal organization shapes how we remember the past.

5.1 Summary of studies

The main goal of Chapter 2 was to investigate explicit recognition memory for the temporal order of items encountered in a real-world environment and contrast it with discrimination of old from similar new items. Participants were presented with pairs of photographs of items encountered in the exhibit three months earlier, and judged whether they were in order, out of order, or new. Lure photographs were taken at a different but thematically related exhibit, and were selected from a larger pool based on the degree to which their perceptual features fit with the encoded exhibit. They were thus relatively conceptually and perceptually similar to targets. Order recognition accuracy was affected by manipulations of cue order and distance – intact cue pairs in which the presentation order matched the encoded order elicited greater accuracy than reordered pairs, perhaps reflecting a facilitative effect of temporal context reinstatement. Furthermore, pairs with greater inter-item distance (two intervening items), elicited greater accuracy than nearer (adjacent) pairs. These effects held across the age-span. We adapted the logic of process dissociation (Jacoby, 1991) to derive scores of spatiotemporal associative (i.e. order) memory and item memory for each participant. Surprisingly, the decline in spatiotemporal associative memory with age was not significant, and there was no effect of age on the raw proportion of order errors. In contrast, age was associated with a decline in item memory, together indicating preserved ability to discriminate temporally intact from reordered photographs but reduced ability to discriminate old from new photographs.

The results from Chapter 2 suggest that, with evocative recognition cues (photographs from a personally experienced event), participants can remember the order of events comprising a one-shot real-world event months after encoding. In Chapter 3, I investigated how memory for temporal order, in contrast to memory for atemporal details (e.g. item colours and auditory information), changes during the intervening time period thought to be critical for systems consolidation (i.e. the first night's sleep and the subsequent days and weeks; Dudai, 2004). Here, I used verbal true/false statements requiring participants to mentally reconstruct the items in question. I hypothesized that temporal order would be better retained in memory compared to specific details, based on evidence and theory that consolidation, particularly during sleep, preferentially stabilizes memory for the spatiotemporal structure of extended episodes. Consistent with our hypothesis, the accuracy and subjective richness with which details were remembered declined considerably across tests (at a roughly logarithmic rate given the spacing of tests), whereas memory for order remained stable from the first to last test and increased significantly overnight. Moreover, as in Chapter 2, memory for order was modulated by the encoded distance between the items in question, and this effect did not change over time. Regarding the effects of age, there was a marked decline in memory for order at all delays, in contrast to Chapter 2 (discussed below). Conversely, the effect of age on detail memory was more subtle and shrank over time.

The results of Chapter 3 provide clear evidence that detail and temporal structure transform differently over time. Chapters 2 and 3 together highlight the durability of explicit temporal order judgements over long delay, and the influence of spatiotemporal distance on such judgements. Chapter 4 built on these findings by investigating whether encoded order and distance shape the way participants spontaneously and freely recall past experiences. Using free recall also let us bridge a gap between measurement tools used in two rich but non-overlapping literatures: word list recall and autobiographical memory. Here, we found strong temporal clustering and forward asymmetry – two hallmark measures of temporal context reinstatement – in participants' recall dynamics after 2 days and 1 week, extending results obtained in the laboratory to recall of real-world experiences at naturalistic delays. Moreover, both measures were significantly reduced in older adults, suggesting that the well-documented loss of detail richness in older adults' autobiographical memories is complemented by a loss of temporal organization. Finally, temporal clustering and forward asymmetry each explained unique variance in detail richness, even within younger and older adult samples. Thus, although detail and sequence memory change differentially over time and serial assessments at the group level, they are associated within individuals at a given point in time.

5.2 Are real-world memories organized by spatiotemporal context?

The studies in this thesis build on prior evidence in humans (Kumaran & Maguire, 2006), monkeys (Templer & Hampton, 2013) and rodents (Fortin et al., 2002) showing that subjects reliably remember the temporal structure of once-encoded sequences of stimuli. In the present studies, the stimuli in question were sub-events or items comprising extended real-world experiences, temporal order was incidentally encoded, and memory was tested at delays as long as weeks or months post-encoding.

Perhaps more interesting than measures of explicit order used in Chapter 2 (picture-based recognition) and Chapter 3 (true/false cued recall) are the ways in which temporal order implicitly shaped participants' memories. The most obvious evidence for the influence of order on memory comes from Chapter 4 (free recall), in which participants spontaneously transitioned between items with a strong forward-going bias, recovering the encoded order of events. This forward asymmetry effect is extremely robust in the word list learning literature (Healey & Kahana, 2014). Under retrieved context models of recall, forward asymmetry results from the lingering influence of one item's representation on the subsequent items, but not the reverse; thus, retrieving one item is more likely to cue the following rather than the preceding neighbouring item (Howard & Kahana, 2002a).

Notably, forward asymmetry is absent or much-reduced in previous investigations of naturalistic free recall in which participants were transitioning across discrete events separated by months or years (Moreton & Ward, 2010; Uitvlugt & Healey, 2018). Forward asymmetry may be more pronounced within single extended episodes, which have an internal organization structured by goals, causality, physical movement and event boundaries (Brunec, Moscovitch, et al., 2018; Ferbinteanu et al., 2006). Accordingly, in laboratory studies, temporal order memory is better for items occurring within versus across events (DeVito & Eichenbaum, 2011; Dubrow & Davachi, 2013; Horner et al., 2016). When recalling details comprising specific autobiographical events, forward-recall instructions produce similar output as free recall instructions, suggesting that forward-ordered recall resembles the intrinsic organization of episodes in the episodic memory system (Anderson & Conway, 1993). This asymmetry is reflected in how the hippocampus represents specific behavioural trajectories – once a rodent learns a route, place cells' receptive fields become asymmetric, with spiking beginning before the rodent enters a given place field, indicating prediction (i.e. memory) of the upcoming location (Mehta et al., 2000; Stachenfeld et al., 2017).

Forward asymmetry was also reflected in the advantage of temporally intact over reordered trials in our recognition data in Chapter 2. Intact pairs may have been more effective retrieval cues because they encouraged sampling the two depicted items in an order that matched their contextual relationship during encoding (St. Jacques & Schacter, 2013; Tulving & Thompson, 1973). Interestingly, this advantage was not seen in verbal true versus false sequence items in Chapter 3, in which true (e.g. 'You encountered A before B) and false (e.g. 'You encountered C before B) items elicited equal performance. Speculatively, photographic cues may trigger context reinstatement (and the converse, context violation) more effectively and automatically than verbal descriptions, which require more reconstructive, internally-generated representations of items and their contextual relations. Naturalistic photographs depict not only the target item but also its immediate surroundings and ambient environmental features, such as lighting. They are thus likely to evoke the larger environmental context in which they were embedded, and indeed, they have been shown to act as particularly potent cues for recollection and visual imagery (Chow & Rissman, 2017). Though Nielson and colleagues (2015) found that photographs captured via wearable cameras evoked a neural contiguity effect spanning events in different spatial locations and when statistically controlling for spatial proximity, suggesting that there is a more purely temporal contextual spillover effect occurring as well (see also Jonker, Dimsdale-Zucker, Ritchey, Clarke, & Ranganath, 2018). This account would also predict that age effects on temporal order memory would be more extreme for free (Chapter 4) and verbal cued recall (Chapter 3) than for picture-cued recognition (Chapter 2) (Craik, 1986; Craik & Schloerscheidt, 2011), as was the case here.

Effects of inter-item distance, observed in all three chapters, provide further evidence for the influence of spatiotemporal structure on memory. In Chapters 2 and 3, greater distance between item pairs (in terms of ordinal positions) elicited greater order accuracy. This extension of the symbolic distance effect (Moyer & Bayer, 1976) has been observed in many previous studies of temporal order memory, including memory for the order events across a week (Skowronski et al., 2003) and the order of items encountered along a real-world route (St. Jacques, Rubin, LaBar, & Cabeza, 2008). Note that a model of temporal order memory based on direct item-to-item associations would make the opposite prediction – that the order of neighbouring items would be better remembered, in virtue of their direct connection, than more separated item pairs. Our observations of forward asymmetry and greater order accuracy at longer lags are both more consistent with the recovery of an extended temporal context representation (Howard & Kahana, 2002a; Templer & Hampton, 2013). Templer and Hampton (2013) demonstrated that a similar distance effect observed in Rhesus monkeys was driven by ordinal distance – that is, the number of intervening items – rather than by the passage of time per se. Though I did not measure absolute time nor metric distance between items in our tour paradigms, I suspect that distance effects in the present data, and their durability over time (Chapter 3), were also driven principally by the number of intervening target items. This assumption is based on evidence that episodic memory and navigation are shaped more by relative spatiotemporal structure rather than absolute elapsed time and space (Dabaghian et al., 2014; Friedman, 2004; Tulving, 1972).

Whereas shorter inter-item distances were ‘bad’ in our recognition and true/false memory tests, they were ‘good’ in free recall (Chapter 4). Participants spontaneously clustered nearby items, as indicated by clear peaks in the conditional response probability curves at lag +/- 1. Furthermore, more tightly clustered memories were observed in younger versus older adults and were associated with more detail-rich memories. Though the distance effects observed in recognition versus recall seem like opposite phenomena (analogous to pattern separation and pattern completion; Long & Kahana, 2018), they may reflect a common underlying mechanism. Items closer in space and time may share greater contextual overlap, leading them to cue each other during free recall, but making them more difficult to discriminate when externally cued. Indeed, experiences that occurred closer in space and time exhibit higher hippocampal pattern similarity (Manns et al., 2007; Nielson et al., 2015), and items sharing greater overlap in pattern similarity are retroactively judged as being closer in time (Ezzyat & Davachi, 2014).

The present studies add to this established literature on temporal structure in episodic memory by objectively measuring the fidelity of sequential organization in memory for real-world episodes, demonstrating that accurate and high-resolution sequence memory shapes the way such episodes are remembered and is preferentially retained in memory over long delays, even after specific details fade away. Together, these findings are consistent with a picture of episodic memory as mental time travel along spatiotemporal trajectories (Buzsáki & Moser, 2013; Hasselmo, 2009). Like scenes and spatial contexts (Hebscher, Levine, & Gilboa, 2016; Maguire & Mullally, 2013; Jessica Robin, 2018; Rubin et al., 2019), representations of sequential associations may serve as scaffolds which support detail retrieval.

People often do not subjectively feel that their episodic memories are precisely ordered records of event sequences. How can the present data be reconciled with such reports? High-performing participants in the present studies may not have retained explicit high-resolution, video-like records of their tour experiences, but rather a latent representation of spatiotemporal relations or topological structure as revealed by the transitions they make. By analogy, hippocampal replay sequences sometimes depict behavioural trajectories in a learned environment that were possible but were never actually experienced (Gupta et al., 2010). Foster (2017) suggested that replay thus represents "traversable distances and thus a model of the world as opposed to the veridical recording of experience", adding that "the model of the world that informs replay is developed very rapidly, after only one to two experiences" (2017, p. 586). If we assume that certain types of information are adaptive to the degree that they are retained in memory over others (Richards & Frankland, 2017), memory for the spatiotemporal structure of past events may be particularly useful for guiding adaptive behaviour. Retention of temporal order information in particular is necessary for retroactively linking sequences of actions to their subsequent consequences (Braun et al., 2018), which is likely useful for constraining online decision making (Lisman & Redish, 2009) and imagination of plausible future scenarios (Buckner, 2010).

5.3 Effects of age

Chapters 3 and 4 found that memories become temporally disorganized with age. In chapter 3, this manifested as an age-related reduction in temporal order memory accuracy at all delays (1 hour to 1 month), even when age groups were matched on detail memory accuracy. In chapter 4, older adults exhibited significantly reduced temporal clustering and forward asymmetry relative to younger adults, in addition to the well-documented age-related decline in internal detail proportion. Both measures of temporal organization control for overall recall quantity, suggesting that the manner in which older adults search through memory is less tethered to the encoded temporal context. All three of these effects were large (Cohen's *d*'s > .8). But they stand in sharp contrast to Chapter 2, where there was not a significant age-related decline on our main measure of temporal associative recognition. Why was this the case?

First, as discussed above, greater age effects should be expected for tasks providing less retrieval support and demanding correspondingly more self-initiated processing (Craik, 1986). Naturalistic photographs of items from a unique and personally-experienced museum exhibit should be relatively potent retrieval cues, providing more retrieval support than verbal true/false statements and free recall. The items in the museum exhibit used in Chapter 2 were also fewer (16 target items, versus 27 in the tours used in Chapters 3 and 4), semantically linked – which has been shown to benefit memory for temporal order (Tzeng & Cotton, 1980).

More to the point, as described in Chapter 2, aging was associated with subtle alterations in memory for spatiotemporal context upon closer inspection of the data: accuracy on reordered trials declined modestly though significantly with age, and this decline was driven by an increase in the tendency to respond 'new' on these trials. In other words, when the temporal context of otherwise valid cues was violated, older adults were more likely to perceive these old cues as new. This finding suggests that aging may compromise the ability to flexibility reconstruct temporal context, which accords with the findings of Chapters 3 and 4, in which participants were provided with limited (verbal true/false statements) or no (free recall) contextual cues. In particular, in Chapter 4, age groups were equally likely to initiate recall from the first item in the tour, and showed equal (though modest) recency effects. Thus, aging may preserve a schematic sense of order and a sense of oldness relative to 'now', but a decline in the ability to jump back in time and reconstruct the temporal relations among events comprising an extended episode. This pattern would be consistent with age-related atrophy and dysfunction in the hippocampus and prefrontal cortex (Leal & Yassa, 2015; Rajah, Kromas, et al., 2010; Rajah, Languay, & Valiquette, 2010; Rosenzweig & Barnes, 2003). When retrieval cues do the work of reinstating contextual relations among items (as in intact pairs), participants can rely on recognition, and no age effect is observed. Rearranged pairs, on the other hand, require a self-initiated recall process, which is more vulnerable to age-related decline (Cohn et al., 2008). Thus, overall older adults performed worse than younger adults on tasks tapping internally organized and internally generated representations of temporal context.

Regarding memory for details irrespective of order, the age-related decline in internal-to-total detail ratio in Chapter 4 builds on established findings from studies on autobiographical memory and future imagination (Addis et al., 2008; Levine et al., 2002). Fixing the event content and encoding-recall delay in the present study rules out the possibility that these effects are artifacts of age-related differences in event selection or remoteness (Aizpurua & Koutstaal, 2015), and further suggests that they reflect a fundamental shift in memory processing with age. With true/false statements probing for specific details in Chapter 3, there was only a subtle effect of aging. This, too, is consistent with the facilitative effect of retrieval support for older adults in particular (Craik, 1986), and with prior evidence that probing for specific details during recall can ameliorate the age gap for delay-matched memories (Levine et al., 2002). As speculated in Chapter 4, the age-related decline in free recall of specific episodic details could be a consequence of disrupted temporal organization. Though we cannot strongly assess this possibility with existing data, this interpretation would be consistent with neurophysiological models of episodic memory suggesting that the hippocampus fundamentally computes structure along temporal (and other) dimensions, providing organized access to details represented in the cortical regions to which the hippocampus is connected (Buzsáki & Tingley, 2018; Howard Eichenbaum, 2013).

5.4 Bridging autobiographical and laboratory approaches to episodic memory

In all experiments in this thesis, we tested memory for immersive events in large-scale spaces that were nonetheless controlled. By controlling the encoding sequence of otherwise rich and complex events, we were able to pair theory and methods from the rodent and laboratory models of episodic memory, often focusing on recall dynamics and organization, with theory and methods from the autobiographical memory literature, often focusing on memory detail and phenomenology. Many others have devised similar encoding paradigms in the past (for recent examples, see: Armson, Abdi, & Levine, 2017; Dede, Frascino, Wixted, & Squire, 2016; Heyworth & Squire, 2019; Willoughby, McAndrews, & Rovet, 2014).

The paradigms developed for the present studies were designed to address a gap in our understanding of episodic memory – specifically, how we remember the temporal order of extended real-world events, how this relates to other aspects of retrieval, and how memory for temporal order changes with age. These paradigms were designed to incorporate low-level component processes and event features that jointly characterize autobiographical experiences, such as volitional control (Voss, Gonsalves, et al., 2011), goal-directedness (Cornwell et al., 2008), self-motion (Holmes et al., 2018; Terrazas, 2005; Wang & Simons, 1999; Winter et al., 2015), and environmental-scale spatial representations (Hegarty et al., 2006; Uttl & Graf, 1993). These processes and features have been shown to shape neural representations of spatiotemporal context or to enhance associative memory performance relative to more standard laboratory encoding conditions (i.e. passive encoding, random sampling, passive displacement, and figural-scale spatial representations).

That said, the encoding paradigms used in this thesis are were not designed to be similar to everyday events at a high level. They were constrained to establish homogeneity across participants and to maintain goal-directedness. Although the audio-guided tours reduced volition, participants were nonetheless required to visually sample a complex immersive environment to identify specific items and then physically move toward them. Even this minimal sense of volition, in combination with kinesthetic and vestibular cues, likely affects temporal binding. Notably, in location-fixed rats, even the potential for exploration elicits canonical hippocampal firing patterns linked to spatial coding (Buzsáki & Moser, 2013), and these patterns are abolished when that potential is removed (e.g. by snugly wrapping the rat in a towel; Foster, Castro, & McNaughton, 1989). In an unpublished experiment, we found that real-world encoding elicited greater accuracy in memory for specific details, as well as higher rates of self-reported re-experiencing, compared to virtualized and passively encoded version of the same event presented in a series of static photographs.

There has been a great deal of debate about the value of naturalistic versus laboratory approaches to episodic memory (Banaji & Crowder, 1989; Conway, 1991; Neisser, 1978), including recent empirical work asking whether fundamentally different brain networks support these types of memory (Cabeza et al., 2004; Chen et al., 2017; Chow et al., 2018; Gilboa, 2004; McDermott et al., 2009; Monge, Wing, Stokes, & Cabeza, 2018; Roediger & McDermott, 2013). I believe that differences will continue to be observed to the degree that the particular tasks engage distinct component processes and representations, but that such approaches may dismiss the heterogeneity within naturalistic and laboratory approaches. Naturalistic and laboratory memory are not natural kinds – although I used these terms for convenience through this thesis, methods and materials within each domain vary widely according to the question at hand. Similarly, though differences have been observed between real-world and virtual (Aghajan et al., 2015; Bohbot, Copara, Gotman, & Ekstrom, 2017; Taube et al., 2013) or video-based (Hegarty et al., 2006; St-Laurent et al., 2016) encoding, these differences do not indicate pros or cons inherent to each method. As virtual reality technology becomes more flexible and immersive, it will likely provide immense value for understanding the component processes underlying memory formation outside of the laboratory. Even highly artificial experimental materials can be seen as ecologically valid to the degree that they engage cognitive processes that generalize to real-world behaviours, even if the materials themselves are not representative of everyday situations (Kvavilashvili & Ellis, 2004).

5.5 Limitations, future directions and conclusions

While the present encoding paradigms were designed particularly to investigate temporal structure, memories are shaped by organization along many different dimensions that may align with or oppose temporal structure, for instance: pre-existing semantic associations (Bousfield, 1953; Howard & Kahana, 2002b), spatial proximity (Miller et al., 2013), narrative structure (Mandler & Johnson, 1977; Xu & Chai, 2017), event boundaries (Clewett, Dubrow, & Davachi, 2019; Zacks & Tversky, 2001), and learned source or category structure (Polyn et al., 2009; Schapiro et al., 2017). The route-like structure of the present encoding paradigms, in addition to the intentionally arbitrary relations among items, likely artificially inflated the influence of pure temporal structure on memory. On the other hand, we could not have assessed temporality at this level of precision without imposing some degree of structure over the sequence of events. Future work using more high-dimensional events is necessary to determine how multiple orthogonal dimensions of experience compete for influence on memory, and how both online (binding) and offline (sleep and replay) forces contribute to memory restructuring.

Similarly, while memory for novel one-time experiences (one-shot learning) is of theoretical interest for models of episodic memory and cognition more generally (Hassabis, Kumaran, Summerfield, & Botvinick, 2017; McClelland et al., 1995), most of our personal experiences (e.g. working in our office or asking our partner if they're in the mood for sushi, Thai or Ethiopian) are highly overlapping and inter-related. Neisser (1981) suggested that many ostensibly episodic memories are rather "repisodic", blurring over multiple similar instances. In such memories, episode-specific information about details and sequence structure will be augmented or supplanted by schematic information. Recent work suggests that trial-unique versus schematic representation of temporal context may be simultaneously instantiated in the hippocampus and posteromedial cortex, respectively (Hsieh & Ranganath, 2015). Looking beyond single episodes also opens up questions about temporal organization within versus across events. It has been proposed that representations of temporal context are scale-invariant, applying in fractal-like manner across memories at all timescales (Brown, Neath, & Chater, 2007; Shankar & Howard, 2012), but there is still little empirical evidence for this (Moreton & Ward, 2010). As above, it is unclear when and how different dimensions shape within- and across-event organization.

Finally, the present studies investigated the effects of healthy aging on memory. Understanding cognitive changes accompanying healthy aging is important for differentiating them from pathological aging. In separate experiments, impairments in temporal order memory and episodic detail richness in autobiographical memory are both observed in in Mild Cognitive Impairment (Murphy et al., 2008; Schmitter-Edgecombe, Woo, & Greeley, 2009) and further in Alzheimer's Disease (Barnabe et al., 2012; Bellassen et al., 2012; Meulenbroek et al., 2010) relative to healthy aging. Future work investigating both of these dimensions within single complex memories may determine whether they uniquely predict cognitive status, and hopefully contribute to increasing the sensitivity of memory testing for normal versus pathological aging.

In conclusion, the temporal structure of memory for extended real-world experiences powerfully shapes the way those experiences are remembered even weeks or months later. This organization comes apart as we age, even when we retain specific details of what happened.

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Appendices

6

6.1 Appendix A: Supplementary material for Chapter 2

6.1.1 Supplemental descriptive statistics

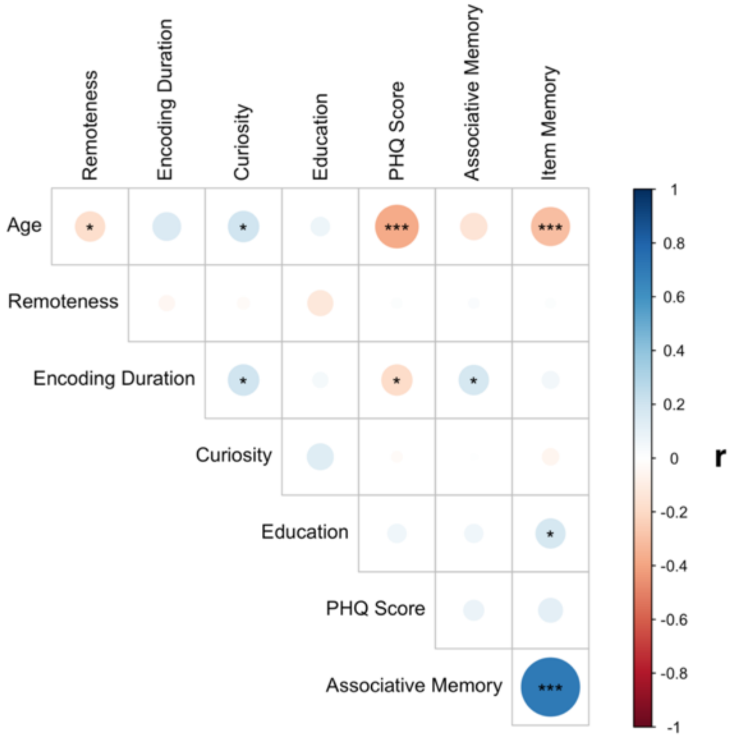

Figure S1. Correlation matrix of the continuous regressors entered into the multiple regression models, including outcome measures (associative and item memory). As described in the Methods section, encoding duration, curiosity, education and PHQ scores were transformed to correct for skewness. Asterisks represent significant correlations (* < .05; ** < .01; *** < .001). Color intensity and the size of the circles are proportional to the Pearson correlation coefficient.

For each of the three categorical variables (gender, handedness, and endorsement of lifetime anxiety), we conducted uncorrected t-tests on each of the continuous variables, including associative and item memory, for descriptive purposes. For the four aforementioned skewed variables, t-tests were conducted on transformed values and raw means are reported. There was a significant effect of gender on curiosity, in which women (M = 5.34, SD = .83) had higher curiosity ratings than men (M = 4.91, SD = .99; $t(52) = 2.48$, p = .016, d = .31). The only other differences that were significant at the *p* = .05 level involved anxiety ("Have you ever suffered from significant anxiety that interfered with your functioning?"). Compared to those who did not report ever having anxiety, those who did had fewer years of education (*M* = 17.59, *SD* = 3.72 and *M* = 16.03, *SD* = 4.16, respectively; *t*(71)=2.21, *p* = .031, *d* = .41) and higher PHQ scores (*M* = 3.29, *SD* = 2.81 and *M* = 5.33, *SD* = 5.65, respectively; *t*(57) = 2.95, *p* = .005, *d* = .62).

6.1.2 Alternative associative and item formulas

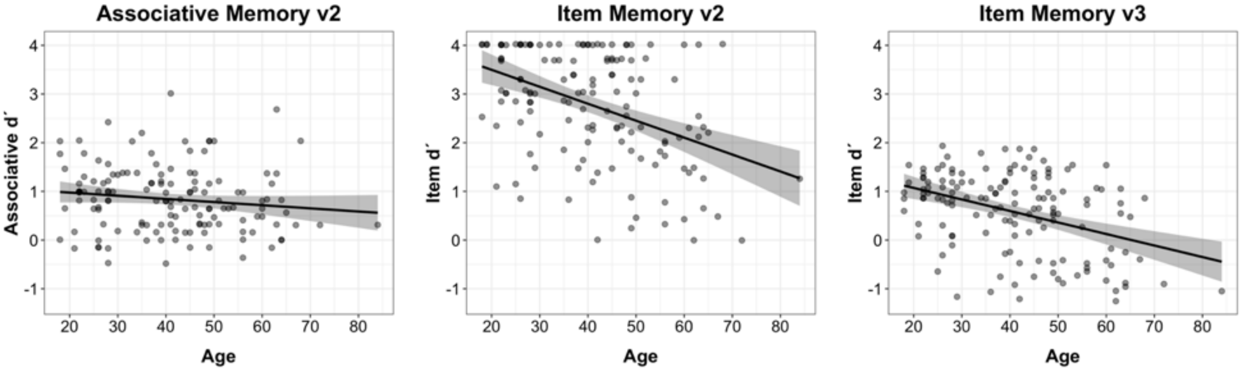

Figure S2. Associative memory v2 subtracts reordered false alarms from intact hits [Z(*P*('intact' | intact)) – Z(*P*('intact' | reordered))], as implemented in previous studies (Troyer et al., 2012; Wolk, Signoff, & Dekoskey, 2008), and is not significantly correlated with age (*r* = -.14, *p* = .089). Item Memory v2 measures old/new discrimination irrespective of order [Z(*P*('intact' or 'reordered' | intact or reordered)) – Z(*P*('intact' or 'reordered' | new))], and is negatively associated with age (*r* = -.42, *p* < .001; Kendall's tau = -.28, p < .001). Item memory v3 measures old/new discrimination in the absence of associative memory [Z(*P*(order errors)) – Z(*P*('intact' or 'reordered' | new))], and is negatively associated with age (*r* = -.4, *p* < .001).

6.1.3 Categorical younger and older groups

To compare our data with past findings, we split our sample into canonical younger (18-35 years; N = 51, M_{age} = 26.06, *SD* = 4.62) and older (60+ years; N = 18; M_{age} = 64.61, *SD* = 5.74) groups and again probed for age-related changes in associative and item memory. We ran a 2x2 mixed-design ANOVA, modelling age as a between-groups factor and memory type as a within-groups factor. There were main effects of age group (*F*(1,67) = 7.35, *p* = .008), whereby younger adults performed better than older adults overall (*t*(25) = 2.43, *p* = .022, *d* = .63), and memory type (*F*(1,67) = 86.85, *p* < .001), whereby item memory was greater than associative memory overall

($t(68) = 11.53$, $p < .001$, $d = 1.39$). Consistent with the main findings in the body of the paper using the full age range, there was a significant interaction between age group and memory type ($F(1,67) = 20.37$, $p < .001$): older adults performed significantly worse than younger adults on item ($M_{younger} = 1.97$, $SD = .78$; $M_{older} = 1.09$, $SD = 1.04$; $t(24) = 3.26$, $p = .003$, $d = .84$) but not associative memory ($M_{younger} = .93$, $SD = .65$; $M_{older} = .73$, $SD = .74$; $t(27) = .99$, $p = .33$, $d = .26$; See Figure S3). Considering age-related changes as percentage loss, older adults had 44.44% lower item discrimination and 20.98% lower associative discrimination. We confirmed that the age groups did not differ in remoteness ($M_{youngers} = 103$ days, $M_{olders} = 98$ days, $t(57) = 1.35$, $p = .18$).

Considering error type, a 2x3 mixed-design ANOVA also revealed a significant interaction between age group and error type ($F(2,134) = 20.47$, $p < .001$□. Older adults made no more order errors than younger adults ($t(29) = -.25$, $p = .801$, $d = .07$), but made marginally more misses ($t(23) = 1.91$, $p = .069$, $d = .48$) and false alarms ($t(21) = 4.199$, $p < .001$, $d = 1.03$) compared to younger adults (see Figure S4).

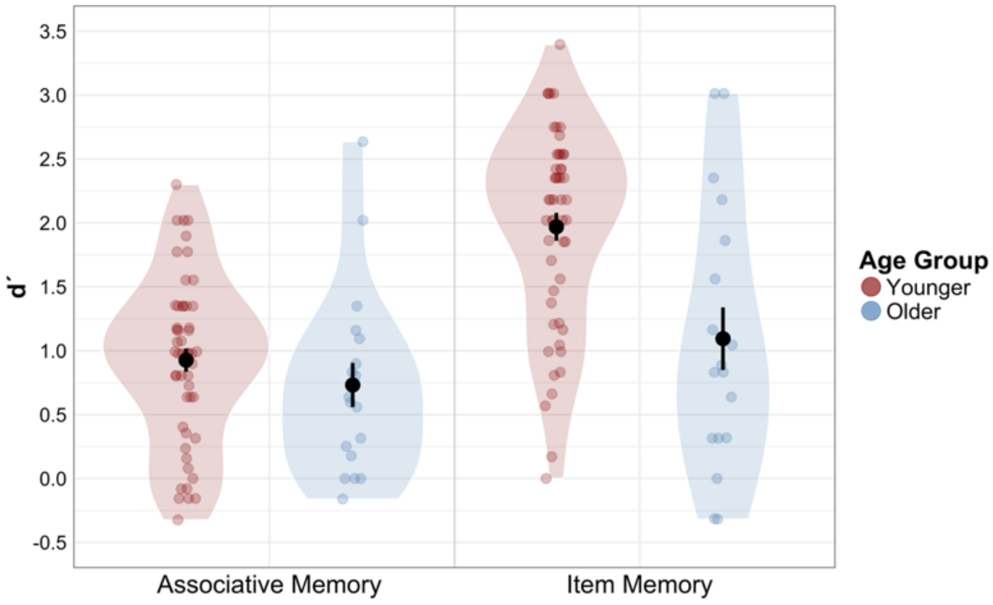

Figure S3. Interaction between age groups and process estimate (associative vs. item memory) depicted using violin distribution plots. Black circles and error bars depict means and standard errors, coloured dots depict individual participants.

Figure S4. Interaction between age groups and error type depicted using violin distribution plots. Proportions of order errors and misses are each out of 32 trials old (intact and reordered) trials. Proportion of false alarms is out of 16 new trials. Black circles and error bars depict means and standard errors, coloured dots depict individual participants.

6.2 Appendix B: Supplementary material for Chapter 3

6.2.1 Test form creation and pilot study

After designing the tour, we built up a pool of 298 true/false test items. There were 151 detail statements (75 true and 76 false) and 147 sequence statements (73 true and 73 false). Detail statements were true or altered descriptions specific features of the tour, including features of the artwork participants were instructed to encode, information spoken by the audio guide, or fixed elements of the tour environment to which participants' attention was directed. As described in the Methods, each feature, or detail (e.g. the colour of a statue), appeared in only one true/false statement – whether it was a true or false statement was often arbitrary. There were multiple statements about each of the main target items of the tour (e.g. one statement about the colour of a statue, another about its shape), and approximately equal numbers of statements were created for each target item. Sequence items were created from a matrix of the 25 main target items, with 'Near' pairs having 0 or 1 intervening target items, 'medium' pairs having 2-3 intervening target items, and 'far' pairs having 4-6 intervening target items, and with true (in order) and false (out of order) items alternating.

In a pilot experiment, 22 participants completed the tour and then were tested once at a 24 hour delay. The pilot test had the same trial structure as the final tests, including true/false responses followed by subjective Remember/Know/Guess responses. The initial pool of 298 test statements were divided into four test blocks with equal or similar numbers of true vs. false, detail vs. sequence, and near vs. medium vs. far statements, and a similar number of statements about each target item in the tour. In other words, forms were designed to have similar 'coverage' of the whole tour. Two of the four blocks were randomly assigned to each pilot participant, so that 10 or 11 participants completed each block.

We averaged accuracy for each statement across participants and discarded statements with less than 50% average accuracy. We then created four new test forms for use in the final experiment, balancing them according to accuracy and proportion Remember/Know/Guess responses based on the pilot data, in addition to the factors described above. Table B1 presents an overview of the four test forms.

Table B1

Overview of the four final test forms. Data are from the pilot study.

Measure	**Form A**	**Form B**	**Form C**	**Form D**
N statements (*true/false)*	69 (36 / 33)	69 (35 / 34)	69 (35 / 34)	69 (35 / 34)
N detail / sequence statements	34 / 35	34 / 35	34 / 35	35 / 34
N near / medium / far sequence statements	12 / 10 / 13	10 / 11 / 14	10 / 11 / 14	10 / 9 / 15
M (SD) accuracy	.786 (.15)	.779 (.16)	.783 (.15)	.779 (.17)
M true / false statement accuracy	.799 / .770	.798 / .760	.804 / .762	.811 / .747
M detail / sequence statement accuracy	.796 / .776	.785 / .773	.812 / .756	.801 / .760
Proportion Remember / Know / Guess responses	.63 / .17 / .20	.62 / .18 / .20	.61 / .20 / .18	.63 / .17 / .20

6.2.2 Master list of final 273 true / false items

Det / Seq	**True / False**	**Seq Lag**	**Statement**
det	T		The piece of weaved artwork is oriented vertically
det	T		The audio guide asked you why you think the "Autumn Song" painting is called that
det	T		The garbage bin is in front of a brick wall

det	T	"The Spiro Family Gardens" sign on the wall is on a gold coloured plaque
det	T	The artwork called "Ruth and Naomi" is rectangular
det	T	The pair of paintings by Dan Christensen - "Jivarro 2" and "illinois" - are mostly white and Blue
det	T	"The Spiro Family Gardens" artwork was on your left as you approached it
det	T	The large white sculpture is in front of a window
det	T	The painting called "Freedom 7" is abstract
det	T	The audio guide asked you to note the colours of the piece of weaved artwork
det	T	In the campaign contributors frames, the names are written in black font
det	T	The sculpture called "One Nine North" is in a corner
det	T	The painting called "Freedom 7" is by Michael Adamson
det	T	The sculpture called "One Nine North" is on a black platform
det	T	The large yellow painting has red in it too
det	T	The artwork called "Ruth and Naomi" is in colour
det	T	The Jean-Paul Riopelle prints have black frames
det	T	The sculpture called "Sails" is in front of a window
det	T	The name that you identified in the campaign contributers was near the left edge of the frame.
det	T	The piece of weaved artwork is mounted on a white wall
det	T	The painting called "Autumn Song" is abstract
det	T	The large yellow painting is square-shaped
det	T	The audio guide asked if you liked the painting called "Autumn Song"

det	T	In the model of Baycrest, you were instructed to look for three cars of a certain colour
det	T	The large white sculpture is oriented at an angle
det	T	When you looked out the window from the mezzanine, you were asked to look at three different buildings
det	T	The painting called "Cradle of the Moon" is purplish
det	T	The artwork called "Head with Armstrong" is wall-mounted
det	T	One of the Jean-Paul Riopelle prints is called "Afternoon"
det	T	The opening of the garbage bin is on top
det	T	The model of Baycrest includes model trees
det	T	In the sculpture called "Sails", the sails are marble-coloured
det	T	The handrail on the stairs is silver coloured
det	T	The nurse in the portrait graduated in 1937
det	T	The audio guide asked you to notice the trees on the first floor
det	T	The pair of paintings by Dan Christensen - "Jivarro 2" and "illinois" - are the same size.
det	T	"The Spiro Family Gardens" artwork is a painting
det	T	In the pair of paintings by Dan Christensen, you examined "Jivarro 2" first and "Illinois" second.
det	T	The bathroom doors that you walked by were on your left
det	T	The piece of weaved artwork is multi-coloured
det	T	In the portrait of the nurse, she is wearing a hat
det	T	The painting called "Cradle of the Moon" is by Gail Ashby
det	T	The painting called "Autumn Song" is by Judy Singer
det	T	The piece called 'Rotation' is made of wood
det	T	The nurse in the portrait's last name was Ungerman

det	T	The sculpture next to "The Tobie Bekhor Wing" sign is called "Ballerina in Motion"
det	T	The piece called 'Rotation' is oriented horizontally
det	T	The fire extinguisher panel had the number 5 on it
det	T	The cluster of photographs that you counted are all the same size
det	T	The large white sculpture is abstract
det	T	You read the information card for the sculpture next to "The Tobie Bekhor Wing" sign
det	T	The cluster of photographs that you counted were mounted on a white wall
det	T	Half of the shapes in the shuffleboard game on the floor are grey
det	T	There are three big trees on the first floor
det	T	The artwork called "Head with Armstrong" is between two elevators
det	T	In the model of Baycrest, you were instructed to look for red cars
det	T	"The Spiro Family Gardens" artwork depicts people
det	T	You stood on two different parts/zones in the shuffleboard game
det	T	The artwork called "Head with Armstrong" is multi-coloured
det	T	The garbage bin is wood-paneled
det	T	The model of Baycrest includes model people
det	T	The cluster of photographs that you counted depict outdoor scenes
det	T	At the painting called "Freedom 7", the audio guide said something about the style of the painting
det	T	The campaign contributors frames have a grey background
det	T	The painting called "Cradle of the Moon" was on the right wall as you approached it
det	T	The sculpture next to "The Tobie Bekhor Wing" is by Jack Culiner

det	T	The number on the fire extinguisher panel is in the top right corner of the panel
det	T	You were asked to touch a sculpture
det	T	The campaign contributors frames are from 1968
det	F	"The Spiro Family Gardens" artwork is square-shaped
det	F	The large yellow painting depicts a sunset
det	F	The floor on which the shuffleboard game is painted is brown
det	F	One of the Jean-Paul Riopelle prints is called "Moon"
det	F	The artwork called "Head with Armstrong" is mounted on a white background
det	F	The piece of weaved artwork is called "Celebration"
det	F	The audio guide told you about the life of the painter of "Cradle of the Moon"
det	F	The sculpture called "One Nine North" is made of wood
det	F	As you approached it, the piece of weaved artwork was on your right
det	F	The sculpture next to "The Tobie Bekhor Wing" sign is green
det	F	The large white sculpture is by Ina Gilbert
det	F	The painting called "Freedom 7" is roughly three feet wide
det	F	The model of Baycrest rests on a silver base
det	F	Half of the shapes in the shuffleboard game on the floor are blue
det	F	The painting called "Freedom 7" is in front of a window
det	F	The bathroom doors that you walked by are grey
det	F	The painting called "Autumn Song" depicts Baycrest
det	F	The artist who made the piece called 'Rotation' is Anne Harris
det	F	When you looked out the window from the mezzanine, the buildings were all the same colour

det	F	The painting called "Cradle of the Moon" depicts a moon floating in space
det	F	The piece called 'Rotation' is flat
det	F	The artwork called "Ruth and Naomi" is a photograph
det	F	The garbage bin is between two elevators
det	F	The sculpture next to "The Tobie Bekhor Wing" sign was to the right of the sign
det	F	The sculpture called "One Nine North" is dark red
det	F	"The Spiro Family Gardens" artwork has a silver frame
det	F	You were asked to note the time twice
det	F	The nurse in the portrait graduated from Ryerson School of Nursing
det	F	The sculpture called "One Nine North" depicts a sailboat
det	F	The artist who made the piece called 'Rotation' graduated from McMaster University
det	F	The audio guide mentioned the word 'sandwich' at some point
det	F	The base of the sculpture called "Sails" is blue
det	F	There are 4 prints in the collection by Jean-Paul Riopelle
det	F	In the portrait of the nurse, her hair falls below her shoulders
det	F	The audio guide asked you if you like the cluster of photographs that you counted
det	F	The artwork called "Ruth and Noami" is mounted on a base on the floor
det	F	The television you examined was on a table
det	F	The model of Baycrest is square-shaped (from a bird's-eye view)
det	F	In the television you examined, you were asked to find a specific word
det	F	You were asked to stand on number 8 on the shuffleboard game

det	F	"The Tobie Bekhor Wing" sign is oriented vertically
det	F	The painting called "Freedom 7" is black and white
det	F	The sculpture next to "The Tobie Bekhor Wing" sign is was made in 1943
det	F	The audio guide asked you to notice the piano on the first floor
det	F	You were asked to touch a plant
det	F	The campaign contributors frames are side-by-side (to the left and right of each other)
det	F	The names in the campign contributors plaques were numbered.
det	F	The piece called 'Rotation' is all one colour
det	F	You were asked to find Gregory Altman in the campaign contributors frame
det	F	The line of chairs near the Shuffleboard were on your left as you passed them
det	F	The title of "The Spiro Family Gardens" artwork is in the top left corner
det	F	The artwork called "Head with Armstrong" depicts a head that is facing left (your left)
det	F	The information card for the Jean-Paul Riopelle prints is on the left wall as you are walking down the hallway
det	F	In the pair of paintings by Dan Christensen, "Jivarro 2" is to the left of "Illinois"
det	F	In the pair of paintings by Dan Christensen called "Jivarro 2" and "Illinois", the paintings were oriented vertically (one on top of the other)
det	F	The audio guide asked you to note the colours of the sculpture called "Sails"
det	F	The artwork called "Head with Armstrong", the man and bicycle are blue

det	F		The cluster of photographs that you counted are arranged in a square shape
det	F		The sculpture called "One Nine North" is roughly waist-high
det	F		In the sculpture called "Sails", there are three sails
det	F		In the portrait of the nurse, the nurse's first name was Rachel
det	F		Each of the campain contributors frames are taller than they are wide
det	F		The garbage bin is rectangular
det	F		The television you examined displayed a clock in the top right corner
det	F		There are 12 photographs in the cluster of photographs that you counted
seq	T	1	You encountered the weaved artwork before "Rotation"
seq	T	1	You encountered the garbage bin before the artwork called "Ruth and Naomi"
seq	T	1	You encountered the painting called "Autumn Song" before the Riopelle prints
seq	T	1	You encountered the sculpture called "Sails" before the shuffleboard game
seq	T	1	You encountered the portrait of the nurse before the shufleboard game
seq	T	1	You encountered the model of Baycrest before the large white sculpture
seq	T	1	You encountered the television before the Riopelle prints
seq	T	1	You encountered the frames with the campaign contibutors before the television
seq	T	1	You encountered the shuffleboard game before "Rotation"
seq	T	1	You encountered "Rotation" before the frames with the names of campaign contributors

seq	T	1	You encountered the painting called "Freedom 7" before the sculpture called "One Nine North"
seq	T	1	You encountered the buildings seen through the window before the painting called "Cradle of the Moon"
seq	T	1	You encountered "Head with Armstrong" before the portrait of the nurse
seq	T	1	You encountered the "Tobie Bekhor Wing" sign before the cluster of photographs
seq	T	1	You encountered the pair of paintings by Dan Christensen called "Jivarro 2" and "Illinois" before the frames with the campaign contributors
seq	T	1	You encountered the painting called "Cradle of the Moon" before the cluster of photographs
seq	T	1	You encountered the artwork called "Ruth and Naomi" before the large white sculpture
seq	T	1	You encountered the "Spiro Family Gardens" painting before the painting called "Cradle of the Moon"
seq	T	1	You encountered the sculpture called "One Nine North" before the artwork called "Ruth and Naomi"
seq	T	1	You encountered the fire extinguisher before the television
seq	T	1	You encountered the first floor trees before the buildings seen through the window
seq	T	2	You encountered "Rotation" before the fire extinguisher
seq	T	2	You encountered the pair of paintings by Dan Christensen called "Jivarro 2" and "Illinois" before the painting called "Autumn Song"
seq	T	2	You encountered the painting called "Cradle of the Moon" before the painting called "Freedom 7"
seq	T	2	You encountered the first floor trees before the "Tobie Bekhor Wing" sign
seq	T	2	You encountered sculpture called "Sails" before the pair of paintings by Dan Christensen called "Jivarro 2" and "Illinois"

seq	T	2	You encountered the sculpture called "One Nine North" before the model of Baycrest
seq	T	2	You encountered the shuffleboard game before the pair of paintings by Dan Christensen called "Jivarro 2" and "Illinois"
seq	T	2	You encountered the fire extinguisher before the first floor trees
seq	T	2	You encountered the cluster of photographs before the garbage bin
seq	T	2	You encountered the Riopelle prints before the "Spiro Family Gardens" painting
seq	T	2	You encountered the frames with the names of contributors before the painting called "Autumn Song"
seq	T	2	You encountered the painting called "Freedom 7" before you encountered the model of Baycrest
seq	T	2	You encountered the "Spiro Family Gardens" painting before the painting called "Freeedom 7"
seq	T	2	You encountered the weaved artwork before the fire extinguisher
seq	T	2	You encountered the artwork cxalled "Ruth and Naomi" before the large yellow painting
seq	T	2	You encountered "Head with Armstrong" before the weaved artwork
seq	T	2	You encountered the portrait of the nurse before the weaved artwork
seq	T	2	You encountered the "Tobie Bekhor Wing" sign before the garbage bin
seq	T	2	You encountered the television before the first floor trees
seq	T	2	You encountered the buildings seen through the window before the "Tobie Bekhor Wing" sign
seq	T	2	You encountered the garbage bin before you encountered the large yellow painting
seq	T	2	You encountered the painting called "Autumn Song" before the "Spiro Family Gardens" painting

seq	T	3	You encountered the weaved artwork before the television
seq	T	3	You encountered the frames with the names of the campaign contributors before the "Spiro Family Gardens" painting
seq	T	3	You encountered the frames with the names of the campaign contributors before the buildings seen through the windows
seq	T	3	You encountered the shuffleboard game before the television
seq	T	3	You encountered the painting called "Autumn Song" before the painting called "Cradle of the Moon"
seq	T	3	You encountered the sculpture called "Sails" before the frames with the names of the campaign contributors
seq	T	3	You encountered the television before the "Tobie Bekhor Wing" sign
seq	T	3	You encountered the pair of paintings by Dan Christensen called "Jivarro 2" and "Illinois" before the Riopelle prints
seq	T	3	You encountered the buildings seen through the window before the garbage bin
seq	T	3	You encountered the potrait of the nurse before the frames with names of campaign contributors
seq	T	3	You encountered the shuffleboard game before the painting called "Autumn Song"
seq	T	3	You encountered the television before you enountered the painting called "Cradle of the Moon"
seq	T	3	You encountered "Head with Armstrong before "Rotation"
seq	T	3	You encountered the "Tobie Bekhor Wing" sign before the artwork called "Ruth and Naomi"
seq	T	3	You encountered the "Spiro Family Gardens" painting before the sculpture called "One Nine North"
seq	T	3	You encountered the painting called "Cradle of the Moon" before the model of Baycrest
seq	T	3	You encountered the painting called "Freedom 7" before the large white sculpture

seq	T	3	You encountered the cluster of photographs before the large yellow painting
seq	T	3	You encountered "Rotation" before the first floor trees
seq	T	3	You encountered the first floor trees before the cluster of photographs
seq	T	3	You encountered the fire extinguisher before you encountered the buildings seen though the window
seq	T	3	You encountered the cluster of photographs before the large white sculpture
seq	T	3	You encountered the portait of the nurse before the fire extinguisher
seq	T	3	You encountered "Rotation" before the Riopelle prints
seq	T	3	You encountered the Riopelle prints before the painting called "Freedom 7"
seq	T	3	You encountered the painting called "Cradle of the Moon" before the artwork called "Ruth and Naomi"
seq	F	1	You encountered the first floor trees before the painting called "Autumn Song"
seq	F	1	You encountered the garbage bin before the painting called "Freedom 7"
seq	F	1	You encountered the "Tobie Bekhor Wing" sign before the painting called "Cradle of the Moon"
seq	F	1	You encountered the model of baycrest before the artwork called "Ruth and Naomi"
seq	F	1	You encountered the model of Baycrest before the garbage bin
seq	F	1	You encountered the fire exit before the pair of paintingd by Dan Christensen called "Jivarro 2 and "Illinois"
seq	F	1	You encountered the fire extinguisher before the frames with the names of campaign contributors

seq	F	1	You encou ntered the garbage bin before the scultpture called "One Nine North"
seq	F	1	You encountered the painting called "Freedom 7" before the "Tobie Bekhor Wing" sign
seq	F	1	You encountered the weaved artwork before the sculpture called "Sails"
seq	F	1	You encountered the pair of paintings by Dan Christensen called "Jivarro 2" and "Illinois" before "Rotation"
seq	F	1	You encountered the pair of paintings by Dan Christensen called "Jivarro 2" and "Illinois" before the weaved artwork
seq	F	1	You encountered the "Spiro Family Gardens" painting before the buildings seen through the window
seq	F	1	You encountered the "Tobie Bekhor Wing" sign before the "Spiro Family Gardens" Painting
seq	F	1	You encountered the "Spiro Family Gardens" painting before the first floor trees
seq	F	1	You encountered the sculpture called "Sails" before the portrait of the nurse
seq	F	1	You encountered the painting called "Autumn Song" before the television
seq	F	1	You encountered the weaves artwork before the shuffleboard game
seq	F	1	You encountered the large yellow painting before the model of Baycrest
seq	F	1	You encountered the first floor trees before you encountered the Riopelle prints
seq	F	1	You encountered the sculpture called "Sails" before "Head with Armstrong"
seq	F	2	You encountered the Riopelle prints before the frames with the names of the campaign contributors
seq	F	2	You encountered the large white sculpture before the garbage bin

seq	F	2	You encountered the painting called "Cradle of the Moon" before the Riopelle prints
seq	F	2	You encountered the large white sculpture before the sculpture called "One Nine North"
seq	F	2	You encountered the shuffleboard game before the "head with Armstrong"
seq	F	2	You encountered "Rotation" before the portrait of the nurse
seq	F	2	You encountered the sculpture called "One Nine North" before the painting called "Cradle of the Moon"
seq	F	2	You encountered the television before "Rotation"
seq	F	2	You encountered the cluster of photographs before the "Spiro Family Gardens" painting
seq	F	2	You encountered the buildings seen through the window before the television
seq	F	2	You encountered the television before the pair of paintings by Dan Christensen called "Jivarro 2" and "Illinois"
seq	F	2	You encountered the cluster of photographs before the buildings seen through the window
seq	F	2	You encountered the sculpture called "One Nine North" before the "Tobie Bekhor Wing" sign
seq	F	2	You encountered the frames with the campaign contributors before the weaved artwork
seq	F	2	You encountered the frames with the name of campaign contributors before the shuffleboard game
seq	F	2	You encountered "Rotation" before the sculpture "Sails"
seq	F	2	You encountered the artwork called "Ruth and Naomi" before the cluster of photographs
seq	F	2	You encountered the artwork called "Ruth and Naomi" before the cluster of photographs

seq	F	2	You encountered the artwork called "Ruth and Naomi" before the painting called "Freedom 7"
seq	F	2	You encountered the Riopelle prints before the fire extinguisher
seq	F	3	You encountered the buildings seen through the window before you encountered the pair of paintings by Dan Christensen called "Jivarro 2" and "Illinois"
seq	F	3	You encountered the painting called "Autumn song" before the weaved artwork
seq	F	3	You encountered the sculpture called "One Nine North" before the "Spiro Family Gardens" painting
seq	F	3	You encountered the "Tobie Bekhor Wing" sign before the Riopelle prints
seq	F	3	You encountered the model of Baycrest before the cluster of photographs
seq	F	3	You encountered the first floor trees before the frames with the name of campaign contributors
seq	F	3	You encountered the painting called "Freedom 7" before the Riopelle prints
seq	F	3	You encountered the first floor trees before you encountered the pair of paintings by Dan Christensen called "Jivarro 2" and "Illinois"
seq	F	3	You encountered the painting called "Autumn Song" before "Rotation"
seq	F	3	You encountered the "Tobie Bekhor Wing" sign before painting called "Autumn song"
seq	F	3	You encountered the painting called "Freedom 7" before the buildingd seen through the window
seq	F	3	You encountered the large yellow painting before the sculpture called "One Nine North"
seq	F	3	You encountered the pair of paintings by Dan Christensen called "Jivarro 2" and "Illinois" before the portrait of the nurse

seq	F	3	You encountered the cluster of photographs before the painting of "Autumn song"
seq	F	3	You encountered the Riopelle prints before the weaved artwork
seq	F	3	You encountered the television before the sculpture called "Sails"
seq	F	3	You encountered the large whire sculpture before the "Tobie Beckhor Wing" sign
seq	F	3	You encountered the garbage bin before the "Spiro Family Gardens" painting
seq	F	3	You encountered the Spiro Family Gardens" painting before the television
seq	F	3	You encountered the fire extinguisher before the shuffleboard game
seq	F	3	You encountered the fire extinguisher before the shuffleboard game
seq	F	3	You encountered the large yellow painting before the painting called "Freedom 7"
seq	F	3	You encounteredthe fire extinguisher before the sculpture called "Sails"
seq	F	3	You encountered the sculpture called "One Nine North" before the first floor trees
seq	F	3	You encountered the frames with the names of the campaign donors before "Head with Armstrong"
seq	F	3	You encountered the garbage bin before the painting called "Cradle of the Moon"
seq	F	3	You encountered the pair of paintings by Dan Christensen called "Jivarro 2" and "Illinois" before "Head with Armstrong"
seq	F	3	You encountered the painting called "Cradle of the Moon" before the fire extinguisher
seq	F	3	You encountered the model of Baycrest before the "Tobie Bekhor Wing" sign