Temporal Dynamics of Memory Integration Processes

Liu, Zhenghao

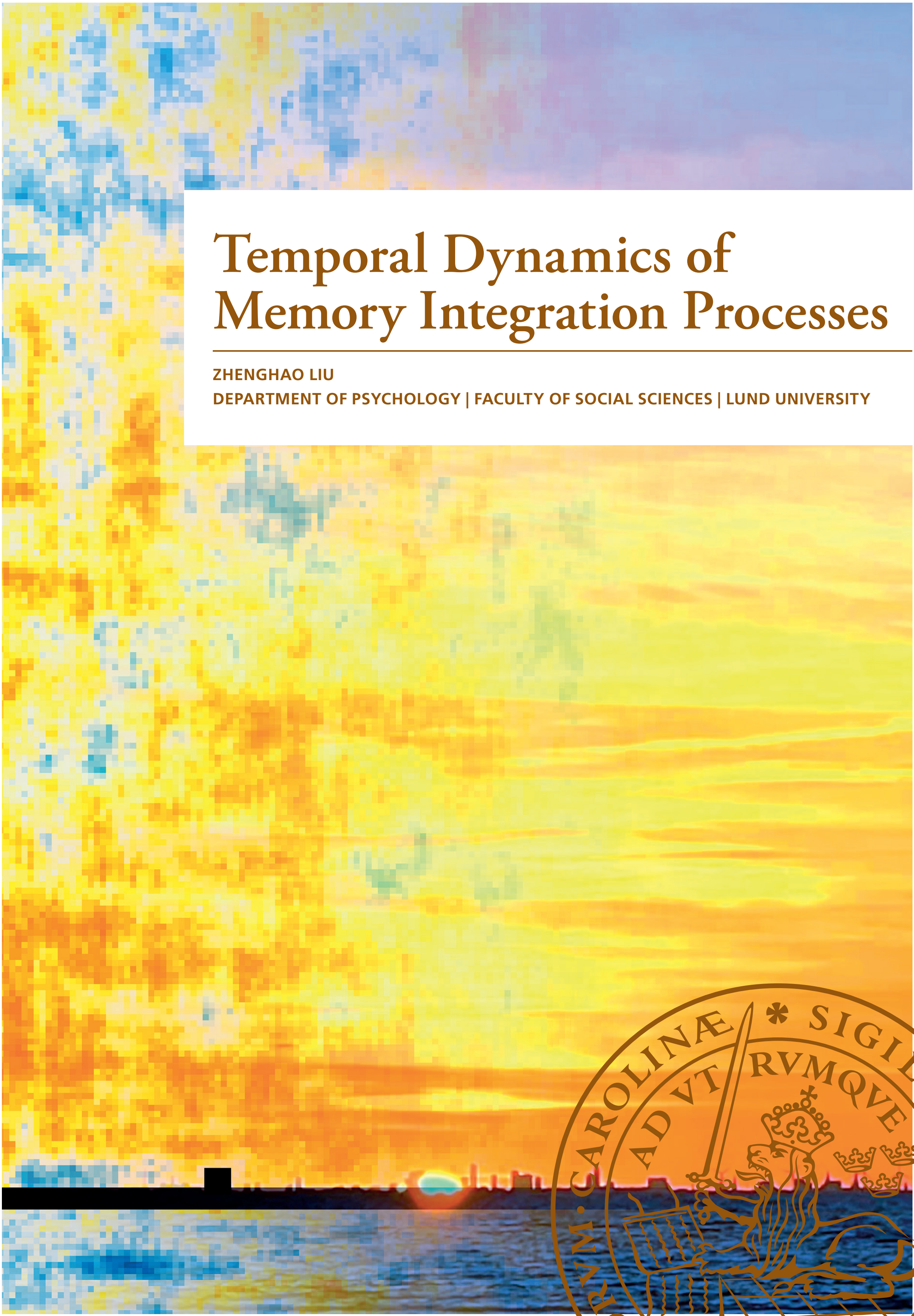
2025

Document Version:
Publisher's PDF, also known as Version of record

Link to publication

Citation for published version (APA):
Liu, Z. (2025). *Temporal Dynamics of Memory Integration Processes*. [Doctoral Thesis (compilation), Department of Psychology]. Lund University.

Total number of authors:
1



Temporal Dynamics of Memory Integration Processes

ZHENGHAO LIU

DEPARTMENT OF PSYCHOLOGY | FACULTY OF SOCIAL SCIENCES | LUND UNIVERSITY

Temporal Dynamics of Memory Integration Processes

Temporal Dynamics of Memory Integration Processes

Zhenghao Liu

DOCTORAL DISSERTATION

Doctoral dissertation for the degree of Doctor of Philosophy (PhD) at the Faculty of Social Sciences at Lund University to be publicly defended on date 3rd of June at 13.15 in Eden Hörsal, Allhelgona kyrkogata 14, Lund

Faculty opponent
Prof. Bernhard Staresina, University of Oxford

Organization: LUND UNIVERSITY

Document name: **Date of issue**

Author(s): Zhenghao Liu **Sponsoring organization:**

Title and subtitle: Temporal Dynamics of Memory Integration Processes

Abstract:

Episodic memories can extend beyond direct experiences. For example, if you see a woman walking a dog and later observe a man walking the same dog, you might infer a connection between them. These inferences, crucial for making novel decisions and extending knowledge to new situations, are thought to rely on memory integration mechanisms.

Two main mechanisms have been proposed for memory integration. The integrative encoding account suggests that novel experiences can trigger the reactivation of past events, promoting the incorporation of new information into existing knowledge structures to form integrated memory representations. A complementary view proposes that memory integration can be achieved on demand, by flexibly retrieving and recombining information from distinct memory representations.

The present thesis employs time-resolved multivariate pattern analysis and representational similarity analysis to measure memory reactivation during new learning and tests of associative inference. This approach enables the investigation of the temporal dynamics of processes underlying memory integration and their boundary conditions. Study 1 investigates the temporal dynamics of integrative encoding and highlights individual differences in the capacity to integrate memories across events. Study 2 examines how the encoding context influences memory integration processes, while Study 3 focuses on the distinct roles of context and semantic schema in memory integration. Finally, Study 4 investigates how both integrated and separate memory representations support episodic memory.

This thesis presents novel evidence on the mechanisms underlying memory integration and elucidates potential boundary conditions for integrating memories across different events. In conclusion, memory integration is a multifaceted phenomenon influenced by processes at multiple mnemonic stages and by various boundary conditions. The resulting integrated and separate representations are adaptively used to support goal-relevant behaviour, highlighting the flexibility and complexity of memory functions.

Key words: memory integration, EEG, MVPA, RSA, context, schema

Classification system and/or index terms (if any) Supplementary bibliographical information

Language **English** **Number of pages**:

ISSN and key title:

ISBN: 978-91-8104-541-3 (print); 978-91-8104-542-0 (electronic)

Recipient’s notes Price Security classification

Signature Date 2025-04-24

Temporal Dynamics of Memory Integration Processes

Zhenghao Liu

LUND
UNIVERSITY

Coverphoto by Zhenghao Liu

Faculty of Social Sciences
Department of Psychology

ISBN (print) 978-91-8104-541-3
ISBN (electronic) 978-91-8104-542-0

Printed in Sweden by Media-Tryck, Lund University
Lund 2024

Acknowledgements

"The way ahead is long and has no ending; yet high and low I'll search with my will unbending." – Qu Yuan

Completing this PhD journey has been both a challenging and immensely rewarding experience, and I owe my deepest gratitude to the many people who supported me along the way.

First and foremost, I would like to express my sincere appreciation to my supervisors, *Inês Bramão* and *Mikael Johansson*, for their invaluable guidance, patience, and encouragement. Their expertise, insightful feedback, and unwavering support have been instrumental in shaping this project. I am really grateful for the opportunity to learn from such inspiring mentors.

Beginning my PhD during the unprecedented challenges of the COVID-19 pandemic was not easy, with remote work, limited lab access, and physical distancing becoming the norm. Despite these obstacles, Lund Memory Lab demonstrated remarkable resilience and adaptability. I am thankful for the efforts of my colleagues, who made even the most difficult days manageable.

I also extend my gratitude to my colleagues at Department of Psychology, Lund University for their support, and to my commentators in the seminars of this project. This journey has been a collective effort, and I am deeply thankful to everyone who played a part in it.

Finally, none of this would have been possible without the love and support of my family, thank you for your endless encouragement, sacrifices, and belief in me, even across distances. Your strength has been my motivation.

The research presented in this thesis is financially supported by the grant of the Swedish Research Council.

It has been a great pleasure and privilege to pursue my doctoral studies in Sweden, a country known for its excellence in research, innovation, and philosophy of life. The supportive academic environment, cutting-edge facilities, and international perspective have profoundly enriched my experience.

Table of Contents

Acknowledgements **7**

Table of Contents **9**

Abstract **11**

List of papers **13**

Abbreviations **15**

Introduction **17**

Encoding and Retrieval of Individual Events **19**

- Short-Term / Working Memory 20
- Long-Term Memory 21
- Cognitive Neural Mechanisms of Encoding and Retrieval 23

Integrating Memories Across Event Boundaries **25**

- Hippocampus-mPFC Interaction in Memory Integration 25
- Assessing Memory Integration 26
  - Integrative encoding 28
  - Flexible retrieval 28
  - Boundary conditions 29
- Integration Versus Separation 30

Detecting Real-Time Memory Reinstatement **33**

- Electroencephalogram (EEG) 33
- Multivariate Pattern Analysis 34
  - From Univariate to Multivariate 35
  - Decoding Memory Reinstatement 35
  - Representational Similarity Analysis 36

Aim of the Present Thesis **39**

Research studies **41**

- Study 1 41
- Study 2 43
- Study 3 45

Study 4 47

General Discussion 51

Temporal Dynamics of Integrative Encoding and Flexible Retrieval......... 51

Boundary Conditions Between Integrative Encoding and Flexible Retrieval 53

The Interplay between Integration and Separation..................................... 55

Limitations and Future Studies 57

Concluding remarks 58

References 59

Abstract

Episodic memories can extend beyond direct experiences. For example, if you see a woman walking a dog and later observe a man walking the same dog, you might infer a connection between them. These inferences, crucial for making novel decisions and extending knowledge to new situations, are thought to rely on memory integration mechanisms.

Two main mechanisms have been proposed for memory integration. The integrative encoding account suggests that novel experiences can trigger the reactivation of past events, promoting the incorporation of new information into existing knowledge structures to form integrated memory representations. A complementary view proposes that memory integration can be achieved on demand, by flexibly retrieving and recombining information from distinct memory representations.

The present thesis employs time-resolved multivariate pattern analysis and representational similarity analysis to measure memory reactivation during new learning and tests of associative inference. This approach enables the investigation of the temporal dynamics of processes underlying memory integration and their boundary conditions. Study 1 investigates the temporal dynamics of integrative encoding and highlights individual differences in the capacity to integrate memories across events. Study 2 examines how the encoding context influences memory integration processes, while Study 3 focuses on the distinct roles of context and semantic schema in memory integration. Finally, Study 4 investigates how both integrated and separate memory representations support episodic memory.

This thesis presents novel evidence on the mechanisms underlying memory integration and elucidates potential boundary conditions for integrating memories across different events. In conclusion, memory integration is a multifaceted phenomenon influenced by processes at multiple mnemonic stages and by various boundary conditions. The resulting integrated and separate representations are adaptively used to support goal-relevant behaviour, highlighting the flexibility and complexity of memory functions.

Key words: memory integration, EEG, MVPA, RSA, context, schema

List of papers

Bramão, I., Liu, Z., & Johansson, M. (2025). Remembering the past affects new learning: The temporal dynamics of integrative encoding. *Neuropsychologia*, *212*, 109148. https://doi.org/10.1016/j.neuropsychologia.2025.109148

(Published paper reprinted with permission from The Elsevier Ltd.)

Liu, Z., Johansson, M., Johansson, R., & Bramão, I. (2024). The effects of episodic context on memory integration. *Scientific Reports*, *14*(1), 30159. https://doi.org/10.1038/s41598-024-82004-7

(Published paper reprinted with permission from Nature Portfolio)

Liu, Z., Bramão, I., & Johansson, M. (manuscript in preparation). Schema congruency impacts the mechanisms supporting memory integration of overlapping events.

Liu, Z., Johansson, M., & Bramão, I. (manuscript in preparation). Episodic events are flexibility encoded in both integrated and separated neural representations.

Abbreviations

CLS	Complementary Learning System
EEG	Electroencephalogram
ERP	Event Related Potential
MVPA	Multivariate Pattern Analysis
mPFC	Medial Prefrontal Cortex
RSA	Representational Similarity Analysis

Introduction

After witnessing an accident, one drives more carefully on the road; after completing a group task, one learns how to facilitate effective cooperation; after visiting different countries, one becomes more open to cultural differences. In this way, events lead people through life's journey – learning from the past informs and guides the future.

An event is 'the segment of time at a given location that is conceived by an observer to have a beginning and an end (Zacks & Tversky, 2001)'. As such, the representation of an event depends on the observer's subjective mental construction, which involves various cognitive functions such as perception, attention, memory, and language, etc.

For example, to watch a basketball game, one must be able to perceive its constituent elements, such as the court, the basket, the players, and the ball. Additionally, one also needs attention allocation, to focus more on players and less on the snack seller, to fully engage with the game. By recollecting players previous performances, one can tell who the star player or the dark horse is in this game. To read the scoreboard and to understand the commentary, a basic knowledge of language is also needed. Through the interplay of these various cognitive processes, the event of 'a basketball game' is represented in mind, which might become the topic of a conversation with other basketball club members in the following week.

Events do not usually stand alone. By sharing common elements, such as people places or objects, individual events often overlap, enabling the formation of connections across distinct experiences (e.g., Morton et al., 2017; Schlichting & Preston, 2015). This process of memory integration, which binds related events into a comprehensive representation, allows learning to happen beyond direct experience and benefits future adaptive behaviour, such as decision making (e.g., Wimmer & Shohamy, 2012) and relational inferences (e.g., Preston et al., 2004). Memory integration can occur at the time of encoding, when encountering a new event overlaps with a previous one, via integrative encoding (Shohamy & Wagner, 2008; Zeithamova, Schlichting, et al., 2012). Alternatively, it can take place during later retrieval, when integration is required to support a given task, via flexible retrieval (Koster et al., 2018; Kumaran & McClelland, 2012). By revealing the real-time memory reactivation during encoding and retrieval that contributes to memory integration, we could gain further insights into the mechanisms by which memory integration is supported through the coordination of various cognitive processes.

Nonetheless, the overlap between events, while enabling the creation of connections between them, also brings memory interference and competition (e.g., Bramão et al., 2022; Kuhl et al., 2011). One proposed mechanism for managing such interference is pattern separation, which is thought to reduce the interference between similar events and help preserve the fidelity of original memory (Kirwan & Stark, 2007; Rolls, 2013; Yassa & Stark, 2011). As such, pattern separation might be recruited when encountering similar events. Therefore, how the brain handles such complementary processes, i.e., integration vs separation, is yet another question to address in the research of memory integration mechanisms.

The present thesis investigated the mechanisms involved in memory integration by examining real-time brain activity during encoding and retrieval. Particularly, the application of multivariate pattern analysis allowed us to track the temporal dynamics of memory reactivation and helped us to elucidate how different mnemonic processes coordinate and jointly lead to the connection that associates distinct but related events. Specifically, the present thesis first revealed the temporal dynamics of the processes involved in memory integration and illustrated how memory reinstatement during new learning may lead to different mnemonic consequences depending on individual differences (Study 1). This thesis thereafter illustrated how the encoding context (Study 2) and schema congruency (Study 3) of an event serve as boundary conditions for the mechanisms supporting memory integration, i.e., integrative encoding vs flexible retrieval. With the last study (Study 4), the present thesis investigated how the brain enables the coexistence of the integrated and separated representations of overlapping events to support different mnemonic functions.

In summary, the present thesis provided new evidence on how people associate distinct but related experiences to generate integrated memory representations across various mnemonic stages, and how these mechanisms vary as a function of encoding context and schema congruency. Finally, the present thesis also shed light on how memory integration coordinates with memory separation, enabling both inference and accurate recollection of individual events.

Encoding and Retrieval of Individual Events

Past events are stored in memory, a complex functional hierarchical system including several subsystems (Squire & Zola, 1996; Tulving, 1987). According to the duration of maintenance, memory can be divided into short-term memory and long-term memory. Short-term memory, commonly referred to as working memory, maintains mental representations for seconds while supporting ongoing cognitive operations. (Baddeley, 1992; Baddeley & Hitch, 1974). As such, it bridges the physical and mental world by temporarily storing the events that are to be transferred into long-term memory (Baddeley & Hitch, 1974; Modigliani & Seamon, 1974; Ranganath et al., 2005). In contrast, long-term memory retains information for periods ranging from minutes to years and comprises two major subsystems: declarative and non-declarative memory (Squire, 1992; Squire & Zola, 1998). Non-declarative memory comprises the memories that are unconscious but behaviourally influential, e.g., the motor skills of driving a car. In contrast, declarative memory refers to the conscious part of long-term memory, which includes semantic knowledge, e.g., thunderstorm may compromise flight safety, and memory for episodes, e.g., receiving a thunderstorm warning yesterday.

Different memory systems are identified based on findings showing their functional independence. For example, non-declarative memories may remain intact in patients who experience degradation in declarative memory systems (Squire, 1992). Such dissociation suggests that these two types of memory rely on different memory systems, so the damage in one system doesn’t affect the other. However, different memory systems usually coordinate to enable the complete functionality of memory. For example, remembering receiving a thunderstorm warning (episodic memory) and knowing that thunderstorms might compromise flight safety (semantic memory), an individual can understand why a flight has been cancelled. If no alternative flight is guaranteed, the person may then choose to drive to the destination (non-declarative procedural memory).

Short-Term / Working Memory

Short-term / working memory refers to the memory system that maintains representations for a few seconds (Baddeley & Hitch, 1974). The capacity of short-term memory is limited and can hold, at maximum, five to nine chunks simultaneously (Miller, 1956). When encoding events in short-term memory, the interrelated elements contained in that event can be organized into chunks (Thalmann et al., 2019), according to the memorizer's experience and skill. Memorizing chunks improves efficiency, compared to memorizing individual elements. For example, by asking a master and a beginner to reproduce the moves of the chess, researchers found that, by combining several moves into a chunk, the master could reproduce the moves better and quicker than the novice, who tended to memorize the moves one by another (Chase & Simon, 1973). Following up studies suggested that the number of chunks was overestimated due to the involvement of proficiency and knowledge (Gobet & Clarkson, 2004), which highlights the interaction between short-term memory and long-term memory.

Beyond holding representations, short-term memory was also suggested to be a working memory system, as it provides a platform where cognitive manipulations over the representations may happen (Baddeley, 1992; Baddeley & Hitch, 1974). Several modules were suggested to support the function of holding and manipulating representations. These modules include the visual sketch pad to maintain visual information, the phonological loop to maintain verbal-auditorial information, the episodic buffer to maintain episodic and contextual information and the central executive to perform cognitive manipulations. Beyond its basic function of short-term maintenance, working memory is also characterized by cognitive operations facilitated by the central executive system. Attentional control—a core executive function supported by working memory—is critically involved in many cognitive processes (McCabe et al., 2010). Besides, some advanced cognitive functions also show reliance on working memory. For example, in a reasoning task, both the storage capacity and the coordination ability were predictive for the reasoning performance, reflecting core functions of working memory (Buehner et al., 2005).

Cognitive tasks typically involve the simultaneous engagement of both short-term and long-term memory systems (Atkinson & Shiffrin, 1968). Consequently, event encoding and retrieval requires frequent interactions between these two memory systems. To efficiently represent events in working memory, chunking serves as a reliable strategy, which depends on the acquired skills, knowledge and experience stored in the long-term memory system (Gobet & Clarkson, 2004; Thalmann et al., 2019). In turn, the events maintained in working memory could be used to update long-term memory representations and form new knowledge structure via consolidation mechanisms (Dudai et al., 2015; Modigliani & Seamon, 1974). Beyond encoding, event retrieval also requires interactions between these two memory systems to facilitate the comparison between the retrieval cue and stored long-term memory traces (Slotnick, 2013), which further underscores their interdependence in supporting cognitive functioning.

In summary, short-term / working memory is a memory system serving as a platform to temporary store representations and perform cognitive operations, which enables the event cognition via the interactions with long-term memory system.

Long-Term Memory

Long-term memory is the memory that can be stored over extended periods of time (Tulving, 1987). With the consolidation mechanisms, such as retention (Modigliani & Seamon, 1974) and experience-based memory template (Gobet & Simon, 1996), memory representations temporarily maintained in short-term memory can be transferred into long-term memory (Cotton & Ricker, 2022; Dudai, 2004, 2012; Dudai et al., 2015).

Based on whether it involves conscious recollection, long-term memory can be categorized into non-declarative memory and declarative memory. Non-declarative memory, featured as *a heterogeneous collection of nonconscious learning capacities* (Squire & Zola, 1996), involves memory formats such as motor skills, priming, classical conditioning, etc. These memories affect human behaviour without intentional conscious recollection, which are thus also named after implicit memory (Roediger, 1990). For example, dancing is a motor skill. Through some training and accumulated experience, one is able coordinate body parts to dance with the music following the standards, which does not rely on intentional recollection of a ‘to do list while dancing’. Non-declarative memory could affect event cognition via the interaction with declarative memory. When looking into how master dancers and non-dancers segment a dancing video into subsections, differences in segmentation boundaries were found related to the mastery of dancing skills, showing that events are more neatly organized if the corresponding skill is better mastered (Bläsing, 2015).

Declarative memory, characterized by conscious recollection of facts and events (Squire & Zola, 1996, 1998), consists of semantic memory and episodic memory. Semantic memory is the memory about the concepts and facts, which enabled the formation of knowledge structure of the world, i.e., the schema (Bartlett, 1932; Piaget, 1929). Events are usually episode specific, which might happen at different times, places and consist of different activities. However, episodic general structure, the schemas, can be abstracted from similar events, which could support and facilitate future event cognition (Radvansky & Zacks, 2014). For example, when discussing trips to the seaside, one would expect to hear about events such as swimming, fishing, and sunbathing, rather than feeding cows. The relationship between seaside and swimming is irrelevant to sensory features of the elements in the event, e.g., colour of the sea, texture of the beach, but embedded in the schema that ‘swimming is a popular way of enjoying a trip to the seaside’ (Gilboa & Marlatte, 2017).

Episodic memory stores the information about what, when, where, and enables the time traveling to revisit the past (Tulving, 1993). In contrast to semantic memory, episodic memory is the declarative memory comprising episode specific information, which is thus directly related to event remembering. Due to the number of elements in episodes, the encoding of episodic memory involves the binding processes connecting various features to form a unified representation of an event (Ranganath, 2010). For example, features such as the time, location and background scene, form the context of an event (Yonelinas et al., 2019), while the objects, as well as their relationships (Mayes et al., 2007) and activities (Gold et al., 2017), form the content of the events. To memorize such an event, one needs to build the connections between the content and the context to form a unified representation of this episode. During episodic memory recollection, the elements of the event are supposed to be recollected to allow for the complete reconstruction of the episodes. Hence, during event retrieval, the brain regions that encode the elements are supposed to engage again to enable its recollection and support the reconstruction of the episode (Johnson et al., 2009).

The complementary learning system (CLS) theory proposed a potential framework of how episodic and semantic memory are formed (McClelland et al., 1995). The CLS theory illustrates the work allocation of two learning systems, the rapid learning system and the slow learning system. The rapid learning system enables rapid encoding of novel information, especially those involving episodic details (Baddeley, 2000; O’Reilly & McClelland, 1994). The rapid encoding of events is thought to rely on the recurrent network structure in CA3 subfield of hippocampus (Nakazawa et al., 2003), which allows the maintenance of memory traces for extended period after just a one-trial exposure. In contrast, the neocortex specializes in slow, incremental learning that extracts statistical regularities and builds schemas (Gilboa & Marlatte, 2017). Neuroimaging studies revealed that cortical learning starts with the greatest changes occurring during initial exposures, followed by progressively smaller updates (Davis & Gaskell, 2009; Frankland & Bontempi, 2005; Takashima et al., 2009; Tompary & Davachi, 2017). This gradual learning process, while computationally efficient for building stable knowledge, creates a vulnerability: direct cortical encoding of new information would distort existing memories due to overlapping representations (McClelland et al., 1995). Hence, it is proposed that the hippocampus initially encodes new memories, which are then gradually integrated with existing cortical knowledge through consolidation (Kumaran et al., 2016; McClelland et al., 1995).

In summary, long-term memory is the system that keeps memory representations for extended periods of time, enabling the reactivation of past experiences to guide future behaviour.

Cognitive Neural Mechanisms of Encoding and Retrieval

Encoding and retrieval of events are prerequisites for past experiences to guide future behaviour. Even though the exact mechanisms of encoding, storage and retrieval remains to be clarified, recent advances in cognitive neuroscience have shown how several brain regions contribute to these processes.

Event encoding starts with the perception of elements. The sensory inputs, usually from visual channel, are transmitted via two brain pathways to the parietal lobe and the medial temporal lobe. The information stream transmitted to the parietal lobe serves the purpose of identifying the spatial location of the different objects, the ‘where pathway’. Furthermore, the information stream transmitted to the medial temporal lobe serves the purpose of recognizing/naming the different objects, the ‘what pathway’ (De Haan & Cowey, 2011). These two streams carry distinctive features about the objects, which are then bound to form the complete knowledge of where and what an object is.

In addition to parietal and temporal lobe, other cortical regions also play vital roles in event representation. For example, the event of a recent family dinner involves the activation of a coherent representation comprising information integrated across these different networks (e.g., Reagh & Ranganath, 2023; Simons et al., 2022). Specifically, the medial prefrontal cortex network (mPFC) captures schematic information at high levels of abstraction (e.g., knowledge about what a family dinner is), the posterior-medial network (PM) represents contextual details of specific events (e.g., the place where a recent family dinner occurred), and the anterior-temporal (AT) network represents specific content, such as objects or people (e.g., who was present at the latest family dinner).

All the information distributed across several brain regions is bind by the hippocampus to form a comprehensive representation of an event. Through the hippocampal binding, the episode, comprising the content and the context, is enclosed as a complete event (Ranganath, 2010; Yonelinas et al., 2019). In addition to information binding, hippocampal functions pattern separation and pattern completion, are also highly involved in memory encoding and retrieval.

Similar memories usually interfere with each other. For example, when an element occurs in two events, the recollection of these events would be worse, compared to the events that comprised of all different elements (Bramão et al., 2022; Kuhl et al., 2011). To cope with such interference, hippocampus encodes these overlapping events into distinct, orthogonally, neural representations, so the activation of one representation would be less interfered with another. Such differentiation in neural representations, i.e., pattern separation, was observed in CA3 subregion of hippocampus, dentate gyrus (Bakker et al., 2008) and adjacent medial temporal lobe (Kirwan & Stark, 2007).

Pattern completion is the hippocampal function that supports memory search. Retrieving the memory of a previous event starts with a retrieval cue–often a fraction of an event, such as an element or a temporal segment (Winocur, 1980). Such fraction is meant to be completed by searching for complementary fractions that together encompass the entire event in long-term memory, a process referred to as ‘pattern completion’ (Horner et al., 2015; Rolls, 2013). When the sensory input of the cue arrives at hippocampus, the brain functional network for memory retrieval, centred at hippocampus and comprising broad cortical regions, would engage to search for the elements of related event to allow for the reconstruction (Rugg & Vilberg, 2013; Ryan et al., 2008).

Memory retrieval covaries as a function of the similarity between cortical activation patterns during encoding and retrieval (e.g., Danker et al., 2016; Johnson et al., 2009; Johnson & Rugg, 2007), suggesting that the accurate reconstruction of a past event relies on the engagement of the cortical regions that were activated during its encoding. Such cortical reinstatement not only highlighted the functional relevance of the cortical regions in both encoding and retrieval of events, but also brings the possibility of detecting real-time memory reinstatement by decoding brain activation patterns without interfering the ongoing task (Haxby et al., 2014).

In summary, the encoding and retrieval of an event engage a distributed brain network spanning broad cortical areas, with the hippocampus at its core.

Integrating Memories Across Event Boundaries

Events often overlap with each other in terms of people, places, and objects, allowing connections to be created between distinct experiences. For example, seeing a person walking a dog and later seeing another person walking the same dog, one may realize that these two people are somehow related. By associating these two episodes via the overlapping content, the memory structure is updated, and the new knowledge is derived by searching through the associations within (person-dog) and across events (person-person). As such, learning can happen beyond direct experience by integrating distinct memory traces (Morton et al., 2017; Schlichting & Preston, 2015), to facilitates human adaptive behaviour such as decision making (e.g., Wimmer & Shohamy, 2012) and relational inferences (Preston et al., 2004).

In classic CLS theory (McClelland et al., 1995), the association across different episodes is supported by the neocortex as the consequence of slow learning. However, recent findings blur such division of labour by showing the involvement of hippocampus in memory integration across experiences and concepts (e.g., Danker et al., 2016; Mack et al., 2018; Zeithamova et al., 2012). Researchers showed that the engagement of hippocampus allows for the rapid generation of new knowledge, by combining information across a small number of events (Zeithamova & Bowman, 2020). In addition to hippocampus, memory integration also relies on the functions of medial prefrontal cortex (Schlichting & Preston, 2015). Through the communication and interaction between these two brain regions, the associations between the distinct experiences can be formed.

Hippocampus-mPFC Interaction in Memory Integration

As the hub for rapid encoding and retrieval, hippocampus enables memory integration via the interplay between the hippocampal binding, encoding and retrieval processes (Schlichting & Preston, 2015). The overlapping content shared by different events facilitates the memory integration. The recognition of the overlapping content would activate the pattern completion mechanism to search for and reactivate the past episodes where the content ever presented (Horner et al., 2015; Rolls, 2013; Staresina et al., 2016). This is thought to rely on the functions of hippocampal subregion CA3 (Rolls, 2013). When a memory is reinstated, the CA1 subregion is thought to compare the current and past events, and if distinctions are detected, it facilitates new encoding in CA3 (Schlichting & Preston, 2015). This forms the connection between two events to generate new knowledge. Importantly, the integration of memories relies not only on the hippocampus but also other cortical areas, such as mPFC.

The medial prefrontal cortex (mPFC) is proposed to store the knowledge of the world, i.e., schema (Ghosh & Gilboa, 2014; Preston & Eichenbaum, 2013; Schacter et al., 2012), and to encode associations between episodes to facilitate adaptive human behaviour (Euston et al., 2012). Memory integration involves the formation of new associations between memories, which thus relies on mPFC. Upon encountering the overlapping content, the hippocampus would activate the related memory structure stored in mPFC, to allow the integration of memories (Kroes & Fernández, 2012; Wilson et al., 2014). Additionally, further evidence also suggested that following the integration in the hippocampus, the memory schemas are updated in mPFC according to the hippocampal inputs (Schlichting & Preston, 2015; Van Kesteren et al., 2012).

In summary, memory integration relies on the interactions between the hippocampus and the mPFC (Schlichting & Preston, 2015). The hippocampus plays a crucial role in recognizing overlapping content, guiding memory search, and forming associations across distinct events, thereby supporting the integration of related experiences into coherent memory representations. On the other hand, the medial prefrontal cortex (mPFC) contributes to this process by reactivating relevant schemas based on prior knowledge and experiences, thereby supporting the updating of existing memory models to accommodate new information.

Assessing Memory Integration

Memory integration may happen when events overlap with each other. To investigate the mechanisms supporting memory integration, researchers have developed several paradigms that allow participants to generate new knowledge derived from distinct experiences (e.g., Preston et al., 2004; Shohamy & Wagner, 2008). Associative inference task is one of those paradigms. In this task, the memory integration is assessed by evaluating the inference making across events encoded in distinct sessions (Preston et al., 2004; Zeithamova, Dominick, et al., 2012; Zeithamova & Preston, 2010). With this paradigm, researchers have previously identified two mechanisms that support memory integration, i.e., integrative encoding (Zeithamova, Dominick, et al., 2012) and flexible retrieval (Kumaran & McClelland, 2012). Additionally, previous work has shown that memory integration might not be an isolated mnemonic process, but rather coordinate with other mnemonic processes, such as memory separation (Schlichting et al., 2015), to enable various memory functions.

The typical associative inference paradigm is shown in Figure 1. This task involves an encoding phase and a retrieval phase separated by a distraction task, which is usually implemented to reduce the influence of short-term memory processes. The encoding phase comprises two sessions (see Figure 1). In the first encoding session, several events comprised of two elements A and B (e.g., a picture and a word) are present for the participant to encode. Then in the second encoding session, one of the previously encoded elements B (e.g., the word) is paired with a novel element C (e.g., another picture). Then, after the distraction task, e.g., consecutively subtracting seven from a random number, a retrieval phase is implemented. In the retrieval phase, the memory integration and the memory for individual events is assessed. The AC inference test is implemented to evaluate if participants can combine the information in AB and BC events to generate AC indirect association, where the picture A or C serves as a retrieval cue for the participant to choose the corresponding picture C or A. Memory tests for the individual AB and BC events may also be implemented, where participants are asked which picture is directly associated with a given cue during the encoding phase.

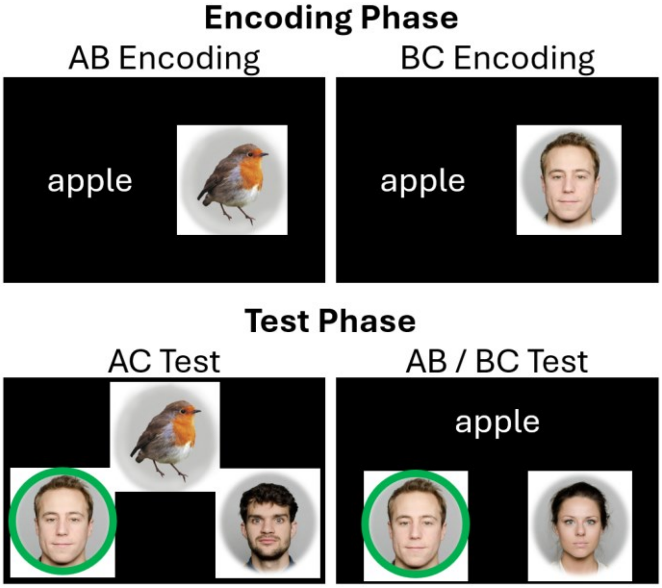


Figure 1 Example of the experimental paradigm of associative inference task. Correct answers are marked out with green circle.

The associative inference task includes two mnemonic stages where memory integration can occur: during BC encoding and/or during AC retrieval. Correspondingly, two distinct but complementary mechanisms, ‘integrative encoding' and 'flexible retrieval', may support memory integration in the associative inference task.

Integrative encoding

The associative inference can be achieved via integrative encoding (Shohamy & Wagner, 2008; Zeithamova, Dominick, et al., 2012). Accordingly, when encoding the BC event, the overlapping element B triggers the reactivation of AB event through pattern completion mechanisms, supported by the hippocampus (Horner et al., 2015; Rolls, 2013). The detection of differences between current experience and reactivated memories, in turn, triggers memory updating mechanisms (e.g., Schlichting et al., 2014). Based on hippocampal and mPFC interactions, the content of the current experience integrates with existing memory structures to allow the update of mental models to incorporate new information and more efficiently represent the world (Morton et al., 2017; Schlichting & Preston, 2015). In the later associative inference task, when the A or C is displayed as the cue, the integrated ABC representation is reinstated, and the corresponding C or A is recollected.

This idea is supported by neural data showing that hippocampal activation during encoding is predictive of later inference performance encoding (Shohamy & Wagner, 2008; Zeithamova, Dominick, et al., 2012). Furthermore, researchers also found that the inference performance was related to the neural representation formed during BC encoding, but not the one formed during AB encoding (Schlichting et al., 2014). This phenomenon was also observed in a study where AB and BC events were constructed in narratives (Cohn-Sheehy et al., 2021). These results suggest that the integrated representation has been formed during BC encoding, so the representation of the individual event (the one formed during AB encoding) does not contribute to performance on the inference task.

In summary, the integrative encoding account proposes that a memory representation, involving both AB and BC events, is formed during the encoding of BC. Such a comprehensive representation plays an essential role in memory integration.

Flexible retrieval

The flexible retrieval account holds that memory integration occurs at the time of the inference test (Kumaran & McClelland, 2012). This account proposes that, due to their similarity, AB and BC events may interfere with each other. Therefore, they are to be encoded in distinct neural representations to best prevent such interferences (Bakker et al., 2008; Kirwan & Stark, 2007; Yassa & Stark, 2011). Then at the test phase, these events would be retrieved in a chained fashion (Holmes et al., 2022) to infer relationships between the events. The big-loop recurrence proposed a feasible way of how this is implemented (Koster et al., 2018). Specifically, the non-overlapping element (A or C) reactivates the memory of the event (AB or BC) via pattern completion. Then the overlapping element (B) would reactivate the other event (BC or AB), which also consisted of this element. Then the linkage between these two events (AB and BC) could be built, which enabled the associative inference task.

This idea is supported by both computational models (Banino et al., 2016) and neural evidence (Koster et al., 2018). Additionally, previous researchers reported more false memories for individual events after making AC inference than before (Carpenter & Schacter, 2017, 2018). This result also aligns with the flexible retrieval account, suggesting that integration only happens by demand, as evidenced by more false memory for original individual events.

Boundary conditions

The involvement of these two complementary mechanisms in memory integration are supported by substantial evidence in literature, suggesting these different accounts are not mutually exclusive. Both integrative encoding and flexible retrieval can contribute to AC inference with their relative contributions depending on particular task demands (Zeithamova, Dominick, et al., 2012; Zeithamova & Bowman, 2020). As such, researchers began the search for the boundary conditions in which people might be in favour of one mechanism over the other. While some of them have been identified, such as task demands (Richter et al., 2016) and temporal proximity of events (Zeithamova & Preston, 2017), more is to be revealed.

This thesis explores the role of the encoding context as a boundary condition for the mechanisms supporting memory integration. The original encoding context is a strong retrieval cue (Godden & Baddeley, 1975, 1980; Herweg, Sharan, et al., 2020). As such, when the original encoding context is revisited, it may facilitate memory integration by promoting the retrieval of relevant events. This is explored in Study 2 of this thesis.

Additionally, schema congruency might also serve as a boundary condition for the memory integration mechanisms. Events congruent with pre-existing schemas demonstrate enhanced encoding and retrieval, which is supported by the medial prefrontal cortex (Brod et al., 2015). Additionally, events incongruent with the schema are also better memorised, after the prediction error induced learning modulated by medial temporal lobe (Greve et al., 2017; Van Kesteren et al., 2013). As schema-congruent and incongruent events are represented differently, the integration across schema-congruent and incongruent events may also rely on different mechanisms. This is explored in Study 3 of this thesis.

Integration Versus Separation

Memory integration is enabled by the overlapping content across events. However, the overlapping content across events can also be a source of memory interference and competition between individual events (Bramão et al., 2022; Kuhl et al., 2011). When memories overlap with each other, they are prone to suffer from proactive and retroactive interference. As such, overlapping events are worse memorized compared to non-overlapping ones (Barnes & Underwood, 1959; Postman & Underwood, 1973). Additionally, the 'fan effect' also shows that, the more events that overlap with each other, the more difficult it is to retrieve any one of them (Radvansky, 1999).

By encoding similar events into distinct representations, pattern separation processes could efficiently control the memory interference and keep the integrity of individual events (Bakker et al., 2008; Kirwan & Stark, 2007; Yassa & Stark, 2011). Moreover, hippocampal function was proposed to vary along its axis, when the anterior hippocampus supporting the formation of integrated memory representations, the posterior hippocampus forming distinct, event-specific memory representations (Brunec et al., 2020). This raise an important question: could the brain encode overlapping events with both integrated and separated representations?

Previous literature has reported the loss in memory for individual events after memory integration, showing trade-off between creating integrated representation and keeping individual events (Banino et al., 2016; Carpenter & Schacter, 2017, 2018). Specifically, the source and the episodic details of individual events were worse memorized after the inference task than before, suggesting that the integrated and separated representations do not co-exist.

However, post-integration impairments in individual event memory were not consistently replicated across studies. Notably, several studies have demonstrated that superior memory for individual events—including direct associations, source, and episodic details—correlates with better associative inference performance (Boeltzig et al., 2023; Bowman et al., 2021; de Araujo Sanchez & Zeithamova, 2023). These findings suggest the possibility that representations of individual events may be preserved following memory integration, which enable both accurate recollection of individual events and successful indirect inference simultaneously.

In summary, both memory integration and memory separation are likely engaged when one performs associative inference task. Particularly, memory integration serves to generate new knowledge and facilitate associative inference across event boundaries, while memory separation serves to keep original events and supports the retrieval of event specific details. Previous fMRI studies have provided evidence that integrated and separated neural representations emerge in different hippocampal subregions (Schlichting et al., 2015). However, the manner in which the brain reconciles these apparently contradictory processes, i.e., integration vs separation, remains to be elucidated.

Detecting Real-Time Memory Reinstatement

The associative inference task involves two key mnemonic stages, i.e., encoding and retrieval, where memory integration can occur. Previous studies have shown that memory integration could happen during both encoding (Shohamy & Wagner, 2008; Zeithamova, Dominick, et al., 2012) and retrieval (Koster et al., 2018; Kumaran & McClelland, 2012). Therefore, to further understand the engagement of the processes enabling memory integration and to reveal how these processes coordinate under various conditions, it is important to detect real-time memory reinstatement and assess how this reinstatement relates to the task performance. Importantly, the detection of the memory reinstatement should not interfere with the ongoing task, which thus requires a 'silent detection' of the real-time memory reinstatement during task performing. For this, the present thesis employed multivariate pattern analysis (MVPA) of electroencephalogram (EEG) to decode real-time memory reinstatement during task performance, which provides a reliable measure of mental reinstatement of past events without interfering with the ongoing task (Bramão et al., 2022; Bramão & Johansson, 2018).

Electroencephalogram (EEG)

Electroencephalogram (EEG) is a non-invasive technique that reveals the real-time brain activity during task performing. By measuring the collective electrophysiological signal of the pyramidal cells, EEG records the brain activities indicated by the postsynaptic potential (Kirschstein & Köhling, 2009). Compared to other non-invasive brain imaging techniques, such as functional magnetic resonance (fMRI) or near-infrared spectroscopy imaging (fNIRS), that measures the blood oxygen level of dependence (BOLD signal), electrical signal recorded by EEG directly reflects the instant brain activities with millisecond-level temporal resolution and is thus better in revealing the temporal dynamics of the cognitive processes involved in memory integration.

EEG has been widely involved in long-term memory research, which comprises wide band signal analysis, i.e., event related potential (ERP) analysis, and narrow band signal analysis, i.e., time-frequency analysis (Friedman & Johnson, 2000;

Jacobs et al., 2006). ERP reveals the brain electrical activities based on the amplitude pattern time-locked to specific stimulus, which is usually tagged by direction and time. For example, P300 indicates a positive component occurred at around 300 milliseconds after the onset of the stimuli, which is a component related to attention and contributing to event encoding (Polich, 2007). ERP studies revealed several components that are relevant to the memory encoding and retrieval, featured by various temporal-spatial patterns. For example, the frontal and left parietal amplitude increases at around 400-500 milliseconds was a typical indicator of recognizing an old event (Rugg & Curran, 2007), which might occur upon the recognition of the overlapping content in a new event. In addition to classic components, ERP could also track slow wave differences at extended time range, i.e., over one second. For instance, the memory interference and competition between overlapping events would elicit reduced frontal positivity, which may sustain for over 1000 milliseconds (Bramão & Johansson, 2017; Hellerstedt et al., 2016).

In addition to ERP, narrow band analysis of EEG allows for more elaborate investigation into specific frequency bands and reveals how they interact to support event cognition. For example, alpha-beta frequency desynchronization was related to better event encoding and retrieval (Griffiths et al., 2019; Karlsson et al., 2020; Martín-Buro et al., 2020; Zappa et al., 2025), while their synchronization indicates inhibitory control over competitive memory (Waldhauser et al., 2012). Besides, theta frequency synchronization was also found to be related to successful encoding and retrieval of event memories (Jacobs et al., 2006; Lin et al., 2017), which also relates to the coding of event structure (Herweg, Solomon, et al., 2020).

In summary, both the wide and narrow band EEG signals could well track the cognitive processes involved in memory encoding and retrieval. Its high reliability in measuring brain activity makes EEG a good tool to reveal the cognitive neural mechanisms of memory integration. Additionally, the high temporal resolution of EEG also ensures the precision of the real-time brain activity detection, which allows the researchers to track the temporal dynamics of the cognitive processes and reveal the temporal dynamics of their potential interplay.

Multivariate Pattern Analysis

To efficiently make use of the advantage of the temporal resolution in EEG, the present thesis combines the classic univariate analysis, i.e., ERP and time-frequency analysis, with the state-of-the-art multivariate pattern analysis (MVPA, Haxby et al., 2014) to reveal the cognitive processes involved in memory integration. These two types of analysis were derived from the same statistical basis but were guided by different pre-assumptions, which hence complement each other in revealing different aspects of the same EEG dataset.

From Univariate to Multivariate

In most cases, statistical contrasts are performed by fitting a generalized linear model, where X denotes the independent variable, Y denotes the dependent variable, the coefficient w denotes their relationship(s) and the activation function $f(\bullet)$ sets up the response mode (see equation 1). Usually, the X and the Y are the known variables, which were used to search for the w that best fits this equation, given the activation function $f(\bullet)$.

$$Y = f(Xw) \tag{1}$$

For classic univariate analysis, the X is the design matrix of the experiment, while the Y is the observed neural response and the activation function $f(\bullet)$ would be a linear function, which can be simply taken as 'multiplied by 1'. For example, in an ERP study involving a task performing condition and a non-task condition, the X would comprise a column vector containing only 0 and 1, denoting whether the observation belongs to the non-task condition or the task condition, and the Y would be the amplitude of each observation at a designated time point. This analysis fits the data in a time-point-by-time-point fashion, resulting in a time series of w denoting how the effect of experimental design varies as a function of time. The following up statistics were then performed on the estimates of w. When the dataset includes more than one channel, the w time-series for different channels would allow the statistical inference of ERP effect to be made on a temporal-spatial basis.

For multivariate pattern analysis, the case is 'reversed'. The observed neural response is now the X in equation 1, and the experimental design is the Y, when the $f(\bullet)$ is a function that transforms the linear combination of X into categorical output Y, e.g., Sigmoid and Softmax (Dubey et al., 2022). When the X contains only one channel, this analysis would be equivalent to the classic univariate analysis. However, when it contains more than one channel, as modern EEG usually does, the accumulation of the information would improve the relationship estimation between the X and the Y to obtain more accurate w. This high accurate w could then be applied to other X, e.g., EEG at anther time point, to infer the corresponding Y, e.g., whether this is a time point during task or non-task. Multichannel EEG data provides a record of the temporal-spatial neural representation in response to the experimental design, by estimating how the neural representations map to the experimental design, it is possible to decode the real-time mental status of a participant from the recoded EEG (Bramão et al., 2022; Bramão & Johansson, 2018).

Decoding Memory Reinstatement

In the associative inference task, memory integration can happen during both the encoding and/or the retrieval phases. Multivariate pattern classification opens a window that could allow the detection of the real-time cognitive process without interfering with the ongoing task. When an old experience is reinstated, and such reinstatement is predictive of better inference task performance, we could infer that such memory reinstatement facilitates memory integration and the creation of an association between two events. In such a classification study, the dataset used to train the classifiers represents the training data and the one to apply the classifiers represents the test data.

As memory reactivation involves cortical reinstatement (Danker et al., 2016; Johnson et al., 2009; Johnson & Rugg, 2007), it is possible to train classifiers using the EEG data during the first session of encoding (AB encoding) and apply them to the EEG data of the second session of encoding (BC encoding) and the retrieval phase (AC test) to capture the mental reinstatement of previously encoded events. By estimating how memory reinstatement relates to the later inference task performance, it is possible to reveal whether mental reinstatement of the old memories contributes to memory integration or interferes with other memories.

Additionally, the time-generalised matrix approach, obtained by applying the classifier trained at one time point in the training data to all time points of the test data, is employed in the studies of the present thesis, which allows us to infer the cognitive stages and their temporal shifts (King & Dehaene, 2014). Specifically, when the representation in the training data reoccurred at the same time point of the test data, the time-generalised matrix would exhibit a diagonal pattern, which indicates a replication of the same cognitive processes. Similarly, when the time generalised matrix shows a reverse diagonal pattern, it might show a reversed, top-down pattern if the training data involves a bottom-up process. Additionally, a horizontal pattern in a time-generalised matrix might show a temporally extended process, while a vertical pattern might indicate a parallel process. In practice, these patterns might co-occur and blend, showing the complexity of the engaged processes (King & Dehaene, 2014).

Based on the multivariate pattern classification, the present thesis tracks the reinstatement of old memories (Studies 1 and 3). By evaluating their time window of occurrence, i.e., during encoding or at retrieval, as well as their behavioural consequences, i.e., predicting better inference performance or related to worse memory for individual events, the present thesis reveals how the memory integration is supported by distinct mnemonic processes in different conditions, and how these processes interplay to allow for various task demands.

Representational Similarity Analysis

Multivariate classification allows the tracking of memory reinstatement based on the real-time EEG data recoded during task performance. However, it does not directly estimate how memory representations shift as a function of time and experimental design. Hence, to estimate the gradual shift in the mental representations, especially how representations of related events approximate or deviate from each other, as the consequence of memory integration and separation (Brunec et al., 2020), the representational similarity analysis (RSA) was also adopted in the present thesis (study 4).

In contrast to the multivariate classification, the RSA directly estimates the distance between the neural representations of two events. This measure describes the relative distribution of the representations corresponding to various stimuli. In the present thesis, it tells how the representations of the novel events are shaped in relation to the representation of the old events during learning. By comparing against the baseline, i.e., the distance between the neural representations of non-corresponding events (Brunec et al., 2020), the systematic RSA variation tracks the outcome of episode learning and reflect the engaged cognitive processes. Previous literature reported systematic representational similarities between the events with overlapping content after learning (Cohn-Sheehy et al., 2021; Schlichting et al., 2015), which shows the engagement of memory integration across these events. In contrast, systematic representational dissimilarities have also been observed to reduce memory interference by maintaining distinctiveness between related events (Bakker et al., 2008; Kirwan & Stark, 2007; Yassa & Stark, 2011).

Therefore, this thesis also implemented the RSA to investigate whether memory integration and separation co-occur during new learning and how they impact later task performances (study 4).

Aim of the Present Thesis

The present thesis aimed to reveal the temporal dynamics of the cognitive processes involved in memory integration, as well as how these processes interact with each other to support various mnemonic functions under different boundary conditions. Specifically, the objectives of the present thesis are threefold.

First, while memory integration mechanisms have been well characterized at the mnemonic stage level, i.e., during encoding vs at retrieval, their fine-grained temporal organization remains to be specified. Examining the integrative encoding and flexible retrieval at a finer temporal resolution is necessary to gain further understanding of how these mechanisms support memory integration. Researchers have attempted to reveal the key time points and neural processes that contribute to successful memory integration with ERP (Varga & Bauer, 2017). However, it remains to be determined whether integrative-encoding mechanisms are expressed during early or later stages, and whether they operate in a sequential or parallel fashion. Hence, the present thesis used EEG-based MVPA to further reveal the temporal dynamics of the processes that enable memory integration during encoding and retrieval.

Second, both the integrative encoding and flexible retrieval accounts are supported by different research studies, suggesting their mutually inclusive nature and emphasising the importance of identifying boundary conditions for one mechanism over the other. Though previous research has revealed that task demand and temporal proximity could serve as boundary conditions (Richter et al., 2016; Zeithamova & Preston, 2017), further work is needed to develop systematic theoretical frameworks. Specifically, are these two processes used by different people, or can people flexibly switch between them depending on the situation? Is the engagement of the mechanisms moderated by encoding context and pre-existing knowledge? To answer these questions, the present thesis evaluated how individual differences affect the memory integration mechanisms and assessed the roles of context and schema congruency in memory integration to test whether they may serve as boundary conditions between integrative encoding and flexible retrieval.

Third, the overlap between events, while enabling the creation of connections between them, also brings memory interference and competition (e.g., Bramão et al., 2022; Kuhl et al., 2011). Hence, overlapping events may be encoded in separated representations in mitigate such interference (Kirwan & Stark, 2007; Rolls, 2013;

Yassa & Stark, 2011). As such, immediate questions would raise, how does the brain balance the integration and separation of overlapping events? Do the integrated and separated representation coexist? Therefore, the present thesis also attempted to reveal how memory integration and separation processes coordinate to allow for the coexistence of integrated and separated memory representations of overlapping events.

In general, to elucidate how integrative encoding and flexible retrieval support memory integration under different boundary conditions, the present thesis applied MVPA, including pattern classification and RSA, to track the memory reinstatement during task performance and evaluated how it supports memory integration. Furthermore, the present thesis also attempted to clarify how memory integration and separation coordinate to support different mnemonic functions and fulfil various task demands.

Research studies

Study 1

This study aimed at revealing the temporal dynamics of the processes engaged in integrative encoding mechanism and investigate how the individual difference moderates the impact of old experience reinstatement on new learning.

Previous researchers have made attempts to reveal the neural activities and key time points during the encoding of related new events that might facilitate later inference performance using ERP (Varga & Bauer, 2017). To further reveal the temporal dynamics of the engaged mnemonic processes that support integrative encoding and elucidate how individual differences moderate their impacts on the learning outcome, the present study used multivariate pattern classifiers to track the mental reinstatement of the old experience during new learning, which depicts the temporal dynamics of the involved cognitive processes and opens a window to test how these processes relate to the memory performances.

Participants performed the associative inference task, comprising an encoding phase and a test phase. In the encoding phase, participants first encoded a few AB events, formed by pairing a picture with a word. Then, participants encoded BC events where the old word was paired to a new picture. At the beginning of the experiment, participants were told to notice the overlap between AB and BC events during BC encoding in preparation for the upcoming AC inference test, a procedure inspired by previous studies to facilitate integrative encoding (Backus et al., 2016; Richter et al., 2016). After a distraction task, the participants were asked to make AC inference and recollect individual AB and BC events. When an AB event comprises a picture of a face, its corresponding BC event would comprise a picture of a bird, and vice versa. Based on this, the face-bird classifiers, trained and validated with EEG data recorded during AB encoding, were applied to the EEG data of BC encoding and AC test, to detect the real-time memory reinstatement during task performing.

Based on their behavioural performance in the inference task, the participants were divided into two groups using median split, i.e., high memory integration group versus low memory integration group. The purpose of this grouping derives from the pre-assumption that when people are showing similar performance in memorizing individual events, they may have different capacity to make inference across them, which shows individual difference in making use of encoded events rather than event encoding itself (see also, Shohamy & Wagner, 2008). The comparison between their behavioural performances aligned with this pre-assumption and assured the validity of grouping that, when these two groups showed differences in inference making, their memory of individual events was comparable.

For the EEG analysis, we used multivariate pattern classifiers to detect the real-time reinstatement of the old event, i.e., AB event, during the task performance and assessed how they interact with the individual differences in inference making. The MVPA results showed that the BC trials started with the processing of the on-screen events, which lasted for around one second. Then, the reinstatement of corresponding AB events followed up, which occurred at around 1.5 to 3 seconds. Such temporal dynamics of memory reinstatement align with previous findings of pattern completion (Horner et al., 2015; Rolls, 2013) that, after encoding the BC event, the overlapping content B would serve as a cue and lead to the reinstatement of the corresponding AB event. Interestingly, such temporal pattern did not show differences between the two participant groups, implying that the performance of inference making across overlapping events might not relate to whether the old event could be reinstated, but whether it could be exploited.

This implication was supported by the correlation between the memory performance in AC and BC tests and the reinstatement of AB events during BC encoding. Specifically, for the high memory integration group, the reinstatement of AB event was related to faster response to AC inference test. However, for the low memory integration group, the reinstatement of AB event was related to longer response time for BC event retrieval. These results suggest that, even though showing a similar level of AB reinstatement, people are exhibiting different capacities in making use of AB events. While some may be capable of utilising the reinstated AB events to generate a comprehensive representation in preparation for the later inference task, others may suffer from interference. The MVPA results also corroborate with the ERP effects. When the high memory integration group showed high left-posterior effect, likely indicating active memory search (Rugg & Curran, 2007), the low memory integration group showed reduced frontal positivity, likely reflecting memory competition (Hellerstedt et al., 2016).

Since AC inference for the low memory integration group was not found to be supported by integrative encoding, we hypothesised that flexible retrieval is the mechanism for this group of participants to facilitate memory integration. As such, the classifiers that capture the reinstatement of AB events were also applied to the EEG data of AC test, at the time window when the cue was solely displayed on screen. This analysis was intended to capture the temporal dynamics of potential flexible retrieval for the low memory integration group, however, no AB reinstatement was detected. This null finding might relate to the specificity of the time window when flexible retrieval operates. More precisely, the critical question is whether flexible retrieval engages immediately upon encountering the retrieval cue or requires the concurrent presence of both cue and potential target (see also, Koster et al., 2018). This question will be revisited in Study 3 and further examined in the General Discussion.

In summary, the present study provided novel evidence showing the temporal dynamics of the integrative encoding mechanism that supports the memory integration across events with overlapping content. In addition, this study also illustrated the individual differences in inference making, when participants showed a similar level of the reinstatement of AB event, some could make use of it to facilitate memory integration, while some might suffer from the interference and subsequent impaired memory.

Study 2

This study aimed to investigate whether context serves as a boundary condition to promote integrative encoding and/or flexible retrieval. Context is a strong cue for episodic memory retrieval (Morris et al., 1977; Tulving & Thomson, 1973), which is thought to rely on the binding between context and content formed during event encoding (Herweg, Sharan, et al., 2020; Shin et al., 2021; Smith & Vela, 2001). Previous studies have shown that revisiting the encoding context facilitates episodic memory retrieval (Godden & Baddeley, 1975; Smith & Vela, 2001), which may thus promote memory integration. Specifically, sharing the context may facilitate integrative encoding across overlapping events, as the context could bring to mind the old event while encoding the new one, which are then integrated to form a comprehensive representation to tackle the later inference task. In addition, the same context may also facilitate flexible retrieval by boosting the retrieval of both events at the time of the inference test.

Two experiments were implemented by employing a context manipulation in the associative inference paradigm to investigate whether revisiting the context would promote memory integration and at which mnemonic stage, encoding or retrieval, such a promotive effect is enabled.

In Experiment 1, participants were asked to memorise AB and BC events during the encoding phase and to make AC inference in the later test phase. AB and BC events comprise a picture of a face or a bird paired to a word and superimposed on an incidental contextual picture. Half of the AB events have the same context as the corresponding BC events, while half were encoded in distinct contexts. Additionally, non-overlapping XY events were also implemented, half of which were encoded together with AB events and the other half with BC events. Similar to AB and BC events, part of the XY events also shared contexts to assess if the associative inference can be facilitated via the shared encoding context. Taken together, this experiment involves two factors, i.e., Event Type (overlapping ABC vs non-overlapping XY) and Context (same vs different). AC test was performed on a black background to evaluate if the same context promotes the associative inference by boosting integrative encoding. If the same encoding context could promote associative inference by facilitating integrative encoding, the inference performance should be better for the events encoded in the same context compared to those encoded in different contexts. Additionally, if the same encoding context could bring to mind the old event and allow for the memory integration, it could probably allow the memory integration across non-overlapping events encoded in the same context as well.

However, the results indicated that, for overlapping events, encoded in the same context, showed no benefit on associative inference performance compared to those encoded in different contexts. Furthermore, the inference across non-overlapping events sharing the same context was not better than guessing, again suggesting no promotive effect of the same context on memory integration during encoding. Hence, the present result does not support the hypothesis that the same encoding context could facilitate integrative encoding.

To assess if the same encoding context could promote flexible retrieval, Experiment 2 was implemented, using the same encoding phase as experiment 1, but with the context of each event displayed at the retrieval phase. If the context promotes associative inference by facilitating flexible retrieval, then the overlapping events encoded in the same context should show better inference performance compared to those encoded in different contexts. In addition, if the context could boost the retrieval of related events, it might also enable the associative inference across non-overlapping events, when their shared context was presented during the inference test.

The data support these hypotheses. The results showed that, associative inference across overlapping events was better when they shared the same context, and the inference across non-overlapping events was also enabled by the shared context. These results highlighted the role of the context in associative inference and demonstrated that when revisiting the encoding context facilitates the flexible retrieval mechanism, which boosts the consequent associative inference.

In terms of individual events, both the shared encoding context and the overlapping content led to lower accuracy and longer response time across the two experiments. This finding likely indicates the interference and competition resulting from the similarity between the events (see also, Bramão et al., 2022; Kuhl et al., 2011), which might thus lead to more engagement of pattern separation while encoding.

In summary, across two experiments, this study examined the role of the encoding context in associative inference. Context provides privileged access to the associated events during retrieval, thus promoting associative inference. However, when the shared encoding context is only revisited during encoding, memory integration is not benefitted.

Study 3

Study 2 illustrates how incidental context promotes memory integration, which leaves the meaningful connections between event content and contexts to be more thoroughly examined. Hence, study 3 aimed to further the exploration and investigate whether the schema congruency between context and content of an event may affect the mechanisms of memory integration.

Schemas are the knowledge structures about the world (Bartlett, 1932; Piaget, 1929). Previous studies have shown that schemas improve both encoding and retrieval of schema-congruent events by providing a scaffold for organising information (Anderson, 1981; Audrain & McAndrews, 2022). Additionally, schema incongruency has also been suggested to promote episodic memory performance, a finding usually attributed to the prediction error driven learning (Frank et al., 2018; Greve et al., 2017; Ortiz-Tudela et al., 2024). Taken together, memory follows a non-linear relationship with schema congruency, which, however, depends on different mechanisms (Van Kesteren et al., 2012). When the encoding of schema-congruent events is mediated by the medial prefrontal cortex (Brod et al., 2015), the encoding of schema-incongruent events mainly relies on the medial temporal lobe that resolves the prediction error (Van Kesteren et al., 2013).

Consequently, memory integration across schema-congruent and incongruent events may also rely on different mechanisms. Specifically, since the schema could promote the encoding and retrieval of the congruent events, it might thus facilitate the integration of the overlapping events already during encoding. On the contrary, as a consequence of prediction error resolution, the schema-incongruent events are more likely to be encoded in separate memory traces. So, the association between them would not be created until required via the flexible retrieval mechanism.

To test these hypotheses, the present study improved the paradigm of study 2 by involving the schema congruency between the content and context of an event. Participants first encoded AB events comprised of a picture-word pair superimposed on a contextual picture. The schema congruency of the AB events was determined by the word and the context, i.e., the word ‘desk’ in a picture of classroom vs the word ‘corn’ in a picture of classroom. Later, participants encoded several BC events comprised of a black background, and the schema congruency of which was inherited from the corresponding AB event. Sixty-four contextual pictures were used as the background of AB events, which comprised eight different exemplars from each of the eight schemas. AC test was also performed with the context absent, allowing the reactivation of AB to be revealed by detecting the schema and context reinstatement during task performance. The present experiment started with a localiser task, when participants watched all the contextual pictures five times. After the localiser task, the associative inference task began. The EEG was recorded throughout the whole experiment.

The behavioural results showed no differences in inference performance between schema-congruent and incongruent events. However, a further analysis showed that the joint accuracy of AB and BC events was predictive of AC inference for the schema-incongruent events, but not for the schema-congruent events. This finding indicated that the associative inference across schema-incongruent events might rely on flexibly retrieving and recombining AB and BC events, so the joint accuracy of their recollection is predictive of AC inference performance. Conversely, the associative inference performance across schema-congruent events depends on the integration of AB and BC events during BC encoding, so whether AB and BC could be simultaneously retrieved was not decisive of the inference making.

For the EEG data, a hierarchical classification strategy was employed to classify the EEG into eight schemas at the first level, and into eight contexts of each schema at the second level. The schema classifiers and the context classifiers were trained with the EEG data during the localiser task, when participants watched all the contextual pictures five times. These classifiers were validated using the AB encoding data, at the time window when the contextual picture was displayed alone. The topography of the classification showed more contribution of the frontal channels for the schema classification, compared to the context classification, which mainly relies on posterior channels. This topography difference indicated that, in addition to the activities around visual areas, schema classification also involves frontal activities, likely reflecting the engagement of mPFC, the hub moderating schema-related memories (Gilboa & Marlatte, 2017).

The validated classifiers were then applied to the EEG of BC encoding and AC test, to capture the schema and context reinstatement. By contrasting the trials with correct and incorrect AC performance, the present study identified the schema and context reinstatement that contributes to the associative inference across schema-congruent and incongruent events respectively.

For schema-congruent events, the schema reinstatement occurred at three time windows successively during BC encoding, i.e., 0.0-1.0 seconds, 2.5-3.1 seconds, and 3.1-4.0 seconds, which contributed to the later AC inference performance. Additionally, the context reinstatement, observed during BC encoding at around 3.3-3.6 seconds, was also leading to better AC inference. Notably, the context reinstatement was mainly observed in the trials with low schema reinstatement, suggesting that the schema and the context complement each other, when both of them could support the integrative encoding across schema-congruent events. Additionally, schema reinstatement related to AC inference was observed during AC test, at the time window when the cue and target coincided. This schema reinstatement at retrieval was found in the trials where the schema reinstatement during encoding was interrupted. This finding further suggested that flexible retrieval might serve as a compensatory mechanism and support the memory integration across schema-congruent events when integrative encoding fails.

For schema-incongruent events, the context reinstatement contributing to AC inference was observed during AC test, at the time window when the cue and target coincided. This finding aligned with our prediction that the memory integration across schema-incongruent events is primarily supported by the flexible retrieval mechanism. Given that schema-incongruent events are more likely to be represented in an individualized manner, deviating from pre-existing knowledge (Greve et al., 2017; Ortiz-Tudela et al., 2024), the integration across them would thus depend on the flexible retrieval and recombination at the time of inference making.

Additionally, the deactivation of the incongruent schema was observed while encoding schema-incongruent BC events. Interestingly, such deactivation was related to the reinstatement of the schema that is congruent with the event. For example, when an incongruent AB event comprises a word ‘corn’ and a picture of a classroom, during the BC encoding, the schema of ‘classroom’ would be deactivated, and the participant might instead reinstate a schema of ‘farm’. Such an event-congruent schema reinstated during BC encoding was predictive of the later AC inference, suggesting the involvement of integrative encoding supported by this schema. Notably, the context-based flexible retrieval, and the event-congruent schema supported integrative encoding was observed in different trials, suggesting that such integrative encoding complements the flexible retrieval and jointly lead to the memory integration across schema-incongruent events.

In summary, both behavioural and neural evidence supported our hypotheses. The memory integration across schema-congruent events mainly relies on the integrative encoding mechanism, which is supported by the reinstatement of the schema and the context while encoding overlapping new events. On the contrary, the memory integration across schema-incongruent events primarily depends on flexible retrieval mechanism, where the separately encoded events were retrieved and recombined to allow novel inferences at the test phase. Furthermore, the present study also reveals complementary mechanisms that jointly support the integration across the schema-congruent and incongruent events.

Study 4

Study 4 investigated how the brain encodes overlapping events into the integrated and separated representations.

Events with overlapping content are prone to mutual interference (Bramão et al., 2022; Kuhl et al., 2011), which are thus encoded as separated memory traces to mitigate such competition (Bakker et al., 2008; Yassa & Stark, 2011). However, they might also be integrated to allow for the novel inferences across event boundaries (Morton et al., 2017; Schlichting & Preston, 2015). Hence, it is important to understand how the brain reconcile such apparently conflicting functions. Additionally, some studies discovered that memory integration often comes at the cost of losing individual memories (Banino et al., 2016; Carpenter & Schacter, 2017, 2018), likely suggesting that memory integration might impair the representations of individual events. However, some studies reported the opposite that better performance in inference task was associated with better memory of individual events (Boeltzig et al., 2023; Bowman et al., 2021; de Araujo Sanchez & Zeithamova, 2023), indicating the coexistence of integrated and separated representations. The present study was implemented to examine whether and how the coexistence of integrated and separated representations is enabled.

In this study, a naturalistic version of the associative inference task was used, where the events were embedded in movies that simulate daily-life events. The movies for this study were created using the life-simulation game *The Sims 4* by Electronic Arts (www.thesims4.com). A movie comprised the following segments: 1) a picture of a character (Sim A/C) for 2 seconds, 2) an animation of this character performing a daily activity in a context (Sim A/C in Context) for 3 seconds, 3) a picture of another character (Sim B) for 2 seconds; and 4) an animation of these two characters interacting in the context (Sim A/C and B in context) for 5 seconds. All AB events have corresponding BC events, which consist of different contexts, so the inference can only be made through the overlapping Sim B. However, only half of the AB events would be presented to the participants, when all BC events were presented. Thus, half of the BC events, whose corresponding AB events were absent, made up the XY events that served as the baseline condition.

At the beginning of the experiment, participants were told to integrate the overlapping events to infer AC indirect associations, and to keep information about the event-specific relationships, i.e., AB, BC and XY direct associations. Then, participants encoded AB movies in five repetitions, which was followed by watching BC and XY movies for another five repetitions. In the retrieval phase, the tests for indirect associations and direct associations were intermingled, with the only constraint that AC indirect association was always tested before its corresponding AB and BC direct associations. After each trial of the association test, the participants would be required to indicate if these two Sims had appeared together, as an assessment of source memory.

Behavioural results demonstrated that when participants correctly responded to AC indirect association test, they simultaneously showed clear awareness that these two Sims had never appeared together in the same movie. This result aligns with previous studies (Boeltzig et al., 2023; Bowman et al., 2021; de Araujo Sanchez & Zeithamova, 2023), showing the coexistence of integrated and separated representations of overlapping events. As such, participants could both make novel inferences and keep source memories.

The EEG was recorded throughout the whole experiment, which allowed us to reveal how the brain enables the formation of both integrated and separated representations. The time-resolved representational similarity between AB and BC events was evaluated, which reveals the temporal dynamics of how the neural representation of BC is shaped in relation to the neural representation of corresponding AB as a function of time. Specifically, the neural representations of AB events were correlated with the neural representations during BC encoding time-point by time-point, which forms a time series depicting how the AB-BC neural representational similarity varies across different segments of the BC movie.

Systematic similarity between AB and BC events was observed while participants were watching the movie segments involving the novel Sim C. As an indicator of memory integration processes, systematic similarity predicted AC inference performance, which, however, also showed a negative impact on the later source memory. In addition, the systematic dissimilarity between AB and the corresponding BC movie was observed at the time window when the overlapping Sim B was presented again in the BC movie, which was predictive of the source memory preservation. Tracking these representations over repeated BC encoding trials revealed incremental shifts in similarity and dissimilarity patterns, indicating a gradual evolution of the memory representations.

Using the XY encoding trials as baseline, we further investigated the time-frequency features of the BC encoding trials to reveal the neural activities engaged in memorizing this overlapping new event. Specifically, we observed alpha-beta desynchronization in the time windows where systematic representational similarity emerged. Interestingly, this alpha-beta desynchronization was predictive of the similarities between neural representations of AB and BC events, likely reflecting the retrieval and encoding processes involved in memory integration. Furthermore, a theta synchronization, followed by an alpha-beta synchronization, was observed at the time window where systematic dissimilarity was observed. This time-frequency effect was predictive of the neural pattern dissimilarity at the same time window, likely reflecting the recognition of the overlapping content and the engagement of cognitive control involved in memory separation.

In summary, this study provides novel evidence that integrated and separated representations for the overlapping events would coexist to flexibly support different memory functions. The systematic similarity, tagging the processes of memory integration, predicted better associative inference performance. While the systematic dissimilarity, indicating the efforts to separate similar events, is related to better source memory. The coordination of these mnemonic processes allows the coexistence of both integrated and separated memory traces.

General Discussion

Yesterday’s river shapes today’s shore—learning from past events equips individuals to make informed decisions in the future. Beyond learning from individual events, overlap between events enables the formation of associations across distinct experiences, offering new insights that support adaptive behaviour. The formation of such associations is believed to rely on memory integration, which is supported by the interaction between the brain’s rapid hippocampal learning system and the slow cortical learning system. Integration may occur either during the encoding of new events or later, when making novel inferences.

The present thesis investigated the mechanisms that support memory integration under various conditions, and how these mechanism coordinate with other mnemonic functions, such as memory separation. Taken together, the findings reveal the temporal dynamics of memory integration processes and define some of the boundary conditions under which complementary mechanisms operate. Furthermore, this work provides evidence for the coexistence of integrated and separated memory representations of the same event—supporting a flexible memory system capable of serving different functional demands.

Temporal Dynamics of Integrative Encoding and Flexible Retrieval

The timing of when associations between overlapping events are formed has long been a focus of investigations into integrative encoding and flexible retrieval. On a rather coarse time scale, i.e., at mnemonic stage level, these two mechanisms have been thoroughly investigated in the previous literatures (e.g., Koster et al., 2018; Schlichting & Preston, 2014). However, what happened on a finer time scale has not yet been well accounted for.

Based on previous finding (Varga & Bauer, 2017), the present thesis aimed to further reveal the temporal dynamics of the integrative encoding and flexible retrieval mechanisms. By adopting state-of-the-art MVPA (Haxby et al., 2014) techniques, the present thesis tracked the reinstatement of past experience and evaluated how it affects the behavioural performances in ensuing memory tests

(Studies 1 and 3). Together with classic techniques such as ERP (study 1), the present thesis elucidates the temporal dynamics of the cognitive processes involved integrative encoding and flexible retrieval.

In Study 1, we encouraged participants to notice the overlap between AB and BC in preparation for the later AC inference test, which is thought to facilitate integrative encoding The EEG data showed that, the reinstatement of the overlapping old memory was captured at around 1.5 seconds after the onset of an overlapping new event, which lasted for around 1.5 seconds. Importantly, this AB reinstatement contributed to the AC inference performance for the high memory integration group, indicating the engagement of integrative encoding. Pattern completion happened around 0.5-1 second after the onset of the probe (Jafarpour et al., 2014; Staresina et al., 2016). Therefore, the data in study 1 suggested that, right after the processing of the on-screen event, which took ~1 second, the pattern completion processes initiated, and resulted in the reinstatement of overlapping memory occurring at around 1.5 second, which led to the integrative encoding for the high memory integration group. Similar temporal dynamics were observed in study 3. During BC encoding, starting from ~2.5 second, we observed the schema reinstatement and context for schema-congruent event, which predicted AC inference performance.

Flexible retrieval has been proposed as another complementary mechanism that associative inference might rely on (Banino et al., 2016; Koster et al., 2018), which was also observed in the present thesis. In study 3, at the time of AC test, both the schema reinstatement for the schema-congruent events and the context reinstatement for the schema-incongruent events led to successful AC inference, indicating the engagement of flexible retrieval. Interestingly, flexible retrieval was observed at the time window when the cue, target and distractor were all displayed on screen, which aligns with previous findings (Koster et al., 2018). This finding might demonstrate a prerequisite to initialise the flexible retrieval mechanism, i.e., it only operates when both the cue and the target coincide.

This finding might explain why flexible retrieval was not observed in study 1 for the low memory integration group, for whom the integrative encoding was inactive. In study 1, the classifiers were trained to discriminate EEG representations of faces versus birds. During AC test, no retrieval of old events occurred in the cue-only time window, leaving no neural signature for classifiers to detect. In the subsequent cue-target window, classifier performance was likely confounded by the visual input of the face and bird presented on screen, resulting in null findings. Hence, although the low memory integration group likely relied on the flexible retrieval mechanism, the neural evidence did not emerge. These null results further suggest that future studies investigating flexible retrieval might employ alternative classifiers to strategically capture the reinstatement of old events.

In summary, across three studies, the present thesis showed the temporal dynamics of processes involved integrative encoding and flexible retrieval. By tracking the memory reinstatement during encoding and retrieval, and evaluating their behavioural consequences, the present thesis illustrates how these mnemonic processes support memory integration.

Boundary Conditions Between Integrative Encoding and Flexible Retrieval

Both integrative encoding and flexible retrieval accounts are supported by empirical evidence (Banino et al., 2016; Kumaran & McClelland, 2012; Shohamy & Wagner, 2008; Zeithamova et al., 2012), implying the differentiation between them is not an ‘either-or’ but rather a ‘where-when’ question (Holmes et al., 2022). Previous researchers have identified a few boundary conditions between these two mechanisms, such as temporal proximity and task demand (Richter et al., 2016; Zeithamova & Preston, 2017). The present thesis offered new insights into the boundary conditions of these two mechanisms as in study 2, study 3, and arguably, study 1.

In study 2, we assessed if the encoding context is a boundary condition between integrative encoding and flexible retrieval. In terms of its positive impacts, revisiting the encoding context facilitates the episodic memory retrieval (e.g., Godden & Baddeley, 1975, 1980; Shin et al., 2021; Smith & Vela, 2001). Presumably, when overlapping events share the same encoding context, this context facilitates the recollection of related events during both encoding and retrieval, thereby promoting memory integration. However, when overlapping events share encoding context, their similarity would increase, leading to more interference and competition (Bramão & Johansson, 2017). Such exacerbated interference may lead to higher engagement of pattern separation, the mechanism that controls similarity-induced interference by separating memory traces (Kirwan & Stark, 2007; Rolls, 2013; Yassa & Stark, 2011). If this is the case, the pattern separation would complicate the integrative encoding across overlapping events with the same encoding context, and might thus make it a boundary condition between integrative encoding and flexible retrieval.

Across two experiments, we demonstrated that the same encoding context benefits the associative inference performance only when re-presented at the time of the inference test. Specifically, when the AC test was performed with the encoding context absent, the inference across overlapping events was not affected by whether they shared the same encoding context. And the inference across non-overlapping events was not better than guessing. These results showed that the same encoding context did not boost integrative encoding. However, when encoding context was re-presented at AC test, the inference across overlapping events was promoted and the inference across non-overlapping events was enabled when they shared the same encoding context. These results showed that, when revisited during retrieval, the context facilitates the accessibility of events and in turn promotes inference making across them via a flexible retrieval mechanism. These results showed that the same encoding context selectively boosts the flexible retrieval, instead of integrative encoding, for memory integration. This effect likely stems from the context's dual role as a strong cue at retrieval and a trigger of pattern separation during encoding, so the events sharing the same context would be encoded into separated representations and the connections between them are formed during retrieval.

In study 3, we evaluated whether schema congruency of an event is the boundary condition between integrative encoding and flexible retrieval. Previous studies have shown that memory for schema-congruent and incongruent events is supported by different mechanisms. While the memory of schema-congruent events is supported by the schema mediated by the medial prefrontal cortex (Brod et al., 2015), the memory of schema-incongruent events is supported by prediction error resolution in the medial temporal lobe (Van Kesteren et al., 2013). Accordingly, we hypothesised that memory integration across schema-congruent and incongruent event are also supported by different mechanisms.

In this study, the schema congruency of an event was determined by the relationship between the content and context (e.g., a word 'desk' or a word 'corn' in a picture of classroom). The results showed that even though the inference performance was comparable across two types of events, it showed different levels of dependency on the accuracy of individual event retrieval. Specifically, for schema-congruent events, the joint accuracy of retrieving the individual events did not predict the inference across them. However, the inference across schema-incongruent events was found to rely on the accurate retrieval of the individual events. This finding suggests that memory integration across schema-congruent events mainly relies on integrative encoding, so it does not show dependency on the retrieval of individual events. However, the schema-incongruent events are likely encoded separately, and therefore the associative inferences across them rely on flexible retrieval. This idea was further supported by neural evidence. The AC inference across schema-congruent events was supported by the reinstatement of the schema during BC encoding. This finding shows that pre-existing knowledge can serve as a scaffold to organize schema-congruent events, facilitating memory integration during encoding. On the other hand, context reinstatement during AC test predicted the associative inference across schema-incongruent events, characterising the flexible recombination of separately stored memory representations to perform the AC inference.

Study 1 demonstrated that the ability to utilize memory reinstatement during learning to construct an integrative encoding representation may also serve as a boundary condition. We observed the reinstatement of an old event during the encoding of overlapping new event. In the high memory integration group, such reinstatement predicted the performance in the later inference test, suggesting the engagement of integrative encoding. On the contrary, for the low memory integration group, the reinstatement of an old event was negatively related to the recollection of the overlapping new event, suggesting another consequence of reinstatement, namely memory interference. This finding demonstrates that for some participants, the reinstatement of old experience was not facilitating integrative encoding but rather bringing to mind competing memories that interfere with the encoding of the new event. Previous studies have shown that retrieval of overlapping memories during new learning may impair the encoding of new information by generating proactive interference (Chanales et al., 2019; Long & Kuhl, 2019). This is likely what happened in this group of participants. Although flexible retrieval was not directly observed in the low memory integration group—possibly due to the time window of flexible retrieval—the contrast between integrative encoding (high memory integration group) and non-integrative encoding (low memory integration group) still suggests that individual differences may serve as a boundary condition for memory integration mechanisms.

Taken together, the present thesis elucidated that encoding context, schema congruency, and arguably, individual differences serve as boundary conditions between integrative encoding and flexible retrieval, showing that both mechanisms are viable for memory integration, but might operate under different conditions.

The Interplay between Integration and Separation

The overlapping content shared across events not only enables memory integration (Morton et al., 2017; Schlichting & Preston, 2015) but also brings memory interference and competition (Barnes & Underwood, 1959; Bramão et al., 2022; Kuhl et al., 2011; Postman & Underwood, 1973; Radvansky, 1999). To resolve the competition the hippocampal mechanism of pattern separation may engage to encode similar event into distinct memory traces (Kirwan & Stark, 2007; Rolls, 2013; Yassa & Stark, 2011). Understanding whether and how the brain balances memory integration and separation is crucial for clarifying how these mnemonic mechanisms support complex memory functions.

Previous studies have reported a loss of episodic detail in individual events following inference-making, suggesting that the brain may not be capable of maintaining both integrated and separated representations of overlapping events. The formation of integrated representations may, therefore, come at the cost of preserving individual event memories (Banino et al., 2016; Carpenter & Schacter, 2017, 2018). However, recent evidence suggests that memory integration is not always accompanied by impairment of individual event memories, highlighting the brain's capacity to simultaneously form integrated representations while preserving distinct event details (Boeltzig et al., 2023; Bowman et al., 2021; de Araujo Sanchez & Zeithamova, 2023). Therefore, to explore whether the integrated and separated representations could coexist, Study 4 was conducted.

With the real-life simulating experimental materials, and the temporally resolved RSA, Study 4 revealed the temporal dynamics of how different mnemonic processes, i.e., integration and separation, coordinated to form both integrated and separated representations to serve different memory functions. In study 4, better source memory was found associated with better memory for indirect associations, implying the coexistence of both integrated and separated representations of the overlapping events. Specifically, the integrated representation would facilitate novel inference across overlapping events, while the separated representations enable individuals to determine whether the elements are from a single event or multiple distinct events.

The time-resolved RSA revealed how the integrated and separated representations were formed across five rounds of movie viewing. While encoding the overlapping new event, the neural representation exhibited both similarities and dissimilarities to the corresponding old event. Interestingly, the systematic similarity was found during the presentation of non-overlapping elements (i.e., Sim C in context), which predicted the performance in later inference making. However, the systematic dissimilarity was found during the presentation of the overlapping element (i.e., Sim B), which predicted the accuracy of source memory. This finding suggests that the mnemonic processes of integration and separation are element-selective. As such, the non-overlapping elements were associated to form an integrated representation that facilitates novel inference, while the overlapping elements were kept distinct to prevent mutual interference and preserve the representations of individual events.

In addition, the movie's structure demonstrated the content-selectivity of the underlying integration and separation processes. In segments containing only novel Sim, systematic similarities were observed, whereas systematic dissimilarities emerged in segments containing overlapping Sim. These findings suggest that memory integration and separation processes are content-selective and that their temporal dynamics may track the presence of overlapping versus non-overlapping content in real-life situations.

Based on the findings in study 4, new insights might derive from the results of study 1. For the group with low memory integration performance, the reinstatement of an old event not only failed to facilitate memory integration but also showed a detrimental effect on the encoding. This result implies that the capacity of memory integration covaries with the ability to control memory interference. In other words, when one is less capable of making use of the reinstated old experience to facilitate integrative encoding, this person may also suffer more from memory interference. This implication is partly supported by previous studies, suggesting that factors like cognitive control and working memory capacity (Brumback et al., 2005; Varga et al., 2019) may influence the performance of memory integration. Together, these findings highlight again that memory integration might require the engagement of various mnemonic processes, the coordination of which is decisive of the final learning outcome.

In summary, memory integration is not an isolated process; rather, it operates in coordination with other mnemonic functions, such as memory separation, to support complex memory operations. This thesis demonstrates that integrated and separated memory representations of overlapping events can coexist, enabling the memory system to flexibly meet different cognitive demands.

Limitations and Future Studies

In the present thesis, MVPA was used to track the memory integration via memory reinstatement. However, memory reinstatement is not uniquely linked to memory integration; it may also give rise to other outcomes such as reconsolidation, interference, etc. To provide a more comprehensive understanding of memory integration within the broader memory system, it is important to consider these additional aspects. Future research could explore these aspects by employing a range of experimental approaches, modalities and analytical techniques to track the diverse outcomes of memory reactivation involved in the memory integration processes.

This thesis also revealed the temporal dynamics of integrative encoding and flexible retrieval using the associative inference task. While the consistency across results strengthens internal, it also raises questions about external validity. Specifically, will the observed temporal dynamics remain consistent across other paradigms that assess memory integration? Findings from Study 4, which demonstrated content selectivity in the integration processes, suggest potential variability in temporal dynamics depending on task characteristics. Future studies should therefore incorporate a broader range of paradigms to more fully characterize the mechanisms underlying memory integration.

Finally, the present studies relied on scalp EEG, which prioritises temporal resolution over spatial resolution. Although MVPA allowed us to track memory reinstatement by decoding overall brain activity, it remains unclear how specific neural subsystems contribute to memory integration. Future research could address this limitation by using techniques such as source-reconstructed EEG or MEG to more precisely evaluate the contributions of distinct neural networks in memory integration.

Concluding remarks

Memory integration serves a vital function: it allows humans to learn more from a limited set of past experiences. This may occur when encountering new events or when reflecting on previous ones. The present work demonstrates how multiple cognitive processes support memory integration, how it may vary across individuals, and how it enables the association of events with distinct attributes. As a key component of event cognition, memory integration operated in concert with other cognitive functions, contributing to our ability to construct a coherent understanding of the world around us.

References

Anderson, J. R. (1981). Effects of prior knowledge on memory for new information. *Memory & Cognition*, *9*(3), 237–246. https://doi.org/10.3758/BF03196958

Atkinson, R. C., & Shiffrin, R. M. (1968). Human Memory: A Proposed System and its Control Processes. In *Psychology of Learning and Motivation* (Vol. 2, pp. 89–195). Elsevier. https://doi.org/10.1016/S0079-7421(08)60422-3

Audrain, S., & McAndrews, M. P. (2022). Schemas provide a scaffold for neocortical integration of new memories over time. *Nature Communications*, *13*(1), 5795. https://doi.org/10.1038/s41467-022-33517-0

Backus, A. R., Schoffelen, J.-M., Szebényi, S., Hanslmayr, S., & Doeller, C. F. (2016). Hippocampal-Prefrontal Theta Oscillations Support Memory Integration. *Current Biology*, *26*(4), 450–457. https://doi.org/10.1016/j.cub.2015.12.048

Baddeley, A. (1992). Working Memory. *Science*, *255*(5044), 556–559. https://doi.org/10.1126/science.1736359

Baddeley, A. (2000). The episodic buffer: A new component of working memory? *Trends in Cognitive Sciences*, *4*(11), 417–423. https://doi.org/10.1016/S1364-6613(00)01538-2

Baddeley, A., & Hitch, G. (1974). Working Memory. In *Psychology of Learning and Motivation* (Vol. 8, pp. 47–89). Elsevier. https://doi.org/10.1016/S0079-7421(08)60452-1

Bakker, A., Kirwan, C. B., Miller, M., & Stark, C. E. L. (2008). Pattern Separation in the Human Hippocampal CA3 and Dentate Gyrus. *Science*, *319*(5870), 1640–1642. https://doi.org/10.1126/science.1152882

Banino, A., Koster, R., Hassabis, D., & Kumaran, D. (2016). Retrieval-based model accounts for striking profile of episodic memory and generalization. *Scientific Reports*, *6*(1), 31330. https://doi.org/10.1038/srep31330

Barnes, J. M., & Underwood, B. J. (1959). "Fate" of first-list associations in transfer theory. *Journal of Experimental Psychology*, *58*(2), 97–105. https://doi.org/10.1037/h0047507

Bartlett, F. C. (1932). *Remembering: A study in experimental and social psychology* (1st ed.). Cambridge University Press.

Bläsing, B. E. (2015). Segmentation of dance movement: Effects of expertise, visual familiarity, motor experience and music. *Frontiers in Psychology*, *5*. https://doi.org/10.3389/fpsyg.2014.01500

Boeltzig, M., Johansson, M., & Bramão, I. (2023). Ingroup sources enhance associative inference. *Communications Psychology*, *1*(1), 40. https://doi.org/10.1038/s44271-023-00043-8

Bowman, C. R., De Araujo Sanchez, M.-A., Hou, W., Rubin, S., & Zeithamova, D. (2021). Generalization and False Memory in an Acquired Equivalence Paradigm: The Influence of Physical Resemblance Across Related Episodes. *Frontiers in Psychology*, *12*, 669481. https://doi.org/10.3389/fpsyg.2021.669481

Bramão, I., Jiang, J., Wagner, A. D., & Johansson, M. (2022). Encoding contexts are incidentally reinstated during competitive retrieval and track the temporal dynamics of memory interference. *Cerebral Cortex*, *32*(22), 5020–5035. https://doi.org/10.1093/cercor/bhab529

Bramão, I., & Johansson, M. (2017). Benefits and costs of context reinstatement in episodic memory: An ERP Study. *Journal of Cognitive Neuroscience*, *29*(1), 52–64. https://doi.org/10.1162/jocn_a_01035

Bramão, I., & Johansson, M. (2018). Neural Pattern Classification Tracks Transfer-Appropriate Processing in Episodic Memory. *Eneuro*, *5*(4), ENEURO.0251-18.2018. https://doi.org/10.1523/ENEURO.0251-18.2018

Brod, G., Lindenberger, U., Werkle-Bergner, M., & Shing, Y. L. (2015). Differences in the neural signature of remembering schema-congruent and schema-incongruent events. *NeuroImage*, *117*, 358–366. https://doi.org/10.1016/j.neuroimage.2015.05.086

Brunec, I. K., Robin, J., Olsen, R. K., Moscovitch, M., & Barense, M. D. (2020). Integration and differentiation of hippocampal memory traces. *Neuroscience & Biobehavioral Reviews*, *118*, 196–208. https://doi.org/10.1016/j.neubiorev.2020.07.024

Buehner, M., Krumm, S., & Pick, M. (2005). Reasoning=working memory≠attention. *Intelligence*, *33*(3), 251–272. https://doi.org/10.1016/j.intell.2005.01.002

Carpenter, A. C., & Schacter, D. L. (2017). Flexible retrieval: When true inferences produce false memories. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *43*(3), 335–349. https://doi.org/10.1037/xlm0000340

Carpenter, A. C., & Schacter, D. L. (2018). False memories, false preferences: Flexible retrieval mechanisms supporting successful inference bias novel decisions. *Journal of Experimental Psychology: General*, *147*(7), 988–1004. https://doi.org/10.1037/xge0000391

Chanales, A. J. H., Dudukovic, N. M., Richter, F. R., & Kuhl, B. A. (2019). Interference between overlapping memories is predicted by neural states during learning. *Nature Communications*, *10*(1), 5363. https://doi.org/10.1038/s41467-019-13377-x

Chase, W. G., & Simon, H. A. (1973). Perception in chess. *Cognitive Psychology*, *4*(1), 55–81. https://doi.org/10.1016/0010-0285(73)90004-2

Cohn-Sheehy, B. I., Delarazan, A. I., Reagh, Z. M., Crivelli-Decker, J. E., Kim, K., Barnett, A. J., Zacks, J. M., & Ranganath, C. (2021). The hippocampus constructs narrative memories across distant events. *Current Biology*, *31*(22), 4935-4945.e7. https://doi.org/10.1016/j.cub.2021.09.013

Cotton, K., & Ricker, T. J. (2022). Examining the relationship between working memory consolidation and long-term consolidation. *Psychonomic Bulletin & Review*, *29*(5), 1625–1648. https://doi.org/10.3758/s13423-022-02084-2

Danker, J. F., Tompary, A., & Davachi, L. (2016). Trial-by-Trial Hippocampal Encoding Activation Predicts the Fidelity of Cortical Reinstatement During Subsequent Retrieval. *Cerebral Cortex*, bhw146. https://doi.org/10.1093/cercor/bhw146

Davis, M. H., & Gaskell, M. G. (2009). A complementary systems account of word learning: Neural and behavioural evidence. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *364*(1536), 3773–3800. https://doi.org/10.1098/rstb.2009.0111

de Araujo Sanchez, M. A., & Zeithamova, D. (2023). Generalization and false memory in acquired equivalence. *Cognition*, *234*, 105385. https://doi.org/10.1016/j.cognition.2023.105385

De Haan, E. H. F., & Cowey, A. (2011). On the usefulness of ‘what’ and ‘where’ pathways in vision. *Trends in Cognitive Sciences*, *15*(10), 460–466. https://doi.org/10.1016/j.tics.2011.08.005

Dubey, S. R., Singh, S. K., & Chaudhuri, B. B. (2022). Activation functions in deep learning: A comprehensive survey and benchmark. *Neurocomputing*, *503*, 92–108. https://doi.org/10.1016/j.neucom.2022.06.111

Dudai, Y. (2004). The Neurobiology of Consolidations, Or, How Stable is the Engram? *Annual Review of Psychology*, *55*(1), 51–86. https://doi.org/10.1146/annurev.psych.55.090902.142050

Dudai, Y. (2012). The Restless Engram: Consolidations Never End. *Annual Review of Neuroscience*, *35*(1), 227–247. https://doi.org/10.1146/annurev-neuro-062111-150500

Dudai, Y., Karni, A., & Born, J. (2015). The Consolidation and Transformation of Memory. *Neuron*, *88*(1), 20–32. https://doi.org/10.1016/j.neuron.2015.09.004

Euston, D. R., Gruber, A. J., & McNaughton, B. L. (2012). The Role of Medial Prefrontal Cortex in Memory and Decision Making. *Neuron*, *76*(6), 1057–1070. https://doi.org/10.1016/j.neuron.2012.12.002

Frank, D., Montaldi, D., Wittmann, B., & Talmi, D. (2018). Beneficial and detrimental effects of schema incongruence on memory for contextual events. *Learning & Memory*, *25*(8), 352–360. https://doi.org/10.1101/lm.047738.118

Frankland, P. W., & Bontempi, B. (2005). The organization of recent and remote memories. *Nature Reviews Neuroscience*, *6*(2), 119–130. https://doi.org/10.1038/nrn1607

Friedman, D., & Johnson, R. (2000). Event-related potential (ERP) studies of memory encoding and retrieval: A selective review. *Microscopy Research and Technique*, *51*(1), 6–28. https://doi.org/10.1002/1097-0029(20001001)51:1<6::AID-JEMT2>3.0.CO;2-R

Ghosh, V. E., & Gilboa, A. (2014). What is a memory schema? A historical perspective on current neuroscience literature. *Neuropsychologia*, *53*, 104–114. https://doi.org/10.1016/j.neuropsychologia.2013.11.010

Gilboa, A., & Marlatte, H. (2017). Neurobiology of Schemas and Schema-Mediated Memory. *Trends in Cognitive Sciences*, *21*(8), 618–631. https://doi.org/10.1016/j.tics.2017.04.013

Gobet, F., & Clarkson, G. (2004). Chunks in expert memory: Evidence for the magical number four … or is it two? *Memory*, *12*(6), 732–747. https://doi.org/10.1080/09658210344000530

Gobet, F., & Simon, H. A. (1996). Templates in Chess Memory: A Mechanism for Recalling Several Boards. *Cognitive Psychology*, *31*(1), 1–40. https://doi.org/10.1006/cogp.1996.0011

Godden, D., & Baddeley, A. (1975). Context-dependent memory in two natural environments: On land and underwater. *British Journal of Psychology*, *66*(3), 325–331. https://doi.org/10.1111/j.2044-8295.1975.tb01468.x

Godden, D., & Baddeley, A. (1980). When does context influence recognition memory? *British Journal of Psychology*, *71*(1), 99–104.

Gold, D. A., Zacks, J. M., & Flores, S. (2017). Effects of cues to event segmentation on subsequent memory. *Cognitive Research: Principles and Implications*, *2*(1), 1. https://doi.org/10.1186/s41235-016-0043-2

Greve, A., Cooper, E., Kaula, A., Anderson, M. C., & Henson, R. (2017). Does prediction error drive one-shot declarative learning? *Journal of Memory and Language*, *94*, 149–165. https://doi.org/10.1016/j.jml.2016.11.001

Griffiths, B. J., Mayhew, S. D., Mullinger, K. J., Jorge, J., Charest, I., Wimber, M., & Hanslmayr, S. (2019). Alpha/beta power decreases track the fidelity of stimulus-specific information. *eLife*, *8*, e49562. https://doi.org/10.7554/eLife.49562

Haxby, J. V., Connolly, A. C., & Guntupalli, J. S. (2014). Decoding Neural Representational Spaces Using Multivariate Pattern Analysis. *Annual Review of Neuroscience*, *37*(1), 435–456. https://doi.org/10.1146/annurev-neuro-062012-170325

Hellerstedt, R., Johansson, M., & Anderson, M. C. (2016). Tracking the intrusion of unwanted memories into awareness with event-related potentials. *Neuropsychologia*, *89*, 510–523. https://doi.org/10.1016/j.neuropsychologia.2016.07.008

Herweg, N. A., Sharan, A. D., Sperling, M. R., Brandt, A., Schulze-Bonhage, A., & Kahana, M. J. (2020). Reactivated spatial context guides episodic recall. *The Journal of Neuroscience*, *40*(10), 2119–2128. https://doi.org/10.1523/JNEUROSCI.1640-19.2019

Herweg, N. A., Solomon, E. A., & Kahana, M. J. (2020). Theta Oscillations in Human Memory. *Trends in Cognitive Sciences*, *24*(3), 208–227. https://doi.org/10.1016/j.tics.2019.12.006

Holmes, N. M., Wong, F. S., Bouchekioua, Y., & Westbrook, R. F. (2022). Not “either-or” but “which-when”: A review of the evidence for integration in sensory preconditioning. *Neuroscience & Biobehavioral Reviews*, *132*, 1197–1204. https://doi.org/10.1016/j.neubiorev.2021.10.032

Horner, A. J., Bisby, J. A., Bush, D., Lin, W.-J., & Burgess, N. (2015). Evidence for holistic episodic recollection via hippocampal pattern completion. *Nature Communications*, *6*(1). https://doi.org/10.1038/ncomms8462

Jacobs, J., Hwang, G., Curran, T., & Kahana, M. J. (2006). EEG oscillations and recognition memory: Theta correlates of memory retrieval and decision making. *NeuroImage*, *32*(2), 978–987. https://doi.org/10.1016/j.neuroimage.2006.02.018

Jafarpour, A., Fuentemilla, L., Horner, A. J., Penny, W., & Duzel, E. (2014). Replay of Very Early Encoding Representations during Recollection. *The Journal of Neuroscience*, *34*(1), 242–248. https://doi.org/10.1523/JNEUROSCI.1865-13.2014

Johnson, J. D., McDuff, S. G. R., Rugg, M. D., & Norman, K. A. (2009). Recollection, Familiarity, and Cortical Reinstatement: A Multivoxel Pattern Analysis. *Neuron*, *63*(5), 697–708. https://doi.org/10.1016/j.neuron.2009.08.011

Johnson, J. D., & Rugg, M. D. (2007). Recollection and the Reinstatement of Encoding-Related Cortical Activity. *Cerebral Cortex*, *17*(11), 2507–2515. https://doi.org/10.1093/cercor/bhl156

Karlsson, A. E., Wehrspaun, C. C., & Sander, M. C. (2020). Item recognition and lure discrimination in younger and older adults are supported by alpha/beta desynchronization. *Neuropsychologia*, *148*, 107658. https://doi.org/10.1016/j.neuropsychologia.2020.107658

King, J.-R., & Dehaene, S. (2014). Characterizing the dynamics of mental representations: The temporal generalization method. *Trends in Cognitive Sciences*, *18*(4), 203–210. https://doi.org/10.1016/j.tics.2014.01.002

Kirschstein, T., & Köhling, R. (2009). What is the Source of the EEG? *Clinical EEG and Neuroscience*, *40*(3), 146–149. https://doi.org/10.1177/155005940904000305

Kirwan, C. B., & Stark, C. E. L. (2007). Overcoming interference: An fMRI investigation of pattern separation in the medial temporal lobe. *Learning & Memory*, *14*(9), 625–633. https://doi.org/10.1101/lm.663507

Koster, R., Chadwick, M. J., Chen, Y., Berron, D., Banino, A., Düzel, E., Hassabis, D., & Kumaran, D. (2018). Big-Loop Recurrence within the Hippocampal System Supports Integration of Information across Episodes. *Neuron*, *99*(6), 1342-1354.e6. https://doi.org/10.1016/j.neuron.2018.08.009

Kroes, M. C. W., & Fernández, G. (2012). Dynamic neural systems enable adaptive, flexible memories. *Neuroscience & Biobehavioral Reviews*, *36*(7), 1646–1666. https://doi.org/10.1016/j.neubiorev.2012.02.014

Kuhl, B. A., Rissman, J., Chun, M. M., & Wagner, A. D. (2011). Fidelity of neural reactivation reveals competition between memories. *Proceedings of the National Academy of Sciences*, *108*(14), 5903–5908. https://doi.org/10.1073/pnas.1016939108

Kumaran, D., Hassabis, D., & McClelland, J. L. (2016). What Learning Systems do Intelligent Agents Need? Complementary Learning Systems Theory Updated. *Trends in Cognitive Sciences*, *20*(7), 512–534. https://doi.org/10.1016/j.tics.2016.05.004

Kumaran, D., & McClelland, J. L. (2012). Generalization through the recurrent interaction of episodic memories: A model of the hippocampal system. *Psychological Review*, *119*(3), 573–616. https://doi.org/10.1037/a0028681

Lin, J., Rugg, M. D., Das, S., Stein, J., Rizzuto, D. S., Kahana, M. J., & Lega, B. C. (2017). Theta band power increases in the posterior hippocampus predict successful episodic memory encoding in humans. *Hippocampus*, *27*(10), 1040–1053. https://doi.org/10.1002/hipo.22751

Long, N. M., & Kuhl, B. A. (2019). Decoding the tradeoff between encoding and retrieval to predict memory for overlapping events. *NeuroImage*, *201*, 116001. https://doi.org/10.1016/j.neuroimage.2019.07.014

Mack, M. L., Love, B. C., & Preston, A. R. (2018). Building concepts one episode at a time: The hippocampus and concept formation. *Neuroscience Letters*, *680*, 31–38. https://doi.org/10.1016/j.neulet.2017.07.061

Martín-Buro, M. C., Wimber, M., Henson, R. N., & Staresina, B. P. (2020). Alpha Rhythms Reveal When and Where Item and Associative Memories Are Retrieved. *The Journal of Neuroscience*, *40*(12), 2510–2518. https://doi.org/10.1523/JNEUROSCI.1982-19.2020

Mayes, A., Montaldi, D., & Migo, E. (2007). Associative memory and the medial temporal lobes. *Trends in Cognitive Sciences*, *11*(3), 126–135. https://doi.org/10.1016/j.tics.2006.12.003

McCabe, D. P., Roediger, H. L., McDaniel, M. A., Balota, D. A., & Hambrick, D. Z. (2010). The relationship between working memory capacity and executive functioning: Evidence for a common executive attention construct. *Neuropsychology*, *24*(2), 222–243. https://doi.org/10.1037/a0017619

McClelland, J. L., McNaughton, B. L., & O'Reilly, R. C. (1995). *Why There Are Complementary Learning Systems in the Hippocampus and Neocortex:InsightsFrom the Successesand Failuresof Connectionist Models of Learning and Memory*. *102*(3), 419–457.

Miller, G. A. (1956). The magical number seven, plus or minus two: Some limits on our capacity for processing information. *Psychological Review*, *63*(2), 81–97. https://doi.org/10.1037/h0043158

Modigliani, V., & Seamon, J. G. (1974). Transfer of information from short- to long-term memory. *Journal of Experimental Psychology*, *102*(5), 768–772. https://doi.org/10.1037/h0036374

Morris, C. D., Bransford, J. D., & Franks, J. J. (1977). Levels of processing versus transfer appropriate processing. *Journal of Verbal Learning and Verbal Behavior*, *16*(5), 519–533. https://doi.org/10.1016/S0022-5371(77)80016-9

Morton, N. W., Sherrill, K. R., & Preston, A. R. (2017). Memory integration constructs maps of space, time, and concepts. *Current Opinion in Behavioral Sciences*, *17*, 161–168. https://doi.org/10.1016/j.cobeha.2017.08.007

Nakazawa, K., Sun, L. D., Quirk, M. C., Rondi-Reig, L., Wilson, M. A., & Tonegawa, S. (2003). Hippocampal CA3 NMDA Receptors Are Crucial for Memory Acquisition of One-Time Experience. *Neuron*, *38*(2), 305–315. https://doi.org/10.1016/S0896-6273(03)00165-X

O'Reilly, R. C., & McClelland, J. L. (1994). Hippocampal conjunctive encoding, storage, and recall: Avoiding a trade-off. *Hippocampus*, *4*(6), 661–682. https://doi.org/10.1002/hipo.450040605

Ortiz-Tudela, J., Turan, G., Vilas, M., Melloni, L., & Shing, Y. L. (2024). Schema-driven prediction effects on episodic memory across the lifespan. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *379*(1913), 20230401. https://doi.org/10.1098/rstb.2023.0401

Piaget, J. (1929). *The children's conception of the world* (J. Tomlinson & A. Tomlinson, Eds.). London, Routledge & K. Paul.

Polich, J. (2007). Updating P300: An integrative theory of P3a and P3b. *Clinical Neurophysiology*, *118*(10), 2128–2148. https://doi.org/10.1016/j.clinph.2007.04.019

Postman, L., & Underwood, B. J. (1973). Critical issues in interference theory. *Memory & Cognition*, *1*(1), 19–40. https://doi.org/10.3758/BF03198064

Preston, A. R., & Eichenbaum, H. (2013). Interplay of Hippocampus and Prefrontal Cortex in Memory. *Current Biology*, *23*(17), R764–R773. https://doi.org/10.1016/j.cub.2013.05.041

Preston, A. R., Shrager, Y., Dudukovic, N. M., & Gabrieli, J. D. E. (2004). Hippocampal contribution to the novel use of relational information in declarative memory. *Hippocampus*, *14*(2), 148–152. https://doi.org/10.1002/hipo.20009

Radvansky, G. A. (1999). The Fan Effect: A Tale of Two Theories. *Journal of Experimental Psychology: General*, *128*(2), 198–206.

Radvansky, G. A., & Zacks, J. M. (2014). *Event Cognition*. Oxford University Press. https://doi.org/10.1093/acprof:oso/9780199898138.001.0001

Ranganath, C. (2010). Binding Items and Contexts: The Cognitive Neuroscience of Episodic Memory. *Current Directions in Psychological Science*, *19*(3), 131–137. https://doi.org/10.1177/0963721410368805

Ranganath, C., Cohen, M. X., & Brozinsky, C. J. (2005). Working Memory Maintenance Contributes to Long-term Memory Formation: Neural and Behavioral Evidence. *Journal of Cognitive Neuroscience*, *17*(7), 994–1010. https://doi.org/10.1162/0898929054475118

Reagh, Z. M., & Ranganath, C. (2023). Flexible reuse of cortico-hippocampal representations during encoding and recall of naturalistic events. *Nature Communications*, *14*(1), 1279. https://doi.org/10.1038/s41467-023-36805-5

Richter, F. R., Chanales, A. J. H., & Kuhl, B. A. (2016). Predicting the integration of overlapping memories by decoding mnemonic processing states during learning. *NeuroImage*, *124*, 323–335. https://doi.org/10.1016/j.neuroimage.2015.08.051

Roediger, H. L. (1990). Implicit memory: Retention without remembering. *American Psychologist*, *45*(9), 1043–1056. https://doi.org/10.1037/0003-066X.45.9.1043

Rolls, E. T. (2013). The mechanisms for pattern completion and pattern separation in the hippocampus. *Frontiers in Systems Neuroscience*, *7*. https://doi.org/10.3389/fnsys.2013.00074

Rugg, M. D., & Curran, T. (2007). Event-related potentials and recognition memory. *Trends in Cognitive Sciences*, *11*(6), 251–257. https://doi.org/10.1016/j.tics.2007.04.004

Rugg, M. D., & Vilberg, K. L. (2013). Brain networks underlying episodic memory retrieval. *Current Opinion in Neurobiology*, *23*(2), 255–260. https://doi.org/10.1016/j.conb.2012.11.005

Ryan, L., Cox, C., Hayes, S. M., & Nadel, L. (2008). Hippocampal activation during episodic and semantic memory retrieval: Comparing category production and category cued recall. *Neuropsychologia*, *46*(8), 2109–2121. https://doi.org/10.1016/j.neuropsychologia.2008.02.030

Schacter, D. L., Addis, D. R., Hassabis, D., Martin, V. C., Spreng, R. N., & Szpunar, K. K. (2012). The Future of Memory: Remembering, Imagining, and the Brain. *Neuron*, *76*(4), 677–694. https://doi.org/10.1016/j.neuron.2012.11.001

Schlichting, M. L., Mumford, J. A., & Preston, A. R. (2015). Learning-related representational changes reveal dissociable integration and separation signatures in the hippocampus and prefrontal cortex. *Nature Communications*, *6*(1), 8151. https://doi.org/10.1038/ncomms9151

Schlichting, M. L., & Preston, A. R. (2015). Memory integration: Neural mechanisms and implications for behavior. *Current Opinion in Behavioral Sciences*, *1*, 1–8. https://doi.org/10.1016/j.cobeha.2014.07.005

Schlichting, M. L., Zeithamova, D., & Preston, A. R. (2014). CA1 subfield contributions to memory integration and inference. *Hippocampus*, *24*(10), 1248–1260. https://doi.org/10.1002/hipo.22310

Shin, Y. S., Masís-Obando, R., Keshavarzian, N., Dáve, R., & Norman, K. A. (2021). Context-dependent memory effects in two immersive virtual reality environments: On Mars and underwater. *Psychonomic Bulletin & Review*, *28*(2), 574–582. https://doi.org/10.3758/s13423-020-01835-3

Shohamy, D., & Wagner, A. D. (2008). Integrating memories in the human brain: Hippocampal-midbrain encoding of overlapping events. *Neuron*, *60*(2), 378–389. https://doi.org/10.1016/j.neuron.2008.09.023

Simons, J. S., Ritchey, M., & Fernyhough, C. (2022). *Brain Mechanisms Underlying the Subjective Experience of Remembering*. *73*, 159–186.

Slotnick, S. D. (2013). The nature of recollection in behavior and the brain. *NeuroReport*, *24*(12), 663–670. https://doi.org/10.1097/WNR.0b013e328362e47e

Smith, S. M., & Vela, E. (2001). Environmental context-dependent memory: A review and meta-analysis. *Psychonomic Bulletin & Review*, *8*(2), 203–220. https://doi.org/10.3758/BF03196157

Squire, L. R. (1992). *Declarative and Nondeclarative Memory: Multiple Brain Systems Supporting Learning and Memory*. *4*(3), 232–243.

Squire, L. R., & Zola, S. M. (1996). Structure and function of declarative and nondeclarative memory systems. *Proceedings of the National Academy of Sciences*, *93*(24), 13515–13522. https://doi.org/10.1073/pnas.93.24.13515

Squire, L. R., & Zola, S. M. (1998). Episodic memory, semantic memory, and amnesia. *Hippocampus*, *8*(3), 205–211. https://doi.org/10.1002/(SICI)1098-1063(1998)8:3<205::AID-HIPO3>3.0.CO;2-I

Staresina, B. P., Michelmann, S., Bonnefond, M., Jensen, O., Axmacher, N., & Fell, J. (2016). Hippocampal pattern completion is linked to gamma power increases and alpha power decreases during recollection. *eLife*, *5*, e17397. https://doi.org/10.7554/eLife.17397

Takashima, A., Nieuwenhuis, I. L. C., Jensen, O., Talamini, L. M., Rijpkema, M., & Fernández, G. (2009). Shift from Hippocampal to Neocortical Centered Retrieval Network with Consolidation. *The Journal of Neuroscience*, *29*(32), 10087–10093. https://doi.org/10.1523/JNEUROSCI.0799-09.2009

Thalmann, M., Souza, A. S., & Oberauer, K. (2019). How does chunking help working memory? *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *45*(1), 37–55. https://doi.org/10.1037/xlm0000578

Tompary, A., & Davachi, L. (2017). Consolidation Promotes the Emergence of Representational Overlap in the Hippocampus and Medial Prefrontal Cortex. *Neuron*, *96*(1), 228-241.e5. https://doi.org/10.1016/j.neuron.2017.09.005

Tulving, E. (1987). Multiple memory systems and consciousness. *Human Neurobiology*, *6*, 67–80.

Tulving, E. (1993). What is episodic memory? *Current Directions in Psychological Science*, *2*(3), 67–100.

Tulving, E., & Thomson, D. M. (1973). Encoding specificity and retrieval processes in episodic memory. *Psychological Review*, *80*(5), 352–373. https://doi.org/10.1037/h0020071

Van Kesteren, M. T. R., Beul, S. F., Takashima, A., Henson, R. N., Ruiter, D. J., & Fernández, G. (2013). Differential roles for medial prefrontal and medial temporal cortices in schema-dependent encoding: From congruent to incongruent. *Neuropsychologia*, *51*(12), 2352–2359. https://doi.org/10.1016/j.neuropsychologia.2013.05.027

Van Kesteren, M. T. R., Ruiter, D. J., Fernández, G., & Henson, R. N. (2012). How schema and novelty augment memory formation. *Trends in Neurosciences*, *35*(4), 211–219. https://doi.org/10.1016/j.tins.2012.02.001

Varga, N. L., & Bauer, P. J. (2017). Using Event-related Potentials to Inform the Neurocognitive Processes Underlying Knowledge Extension through Memory Integration. *Journal of Cognitive Neuroscience*, *29*(11), 1932–1949. https://doi.org/10.1162/jocn_a_01168

Waldhauser, G. T., Johansson, M., & Hanslmayr, S. (2012). Alpha/Beta Oscillations Indicate Inhibition of Interfering Visual Memories. *The Journal of Neuroscience*, *32*(6), 1953–1961. https://doi.org/10.1523/JNEUROSCI.4201-11.2012

Wilson, R. C., Takahashi, Y. K., Schoenbaum, G., & Niv, Y. (2014). Orbitofrontal Cortex as a Cognitive Map of Task Space. *Neuron*, *81*(2), 267–279. https://doi.org/10.1016/j.neuron.2013.11.005

Wimmer, G. E., & Shohamy, D. (2012). Preference by Association: How Memory Mechanisms in the Hippocampus Bias Decisions. *Science*, *338*(6104), 270–273. https://doi.org/10.1126/science.1223252

Winocur, G. (1980). The hippocampus and cue utilization. *Physiological Psychology*, *8*(2), 280–288. https://doi.org/10.3758/BF03332859

Yassa, M. A., & Stark, C. E. L. (2011). Pattern separation in the hippocampus. *Trends in Neurosciences*, *34*(10), 515–525. https://doi.org/10.1016/j.tins.2011.06.006

Yonelinas, A. P., Ranganath, C., Ekstrom, A. D., & Wiltgen, B. J. (2019). A contextual binding theory of episodic memory: Systems consolidation reconsidered. *Nature Reviews Neuroscience*, *20*(6), 364–375. https://doi.org/10.1038/s41583-019-0150-4

Zacks, J. M., & Tversky, B. (2001). Event structure in perception and conception. *Psychological Bulletin*, *127*(1), 3–21.

Zappa, A., León-Cabrera, P., Ramos-Escobar, N., Laine, M., Rodriguez-Fornells, A., & François, C. (2025). *Alpha and beta desynchronization during consolidation of newly learned words*. https://doi.org/10.1101/2025.01.09.632010

Zeithamova, D., & Bowman, C. R. (2020). Generalization and the hippocampus: More than one story? *Neurobiology of Learning and Memory*, *175*, 107317. https://doi.org/10.1016/j.nlm.2020.107317

Zeithamova, D., Dominick, A. L., & Preston, A. R. (2012). Hippocampal and Ventral Medial Prefrontal Activation during Retrieval-Mediated Learning Supports Novel Inference. *Neuron*, *75*(1), 168–179. https://doi.org/10.1016/j.neuron.2012.05.010

Zeithamova, D., & Preston, A. R. (2010). Flexible memories: Differential roles for medial temporal lobe and prefrontal cortex in cross-episode binding. *The Journal of Neuroscience*, *30*(44), 14676–14684. https://doi.org/10.1523/JNEUROSCI.3250-10.2010

Zeithamova, D., & Preston, A. R. (2017). Temporal proximity promotes integration of overlapping events. *Journal of Cognitive Neuroscience*, *29*(8), 1311–1323. https://doi.org/10.1162/jocn_a_01116

Zeithamova, D., Schlichting, M. L., & Preston, A. R. (2012). The hippocampus and inferential reasoning: Building memories to navigate future decisions. *Frontiers in Human Neuroscience*, *6*, 1–14. https://doi.org/10.3389/fnhum.2012.00070

Printed by Media-Tryck, Lund 2025 NORDIC SWAN ECOLABEL 3041 0903

LUND
UNIVERSITY

Faculty of Social Sciences
Department of Psychology

ISBN 978-91-8104-541-3

9 789181 045413